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Landscape Influences on Stream Habitats and Biological Assemblages

Landscape Influences on Stream Habitats and Biological Assemblages

Robert M. Hughes,
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and
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editors

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Preface

Viewing rivers in the context of their landscape settings is a relatively young and rapidly developing discipline. The linkages among landscape and associated physicochemical and biological characteristics of rivers have long been recognized. However, the development of conceptual frameworks and tools for measuring and synthesizing such linkages has only recently been fueled by growth in related fields, including landscape ecology and geographic information systems. We are at an important moment in the emergence of landscape-based river science. To facilitate communication among researchers, resource managers, and policy makers, Lizhu Wang and Bob Hughes began organizing a symposium on landscape effects on streams at the 2003 annual meeting of the American Fisheries Society (AFS). The AFS Water Quality Section agreed to sponsor both the symposium and this resulting book, Paul Seelbach agreed to coedit,

and AFS agreed to publish the book. Twenty-eight presentations were given in a special session at the 2004 AFS annual meeting in Madison, Wisconsin. From these, 26 acceptable manuscripts and five additional chapters were prepared within the following year, with the capable assistance of 80 peer reviewers, bringing the total to 31 chapters. Also, the USGS-Biological Resources Discipline, USGS-Forest & Rangeland Ecosystem Science Center, and the Natural Resources Research Institute of the University of Minnesota-Duluth assisted with publication costs. And the USEPA guaranteed purchase of 50 books. We offer our sincere gratitude to the sponsors, peer reviewers, authors, and AFS copy editor—Debby Lehman—for bringing this book to fruition. We hope this collection of thoughts and experiences will help us to better see, understand, and manage rivers as landscape ecosystems.

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Introduction to Landscape Influences on Stream Habitats and Biological Assemblages

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Abstract.—Viewing river systems within a landscape context is a relatively new and rapidly developing approach to river ecology. Although the linkages among landscapes and associated physicochemical and biological characteristics of rivers have long been recognized, the development of conceptual frameworks and tools for measuring and synthesizing such linkages is relatively recent. In this book, authors from the United States and Canada explore new ideas about landscape–river relationships, river research, and river management; compile large regional, spatially referenced, survey data sets on river network characteristics; explore and describe patterns and relationships across survey sites, reaches, and catchments; and develop management and decision tools. In synthesizing these chapters, we have identified key challenges to studying and managing landscape–river systems. Key challenges include identifying appropriate units of measurement and interpretation of the river network, understanding how human alterations of land cover modify river characteristics and biological assemblages, understanding and measuring how various spatial-scale factors interactively influence instream habitat and biota, and collecting and gathering appropriate landscape and instream habitat data. This book also reveals the major current knowledge gaps that deserve more attention in landscape–river ecology. These include improving river–landscape classification, capturing appropriate spatial- and temporal-scale data, developing accurate predictive models where study data are limited, and improving our ability to measure connectivity among river segments and their networks. Future research that focuses on overcoming the challenges and filling the knowledge gaps will substantially improve our understanding of river ecosystems, fuel the development of tools for linking the functions and processes operating at different spatial- and temporal-scales, and stimulate the development of new hypotheses and frameworks to provide foundations for the next phases of riverine science and management.

INTRODUCTION

Understanding, measuring, and predicting the key landscape factors and how they influence the characteristics of running-water systems has been a central concern of those who study, manage, and use river systems. The view of lotic sys-

tems longitudinally from headwaters to river mouths and laterally from water boundaries through their riparian floodplains to their catchment divides has progressed from generating descriptive concepts to testing generalized theories and, more recently, towards developing and applying statistical models and management tools at local, regional, and national scales. As this book illustrates, the recent acceleration of efforts to identify and measure key landscape factors and

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their effects on characteristics of stream/river (hereafter, river refers to both stream and river) systems has been largely driven by the emergence of concepts from the disciplines of landscape and river ecology, wider availability of regional databases, and rapid development of geographic information technologies. Our objectives for this book are to (1) assemble and synthesize current knowledge of the influences of landscape on river ecosystems, (2) highlight the challenges encountered when measuring and linking landscapes with river systems, (3) describe current approaches of resolving these challenges, and (4) identify major knowledge gaps to direct future research. Throughout the book, we follow Fauth et al. (1996) and use the term “assemblage,” when referring to taxonomic subgroups such as fish or macroinvertebrates, and the term “community,” when referring to all biota in an ecosystem. Our book focuses on the United States and Canada.

RECOGNIZING THE MULTISCALE STRUCTURE OF LANDSCAPE–RIVER SYSTEMS

It has long been recognized that river chemical properties, channel hydraulics, morphology, bottom composition, and associated biological communities are shaped by many landscape factors that operate at a variety of spatial and temporal scales (Ross 1963; Hynes 1975; Hughes and Hunsaker 2002; Wang et al. 2003; Allan 2004). Landscape influences on river systems can be generalized to occur at three spatial scales. These scales are (1) landscape areas having immediate contact with the river channel at or below bank-full conditions, (2) landscape areas within the floodplain and riparian areas, and (3) landscape areas that have indirect connections with the river channel through contribution of surface and groundwater flows, sediments, and other materials that influence water physicochemical properties (i.e., the catchment area beyond the floodplain and riparian zone). Understanding and measuring the

physical and biological functions and processes at each of the scales and their interactions among the three scales are critical to river ecosystem management and have progressed with increased availability of large scale databases and improved information technologies.

Early studies on the influences of landscape at the channel scale concentrated on understanding how local river channel physical and geomorphologic properties varied under different landscape settings. Attempts to understand ecological functions focused on local phenomena that influence biological communities directly, such as water temperature, flow regime, water physicochemical properties, channel hydraulics, pool-riffle complexity, and substrate composition (Southwood 1977; Gorman and Karr 1978; Karr and Dudley 1981). This organisms’ view of habitat heterogeneity provided good descriptions of habitat distributions, uses, and preferences.

Expanding the view outward, studies explored how the floodplain and riparian zone constrain channel form, slope, and bed materials. Floodplains have been shown to provide functions of storing and releasing waters and nutrients during flood pulses, storing inorganic and organic matter, and providing spawning and nursery grounds for aquatic organisms during high flow seasons (Junk et al. 1989; Welcomme 1995). Riparian vegetation also regulates light and water temperature, protects riverbanks, filters runoff sediments and nutrients, and provides seasonal habitats for aquatic life (Gregory et al. 1991). The influence of riparian areas decreases as rivers grow in size, but floodplain importance increases with river size.

The classic statement that “in every respect the valley rules the stream” (Hynes 1975) provides an overarching view of landscape influence at the catchment scale. The riverine landscape or riverscape (Ward 1998; Fausch et al. 2002; Wiens 2002) offers a holistic perspective that river channels are only part of an extensive interconnected series of biotopes and environmental gradients that constitute lotic ecosystems, and rivers at any scale express the essential feature of

landscape: locational variance or heterogeneity. The riverine landscape incorporates multiple interactive pathways operating across a range of spatiotemporal scales that determine river system characteristics, and the mosaic structure and dynamic nature of river systems maintain their functional integrity. Landscape influences on rivers include controlling deliveries of water, nutrients, minerals, wood, and sediments into the river system and determining regimes for flow, sediment inputs, nutrient levels, and water temperatures. These influences are determined by the catchment characteristics of climate, elevation, vegetative cover, land use, soil permeability, landscape slope, topography, and overall surficial geology (Omernik 2004). Hence, effective management and research of river systems relies on a strong understanding of the structural and functional components of river–landscape ecosystems.

PROGRESS TOWARDS UNDERSTANDING CROSS-SCALE LINKAGES FOR RIVER SYSTEMS

Viewing a river ecosystem at any one of the three spatial scales mentioned above provides an incomplete understanding. Only when the entire system is considered—from upland to flood plain/riparian to river channel, along with all the processes taking place throughout—can we understand a river as an integrated, functioning system (Waters 2000; Rabeni and Sowa 2002). Such incomplete views of rivers have been largely the result of basing our concepts on personal observations and measurements within the short river sections that could be viewed or quickly traversed by foot. Another factor was the divergent interests of the various disciplines involved in river study. Hydrologists focused on how landscape influences flow patterns. Geomorphologists emphasized valley characteristics that control sediment budgets and hydraulic behaviors. Engineers have paid most attention to flood patterns and control and navigation needs. Most ecologists have been interested in how local

instream physicochemical habitats relate to distributions of single species or assemblages. One challenge to understanding rivers as ecological systems has been the integration of concepts and knowledge sets from these separate sciences.

A milestone in river systems thinking was the river continuum concept (Vannote et al. 1980) and the subsequent river “discontinuum” perspective (e.g., Perry and Schaeffer 1987; Townsend 1989; Montgomery 1999; Poole 2002; Rice et al. 2001). The river continuum concept integrated the longitudinal changes in structure and ecological function along an entire river into a general, holistic model. It described a gradient of physicochemical and geomorphic conditions from headwater streams to river mouths that control habitat characteristics, energy relationships, and corresponding biota. The river discontinuum perspective recognized that the downstream physicochemical and biological continuum are periodically interrupted in response to channel and valley morphological variations, such as those caused by ecoregion boundaries, alternating canyons and floodplains, bedrock intrusions, tributary confluences, lakes, and landslides. This discontinuum perspective stresses that fluvial systems are hierarchically organized from valley segments to riverbed particles, which create highly heterogeneous network systems. The river continuum concept emphasizes the influence of catchment size and channel width, with longitudinal variation at channel and riparian/floodplain scales, while the discontinuum notion focuses more on the longitudinal heterogeneity resulting from ecoregional and local changes in geologic formation, soil type, land cover, and landscape topography. Although each of these two views focuses on different aspects of linkages between rivers and their landscapes, together they present the landscape–river as one integrated ecological system.

Ward (1989) extended the continuum and discontinuum concepts to view rivers holistically and proposed a four-dimensional framework to conceptualize the dynamic and hierarchical nature of river ecosystems. This framework stated

that upstream–downstream interactions constitute the longitudinal dimension, interactions between the channel and floodplain form the lateral dimension, the connections between the channel and groundwater constitute the vertical dimension, and changes through time provide the temporal dimension. This spatial–temporal framework provided a holistic approach to perceive major interactive pathways and led to a more complete understanding of the dynamic and hierarchical structure of river ecosystems.

Following the same line of thinking, Schlosser (1991) further extended the framework of viewing river systems holistically by linking requirements of various life stages and species of riverine fish with a river's longitudinal continuity, hierarchy, heterogeneity, lateral connectivity, and catchment. His landscape model illustrated the spatial upstream–downstream and channel–riparian/floodplain arrangements of habitats for spawning, feeding and rearing, and refuges for different life stages, and the critical need for fish to be able to move among them to complete their life cycles. To apply Schlosser's model, Fausch et al. (2002) and Hughes et al. (2002) concluded that the traditional sampling schemes and methods used by river ecologists are largely inadequate for gathering appropriate data because of the large scale involved, the hierarchical and heterogeneous nature of river habitats, and the extensive daily movements displayed by many riverine fishes. They proposed sampling river habitat at an intermediate river segment scale of 1–100 km, or 50–100 times the mean wetted channel width, and 5–50 years rather than the current sampling done at ≤ 200 m and ≤ 2 years. The riverscape view and the sampling scale framework proposed by Fausch et al. (2002) emphasized understanding how continuous, hierarchical, and heterogeneous river habitats are arrayed in space and time and how they are linked to river biological communities, especially fish assemblages.

Another milestone in viewing landscape–river systems was the development of the natural flow regime paradigm (Dunne and Leopold 1978; Junk et al. 1989; Poff and Ward 1989; Poff et al.

1997). This paradigm recognizes that flow regimes show regional patterns that are determined largely by river size and geographic variations in climate, geology, topography, and vegetative cover. These factors determine both the supply of water and the pathways by which precipitation reaches the channel. The magnitude, frequency, duration, timing, and rate of change in hydrologic conditions are the five critical components of the flow regime. These five components regulate channel and floodplain morphology and connectivity, thermal regime, substrate size and heterogeneity, abundance and transportation of sediment and woody debris, physicochemical characteristics, and hence, biological communities of river systems. This paradigm provides a holistic view of the key functional roles that natural flow regimes play in connecting different temporal- and spatial-scale landscape factors with instream characteristics, functions, and processes. Most importantly, this paradigm emphasizes that not only minimal flow, but also natural stream flow variability, are critically important in maintaining the ecological functions of a river system, a view that has been virtually ignored in river management until recently (Poff et al. 1997).

The process domain concept (Montgomery 1999) is also worth mentioning as a major contribution to viewing and measuring landscape–river systems. This concept is a multiscale hypothesis that spatial variability in geomorphic processes governs temporal patterns of disturbances that influence ecosystem structure and dynamics. It states that at a coarse scale, regional climate, geology, vegetation, and topography control the suite of geomorphic processes that are distributed over a landscape. Process domains are spatially identifiable areas within a river network characterized by distinct suites of geomorphic processes. The process domain concept implies that a river channel network can be divided into discrete regions in which community structure and dynamics respond to distinctly different disturbance regimes. Although this concept has not been widely accepted, its recognition

of the fundamental differences in landscape process allows the identification of landscape units and discrete areas in channel networks that correlate with differences in river system organization. Such a view provides a foundation for identifying river units where distinctly different ecological processes and process rates occur.

A more recent, overarching theme is the conceptual framework that considers terrestrial-aquatic linkages from a hierarchical perspective. This framework recognizes that a variety of factors at multiple spatial and temporal scales influence variation in riverine physicochemical properties, hence biological communities. It has become clear that the instream and riparian physical and chemical factors, such as water quality, energy source, substrate, channel morphology, and flow and thermal regimes, help determine the structure and composition of biological communities and are largely determined by landscape factors (Hughes et al. 1987; Richards et al. 1996; Wiley et al. 1997). These linkages among channel, riparian/floodplain, and catchment factors have led to the development of hierarchical models that describe the spatial relationships among the units of a river system as a nested series from biota to local habitat to river reach to river segment to sub-catchment to basin (Frissell et al. 1986; Hawkins et al. 1993; Poff 1997; Parsons et al. 2003).

These conceptual models, in principle, state that the array of local instream conditions found within fluvial systems are created and constrained by predictable hydrologic and geomorphic processes (e.g., Harper and Everard 1998; Parsons et al. 2004). These processes operate hierarchically; large-scale processes constrain the expression of processes at successively smaller scales, and hence, riverine systems can be divided into, and viewed at, discrete scales that reflect relationships between hydrologic and geomorphic processes and local river features (Parsons et al. 2003). Consequently, the distribution and character of local river conditions determine the types of biological assemblages found in them (Southwood 1977).

CHALLENGES TO MEASURING AND DESCRIBING LINKAGES BETWEEN LANDSCAPE AND RIVER SYSTEMS

Current conceptual models have provided a framework for considering linkages between rivers and their landscapes and improved our understanding of hierarchical processes at work. However, there are many challenges in actually measuring components and functions of the landscape–river ecosystem and in developing tools for aquatic resource management.

Challenges in Identifying Meaningful Spatial Units within the River Network

One current challenge is to identify meaningful spatial units for measuring and interpreting river networks. Currently, most river fish surveys are based on data collected from relatively small sections of the network, typically 100–1,000 m depending on river size (Gammon 1976; Meador et al. 1993; Penczak and Mann 1993; Yoder and Smith 1999; Flotemersch and Blocksom 2005). Although such data may provide relatively reliable information about the sites, they do not provide information for extrapolating a single site-scale result to unsampled areas in the same river (Fausch et al. 2002; Fayram et al. 2005). Extrapolating results from sampled sites to sections without data is extremely important because we will never have enough resources to directly sample every river section across a state or nation. National sampling programs, such as the U.S. Environmental Protection Agency's Environmental Monitoring and Assessment Program (EMAP), are addressing this issue by randomly selecting river sites stratified geographically and by size. Although this approach has markedly improved the accuracy of regional data summaries (USEPA 2000; Stoddard et al. 2005), the data are inappropriate for generalizing to unsampled parts of a river in different landscape settings. This is because the sampling data are from only a small percent of the sections

of the network, and one does not know what parts of the network that the collected data could represent. For example, one does not know if data collected from a second order section of a stream represents all second-order streams in the same ecoregion. However, EMAP's random design can be intensified to allow accurate and precise inference at multistate, (McCormick et al. 2001; Klemm et al. 2003), ecoregion (Hughes et al. 2004; Ode et al. 2005; Stoddard et al. 2005), or basin (Nicholas et al. 2005) scales.

The initial approach of a landscape-based ecological classification system for ecological river valley segments (VSEC) in lower Michigan (Seelbach et al. 1997, 2006, this volume) offers one option to meet this challenge. This framework proposes to identify and describe naturally occurring, ecologically distinct river segments for data collection, data interpolation, segment type classification, and aquatic resource management. This framework divides the heterogeneous river network into segments that are relatively homogeneous in physicochemical, geomorphological, and biological characteristics. A classification system based on the natural characteristics of the three spatial landscape scales mentioned earlier provides a way for data collected from one segment to be interpolated to other segments of the same type and region.

This approach has been further improved by the increased availability of large-scale landscape databases, such as the national hydrography dataset, the national digital elevation model, regional surficial geology and soil permeability data, and multistate land use/cover databases, which aid gathering different scales of landscape information. The VSEC approach is also enhanced by the advancement of geographic information technology that helps quantify and automate the identification of river segments, delineate catchment boundaries of each segment, calculate different spatial scale landscape and instream attributes associated with each segment, and classify segments for all rivers at a state or multistate scale. However classification accuracy related to local-scale factors, model variance,

map accuracy, absolute versus fuzzy segment boundaries, and fish movements limit prediction accuracy (Seelbach et al. 2006).

Improved river unit identification, catchment delineation and data gathering, and classification are presented by Brenden et al. (2006, this volume). This framework aids development of models for large scale fish occurrence prediction (Gido et al. 2006; McKenna et al. 2006; Steen et al. 2006; Wall and Berry 2006; all this volume) and evaluation of relationships between fish assemblages and landscapes (Stanfield et al. 2006, this volume).

Challenges in Understanding How Human Activities Modify River Characteristics and Biological Assemblages

The second challenge is to understand how extensive alterations of land cover by human activities at riparian and catchment scales modify natural river characteristics and their associated biological communities and assemblages (i.e., environmental assessment). In natural or minimally disturbed systems, catchment, riparian, and instream conditions are at a dynamic equilibrium that typically permits internal adjustment of factors without producing rapid or dramatic change in many of those systems. The resilience or ability to maintain this dynamic equilibrium results from factors acting together across different spatial scales. The biota in such systems are adapted to dynamic equilibrium conditions and natural disturbance levels. When anthropogenic disturbances break the dynamic equilibrium among catchment, riparian, and instream conditions, the instream factors tend to reestablish new equilibria with their environments and different and generally degraded physicochemical habitat and biological assemblages occur.

The most common approach for conducting environmental assessments is to compare least-disturbed reference conditions for physicochemical habitat and biological assemblages of a river site with those of test segments. Hence,

the central theme of environmental assessment is identifying appropriate reference conditions. The recommended method of establishing reference conditions is to use a combination of methods of least-disturbed reference sites, historical data, simulation models, and expert consensus (Hughes 1995; USEPA 1996). Such a method requires that the river segments where the historical data originate, simulation models are built, expert opinion is generated, and reference sites are selected have comparable natural conditions with the test segments.

The three steps recommended by USEPA (1996) for characterizing reference conditions for multiple test rivers include (1) classification of resources, because not all rivers are alike and reference conditions naturally differ among geographic regions and river types; (2) selection of least-disturbed sites in each resource class as candidate reference sites; and (3) confirmation and refinement of reference site quality through data evaluation or modeling. One key difficulty in carrying out these steps is that least-disturbed reference sites vary in level of disturbance among regions, and some are actually quite disturbed (Stoddard et al. 2005; Whittier et al. 2006, this volume). Another drawback is that few river segments have sufficient instream and landscape data for accurate classification. This produces highly variable reference site data. Brenden et al. (2006), Seelbach et al. (2006), and Stanfield et al. (2006) have explored feasible ways to produce such data. Similar approaches have also been used by the U.S. Geological Survey Aquatic Gap program in Missouri, Kansas, and South Dakota (Sowa et al. 2005).

An alternate way of conducting environmental assessment is to use a landscape-based modeling and regional normalization process (Moss et al. 1987; Bailey et al. 1998; Davies et al. 2000; Hawkins et al. 2000; Oberdorff et al. 2002; Wiley et al. 2003; Baker et al. 2005; Tejerina-Garro et al. 2005; Pont et al. 2006). In this process, the relationships between physicochemical habitat and biological assemblages and their associated landscape conditions are described using linear

or nonlinear models. The physicochemical habitat and biological assemblage reference conditions for the test segments can be estimated from the specific natural landscape context of those sites while eliminating human induced factors, such as dams, land use, and point source pollution. Environmental assessments are done by comparing actual conditions of habitat and biological assemblages at the test sites with predicted reference condition. This approach is represented by Kilgour and Stanfield (2006, this volume) and Riseng et al. (2006, this volume). Such models can also be used to predict future conditions, for example those expected to result from increased catchment urbanization (Van Sickle et al. 2004; Stanfield and Kilgour 2006, this volume). A basic drawback of such modeling is its requirement for a large and diverse data set, including both biological and physicochemical data for model development and validation.

Challenges in Understanding and Measuring How Various Spatial Factors Interactively Influence Instream Habitat and Biota

This challenge also includes the identification of key landscape factors that are most influential, and the spatial scales at which they are manifest, so that rehabilitation and conservation efforts can be directed towards the factors and scales where management activities are most effective. During the last two decades, considerable efforts have been directed toward this challenge; so does our book, with 20 chapters devoted to this issue. However, the conclusions from these studies are varied and inconsistent in the current literature and this book, largely because of variations in statistical methods used and the sizes and conditions of the study regions.

Commonly used statistical approaches for these tasks in the current literature and this book are correlations, multiple regression, multivariate regression, multivariate gradient analysis, and structure equation modeling. Correlation analysis examines relationships between dependent

and independent variables at one data-set-pair at a time without considering the influence of other variables. It is more suitable for variable screening or evaluating simple relationships. Multiple regression approaches identify the most important independent variables in predicting a single dependent variable. The contributions of other independent variables in the regression model do not necessarily indicate how important they are in determining the dependent variable. Multivariate regression is similar to multiple regression, but can have multiple dependent variables. It is more suitable for building predictive models. Both multivariate gradient analysis and structure equation modeling evaluate multiple, complex relationships among dependent and independent variables. Multivariate gradient analysis emphasizes relationships in multiple dimensions, and structure equation modeling focuses on building theoretical models and on clarifying the direct and indirect paths of the influences.

The influence of study region size on identifying key landscape factors is evident. If the study region is a large area, such as the entire United States, one would expect latitude, longitude, elevation, and catchment size to be among the key factors influencing fish distribution. In contrast, if the study region is relatively small, such as a county in Iowa, one would not expect latitude, longitude, and elevation to be influential factors.

The influence of study region condition on the outcome of the assessment is somewhat difficult to understand and the true natural patterns and processes can be identified and analyzed only under undisturbed conditions. Studies on catchments with strong agriculture- or urban-forest gradients indicate that land uses are the main factors influencing river fish and macroinvertebrate assemblages and that local-scale physical habitat plays a less important role (Wang et al. 2001, 2002; Wang and Lyons 2003). When there are large elevation, geological, or slope gradients among study sites and catchments, such natural factors must be factored out to detect anthropogenic gradients (Burnett et al. 2006;

Kaufmann and Hughes 2006; both this volume). Studies from mixed forest-agriculture catchments indicate that both catchment- and reach-scale factors are important (e.g., Richards et al. 1996; Allan et al. 1997). There is limited understanding of the role of different spatial scales for relatively undisturbed and for highly disturbed catchments. Heitke et al. (2006, this volume) provide an example of such studies on highly disturbed agricultural catchments, in which they found that catchment scale agriculture was less important than other environmental factors in determining fish assemblages. This does not mean that agricultural land use had no effect on river fish assemblages, but it does mean that all study rivers had similar level of agricultural degradation. As Wang et al. (2006, this volume) demonstrate, in largely undisturbed Midwestern catchments, fish assemblages are predominantly influenced by local factors or natural gradients, but as disturbance increases in catchments and riparian areas, the relative importance of local factors declines and that of catchment increases. Hughes et al. (2005) found a similar shift in importance from local/natural factors to network scale factors with increased disturbance from dams and alien species in large rivers.

Challenges in Collecting and Gathering Landscape and Instream Data

Our ability to understand influences of landscape on river systems is largely driven by the availability of large-scale databases and development of information technologies. Many federal and state monitoring programs have been collecting high quality physicochemical and biological data for 10–15 years. However, the river segment length these data represent remains a question. There is limited effort in national and state monitoring programs to gather landscape data at various scales, although the recent emergence of landscape ecology concepts, coupled with an explosion of capabilities for computerized spatial

data analyses and visualization, are now allowing us to begin to truly see and understand rivers as spatially extensive, landscape-integrated ecosystems. As several authors illustrate (Brenden et al. 2006; Gresswell et al. 2006, this volume; Seelbach et al. 2006; Torgersen et al. 2006, this volume), the river segments and their associated landscape databases are essential and powerful for understanding the influences of landscape on river systems, for environmental assessment, and for developing resource management tools. Brenden et al. (2006) also demonstrate the feasibility of building such databases for multiple states or entire nations.

STRUCTURE OF THE BOOK AND KEY FINDINGS

This book is organized by topics on (1) general principles and concepts in viewing the linkage between river and landscape systems, (2) landscape and instream physicochemical relations, (3) influences of spatial and temporal scales on the effects of the natural landscape and land use on river conditions, (4) landscape and prairie/plains fish relations, (5) landscape and Midwestern fish relations, (6) landscape influences on fish and macroinvertebrates in largely forested catchments, (7) landscape influences on large rivers, (8) landscape in fish predictive modeling, and (9) distinguishing natural variation from human disturbance on river physicochemical and biological characteristics. In some cases, a chapter may include more than one topic, and in other cases, several chapters may deal with the same topic using different approaches or at different geographic locations.

The first four chapters deal with general principles. Seelbach et al. (2006) synthesized the current views of river-landscape systems and proposed that rivers can be divided into segments with relatively homogeneous physicochemical, morphological, and biological characteristics. In lower Michigan, the characteristics of those segments are determined by the surrounding landscape features, such as surficial geology, soil type,

landscape slope, bedrock depth, and position of the segment within the network. Brenden et al. (2006) described how to identify river segments using statistical and geographic information system (GIS) tools. This chapter extensively explored how those tools can be applied to all rivers in multiple states, and the potential usefulness of those identified river segments. Hitt and Angermeier (2006, this volume) tested the hypotheses that fish dispersal from adjacent streams influences local fish assemblage structure, and the effects of interstream dispersal are mediated by local environmental conditions. They found significant effects of adjacent stream size on local species richness, mean reproductive age, and riverine species richness in Virginia. Large adjacent streams (>fourth-order) were associated with increased species richness in second-order sites. Measures of channel shape (i.e., depth, width, and sinuosity) and microhabitat complexity (i.e., mean substrate size and woody debris) were associated with local assemblage structure, in some cases, but did not account for significant variation in fish metrics explained by adjacent stream size. Herlihy et al. (2006, this volume) analyzed data from 5,951 sample sites across the United States to conduct a fish-based biological classification and to evaluate its relation with landscape-based classification. They found 12 fish assemblage groups that were well described by indicator fishes. Landscape classifications, whether based on ecoregion, physiography, hydrologic units, or political boundaries, had very similar and low classification strength for explaining fish assemblage similarities and differences.

The next three chapters evaluated landscape and instream physicochemical habitat relations. Wehrly et al. (2006, this volume) described how landscape characteristics determine river water temperature regime in lower Michigan. They found that catchment area, latitude, local groundwater inputs, local forest cover, air temperature, percent agriculture in the catchment, percent lakes and wetlands in the catchment, and percent coarse-textured geology in the catchment were important factors structuring spatial

variation in river temperatures. Rosen et al. (2006, this volume) evaluated how landscape influences river flow and water chemistry and, hence, how they influence river toxicity. They found that Truckee River sites in Nevada and California with high percentages of urban land use had increased toxicity and hydrologic flow was less important in determining the amount of toxicity present at each site. Johnson et al. (2006, this volume) described how landscape factors influence the amount and character of instream woody debris. They found that mean log size was greater, but total abundance was lower in Minnesota than Michigan. The greatest wood abundance and extent of accumulations were associated with high substrate heterogeneity and riparian vegetation in Minnesota. The largest densities and accumulations of wood were associated with catchments in hilly regions containing urban centers, with low soil water capacity, wide and shallow river channels, and woody riparian zones.

Two chapters evaluated the influences of spatial and temporal scales on the effects of the natural landscape and human induced land cover on river conditions. Burnett et al. (2006) compared riparian and catchment influences on habitat in a forested-montane basin of western Oregon. They found that multiscale assessments can identify areas and suggest processes most closely linked to stream habitat and, thus, can aid in designing land management to protect and restore stream ecosystems. Wang et al. (2006) demonstrated that in largely undisturbed Midwestern catchments, fish assemblages are predominantly influenced by instream habitat, but as disturbance increases in catchment and riparian areas, the relative importance of instream habitat declines and that of catchment increases.

Four chapters evaluated the relationships among landscape characteristics and fish assemblages in prairie or plains catchments. Hoagstrom and Berry (2006, this volume) studied native fish zoogeography in the Great Plains and used island biogeographical approaches to

study the influence of basin area and isolation on faunal composition. They reported that 25 widespread species were either present among tributary basins during glaciation or colonized the region during recession of the continental glaciers, and 66 more restricted species presumably colonized more recently. Gido et al. (2006) quantified the relative increase in predictive ability as they added habitat measurements (catchment, reaches, and sites) from increasingly finer spatial scales in the Kansas River basin. They concluded that field habitat measurements were less informative for predicting species occurrences than catchment data, but a refined understanding of the relationship between catchment-, reach- and site-scale habitats provides a mechanistic understanding of fish-habitat relations across spatial scales. Heitke et al. (2006) provided an example of how natural variation among river systems can hinder detection of anthropogenic impacts on river health. They demonstrated that study of 37 second- to sixth-order river sites from seven ecoregions in Iowa could not detect the degradation of fish assemblages caused by intensive and extensive agriculture. They concluded that this occurred because the natural variations in fish assemblages among the river sizes and ecoregions were greater than the variance in agricultural land use. Wall and Berry (2006) found that the distribution of endangered Topeka shiner *Notropis topeka* in South Dakota is associated with river size, groundwater potential, channel slope, river flow, network position, and percentages of pasture and trees at the river segment scale. At the reach scale, Topeka shiner distribution is associated with low grazing and small trees in riparian zones, low bank height, less submerged vegetation, and coarse substrates.

Four chapters described the relationships among landscape characteristics and fish assemblages in Midwestern rivers. Moerke and Lamberti (2006, this volume) quantified the relationships between different types of land uses and river physicochemical variables and resident

fish assemblages in southwestern Michigan rivers. They found that forested rivers have the least degraded water quality, physical habitat, and fish assemblages, and agricultural rivers lacking buffers were the most degraded. Urban and agricultural rivers with buffers displayed characteristics intermediate to forested and agricultural rivers lacking buffers. Infante et al. (2006, this volume) investigated the effects of channel shape on the fish assemblages of rivers in Michigan's Lower Peninsula. They concluded that with increasing channel incision, total fish biomass decreased and that decreasing low flow hydraulic radius led to a reduction in the biomass of intolerant fishes. The catchment- and reach-scale measures affected fish assemblages through their effects on catchment hydrology, river hydraulics, and channel shape. Diana et al. (2006, this volume) studied the influence of land use and instream physical habitat on biotic condition of fish assemblages for rivers in southeastern Michigan and found that the amount of agriculture and wetland in the catchment and 100-m buffers had the strongest relationships with instream physical habitat and biological assemblages. Zorn and Wiley (2006, this volume) quantitatively described relations between catchment- and local-scale habitat variables and fish biomass in rivers of lower Michigan. They found that catchment-scale variables characterizing river size, land use, and surficial geology had significant effects on mean water depth, velocity, water temperature, base flow yield, and total phosphorus. Site scale water depth, total phosphorus, percent cobble, catchment area, and agricultural and urban land use most affected fish biomass.

Four chapters studied relationships among landscape characteristics and river fish or macroinvertebrate assemblages in forest-dominated catchments. Woodcock et al. (2006, this volume) evaluated macroinvertebrate assemblages in catchments with different forest management in New York. They reported that unlogged catchments had deeper and wider river channels, despite steeper channel slopes, while

logged catchments had more stored organic matter and finer substrate particles. Macroinvertebrate taxa richness was significantly reduced in logged catchments. Distribution of macroinvertebrates was related to water quantity, channel geomorphology, and particle size at the channel scale and to circularity (ratio of the catchment area to the area of a circle with the same perimeter), ground and surface water drainage patterns, and sediment load at the catchment scale. Hemstad and Newman (2006, this volume) investigated the influence that various land cover types (including recent forest harvest) had on northeastern Minnesota fish assemblages at multiple spatial scales and compared these results to the influences of local instream habitat variables. They found that forest harvest within the past 2 years had negative influences on fish assemblages at the local and catchment scales. The cumulative effect of increasing forest harvest from up to 8 years throughout the catchment was associated with lower quality fish assemblages and instream habitat. Kaufmann and Hughes (2006) examined associations among physical and chemical habitat, land use, geomorphology, and aquatic vertebrate assemblages in western Oregon and Washington and found that variations in aquatic vertebrate assemblages and habitat characteristics were predetermined by drainage area, channel slope, and basin lithology. Streambed instability and excess fines were associated with riparian disturbance and road density. The vertebrate index of biotic integrity was associated with excess streambed fines, bed instability, higher water temperature, higher dissolved nutrient concentrations, and lack of deep pools and cover complexity. Gresswell et al. (2006) evaluated relations between coastal cutthroat trout *Oncorhynchus clarkii clarkii* populations and physical habitat template at a variety of spatial scales in western Oregon. They found that some cutthroat trout congregated in areas of suitable habitat and formed local populations that may exhibit unique genetic attributes and concluded

that it is important to include fish movement needs when viewing habitats that are critical to the fitness and persistence of cutthroat trout populations.

Two chapters examined relationships among landscape characteristics and fish assemblages in nonwadeable rivers. Torgersen et al. (2006) examined spatially continuous longitudinal profiles of fish distribution and aquatic habitat for three northeastern Oregon rivers. They found that spatial structuring of fish assemblages exhibited a generalized pattern of cold- and cool-water fish assemblage zones but was variable within thermal zones. Landscape geographic setting and thermal condition influenced the observed relationship between species distribution and channel gradient. Weigel et al. (2006, this volume) analyzed data from 38 large-river sites in Wisconsin to characterize the influence of environmental variables at basin, reach, and site scales on fish assemblages. They reported that site and basin scales defined fishes along a gradient from high conductivity, fine substrate, and agricultural land cover to low conductivity, rocky substrate, and forest land cover.

Two chapters explored methods for using different spatial-scale landscape characteristics to predict fish assemblages. Steen et al. (2006) evaluated methods for modeling associations between fish species and landscape characteristics in lower Michigan. They compared landscape models generated by multiple regression, logistic regression, neural networks, and classification trees for predicting brook trout *Salvelinus fontinalis*. They concluded that differences in accuracy among the models were small, but the logistic regression model predicted with the least amount of error, followed by multiple regression, classification trees, and neural networks. McKenna et al. (2006) described a methodology for developing species–habitat models for the Genesee basin, New York. Multiple linear regression, stepwise multiple linear regression, linear discriminant analysis, and neural network were developed and compared for 11 fish species. They concluded that predictive models used as many

as 25 habitat variables and explained 35–91% of observed species abundance variability. Neural network models performed best for the majority of the fish species.

Five chapters aimed to develop methods on reference site selection for environmental impairment assessment. Riseng et al. (2006) compared three data sets of differing geographic extents and sampling intensities to examine how data structure affects the outcome of biological assessment. They compared results from a fine-scale data set from a single catchment, a medium-size data set from an ecoregion, and a coarse Michigan-wide data set and concluded that the scale and specificity of data used to determine reference condition influences the results of a biological assessment. Reference conditions determined by the coarse statewide data were more sensitive to land-use stresses and data sets with broader spatial range appeared to produce the most sensitive and accurate watershed impairment assessment. Stanfield and Kilgour (2006) evaluated the effects of PIC on fish assemblages, benthic invertebrate assemblages, instream physical habitat, and temperature, after statistically removing the effects of natural landscape features (i.e., catchment area, slope, base flow) for Lake Ontario tributary rivers. Both coldwater sensitive and warmwater intolerant fish and diverse macroinvertebrate assemblages were found in catchments with low PIC; both fish and macroinvertebrate assemblages consisted of mainly warmwater or tolerant assemblages in catchments with high PIC. Stanfield et al. (2006) used a hierarchical approach to evaluate the predictive capabilities of landscape conditions, local habitat features, and potential effects from cooccurring salmonids on the distribution and densities of three trout and a salmon species within the majority of the Canadian tributaries to Lake Ontario. They found that catchment percent impervious cover (PIC), base flow index, and barriers were the most important predictors of salmonid distribution. Landscape features were the best predictors of densities of rainbow trout *O. mykiss* and brook trout and

local habitat features and presence of other salmonids produced the best predictive model for brown trout *Salmo trutta*. Kilgour and Stanfield (2006) developed a series of models that relate biophysical conditions of rivers (i.e., fish, macroinvertebrates, and instream habitat) to landscape (i.e., slope, geology, catchment area) and PIC to estimate the expected biophysical condition at a variety of land-use scenarios. The difference between the expected and present conditions is an estimate of present-day impacts. Results from this exercise provided an estimate of the magnitude of impairment of streams in the Canadian portion of the Lake Ontario region. Whittier et al. (2006) defined least-disturbed conditions for a set of water chemistry, catchment, and site-scale indicators of disturbance for 835 river sites in the Mountains, Xeric, and Plains regions in the conterminous western United States. The least-disturbed condition for each indicator was adjusted by the sites' locations along the primary natural gradients. The importance of disturbance types varied regionally and along natural gradients. They also reported regional-scale patterns in aquatic vertebrate and macroinvertebrate assemblage metrics at least- and most-disturbed sites.

KNOWLEDGE GAPS IN LINKING LANDSCAPE FEATURES AND INSTREAM PHYSICOCHEMICAL AND BIOLOGICAL CONDITIONS

By examining chapters in this book and peer-reviewed journal publications, it is not difficult to conclude that the field of viewing and measuring river systems from a landscape perspective is a relatively young, but rapidly developing ecological discipline. As we outlined above, there are many challenges to applying current knowledge in measuring components and function of river-landscape systems and in developing tools for aquatic resource management. These challenges are mainly the result of gaps in our current levels of data collection, data analysis, and concept and principle development. We call spe-

cial attention to those areas for future resource investment and research efforts.

Improving River-Landscape Classification

Although many different conceptual classification schemes have been proposed, early methods mainly involved longitudinal zonations that tie discontinua of biological assemblages to key physical factors such as temperature, substrate, water depth, current velocity, and network position (Hawkes 1975; Hudson et al. 1992). During the last two decades, greater emphasis has been placed on describing physical drainage (catchment, subcatchment) and channel (segment, reach, mesohabitat, microhabitat) units or habitat patches, at a series of nested scales as a fundamental habitat template (Frissell et al. 1986; Maxwell et al. 1995; Snelder and Biggs 2002; Benda et al. 2004). The characteristics of biological assemblages for a particular river location are recognized as a result of multiple spatial scale filters (Tonn 1990; Poff 1997). This current knowledge permits us to zoom out from a traditional sampling reach perspective to view patterns at a broad landscape scale that can be used for understanding and describing processes and characteristics controlling finer-scale units. However, there is no single commonly accepted river classification unit. One common unit is the catchment or subcatchment, which is ambiguous because not all river sections in the same catchment or subcatchment are the same, especially those in large catchments or those crossing ecoregion boundaries. For example, Omernik and Bailey (1997) and Omernik (2003) found that hydrologic units are true catchments less than half the time, and Omernik (2003) reported substantial differences in 8-digit hydrologic units and catchments draining different ecoregions. Another classification unit is the river sampling site, typically 100–1,000 m. Such sites can only classify river sections where data have been collected. A recent approach uses river reach, defined by confluence to confluence, as a classification

unit, which is promising because regimes of flow, temperature, and sediment of a river section are often noticeably different before and after a major confluence (Benda et al. 2004). In cases when differences among adjacent reaches are not substantial, they can be classified as the same class and easily merged into larger segments using GIS tools. Dividing continuous river systems into relative distinct segments and classifying those segments into relative homogeneous classes permits expansion of site-specific information, supplies a framework for organizing data, and aids generalization among relatively similar spatial units.

Data Capturing

Limitations to data capturing hinders the progress of viewing and measuring river-landscape systems. Instream physicochemical and biological data collection and out-of-river landscape data gathering are the major areas of concern in data capturing. As represented by the chapters of this book and existing state and federal monitoring programs, current data capturing is a piece-meal approach that samples river sites, gathers landscape information associated with the sites, then uses such captured information to represent areas where data are lacking. There are five major weaknesses of this approach. (1) We cannot study all river sites for a state or a large region. (2) We typically do not know the length of the river segment that the sampled data represent within the same system. (3) We are unsure of the degree that the sampled data represent segments of similar size in the same or different river networks. (4) The landscape data captured for individual sites is often duplicated or not comparable among different agencies and projects. (5) Some important data layers are at too coarse a scale, inconsistent, or lacking (e.g., dam size and location, size and date of logged areas, extent and intensity of livestock grazing, and type and amount of biocide application)

The aforementioned approach that identifies river segment, gathers different spatial scale land-

scape data for each segment, and classifies segments into classes seems promising. Such an approach can improve our ability to determine the length of the river segment that the study data represent (random samples from a segment can represent the entire segment) and can indicate whether the study data represent segments of different rivers (random samples from a set of segments can represent all segments in the same class). Another advantage of this approach is that once the landscape data have been captured for a region, all programs and projects in the region can share the same information to reduce duplication of efforts and to increase data comparability.

Although this approach has promise, it is still in its early stage of development, and it has not been widely used mainly because of the unavailability of large scale landscape databases and the resources required to delineate segments and associated different scale catchment boundaries of each segment. Presently, many agencies, such as those described in this book (Brenden et al. 2006), the U.S. Geological Survey Aquatic Gap Program, and The Nature Conservancy, have invested considerable resources working toward this direction. Available landscape databases, such as the National Hydrographic Data, National Elevation Dataset, and National Land Cover Dataset, meet preliminary needs. Many other databases that are essential to such an approach, such as surficial geology and bedrock type and depth, are available only locally. More resources and efforts are needed to develop multistate or national databases, to identify river units, to delineate catchment boundaries of the units, and to capture landscape data associated with the units. In many parts of the United States, better landscape data on livestock grazing intensity, logging intensity, road density and crossings, dams, and water diversion are needed. In particular, the upstream effects of downstream dams and other migratory barriers is poorly rendered by catchment-based data sets.

Improving Accuracy of Predictive Models

Model development for predicting conditions where instream data are not available also deserves more attention. Because instream physicochemical conditions are largely controlled by different spatial-scale landscape settings, many instream physicochemical characteristics can be predicted from landscape features to varying degrees of accuracy. The major advantage of such an approach is that landscape data can be obtained from readily available databases; hence, landscape-based model prediction is much cheaper than field sampling—although field data are required for initial model calibration and validation. Additionally, by using models, one can predict key instream variables, such as water temperature and discharge for each river segment. Such models are useful for hindcasting historical or predevelopment conditions or for predicting consequences of alternative future development (Van Sickle et al. 2004; Kilgour and Stanfield 2006; Stanfield and Kilgour 2006).

Although catchment-scale models have been developed locally for predicting key physicochemical and biological characteristics, few models have been developed for an entire state or multiple states (e.g., Studdard et al. 2005; Pont et al. 2006). Additionally, current model accuracy is far from satisfactory, and accuracy depends on large, rigorous data sets for model calibration and validation. Nonetheless, landscape based models for predicting instream physicochemical and biological characteristics have great potential and deserve more attention.

Improving Our Ability to Measure Connectivity among River Segments and Their Networks

The connection of a river site to its network influences the local distribution and abundance of organisms. River fish, in particular, may disperse to access remote resources, escape local

habitat stressors, colonize adjacent habitats, or migrate to specific habitats that are essential to a specific life stage. Hence, local fish assemblage composition at a particular time is not only regulated by local environmental condition, but also by the spatial distribution of source populations and the connectivity between a site and the river network.

Presently, we know that some fish species and individuals of a species have distinct home ranges with defined habitat requirements, while others require large home ranges with more complex habitat conditions. We know that headwaters typically support fewer fish species than rivers of equal size directly connected to large rivers (e.g., Hitt and Angermeier 2006) and lakes. However, we have only limited knowledge of how the distance from a site to a larger river or how big a size difference between the site and the larger river affects local fish assemblage structure. More knowledge is also needed on how fragmentation by dams, waterfalls, channel modification, physicochemical interruption in the river network (including side channels and flood plains), and how proximity of a river reach to lakes or large rivers affect local and network fish assemblages, especially on how to measure and evaluate the effects of such fragmentation.

By recognizing the importance of network connectivity, Fausch et al. (2002) proposed to measure all components of instream habitat structure, including connectivity with side channels and floodplains, at a scale between 1 and 100 km of river length because of the longitudinal heterogeneity of river conditions. This approach provides accurate assessment, but it is not practical to apply at state or national scales. Although Seelbach et al. (2006) and Brenden et al. (2006) explored a way to measure connectivity and Hitt and Angermeier (2006) evaluated the importance of connectivity, more research is needed on how to measure and evaluate the effects of connectivity and fragmentation at multiple spatial scales from intermittent tributaries to large navigable rivers.

Additional research and understanding on the temporal scale of connectivity, and how it changed with climate change and anthropogenic alterations, is needed. For example, Hocutt and Wiley (1986), Tedesco et al. (2005), and Hoagstrom and Berry (2006) document the effects of glacial advances and recession on fish distribution. Such information provides important temporal context for current conditions, and continued research and revisions are needed in this area. But it is equally important to determine how historical changes in river habitat, flow regime, and land use over the past two centuries have altered species distribution and abundance in individual river basins (Jungwirth et al. 2003; Rinne et al. 2005; Kilgour and Stanfield 2006). Without historical habitat and assemblage information, our models and status and trend assessments will remain partially veiled.

SUMMARY

Although this book covers a variety of topics directly related to the influences of landscape on river habitats and biological assemblages, it provides only a snapshot of the status of this rapidly developing field. In this book, the authors have explored new ideas about landscape-river relationships and about river research and management and have produced interesting hypotheses as a foundation for the next phases of riverine science. We hope this book will help outline a whole new generation of questions about the relationship between landscape and lotic systems.

By examining the chapters of this book, one can easily identify key challenges in landscape-lotic systems that we are facing today. This book also reveals some major current knowledge gaps that deserve more attention in landscape-river ecology. To overcome the challenges and fill the knowledge gaps in understanding and measuring landscape influences on river systems at large spatial scales, we call for the development of national or regional standard landscape databases, such as soil, digital elevation, surficial geology, climate, and bedrock, from the existing, incon-

sistent pieces across the United States. National standardized catchment boundary delineations for all river segments based on the National Hydrographic Database (NHD-plus) are in progress (http://nhd.usgs.gov/newsletter_list.html). These databases and river measurement units with defined catchment boundaries will improve our ability to measure, evaluate, and understand relationships among a particular river segment and its fluvial network and surrounding landscape. We also call for an investment in developing readily available GIS tools. Presently, GIS tools developed by different federal, state, non-profit/profit, and university agencies are diverse, inconsistent, repetitive, and often unavailable to others. Such readily available tools will enable us to effectively develop and use the databases and to appropriately evaluate river segment conditions and river-landscape relationships. Most importantly, these databases and technology will enable us to distinguish natural variation in physicochemical and biological conditions among river units from the changes caused by human activities. This, in turn, aids development of appropriate resource management plans and policies for preserving and rehabilitating river habitats and biological assemblages. Last, we call for implementation of a rigorous, national river monitoring program similar to those developed by some U.S. states (e.g., Klauda et al. 1998; Yoder and Smith 1999; Nicholas et al. 2005), eastern Ontario (Stanfield et al. 2006), and the USEPA's EMAP (USEPA 2000; Stoddard et al. 2005). Without such a program, our models and status and trend assessments will remain inaccurate and limited to those few areas with adequate field data.

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Initial Classification of River Valley Segments across Michigan's Lower Peninsula

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Abstract.—Describing the unique spatial context of any river unit requires integrating catchment and local valley characters. We believe that adding hydrologic regime and key fish species to standard geomorphic variables improves the delineation and characterization of river valley segments as ecological units. Valley segments constrain habitat units, and several segments together can encompass home ranges of mobile fishes. Segments can be accurately defined and characterized using maps and then analyzed across large geographic areas, making them practical for statewide planning and management. By incorporating prior knowledge from modeling landscape–river relationships, we interpreted multiple landscape maps to delineate and assign initial attributes to river valley segments. The resulting classification system provides a new, ecologically informed view of Michigan's rivers that has helped managers better perceive and consider environmental patterns that constrain habitat and biological variation within and among individual rivers. It is being used throughout Michigan and regionally as a framework for fisheries and water management, conservation planning, and education.

INTRODUCTION

Tremendous diversity in the ecological character of rivers hinders extrapolating our experiences and management protocols from place to place. River classification presents a means of describing and managing this heterogeneity by aiding inference from site-specific information and

model estimates, supplying a framework for organizing data, and facilitating generalizations among similar spatial units (Hudson et al. 1992; Maxwell et al. 1995; Goodwin 1999). Classification also provides a means for thinking and communicating about the consequences of complex ecological processes (Bailey et al. 1978; Spies and Barnes 1985).

Many conceptual schemes for river classification have been proposed. Early methods involved

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longitudinal zonations that tied fish species to key physical variables such as temperature, substrate, and network position (Hawkes 1975; Hudson et al. 1992). Recently, emphasis has been placed on describing physical drainage (catchment, subcatchment) and channel units (segment, reach, mesohabitat, microhabitat) at a series of nested scales (Frissell et al. 1986; Maxwell et al. 1995; Montgomery 1999; Snelder and Biggs 2002; Benda et al. 2004).

With the exception of a segment classification based on trout distributions (Anonymous 1981), no ecological classification previously existed for Michigan rivers or similarly glaciated and mixed-land use terrain. Similar to Maxwell et al. (1995), our objective was to develop a river classification that would (1) encompass decadal temporal and statewide spatial scales, (2) integrate segment-scale ecosystem structure and function, (3) convey mechanisms that drive segment-scale ecological responses, (4) be inexpensive, and (5) promote consistency among managers. In this chapter, we (1) highlight several concepts and elements that we believe provide an expanded view of riverine habitat structure and that are fundamental to developing a river classification, (2) describe implementation of a new classification of valley segments for Michigan's Lower Peninsula (MLP) rivers, and (3) discuss current management applications.

Keys to Enhanced River Classification

Frissell et al. (1986) described a conceptual model for classifying riverine habitats. Their model framed a hierarchically nested series of drainage and channel units (segment, reach, mesohabitat, and microhabitat) and explained that each successively broader scale structures those beneath. Their model has been accepted and used as a basic framework for river classification (e.g., Maxwell et al. 1995). However, as we began classifying Michigan rivers, we identified additional key elements that are missing or underemphasized in current approaches, but fundamental to improved river classification,

including catchment character, key fish species, and hydrologic regime.

Catchment character.—Landscape ecology supports the hierarchical view of Frissell et al. (1986), encouraging river ecologists to broaden their perspectives from sampling site or reach, to catchment patterns useful for understanding characteristics of those finer-scale river units (Risser et al. 1984; Allan and Johnson 1997; Wiley et al. 1997). A landscape approach stresses the catchment, hydrologic, geomorphic, and river network contexts of a reach that control its physical and biological characteristics (Montgomery 1999; Poole 2002; Baker et al. 2003; Benda et al. 2004; Riseng et al. 2004; Thorp et al. 2005).

Clarification is needed regarding use of catchments in river analyses. In the Frissell et al. (1986) model, multiple valley segments are nested within a single subwatershed (Figure 1). At the valley segment scale, application of this structure is limiting because neighboring segments cannot be differentiated from each other based on catchment differences. To emphasize hydrologic processes, we favor using each unique catchment as the drainage unit for each valley segment. We define catchment as the land area that drains to a specific river site. In contrast to the subwatershed concept, catchments overlap spatially and accumulate in a hierarchical fashion down the river network (Figure 1). This "accumulating drainage" conceptual model is standard in hydrologic analyses, but represents a modification to the nested-hierarchy thinking often used in river ecology.

A site's, or valley segment's, unique position in the catchment character provides a basis for developing statistical models that relate mapped catchment patterns to site- or segment-scale response variables (Biggs et al. 1990; Seelbach and Wiley 1997; Wiley et al. 1997; Montgomery 1999). Conceptual and empirical models help define the range of catchment and valley scale characteristics that appear to be key valley segment drivers (Seelbach et al. 2002). The spatially explicit predictions of such models can illustrate relationships (including error terms) between

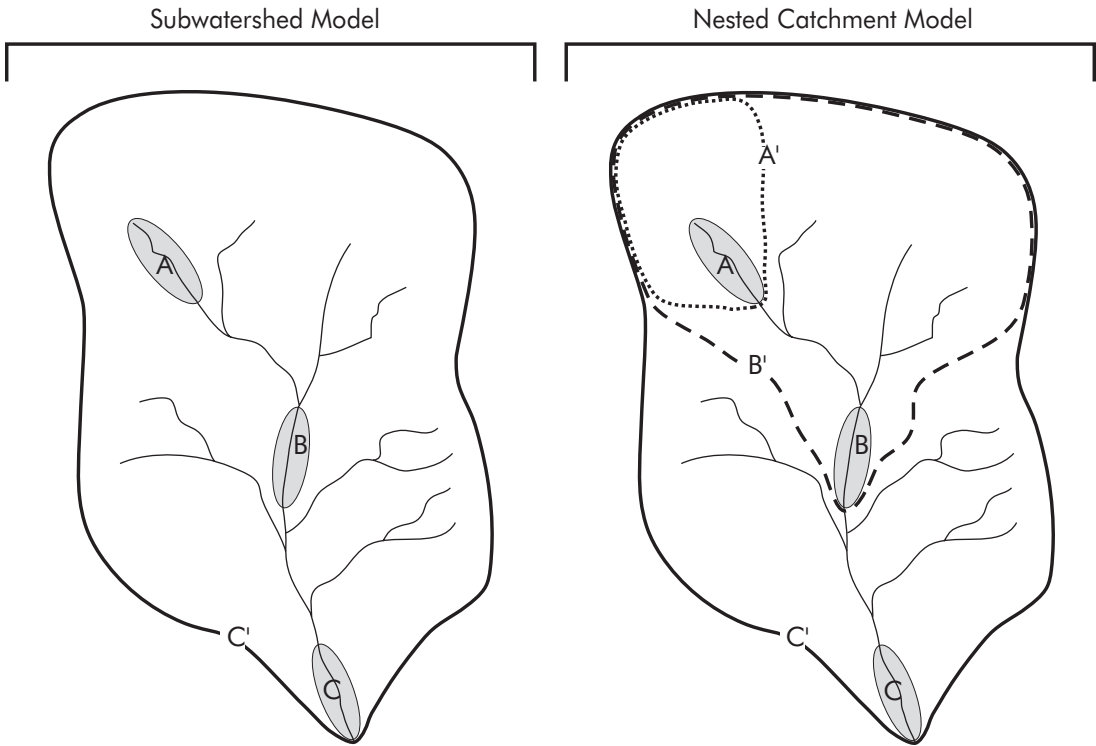


Figure 1. A hypothetical stream network with three segment units, A, B, and C, and corresponding catchments A', B', and C'. In the subwatershed model, all three segments are nested within catchment C', and characteristics of C' are assumed to influence segments A, B, and C equally. In the alternative nested catchment model, characteristics of each catchment (A', B', and C) are applied to segments A, B, and C, respectively. Note that scale relationships between A and its catchment differ in the two models (C' versus A'). Note that catchment unit outer boundaries A', B', and C' typically would be overlapping but have been offset for clarity.

catchment characteristics and key aquatic habitat and biotic variables, making them informative precursors for valley segment classification.

Fish species associations.—Recent river classification approaches emphasized a physical habitat template only, with biotic responses inferred (Naiman 1998; Goodwin 1999; Montgomery 1999). In contrast, forest ecologists (Spies and Barnes 1985; Rowe and Barnes 1994) and geographers (Bailey et al. 1978; Omernik 2004) have argued for ecological classification incorporating biological information. Similarly, Wu and Loucks (1995) described ecological patchiness in terms of biological patches overlying physical patchiness, and Thorp et al. (2005) argued that this concept is central to the ecological structuring of rivers. In an ecological river classification, distributions

of fish species are incorporated to help delimit ecologically relevant valley segments.

Hydrologic regime.—Despite strong agreement among scientists on the importance of the hydrologic regime to river ecosystems, this surprisingly is not explicitly featured in many current river classification approaches. Most important riverine characteristics are shaped by the hydrologic regime (Poff and Ward 1989; Poff et al. 1997; Montgomery 1999; Zorn et al. 2002; Benda et al. 2004); indeed, temperature, chemistry, and hydraulics are all major habitat variables governed by the conservative character of the water mass. The hydrologic regime largely defines patterns of delivery and transport of water, wood, and sediments, which, in turn, interact with local valley and channel constraints

to create the unique habitat characteristics found at any place or time. On one hand, many aspects of stream habitat are influenced by the geology and physiography of the immediate valley segment. On the other hand, the hydrologic regime at any particular location is strongly dependent on aspects of the catchment. Thus, landscape characterizations at both valley segment and catchment levels are needed to better understand variation in the physical and biotic character of rivers (Montgomery 1999; Poole 2002; Snelder and Biggs 2002; Benda et al. 2004).

Valley segment scale.—River channel networks are composed of many distinct ecological patches with relatively distinct boundaries created by stream confluences, variable local landscape features, and lakes and impoundments (Naiman et al. 1988; Hudson et al. 1992; Montgomery 1999; Poole 2002; Thorp et al. 2005). The confluence of streams draining markedly different catchments can result in abrupt changes in thermal regime, hydraulics, chemical and sediment loads (Minshall et al. 1985; Statzner and Higler 1985; Poole 2002; Benda et al. 2004), and biota (Osborne and Wiley 1992; Rice et al. 2001; Hitt and Angermeier 2006, this volume). As a river moves across a landscape, it passes through a mosaic of landscape types with abrupt or subtle boundaries (Naiman et al. 1988; Maxwell et al. 1995; Bryce and Clarke 1996; Montgomery 1999), encountering diverse local geologic and physiographic features that influence valley floor slopes, hydraulics, channel cross sections, meander patterns, pool and riffle development, substrates, sediment supply, and groundwater inputs (Statzner and Higler 1985; Cupp 1989; Rosgen 1994; Montgomery 1999; Baker et al. 2003). Local geomorphology (e.g., plains, hills or mountains, or glacial river valleys) also affects channel forms, including floodplain structures (Hupp 1982; Cupp 1989; Rosgen 1994; Baker and Barnes 1998). Mid-river lakes and impoundments alter upriver grades and biota (Statzner and Higler 1985; Pringle 1997) and affect downstream biological, chemical, thermal, and material conditions (Ward and Stanford 1983; Minshall et al. 1985).

The whole river channel network, then, is a branched linear mosaic of ecological transitions bounding relatively homogeneous units (Montgomery 1999; Poole 2002; Thorp et al. 2005) that we call valley segments. These valley segments can be identified by simultaneously examining accumulating catchment effects (e.g., discharge, water character, land surface form, soil, and land use) and localized discontinuities (e.g., tributary junctions, in-river lakes, geological contact zones, and shifts in channel morphology and key fish species) (Figure 2). Valley segments were characterized by Frissell et al. (1986), Cupp (1989), and Maxwell et al. (1995) as displaying relative homogeneity in flows, water quality, valley and channel morphology, and riparian/floodplain dynamics that typically change at stream junctions, slope breaks, and land form boundaries.

Valley segments are attractive as river classification units for several conceptual and practical reasons. Valley segments define relatively persistent features of channel and riparian habitats on the orders of 10^2 – 10^3 years and 10^1 – 10^2 km (Hudson et al. 1992; Baker and Barnes 1998). Several adjacent segments are often large enough to contain the multiple habitats required by many mobile, resident lotic fishes during their life cycles (Hawkes 1975; Schlosser 1991; Maxwell et al. 1995). Because many riverine fishes are extremely mobile, especially among seasonal habitats (Gowan et al. 1994; Fausch et al. 2002; Gresswell et al. 2006; Torgersen et al. 2006; both this volume), smaller units such as reaches or habitat units are inappropriate for state- or regional-scale management. Furthermore, valley segments have internal organization represented by a predictable series of smaller-scale reaches (e.g., alternating stretches of relatively uniform slopes within the segment) and further-nested habitat units (e.g., pools, riffles; Frissell et al. 1986; Hudson et al. 1992) that are used selectively by fishes during specific life stages and seasons (Hawkins et al. 1993; Rabeni and Sowa 1996). Thus, valley segments limit the character of reaches and habitat units and provide a framework for smaller-scale classifications where

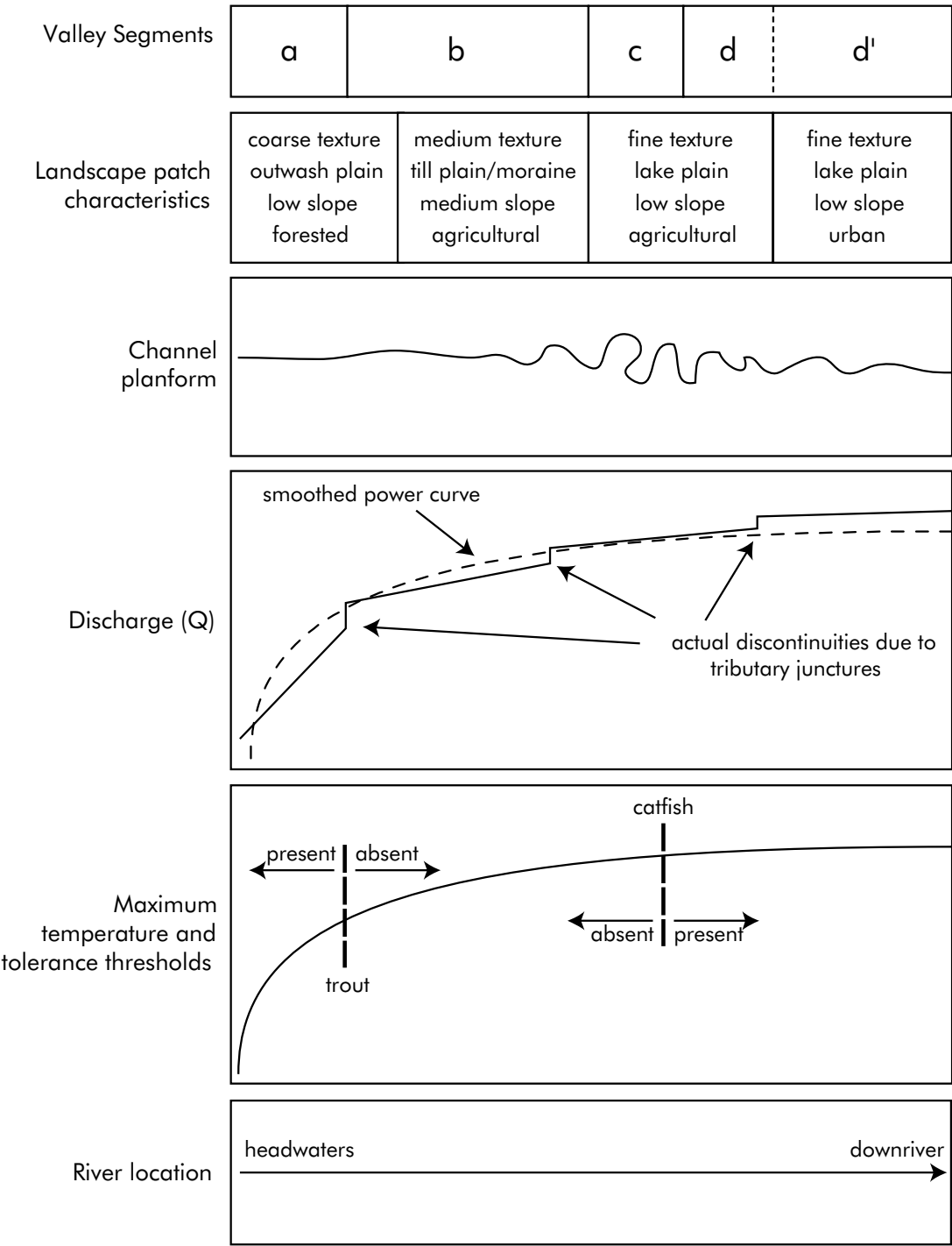


Figure 2. Valley segments emerge from the interaction between local characteristics that constrain longitudinal processes and changes driven by catchment characteristics (energy and associated planform, discharge, and temperature). We used fish species associations as primary indicators of substantive ecological change. Note that valley segment d’ is a subunit of valley segment d. The vertical dashed line separating these units could be removed depending on the goal of classification.

desired. And importantly, valley segments are the smallest river unit that can be accurately interpreted from maps and analyzed comprehensively across states or regions. The primary landscape features of interest (i.e., river networks, elevations, slopes, climate character, geologic materials, valley character, and land uses) can be readily determined from maps at 1:100,000 or 1:500,000 scales (Omernik 2004).

Valley segments are relevant for management and planning, since they reflect the scales at which important physical and biological processes operate (Montgomery 1999; Fausch et al. 2002; Benda et al. 2004; Parsons et al. 2004). Fish assemblages and water quality can be predicted from valley segments, so comprehensive river network and regional data frameworks (essentially the riverscapes envisioned by Ward 1998 and Fausch et al. 2002) can be developed. Also valley segments are few enough that information can be readily compiled for state and regional analyses.

A flexible system for classifications.—The traditional approach to river classification has been to create a single map showing the distribution of a finite set of river types. However, Davis and Henderson (1978) argued that every classification is question specific and that we should first develop data-rich information systems that can be flexibly queried to create multiple classifications. We were interested in creating a stable set of valley segments as a data framework from which slightly different river classifications might be created for uses like aquatic conservation, trout fishery management, or water quality management at a statewide scale.

METHODS

Study Area

Despite its relatively small area and little variation in climate and elevation, MLP contains a variety of river types (Seelbach and Wiley 1997). Successive glaciations created a mosaic of glacial lake plains, outwash sand plains, moraines,

and tills of varying depths and textures (including some of the deepest deposits of glacial outwash sands and gravels in North America; Farrand and Eschman 1974; Albert et al. 1986). This peninsula is laced with glacial-fluvial channels and bedrock protrudes in a few locations. Local valley characteristics and constraints vary as stream channels cross these terrains and glacial-fluvial channels (Crow et al. 2000; Baker 2002). River catchment hydrology—the routing of precipitation among evapotranspiration, groundwater, and overland flow pathways—therefore varies tremendously across watersheds (annual 90% exceedence yields range from ~0.0 to ~0.011 cm/km², and the ratio of discharge to precipitation ranges from 0.20 to ~1.00 (Hendrickson and Doonan 1972; Seelbach et al. 1997; P. W. Seelbach, unpublished data).

In terms of valley geomorphology, many local valley characteristics and constraints are encountered as stream channels move among specific glacial terrains and in and out of remnant glacial-fluvial channels (Crow et al. 2000; Baker 2002).

River Modeling

We established a river modeling program (Seelbach and Wiley 1997) to explore relationships between landscape and riverine attributes. We built a relational database linking catchment and site-scale landscape data with existing river and stream site survey data. We then developed a series of statistical models describing landscape-river relationships across MLP. From the models, we predicted flow regime (Wiley et al. 1997), nutrient chemistry (Kleiman 1995; Baker et al. 2001), summer temperature regime (Wehrly et al. 2006, this volume), and fish assemblage structure (Zorn 2002; Zorn et al. 2002). These models indicated how, and at what scales, various landscape attributes influenced riverine attributes. Because the preceding models were derived from independent variables obtained from maps, we were able to develop rules for assigning riverine attribute classes based on map

interpretations. The resulting attributes represent an implementation of the hierarchical landscape filters concept (*sensu* Poff 1997) to map MLP riverscapes where flow regime limits water temperature and then fish distribution. We then used the following steps in developing our classification (modified from Davis and Henderson 1978).

Ecological attributes.—We sought river classification attributes that are temporally stable; that are easily quantified; that are representative of either catchment-scale hydrologic, or local-scale geomorphic, processes; and that determine habitat and biotic characteristics (Vannote et al. 1980; Lotspeich and Platts 1982; Frissell et al. 1986; Hudson et al. 1992; Maxwell et al. 1995; Montgomery 1999; Appendix A). We selected catchment size, discharge, nutrient concentration, summer water temperature, valley character, channel character, and key fish species as classification attributes. Catchment size indexes important longitudinal gradients in river habitats and has long been recognized as a primary classification variable (Hawkes 1975; Vannote et al. 1980; Goodwin 1999; Benda et al. 2004). Discharge, nutrient concentration, and water temperature integrate natural and anthropogenic catchment processes (Poff et al. 1997; Montgomery 1999; Wehrly et al. 2003). Valley character constrains channel development and local hydraulics and, therefore, the patterning of habitat units (Frissell et al. 1986; Baker and Barnes 1998; Montgomery 1999; Peterson and Rabeni 2001; Poole 2002). Key fish species integrate these environmental conditions (Fausch et al. 1990; Naiman 1998).

Map variables.—Identification of key map variables was guided by relationships highlighted in the landscape-based statistical models. Important map variables included catchment area, catchment surficial geology, catchment slope, catchment land use, valley width, valley wetlands, and channel sinuosity (Wiley et al. 1997; Baker et al. 2001; Zorn et al. 2002; Wehrly et al. 2006). We also used an explicit combination of topography and surficial geology to map shallow groundwater flux in catchments and valleys (Baker et al. 2003).

Regionalization.—Statewide river classification is daunting because comprehensive river survey data are lacking. Recognizing the constraints imposed by broad-scale landscape phenomena, we approached the delineation of spatial units by examining coincident patterns among a series of regional landscape maps (Spies and Barnes 1985; Rowe and Barnes 1994), thereby classifying the presumed causes of ecosystem structure instead of the outcomes (Klijn 1994; Seelbach et al. 2002; Snelder and Biggs 2002). This top-down form of delineation is called regionalization (Bailey et al. 1978; Klijn 1994; Omernik 2004). We assumed that relatively large, homogeneous ecological units exist and can be recognized in the spatial correspondence of selected physical and biological traits (Spies and Barnes 1985; Rowe and Barnes 1994). Traits that drive numerous ecological processes are sometimes given extra weight; for example, in terrestrial work, land form is emphasized because it shapes local climate, soil, and vegetation (Spies and Barnes 1985). For rivers, we considered land form and hydrologic regime as fundamental drivers. Known distributions of key fish species were also weighted because they integrate many local and catchment variables. Our regionalization approach was subjective, yet grounded in hierarchical concepts, landscape-based statistical modeling, and extensive regional field experience.

Delineating valley segment boundaries.—We first integrated terrain features observed on multiple thematic maps (Barnes et al. 1982; Rowe and Barnes 1994; Omernik 2004; Figure 3). We identified segment boundaries by interpreting digital terrain maps on a geographical information system (GIS). The GIS facilitated moving among maps, overlaying maps or data points, and gaining various perspectives by changing focus and scale. Two aquatic ecologists with field knowledge of Michigan rivers worked together, interpreting map information on catchment and valley characteristics (Spies and Barnes 1985). We began with the headwaters and worked down-river. Catchment and valley boundaries were coarsely interpreted during the initial delineation process. We first examined several maps to

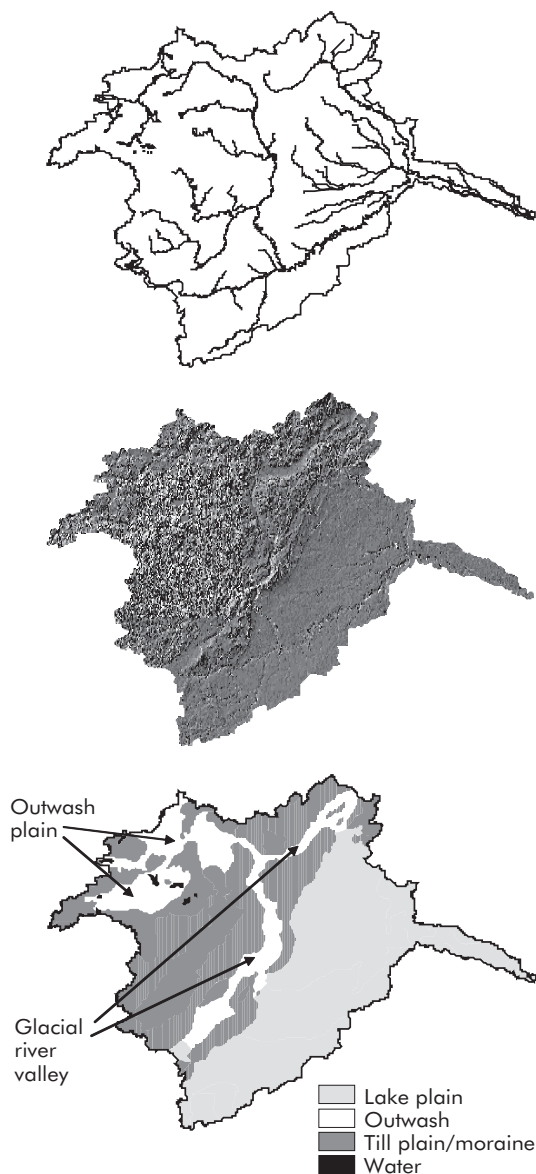


Figure 3. Multiple map themes were studied simultaneously to discern major network junctions or landscape patch boundaries that would define river segment boundaries. Shown are drainage network (upper panel), elevation (middle panel), and quaternary geology (lower panel) for the River Raisin watershed, Michigan.

familiarize ourselves with the landscape patterns of a particular catchment and to identify preliminary catchment and valley segment boundaries.

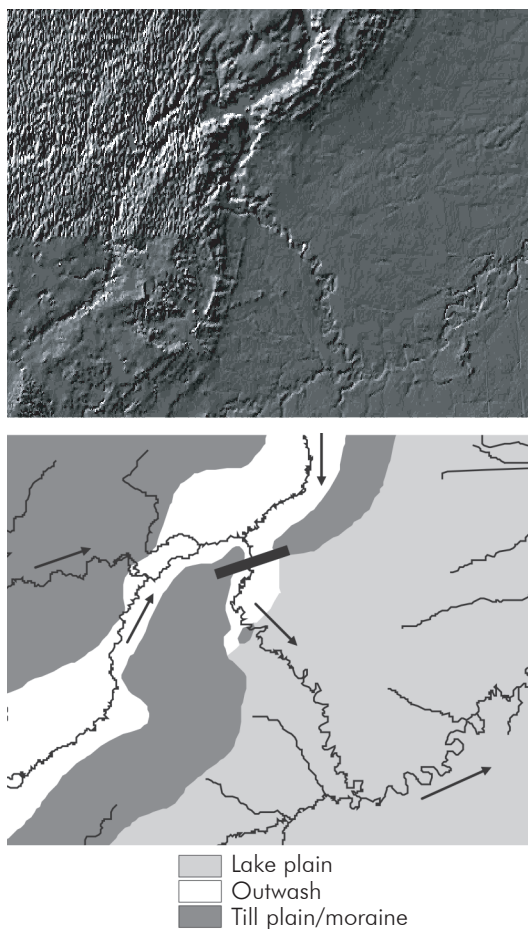


Figure 4. A close up view of the River Raisin showing changes in topography, valley character, and plan-form (upper panel) as the river flows from a landscape dominated by tillplain/moraine and outwash to lacustrine plain. Arrows in lower panel indicate direction of stream flow and the dark bar represents a valley segment boundary identified where the river leaves a moderate-gradient, confined glacial valley and moves onto a very low gradient, unconfined lacustrine plain.

Definition of an ecological boundary began with integration of terrain features observed on multiple thematic maps (Barnes et al. 1982; Rowe and Barnes 1994; Figures 3 and 4). Elevation and wetland maps were examined for changes in valley slope, width, and geological origin (glacial or alluvial) and floodplain wetlands. We examined surficial geology maps and predicted groundwater velocity from catchment-level changes in

land form, soil texture, location of glacial-fluvial channels, and groundwater sources. We analyzed hydrography maps for locations of major network junctions, large lakes, and large wetlands and for changes in channel sinuosity. Land-use maps were evaluated for boundaries between forested, agricultural, and urban areas. We determined segment boundaries by applying the following priority criteria: (1) junctions of similar order tributaries, (2) corresponding breaks in land surface form, (3) changes in local groundwater source (often corresponding with 2), (4) abrupt changes in major land uses, and (5) observed or expected changes in key fish species. Despite local variation in some areas, we sought to keep valley segments large. Frissell et al. (1986) recommended that lakes within river networks be treated as individual valley segments, in essence as ecological units. We agree but only included the larger lakes and impoundments, leaving thousands of smaller lakes for future iterations.

Valley segment descriptors.—Once segment boundaries were identified, the two ecologists assigned values or categories of ecological attributes to each valley segment by interpreting maps (Seelbach et al. 1997; Snelder and Biggs 2002). Attributes included basin name, major watershed name, segment identification number, segment link number (an index of catchment size), segment position, connection to the Great Lakes, hydrologic type, water chemistry type, water temperature type, valley slope type, valley character type, channel character type, and fish species associations (Appendix A).

We again began with headwater segments and worked systematically downriver, assigning categories to each valley segment based on the following general map interpretation rules but also considering how categories might change relative to attributes of neighboring segments. We confirmed that at least one coded ecological trait changed between adjoining segments. If this criterion was not met, we joined the segments in question. Attribute values and categories for

each valley segment were entered into a unique field, or column, in the resulting attribute data table. We identified categories or types for each key attribute through data plots, seeking natural groupings or groupings related to fish distributions. Brief descriptions of the selected attributes are provided in Appendix A, along with descriptions of attribute categories used in map interpretation.

Classification system.—We classified the 19 largest river networks in MLP, calling the product the Michigan Valley Segment Ecological Classification Version 1.0 (MI-VSEC-1). Segment boundaries and segment attributes were combined within a GIS as an ArcView (ESRI, Inc., Redlands, California) shape-file and associated data table. We used the U.S. Environmental Protection Agency's Reach File 3 (RF3), 1:100,000 scale, hydrography as our digital base map. Reach file reaches were agglomerated into valley segments or split to match major landscape breaks, using the Reach Indexing Tool software (Research Triangle Institute, Research Triangle Park, North Carolina). This GIS could be queried through map or data table interfaces and used to develop segment groupings for answering questions posed at catchment, regional, or state scales.

Evaluation.—We evaluated the assumptions that valley segments are homogeneous relative to neighboring segments, segments within the same major watershed, or segments statewide by examining similarity in fish assemblage structure among surveyed sites. We used fish assemblage data from 454 sites that included those used in the initial models relating landscape to fish species associations. Thus, this evaluation was circular for those species but still offers a useful demonstration that use of valley segments can increase assemblage similarity. We calculated Sorenson's similarity coefficient for pairwise comparisons of the presence of all fish species at sites. This index is well suited for analyzing fish assemblages that often have few species, a wide range in total abundance, and some rare species and is commonly used in ecological studies.

We also used two sets of independent data to evaluate our segment classification in three ways. First, we visually compared the overall distribution of brown trout *Salmo trutta* described by the MI-VSEC-1 system with that mapped in Bailey et al. (2004). We then evaluated the validity of our segment classification through use of the key ecological attributes of key fish species and summer temperature regime. We used fish assemblage samples from 100 sites and another 100 temperature regime sites that were randomly selected from spatially representative surveys and had not been used in developing the initial landscape-fish species or landscape-temperature models, thus providing an independent validation. We assigned thermal and fish association classes to each test site as described in Appendix A and then compared test classes with those assigned in the MI-VSEC-1 system for the valley segments containing those sites.

RESULTS

We initially identified and described 1,956 valley segments that covered river main stems and major tributaries within 19 major river basins. The mean number (and range) of main-stem valley segments per river was 6 (1–14). The mean number (and range) of tributary valley segments per river was 78 (28–211). Main-stem segments averaged 26 km long and ranged from 12 to 38 km long; segments were generally longer in larger rivers.

Summaries of the assigned attributes provide a preliminary description of MLP riverine resources. Due to relatively short drainages to the Great Lakes, the downriver-most link number averaged 195 (range 27–492). Despite their proximity, only 5% of valley segments were directly connected to the Great Lakes because of dams. High groundwater inputs (annual 90% exceedence yields of $\sim 0.007\text{--}0.011\text{ m}^3\text{s}^{-1}\text{km}^{-2}$) occur in almost a third of valley segments and moderate groundwater inputs (yields of $\sim 0.003\text{--}0.006\text{ m}^3\text{s}^{-1}\text{km}^{-2}$) occur in another third. Some valley segments show relatively low nutrient lev-

els (soluble reactive phosphorus $<15\text{ }\mu\text{g/L}$; nitrate plus nitrite $<100\text{ }\mu\text{g/L}$), reflecting catchments composed largely of sands and gravels, but most have substantial nutrients (SRP 15–30 $\mu\text{g/L}$; NO_3+NO_2 100–700 $\mu\text{g/L}$), due to more loamy soils and anthropogenic influences. Most valley segments have very low or low valley slopes ($<0.002\%$) and flow through unconfined valleys across outwash, till, and lake plains. Valley segments with moderate valley slopes (0.002–0.008%) and confined channels containing rocky substrates, distinct riffle-pool sequences or rapids are uncommon. Previously Michigan streams were considered either coldwater or warmwater (Anonymous 1981); yet, July weekly mean temperature for nearly half the segments was 19–22°C. These thermal conditions are suitable for certain coolwater fishes but are not ideal for most game fishes (Wehrly et al. 2003). About one-fourth the segments had July weekly mean temperatures below this range, and the remaining fourth had temperatures above this range.

Comparisons of fish assemblage similarity indices indicated that valley segments were relatively homogeneous or that increased proximity yielded increased similarity (Herlihy et al. 2006, this volume). Random site comparisons had low mean fish assemblage similarity and wide range (Figure 5). Sites from differing MI-VSEC-1 types within the same basin had higher mean similarity but large range. Sites within the same MI-VSEC-1 type but in different basins were about as similar as sites within a basin, but with less range. Similarity increased further for sites in the same basin and MI-VSEC-1 type. Sites within a basin but from adjacent MI-VSEC-1 of different type had similar similarity scores as sites in the same basin and same MI-VSEC-1 type. Sites from the same basin and valley segment had the highest similarity, but still had a large range.

The MI-VSEC-1 closely approximated the general distribution pattern of brown trout across MLP (Figure 6). Fish association classes were 69% accurate when compared to independent observations from both primary and nearest neighbor associations (Table 1). There was

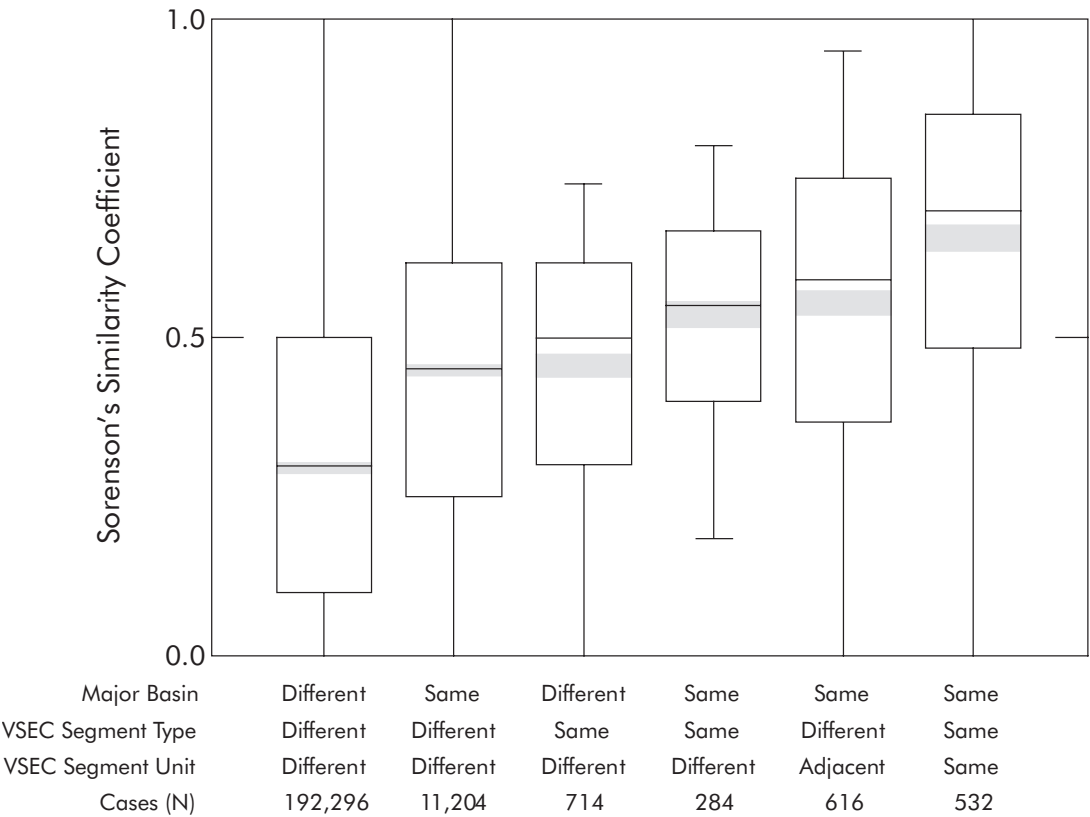


Figure 5. Box plots showing the effect of stream classification and spatial proximity on pair-wise distributions of fish assemblage similarity. Medians are indicated by horizontal lines, shaded areas represent 95% confidence limits around the mean, boxes are one standard deviation, and whiskers represent ranges.

some tendency to underpredict occurrence of cold water associations. Larger-river associations were not well represented in this test, as data were from wadeable stream surveys only. July thermal regime classes were 39% accurate when compared to independent observations for the primary thermal class. When the nearest neighbor class was included, classification accuracy improved to 69% (Table 2).

DISCUSSION

The values of MI-VSEC-1 as a learning and communications framework for riverine management have been illustrated through its use by Michigan fisheries and water quality managers in recent years. Managers have found the scale

of valley segments consistent with their field experiences and communication needs. The framework has helped managers understand the multiple processes influencing rivers, landscape-water connections, and patterns within and among rivers. The MI-VSEC-1 is used by the Michigan Department of Natural Resources (MDNR) as the stratification framework in state-wide and regional inventory, assessment, and research on lotic fishes and habitats. It is being used to analyze potential habitats for sea lamprey *Petromyzon marinus*, salmonids *Oncorhynchus* spp. and lake sturgeon *Acipenser fulvescens* (E. S. Rutherford, University of Michigan, personal communication; T. G. Zorn, Michigan Department of Natural Resources, personal communication). The MI-VSEC-1 forms the

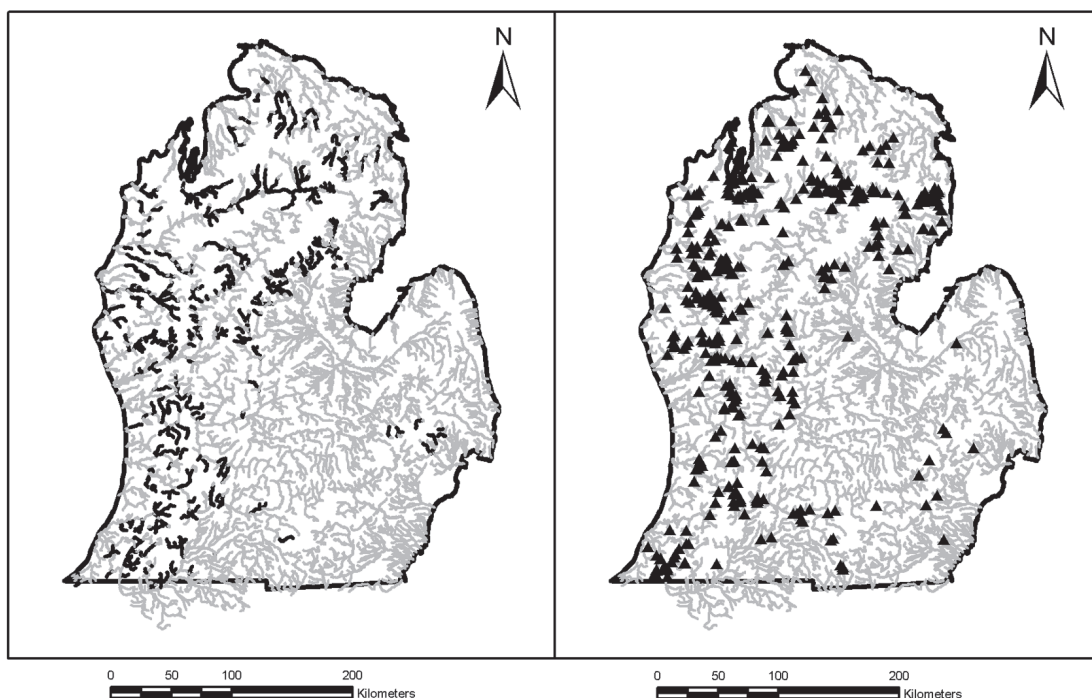


Figure 6. Comparison of brown trout distributions generated by MI-VSEC-1 for Michigan's Lower Peninsula with actual distributions of individuals recorded in Bailey et al. (2004).

riverine framework for a new MDNR statewide wildlife conservation plan (Clark Eagle et al. 2005), and main-stem MI-VSEC-1 segments are the framework for MDNR river fishery management plans (Wesley 2005). The system provides the spatial framework for privately funded, intensive management plans on several Lake Michigan tributaries (Wiley et al. 2005). The MI-VSEC-1 system provides a holistic basis for judging sensitivities to nutrient, sediment, and thermal impacts on river resources and for ranking protection and rehabilitation strategies (Wiley et al. 1998, 2004, 2005).

While considering the context of surrounding natural landscapes, the MI-VSEC-1 uses current observations of land use and river conditions to characterize the nature and potentials of valley segments. Thus, it is a classification of current, clearly altered conditions and can only be used to either describe the current state or when the current state is chosen as the reference state.

This can be a very pragmatic and useful reference point. It accepts some degree of human presence in the ecosystem and provides a solid empirical basis for setting environmental goals. If a less-disturbed reference state is desired, valley segment attributes can be estimated using low values of urban or agricultural land use in the landscape-river ecosystem predictive models (Wiley et al. 2003; Baker et al. 2005; Wiley et al. 2005; Kilgour and Stanfield 2006, this volume).

There is considerable interest in developing regional information and classification systems for rivers. Within the Great Lakes region, several agencies have developed valley segment classification systems in parallel with, or as expansions of, the MI-VSEC-1. E. Baker (Michigan Department of Natural Resources, personal communication) expanded MI-VSEC-1 to include Michigan's Upper Peninsula. The Nature Conservancy (TNC) completed a similar framework for the U.S. portion of the Great Lakes basin

		Observed																			
Predicted		brook stickleback	mottled sculpin	white sucker	burbot	brown trout	brook trout	northern pike	walleye	freshwater drum	northern logperch	hornyhead chub	rock bass	smallmouth bass	rosyface shiner	golden redbhorse	sample size	association group	total agreement		
		creek chub	17	1	12	13	3	1	1	3								51		A	0.84
	brook stickleback	4	1	5	4		6										22	A	0.64		
	mottled sculpin	10		19	8		9	2				1	1				68	A	0.54		
	white sucker	9		4	8	1		3				1	2				28	A	0.75		
	burbot	3		3	2	3	1										15	B	0.80		
	brown trout	4		11	10	3	3				1	1					55	B	0.89		
	brook trout	2		7	1	1	7	12									30	B	0.93		
	northern pike	3		1	3	3		10			2	2	3	3			30	C	0.40		
	walleye								5	2						1	8	C	0.88		
	freshwater drum								1	1							3	C	0.67		
	northern logperch																0	C	0.00		
	hornyhead chub	4		2	4	1	7	2			1	2	3	1	1		30	D	0.43		
	rock bass							2			1	1	2	3		1	11	D	0.45		
	smallmouth bass							1			1			3	3		7	E	0.71		
	rosyface shiner										1		1				3	E	0.67		
	golden redbhorse	1						2	1				1			1	7	E	0.14		
weighted average																					0.68

Table 1. Comparison of observed to predicted MI-VSEC-1 classes for summer fish species associations in streams in lower Michigan. Associations were based on Zorn et al.'s (2002) hierarchical cluster analysis and are defined in Table A.1. Observed data were from wadeable sites not used to build the relationships underlying the MI-VSEC-1 system. Association classes were assigned based on the most abundant fish species at each site. Counts in bold boxes show percent concurrence of observations with each predicted primary fish association. Counts in light boxes show concurrence to nearest neighbor associations as defined in the hierarchical cluster analysis (Table A.1, with some modifications according to macrohabitat relationships shown in Figure A.1). As we did not expect observations to fall solely within the primary class, the neighbor agreement value reflects total counts from both primary and neighbor boxes.

		Observed									Sample size	Primary agreement	Neighbor agreement
		Cold/low	Cold/moderate	Cold/high	Cool /low	Cool/moderate	Cool/high	Warm/low	Warm/moderate	Warm/high			
Predicted	Cold/low	14	14		3	4		1			36	0.39	0.78
	Cold/moderate	5	18	1	4	12				1	41	0.44	0.73
	Cold/high										0		
	Cool/low			1	4	6					11	0.36	0.91
	Cool/moderate	1	15	3	6	31	1	2	3	1	63	0.49	0.73
	Cool/high		2		1	5					8	0.00	0.63
	Warm/low							2			2	1.00	1.00
	Warm/moderate		1		2	3		0	7	0	13	0.54	0.77
	Warm/high	6		1	2	8	1		4	2	24	0.08	0.25
Weighted average												0.39	0.69

Table 2. Comparison of observed to predicted MI-VSEC-1 classes for July stream temperature regimes in streams in lower Michigan. Classes were based on Wehrly et al.'s (2003) matrix of weekly mean classes (cold < 19°C, cool 19–21°C, warm > 21°C) and weekly variation classes (low < 6°C, moderate 6–11°C, high > 11°C). Observed data were from sites not used to build the relationships underlying the MI-VSEC-1 system. Counts in bold boxes show percent concurrence of observations with each predicted primary thermal class. Counts in light boxes show the highest nearest neighbor class concurrence. Neighbor agreement reflects total count from both primary and neighbor boxes.

(Higgins et al. 1998) and is currently working with TNC Canada and the Ontario Ministry of Natural Resources (OMNR) to complete the Canadian portion (M. DePhilip, The Nature Conservancy, personal communication). The TNC version is used to aid aquatic conservation planning for the Great Lakes and several other regions, and to integrate aquatic and terrestrial planning efforts (Higgins et al. 2005). The OMNR has linked stream fisheries and habitat data with landscape data for developing management decision tools (Stanfield and Kuyvenhoven 2002; Kilgour and Stanfield 2006; Stanfield and Kilgour 2006, this volume). The U.S. Geological Survey has developed valley seg-

ment frameworks in Missouri and Ohio for regional aquatic conservation planning (Covert and Kula 2003; Sowa et al. 2005). Two large regional research projects have coordinated efforts to begin building an improved, multi-state valley segment framework (VSEC-2; Great Lakes Aquatic GAP). J. Stewart (U.S. Geological Survey, Middleton, Wisconsin) is coordinating with the senior author to develop a mostly automated and quantitative process for delineating and attributing segments (Brenden et al. 2006, this volume). This process takes advantage of advances in technologies and geographical data developed since our original efforts, including the new National Hydrography Dataset (NHD), and

combines some of the strengths of both regionalization and agglomeration approaches. Staff at TNC, OMNR, and the Great Lakes states are included in the project, and completion of VSEC-2 should yield a standard for rivers in the Great Lakes region. This new system will aid in visualizing the region's riverine resources, analyzing river habitat and biological data across the region, and encourage a common language of riverine habitat among agencies.

The MI-VSEC-1 has several significant limitations and weaknesses. (1) Classification requires the placement of absolute boundaries on what are usually true continua. Although valley segment boundaries are predicated on describing rather abrupt ecological changes, transition zones certainly occur. And our assigned attribute classes are merely a framework placed over true continua of characteristics. (2) Our interpretations were limited by scales of the available digital maps. These provided good descriptions of the dominant landscape features and patterns; however, we were unable to discern features like small river valleys or localized geologic deposits. Additional independent measures of flow, temperature, and fishes are needed to ground truth or modify the MI-VSEC-1 classifications, for local management assessments. (3) Fishes certainly move among valley segments during their lives, and future analyses should consider connectivity among valley segments as critical to assemblage structuring.

We view MI-VSEC-1 as an important pilot project, illustrating the feasibility and usefulness of delineating meaningful riverine units across a state or region, while providing a framework for revisions. It is a subjective, preliminary classification that shows promise but needs further testing, modification, and ground truthing. Our initial validation results illustrate both promise and the need for additional revision and improvements. Although the relationships we describe between valley segments and predictors are specific to our region, the general approach should be useful and informative in other lotic settings.

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APPENDIX A. MICHIGAN VALLEY SEGMENT ATTRIBUTES AND CATEGORIES

To illustrate the classification process, here we describe map interpretation rules for assigning hydrologic and fish association types. See Seelbach et al. 1997 for details for other attributes.

Basin and Watershed Names, and Unique Segment ID Number

The Great Lake basin and major river watershed to which each segment belonged were identified. Lake Michigan: St. Joseph, Kalamazoo, Grand, Muskegon, White, Pere Marquette, Manistee; Lake Huron: lower Saginaw, Cass, Shiawassee, Tittabawassee, Rifle, Au Sable, Thunder Bay, Cheboygan; Lake Erie: Raisin, Huron, Rouge, Clinton, Black. Each segment was given a unique identification number.

Link Number

Segment catchment size was indexed as the link number determined at the downstream end of each segment (range 1–492). Link number is the number of first-order streams in the catchment (Osborne and Wiley 1992). We interpreted link number from a stream network map built from 1:24,000 USGS topographic maps (Michigan Resource Information System, Michigan Department of Natural Resources, Real Estate Division, Lansing).

Segment Position

Network position relative to river size indicates proximity of a segment to potential downstream source populations and has been shown to influence fish assemblage composition (Osborne and Wiley 1992; Osborne et al. 1993) and was measured as d-link number (Osborne and Wiley 1992) at the downstream node of each segment. The d-link number is the link number at the next-downstream network juncture (we ex-

cluded junctures with tributaries having link numbers < 10% of the existing link number).

Connection to the Great Lakes

Similar to network position, connection to a Great Lake indicates potential faunal sources influencing assemblage structure. We recorded whether a segment was openly connected to the Great Lakes or isolated by a dam or waterfall.

Hydrologic Type

We coded hydrology for each segment as one of six general discharge patterns observed in Michigan hydrologic data. For this and the following attributes, we also assigned a secondary code to indicate transitional situations. A hydrologic type was inferred by examining composition of catchment topography, surficial geology, and land cover. These patterns were considered independent of catchment size, and discharges were considered in terms of yields (discharge/catchment area). This and the following codings were required to change along the system in a reasonable, stepwise pattern. The six most common patterns represent a continuous series illustrating water budget trade-offs between groundwater and runoff sources. These were divided into a group of two mostly groundwater-driven types and a group of four mostly runoff-driven types. Each group was further broken down into the following types having specific base flow and peak flow yields, based on correspondence with recurring patterns in catchment glacial geology (Seelbach et al. 1997).

- Groundwater-driven, with very high base flow (annual 90% exceedence yield $\sim 0.011 \text{ m}^3 \text{ s}^{-1} \text{ km}^{-2}$) and low peak flow (annual 10% exceedence yield $\sim 0.017 \text{ m}^3 \text{ s}^{-1} \text{ km}^{-2}$). Catchment physiography is fairly high-relief, ice-contact hills and coarse-textured end moraines surrounding extensive outwash plains.
- Groundwater-driven, with high base flow (~ 0.008) and moderate peak flow (~ 0.019).

Catchment physiography is relatively high-relief coarse end moraines draining onto outwash plains, often with some coarse till plains, medium-textured end moraines, or medium till plains present.

- Runoff-driven, with fair base flow (~ 0.004) and moderate peak flow (~ 0.021). Catchment physiography is a mixture of moderate-relief coarse end moraines, coarse till plains, and outwash plains.
- Runoff-driven, with moderate base flow (~ 0.003) and fair peak flow (~ 0.024). Catchment physiography is a mixture of low-relief coarse and medium end moraines, and medium till plains, with some outwash plains.
- Runoff-driven, with low base flow (~ 0.001) and high peak flow (~ 0.027). Catchment physiography is primarily medium and fine-textured till plains, and lacustrine plains, with some low-relief medium and fine end moraines present.
- Runoff-driven, with very low base flow (~ 0.000) and very high peak flow (~ 0.034). Catchment physiography is primary very low-relief glacial lake plains.

Trophic State Type

Segment water chemistry is a product of catchment hydrology and land cover, and was determined from hydrology codes and interpretation of soils and land-cover maps (Kleiman 1995). Chemistry was first categorized as either oligotrophic ($\text{SRP} < 15 \text{ } \mu\text{g/L}$, $\text{NO}_3 + \text{NO}_2 < 100 \text{ } \mu\text{g/L}$), mesotrophic ($\text{SRP} 15\text{--}30 \text{ } \mu\text{g/L}$, $\text{NO}_3 + \text{NO}_2 100\text{--}700 \text{ } \mu\text{g/L}$), or eutrophic ($\text{SRP} > 30 \text{ } \mu\text{g/L}$, $\text{NO}_3 + \text{NO}_2 > 700 \text{ } \mu\text{g/L}$). These categories were further divided based on effects of upstream lakes and wetlands, and land-cover intensity.

Water Temperature Type

Patterns in summer temperature means and diurnal fluctuations are driven primarily by catchment hydrology and size, modified by upstream

lake and shading effects (Wehrly et al. 2006, this volume). Our temperature codes described the following matrix of three categories for July weekly mean and three for July weekly variation (Wehrly et al. 2003). Categories were based on observed summer temperature boundaries in relation to distributions of common fishes, with emphasis on brown trout *Salmo trutta* and small-mouth bass *Micropterus dolomieu*.

- Cold mean ($<19^{\circ}\text{C}$) and low variation ($<6^{\circ}\text{C}$).
- Cold mean and moderate variation (6–11).
- Cold mean and high variation (>11).
- Cool mean (19–22) and low variation.
- Cool mean and moderate variation.
- Cool mean and high variation.
- Warm mean (>22) and low variation.
- Warm mean and moderate variation.
- Warm mean and high variation.

July temperature code assignments were based on hydrology codes and relative catchment size (i.e. small, medium, or large), using known relationships for MLP (Wehrly et al. 2006). Assignments were sometimes modified according to potential impacts of catchment land cover, upstream lakes, and latitude. We also considered the downstream sequence of codes among neighboring segments.

Valley Slope Type

Valley slope was interpreted by eye from elevation and topography maps and assigned to one of three broad categories: very low ($<0.00076\%$), low ($0.00076\text{--}0.0019\%$), and moderate ($0.0019\text{--}0.008\%$).

Valley Character Type

Valley character codes described the degree of channel confinement, either by coarse-textured morainic features, old glacial-fluvial channel walls, or deeply incised alluvial channel walls. The following codes were assigned based on in-

terpretation of local elevation, topography, surficial geology patterns, and wetland patterns.

- Channel flows unconfined within a relatively broad glacial-fluvial valley.
- Channel is confined within a relatively narrow glacial-fluvial valley.
- Channel is confined by alluvial incision in a broad glacial-fluvial valley.
- Channel is sporadically confined by moraines within a broad glacial-fluvial valley.
- Channel is unconfined as it cuts across broad till, outwash, or lacustrine plains.
- Channel is confined in an alluvial valley.
- Channel is sporadically confined by moraines within broad till, outwash, or lacustrine plains.
- Channel cuts alternatively across moraines and till, outwash, or lacustrine plains.

Channel Character Type

We noted whether a channel was single and meandering, multiple (braided or anastomosing), or channelized, by viewing the river network map.

Fish Associations

We coded the fish associations most likely to occur at each segment. Fish associations were determined by Zorn et al. (2002) through a hierarchical cluster analysis using relative abundance data for the 69 most common riverine fish species, at 225 sites throughout MLP. Each cluster is represented by the name of a key species (Table A.1). Zorn et al. (2002) calculated mean base flow yield and catchment drainage area for sites where each association occurred (Figure A.1). We estimated likely associations for each segment by interpreting hydrologic type and catchment size and estimating where the segment fell on Figure A.1; we then considered additional map variables (land-cover patterns, river net position, and connectivity), relevant file notes, and field experiences.

Table A.1. Common and scientific names of fishes found in statistical fish species associations for lower Michigan rivers (from Zorn et al. 2002). Key fish species used as group labels are in bold. Associations found to cluster together at the next higher level are shown by letters (A–E), preceding the group label.

A	creek chub <i>Semotilus atromaculatus</i> bluntnose minnow <i>Pimephales notatus</i> common shiner <i>Luxilus cornutus</i> johnny darter <i>Etheostoma nigrum</i> redfin shiner <i>Lythrurus umbratilis</i> central stoneroller <i>Campostoma anomalum</i> brook stickleback <i>Culaea inconstans</i> bluegill <i>Lepomis macrochirus</i> northern redbelly dace <i>Phoxinus eos</i> mottled sculpin <i>Cottus bairdii</i> western blacknose dace <i>Rhinichthys obtusus</i> white sucker <i>Catostomus commersonii</i> fathead minnow <i>Pimephales promelas</i>	D	hornyhead chub <i>Nocomis biguttatus</i> grass pickerel <i>Esox americanus</i> lake chubsucker <i>Erimyzon sucetta</i> rock bass <i>Ambloplites rupestris</i> brown bullhead <i>Ameiurus nebulosus</i> largemouth bass <i>Micropterus salmoides</i> longear sunfish <i>Lepomis megalotis</i> rainbow darter <i>Etheostoma caeruleum</i>
	burbot <i>Lota lota</i> longnose dace <i>Rhinichthys cataractae</i> brown trout <i>Salmo trutta</i> chinook salmon <i>Oncorhynchus tshawytscha</i> rainbow trout <i>O. mykiss</i> brook trout <i>Salvelinus fontinalis</i> slimy sculpin <i>Cottus cognatus</i> coho salmon <i>Oncorhynchus kisutch</i>		smallmouth bass <i>Micropterus dolomieu</i> black redbhorse <i>Moxostoma duquesnei</i> northern hog sucker <i>Hypentelium nigricans</i> striped shiner <i>Luxilis chrysocephalus</i> stonecat <i>Noturus flavus</i> river chub <i>Nocomis micropogon</i> greenside darter <i>Etheostoma blennioides</i> yellow perch <i>Perca flavescens</i> rosyface shiner <i>Notropis rubellus</i> silver redhorse <i>Moxostoma anisurum</i> greater redhorse <i>M. valenciennesi</i> golden redhorse <i>M. erythrurum</i>
B		E	
C	black bullhead <i>Ameiurus melas</i> yellow bullhead <i>A. natalis</i> green sunfish <i>Lepomis cyanellus</i> northern pike <i>Esox lucius</i> pumpkinseed <i>Lepomis gibbosus</i> pirate perch <i>Aphredoderus sayanus</i> golden shiner <i>Notemigonus crysoleucas</i> central mudminnow <i>Umbra limi</i> blackside darter <i>Percina maculata</i> bowfin <i>Amia calva</i> walleye <i>Sander vitreus</i> tadpole madtom <i>Noturus gyrinus</i> black crappie <i>Pomoxis nigromaculatus</i> white crappie <i>P. annularis</i> spotted sucker <i>Minytrema melanops</i> common carp <i>Cyprinus carpio</i> flathead catfish <i>Pylodictis olivaris</i> freshwater drum <i>Aplodinotus grunniens</i> quillback <i>Carpionides cyprinus</i> gizzard shad <i>Dorosoma cepedianum</i> northern logperch <i>Percina caprodes</i> channel catfish <i>Ictalurus punctatus</i> mimic shiner <i>Notropis volucellus</i> spotfin shiner <i>Cyprinella spiloptera</i> shorthead redhorse <i>Moxostoma macrolepidotum</i> brook silverside <i>Labidesthes sicculus</i> sand shiner <i>N. stramineus</i>		

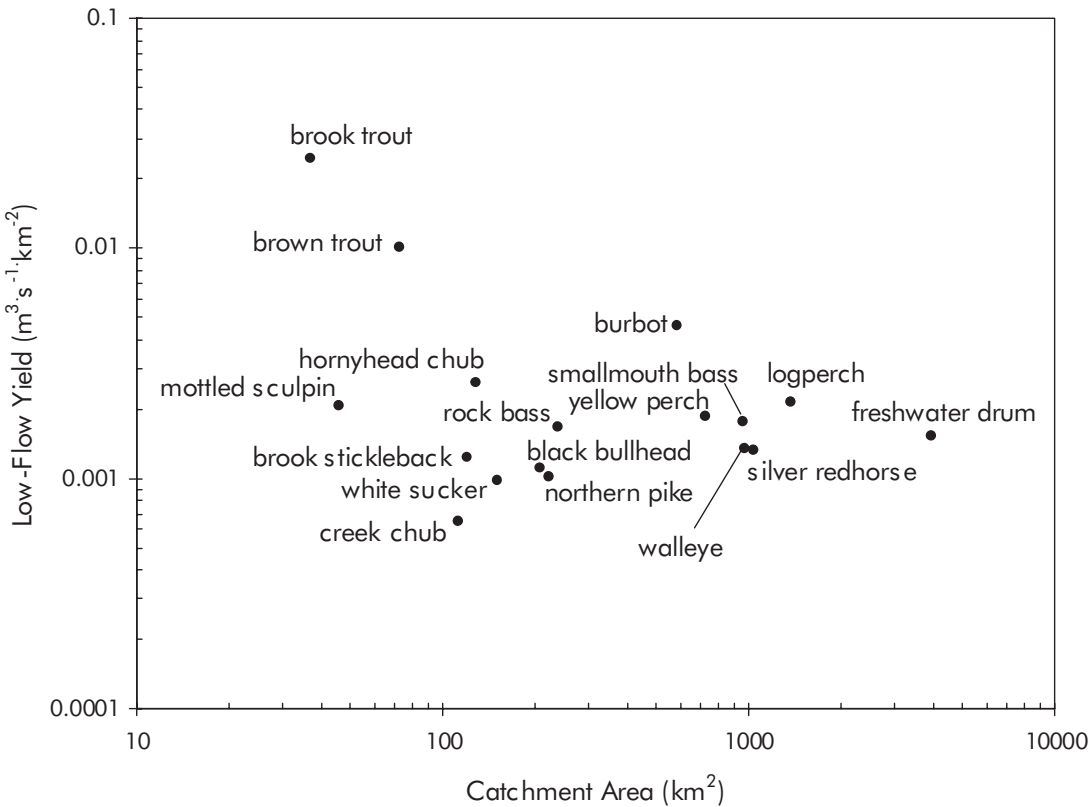


Figure A.1. Mean low-flow yield (LFY) and catchment area conditions of sites on lower Michigan streams where each of 17 fish assemblage clusters was most abundant (figure with permission from Zorn et al. 2002). Assemblages are identified by a key species.

A GIS Framework for Collecting, Managing, and Analyzing Multiscale Landscape Variables across Large Regions for River Conservation and Management

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Abstract.—We describe a geographic information systems (GIS) framework for conducting research related to the functional linkages between rivers and multiscale landscape descriptors. Our purpose in presenting this framework is to provide a template for those wishing to conduct their own research and to encourage the adoption of standardized GIS methodologies when conducting stream ecological research. A standardized framework will strengthen the abilities of stream ecologists to communicate and reach broad conclusions regarding the relationships between rivers and conditions in the surrounding landscape and ultimately will improve conservation and management efforts. The GIS framework consists of three spatial units: stream reaches, riparian buffers, and catchments. The basic spatial unit is a stream reach, which is defined primarily as interconfluence stretches of water. A riparian buffer is that portion of the landscape within a bounded distance (e.g., 60 m) of a reach, while a catchment is the total land area draining to a reach. We distinguish between two forms of riparian buffers and catchments, reach and network, which helps with variable attribution and provides a method for differentiating between local and accumulative upstream conditions. Each of these spatial units can be delineated from the national hydrography and elevation data sets using ArcInfo GIS functions. Variables that are attributed to the spatial units either occur in preexisting GIS data sets (e.g., land use) or else are calculated (e.g., reach sinuosity) or statistically modeled (e.g., river temperature) using attributes available in preexisting GIS data sets. Several potential applications (landscape-based statistical modeling of reach-scale characteristics, identification of conservation gaps, and environmental impairment assessment and management) of this GIS framework are described to illustrate the benefits and flexibility of this approach in addressing common river conservation and management objectives.

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INTRODUCTION

Functional linkages between instream habitat, biotic conditions, and conditions in surrounding landscapes exist at a variety of spatial scales. Past studies exploring these functional linkages often have focused on landscape variables defined locally (Barton et al. 1985; Platts and Rinne 1985; Li et al. 1994). Research currently is focused more on the conjoint influence of local-, catchment-, and regional-scale landscape descriptors (Vinson and Hawkins 1998; Zorn et al. 2002; Wang et al. 2003). This greater emphasis on multiscale relationships largely has resulted from technological advances in remote sensing and geographic information systems (GIS), which have facilitated incorporating multiscale landscape descriptors within a unified analytic framework (Johnson and Gage 1997; Mertes 2002). In particular, development of GIS and the increased availability of GIS data have allowed spatial units to be delineated at a variety of scales and for a large number of variables to be attributed to these units.

One challenge resulting from the emergence of GIS within stream ecological research is that an explicit framework as to how a GIS analysis of rivers and landscapes should be conducted has not yet been established. Therefore, studies differ in the manner in which spatial units are delineated, which variables are attributed to the spatial units, and how the variables are measured. Such a discordant approach is similar to fishery biologists sampling fish populations without standardized methods, thus restricting the identification of consistent themes across broad spatial or temporal bounds (Bonar and Hubert 2002). If stream ecologists adopted a more standardized GIS approach of how spatial units are delineated and what landscape characteristics are attributed to those spatial units, our ability to draw broad conclusions would be greatly enhanced. In particular, the relative importance of local and catchment landscape factors on aquatic assemblages under different land management scenarios might be clarified. Additionally, a stan-

dardized GIS approach would help investigators combine independently derived GIS data sets into broader scale layers, thus facilitating future investigations at regional, national, and continental scales. Conducting such analyses without a standardized approach requires substantial effort to combine individual GIS data sets, making broad-scale analyses largely unfeasible.

We describe a GIS framework that was developed cooperatively by personnel at the University of Michigan, U.S. Geological Survey (USGS), and the Illinois, Michigan, and Wisconsin Departments of Natural Resources. This framework is being used in two river conservation and management projects in the Great Lakes region, a Classification and Impairment Assessment of Upper Midwest Rivers (CIAUMR; UM 2004) project and a Great Lakes Gap Analysis Program (GLGAP; GLSC 2004) project. Although the specific goals of the CIAUMR and GLGAP projects differ, their data requirements are similar, so we decided to work together during the initial GIS development stages. Both projects encompass multistate regions (Figure 1), and personnel from several natural resource agencies are responsible for completing many of the preliminary GIS tasks (e.g., spatial unit delineation, variable attribution). Thus, it was important to develop an explicit framework that could be easily replicated by many users. We believe the GIS framework that we developed for these projects can serve as a template for those wishing to conduct their own riverine and landscape GIS studies. We further believe that presentation of this framework will stimulate discussion concerning how riverine-landscape research should be conducted, which may help lead to more standardized methodologies.

METHODS

Framework Structure

Our GIS framework is structured around three spatial units: stream reaches, riparian buffers, and catchments. The fundamental spatial unit is a



Figure 1. States involved in the Classification and Impairment Assessment of Upper Midwest Rivers (CIAUMR) and Great Lakes Regional Aquatic Gap Analysis Program (GLGAP) projects for which this GIS framework was developed.

stream reach, which we define primarily as interconfluence stretches of water. Because an interconfluence reach definition allows reaches to be objectively identified, this definition assures a consistent starting point across studies. Although interconfluence reaches are not spatial units that stream and land managers use from a decision-making perspective (Fausch et al. 2002),

they can be combined into more appropriate management units (e.g., valley segments or hydrologic units). The only exception to our interconfluence reach definition is when a lake or reservoir interrupts the stream network, in which case the transition between lentic and lotic environments serves as a reach break. For example, if a reservoir interrupts an otherwise continuous

stretch of water, then that stretch of water is considered to consist of three reaches: the first reach extends from the upstream confluence to the beginning of the reservoir, the reservoir itself is considered the second reach, and the third reach extends from the reservoir effluent to the next downstream confluence (Figure 2). Because conservation and management of streams is the primary concern for the CIAUMR and GLGAP projects, a reservoir or lake lying within the stream network that consists of multiple tributary backwaters is regarded in its entirety as one reach (Figure 3).

One problem with an interconfluence reach definition is the effect that map scale has on the delineation of stream segments. Higher resolution data sets will contain a higher number of streams. As a result, the number of reaches identified for a particular area will differ depending on the scale of the data set. Additionally, the potential for including intermittent streams increases with higher resolution data sets; thus,

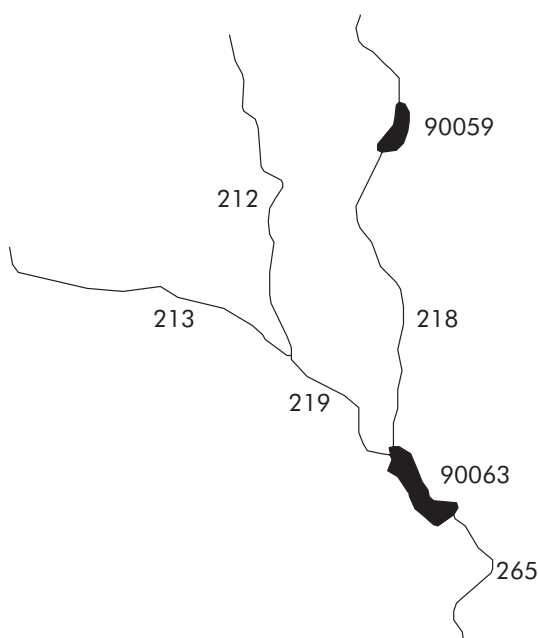


Figure 2. Examples of how a lake or reservoir (solid black regions) lying within a stream network affects stream reach delineation (numbers shown are shortened NHD "reach codes").

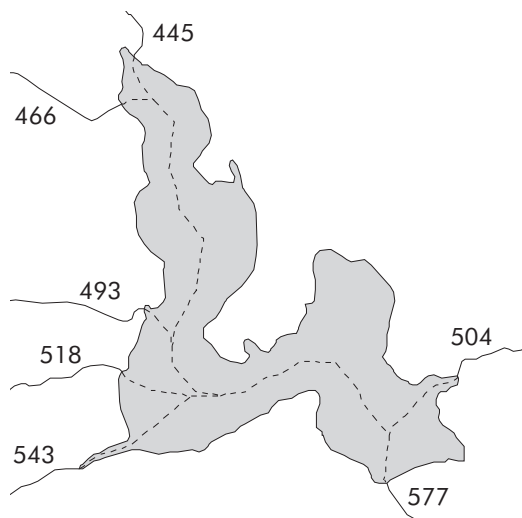


Figure 3. Example of how a lake or reservoir (shown in gray) consisting of multiple tributary backwaters is considered a single reach within our GIS framework (numbers shown are reference codes). The path of each tributary and the main stem (shown as dashed lines) within the lake has a reference code of 90077.

there may be some uncertainty as to whether stream confluences result in a marked change in habitat. These map scale issues suggest that a reach definition based on hydrologic (e.g., discharge) or geomorphic (e.g., gradient) stream characteristics may be more appropriate than an interconfluence reach definition. However, use of such characteristics to identify reaches also would be affected by map scale and would require detailed site-specific information that may not be available for very large areas. Additionally, the use of hydrologic or geomorphic stream characteristics to delineate reaches would require subjective decisions regarding the amount of change needed for a reach break to occur. Alternatively, an interconfluence reach definition provides an objective point for river conservation research and management to begin, even in areas with little or no site-specific data.

Our definitions for riparian buffers and catchments are based on definitions from Armantrout (1998). A riparian buffer is defined as that portion of a terrestrial landscape within

a bounded distance (e.g., 30 m, 60 m, or 120 m) of a stream reach, while a catchment is defined as the total upstream land area draining to the most downstream point of a reach. We discriminate two forms of riparian buffers and catchments, reach and network. Reach and network riparian buffers and catchments differ in how they are bounded. The upstream and downstream boundaries for a reach riparian buffer and reach catchment only extend as far as the boundaries with neighboring reaches (Figure 4). Network riparian buffers and catchments, on the

other hand, are an aggregation of all reach riparian buffers and catchments located upstream from the particular reach of interest (Figure 4).

The major advantage of distinguishing between reach and network riparian buffers and catchments is for data attribution. Because network riparian buffers and catchments are a combination of reach riparian buffers and catchments, variables only need to be attributed for reach riparian buffers and catchments. Variable attribution for network riparian buffers and catchments can be based on area-weighted

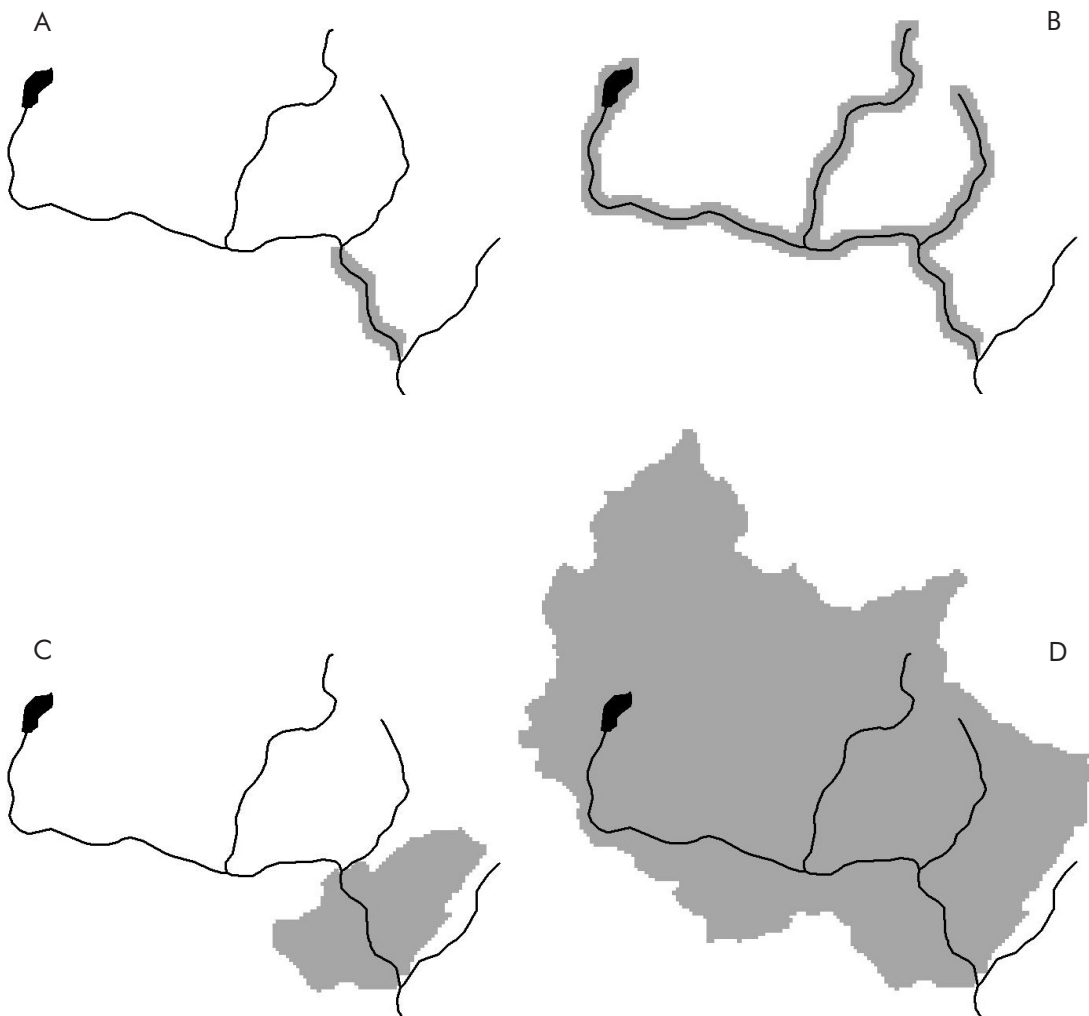


Figure 4. Differences, relative to a reach of interest, between a reach riparian buffer (shown in gray, A), a network riparian buffer (shown in gray, B), a reach catchment (shown in gray, C), and a network catchment (shown in gray, D).

averaging or summation of reach riparian buffer and catchment estimates. This alleviates the need to create a data set consisting of network riparian buffers and catchments for each reach, which would result in a data set comprised of many overlapping regions. Distinguishing between reach and network riparian buffers and catchments also may be useful from an ecological standpoint. For example, if the objective of a project were to study the impact of industrial pollution on stream biota, researchers possibly would be interested in separating local pollution inputs from cumulative upstream inputs.

Neither reach nor network catchments should be considered synonymous with hydrologic units (Seaber et al. 1987). Hydrologic units, which are commonly referred to as HUCs, are often mistakenly assumed to be the same as catchments, but there are substantial differences between them (Griffith et al. 1999; Omernik 2003). Catchments are delineated solely based on topography of surrounding regions. However, a single catchment may consist of several 8-digit hydrologic units, suggesting that delineation of hydrologic units is more complex than for catchments (Omernik 2003). We selected catchments instead of hydrologic units because hydrologic units often have catchments extending far beyond the hydrologic unit boundaries (Omernik 2003). Consequently, using a hydrologic unit to summarize a variable that has the potential to affect sites located substantial distances downstream (e.g., amount of urban land use) may prevent us from being able to definitively link this variable's effect on instream habitat or biotic conditions.

Stream reaches, riparian buffers, and catchments occur as a hierarchical series, with reaches nested within buffers and buffers nested within catchments (Fisher and Rahel 2004). One consequence of this nested structure is that factors defined at lower levels may be influenced by factors defined at higher levels (Wang et al. 1997; Wang et al. 2001). This nested structure has important implications from a modeling standpoint in that it suggests that lower-level (e.g.,

riparian buffer and reach) parameters should be at least partly modeled as functions of higher-level (catchment) parameters. Multilevel modeling techniques, such as multilevel linear regression and multilevel confirmatory factor analysis, have been specifically developed for analyzing nested models (Heck and Thomas 2000) and can be implemented through a number of statistical software packages (see CMM 2004 for software reviews).

Delineation of Spatial Units

Selection of a water feature layer.—Our basic water feature data set was derived from the 1:100,000 scale national hydrography data set (NHD; USGS 2004a). This scale was selected because it was the most detailed resolution available for the entire Great Lakes region. The NHD divides water features into several types (e.g., stream/river, lake/pond, canal/ditch, spring/seep). Each water feature type is portrayed in a GIS as points, lines, or areas (polygons). Line features such as stream networks consist of numerous arcs, each of which has a from- and to-node that indicates direction of water flow. Although point features (e.g., springs) may be important for some research and management objectives, we did not use point features in the CIAUMR and GLGAP projects; therefore, we make no reference to point features in this framework.

“Reaches” comprise the basic water features of the NHD. An NHD reach is defined as “a continuous piece of surface water with similar hydrologic characteristics” (USGS 2004b). Reaches can be one of three types: coastline, transport, or water body. Transport reaches include streams, rivers, and artificial paths (centerline representations) of lentic water bodies or large rivers. Water body reaches are those hydrographic features that are delineated as areas (polygons) and include lakes, ponds, reservoirs, and large rivers. All NHD reaches are uniquely identified with a reach code, which permits the incorporation of future NHD modifications in preexisting projects (USGS 2004b).

Identification of NHD reaches is based on a set of predefined rules (e.g., underlying-feature rule, confluence-to-confluence rule, branched-path rule; USGS 2004b). These rules largely delineate NHD reaches that are similar to the reach definitions we described earlier. However, the NHD does make several exceptions to its delineation rules (USGS 2004b), which we did not want incorporated in our GIS framework. For example, an NHD reach break will only be inserted at a lake or reservoir lying within the stream network if the surface area of the lake or reservoir is greater than ≈ 4 ha. However, even small water bodies can affect habitat conditions (e.g., water temperature) or impede fish movement, so we preferred to have all water bodies identified as separate reaches. Such exceptions to the NHD reach delineation rules required us to make some modifications to the water feature data set in order for it to match our desired structure.

Our modification of the water feature data set began by joining the tables associated with route drain and route reach subclasses with the arc attribute table for the line feature type. The route drain and route reach tables include information such as each arc's reach code, whether an arc is an artificial path or an actual stream, and the name associated with each arc. After joining the tables, the NHD reaches that spanned multiple confluence-to-confluence segments of water were split so that each confluence-to-confluence section of water comprised one uniquely coded reach (unless the section of water was interrupted by a lake or reservoir). Confluence-to-confluence sections of water that were separated into multiple NHD reaches were converted to a single reach by deleting all pseudo nodes (i.e., nodes that mark the intersection of only two arcs). To ensure that a reach break occurred wherever a lake or reservoir interrupted the river network, we first used ArcInfo's REGIONPOLY function to convert the NHD area (polygon) feature type into a stand-alone GIS data set. Next, ArcInfo's IDENTITY function was used to perform a line-in-polygon over-

lay, which inserted reach breaks wherever a lake or reservoir interrupted the stream network. This overlay also assigned the unique reach code of each lake or reservoir to the arc (or arcs) they overlaid.

Other modifications of the NHD included breaking headwater arcs that were incorrectly joined, joining arcs that were incorrectly separated, and ensuring that all arcs flowed downstream. Braided channels, which occurred as multiple arcs in the NHD, were changed to single centerline representations. Reducing braided channels to single centerlines was needed for accurate identification of stream order, delineation of catchments, and data attribution. However, braided channels provide important habitat to fish, particularly during juvenile stages (Mosley 1982). Therefore, it is worthwhile to include an attribute field within the GIS data set identifying reaches associated with braided channels or to add braided channels back into the data set once all data attribution steps have been completed.

Although modifying the structure of the NHD water features might prevent us from being able to incorporate future NHD changes (e.g., the reach codes for some arcs were deleted when pseudo nodes were deleted), many of these modifications were necessary to assure that data attribution was correct. Also, a majority of arcs in our modified structure retained their original reach codes, thus many NHD changes could still be incorporated in GIS projects based on this framework. Conflation, which is a process for transferring attributes between GIS data sets, also could be used to incorporate some NHD changes. As a result, we do not believe that our modifications of the NHD water feature structure should be of great concern to potential users of this framework.

Delineation of riparian buffers.—Riparian buffers were delineated by first converting the modified NHD line feature type from a vector to a raster format. A pixel size of 30 m was used for the CIAUMR and GLGAP projects so that the rasterized NHD line feature type would match the resolution of the digital elevation

model used for delineating catchments (see below). Alternatively, pixel size could be chosen based on the scale of the water feature data set. According to National Map Accuracy Standards, 90% of horizontal points errors for a 1:100,000-scale map will be within 50 m (USGS 2004c). Thus, a pixel size of 50 m may be a better standard to account for locational error in GIS data.

Conversion of the NHD line feature type to a raster format resulted in an integer grid in which individual pixels had the same reach code as the

arcs they overlaid. Pixels that did not overlay arcs were coded as “no data” cells. Riparian buffer zones were then created by using ArcInfo’s EXPAND function to expand the reach-coded pixels of the NHD grid by two cells on all sides. This expansion of grid cells resulted in 60-m-wide riparian buffer zones on either side of a 30-m channel (Figure 5). When delineating riparian buffers for large rivers, lakes, and reservoirs, the stand-alone water body data set created from the NHD area feature type was converted to a raster

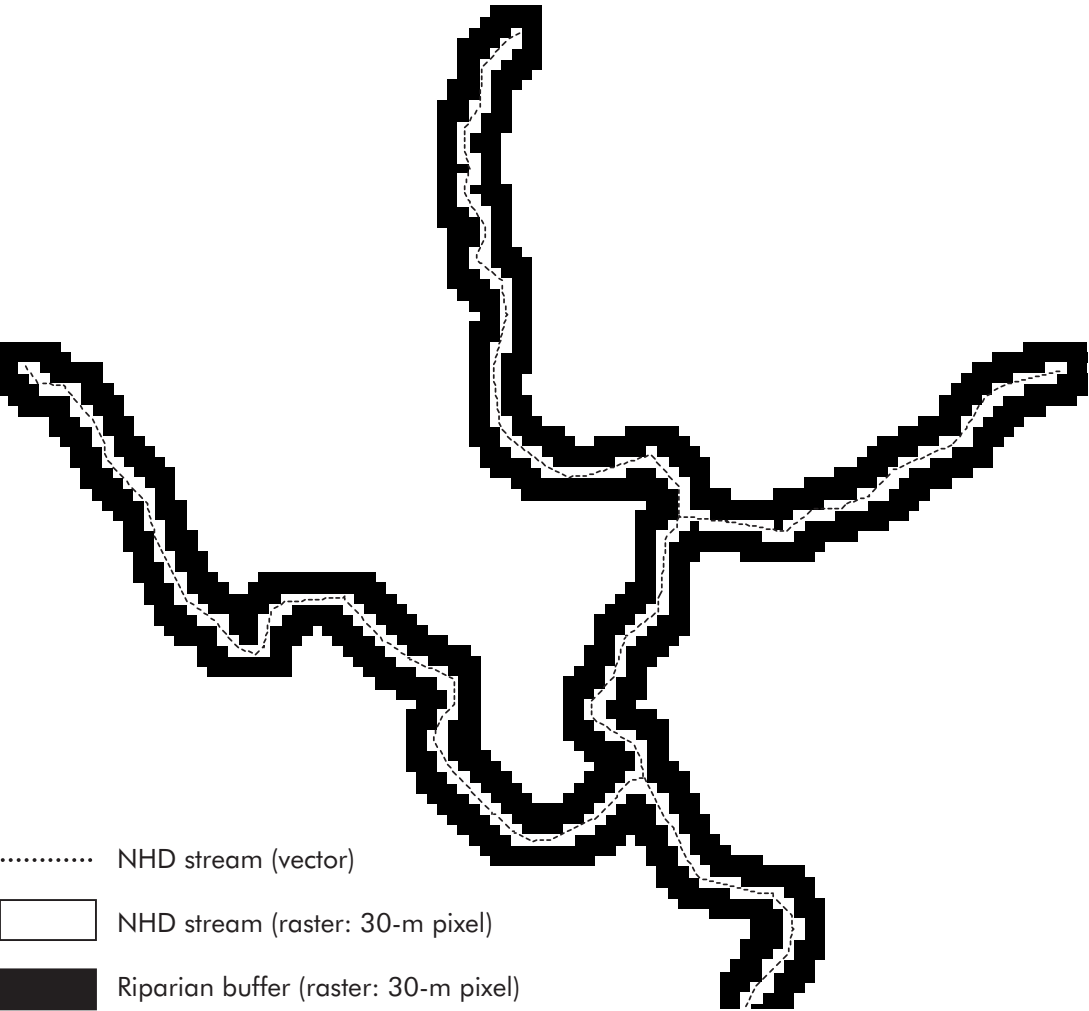


Figure 5. Illustration of riparian buffer delineation by conversion of the NHD line feature type to a grid (30-m pixel) and cell expansion (number of expanded cells = 2).

format and expanded. If riparian areas were delineated using the centerline representations of large rivers, lakes, and reservoirs, the delineated buffer zones may not have extended beyond the shoreline (Figure 6), which would have caused errors when defining variables at riparian buffer scales.

Identifying the appropriate width for riparian buffers is a difficult aspect for stream ecological research because of the conditional functionality of riparian buffers. For trapping

sediment, 30-m-wide riparian buffers may be sufficient, while providing terrestrial animal habitat may require riparian buffers of 300 m or greater (Brososke et al. 1997). A 60-m-wide riparian buffer was selected for the CIAUMR and GLGAP projects based upon the resolution of the land use data and because prior research has found significant correlations between fish assemblage measures and land-use conditions at this approximate distance (Roth et al. 1996; Stancil 2000). For other studies with different

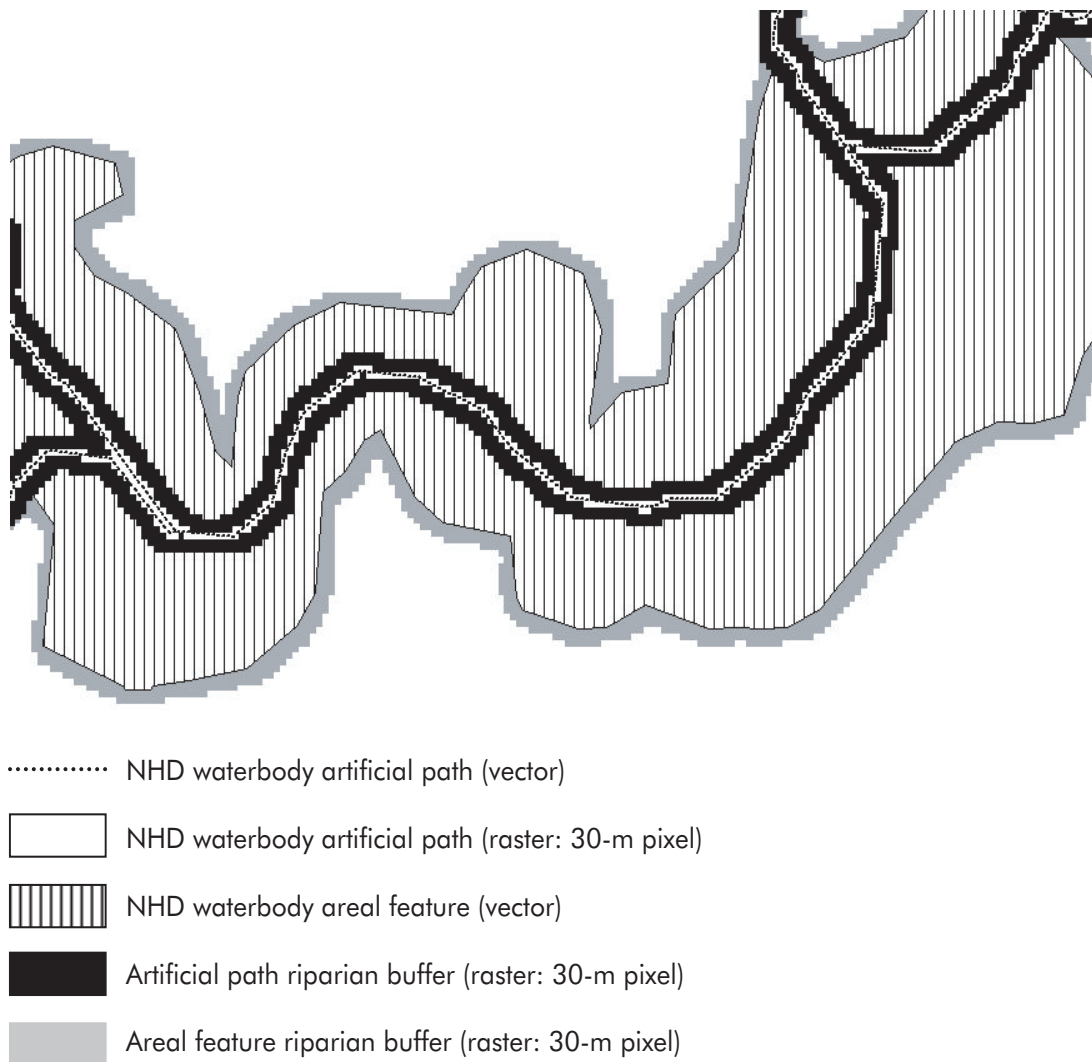


Figure 6. Comparison between riparian buffers delineated by NHD grid conversion and expansion of the artificial path of a water body versus the polygon boundary of the water body.

objectives, this distance may need to be either increased or decreased. Alternatively, appropriate riparian buffer widths might be identifiable as a function of landscape characteristics, such as stream gradient (Nieswand et al. 1990) or rate of overland flow (Mander et al. 1997). Wenger (1999) provides an overview of several models that have been developed for identifying riparian buffer widths.

While it is not necessary to convert the NHD to a raster format when delineating riparian buffers, doing so helps to account for deviation in reach location within a GIS from actual reach location within a landscape. Such uncertainties as to reach location would not have been accounted for if riparian areas were delineated by buffering the NHD line feature type, which ultimately may have led to errors when attributing variables for riparian buffers. While it might be argued that conversion of the NHD to a raster format sacrifices locational precision of the NHD layer, the NHD is overly precise in that all rivers have both lengths and widths and are not one-dimensional features as depicted in a GIS.

The delineation of riparian buffers by NHD raster conversion and grid expansion does cause some problems at stream confluences. Because grid pixels can only be assigned a single value, grid cells near stream confluences will only be identified as lying within the riparian buffer zone for one of the stream reaches (Figure 7). Which riparian buffer zone that each cell will be identified with will depend on the cell assignment of a majority of its surrounding neighbors. This will lead to some inaccuracies when attributing variables at reach riparian buffer scales as limited portions of riparian buffer zones may be excluded from each reach. However, this also will prevent double- or triple-counting of information when attributing reaches with network riparian buffer information, which would be an issue if riparian buffers were delineated by buffering the NHD in its original vector format (Figure 7).

Delineation of catchments.—Reach catchments were delineated using the NHD and the

national elevation data set (NED; USGS 2004d). The NED is a raster data set of elevation values. A major advantage of using the NED over other digital elevation models is that NED layers are available as seamless data sets. Thus, users do not need to merge, filter, mosaic, and smooth several files into one usable layer, which are common tasks with other elevation data sets (Gesch et al. 2002). The NED is available, depending on area of interest, at resolutions of one-third-, 1-, and 2-arc-second resolutions (USGS 2004d). In the Great Lakes region, these resolutions equate to pixel sizes of approximately 10, 30, and 60 m, respectively. For the CIAUMR and GLGAP projects, 1-arc-second resolution was the smallest resolution available for all areas. As with the NHD, some modification of the NED was necessary to assure that catchment boundaries were properly delineated. Ridgeline elevations were increased so that water would not flow across catchment divides. Additionally, elevation sinks and peaks that possibly stemmed from NED errors were filled and leveled. The NED was used as the basis for spatially registering all rasterized data sets (e.g., NHD water features) so that the cell boundaries between data sets aligned.

Only a subset of NED elevations was used to delineate reach catchment boundaries. In any continuous surface, the marginal value of individual data points decreases as the number of points increases. Therefore, delineating catchment boundaries with all elevation values rather than just a subset of points may not significantly increase the accuracy of catchment boundaries. However, delineating catchment boundaries is a very computer-intensive process and even high-end desktop computers by today's standards (e.g., 3.20-GHz processor and 2 GB RAM) may have insufficient memory and storage space to delineate catchment boundaries for very large areas. Some data sets associated with large catchments also may exceed the maximum file size imposed by 32-bit software applications (2.147 GB), so it may not even be possible to work with all elevation values for a particular catchment. Therefore, using a subset of elevation values may save a

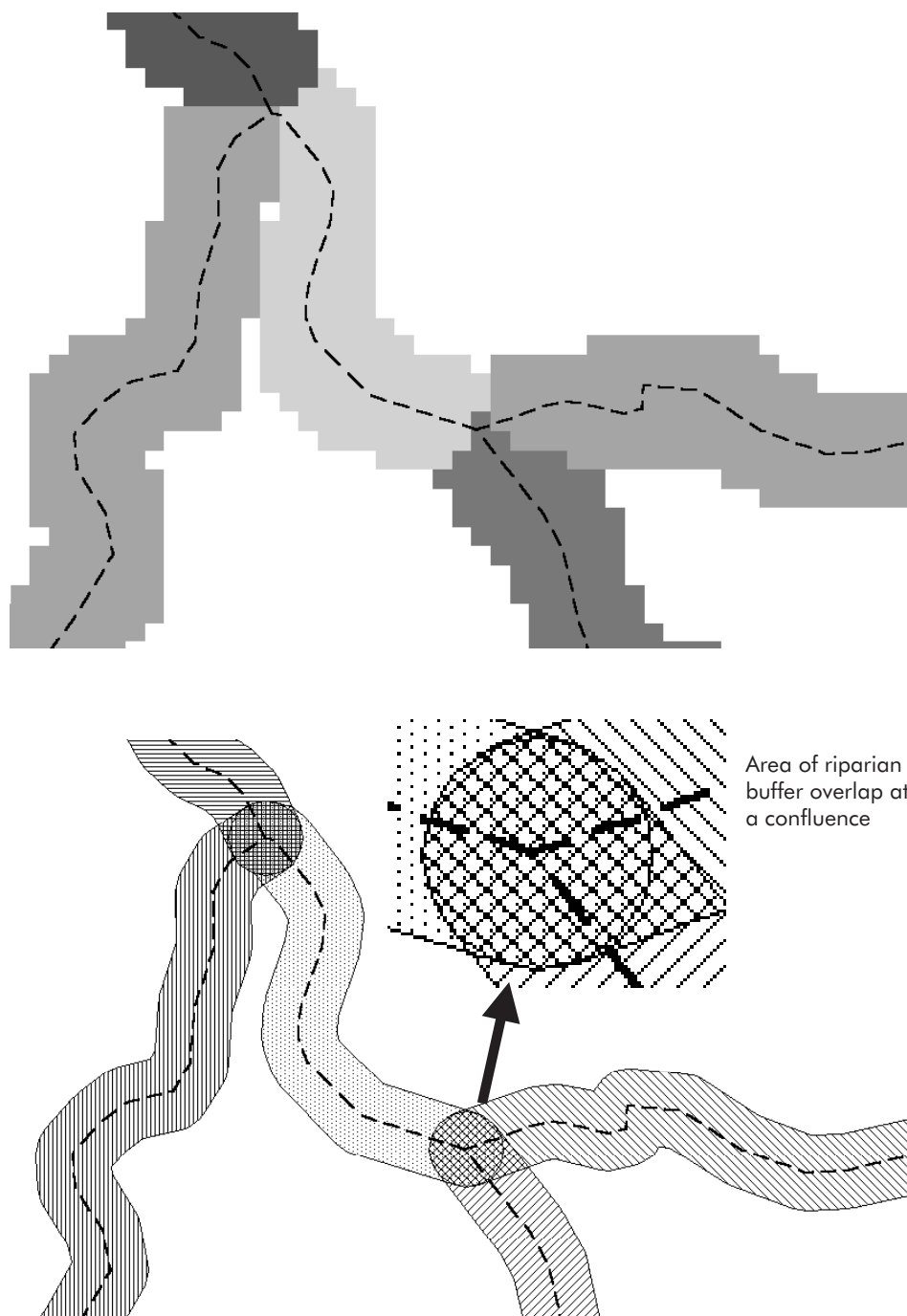


Figure 7. Illustration of the problems associated with delineating riparian buffer zones near stream confluences by NHD grid conversion and expansion (top figure) and by buffering the NHD in its original format (bottom figure). With rasterization and grid expansion, cells in regions where riparian buffers overlap will only be identified as lying within the riparian buffer for one reach (top figure). Buffering the NHD in its original vector format will result in overlapping riparian buffers (bottom figure) that would cause information to be duplicated when attributing variables at network scales. Different cell shades and fill patterns identify reach riparian buffers associated with different reaches.

significant amount of processing time and may be the only option for delineating catchment boundaries for some areas.

To identify the most important features on the landscape, ArcInfo's VIP (Very Important Point) algorithm was used to convert the NED to a point data set and to identify the local maximum and minimum elevations within the data set. The VIP function also assigns a level of significance to each point based on its degree of elevation change in comparison to its neighboring points. A frequency plot was then generated of the ranked points and their cumulative elevation "significance." Typically, between 5% and 20% of the data points in the original NED explained 80% or more of the total variation in the landscape. The subset of elevation points was then used along with the NHD drainage network to interpolate a new elevation surface using ArcInfo's TOPOGRID function, which minimized errors in flow direction on the landscape by ensuring all points in a catchment drained to the NHD network. The newly interpolated elevation surface was then used to determine flow direction (ArcInfo's FLOWDIRECTION function) and to delineate individual reach catchments (ArcInfo's WATERSHED function). Reach catchments were delineated for all stream reaches using an automated GIS script. The pour point for reach catchment delineation was the to-node associated with each stream segment.

Variable Selection

Variable selection requires significant forethought to assure that potentially important variables are not excluded from study. A convenient way to choose GIS variables is according to availability. Some variables may exist as attributes in freely available GIS data sets. Before using such data, one should know the source, datum, projection, scale, geographic reference coordinates, and accuracy of the data set. Much of this information should be documented or described in metadata that often accompany GIS data sets. Metadata also should contain details about the

information content of the data set, including attribute names, detailed descriptions of how the data were collected, range of values, units of measure, and measurement resolution. The importance of metadata to having a clear understanding of a data set and its contents cannot be over emphasized, and we strongly discourage use of any GIS data set that is not appropriately documented.

Other variables considered important for a GIS study of rivers may not be available in GIS data sets, but it might be possible to compute them directly from GIS data. For example, reach sinuosity can be calculated using GIS functions that measure reach length and Euclidean distance between reach endpoints.

An additional category is variables that do not exist in GIS layers but which can be modeled from information contained in GIS data sets. Such variables (e.g., water temperature, river discharge, fish presence/absence, fish abundance) often are measured in field surveys. If such variables are considered important to the research question at hand but have not been previously measured, it might be possible to model these variables through a method such as linear regression. We regard statistical modeling as different from direct computation of feature attributes, such as reach sinuosity, in that statistical modeling is more complex because of unknown structural relationships between variables. Consequently, model error must be considered, and these models need to be carefully evaluated to ensure that their predictions are appropriate and useful. One option for evaluating the effect of model error is to use Monte Carlo simulations to incorporate model error effects into final analyses, which will result in distributions for possible outcomes (Van Sickle et al. 2004). Despite the potential problems associated with statistical modeling, we believe this approach can be useful for obtaining information at a detailed resolution across large spatial regions.

Reach variables.—Availability of data sets containing reach-scale habitat variables for large scales is rather limited (Fisher and Rahel 2004).

As a result, unless a concerted reach-scale monitoring program has been ongoing, research investigations conducted across spatially extensive areas will be limited to using reach-scale variables that can be directly calculated or modeled.

For the CIAUMR and GLGAP projects, we directly calculated from the modified NHD several reach variables that addressed channel shape, size, and position within the stream network. Reach sinuosity was calculated using the sinuosity index, which is the ratio of channel length to downvalley distance (Allan 1995). Reach gradient was calculated by attributing elevations to reach endpoints, determining the elevation change between endpoints, and dividing the change in elevation by channel length. Stream position within the river network was referenced using three metrics: Strahler order (Strahler 1957), link magnitude (Shreve 1966), and downstream link magnitude (Osborne and Wiley 1992). Connectivity and proximity to the Great Lakes, dams, and lakes/reservoirs also were determined for each stream reach as we felt this information was beneficial for understanding differences in aquatic assemblages.

In addition to variables that were computed directly from the NHD, statistical modeling was used to predict 5%, 10%, 25%, 50%, 75%, 90%, and 95% annual exceedence discharges and mean July temperature for each reach. Statistical models were created for each state individually. For example, Michigan percent annual exceedence discharges were calculated from multiple linear regression models containing network catchment area (DA), mean annual precipitation in the network catchment (PPT), mean slope in the network catchment (SLOPE_NC), percent of network catchment consisting of coarse textured surficial geology (COARSE), percent of network catchment consisting of glacial outwash surficial geology (OUTWASH), percent of network catchment consisting of peat and muck surficial geology (PM), percent of network catchment consisting of medium textured surficial geology (MED), percent of agricultural land use in the network

catchment (AGRICU), percent of urban land use in the network catchment (URBAN), and percent forest land cover in the network catchment (FOREST) as independent variables (Table 1; L. Hinz, Illinois Natural History Survey, personal communication). Mean July water temperatures were estimated for Michigan via multiple linear regression with network catchment area (DA), mean soil permeability in the network catchment (SOILPER), percent of network catchment with soil permeability greater than 1.27 m/100 h (Q75P500W), percent of network catchment covered in water (WATER), mean annual precipitation in the network catchment (PPT), mean slope of the reach catchment (SLOPE_RC), percent of reach catchment with igneous/metamorphic bedrock geology (BIGNME), percent of network catchment with bedrock depths less than 100 m (BDEPL1H), mean July air temperature (AIR), an indicator variable identifying ecoregion (ECOREGION), and reach gradient (GRAD) as model parameters (Table 1; K. Wehrly, Michigan Department of Natural Resources, personal communication). However, at press time for this paper, we also were evaluating whether estimation by neural networks, model averaging, or geostatistical modeling would improve temperature predictions.

Riparian buffer and catchment variables.—Unlike reach-scale habitat variables, there exists a number of GIS data sets that provide useful information at riparian buffer and catchment scales (Fisher and Rahel 2004). For the CIAUMR and GLGAP projects, we obtained data sets describing climate (i.e., amount of precipitation, air temperature, or growing degree-days), bedrock depth, bedrock geology, land cover and land use, surficial geology, and soil permeability. Attributes directly calculated for both riparian buffers and catchments were total surface area, average slope, and potential groundwater delivery. Potential groundwater delivery maps for all states involved in the CIAUMR and GLGAP projects were created using the MRI-DARCY groundwater model (Baker et al. 2001, 2003). This model calculates

Table 1. Variables attributed to river reaches, reach and network riparian buffers, and reach and network catchments for the CIAUMR and GLGAP projects. For variables available in preexisting GIS data sets, the map type (raster or vector), map scale, source, and Web site address from where the data set was downloaded (CIAUMR project only) are shown. For variables that were calculated or modeled, the equation or statistical model used to calculate the variable also is shown.

Variable	State(s)	Type	Scale/resolution	Citation/equation/statistical model ^a
Preexisting attributes				
Air temperature	All	Raster	2,000 m	OSU/SCAS (2004a)
Growing degree-days	All	Raster	2,000 m	OSU/SCAS (2004b)
Land cover/land use	IL	Raster	30 m	INRGDC (2004a)
Land cover/land use	MI	Raster	30 m	MCGI (2004a)
Land cover/land use	WI	Raster	30 m	WDNR (2004)
Precipitation	All	Raster	2,000 m	OSU/SCAS (2004c)
Bedrock depth	All	Vector	1:1,000,000	USGS (2004e)
Bedrock geology	IL	Vector	1:500,000	INRGDC (2004b)
Bedrock geology	MI and WI	Vector	1:1,000,000	USGS (2004f)
Channel length	All	Vector	1:100,000	USGS (2004a)
Surficial geology	IL	Vector	1:500,000	INRGDC (2004c)
Surficial geology	MI	Vector	1:500,000	MCGI (2004b)
Surficial geology	WI	Vector	1:1,000,000	USGS (2004g, 2004h, 2004i)
Soil permeability	All	Vector	1:250,000	USGS (2004j)
Calculated attributes^b				
Catchment area	All	NA	NA	900 × total number of reach or network catchment grid cells
Catchment slope	All	Raster	30 m	ArcInfo SLOPE command: $\arctangent(\text{rise/run}) \times 57.296^c$
Channel gradient	All	NA	NA	$((\text{Elevation of from-node}) - (\text{elevation of to-node})) / \text{channel length}$
Connectivity/proximity	All	NA	NA	ArcInfo TRACE command: sum of channel lengths to points of interest
Downstream link	All	NA	NA	Gap_down.aml: calculated based on stream network structure
Groundwater delivery	All	Raster	30 m	$(\text{Topographic slope}) \times (\text{subsurface hydraulic conductivity})$
Link	All	NA	NA	Gap_shreve.aml: calculated based on stream network structure
Riparian area	All	NA	NA	900 × total number of reach or network riparian buffer grid cells
Riparian slope	All	NA	NA	ArcInfo SLOPE command: $\arctangent(\text{rise/run}) \times 57.296^c$
Sinuosity	All	NA	NA	$(\text{Channel length}) / (\text{downstream distance})$
Strahler order	All	NA	NA	Gap_strahler_sord3.aml: calculated based on stream network structure
Modeled attributes				
July water temp.	All	NA	NA	Mult. linear regression ^d
Exceedence discharge	All	NA	NA	Mult. linear regression ^e

^{NA} Maps were not created for these variables so no map type or scale/resolution exists.

^a Identified statistical models are just some of the models that were evaluated.

^b Identified ArcInfo AMLs will be available to the public in the future. Please check <http://sitemaker.umich.edu/riverclassproject> for information as to when and where the AMLs can be obtained.

^c Cell slope is calculated from the cell's 3-cell × 3-cell neighborhood using the average maximum technique (Burrough 1986)

^d Michigan mean July water temperature model: $y = 13.76 + 0.71 \cdot (\log_e DA) - 3.26E-03 \cdot (SOILPER) + 0.52 \cdot (AIR) - 0.35 \cdot (SLOPE_RC) - 1.72E-02 \cdot (BIGNME) - 8.39E-03 \cdot (PPT) + 9.41E-03 \cdot (BDEPL1H) + 0.148 \cdot (WATER) + 8.96 \cdot (GRAD) + 0.685 \cdot (COREGION) - 1.51E-02 \cdot (Q75P500W)$

^e Michigan 50% exceedence discharge model: $y = -20.73 + 1.05 \cdot (\log_e DA) + 2.04 \cdot (\log_e PPT) + 0.38 \cdot (\log_e SLOPE_NC) + 0.78 \cdot (\exp COARSE) + 0.48 \cdot (\exp OUTWASH) + 1.98 \cdot (\exp PM) + 0.32 \cdot (\exp MED) - 0.45 \cdot (\exp AGRICU) - 0.66 \cdot (\exp URBAN) - 0.60 \cdot (\exp FOREST)$

groundwater delivery based on landscape elevation and subsurface water conductivity.

Feature Attribution

Once the spatial units were delineated and the variables selected, attribution of the spatial units proceeded. Variables defined for individual stream reaches were linkable by reach codes. ArcInfo's ZONALSTATS function was used to summarize variables for the reach riparian buffers and catchments. Different statistics were calculated depending on whether the attribute of interest was on a nominal, interval, or ratio scale. With interval or ratio scale variables, we computed the mean value for the spatial units (e.g., mean precipitation or mean July temperature for each reach catchment). With variables classified on a nominal scale, we determined the proportions of the spatial unit in each of the variable classes (e.g., percentages of each land use class within each reach riparian buffer). Attribution for network riparian buffers and catchments was accomplished using the ArcInfo TRACE function to identify all reaches that were located upstream from a particular reach. The attributes associated with all upstream riparian buffers and catchments were then combined, along with the attributes for the reach of interest, into a single data set for network summarization. For variables defined on a ratio or interval scale (e.g., precipitation, July temperature), reach riparian buffer and catchment information were summarized into network measurements by computing area weighted-averages of the variables. For variables defined on a nominal scale (e.g., land use), riparian buffer and catchment information were summarized into network measurements by summing the cell counts of each variable class.

Because of the spatial extent of the CIAUMR and GLGAP projects, attribution of all features was accomplished using automated ARC Macro Language (AML) applications that were written specifically for these projects (S. S. Aichele and E. G. Bissell, unpublished data). In the future, these AML applications will be made available

for public use. Those interested in obtaining the applications should refer to the CIAUMR project Web site (<http://sitemaker.umich.edu/riverclassproject>) for information as to when and where copies may be obtained.

RESULTS

The framework described above has been used to attribute approximately 300 habitat variables (including variables defined at reach and network riparian buffers and catchments) for more than 130,000 stream reaches, covering all watersheds in Illinois, Michigan, and Wisconsin. Habitat variables are currently being used in identifying/describing valley segments, and in predicting potential distributions of stream fish. The vast majority of habitat variables were attributes within downloaded GIS data sets (Table 1). One issue that arose when working with data sets obtained from multiple sources was that the classification scheme used for an attribute sometimes differed between sources. For example, a land cover/land use data set obtained for one state might have five classes describing upland deciduous forest, while another state might have eight classes for upland deciduous forest. When classification systems differed between sources, we found that developing a crosswalk between classification systems and reclassifying the data sets to the common system was the easiest way to resolve differences. While the classification systems developed for the CIAUMR and GLGAP projects may not be appropriate elsewhere, we have nevertheless provided the classification systems that we used to reclassify surficial geology, bedrock geology, and land cover/land use data sets (Table 2). Consultation with field experts greatly facilitated the development of these classification systems, and we encourage those wishing to develop similar systems to consult with experts as well.

DISCUSSION

To be most advantageous for stream ecological research, GIS standardization must go further

Table 2. Classification schemes used for surficial geology, bedrock geology, and land cover/land use in the CIAUMR and GLGAP projects.

Surficial geology ^a		Bedrock geology	Land cover/land use
Alluvium/fluviial (c)	Ice-contact (c)	Carbonate	Agriculture (row crop)
Alluvium/fluviial (nt)	Lacustrine (c)	Metamorphic	Agriculture (non-row crop)
Attenuated-drift (c)	Lacustrine (f)	Igneous	Barren
Attenuated-drift (m)	Loess (f)	Sandstone	Forest (upland coniferous)
Bedrock (nt)	No landform (c)	Igneous/metamorphic (crystalline)	Forest (upland deciduous)
Colluvium	No landform (f)	Shale	Forest (mixed deciduous/coniferous)
Dune (c)	No landform (m)		Open (nonforested)
End-moraine (c)	No landform (nt)		Open (water)
End-moraine (f)	No landform (pm)		Wetland (nonwooded)
End-moraine (m)	Outwash (c)		Wetland (wooded lowland coniferous)
Ground-moraine (c)	Stagnation-moraine (c)		Wetland (wooded lowland deciduous)
Ground-moraine (f)	Stagnation moraine (m)		Wetland (wooded lowland mixed)
Ground-moraine (m)	Water		Wetland (wooded shrubland)
			Urban (commercial)
			Urban (other)
			Urban (residential)

^a Texture categories: c = coarse, f = fine, m = medium, nt = no texture, pm = peat and muck.

than simply using similar spatial units. Consolidation of independently derived GIS data sets will proceed more smoothly if data sets are populated with similar variables that are attributed in the same manner. In our GIS framework, we tried to be as explicit as possible in describing the different types of spatial units, how the spatial units can be delineated, the type of variables that can be attributed to the spatial units, and how attribution of spatial units can proceed. As a result, we believe that those wishing to begin their own stream ecological research will benefit by following a framework such as ours. Other GIS frameworks that have been developed have sometimes focused more on GIS structure. For example, the Arc Hydro data model (Maidment 2002) goes into great detail regarding type of features, including how to delineate a three-dimensional view of a river based on cross-sectional profiles of a channel using triangulated irregular networks (TIN). Users of the Arc Hydro data model also benefit by the availability of a prepackaged set of ArcGIS tools that facilitate working within the Arc Hydro framework. While we are fully sup-

portive of the Arc Hydro data model and believe that widespread adoption of that framework will be a first step towards GIS standardization, this by itself will not necessarily lead to complete standardization.

Resistance to methodological standardization often can be high as it may be felt that it will stifle researcher creativity (Bonar and Hubert 2002). Even with standardization of data production and collection procedures, however, researchers still retain substantial flexibility in the types of research questions they can explore and the types of analytic methods they can use. Standardization thus does not stifle research creativity, rather it shifts creativity back to the areas where it can be most beneficial (e.g., research question development, analytic methods). In the following sections of this paper, we discuss how our GIS framework can be used to address three common stream conservation/management objectives. These examples are presented to illustrate the flexibility and applicability of our framework. The objectives discussed are landscape-based statistical modeling of reach-scale characteristics, identification of conservation

gaps, and environmental impairment assessment and management.

Landscape-Based Statistical Modeling of Reach-Scale Characteristics

Sufficient resources are rarely available to collect data at the level of detail believed to be most relevant to river conservation and management (Seelbach et al. 1997). This is particularly true for spatially extensive studies, such as those involving multiple states or ecoregions. When insufficient resources are available, researchers must either conduct the research without the variable or estimate the variable with an appropriate statistical model using available data. Landscape-based statistical modeling of reach-scale characteristics is frequently recognized as a cost-effective and practical approach to obtaining information at detailed resolutions across large regions (Seelbach et al. 2002; Gardner et al. 2003). The premise for landscape-based statistical modeling comes from basic stream hierarchical theory, which states that large-scale variables constrain and shape the character of smaller scale variables (Frissell et al. 1986; Maxwell et al. 1995). Because our GIS structure directly links catchments, riparian buffers, and stream reaches, a variety of reach-scale habitat variables can be readily modeled. Reach-scale characteristics that frequently are predicted from statistical models include temperature (Stefan and Preud'homme 1993; Wehrly et al. 1998; Neumann et al. 2003), hydrology (Holtschlag and Croskey 1984; Wiley et al. 1997), and species occurrence or abundance (Hawkins et al. 2000; Zorn 2002; Wall et al. 2004).

Stream temperature and hydrologic models.—Stream temperature and hydrology (e.g., discharge) are regarded as two of the most important factors influencing aquatic assemblages (Moyle and Cech 1988; Allan 1995; Hynes 2001). Although temperature and hydrologic characteristics can be intensively monitored using temperature data loggers, forward looking infrared videography (Torgersen et al.

2001), and acoustic Doppler profilers (Gard and Ballard 2003), the expense of such technology limits its use across large regions. As a result, statistical modeling is an attractive alternative for obtaining estimates of these variables. Modeling approaches that have been used to predict stream temperature and hydrologic characteristics have included multiple linear regression (Wiley et al. 1997; Wehrly et al. 1998; Neumann et al. 2003), nonlinear regression, (Mosheni et al. 1998), geostatistical models (Gardner et al. 2003; Gardner and Sullivan 2004), and physical process models (Newcomb and Coon 1997).

Stream temperature and hydrology can each be influenced by a large number of landscape factors operating at a variety of potentially interacting spatial scales. At catchment scales, stream temperature and hydrology can be influenced by regional climates (e.g., air temperature, precipitation, amount of direct solar input) and by landscape conditions (e.g., land use, land cover, soil type). Locally, stream temperature and hydrology can be influenced by channel width, channel gradient, and amount of groundwater input to the stream (Wiley et al. 1997; Wehrly et al. 1998 and 2006, this volume; Neumann et al. 2003).

Our GIS framework offers several advantages for developing stream temperature and hydrologic models. Changes in temperature and hydrology within a stream network will often occur at stream confluences and at junctures of lentic and lotic system. Since stream confluences and lentic-lotic junctures are directly incorporated in our reach definitions, predictive models developed within our GIS framework can account for substantial variability in both temperature and hydrology. In addition, both stream temperature and hydrologic measurements can be expected to exhibit some degree of spatial dependency (i.e., autocorrelation) between reaches. In other words, both temperature and hydrologic characteristics at any particular stream reach can be partially estimated from neighboring reach measurements. Incorporating an autocorrelative

element in predictive models thus can potentially improve temperature or hydrologic estimates by “lending” information from neighboring reaches. There are a number of ways for spatial autocorrelation to be incorporated within a statistical model. Bailey and Gatrell (1995) suggest including the geographic coordinates of the sites within the predictive model itself to identify regionalization in the variable of interest. Alternatively, a spatial lag variable consisting of the weighted average of values in adjacent regions could be incorporated in the prediction model (Haining 1990). Another option would be to use a geostatistical method such as kriging to predict the variable of interest (Gardner et al. 2003; Gardner and Sullivan 2004). The network structure of the NHD facilitates the incorporation of spatial autocorrelation in prediction models using any of the above methods.

Biological models.—Landscape-based statistical modeling also is frequently used for predicting biological attributes such as fish presence/absence, fish abundance, and fish production within rivers. Such predictions may serve as a basis for identifying regions potentially important for conservation (Jennings 2000; Wall et al. 2004), estimating the biological condition of a river (Hawkins et al. 2000; Oberdorff et al. 2002), or forecasting the future recreational quality of a fishery (Bradford et al. 1997). Additionally, predictive biological models are routinely used to develop and test hypotheses about the influence of various habitat characteristics on aquatic species in order to evaluate the effects of environmental changes (Dunham et al. 1997; Boisclair 2001; Olden et al. 2002).

For aquatic biota to occupy specific sites within streams, they must possess certain traits that allow them to pass through habitat filters, which limit the members of a species pool that can occupy certain areas (Tonn 1990; Poff 1997). These filters operate across all spatial scales, from microhabitat to continental scales. As a result, the most robust models of aquatic assemblages are those incorporating relevant

habitat descriptors across a multitude of spatial scales (Zorn 2002; also see modeling chapters in this volume).

The spatial structure of our GIS framework improves the ability of researchers to develop accurate predictive biological models because it allows filters at a number of spatial scales to be incorporated in the models. Additionally, adoption of a more standardized GIS approach facilitates validity testing of biological models since it increases availability of appropriately structured data sets. Model validation is an often-ignored step in biological model development, but is nevertheless crucial for assuring accurate and useful models (Olden et al. 2002).

Identification of Conservation Gaps

Biodiversity loss in rivers and streams stemming from intensive land use, dams, habitat degradation, pollution, and nonnative species invasion has been pervasive and well documented (Benke 1990; Allan and Flecker 1993; Rinne et al. 2005). In response to these losses, a number of programs have been developed to conserve biological diversity in running waters (Groves et al. 2002). One such program is the National Gap Analysis Program (NGAP), which is administered by the U.S. Geological Survey. The purpose of NGAP is to keep “common species common” by identifying species and communities not adequately protected under current conservation strategies (Jennings 2000). The GLGAP project specifically targets the identification of species and communities within the Great Lakes basin. Protection of biodiversity in the Great Lakes basin is globally important because it contains approximately 20% of the world’s fresh surface water and it supports a number of globally unique biological assemblages (TNC 2004; USEPA 2004).

The GLGAP project developed this GIS framework in cooperation with the CIAUMR project to predict a number of reach-level habitat characteristics, including stream temperature and discharge, and to predict presence/absence of several fish species throughout rivers and

streams within the Great Lakes basin. Once fish presence/absence has been predicted, a GIS data set of predicted fish distributions can be compared to land stewardship levels. This helps to identify locations with a high likelihood of fish occurrence, but few conservation measures (i.e., conservation gaps). Scientists, land and water managers, and policy makers can then use this information to make informed decisions when prioritizing conservation activities within the Great Lakes basin.

Environmental Assessment and Management

Environmental assessment and management includes identification and rehabilitation of degraded habitat, evaluation of the potential for future habitat degradation, water conservation and allocation, and conservation or enhancement of native fish populations. Because the basic structural unit of our GIS framework is the stream reach, using this framework to evaluate management decisions may not seem outwardly advantageous since management decisions rarely are made at such a detailed resolution (Fausch et al. 2002). However, one of the major strengths of attributing variables to stream reaches is that reaches can be combined into larger units closer to the scale at which management decisions are being made. Although different perceptions exist as to what size spatial unit is most appropriate for evaluating management decisions, valley segments are increasingly popular (Seelbach et al. 1997; Wall et al. 2004; Burnett et al. 2006, this volume). Valley segments typically span multiple stream reaches and are relatively homogeneous in hydrology, limnology, channel morphology, and riparian dynamics (Frissell et al. 1986; Maxwell et al. 1995). Valley segments can be as long as 60 river kilometers, which increases their value for evaluating management decisions because they are closer to the scale at which many fish species complete their life cycles (Seelbach et al. 1997; Fausch et al. 2002).

Two methods have been developed for delineating valley segments. Seelbach et al. (1997) overlaid water feature, hydrology, water chemistry, water temperature, land use, and surficial geology data sets and made subjective determinations as to where valley segment breaks occurred using a GIS. Kilgour and Stanfield (2001) reduced the subjectivity of the Seelbach et al. (1997) method by defining variable classes and then programming a GIS function that would insert a valley segment break wherever at least one variable class changed. Either of these approaches for delineating valley segments could be implemented in our GIS framework. Alternatively, an algorithmic approach that compared variable similarity and that joined stream reaches with the least amount of differences between them could be implemented (T. O. Brenden, R. D. Clark, P. W. Seelbach, and L. Wang, unpublished method). Such an approach could mimic the process, but reduce the subjectivity, of the Seelbach et al. (1997) method. Additionally, it would eliminate the need to divide each variable into classes, which might be arbitrary and difficult to defend.

An additional step needed for identifying management units from stream reaches is classification. The purpose of classification is to group like with like (Gerritsen et al. 2000) and is advantageous in that it helps identify standards to which management units can be compared (Frissell et al. 1986; Hawkins and Vinson 2000; Hawkins et al. 2000). Classification is needed because rivers exhibit a remarkable amount of complexity in ecological attributes (e.g., water chemistry), even within regions of limited size, such as hydrologic units and catchments (Karr 1991; Omernik 2003). Thus, from an environmental assessment standpoint, classification allows us to better approximate the extent to which streams have been degraded (Hawkins and Vinson 2000). From a fisheries management standpoint, classification can help determine the need or likelihood of success of fish rehabilitation efforts. Techniques used to classify spatial units can range from standard hierarchical or

nonhierarchical clustering methods (Gauch 1982) to more complicated clustering techniques, such as model-based clustering (Banfield and Raftery 1993). The strength of a classification system can be measured using neutral-model classification (Van Sickle and Hughes 2000; Herlihy and Hughes 2006, this volume).

Once management units have been delineated and classification has identified management unit domains, management actions or strategies can be evaluated within our GIS framework. For illustrative purposes, we describe in more detail the CIAUMR project, which uses our GIS framework to evaluate the impairment of streams and rivers relative to land use changes.

CIAUMR project.—The goal of the CIAUMR project is to use valley segment classification and landscape-based statistical modeling to provide a comprehensive impairment assessment (both current and future) of river systems for the upper Midwest states of Illinois, Michigan, and Wisconsin. Its purpose is to evaluate how past, present, and future patterns in land use, specifically increased levels of urbanization, have affected or will affect algal, macroinvertebrate, and fish biodiversity. The CIAUMR project entails nearly every application of our GIS framework: temperature modeling, discharge modeling, aquatic assemblage modeling, merging of stream reaches into valley segments, and classification of valley segments. The current status of rivers is being evaluated by modeling algal, macroinvertebrate, and fish presence/absence and abundance for individual stream reaches relative to landscape descriptors at reach and catchment scales. Stream reaches are then merged into valley segments based on similarities between habitat descriptors, and classified according to aquatic assemblage structure and large-scale landscape factors to facilitate the identification of baseline conditions for different species.

An additional aspect of the CIAUMR project involves the evaluation of future risks to rivers in Illinois, Michigan, and Wisconsin based on predicted changes in land use patterns. Land use changes within Illinois, Michigan, and Wisconsin

are being predicted with a land transformation model (LTM; Pijanowski et al. 2000, 2002). The LTM predicts areas having the highest likelihood of being developed based on factors such as quality of view, distance to recreational areas, and distance to other urban areas. These likely land use patterns can then be incorporated in models predicting aquatic assemblages to determine how assemblages may change in the future. As with GAP analysis, this information permits stream and land managers to make informed proactive decisions regarding conservation priorities for the Great Lakes region. The LTM also can be used to predict historical land use condition, which is beneficial for understanding the extent streams have been altered and the likelihood that rehabilitation efforts will be able to revert streams to historical condition (Van Sickle et al. 2004; Kilgour and Stanfield 2006, this volume).

Suggestions for the Future

Our purpose in presenting this GIS structure and framework was to provide a basic template from which to begin research concerning functional relationships between river and landscape conditions. Our other objective was to stimulate discussion among stream ecologists as to how research into functional relationships between river and landscape conditions should proceed in hopes that greater GIS standardization would materialize. While the emergence of a single GIS framework that can be applied across the globe or even across entire continents seems unlikely, we believe it is feasible and beneficial for a few frameworks to be developed from which researchers can select based upon their study area locations.

During the development of this GIS framework for the CIAUMR and GLGAP projects, we identified several factors that we believed would be beneficial for studies involving functional relationships between streams and conditions in surrounding landscapes. Development of evapotranspiration GIS data sets for large regions would improve our ability to predict stream

discharge and would be useful for water allocation management and research. Studies such as the CIAUMR and GLGAP projects also would benefit from increased availability of reach-scale data sets containing such attributes as water chemistry, discharge, and availability of cover. While statistical modeling can predict some of these attributes, the value of quantitative field monitoring cannot be overlooked. Coordinated monitoring programs such as the U.S. Environmental Protection Agency's Environmental Monitoring and Assessment Program (USEPA 2005) hold great promise for increasing the availability of reach-scale data sets and we hope that this program expands in scope. Continued advances in remote sensing technology in the form of enhanced image resolution, greater number of water-penetrating spectral bands, and narrower sensor bandwidths also should help increase availability of reach-scale data sets (Mumby and Edwards 2002). Finally, greater comparability in data set resolution would prove beneficial for management and research. As evident in Table 1, there are wide discrepancies between GIS data sets in terms of spatial scale. Such discrepancies in scale limit the usefulness of some data sets. For example, a 1:24,000 scale NHD is being developed for the United States. While this certainly will enhance delineation of stream reaches, the resolution of other data sets such as bedrock geology, surficial geology, and soil permeability will remain at 1:1,000,000–1:250,000 scales. As a result, even though stream ecologists will be able to identify more stream reaches, the data attributed to the many of the reaches will remain constant, which means that nothing may really be gained in identifying factors affecting river condition. The full benefits of GIS from a river conservation and management standpoint may not be realized until all data sets are available at more detailed resolutions.

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Effects of Adjacent Streams on Local Fish Assemblage Structure in Western Virginia: Implications for Biomonitoring

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Abstract.—A key challenge in stream fish ecology and biomonitoring is to partition local and regional influences on assemblage structure. Numerous studies have identified local determinants of species composition (i.e., competition, predation, habitat availability), but regional influences remain poorly understood. Here, we test the hypotheses that (1) fish dispersal from adjacent streams influences local fish assemblage structure, and (2) the effects of interstream dispersal are mediated by local environmental conditions. We evaluated fish and physical habitat data from the U.S. Environmental Protection Agency's Environmental Monitoring and Assessment Program in western Virginia streams ($n = 55$). We found significant effects of adjacent stream size on local species richness, mean reproductive age, and riverine species richness. Large adjacent streams (greater than third-order) were associated with increased species richness in second-order sites. Fourth-order sites showed increased riverine species richness and decreased mean reproductive age in the presence of large adjacent streams. The nonrandom effects of adjacent stream size among sites of various stream orders suggests that local environmental conditions mediate the effects of dispersal from adjacent streams. Measures of channel shape (i.e., depth, width, and sinuosity) and microhabitat complexity (i.e., mean substrate size and woody debris) were associated with local assemblage structure in some cases, but did not account for significant variation in fish metrics explained by adjacent stream size. These results indicate that the ability of fish biomonitoring metrics to detect anthropogenic impacts may be improved by calibrating scoring criteria based on the size of adjacent streams.

INTRODUCTION

Dispersal is a landscape-scale process that influences the local distribution and abundance of organisms (Wiens 2001). Stream fishes may disperse to access remote resources, escape local habitat conditions, or colonize adjacent habitats (Schlosser 1990; Fagan et al. 2002, 2005). As such,

local fish assemblage structure is regulated not only by local environmental conditions but also by the regional distribution of source populations (Angermeier and Schlosser 1989; Schlosser and Angermeier 1995; Angermeier et al. 2002). In this paper, we evaluate the effects of adjacent streams as potential sources of fish dispersal and explore the implications for fish biomonitoring.

Fish biomonitoring requires an understanding of how dispersal from adjacent areas influences

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local assemblage structure. First, immigrating fishes may not be exposed to the full range of environmental conditions occurring at the sample site. For instance, immigration of gravel-spawning fishes from adjacent areas would not necessarily indicate high substrate quality in the sample site, although their presence would be interpreted as such in most biomonitoring studies. Second, dispersal of “new” species from adjacent habitats would inflate local species richness. Third, disproportionate immigration of intolerant or tolerant fishes may bias biomonitoring scores towards overestimating or underestimating site quality. As a result, dispersal from adjacent areas can bias biomonitoring assessments towards either false identification of local degradation (i.e., type I errors) or failure to detect local degradation (i.e., type II errors).

The spatial distributions of stream fishes suggest that dispersal among adjacent streams is an important determinant of local fish assemblage structure. Within North America, river systems flowing directly into the ocean generally contain fewer fish species than rivers of equal size connected to other river systems (Sheldon 1988), suggesting that dispersal from adjacent streams and rivers provides an important source of immigrants. Analogous patterns have been reported within smaller watersheds: headwater streams typically support fewer fish species than streams of equal size connected to larger rivers (Gorman 1986; Osborne and Wiley 1992; Schaefer and Kerfoot 2004). Local fish assemblages often exhibit positive spatial autocorrelation among stream sites (Matthews and Robison 1998; Wilkinson and Edds 2001; Hitt et al. 2003; Grenouillet et al. 2004), suggesting dispersal-mediated distributions. Empirical fish movement studies have also documented interstream dispersal events (e.g., Albanese et al. 2004; Gresswell et al. 2006, this volume).

To predict the effects of interstream dispersal on local fish assemblage structure, it will be necessary to consider how conditions in adjacent streams regulate the composition of potential immigrants (i.e., regional species pool; Tonn et

al. 1990) and the suitability of local sites for immigrating fishes. Stream size provides one framework within which to develop such predictions. Several assemblage attributes are known to vary with stream size. First, fish species richness tends to increase with stream width and volume (Shelford 1911; Burton and Odum 1945; Sheldon 1968; Angermeier and Schlosser 1989; Goldstein and Meador 2004). Second, fish life histories tend to vary with stream size, in that headwater fishes tend to have shorter life spans, smaller adult body sizes, and earlier reproductive ages than riverine fishes (Schlosser 1990).

Longitudinal patterns in fish assemblage structure therefore suggest two predictions based on the size of a site’s adjacent streams. First, dispersal from large streams should tend to increase species richness, mean adult body size, mean reproductive age, and mean life span in assemblages of smaller receiving streams. Second, the relative importance of dispersal from adjacent streams should increase with site stream size because larger sites would tend to have fewer “filters” (sensu Tonn et al. 1990; Poff 1997) operating on immigrants. We tested these predictions by comparing stream fish assemblages from sites with similar local habitat conditions but different regional habitat conditions (i.e., adjacent stream sizes) in western Virginia.

METHODS

Data Source

We used fish and physical habitat data from the Environmental Monitoring and Assessment Program (EMAP) of the U.S. Environmental Protection Agency. The EMAP site locations were established using a systematic random methodology (Herlihy et al. 2000). U.S. Environmental Protection Agency personnel sampled stream sites using standardized methods during base flow conditions during the summers of 1993, 1994, 1997, and 1998. We evaluated sites in second-, third-, and fourth-order streams (Strahler 1957) in western Virginia containing both fish and physical

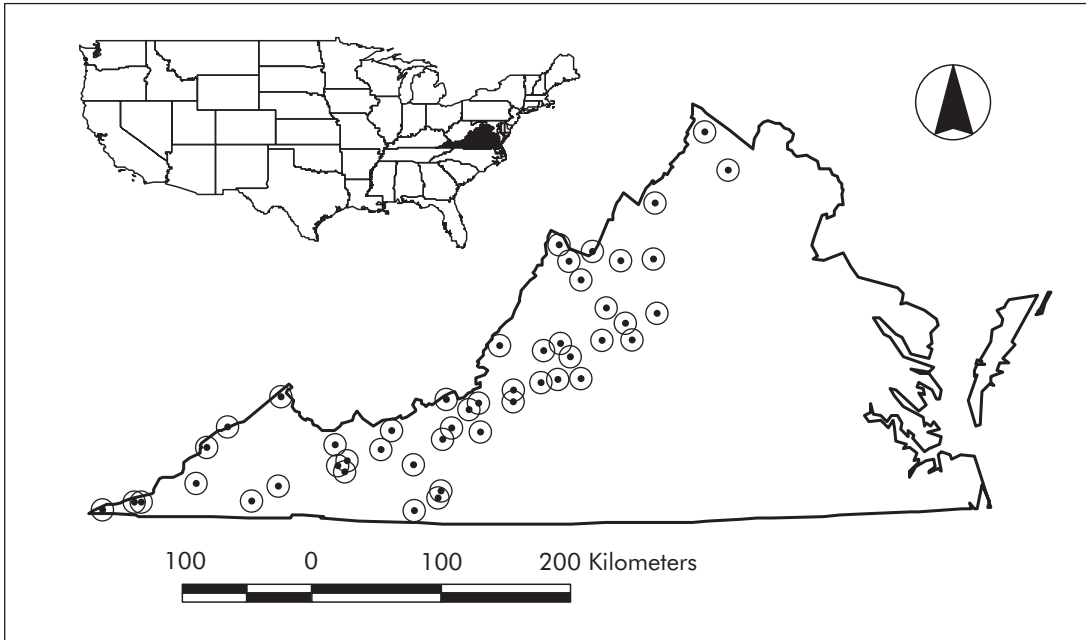


Figure 1. EMAP stream sites evaluated in the current study ($n = 55$). Sites were represented by fish and physical habitat data from second-, third-, and fourth-order streams.

habitat data ($n = 55$; Figure 1). This area includes portions of the Blue Ridge and Ridge and Valley physiographic provinces and portions of the Potomac, James, New, Tennessee, and Big Sandy River basins. We chose this study area because it represents a region that has been recommended for fish biomonitoring development in Virginia (Smogor and Angermeier 2001). Raw data are available at <http://www.epa.gov/emap>.

Physical habitat data included quantitative measures of substrate size, woody debris volume, fish cover, riparian vegetation, thalweg depths, and mesohabitat dimensions (Kaufmann and Robison 1998). Data were collected with a systematic, randomized protocol that encompassed the entire sampling reach; reach lengths were 40 times mean wetted width (Kaufmann and Robison 1998). We used these data to characterize local site conditions because they exhibit significant variation among sites in our study area (Yuan and Norton 2003) and because they are known correlates of fish distribution and abundance (McCormick et al. 2001). We assumed that local physical habitat conditions would covary

with other local physicochemical conditions that were not measured. For sites sampled more than once, we calculated mean values for all variables and used these in our analyses.

Fish assemblage data were collected with single-pass backpack electrofishing methods at each site following McCormick and Hughes (1998). Fishes were identified to species, counted, and returned to the sampling reach. We rejected 12 EMAP fish records based on Jenkins and Burkhead (1994) and replaced rejected records with the probable species or used mean values for adult body size, reproductive age, and life span calculated from congeners occurring in Virginia (see Appendix 1). Previous electrofishing surveys in the study area using the EMAP sampling reach length (i.e., 40 times mean stream width) detected more than 70% of the fish species present in local sites (Angermeier and Smogor 1995).

Adjacent Stream Classification

In this analysis, we defined “adjacent streams” as streams confluent to sampling sites within three

river kilometers (rkm) downstream from sample site locations. We evaluated only downstream habitats to permit comparisons among large and small stream sites without confounding the effects of upstream flow variability. We chose this spatial extent because some common stream fishes can disperse this distance (Logan 1963; Gorman 1986; Osborne and Wiley 1992; Gatz and Adams 1994; Albanese et al. 2004) and exploratory analyses revealed sufficient numbers of sites in small and large adjacent stream categories to permit comparisons.

First, stream channels were mapped from the 1:24000-scale national hydrography data set (<http://nhd.usgs.gov>) and converted to raster data (30-m² cells). Second, we calculated Strahler (1957) stream orders for each grid cell using a geographic information system. Third, we classified sites based on the size of adjacent stream habitats in the analysis zone. We defined first- to third-order streams as “small” and streams larger than third-order as “large” following Jenkins and Burkhead (1994). This stream size criterion typically distinguishes wadeable from nonwadeable streams in the mid-Atlantic highlands region (Herlihy et al. 2000). Site categories therefore indicate whether or not large or small adjacent streams were available to provide immigrants into each sample site. Sites with large and small adjacent streams encompassed a wide range of catchment areas, but large adjacent streams tended to occur more frequently at lower elevations than small adjacent streams (Figure 2).

We characterized fish assemblage structure with four metrics: species richness, mean body size, mean reproductive age, and mean life span. We chose these metrics because they typically increase from small to large stream sites (Schlosser 1990) and they provide a framework to test hypothesized patterns of dispersal from adjacent streams. Data on adult body size (total length [TL]), reproductive age (years), and life span (years) were taken from Jenkins and Burkhead (1994) and Smogor (1996). Congeneric surrogate species or family averages calculated for Virginia taxa were used where primary

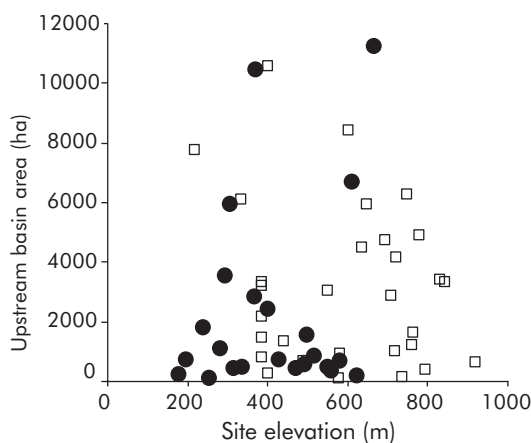


Figure 2. Distribution of EMAP sites with small (\leq third order, squares) and large ($>$ third order, circles) adjacent streams along gradients of catchment area and site elevation.

data were not available. Of 109 species identified, 25 (23%) required surrogates or family averages for at least one metric.

We also categorized species according to the stream size they tended to occupy based on distribution data in Jenkins and Burkhead (1994). To identify large and small stream specialists, we excluded species that were reported to inhabit all stream sizes (i.e., stream size generalists) by Jenkins and Burkhead (1994). “River” and “creek” species therefore represent obligate habitat associations in large and small streams. Of the 109 species in EMAP sites, 32 (29%) were classified as “river” species and 20 (18%) were classified as “creek” species. We compared local richness of river and creek species between sites with large and small adjacent streams to assess the potential role of dispersal.

Statistical Analyses

The primary challenge in this analysis was to control for local environmental variability while evaluating the regional effect of adjacent stream size. First, we used principal components (PC) analysis from correlation matrices to characterize physical habitat conditions among sites.

Principal components scores encompassed 68% of the variance in physical habitat conditions in two principal components for all eigenvalues greater than 1. Eight variables loaded strongly (i.e., variable loadings > 0.5) into the first two components (Table 1). PC I represented a gradient of channel size and shape and PC II represented a gradient of structural complexity (woody debris volume, substrate size).

Second, we grouped sites by stream order (i.e., second, third, and fourth) and compared 95% confidence intervals of fish metrics among sites with small and large adjacent streams (Pearson 2002). We assumed that by evaluating the effects of adjacent streams among sites of the same stream order, we would control for some local environmental variability. We also used nonparametric techniques to compare fish metrics in sites with small and large adjacent stream sizes (Kruskal–Wallis tests). We chose nonparametric methods because our sample sizes did not permit us to test the assumption that the data were normally distributed.

Third, we used Mantel tests (Mantel 1967) to evaluate associations between adjacent stream size and fish metrics while controlling for the potentially confounding effects of local physical habitat. We calculated three categories of site-by-site dissimilarity matrices for these tests: (1)

fish metrics, (2) adjacent stream size, and (3) local physical habitat (i.e., PC I and PC II scores). All matrices were calculated from Euclidean distances and standardized from 0 to 1 (SPSS 10.0). When significant associations between adjacent stream size and fish metrics were observed, we used partial Mantel tests with local habitat data as a blocking matrix to test for covariation. All Mantel statistics were calculated from matrix correlations with *Mantel zt* (MS-DOS program by E. Bonnet, Ghent University, Belgium) using 10,000 randomized resampling iterations.

RESULTS

EMAP surveys reported 109 fish species in western Virginia streams, representing 52% of the species occurring in freshwaters of Virginia (Jenkins and Burkhead 1994). Fish metrics varied consistently along a stream order gradient. Species richness, adult body size, and life span increased with increasing stream order (Figure 3). River species richness changed in the expected direction, but creek species richness was not monotonically related to stream order (Figure 3). Mean reproductive age increased slightly from second- to third-order sites but did not increase from third- to fourth-order sites (Figure 3).

We found significant effects of adjacent stream size on species richness, mean body size, mean reproductive age, and riverine species richness in local assemblages. Second-order sites with large adjacent streams tended to have more species than similar-order sites with small adjacent streams (Table 2; Figure 4A). In fourth-order sites, large adjacent streams were associated with younger mean reproductive age and increased river species richness (Table 2; Figure 4C and 4E). Large adjacent streams were negatively associated with mean body size and life span in fourth-order sites (Figures 4B and 4D) but these effects were not statistically significant. We detected no significant relationships between fish metrics and adjacent stream size among third-order sites. Among all sites, adjacent stream size influenced mean body size (Table 2) but this effect was not

Table 1. Principal components (PC) analysis loadings for physical habitat data at EMAP sites ($n = 55$). The first two components (PC I and PC II) explained 68% of the total variance for all eigenvalues greater than 1. Values represent loadings of variables onto components. Variable loadings greater than 0.5 are indicated in bold.

Variable	PC I	PC II
Standard deviation of stream depth	0.909	0.204
Residual pool mean depth	0.768	0.068
Sinuosity	0.528	0.097
Mean volume fine woody debris	-0.399	0.851
Mean volume coarse woody debris	-0.353	0.856
Mean stream depth	0.924	0.175
Mean stream width	0.813	0.278
Log of mean substrate diameter	-0.063	0.564
Variance explained (%)	43.7	24.2

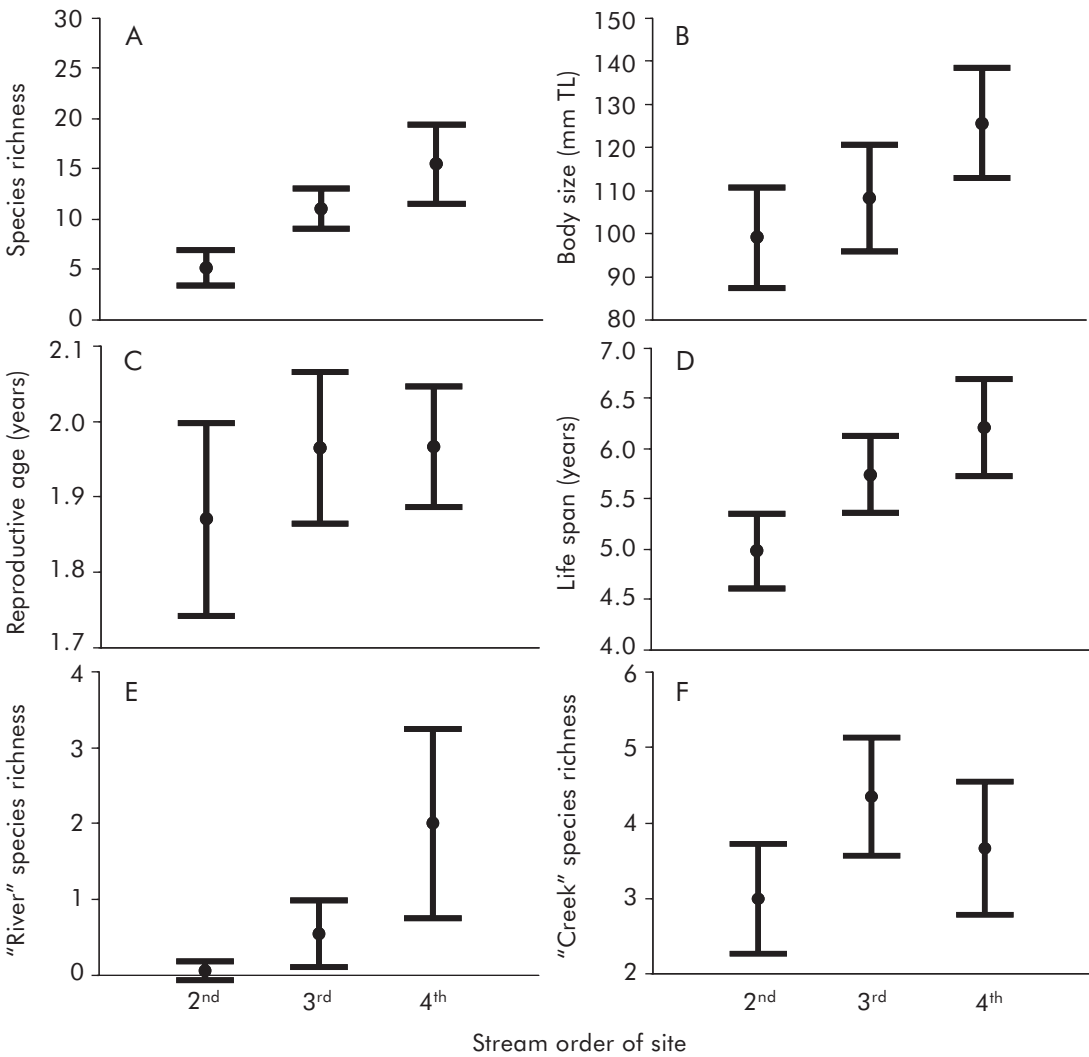


Figure 3. Effects of site stream order on local species richness (A), mean adult body size (B), mean reproductive age (C), mean life span (D), “river” species richness (E), and “creek” species richness (F). See text for definitions of river and creek species. Mean values (circles) and 95% confidence intervals (whiskers) are shown. TL refers to total length of fishes.

Table 2. Effects of adjacent stream size on fish assemblage metrics. Kruskal-Wallis chi-square statistics are presented for each fish metric (column) for comparisons of small and large adjacent streams within stream size categories. Asterisks indicate significance at $P < 0.05$. Significant adjacent stream size effects are shown in Figure 5.

Site stream order	Species richness	Body size	Reproductive age	Life span	River species richness	Creek species richness
2,3,4	0.01	5.95*	0.35	2.26	0.00	0.11
2	5.24*	0.43	0.85	2.04	1.83	3.63
3	0.56	0.82	0.80	1.86	0.09	0.06
4	0.80	1.72	4.81*	2.55	4.26*	0.23

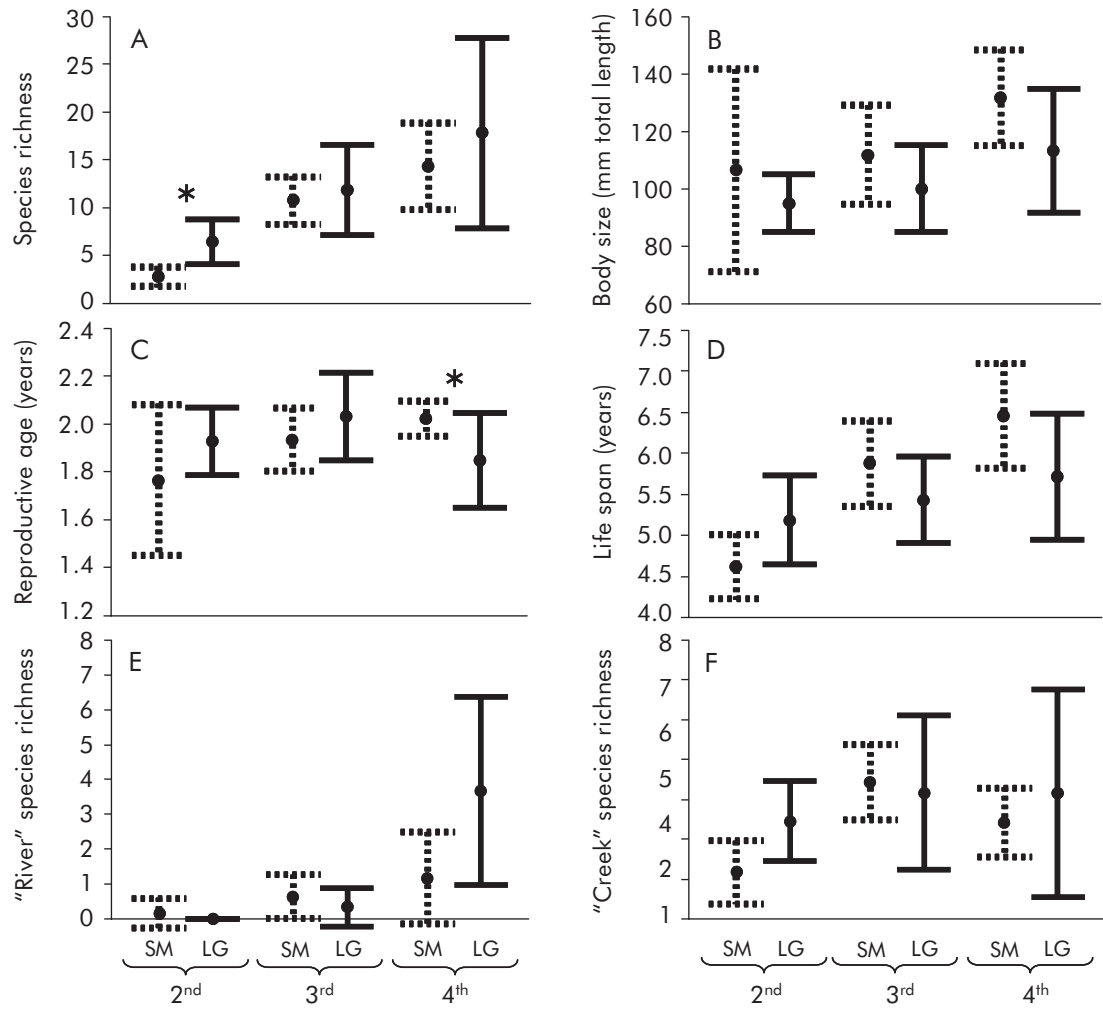


Figure 4. Effects of adjacent stream size on local species richness (A), mean adult body size (B), mean reproductive age (C), mean life span (D), "river" species richness (E), and "creek" species richness (F) across stream orders. Mean values (circles) and 95% confidence intervals (whiskers) are shown. Small adjacent streams (SM) are indicated with dashed lines; solid lines indicate the presence of large adjacent streams (LG). See text for definitions of river and creek species and adjacent stream size categories. Asterisks indicate significant differences ($P < 0.05$) between large and small adjacent streams (Table 2).

observed within comparisons of same stream order. Only 4 of 24 tests showed significance at the $P < 0.05$ level, suggesting weak experiment-wise effects of adjacent stream size on local fish assemblage structure.

Mantel tests provided additional evidence for the effect of large adjacent streams on mean reproductive age and river species richness in fourth-order sites (Table 3). However, Mantel

tests did not identify significant effects of adjacent stream size in second- or third-order sites. These tests also revealed effects of local physical habitat on some fish metrics. Channel size and shape (i.e., PC I) were significantly associated with species richness in second- and fourth-order sites (Table 3). Physical habitat complexity (i.e., PC II) was significantly associated with species richness in fourth-order sites. However,

Table 3. Effects of adjacent stream size and local physical habitat on fish assemblage metrics. Mantel test statistics (Mantel r) are presented for site-by-site matrix correlations of adjacent stream size ("adjacent") and physical habitat (PC I and PC II) within four stream size categories. Single asterisks indicate significance at $P < 0.05$. Double asterisks indicate significance of partial Mantel tests (using PC I and PC II as blocking matrices) at $P < 0.05$.

Variable	Site stream order	Species richness	Body size	Reproductive age	Life span	"River" species richness	"Creek" species richness
Adjacent	2,3,4	-0.01	0.01	0.00	-0.01	0.01	0.00
PC I	2,3,4	0.34*	0.07	-0.07	0.10	0.19*	0.00
PC II	2,3,4	0.04	-0.11	-0.09	-0.09	-0.05	-0.03
Adjacent	2	0.07	0.16	0.06	0.00	0.15	0.03
PC I	2	0.46*	0.09	-0.15	-0.10	-0.11	0.44
PC II	2	-0.07	0.07	-0.09	-0.18	0.06	-0.04
Adjacent	3	0.00	-0.12	-0.04	-0.07	-0.10	-0.03
PC I	3	-0.06	-0.18	-0.16	-0.08	-0.10	0.02
PC II	3	0.03	-0.18	-0.09	-0.17*	0.08	0.07
Adjacent	4	0.06	-0.02	0.34**	0.00	0.25**	0.15
PC I	4	0.26*	0.15	0.00	0.03	0.01	-0.11
PC II	4	0.21*	-0.11	-0.10	-0.04	0.04	-0.04

partial Mantel tests using physical habitat data as blocking matrices did not diminish the significance of adjacent stream size effects on mean reproductive age or river species in fourth-order sites (Table 3). Among all sites, Mantel tests showed no significant effects of adjacent stream size on fish metrics but did show effects of channel size and shape on species richness and riverine species (Table 3). Overall, we detected the greatest number of correlations with species richness and fewest with body size and creek species richness; these correlations were most common in fourth-order sites and least common in small stream sites (Table 3).

DISCUSSION

Our results suggest that (1) dispersal from adjacent streams can affect local fish assemblage structure, (2) dispersers from large adjacent streams tend to be smaller-bodied fishes with earlier ages of reproduction, and (3) local site conditions may mediate the influence of dispersal from adjacent streams. Our first prediction was that dispersal from large adjacent streams would tend to increase local species richness, mean adult body size, mean reproductive

age, and mean life span in local assemblages. We found that large adjacent streams tended to increase local species richness, consistent with previous studies (Osborne and Wiley 1992; Schaefer and Kerfoot 2004). However, large adjacent streams tended to decrease mean reproductive age, contrary to our expectations. This suggests that large nearby streams may act as sources of dispersal of early-maturing fishes into adjacent stream sites. Gorman (1986) speculated that adventitious stream effects might be driven by dispersal of small-bodied schooling fishes from large rivers. Our data support this notion.

Our second prediction was that the effects of dispersal would be greatest in larger sites because these areas would tend to support fewer environmental "filters" (Tonn et al. 1990; Poff 1997) for immigrant fishes. Our data provide some support for this prediction. Pooled analysis of second-, third-, and fourth-order sites revealed inconsistent effects of adjacent stream size on fish metrics, but several significant effects were detected when comparisons were partitioned into sites of the same stream order. Fourth-order sites supported a greater number of significant adjacent stream effects than did second- or third-order sites. Moreover, the effects of large adjacent

streams on fourth-order sites were not explained by channel size and shape (i.e., PC I) or physical habitat complexity (i.e., PC II). However, second-order sites also showed an effect of large adjacent streams on species richness, in contrast to our expectations.

These results have important consequences for stream fish biomonitoring development and interpretation. In cold- and cool-water streams, low levels of enrichment increase fish species richness by addition of more tolerant species (McCormick et al. 2001; Scott and Helfman 2001; Hughes et al. 2004). However, fish bioassessments typically evaluate species richness, given that degraded streams tend to support fewer species than less disturbed streams (Fausch et al. 1984). On average, the presence of large adjacent streams increased local richness by five species in second- and fourth-order sites. These additional species would have inflated metric scores in previous stream biomonitoring studies in the mid-Atlantic highlands region (Angermeier et al. 2000) and Midwestern United States (Karr et al. 1987; Angermeier and Schlosser 1989). Smogor and Angermeier (2001) recommended several metrics for fish biomonitoring in western Virginia streams, including the number of cyprinid species in a sample. In the current study, cyprinids constituted the majority of the additional species associated with large adjacent streams. As a result, the presence of large adjacent streams may tend to mask local habitat degradation and contribute to type II errors. Additional research is necessary to understand how inter-stream dispersal influences the overall tolerance of local assemblages to environmental stressors. We would expect that increasing dispersal from adjacent areas would decrease metric sensitivity to local stressors, and increase sensitivity to distal stressors like migration barriers but these hypotheses remain to be tested empirically.

Osborne et al. (1992) recommended that fish biomonitoring studies calibrate metrics for adventitious and headwater streams due to the potential effects of dispersal from adjacent source

populations. Our findings suggest that the size of the stream site may provide a useful framework to develop expectations for the influence of inter-stream dispersal. Analogous methods were developed by Fausch et al. (1984) to account for natural variation in local species richness as a function of stream size. However, calibrating for adjacent stream sizes will require additional consideration of the spatial scale at which dispersal influences local assemblages. The spatial extent of such influence in our analysis was limited to 3 rkm downstream from sample sites. Future studies should evaluate whether inter-stream dispersal is limited to confluence zones or has more extensive upstream effects.

This study provides new insight into ways that inter-stream dispersal may influence local assemblage structure. More mechanistic models will require a clearer understanding of the factors that regulate the distribution and proximity of immigrant sources within and among streams (Schlosser and Angermeier 1995). Future studies aiming to resolve local and regional influences on fish assemblage structure may benefit by considering how watershed shape constrains the configuration and connectivity of source population habitats (Fagan 2002). For instance, trellis-shaped watersheds are characterized by a relatively high proportion of adventitious streams, whereas dendritic-shaped watersheds contain more confluences of larger streams (Zernitz 1932; Shreve 1969; Benda et al. 2004). Watershed shape may thereby provide a spatial framework to predict dispersal dynamics at smaller spatial scales.

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Appendix 1. Changes to EMAP fish data incorporated in the current analysis. We replaced problematic records with the likely species or calculated mean metric values from congeners in Virginia (Jenkins and Burkhead 1994). Our rationale for all changes was based on data in Jenkins and Burkhead (1994).

EMAP site code	EMAP record	Current analysis	Rationale
MAIA97-052	Spotted bass <i>Micropterus punctulatus</i>	Smallmouth bass <i>M. dolomieu</i>	<i>M. punctulatus</i> is not reported in northern Virginia.
MAIA97-052	Pallid shiner <i>Hybopsis amnis</i>	<i>Notropis</i> spp.	<i>H. amnis</i> is not reported in Virginia.
MAIA97-178	Silver shiner <i>Notropis photogenis</i>	<i>Notropis</i> spp.	<i>N. photogenis</i> is not reported in the James River basin.
MAIA97-179	Redfin pickerel <i>Esox americanus</i>	Chain pickerel <i>E. niger</i>	<i>E. americanus</i> is not reported in the upper Roanoke River basin.
MAIA97-186	Sauger <i>Sander canadensis</i> (also known as <i>Stizostedion canadense</i>)	Walleye <i>Sander vitreus</i> (also known as <i>S. vitreum</i>)	<i>S. canadensis</i> is not reported in upper Big Sandy River basin; <i>S. vitreus</i> is native to this basin.
VA526S	Longnose dace <i>Rhinichthys cataractae</i>	Eastern blacknose dace <i>R. atratulus</i>	<i>R. cataractae</i> is unlikely in Big Sandy River basin.
VA770S	Emerald shiner <i>N. atherinoides</i>	<i>Notropis</i> spp.	<i>N. atherinoides</i> is not reported in the Big Sandy River basin in Virginia.
VAR01S	Stripetail darter <i>Etheostoma kennicotti</i>	Fantail darter <i>E. flabellare</i>	<i>E. kennicotti</i> is not reported in Virginia.
VAR09S	River darter <i>Percina shumardi</i>	<i>Percina</i> spp.	<i>P. shumardi</i> is not reported in Virginia.
VAR09S	Fallfish <i>Semotilus corporalis</i>	Creek chub <i>S. atromaculatus</i>	<i>S. corporalis</i> is not reported in the New River basin in Virginia.
VAR09S	Southern redbelly dace <i>Phoxinus erythrogaster</i>	Mountain redbelly dace <i>P. oreas</i>	<i>P. erythrogaster</i> is not reported in Virginia.
VAR12S	<i>P. erythrogaster</i>	<i>P. oreas</i>	<i>P. erythrogaster</i> is not reported in Virginia.

Landscape Clusters Based on Fish Assemblages in the Conterminous USA and Their Relationship to Existing Landscape Classifications

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Abstract.—Conducting biological assessments at a national scale requires a classification scheme to report results, define reference conditions, and interpret data. We believe that such a classification should be based largely on biota. Analyzing stream biological assemblage data across the conterminous United States is difficult due to the lack of synoptic assemblage data. In the last 10 years, however, the number and scope of bioassessments has increased dramatically. We compiled a national-scale database of lotic fish assemblages containing 5,951 sample sites from available national and state agency data. Cluster analysis (Bray-Curtis distance) and indicator species analysis were used to cluster the data, identify clusters, and describe them. We developed 12 national clusters of fish assemblage groups that were well described by indicator fish species and predicted using both discriminant function analysis and classification tree analysis. We also examined the relationship of existing landscape classification schemes to fish assemblage similarity. Existing schemes captured about half the within-group similarity expressed in biologically derived clusters. Schemes based on ecoregion, physiography, hydrologic units, and geopolitical boundaries had very similar mean within-group fish assemblage similarities. Cluster and mean similarity analyses were not strongly influenced by using data subsets that removed nonnative fish species and disturbed sites. This suggests that the underlying mechanisms responsible for controlling fish assemblage patterns at the national scale are fairly robust to the effects of nonnative species and anthropogenic disturbances.

INTRODUCTION

Aquatic ecosystem classification has long been, and remains, an important part of how we study and manage streams and rivers. Some of the earliest techniques proposed in the late 19th century focused on reaches or zones (Hawkes 1975). Typically, these were based on the dominant fish

species. Although the transition from one assemblage to another among sites or along a river's course from headwaters to the sea is often obvious, scientists have sought to explain what causes it. Chief among these explanations are landscape conditions, river basins, and river size.

Pflieger (1971) used physiographic regions and river size to describe different fish faunal regions. Ecoregions are used by many state water quality agencies (Hughes et al. 1994), as well as New Zealand (Biggs et al. 1990), for developing

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expectations for aquatic assemblages. Matthews (1998), however, argued that river basins offer more appropriate schemes for regionalizing fish assemblages than ecoregions. Meek (1891) employed river basins to explain patterns in fish distribution, and Hocutt and Wiley (1986) organized their book chapters by them. Because native freshwater fish disperse mostly by swimming, Gilbert (1980) and Matthews (1998) considered basins as the single most important factor in regional ichthyogeography. Nonetheless, Legendre and Legendre (1984) found climatic, geomorphic, and vegetation patterns more closely associated with fish assemblage patterns in Quebec than basins. Omernik and Bailey (1997) and Omernik (2003) argued that what many call basins are hydrologic units, which represent true river basins only about half the time.

River zonation appears to be a function of river size, gradient, and temperature. Kuehne (1962) and Lotrich (1973) observed that fish assemblage structure changed with stream order in two Kentucky streams. Vannote et al. (1980) linked zones with stream width or stream order, predicting that fish, benthos, and algae assemblages would change with increasing distance from headwaters. On the other hand, Hynes (1970) summarized zonal patterns in fish, macrobenthos, and algae, concluding that zones are of mostly descriptive value. Also, both Hughes and Gammon (1987) and Omernik and Griffith (1991) observed marked changes in fish assemblages along two Oregon rivers without any change in stream order.

Several U.S. agencies use ecoregions and ecoregional reference sites for setting biological criteria when assessing fish assemblage condition (Yoder and Rankin 1994; Kentucky DEP 2002; Linam et al. 2002; Wilton 2004); others use river basins (McDonough and Barr 1977; Hawkes et al. 1986; Chilcote et al. 2005) or hydrologic units (Abell et al. 2000; Master et al. 1998). All three forms of landscape classification are broad and general, therefore they include considerable heterogeneity. Regardless of the fish assemblage heterogeneity within a basin or ecoregion, agencies

can stratify and reduce the apparent variability occurring at the scale of an entire state. This is clearly an improvement. But is it enough?

States that set quantitative biological criteria for naturally heterogeneous regions or basins run the risk of overprotecting some waters and underprotecting others. For example, Ohio EPA's criterion for fish assemblage condition in the eastern corn belt plains ecoregion is 40, but the interquartile and total ranges in scores at regional reference sites are 40–50 and 31–59, respectively, for wadeable streams (Yoder and Rankin 1994). Some of this variation results from natural environmental and fish assemblage heterogeneity. Similarly, a population viability criterion for coho salmon *Oncorhynchus kisutch* in Oregon is 50% distribution throughout a basin, but distribution ranges from 0% to 100% for coho among Oregon Coast Range basins and 25–56% in subbasins of a single large basin (Chilcote et al. 2005). When it comes to listing or delisting a species as threatened, such wide variations are problematic, especially when much of the variation results from natural heterogeneity in the Coast Range (Gresswell et al. 2006; Kaufmann and Hughes 2006; both this volume). Regardless of scale, we believe that using robust fish assemblage data sets to determine fish assemblage patterns, which are then linked to naturally varying environmental variables, is preferable to using preexisting landscape classifications for developing expectations.

Analyzing biological assemblage data at a national scale is difficult and rarely attempted due to the problems of compiling the necessary database. In the United States, in the past 10 years, there has been a dramatic increase in the collection of stream biological data for the purposes of assessing the ecological condition of lotic systems. At the national scale, both the U.S. Environmental Protection Agency's (EPA), Environmental Monitoring and Assessment Program (EMAP) and the U.S. Geological Survey's (USGS), National Water Quality Assessment Program (NAWQA) have been collecting data nationwide. In addition, many state agencies have

established synoptic biomonitoring programs. With the advent of these national and state databases, there are sufficient data to attempt to analyze national patterns in biological assemblage data. Our objective was to start the process of developing a biologically driven classification system for lotic systems at the scale of the conterminous 48 states and to compare the classification strength of existing national landscape classifications to that observed with our biological classes.

METHODS

National Database Development

Since 1993, EMAP and its smaller scale regional counterpart (Regional EMAP or REMAP) have been conducting probability-based surveys to determine the ecological condition of streams and rivers in many parts of the United States. In EMAP, sample sites are selected using a systematic, randomized sample providing a sound statistical basis for assuming that the data are representative of all the streams and rivers of the study region (Hughes et al. 2000). Sites were sampled for a suite of biological, chemical, and habitat indicators of ecological condition. NAWQA is designed to assess the condition of the nation's streams and groundwater and how natural and human factors affect condition (Gilliom et al. 1995). NAWQA sampling has taken place within 50 major hydrologic basins across the country. Within each basin, sites were hand-picked, with smaller streams being indicator sites selected to represent relatively homogeneous environmental settings and larger streams/rivers used as integrator sites affected by complex combinations of land use and natural influences.

Our initial attempt at compiling a national database used all available EMAP and REMAP probability survey data (Table 1). Examination of the national map from this compilation revealed a number of spatial gaps, particularly in the southeastern United States. Thus, we at-

tempted to fill in these gaps by requesting agency data from states where we had no EMAP/REMAP data (Table 1). At about this time, the USGS released data from the NAWQA project, which also helped fill in gaps. Although the state and NAWQA data were not collected from randomly selected sites, the surveys were synoptic in scope and sampled sites from a broad range of stream types and sizes. All of the surveys sampled Wadeable streams and about half of them also included river samples (Table 1). A primary objective of all the surveys was bioassessments, using stream biota to assess stream condition. All fish species and site data were compiled from the individual surveys into one combined SAS database.

Fish sampling in all the surveys used in our compilation were designed to characterize the entire fish assemblage at each sample site. Fish sampling methods varied somewhat among surveys but all involved sampling a defined sample reach length and identifying and enumerating all captured individuals. Environmental Monitoring and Assessment Program field methods are detailed in Lazorchak et al. (1998). Streams were backpack electrofished within sample reaches 40 times the mean wetted width in length, a distance shown to capture more than 90% of the species in western Oregon streams (Reynolds et al. 2003). Rivers in EMAP were sampled by raft electrofishing along longer reaches (100 times the mean wetted width) to achieve a similar sampling sufficiency (Hughes et al. 2002). In other surveys, electrofishing was the normal method of fish sampling although some data were collected by seining. Sample reach lengths were similar but not exactly the same as EMAP methods. Sample reach lengths in NAWQA were 150–300 m for Wadeable streams and 500–1,000 m in nonwadeable rivers (Meador et al. 1993); Ohio EPA requires 150–200 m and 500 m, respectively. Sample reach lengths in Iowa streams were 150–320 m depending on width and habitat form.

We compiled all fish species data and converted all species names into one set of consistent species

Table 1. Survey data included for analysis in the national fish database.

Survey	N	S	Waterbodies*	Reference or agency
EMAP surveys				
Mid-Atlantic	541	201	S&R	McCormick et al. 2000
Oregon Pilot	141	56	S&R	Peterson et al. 2002
Western	365	137	S&R	U.S. EPA 2001
REMAP surveys				
New England	33	27	S	EPA New England Lab
Savannah Basin	108	48	S	U.S. EPA 1999
Eastern Corn Belt	342	107	S	Simon and Dufour 1998
Northern Lakes and Forests	94	65	S	Wang et al. 2003
New Mexico Chama/Gila basins	20	22	S&R	Joseph 2004
Kansas/Missouri/Nebraska	286	142	S&R	Kansas DWP 2002
Southern Rockies	64	15	S	Griffith et al. 2001
California Central Valley	72	36	S	Griffith et al. 2003
Coast Range/Yakima	108	31	S	Herger and Hayslip 2000
Cascades	39	12	S	Hayslip et al. 2004
Upper Deschutes Basin	39	17	S	Hubler 2000
NAWQA	883	437	S&R	Meador et al. 1993
State agency surveys				
Iowa	195	95	S	Wilton 2004
Illinois	139	116	S	Illinois DNR
Kentucky	247	158	S	Kentucky DEP 2002
Minnesota	1249	114	S&R	Minnesota MPCA
Ohio	500	118	S&R	Ohio EPA 1987
Oregon	186	26	S	Oregon DEQ
Texas	60	95	S	Linam et al. 2002
Vermont	240	47	S	Vermont DEC 2002
ALL DATA	5951	530		

N = Number of unique sample sites in survey used in this analysis

S = Number of fish species in survey data used in this analysis.

* Indicates whether survey was for wadeable streams only (S) or streams and rivers (S&R).

names using Robins et al. (1991). For purposes of this analysis, we only used fish data and deleted all amphibian and reptile species from the analysis. When multiple sampling visits were made to the same site, we used the most recent sampling visit in our analyses so that each site was only represented by one sampling visit. In total, there were 5,951 unique sampling sites in our database and 530 different fish species (Table 1). For each site, we calculated the proportionate abundance of each fish species. Proportionate abundance was used in all statistical analyses to minimize the effects of varying sampling effort among surveys on total abundance. Individuals that were not identified to species (e.g., *Cottus* sp.) and individuals that were identified

as hybrids were deleted. Twenty sites in which more than 25% of the individuals were hybrids or not identified to species were deleted entirely.

We compiled available site information, water chemistry, and physical habitat data for all sites with fish data. Available environmental data varied enormously among surveys. Very few variables were measured at all sites. In this analysis, we only used the watershed area and channel slope data that were available for more than 90% of the sites. We also used available GIS data layers and site latitude and longitude to determine each site's Omernik (1987) ecoregion, 8-digit USGS hydrologic unit code, Fenneman (1946) physiographic province, and aquatic zoogeographic region (Maxwell et al. 1995). We also

used a GIS to determine site elevation from 30-m digital elevation models (DEM) and mean August air temperature from PRISM data layers (Daly et al. 2002).

Data Analysis

To examine biologically driven clusters of fish assemblage types, we performed a cluster analysis on the compiled national data set. To help describe the individual clusters derived from the cluster analysis, we used indicator species analysis, visual examination of each cluster's spatial distribution, and bar diagrams of overall species composition in each cluster. We also used discriminant function analysis (DFA) and classification tree analysis (CTA) to predict cluster membership from the fish assemblage data. With these tools, it is possible to predict cluster membership for any site outside our data based on its fish assemblage. Last, we used mean similarity analysis to evaluate the similarity of fish assemblages within a number of different landscape classification schemes.

Before conducting any analyses, we screened out rare species. Extracting patterns with multivariate analyses is often facilitated by excluding rare species that add noise to the patterns. Following the rule of thumb proposed by McCune and Grace (2002), we deleted species that were present in fewer than 5% of the sites. Removal of rare species reduced the number of species analyzed from 530 to 63 (Table 2). A small number of sites (58) only contained rare species and were dropped from the analyses. These sites were generally small streams with low total species richness (1–4), in no particular region of the country. All analyses were then conducted on this screened matrix of 5,873 sites by 63 species.

We did the cluster analysis using PC-ORD version 4 software (McCune and Mefford 1999) using the fish species proportionate abundances, Bray-Curtis (Sorensen) distance, and the flexible-beta linkage method with a beta of -0.25 . We also conducted indicator species analysis

(Dufrêne and Legendre 1997) using PC-ORD. This analysis shows how indicative individual species were of each of the clusters. Species indicator values were calculated for each cluster as the product of percent faithfulness (all sites in the cluster should contain the species) and percent exclusiveness (species should only be in the cluster and not others). We reported the percent indication of individual species to particular clusters. Values ranged from 0% (no indication) to 100% (perfect indication). A perfect score would indicate that the species is both 100% exclusive and faithful to that particular cluster. We also calculated the statistical significance of the percent indication for each species using the Monte Carlo method in PC-ORD, by running 10,000 simulations and randomly assigning sites to groups. The type I error (P -value) for each species is the proportion of times that the percent indication in the random simulations exceeds the observed percent indication in the data (McCune and Grace 2002). With 10,000 simulations, the lowest possible species P -value is 0.0001 (the observed percent indication is greater than all of the random simulations).

We examined the dendrograms from the cluster analysis and evaluated models that had between 2 and 100 clusters. We ran the indicator species analysis for a number of different cluster sizes to help determine the optimum number of clusters to choose from the dendrogram. Following the suggestion of Dufrêne and Legendre (1997), we calculated the mean P -value for all species from the indicator species analysis and plotted it as a function of increasing number of clusters. The cluster size with the lowest P -value can be considered the best place to prune the dendrogram in terms of species ability to distinguish among clusters.

Discriminant function analysis and CTA were performed in R version 1.9.1 to predict cluster membership using the relative abundance of the 63 fish species as predictors. Predicted versus observed matrices of the results for both methods provided an overall classification rate, as well as probabilities associated with how well each

Table 2. The 63 fish species present at greater than 5% of the sites in the national database that were used for the national cluster analysis. Species are sorted in descending order of percent occurrence.

Species name	% of sites	Species name	% of sites
Creek chub <i>Semotilus atromaculatus</i>	47.2	Logperch <i>Percina caprodes</i>	11.0
White sucker <i>Catostomus commersonii</i> *	45.4	Brook stickleback <i>Culaea inconstans</i> *	9.8
Green sunfish <i>Lepomis cyanellus</i> *	33.9	Black bullhead <i>Ameiurus melas</i> *	9.6
Bluntnose minnow <i>Pimephales notatus</i> *	31.2	Hornyhead chub <i>Nocomis biguttatus</i>	8.8
Bluegill <i>Lepomis macrochirus</i> *	29.7	Bigmouth shiner <i>Notropis dorsalis</i>	8.6
Eastern blacknose dace <i>Rhinichthys atratulus</i>	29.2	Brown trout <i>Salmo trutta</i> **	8.5
Johnny darter <i>Etheostoma nigrum</i>	27.9	Northern pike <i>Esox lucius</i> *	8.5
Central stoneroller <i>Campostoma anomalum</i>	27.7	Gizzard shad <i>Dorosoma cepedianum</i> *	7.8
Northern hog sucker <i>Hypentelium nigricans</i>	22.8	Yellow perch <i>Perca flavescens</i> *	7.7
Largemouth bass <i>Micropterus salmoides</i> *	22.2	Pumpkinseed <i>Lepomis gibbosus</i> *	7.7
Common carp <i>Cyprinus carpio</i> **	22.1	Silver redhorse <i>Moxostoma anisurum</i>	7.4
Rock bass <i>Ambloplites rupestris</i> *	21.0	Silverjaw minnow <i>Notropis buccatus</i>	7.4
Fathead minnow <i>Pimephales promelas</i> *	20.8	Red shiner <i>Cyprinella lutrensis</i> *	7.4
Smallmouth bass <i>Micropterus dolomieu</i> *	19.8	Stonecat <i>Naturus flavus</i>	7.4
Common shiner <i>Luxilus cornutus</i>	19.2	Redbreast sunfish <i>Lepomis auitus</i> *	6.9
Yellow bullhead <i>Ameiurus natalis</i> *	17.3	Suckermouth minnow <i>Phenacobius mirabilis</i>	6.9
Sand shiner <i>Notropis stramineus</i> *	17.0	Quillback <i>Carpoides cyprinus</i>	6.7
Longnose dace <i>Rhinichthys cataractae</i>	16.7	Walleye <i>Sander vitreus</i> *	6.7
Spotfin shiner <i>Cyprinella spiloptera</i>	16.7	Freshwater drum <i>Aplodinotus grunniens</i>	6.7
Golden redhorse <i>Moxostoma erythrurum</i>	16.6	Cutthroat trout <i>Oncorhynchus clarkii</i>	6.6
Fantail darter <i>Etheostoma flabellare</i>	15.7	Black redhorse <i>Moxostoma duquesnei</i>	6.4
Striped shiner <i>Luxilus chrysocephalus</i>	14.8	Rosyface shiner <i>Notropis rubellus</i>	6.2
Longear sunfish <i>Lepomis megalotis</i> *	14.4	Spotted bass <i>Micropterus punctulatus</i> *	6.1
Rainbow trout <i>Oncorhynchus mykiss</i> *	13.9	Golden shiner <i>Notemigonus crysoleucas</i> *	6.1
Greenside darter <i>Etheostoma blennioides</i>	13.6	Banded darter <i>Etheostoma zonale</i>	6.0
Mottled sculpin <i>Cottus bairdii</i>	12.9	Orangethroat darter <i>Etheostoma spectabile</i>	6.0
Channel catfish <i>Ictalurus punctatus</i> *	12.6	Brassy minnow <i>Hybognathus hankinsoni</i>	5.5
Shorthead redhorse <i>Moxostoma macrolepidotum</i>	12.6	Western mosquitofish <i>Gambusia affinis</i> *	5.4
Rainbow darter <i>Etheostoma caeruleum</i>	11.4	Emerald shiner <i>Notropis atherinoides</i>	5.4
Blackside darter <i>Percina maculata</i>	11.4	Black crappie <i>Pomoxis nigromaculatus</i> *	5.3
Central mudminnow <i>Umbra limi</i>	11.4	Orangespotted sunfish <i>Lepomis humilis</i> *	5.2
Brook trout <i>Salvelinus fontinalis</i> *	11.3		

* = Present as a nonnative species in some portion of the United States in our database.

** = Nonnative species throughout the United States.

cluster group was predicted. We constructed the models using 90% of the data. The remaining 10% were used to validate the models. We repeated the 90/10 splits of the data 1,000 times and report the mean and standard deviation of the percent correctly classified values. Discriminant function analysis finds a rule that best discriminates the cases into different groups by finding a linear combination of the predictor variables that maximizes the one-way analysis of variance (ANOVA) F-statistic (Ramsey and Schafer 2002). We used stepwise DFA to fit the model using an arc sine square root transformation of the relative abundance predictor data. A *P*-value of 0.001 was used

as the criterion for a variable to be included in the model. With a 50 variable model, an effective alpha value of 0.001 is equivalent to a nominal alpha of 0.05. Classification tree analysis is a nonparametric method for data analysis, with models fit by binary recursive partitioning of the data. The data set is split into two groups by choosing the predictor variable that best divides the cases into homogeneous subsets (Clark and Pregibon 1992). The procedure is repeated until all nodes have pure class membership, the nodes have some minimum size, or some other stopping rule is applied (either during the growing process or after, e.g., pruning).

We used mean similarity analysis (Van Sickle 1997) to evaluate fish assemblage similarity against a number of different landscape classification schemes. The method calculates the mean similarity between all the pairs of sites within each group and then calculates an overall mean similarity by averaging (sample size weighted) the individual mean similarities across all the groups in the classification. We used the MRPP procedure in PC-ORD to calculate the individual group and overall classification mean similarities using the fish proportionate abundance data and Bray-Curtis similarity. The landscape classification schemes we tested included three different levels of ecoregions (Omernik 1987), hydrologic units (2 digit and 4 digit USGS hydrologic units), Fenneman (1946) physiography (division, province, and section level), aquatic zoogeography (subzone, region, and subregion levels; Maxwell et al. 1995), and political boundaries (10 EPA regions and 48 states). For this analysis, we only used groups that contained 10 or more sample sites. For example, only 42 of the 48 states had 10 or more sample sites, so our state level analysis is based on 42 states.

We initially ran all of the above analysis on all of the 5,873 sites in the data. We also ran all the analyses on two subsets of the data to investigate the effects of nonnative species and human disturbance. Our first subset excluded alien fish species from the analysis. We plotted national maps of species distribution from our database and compared them to native distribution maps (Lee et al. 1980). Species found outside their native ranges were considered nonnatives and deleted from this data subset. If greater than 25% of the individuals at a site were nonnative, the entire site was deleted from the subset. The natives-only data subset had 5,224 sites and 61 species (brown trout *Salmo trutta* and common carp *Cyprinus carpio* are nonnative everywhere in the United States). We also created a “least-disturbed” data subset by screening the natives only subset and deleting sites that were not in good condition. For the state and NAWQA data, reference sites were identified in the database and

we deleted any sites that weren’t listed as reference as being disturbed. In the EMAP and REMAP data, we screened sites based on site water chemistry and physical habitat criteria as done in the mid-Atlantic EMAP surveys (Waite et al. 2000). Criteria values varied regionally as levels of what can be considered impairment can be quite different in different regions. EMAP and REMAP sites that exceeded criteria were deleted. The final least-disturbed data subset had 1,184 sites. A complete list of the criteria in different regions is given in Appendix 1. This least-disturbed data subset had only native species and sites that were least affected by anthropogenic activities. Analysis of this data subset should represent the most natural fish clusters.

RESULTS

As expected from such a spatially extensive database, there is a wide variety in stream sizes, elevations, and slopes among study sites. Sample watershed areas range from less than 0.1 to just over 200,000 km² (median = 72, interquartile range [IQR] = 19–371 km²). Channel slopes range from 0% to 29% (median = 0.3, IQR = 0.1–1.3%) and elevations range from 6 to 3,780 m (median = 299, IQR = 213–421 m). The most commonly occurring fish species in the database is creek chub *Semotilus atromaculatus* found in 47% of the sites in the national database (Table 2). The next three most commonly occurring species, found at more than 30% of the sites, are white sucker *Catostomus commersonii*, green sunfish *Lepomis cyanellus*, and bluntnose minnow *Pimephales notatus*. Based on our data, of the 63 common fish species in Table 2, 30 of them have been introduced outside their native ranges in some part of the United States. In addition, 31% of the sites in our data contain one or more nonnative individuals.

It is difficult to determine how many clusters should be pruned from the full dendrogram. To help decide, we examined the relationship between the mean fish species *P*-value from the indicator species analysis and increasing number

of clusters for each of the three data subsets (Figure 1). The line for all-data shows the expected trough pattern with a rapid decline in P -value as the number of clusters increase from two to five followed by an increase in P -value for cluster sizes above 11. The least-disturbed subset has a similar but less well-pronounced pattern. The natives-only subset shows an initial increase, then decrease to a trough. The minimum P -value from this analysis would indicate an optimal cluster size of 11 for all data, 12 for the natives-only data, and 9 for the least-disturbed site data. We opted to use a cluster size of 12 groups for all three data subsets.

Dendrograms from the cluster analysis for all three data subsets were pruned to 12 clusters (Figure 2). The resulting dendrogram using all the data shows four major groupings of the clusters. For labeling, we used the letters A–D to indicate these four major groups and the numbers 1–4 to indicate a cluster number within the four major groups (Figure 2). We used indicator species analysis to identify species associated with

each cluster (Table 3). In the dendrograms for the natives-only and least-disturbed subsets, we preserved the cluster label from the all data analysis when the cluster had many of the same indicator species. In cases where a cluster from the all-data analysis appeared to be split in the other subsets, we added a small a/b to the cluster label (e.g., cluster C2a and C2b in the native-only dendrogram is a split of cluster C2). In cases where it looked like two of the all-data clusters were joined together, we combined numbers (e.g., cluster B12 in the least-disturbed subset is a combination of cluster B1 and B2). In comparing dendrograms, it is helpful to note that dendrograms are really nondimensional representations and are better visualized as a mobile hanging from the top link free to pivot in three dimensions rather than the two dimensions seen on paper (McCune and Grace 2002).

Overall, the dendrograms from the all-data and natives-only cluster analyses are very similar. The A and D groups identify identical clusters with many overlapping indicator species. In going from the all- to the native-only subset, Cluster C1 disappears (almost all observations went into cluster B1) and cluster C2 splits into two clusters (Table 3). Overall, 71% of the sites occur in the same cluster in both dendrograms. The major difference between the two is a bigger B1 cluster (852 sites) in the natives-only subset that has sites originally from all of the A, B and C clusters in the all-data dendrogram. The dendrogram from the least-disturbed subset shows the same D group of clusters as the other analyses and the A group expanded from 4 to 6 clusters by splitting clusters A1 and A2. The B and C groups were reduced to two clusters each (Table 3). Overall, 72% of the sites are in the same cluster between the natives-only and least-disturbed dendrograms and 62% of the sites are in the same cluster between the all- and least-disturbed dendrograms. Agreement is even higher by major group (A, B, C, or D); 89% of the sites are in the same major group between natives-only and least-disturbed and 83% for all- versus least-disturbed.

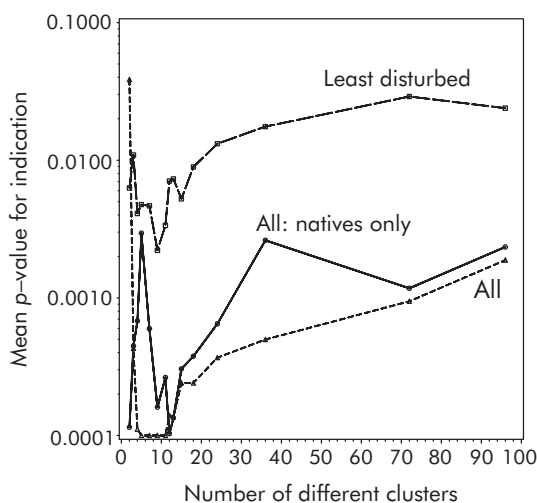


Figure 1. Mean P -value for all species from the indicator species analysis as a function of increasing number of clusters pruned from the dendrograms for the three separate data analyses. Note that with 10,000 Monte Carlo simulations to determine the P -value, a value of 0.0001 is the lowest possible P -value.

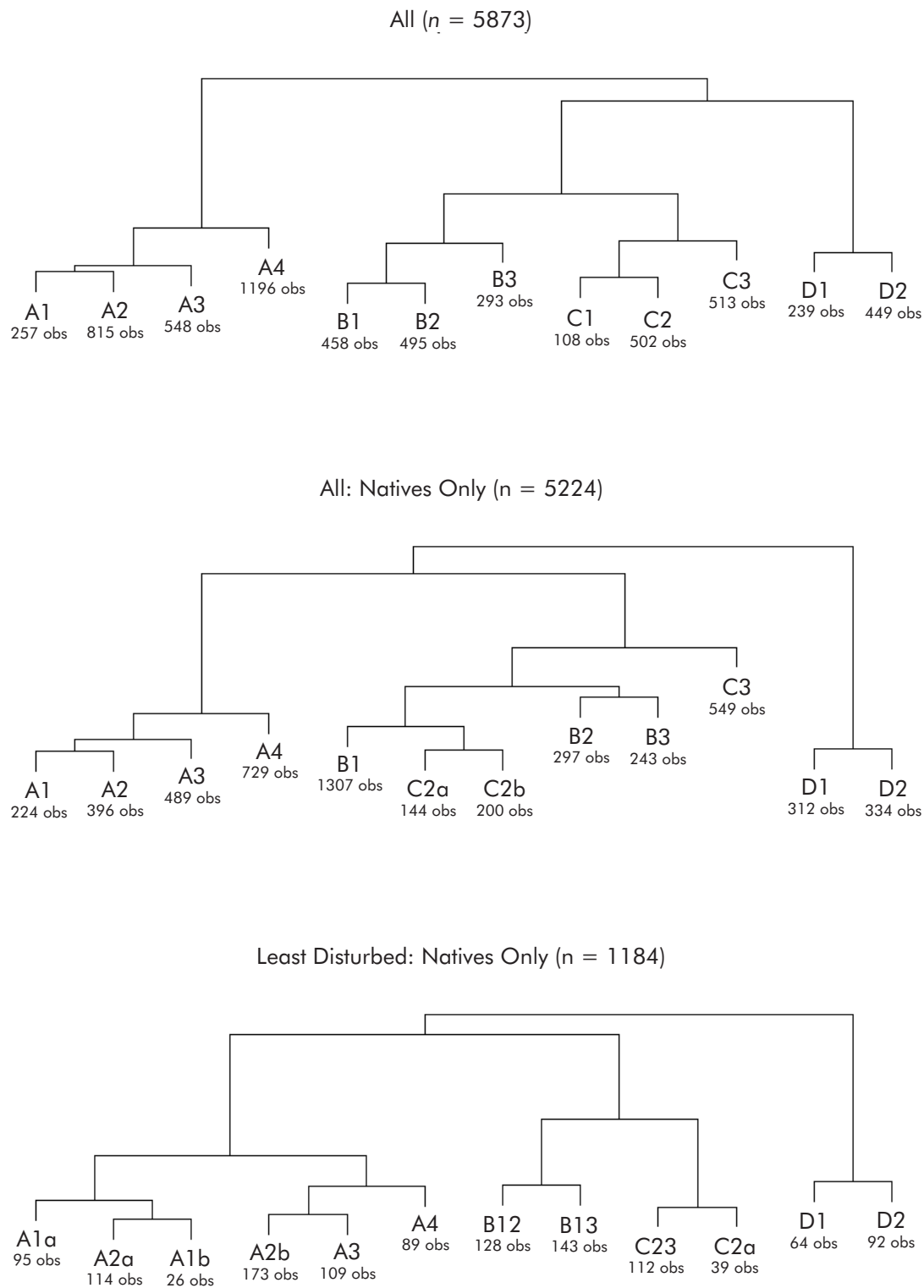


Figure 2. Dendrograms from the three separate cluster analyses of the national fish database. Dendrograms were pruned to show only the top 12 clusters.

Table 3. Fish species indicative of each biological cluster as determined from indicator species analysis. The top three species in each cluster that had percent indication greater than 10% are shown. The value in parentheses below the cluster ID is the mean within cluster similarity.

All		All: natives only		Least disturbed: natives only	
Cluster ID (similarity)	Indicator species (% indication)	Cluster ID (similarity)	Indicator species (% indication)	Cluster ID (similarity)	Indicator species (% indication)
A1 (0.28)	<i>C. lutrensis</i> (66%) <i>G. affinis</i> (47%) <i>I. punctatus</i> (21%)	A1 (0.32)	<i>C. lutrensis</i> (74%) <i>N. stramineus</i> (53%) <i>N. dorsalis</i> (33%)	A1a (0.30) A1b (0.52)	<i>C. lutrensis</i> (49%) <i>N. stramineus</i> (43%) <i>N. dorsalis</i> (39%) <i>G. affinis</i> (97%) <i>C. lutrensis</i> (26%) <i>M. salmoides</i> (19%)
A2 (0.09)	<i>L. macrochirus</i> (26%) <i>M. salmoides</i> (19%) <i>L. cyanellus</i> (16%)	A2 (0.19)	<i>L. macrochirus</i> (53%) <i>L. cyanellus</i> (31%) <i>L. megalotis</i> (28%)	A2a (0.09) A2b (0.28)	<i>L. macrochirus</i> (19%) <i>L. auritus</i> (13%) <i>P. notatus</i> (31%) <i>L. megalotis</i> (28%) <i>L. cyanellus</i> (28%)
A3 (0.20)	<i>C. spiloptera</i> (55%) <i>M. macrolepidotum</i> (50%) <i>C. carpio</i> (45%)	A3 (0.23)	<i>C. spiloptera</i> (61%) <i>M. erythrurum</i> (53%) <i>M. macrolepidotum</i> (50%)	A3 (0.32)	<i>C. spiloptera</i> (64%) <i>M. erythrurum</i> (60%) <i>H. nigricans</i> (44%)
A4 (0.23)	<i>C. anomalum</i> (41%) <i>L. chrysocephalus</i> (40%) <i>E. blennioides</i> (36%)	A4 (0.26)	<i>E. blennioides</i> (41%) <i>L. chrysocephalus</i> (39%) <i>C. anomalum</i> (37%)	A4 (0.49)	<i>C. anomalum</i> (57%) <i>L. chrysocephalus</i> (16%) <i>E. caeruleum</i> (16%)
B1 (0.30)	<i>L. cornutus</i> (42%) <i>C. commersonii</i> (37%) <i>E. nigrum</i> (32%)	B1 (0.16)	<i>C. commersonii</i> (22%) <i>L. cornutus</i> (19%) <i>E. nigrum</i> (17%)	B12 (0.27)	<i>L. cornutus</i> (52%) <i>U. limi</i> (50%) <i>P. flavescens</i> (26%)
B2 (0.22)	<i>P. promelas</i> (53%) <i>C. inconstans</i> (33%) <i>U. limi</i> (30%)	B2 (0.27)	<i>P. promelas</i> (58%) <i>C. inconstans</i> (42%) <i>U. limi</i> (40%)	B13: (0.36)	<i>S. atromaculatus</i> (44%) <i>C. commersonii</i> (22%) <i>E. flabellare</i> (22%)
B3 (0.55)	<i>S. atromaculatus</i> (52%)	B3 (0.56)	<i>S. atromaculatus</i> (52%)		
C1 (0.53)	<i>R. cataractae</i> (75%)				
C2 (0.25)	<i>S. fontinalis</i> (49%) <i>C. bairdii</i> (30%) <i>S. trutta</i> (24%)	C2a (0.41) C2b (0.41)	<i>S. fontinalis</i> (89%) <i>C. bairdii</i> (81%)	C2a (0.57)	<i>S. fontinalis</i> (93%) <i>R. atratulus</i> (12%)
C3 (0.48)	<i>R. atratulus</i> (65%)	C3 (0.49)	<i>R. atratulus</i> (67%) <i>R. cataractae</i> (11%) <i>S. atromaculatus</i> (11%)	C23 (0.37)	<i>R. atratulus</i> (52%) <i>C. bairdii</i> (39%) <i>S. atromaculatus</i> (15%)
D1 (0.50)	<i>O. clarkii</i> (96%)	D1 (0.33)	<i>O. clarkii</i> (81%)	D1 (0.55)	<i>O. clarkii</i> (95%)
D2 (0.53)	<i>O. mykiss</i> (91%)	D2 (0.55)	<i>O. mykiss</i> (97%)	D2 (0.62)	<i>O. mykiss</i> (99%)

Focusing on the all-data analysis, in terms of relative abundance of fish families, group A streams are dominated by cyprinids, catostomids and centrarchids whereas group D streams are dominated by salmonids and cottids (Figure 3). Group B is more similar to group A in terms of family composition and group C is a mixture. Group C2 is dominated by salmonids while the other two C group clusters are dominated by

cyprinids. The indicator fish species and overall cluster species composition of the all-data subset were used to develop qualitative cluster attributes (Table 4).

Group A streams are located throughout the country (Figure 4). They tend to have higher August air temperatures, lower elevation, and lower slope than the other groups. Cluster A3 is a larger river group with 75% of the sites having

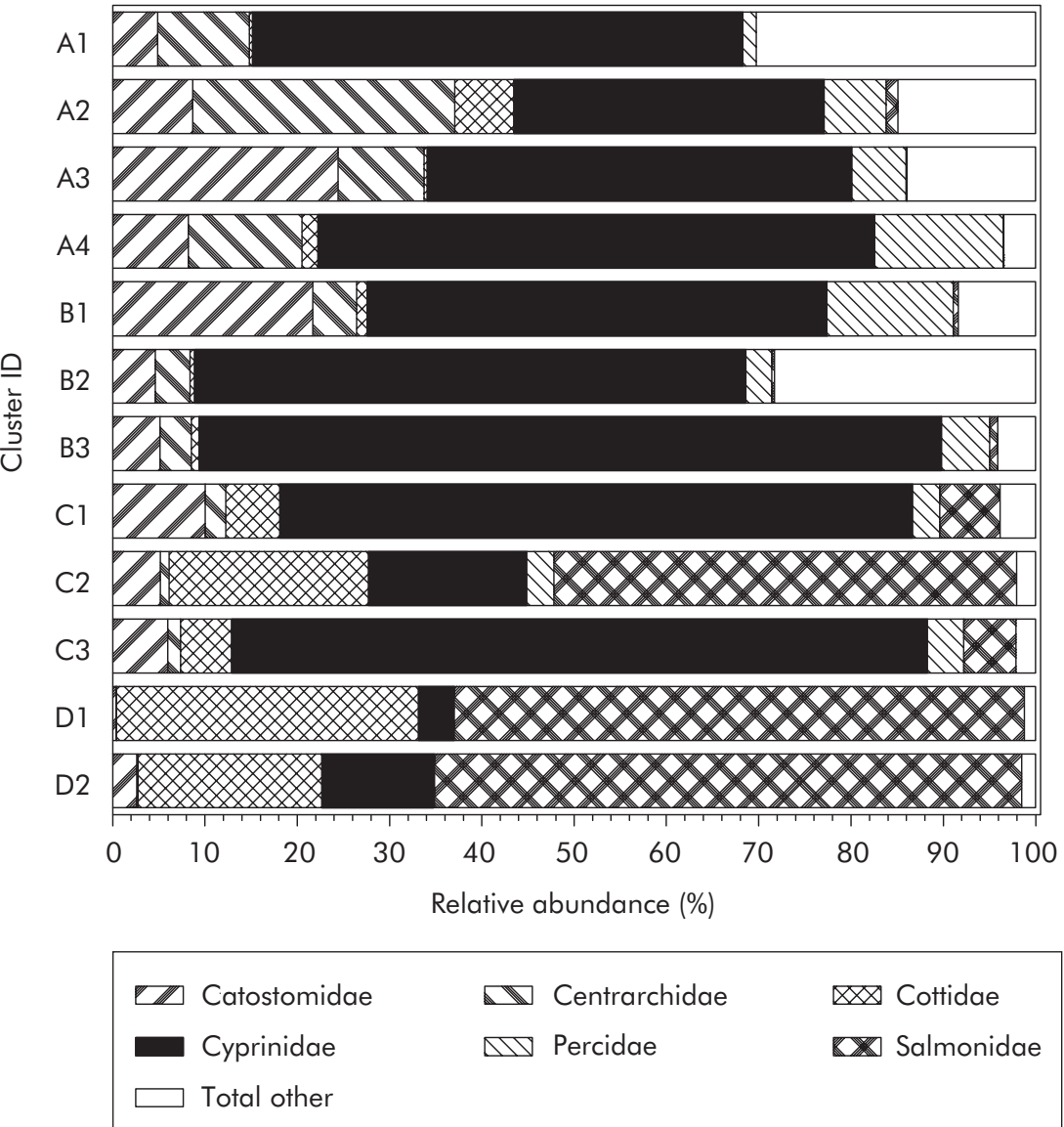


Figure 3. Mean fish assemblage family composition for each of the 12 clusters in the all data analysis.

Table 4. Qualitative stream types derived from indicator fish species.

Cluster	U.S. location	Size	Nutrients	Temperature	Turbidity	Habitat
A1	Central & south	small rivers	high	warm	high–moderate	macrophytes
A2	Nationwide (aliens in West)	small rivers	high	warm	high–moderate	ponded macro- phytes
A3	North & central	boatable rivers	high	warm	high	sand & gravel
A4	Corn Belt	small rivers	high	warm	moderate	high algae
B1	North	small rivers	high	cool–warm	moderate	sand & cobble
B2	Central	small streams	high	warm	moderate	weedy ditches
B3	Corn Belt & eastern mountains	small streams	moderate	cool	moderate	pioneer
C1	North & western mountains	streams & rivers	moderate	cool	moderate	gravel & cobble
C2	East & north central (alien in West)	streams	low	cool–cold	low	gravel & cobble
C3	East & Corn Belt	headwaters	high-moderate	cool	high-moderate	pioneer
D1	West	small streams	low	cold	low	gravel & cobble
D2	Pacific West (alien elsewhere)	rivers & small streams	low	cold	low	gravel & cobble

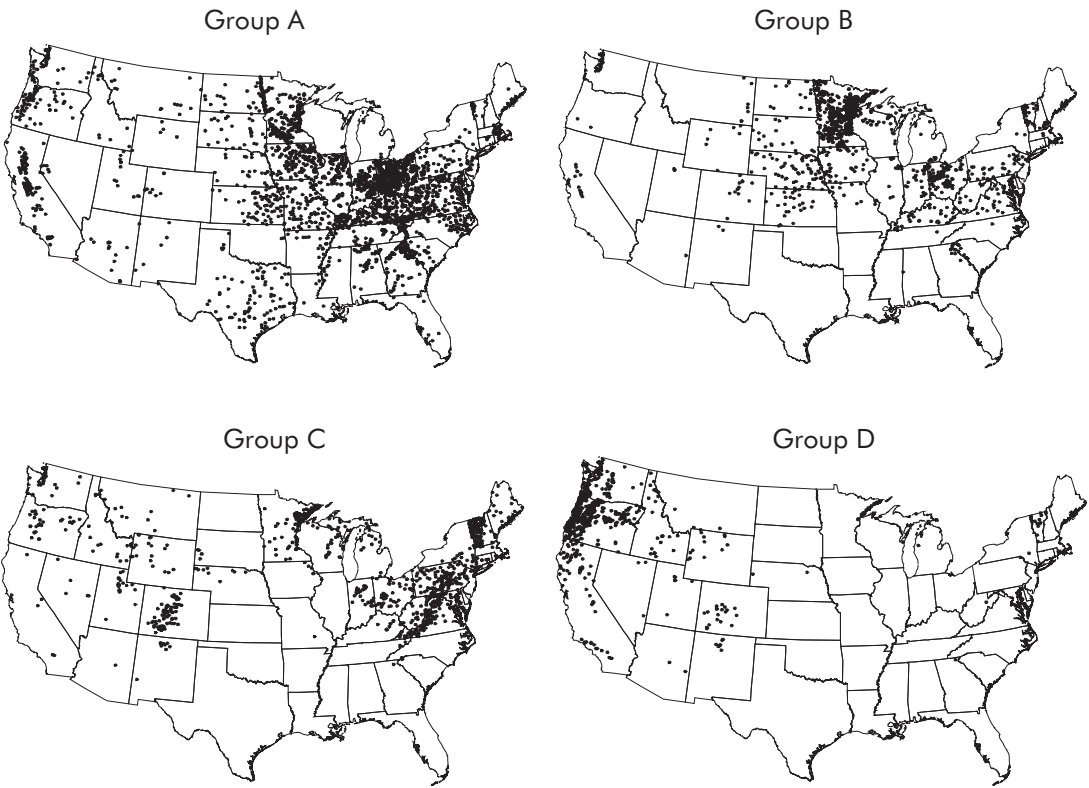


Figure 4. Location of the sample sites in each of the four major fish cluster groups in the conterminous United States for the all data analysis.

watershed areas greater than 1,000 km². Slopes are also the lowest of any cluster. The indicator species for group A3 (spotfin shiner *Cyprinella spiloptera*, shorthead redhorse *Moxostoma macrolepidotum*, and common carp) are all river species (Table 3). Cluster A2 is a catch all cluster with a very low within-cluster similarity (0.09). It consists of many different warm water species that didn't get aggregated into one of the other clusters. Sites from this cluster are found nationwide. It lacks a strong indicator species. Bluegill *Lepomis macrochirus* has the highest indicator species value for this group (26%), but that is low relative to the top indicator species in other groups. In the least-disturbed dendrogram, this cluster was divided into one cluster with very low within cluster similarity indicated by bluegill (A2a) and another with a higher within cluster similarity indicated most strongly by bluntnose minnow (A2b). Cluster A1 sites were concentrated in the central and southern United States and were indicated by red shiner *Cyprinella lutrensis* (66% perfect indication; Table 3). In the least disturbed dendrogram, this cluster is split into two clusters indicated by red shiner (A1a) and western mosquitofish *Gambusia affinis* (A1b). Cluster A1b has the highest mean August air temperature of any cluster. Cluster A4 sites are found in the Midwest Corn Belt and are indicated by central stoneroller *Camptostoma anomalum* (41%) and striped shiner *Luxilus chrysocephalus* (40%).

Group B streams are located in the eastern and north-central portions of the United States (Figure 4). They are generally lower elevation, low gradient streams that are cooler than group A streams but warmer than group C and D streams (Figure 5). Using all-data, Cluster B3 is the most homogeneous cluster of all the clusters (within cluster mean similarity = 0.55). It is strongly indicated only by creek chub (Table 3), and located primarily in small streams in the Corn Belt and eastern United States. Cluster B1 is less homogeneous and found in larger, lower gradient streams. The two best indicator species are common shiner *Luxilus cornutus* and white sucker. Cluster B2 is

the least homogeneous cluster of the three group B clusters and has intermediate slopes, watershed areas, and air temperatures for group B. The primary indicator species for cluster B2 is fathead minnow *Pimephales promelas*. In the least-disturbed dendrogram, group B is represented by two clusters; one indicated strongly by common shiner and central mudminnow *Umbra limi* (B12), and the other by creek chub and white sucker (B13).

Group C streams are a group of dace and trout streams located in the mountainous western, eastern, and north-central United States (Figure 4). Using all-data, they have intermediate slopes and August air temperatures between group B and D streams (Figure 5). Cluster C2 is indicated by brook trout *Salvelinus fontinalis*, brown trout, and mottled sculpin *Cottus bairdii* (Table 3). They are smaller streams at higher elevations in the mountainous West, Appalachian Mountains, and Great Lakes regions. In the natives-only dendrogram, brown trout are eliminated as they are all nonnatives and this cluster is split into a brook trout cluster (C2a) and a mottled sculpin cluster (C2b). Cluster C1 is strongly indicated only by longnose dace *Rhinichthys cataractae* and has the smallest sample size of any of the clusters. C1 sites are found in larger streams than the other two C group clusters in the northern United States. The last C group cluster, C3, is strongly indicated by eastern blacknose dace *Rhinichthys atratulus*. They are smaller streams primarily located in the Appalachian Mountains. In the least-disturbed dendrogram, group C is represented by a brook trout cluster (C2a), and a cluster indicated by longnose dace and mottled sculpin (C23).

Group D streams have the highest elevations, steepest slopes and coolest air temperatures of any of the groups. They are located in the mountainous areas of the western United States (Figures 4 and 5). These are trout streams with high mean within cluster similarity scores (greater than 0.5). Group D1 sites are indicated by cutthroat trout *Oncorhynchus clarkii* with an almost perfect indicator species score of 96% (Table 3). Rainbow trout *O. mykiss* is a very strong indicator species

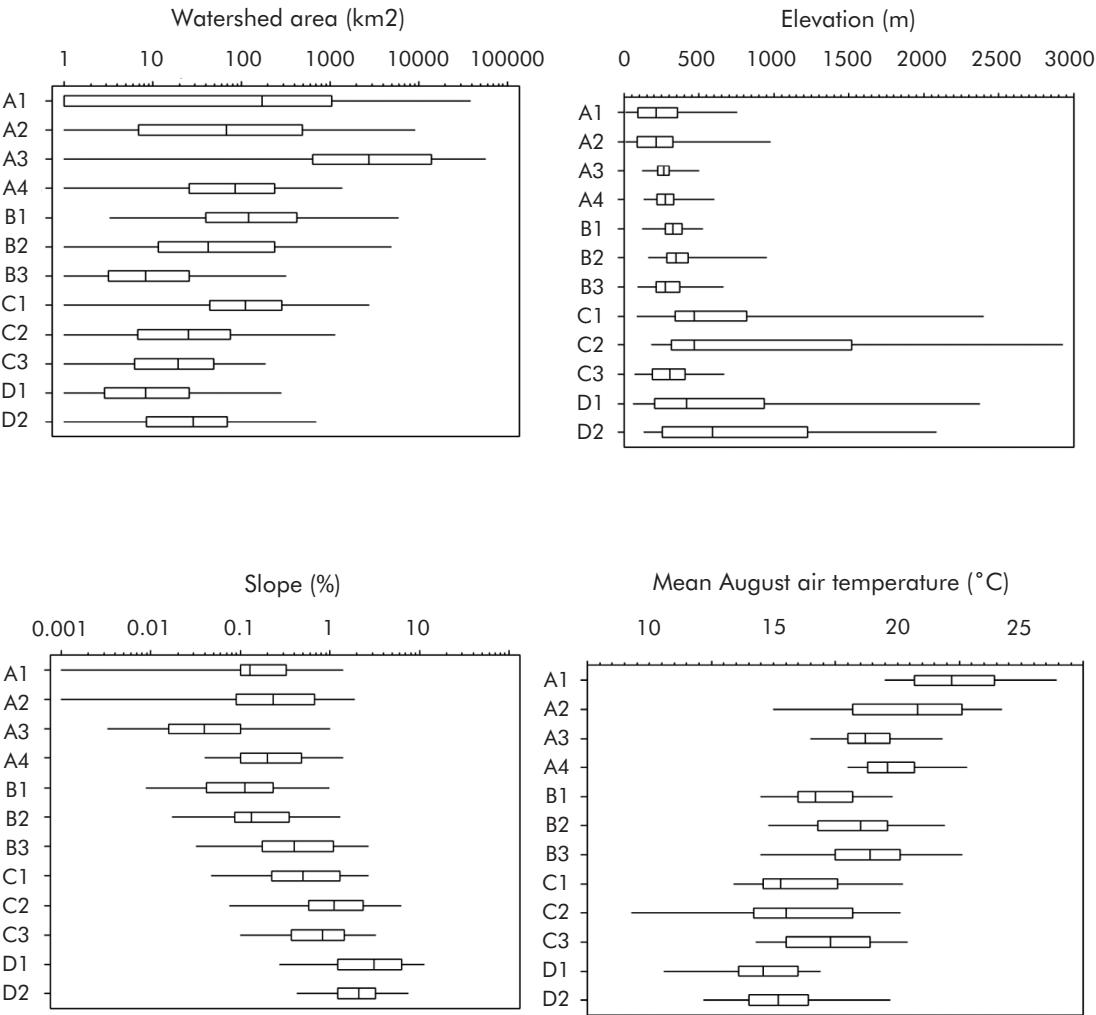


Figure 5. Box and whisker plots showing the distribution of four environmental variables across the sample sites in each of the 12 fish clusters for the all data analysis. Boxes show the interquartile range and median, whiskers show the 5th and 95th percentiles.

for Group D2 sites (91% perfect indication). A few rainbow trout streams (D2) are found in our data in the eastern United States (Vermont and eastern Minnesota), where rainbow trout has been introduced. The two group D clusters are found consistently as a major group with these two clusters indicated by the same species in the all-, natives-only, and least-disturbed dendrograms.

Using all-data, we used the fish proportionate abundance data to predict cluster membership with both DFA and CTA. Of the 63 species

in Table 2, 59 entered the DFA model using the stepwise procedure with a *P*-value less than 0.001. Only orangespotted sunfish *Lepomis humilis*, spotted bass *Micropterus punctulatus*, stonecat *Noturus flavus*, and black crappie *Pomoxis nigromaculatus* do not enter the model. These species are all found at less than 8% of the sites in the database. In the 10% of the data that was used to validate the model, 83.3% (SD = 1.5%) of the sites are correctly classified by the discriminant function model. Similar DFA analyses for

the natives-only and least-disturbed subsets show correct classification rates of 81.8% (SD = 1.7%) and 83.3% (SD = 3.4%), respectively. For all data, the classification rate for individual clusters ranges from 64% correct in cluster D2 to 94% in A2.

For the all-data CTA made with the full data set (no cross validation), a 16 node classification tree is required to predict all 12 of the cluster groups (Figure 6). All species that appear in the tree are also important indicator species from the

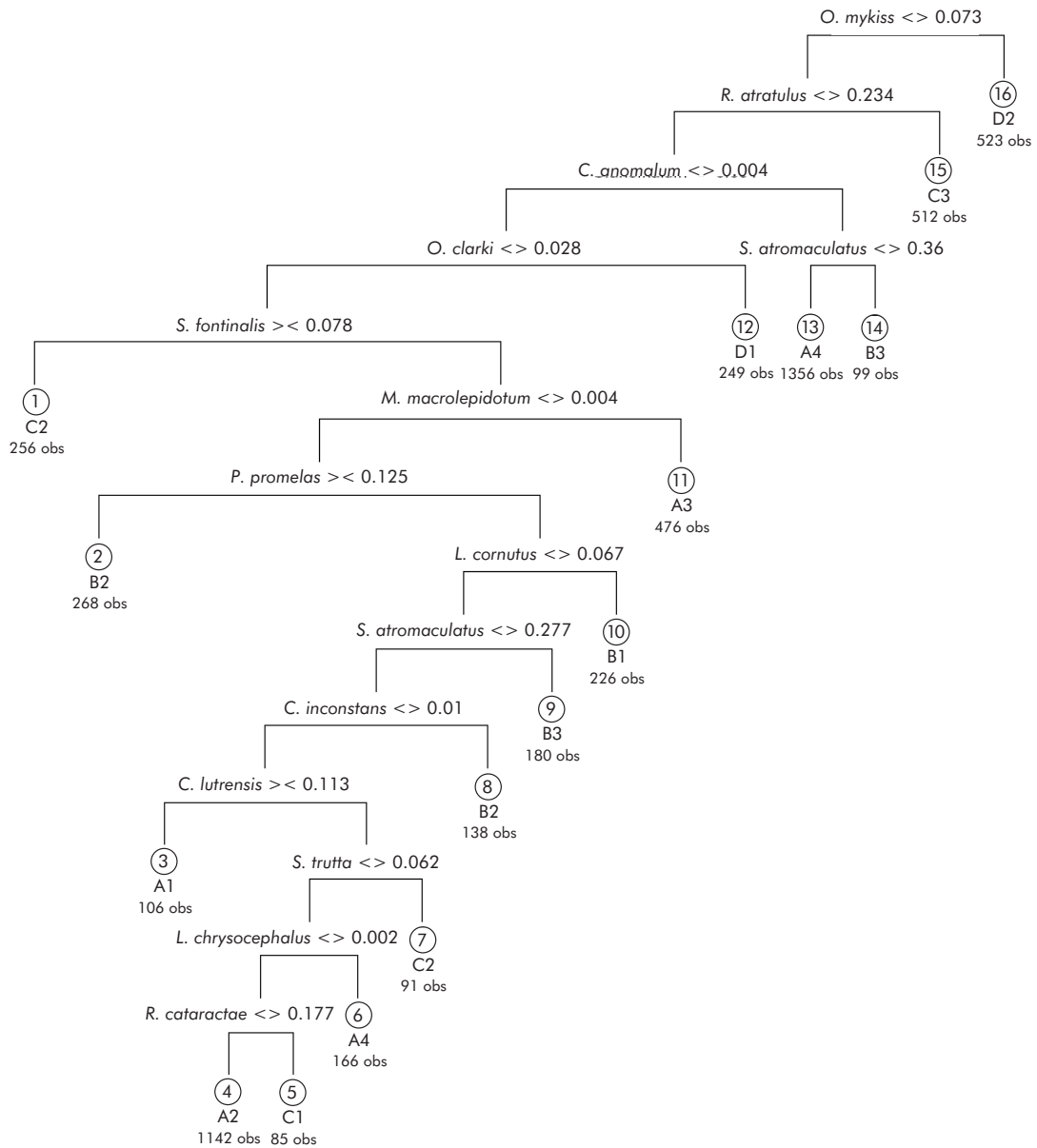


Figure 6. Sixteen node classification tree predicting cluster membership from the fish assemblage proportionate abundance data based on all sites using all data. The circled numbers are the terminal tree nodes. Cluster IDs predicted by that node are given below the circled number along with the number of sites predicted to occur in that node. The tree can be read like a dichotomous key with the equation at each split indicating that the cases with the lower values go left (<=) or right (>=) at the split.

indicator species analysis (Table 3). In most cases, the species with the highest percentage perfect indication for the cluster is the species that appears in the tree as the variable indicating the node for the cluster. The four clusters that appear in two different nodes on the tree are A4, B2, B3, and C2. In these cases, the cluster is either predicted by two different proportionate abundance levels of the same species or two different species that have high percent perfect indication for that cluster. For example, cluster C2 membership is predicted at one node by brook trout relative abundance and at another node by brown trout relative abundance. On cross validation, the CTA correctly classifies 70.6% (SD = 1.9) of the sites. The classification trees for the natives-only and least-disturbed subsets (not shown) are similar to the all-data tree in Figure 6. The cross validation of the CTA for the natives-only subset correctly classifies 68.8% (SD = 2.1) of the sites and for the least-disturbed subset correctly classifies 69.4% (SD = 4.2) of the sites.

The classification strengths of a number of different landscape classification schemes were analyzed by calculating mean within-group similarity in fish assemblages at different types and scales of spatial resolution (Figure 7). For comparison, the results from the same analysis using increasing numbers of biological clusters are also plotted in Figure 7. The biological cluster curve represents a theoretical maximum for within-group similarity because the cluster analysis used to select the clusters attempts to maximize within-group similarity. The mean similarity between all pairs of sites in the database is 0.08 for all data and 0.11 for the least-disturbed subset and these values are plotted as horizontal lines on Figure 7 to represent a theoretical minimum for within-group similarity. Any random grouping of sites would have a similarity near these values. As expected, within-group similarity increases with higher spatial resolution (increasing number of landscape groups). Surprisingly, all the landscape classification schemes, from political to ecoregional to hydrological, have

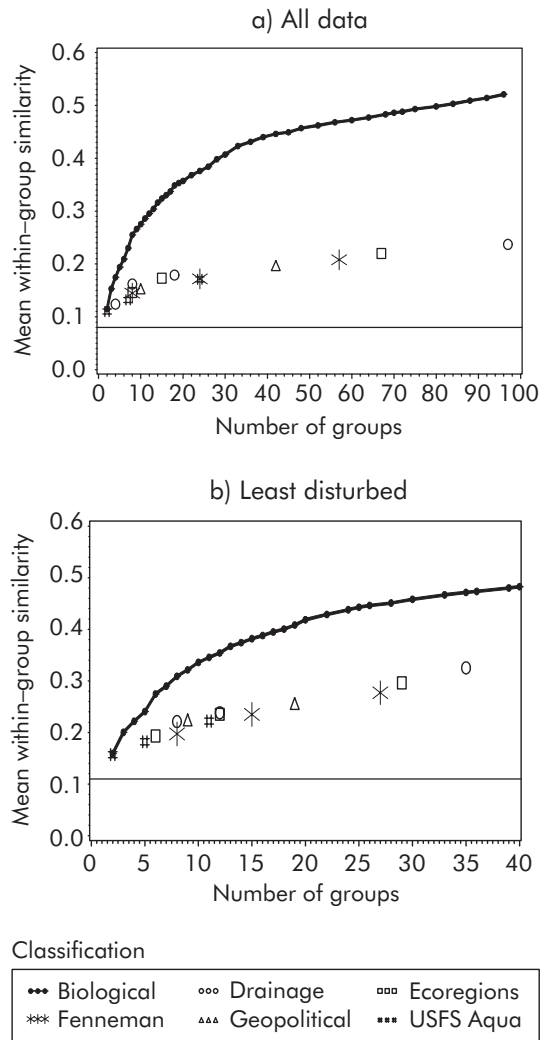


Figure 7. Relationship between mean within-group Bray-Curtis fish assemblage similarity and increasing spatial resolution for different landscape classification schemes for (a) all data and (b) least-disturbed/all native sites. The analogous curves for the biologically derived clusters are also shown. The horizontal line represents the overall mean similarity of all pairs of sites in the database.

similar classification strengths and gains in classification strength with increasing spatial resolution. Using all the data, mean similarities of landscape classification schemes are usually about half that seen for equivalent sized biological clusters. If we regress mean similarity against

log transformed number of groups in Figure 7, the biological clusters have a slope of 0.25 ($r^2 = 0.996$). Thus, mean similarity of the biological clusters increases by 0.25 with each 10-fold increase in number of cluster groups. Using all the data, similar slopes for the various landscape schemes in Figure 7 range from 0.056 to 0.079, indicating that the gain in similarity with increasing resolution is much more rapid with the biologically based cluster groups than the landscape groups. Examination of the standard errors of the slopes indicated that there is no significant difference in slopes among the different landscape schemes.

Human disturbances may influence this analysis by altering assemblage composition in some sites, resulting in reduced within group similarity. To assess the effects of human disturbance, we reran the landscape mean similarity analysis on the least-disturbed subset of sites (Figure 7). The resulting graph for the least-disturbed sites shows an almost identical pattern to that observed using all the data. Overall mean similarity, however, is higher for all landscape schemes using the least disturbed subset. As in the all-data analysis, there is very little difference in the mean similarity-number of groups relationship among the tested landscape classification schemes, and biological clusters have a higher mean similarity for a fixed number of groups. The slope of the log transformed biological cluster line for the least-disturbed sites (0.25) is the same as the slope in the all-data analysis. Slopes for the various landscape schemes in the least-disturbed subset (0.09–0.17), however, are significantly higher than those observed using all the data (0.06–0.08). Even in least-disturbed sites, there remains a large amount of similarity that can be accounted for by biological clusters that is not accounted for by any of the landscape classification schemes.

In addition to mean similarities, we also examined the distribution of the individual within-group similarities for each landscape group (Table 5). The similarity within individual Omernik ecoregions ranges from 0.08 to 0.22 for

level I and 0.08–0.41 for level III in the all data analysis versus ranges of 0.10–0.31 and 0.15–0.75, respectively, for the least disturbed data subset. For reference, at level I, there are nine ecoregions in the conterminous United States (e.g., Northwestern Forested Mountains, Great Plains). At level III, there are 84 ecoregions (e.g., Willamette Valley, Northern Glaciated Plains). Similarity distributions within varying levels of hydrologic groupings are very similar to those observed at the same levels of ecoregions. In terms of hydrologic units, there are 18 “two digit” hydrologic unit codes (HUCs) in the conterminous United States (e.g., South Atlantic-Gulf, Upper Mississippi) and 178 four digit HUCs (e.g., Willamette, West Branch Susquehanna, Upper Arkansas) represented by sites in our database. Political classes based on the 42 states had virtually the same similarity distribution as those observed for the 67 level III ecoregions and 97 four-digit USGS hydrologic units represented in our database. For comparison purposes, we also present similar distributions for the biological clusters in Table 5 at two levels of resolution, coarse (12 clusters) and fine (92 clusters for all-data, 65 for least-disturbed).

DISCUSSION

The primary objective of our study was to define a set of biologically driven fish assemblage clusters from an analysis of a national scale fish assemblage data set independent of any preexisting classification scheme. As such, it is dependent on the parameters of the cluster analysis. The details of how a cluster analysis is conducted can have a large impact on the results. To examine these effects, we performed the national cluster analysis a number of different times using a variety of other linkage methods, different beta coefficients for the flexible beta method, different distance measures (Jaccard, Euclidean), and rare species screens. Nearest and farthest neighbor, median, group average and centroid linkage methods run in PC-ORD yielded extremely chained clusters (most sites in one generic cluster

Table 5. Minimum, maximum, and median values for individual within-group fish assemblage similarity values for various landscape classification schemes for all data and for the subset of least disturbed/all native sites.

Level	Total number of groups	All data within-group similarity				Least disturbed within-group similarity			
		N ^a	Min.	Median	Max.	N ^a	Min.	Median	Max.
Ecoregion									
level I	9	8	0.08	0.13	0.22	6	0.10	0.20	0.31
level II	20	15	0.08	0.16	0.30	12	0.14	0.25	0.35
level III	84	67	0.08	0.22	0.41	29	0.15	0.28	0.75
Hydrologic									
Major basins	8	8	0.10	0.14	0.23	8	0.14	0.21	0.45
HUC-2 digit	18	18	0.09	0.17	0.27	12	0.12	0.21	0.73
HUC-4 digit	178	97	0.08	0.25	0.47	35	0.18	0.31	0.95
Zoogeographic									
Subzone	2	2	0.11	0.12	0.13	2	0.13	0.21	0.29
Region	7	7	0.10	0.12	0.16	5	0.12	0.16	0.31
Subregion	30	24	0.07	0.17	0.29	11	0.16	0.22	0.45
Physiographic									
Division	8	8	0.13	0.15	0.19	8	0.14	0.21	0.39
Province	21	21	0.08	0.17	0.29	15	0.14	0.23	0.53
Section	73	57	0.08	0.21	0.41	27	0.16	0.27	0.65
Political									
EPA region	10	10	0.09	0.17	0.27	9	0.11	0.21	0.68
States	48	42	0.08	0.22	0.40	19	0.10	0.26	0.37
Biological clusters ^b									
12 clusters	12	12	0.09	0.29	0.55	12	0.09	0.37	0.62
92 clusters	92	90	0.06	0.47	0.78	65	0.09	0.49	0.84

^a Number of groups analyzed; only groups with 10 or more sample sites were used in this analysis.

^b Identical analysis for biologically based clusters are presented for comparison.

with the other clusters containing just a few sites) that were clearly inappropriate for our objectives. Not screening the data for rare species and deleting species found at fewer than 1% of the sites yielded a set of fish clusters similar to the screen based on rare species found at fewer than 5% of sites that we presented in this chapter. Ward’s linkage method with both Euclidean and Bray-Curtis distance also yielded a pattern similar to what we saw with the flexible-beta method. Results were not identical but the indicator species identifying the clusters were very similar and most sites were put in the same cluster. The factor that seemed to make the most difference was output generated using Jaccard distance on presence-absence data instead of Bray-Curtis distance with relative abundance data. Results were not drastically different but they were more dif-

ferent than for any of the other tested factors. For this analysis, however, we felt that the relative abundance data were more appropriate. We did not use any partitioning cluster techniques (e.g., k-means) as they require some a priori decision about how many clusters there should be, and we preferred to let those decisions be driven by patterns in the data.

To our knowledge, there are no other existing classification analyses based on site specific survey data at the continent-wide scale of this analysis, although a species richness study on a one degree latitude-longitude grid across the United States (McAllister et al. 1986) comes close. There have been, however, a number of analyses classifying fish assemblages at the state or province scale for western Oklahoma (Stevenson et al. 1974), Quebec (Legendre and Legendre 1984),

Kansas (Hawkes et al. 1986), Ohio (Larsen et al. 1986), Oregon (Hughes et al. 1987), Arkansas (Matthews and Robison 1988), and Wisconsin (Lyons 1996). Almost all of these studies performed either a factor analysis or some type of ordination analysis on the site by species matrix as a first step to reduce the data into a smaller number of component axes. Axis scores were then clustered into fish assemblage groups either by cluster analysis, correlation analysis or visually by expert judgment. Hawkes et al. (1986) took things one step further and plotted the resultant fish clusters on a map of Kansas to derive spatially contiguous fish ecoregions. In Quebec, Legendre and Legendre (1984) conducted their cluster analysis with a spatial constraint to derive 21 contiguous fish subregions. All of these researchers found that a mixture of climatic, landscape, and drainage basin factors played a role in defining fish assemblage patterns. Ecoregions, basins, or physiographic classifications in isolation could not explain all of the fish groupings.

Both river basins and geomorphology have been used to explain patterns in fish assemblages at the continental scale. Cavender (1986) and Briggs (1986) indicated that western and eastern fish faunas likely differed since the late Cretaceous (65 mya), when a sea separated what is now eastern and western North America, which were also joined, respectively with Asia and Europe. Fossil records are better in western than eastern North America, and they offer insights into the origins of the indicator species we found. Catostomids existed in the West since the Paleocene (50 mya) and are believed to have had an Asian origin (Briggs 1986), but only one species remains in Asia. Diverse salmonids existed in Pacific drainages since the Eocene (40 mya). Cyprinids were present in the West since the Oligocene (30 mya), but likely had a Eurasian source. Eocene centrarchids were found in Montana and by the Miocene (20 mya) they were widespread in the West. A diverse number of cottids occurred in Oregon since the late Miocene (5 mya). Climatic cooling, mountain

building, and drainage disruptions began in the late Eocene, resulting in extinctions of subtropical species and expansions of salmonids in the west. Warming in the late Miocene facilitated a round of range extensions, which was followed by another cycle of mountain building, cooling, drainage disruptions, and extinctions of the western warmwater fauna in the late Cenozoic (9 mya). During the Pleistocene glaciations (8 to 10 kya) there were fewer extinctions in the Mississippi Basin because of the lack of major migration barriers north and south across a large area. Along the Atlantic and Gulf of Mexico coasts, sea level lowering allowed presently disconnected rivers to connect and facilitate fish dispersal (Matthews 1998). In the west, however, the continental shelf is narrower and more steeply sloping, and basins were smaller, drier, climatically and tectonically less stable, often endorheic, and with major mountain ranges and barriers that hindered Pleistocene migrations during repeated glacial advances and retreats. Salmonids and cottids, however, were well adapted to such conditions and survived to be the cold water indicator species we now see in the western United States (group D). Similarly, although group C has strong Mississippi Basin connections, it represents a northern cool water fauna on a landscape recently covered by Pleistocene ice.

The factors that appear to control the distribution of fish assemblages will vary by scale and scope of the database. Apparent controlling factors in a small basin will not necessarily be the same when that basin is a small piece of a state or national-scale analysis. In our data, at the national scale, the 12 clusters show a strong gradient in warmwater to coldwater assemblages (Table 4). This is also apparent in the box and whisker plot of mean August air temperature (Figure 5) which we used as a surrogate for stream temperature. The clusters have a highly significant air temperature effect (one way ANOVA; F -value = 442, $p < 0.0001$). Lyons (1996) also found that summer water temperature patterns were the strongest gradient related

to fish assemblages in Wisconsin. Stream size also plays a role in our clustering. One of our clusters (A3) is a large river cluster with large river fish assemblages and watershed areas larger than any of the other clusters. Hawkes et al. (1986), Matthews and Robison (1988), and Pflieger (1971) also noted a large river cluster in their analyses of Kansas, Arkansas, and Missouri fish assemblages, respectively.

In order for a fish classification based on biologically derived clusters to be useful, one must define the clusters so that they can be employed by others. Data from any sampled site has to be assignable to a cluster. We used DFA and CTA as a means of taking observed fish assemblage data at a site to assign cluster membership. Overall, DFA provide lower misclassification rates than CTA. There are properties of CTA, however, that make it more practical for general use. The tree output is easy to understand and interpret and the recursive hierarchical nature can be useful for many types of data. In addition, classification trees require no distributional assumptions, allow for unspecified interactions between variables, are invariant to monotonic transformation of the predictor variables and therefore outliers do not pose a problem. They can handle mixtures of data types and have provisions for missing values (Clark and Pregibon 1992). For spatial data, mapping the tree provides an easy graphical display and aids interpreting results. Discriminant function analysis results are somewhat more difficult to package for easy use and visualization.

At a national scale, the mean similarity analysis shows that existing landscape classification schemes do not capture the major part of the similarity in fish assemblages that can be obtained by biologically derived fish assemblage clusters. This observation is evident in all the data as well as in the least-disturbed data subset. Within group similarity is higher in the least-disturbed sites presumably due to fish assemblage perturbations as a result of anthropogenic activities. However the gain in similarity seen after screening out disturbed sites is similar for both landscape and biological classifications.

Thus, smaller scale, local environmental factors appear to play a major role in structuring fish assemblages that appear to be unaccounted for by ecoregion, hydrologic, political, or physiographic national classifications. Hawkins and Vinson (2000) suspected that weak landscape classifications occur because aquatic organisms vary independently and continuously along environmental gradients and do not cluster into discrete groups. Similar levels of landscape classification strengths to what we observed at the national scale have also been observed in smaller-scale studies. McCormick et al. (2000) analyzed the EMAP fish data in the mid-Atlantic United States and found that eight biologically based fish clusters had a mean Bray-Curtis similarity of 0.46 versus values of 0.25 for nine level III Omernik ecoregions, 0.27 for eight USGS 4-digit hydrologic units, and 0.27 for three stream-order classes. They suggested that the interaction of complex zoogeographic patterns and a long history of human disturbance had masked the fine-scale structure of regional fish assemblages. Oswood et al. (2000) used published distributions of freshwater fishes of Alaska to study faunal similarity among ecoregions and hydrologic units and found that while some individual regions worked well, neither ecoregions nor hydroregions alone were sufficient as frameworks for managing aquatic ecosystems across diverse landscapes. In western Oregon, Van Sickle and Hughes (2000) found that classifications based on fish assemblages alone had twice the classification strength of any landscape classification scheme. They concluded that while ecoregions and catchments have utility for classifying streams, much of their classification strength in western Oregon may be a result of spatial autocorrelation effects, rather than ecological factors that determine class boundaries. Our results strongly support this observation at the national scale in that ecoregions, hydrologic units, physiographic units, and simple political units like states all had the same classification strength. It appears as if the increase in fish assemblage similarity with all these landscape classifications is primarily a result of

drawing lines around spatially smaller units and not some kind of environmental factor. It is hard to imagine something other than spatial autocorrelation being responsible for the gains in fish assemblage similarity associated with state boundaries.

Over the past 20 years, there has been a marked increase in the use of biomonitoring to assess the condition of aquatic systems, and we expect that trend to continue as the cost effectiveness of bioassessment is increasingly demonstrated. As the natural variability in aquatic biota is extremely large, reporting and analyzing the results of biomonitoring requires a classification framework that minimizes this variability so that reference expectations and the effects of anthropogenic disturbance can be more clearly defined. As noted in our study, Houghton (2003) found that biologically derived regions had twice the classification strength of basins or ecoregions for caddisflies in Minnesota. Houghton (2003) stated that failure to consider this disparity may lead to spurious information about human disturbance due to natural faunal differences, and if this pattern were shown in other aquatic organisms that it may be valuable to replace geographic regions with organismal regions. The results from our study show that while variability in fish assemblages is large at the national scale, it is possible to divide the sites into 12 clusters that could be defined by specific indicator species. These clusters work much better than existing landscape classification schemes for defining more homogeneous fish assemblage groups. Cluster results were not strongly influenced by using data subsets that removed non-native fish species and disturbed sites. This suggests that the underlying mechanisms responsible for controlling fish assemblage patterns at the national scale are fairly robust to the effects of nonnative species and anthropogenic disturbances.

Recently, quantitative modeling has been used to predict fish assemblage indices. Oberdorff et al. (2001) employed hydrographic units, climate, and local habitat variables to predict fish assem-

blage indices of lotic systems in France based on 34 common fish species. Pont et al. (2006) expanded this model to Europe. Joy and Death (2002) predicted fish assemblages for 13 species in the Manawatu-Wanganui region of New Zealand from location, stream size, temperature, and habitat type. Our results, based on a subset of common fish species, and linked to a small set of environmental variables offer similar possibilities for the United States—but only where quantitative and consistent landscape and physical and chemical habitat data are collected along with the fish assemblage data. Until that time, ecoregions and basins with half the explanatory power, and perhaps twice the misclassification error, of fish assemblage classes must suffice for predicting expected fish assemblages. Landscape classifications also remain essential for designing sampling programs and communicating information.

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Appendix 1. List of chemical and physical habitat exclusion criteria used to identify least disturbed sites in the different EMAP and REMAP survey databases. Any site that exceeded any one of the listed criteria for that survey were excluded from the least disturbed subset. EMAP physical habitat metrics are defined in Kaufmann et al. (1999).

REMAP surveys [*] Criteria	New England	North. Lake and Forests	New Mexico Chama/ Gila	KS/ MO/ NE Uplands	KS/MO/ NE E. Low- lands	KS/MO/ NE Western Plains	Southern Rockies	CA Central Valley
Total P (ug/L)	>20	>50	>50	>100	>150	>150	–	>150
Total N (ug/L)	>1000	>1000	–	>3000	>4500	>4500	–	–
Nitrate (ueq/L)	–	–	–	>150	–	–	>100	>100
Chloride (ueq/L)	>100	–	–	–	–	–	>100	>300
Sulfate (ueq/L)	>250	–	>1000	–	–	–	>100	>300
pH	–	>9	–	–	–	–	–	–
ANC (ueq/L)	<50	–	–	–	–	–	<50	–
Turbidity (NTU)	–	–	>10	>25	>50	>50	–	–
Dissolved oxygen (mg/L)	–	<5	–	–	–	–	–	–
Mean RBP habitat score	<15	–	–	–	–	–	–	–
Riparian disturbance index	–	>0.33	>2	–	>2	>3	–	–
% canopy density-bank	–	–	–	–	<25	<25	–	<40
Mean wetted width (m)	–	–	–	–	–	–	–	<1
% fine substrate	–	>65	–	–	>90	>90	–	–
% reach channelized	–	>0	–	–	–	–	–	–
% developed riparian zone	–	>1	–	–	–	–	–	–

EMAP surveys [*] Criteria	Western EMAP Mountain ecoregions	Western EMAP Plains ecoregions	Western EMAP Xeric ecoregions	EMAP Mid-Atlantic
Total P (ug/L)	>20	>150	>50	>20
Total N (ug/L)	>750	>4500	>1500	>750
Chloride (ueq/L)	>200	>1000	>1000	>100
Sulfate (ueq/L)	>200	–	–	>400
pH	>9	>9	>9	–
ANC (ueq/L)	–	–	–	< 50
Turbidity (NTU)	–	>50	>25	–
Mean RBP habitat score	–	–	–	<15
Riparian disturbance index	>0.5	>2	>2	–
% canopy density-bank	<50	<25	<25	–
% fine substrate	>15	>90	>90	–

^{*} EMAP Oregon Pilot and REMAP Coast Range, Cascades, and Deschutes surveys used the western EMAP criteria.

Influence of Landscape Features on Summer Water Temperatures in Lower Michigan Streams

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Abstract.—Relatively little information is available regarding the environmental factors influencing water temperature in streams draining low-elevation, glaciated landscapes in the upper Midwest. We used multiple regression analysis and covariance structure analysis (CSA) to identify the landscape features that influence spatial variation in mean July water temperature in 282 lower Michigan stream sites and to determine the spatial scales over which these features operate. Both modeling approaches explained from 63% to 65% of the spatial variation in stream temperatures and suggested that thermal regimes in lower Michigan are influenced by a suite of landscape factors operating at catchment and local scales. However, CSA, because it incorporated both direct and indirect effects, provided a more robust approach for identifying the relative influence of landscape features on stream temperature. Our CSA model suggested that catchment area, latitude, local groundwater inputs, local forest cover, air temperature, percent catchment agriculture, percent catchment lakes and wetlands, and percent catchment coarse-textured geology were important factors structuring spatial variation in stream temperatures. Our analysis also suggested that impacts on stream temperature from land cover/land use changes are of similar or greater magnitude as those resulting from increases in air temperature associated with global climate warming.

INTRODUCTION

Spatial variation in stream temperature has been shown to be a key factor shaping the abundance and regional assemblage characteristics of stream fishes (Huet 1959; Cech et al. 1990; Rahel and Hubert 1991; Lyons 1996; Wang et al. 2003b; Wehrly et al. 2003) and aquatic invertebrates (Vannote and Sweeney 1980; Ward and Stanford

1982; Haro and Wiley 1992; Hawkins et al. 1997). These relationships stem from the pervasive influence of temperature on the physiology of ectotherms. Consequently, water temperature is often viewed as one of the most important habitat variables affecting stream biota. As knowledge of the effects of temperature on aquatic organisms has grown, interest in identifying the environmental variables that influence stream temperature has increased. Interest results from the need not only to understand present species

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distribution patterns, but also to assess the impacts of anthropogenic landscape alteration (e.g., LeBlanc et al. 1997) and to identify potential impacts of changes in global climate patterns (e.g., Keleher and Rahel 1996).

Most empirical studies investigating the factors influencing stream temperature have focused on either a single stream or a limited number of stream sites draining relatively small, homogeneous catchments (Macan 1958; Crisp and Le Cren 1970; Smith and Lavis 1975; Crisp and Howson 1982; Barton et al. 1985; Webb and Walling 1986; Mackey and Berrie 1991; Li et al. 1994; Webb and Nobilis 1994; Mellina et al. 2002). Collectively, these studies have contributed much to our understanding of the importance of groundwater accrual, riparian vegetation, and regional heat budget (approximated by air temperature) on fluvial thermal regimes at specific sites. However, resource managers developing regional conservation and management strategies need to understand how these factors interact to produce the often complex spatial patterns of stream temperature observed across larger geographic extents (e.g., states, ecoregions).

A limited number of studies have quantified the relative importance of variables influencing stream temperature over large spatial scales. Stanfield and Kilgour (2006, this volume) found that summer maximum stream temperature varied as a function of catchment area, slope, surficial geology, and amount of impervious land cover in streams draining into the North shore of Lake Ontario. Keleher and Rahel (1996) found that latitude and elevation explained much of the variation in stream temperature across Wyoming and across eight states in the Rocky Mountain region. Hawkins et al. (1997) identified channel morphology as the dominant factor structuring stream temperature across three ecoregions in California. Vannote and Sweeney (1980) found that latitude explained most of the variation in mean annual water temperature in streams in both the eastern and central United States. However, relatively little information is

available regarding the environmental factors influencing water temperature in streams draining low-elevation, glaciated landscapes in the upper Midwest.

Because stream thermal regimes are strongly influenced by large-scale geological and climatic variables, they are particularly well suited for landscape-scale analyses (Wiley et al. 1997). Our objectives were to (1) identify the landscape features that influence spatial variation in mean July water temperature in lower Michigan streams, and (2) determine the spatial scales over which these features operate.

METHODS

Study Area

In Michigan's lower peninsula, variation in climate and elevation is relatively low. Summer (May–September) average air temperatures range from 15.9°C to 19.3°C and total precipitation varies from 360 to 440 mm (Albert et al. 1986). Elevation ranges from 177 to 418 m and 96% of the peninsula is between 177 and 366 m (Leverett 1912). The landscape, however, is characterized by a diverse mosaic of surficial deposits, including glacial lake plains, moraines, outwash plains, and tills of varying depths and textures (Farrand and Bell 1984). Land use and land cover types also vary considerably across the Lower Peninsula. Within the major catchments, the amount of agriculture ranges from 6% to 92% and the amount of forest varies from 2% to 77% (Gooding 1993).

Stream Temperature Data

Our stream temperature data consisted of hourly temperature measurements (147 sites) and weekly maximum–minimum (135 sites) readings taken during July across lower Michigan from 1989 to 2002 (Figure 1). In most cases only data from a single year were available for each site. When multiple years of data were available for a site, data from a single year were randomly

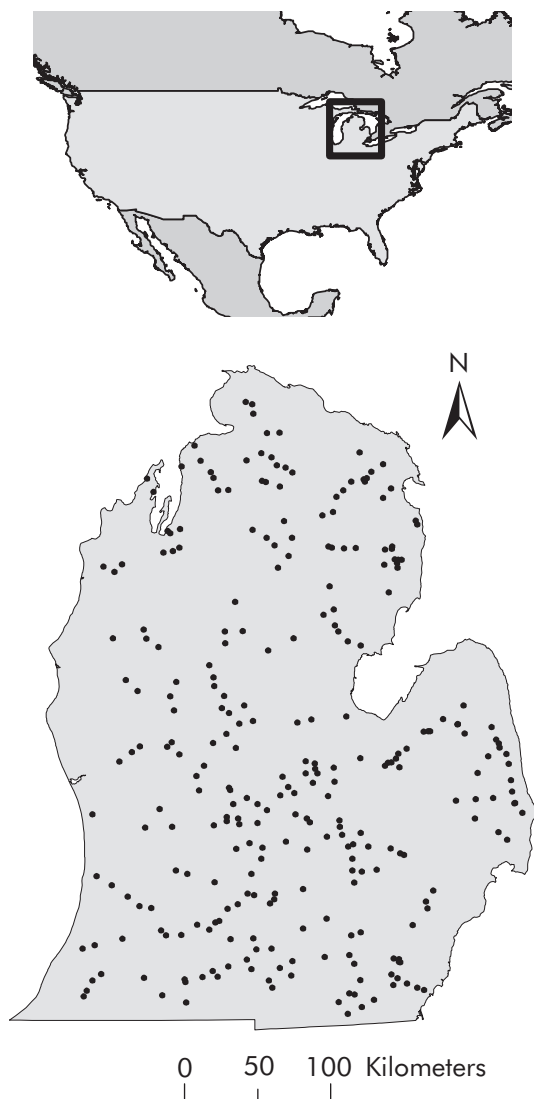


Figure 1. Locations of the 282 study sites.

chosen to calculate July temperature summaries. We used July temperatures for each site because this is when Michigan streams approach the lethal limit for some taxa and also when differences in thermal behavior among sites are most pronounced. For sites with continuous temperature data, mean July temperature was determined by averaging the hourly readings. For sites with maximum–minimum data, mean July temperature was calculated by averaging the mean of the

weekly maximum and minimum readings. Mean July temperatures calculated with maximum–minimum data are typically within 1°C of the true monthly mean temperature calculated from hourly temperature data (K. E. Wehrly, unpublished data). Hereafter, mean July stream temperature will be referred to as stream temperature.

Landscape Characterization

Landscape features associated with each sampling site were characterized with existing databases from the Michigan Rivers Inventory (Seelbach and Wiley 1997). Primary map layers were converted into a 1-ha raster format and all landscape data were maintained and accessed with a geographic information system (GIS).

Land use and land cover data consisted of Michigan Department of Natural Resources (MDNR) Michigan Resource Information System vector format maps developed from 1981 to 1986 aerial photos at a scale of 1:24,000. Surficial geology data were obtained from a 1:500,000 scale digital version of the map created by Farrand and Bell (1984). Groundwater velocity data were obtained from a spatial model (map layer) predicting potential groundwater velocity based on Darcy's Law (Wiley et al. 1997; Baker et al. 2003). Reach gradient was determined from U.S. Geological Survey (USGS) topographic maps at a scale of 1:24,000. Reach gradient was calculated as the difference between successive contour intervals upstream and downstream from a sampling site, divided by the length of stream between the contour intervals. Mean July air temperature was calculated for each site for the year that water temperature was sampled. Air temperature data were based on National Oceanic and Atmospheric Administration (NOAA) climate records from weather stations closest to each stream temperature site.

Catchment boundaries were delineated for each site based upon subcatchment divides mapped by the MDNR from 1:24,000 scale USGS topographic maps. Catchment boundaries were then locally modified for each sample site

with a 3 arc-second digital elevation model (at a scale of 1:250,000). Stream channel networks were based on USGS 1:100,000 digital line graphs.

To evaluate the influence of landscape features at multiple spatial scales, land use, land cover, surficial geology, and groundwater velocity data were summarized for each site's catchment; for a 250-m riparian network buffer (125 m on each side of the stream); and for the region of the catchment intersected by a 4-km radius circular buffer centered over each site. Hereafter, these spatial scales will be referred to as catchment, network, and local.

Data Analysis

Stepwise multiple regression analysis was used to construct models relating landscape features to mean July stream temperature. All variables that were correlated with stream temperature were considered during model development. Because land-use variables were highly correlated with one another, two regression models were created; in the first model, land development variables (e.g., agriculture and urban land use) were excluded from the analysis, and in the second model, land development variables were entered first and additional variables were then added to the model. Multiple regression analyses were performed with SPSS 11.0.

Covariance structure analysis (CSA) was used to further assess the relative influence of individual landscape features on stream temperature. In CSA, the investigator begins by developing a path diagram representing a set of hypothesized linear relationships among all variables in the model. Covariance structure analysis allows variables to have both direct and indirect effects and also enables the investigator to account for noncausal correlations in the model. Covariance structure analysis models are parameterized by fitting the implied system of linear equations to the observed variance–covariance matrix with one of several estimation procedures. The soundness, or fit, of the CSA model is evaluated by testing whether the structure of the sample

covariance matrix is significantly different from the covariance structure imposed in the path diagram (Shipley 2000).

Unlike the multiple regression analysis where all variables were free to enter the model, only those variables believed to be causally related to stream temperature were included in the CSA model (Figure 2). Exogenous (independent) variables in the CSA model were catchment area, site latitude, percent of the catchment in urban land use, and percent of the catchment in lakes and wetlands. Endogenous variables (variables caused by other variables in the model) in the CSA model were local groundwater, local forest cover, mean July air temperature, percent coarse geology in the catchment, percent agriculture in the catchment, and stream temperature. Exogenous variables and error terms for endogenous variables in the model were allowed to freely correlate to account for noncausal correlations.

AMOS 4.0 software (Arbuckle and Wothke 1999) was used to develop the CSA model. Sample data were fit to the hypothesized model with the maximum likelihood function. Squared multiple correlations were used to determine how much of the variability in endogenous variables was explained by the model. Significance of direct, indirect, and total effect coefficients was assessed with 95% biased corrected confidence intervals generated from a Monte Carlo bootstrap procedure and *t*-distribution based on the degrees of freedom for each model. Overall fit of the model was determined with Chi-square (χ^2), root mean square error approximation (RMSEA), Tucker-Lewis index (TLI), and normed fit index (NFI).

All variables except air temperature, latitude, and stream temperature were transformed to meet assumptions of normality. Catchment area and reach gradient were transformed with Log10 *X*, groundwater velocity variables were transformed with Log10 (*X* + 1), and land use and land cover variables were transformed with Log10 (*X* + 0.01). Transformed variables were used in both multiple regression models and the covariance structure analysis models. In all analyses, significance was set at $p < 0.05$.

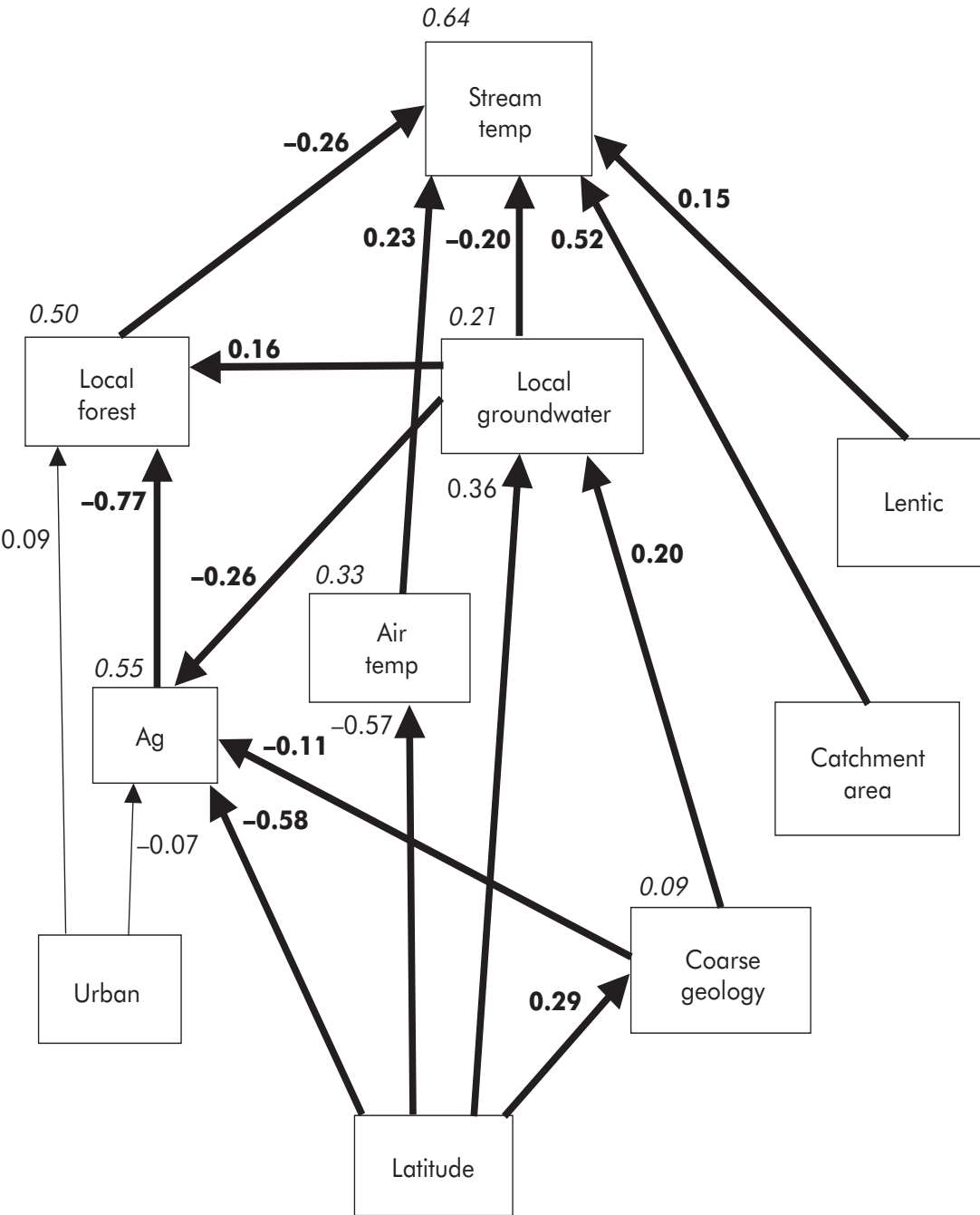


Figure 2. Simplified path diagram showing results of covariance structure analysis (CSA) of the effects of landscape features on stream temperature. In the actual model, variables were free to correlate with each other and with the error terms of endogenous variables. Rectangles are measured variables, arrows indicate direct effects, and adjacent numbers are the magnitude of direct effects. Bold numbers and thick arrows represent significant effects at $p < 0.05$. Italicized numbers are squared multiple correlations and indicate how much variability in endogenous variables was explained by the model. See Table 1 for definition of variables.

Table 1. Description and characteristics of variables included in the final multiple regression and covariance structure models.

Variable	Description (units)	Minimum	Median	Maximum
Stream temp	Mean July stream temperature (°C)	9.2	21.2	26.4
Local groundwater	Mean groundwater velocity in local buffer (m/d)	0.0	67.1	1239.4
Local forest	Proportion of local buffer in forest (%)	0.0	13.7	100.0
Gradient	Gradient of sampling reach (m/km)	0.0	0.8	51.2
Air temp	Mean July air temperature (°C)	17.9	21.6	25.0
Coarse geology	Proportion of catchment in coarse-textured geology (%)	0.0	59.8	100.0
Lentic	Proportion of catchment in lakes and wetlands (%)	0.0	14.6	59.4
Ag	Proportion of catchment in agriculture (%)	0.0	50.4	90.3
Urban	Proportion of urban in catchment (%)	0.0	3.6	77.2
Catchment area	Catchment area (km ²)	1	332	14182
Latitude	Latitude of stream temperature site (°)	41.8		45.6

RESULTS

Characteristics of Study Sites

Individual sites used in this analysis represented a large range in temperature and in catchment characteristics (Table 1). Although sites were distributed across a relatively low range in latitude (3.8°), observed stream temperatures showed considerable variation. Mean July water temperature ranged from 9.2°C to 26.4°C. Mean July air temperature was less variable and ranged from 17.9°C to 25.0°C. Catchment area ranged from 1 to 14,182 km². Coarse-textured geology in the catchment ranged from 0% to 100%. Amount of lakes and wetlands in the catchment ranged from 0% to 59.4%. Urban land use in the catchment ranged from 0% to 77.2%. Agricultural land use in the catchment ranged from 0% to 90.3%.

Multiple Regression Models

Stepwise regression analyses indicated that spatial variation in stream temperatures was influenced by a suite of landscape factors operating at the catchment and local scales. The best fitting model when land development data were excluded from the analysis was

$$\begin{aligned} \text{Stream temperature (°C)} = & 8.239 - (0.810 \cdot \text{lgw}) \\ & - (1.463 \cdot \text{lfor}) - (1.156 \cdot \text{rgra}) + (0.466 \cdot \text{airt}) \\ & + (1.644 \cdot \text{lent}) + (1.728 \cdot \text{catc}) \end{aligned} \quad (1)$$

where lgw = local groundwater velocity, lfor = local forest cover, rgra = reach gradient, airt = local mean July air temperature, lent = percent of catchment in lakes and wetlands, and catc = catchment area.

The best fitting model when land development data were included in the analysis was

$$\begin{aligned} \text{Stream temperature (°C)} = & 12.108 - \\ & (1.020 \cdot \text{lgw}) - (1.351 \cdot \text{rgra}) + (0.422 \cdot \text{airt}) + \\ & (1.604 \cdot \text{lent}) + (1.493 \cdot \text{catc}) + (0.887 \cdot \text{ag}) \end{aligned} \quad (2)$$

where lgw = local groundwater velocity, rgra = reach gradient, airt = local mean July air temperature, lent = percent of catchment in lakes and wetlands, catc = catchment area, and ag = percent of catchment in agriculture. Both model 1 and model 2 were highly significant ($p < 0.001$) and explained 65% and 63% (adjusted R^2) of the regional variation in stream temperature, respectively. Comparisons of observed versus predicted temperatures showed that both models tended to overestimate temperatures at cold sites and underestimate temperatures at warm sites. Standard deviation between predicted and observed temperatures was 1.9°C in both models.

Standard partial regression coefficients for the regression models (Table 2) provide some measure of the relative influence of the predictors on the dependent variable, assuming interactions between independent variables are minimal. In

Table 2. Relative importance of landscape variables on mean July stream temperature as determined by their standard partial regression coefficients from multiple regression models. Land development variables were excluded from Model 1 and included in Model 2. See Table 1 for definition of variables.

Variable	Regression coefficient	
	Model 1	Model 2
Local groundwater	-0.18	-0.23
Local forest	-0.22	
Gradient	-0.18	-0.21
Air temp	0.21	0.20
Lentic	0.12	0.12
Catchment area	0.42	0.36
Ag		0.14

model 1, catchment area had the greatest influence on stream temperature followed by local forest cover, mean July air temperature, local groundwater velocity, reach gradient, and percent lakes and wetlands in the catchment. Although model 2 contained most of the same variables, the agriculture variable led to the exclusion of percent forest in the local buffer because of strong collinearity. In model 2, catchment area had the greatest influence on stream temperature followed by local groundwater velocity, reach gradient, mean July air temperature, percent agriculture in the catchment, and percent lakes and wetlands in the catchment. These differences in the two models as well as the covariances observed among predictors (Table 3) indicated that a meaning-

ful evaluation of the relative effects of these variables on stream temperature would require an explicit causal hypothesis and analysis of the covariance structure.

Covariance Structure Analysis Model

Our causal hypothesis for the relationships among landscape variables and stream temperature is represented in the path diagram in Figure 2. Standard fit statistics (Table 4) indicated a good fit between the CSA model and the covariance matrix from the observed data (Table 3). The model explained 21% of the variance in local groundwater velocity, 50% of the variance in the amount of local forest cover, 33% of the variance in mean July air temperature, 9% of the variance in the amount of coarse geology in the catchment, 55% of the variance in the amount of agriculture in the catchment, and 64% of the variance in stream temperature (Figure 2). Multivariate kurtosis in the data was 12.27 suggesting only moderate departures from multivariate normality. Sample size ($n = 282$), however, was large enough to result in reasonably robust estimates of model fit and parameter values (Shipley 2000).

Standardized effects from the model (Table 5; Figure 2) showed a significant north-south gradient in climate, land use, geology, groundwater velocity, and land cover. Latitude had strong, negative direct effects on both air temperature (-0.57) and the amount of catchment

Table 3. Variance/covariance sample matrix for computing covariance structure analysis (CSA). See Table 1 for definition of variables.

	Stream temp	Local groundwater	Local forest	Air temp	Coarse geology	Lentic	Ag	Urban	Catchment area	Latitude
Stream temp	9.996									
Local groundwater	-0.898	0.501								
Local forest	-0.741	0.197	0.230							
Air temp	1.649	-0.268	-0.204	2.051						
Coarse geology	-0.281	0.124	0.103	-0.104	0.352					
Lentic	0.176	0.027	0.002	-0.023	-0.007	0.057				
Ag	0.834	-0.178	-0.160	0.226	-0.099	0.005	0.240			
Urban	0.345	-0.029	-0.051	0.110	-0.013	0.007	0.044	0.104		
Catchment area	1.446	-0.018	-0.036	0.033	-0.019	0.048	0.108	0.068	0.578	
Latitude	-1.669	0.305	0.316	-0.847	0.180	-0.001	-0.351	-0.172	-0.209	1.075

Table 4. Model fit indices, decision rules, and test statistics used to determine how well the covariance structure analysis (CSA) model developed in this study fit the observed data set.

Model fit index	Rule for good fit	Test statistic
Chi-square (χ^2)	$P > 0.05$	$\chi^2 = 27.05, df = 19, p = 0.10$
Root mean square error approximation (RMSEA)	$RMSEA \leq 0.05$	0.04
Tucker-Lewis index (TLI)	$TLI > 0.9$	0.98
Normed fit index (NFI)	$NFI > 0.9$	0.98

Table 5. Standardized direct, indirect, and total effects for the fitted covariance structure analysis (CSA) model. Direct effects are interpreted like standardized regression coefficients (effect of one variable on another with all other variables held constant) and indirect effects are the effects between two variables mediated by intervening variables. Total effects are the sum of direct and indirect effects. Bold indicates significance at $p < 0.05$. See Table 1 for definition of variables.

	Effects		
	Direct	Indirect	Total
Local groundwater			
Coarse geology	0.20		0.20
Latitude	0.36	0.06	0.42
Local forest			
Local groundwater	0.16	0.20	0.36
Coarse geology		0.16	0.16
Ag	-0.77		-0.77
Urban	-0.09	0.05	-0.04
Latitude		0.62	0.62
Air temperature			
Latitude	-0.57		-0.57
Coarse geology			
Latitude	0.29		0.29
Agriculture			
Local groundwater	-0.26		-0.26
Coarse geology	-0.11	-0.05	-0.16
Urban	-0.07		-0.07
Latitude	-0.58	-0.14	-0.72
Stream temperature			
Local groundwater	-0.20	-0.09	-0.29
Local forest	-0.26		-0.26
Air temperature	0.23		0.23
Coarse geology		-0.08	-0.08
Lentic	0.15		0.15
Ag		0.20	0.20
Urban		0.01	0.01
Catchment area	0.52		0.52
Latitude		-0.37	-0.37

agriculture (−0.58), and positive direct effects on catchment coarse geology (0.29) and local groundwater velocity (0.36) (Figure 2). Latitude had a strong positive, but indirect effect, on the amount of forest in the local buffer (0.62) mediated by its strong negative effect on the amount of agriculture in the catchment (−0.58) (Table 5; Figure 2).

Stream temperature was clearly influenced by a suite of landscape features (Table 5). Catchment area had a positive direct effect on stream temperature, and had the strongest total effect of all variables in the model (0.52 in both cases). Latitude had a strong, negative indirect effect (−0.37) mediated through its effects on air temperature, land use, geology, groundwater velocity, and land cover. The amount of agriculture in the catchment had a strong, positive indirect effect on stream temperature (0.20) because it negatively affected forest cover in the local buffer. Coarse geology had a negative indirect effect (−0.08) mediated through its effects on percent agriculture in the catchment and local groundwater velocity. Mean July air temperature (0.23) and percent lakes and wetlands in the catchment (0.15) had positive direct effects; while local forest cover (−0.26) and local groundwater velocity (−0.20) had negative direct effects on stream temperatures. However, the analysis suggested that local groundwater significantly affects local forest cover and the amount of agriculture in the catchment, so that the total effects of groundwater and riparian forest cover were not statistically different in magnitude (−0.29 and −0.26, respectively). The rank of total (direct + indirect) effects from highest to lowest for variables

affecting observed temperatures in Michigan streams was (1) catchment area, (2) latitude, (3) local groundwater velocity, local forest cover, mean July air temperature and percent agriculture in the catchment, (7) percent of lakes and wetlands in the catchment, and (8) percent coarse geology in the catchment. Significant models could not be developed when we included direct and indirect causal paths between percent urban land use in the catchment and stream temperature. Likewise, a significant model could not be developed when we allowed a direct causal link of percent agriculture in the catchment to stream temperature.

DISCUSSION

The multiple regression models developed in this study could be reasonably used to estimate site-specific stream temperatures throughout the lower Peninsula of Michigan. However, results of the covariance structure analysis implies that some conclusions about the effects of predictor variables on stream temperature, based on the regression coefficient values, are likely to be misleading. This limitation results from (1) an inability of purely statistical procedures to distinguish between causal and noncausal (spurious) correlations, (2) an inability to distinguish between direct and indirect effects, and (3) the highly collinear and autocorrelated nature of landscape data (Johnson and Gage 1997). For example, reach gradient was a strong predictor in our regression models but has no demonstrated mechanistic linkage to stream temperature. It is, in fact, correlated with catchment area, local groundwater velocity, and with coarse geological deposits. We believe that the correlation between local channel gradient and stream temperature is spurious and results from covariation with multiple shared antecedent variables (see Shipley 2000). Correlative approaches (e.g., regression analysis) are often used to explain ecological patterns. Such nonmechanistic approaches, while often meeting immediate conservation and management needs (e.g., eco-

logical assessment and inventory), may not capture important ecological realities of the system in question (Levin 1992; Poff 1997), and provide a weak basis for prescriptive management. Covariance structure analysis, because it incorporates a mechanistic set of causal constraints, provides a more robust approach for identifying the causal relationships between landscape variables and stream temperature.

An emerging theme in stream ecology is that the landscape influences both physical and biological characteristics of streams through multiple pathways operating at different spatial scales (Allan and Johnson 1997). Our results support this theme and suggest that a suite of catchment and local-scale landscape features directly and indirectly influence regional water temperature patterns in lower Michigan streams.

Catchment area had the strongest influence in our models implying that longitudinal position in the catchment is the most important feature governing stream temperatures in Michigan. This result is consistent with a growing body of literature suggesting that relative position in the landscape is an overriding factor structuring physical and biological characteristics in both streams (Vannote et al. 1980; Wiley et al. 1997; Stanfield and Kilgour 2006) and lakes (Kratz et al. 1997; Soranno et al. 1999). In the case of stream temperature, longitudinal position controls the amount of time that a unit volume of water has spent in the channel network, which, in turn, determines the amount of exposure to heat exchange with the atmosphere (Smith and Lavis 1975; Theurer et al. 1984; Bartholow 1989). As a result, cool water tends to accumulate heat as it flows downstream and gradually approaches what is known as the equilibrium temperature; the point where net heat exchange with the atmosphere is zero (Theurer et al. 1984; Bartholow 1989). Therefore, the average temperature of small headwater sites, originating from cool or cold water sources, tends to be cooler than larger downstream reaches on the same stream. Exceptions include some lake and wetland drainage streams where the source system acts as a heat

storage reservoir and small streams exit at relatively warm temperatures. In Michigan and in other regions, warm headwater streams often cool as they flow downstream because of both groundwater accrual (Hendricks and White 1995; Mellina et al. 2002; Zorn et al. 2002) and thermal equilibration with the atmosphere.

Latitude helps set the regional heat balance (approximated by air temperature) and can be an important predictor of stream temperature when sites are viewed across large regions (e.g., multiple states or ecoregions) (this study; Vannote and Sweeney 1980; Eaton and Scheller 1996; Keleher and Rahel 1996). However, our CSA model suggests that the north-south gradient in stream temperatures observed in Michigan is largely due to latitudinal gradients in land use and subsequent riparian forest cover, and to a lesser extent on regional variation in mean summer air temperature, groundwater dynamics, or geology. In Michigan, agriculture is largely confined to the southern half of the lower Peninsula. This pattern results from north-south gradients in geology (fine- and medium-textured till plains versus coarse-textured outwash sand and gravel) and length of the growing season (long versus short). The positive effect of latitude on groundwater reflects the combined effects of north-south gradients in geology, groundwater availability (due to higher rates of precipitation and lower rates of evapotranspiration in the northern portion of the state; M. J. Wiley, unpublished data) and in groundwater temperature (range = 8.2°C to 11.3°C; Leverett 1906).

Riparian forest cover has been reported by many authors to be the major factor controlling stream temperature (Barton et al. 1985; LeBlanc et al. 1997; Li et al. 1994; Abell and Allan 2002). Riparian vegetation intercepts direct solar radiation that would otherwise be absorbed at the stream surface and is, therefore, important in moderating maximum temperature. In our models, riparian forest cover was important, but was not the dominant factor controlling stream temperature. This difference may be attributed, in part, to the fact that most studies investigat-

ing the influence of riparian forest have been conducted in relatively small homogeneous catchments where the variance of other factors may be minimal. This difference might also result from indirect effects and spurious correlations not typically accounted for in the models developed in other studies. Extent of riparian forest cover covaries with longitudinal position (i.e., catchment area; see Vannote et al. 1980 and Wiley et al. 1990 for examples of both negative and positive correlations) and thus its correlation with stream temperature can be inflated in a purely statistical analysis. In our CSA model, agricultural land use in the catchment had a strong, negative effect on the amount of riparian forest cover. Indeed, it was the only significant pathway through which agriculture affected stream temperature. This finding provides more evidence for the need to protect and restore riparian corridors.

Groundwater accrual within several kilometers upstream from a site had a strong negative effect in our model. Groundwater can directly affect stream temperature through advective processes that buffer the water mass against sources of heat input (Evans et al. 1998). Consequently, streams receiving a relatively large proportion of their discharge from groundwater tend to be cold. In low-elevation temperate streams, groundwater inputs are critical to the maintenance of appropriate thermal habitat for cold adapted species (Bowlby and Roff 1986; Meisner 1990; Wiley et al. 1997; Zorn et al. 2002). Groundwater can also indirectly influence stream temperature through effects on local forest cover. Our model suggested that local groundwater inputs can affect local forest cover through two pathways. First, local groundwater can directly influence the amount of forest cover in the local buffer. This finding is consistent with our observations in Michigan streams and is supported by a number of studies showing strong linkages between riparian hydrology and the structure (Pautou and Decamps 1985; Baker and Barnes 1998) and function of riparian forests (Baker et al. 2001; Baker and Wiley 2004). Second, local

groundwater can indirectly influence the amount of forest cover in the local buffer through its effect on percent agriculture adjacent to the stream. This result suggests that portions of the landscape receiving relatively larger inputs of groundwater tend to be less suitable for farming and subsequently support more forest cover.

Percent of the catchment in lakes and wetlands had a positive effect on mean summer temperature in our causal model. Lakes and wetlands can increase stream temperature in two ways. First, they can act as competing sinks for groundwater in the catchment by intercepting and storing a proportion of the groundwater before it reaches the stream network. Second, thermal stratification and differential surface heating across relatively large areas can lead to an accumulation of heat energy. Consequently, lakes and wetlands with outlets to a stream can elevate stream temperature by providing a direct source of heat energy (Hendricks and White 1995; Mellina et al. 2002).

Urban land use has been reported to increase stream temperature through reductions in base flows, changes in channel morphology, and reductions in riparian forest cover (LeBlanc et al. 1997). Although the lower Peninsula of Michigan contains a number of large urban areas, we were unable to detect any significant effects of urban land use in our models. The lack of effect may have resulted from inadequate sampling of stream sites having a high percentage of urban land use in the catchment. Inclusion of more sampling sites with urban land use might result in the detection of significant effects similar to those observed in other regions (LeBlanc et al. 1997; Wang et al. 2003a).

As hypothesized in our CSA model, the causal relationships among landscape features and stream temperature were hierarchical and complex. This complexity makes it difficult to interpret broad generalizations about the thermal responses of streams to changes in driving factors. One practical application of our model would be to estimate the response of stream temperatures to human perturbations and to differ-

ent mitigation scenarios. For example, using the unstandardized effects of mean July air temperature and local forest cover on stream temperature from the CSA model, we estimated the relative sensitivity of water temperature to changes in these factors. Based solely on the effects of air temperature, a 5°C increase in mean July air temperature is predicted to result in a 2.3°C increase in water temperature (Figure 3), less than the 4.6°C water temperature increase predicted by Eaton and Scheller (1996) for streams in lower Michigan following a doubling

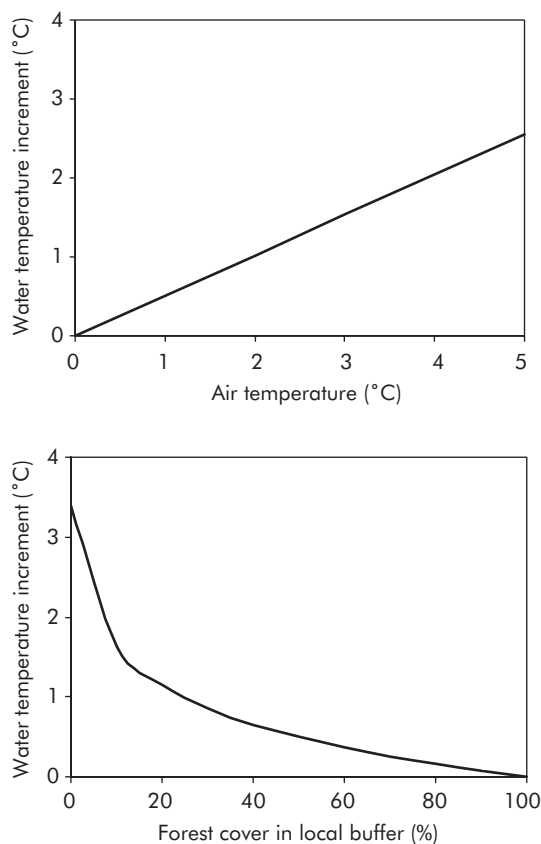


Figure 3. The effects of air temperature (upper panel) and percent forest cover in the local buffer (lower panel) on stream temperature. Increment change in stream temperature was calculated from the unstandardized total effects from the covariance structure analysis (CSA) model and does not account for the influence of other variables in the CSA model.

of atmospheric CO₂ concentration. Based solely on the effects of forest cover, the maximum amount of change in water temperature was 3.4°C and occurred when all forest cover was eliminated within the local buffer (Figure 3). This result suggests that impacts from changes in land cover or land use may be similar or greater than those resulting from increases in air temperature associated with global climate change. In addition, our analysis suggests that most of the potential temperature reduction associated with forest cover can be achieved by protecting at least 30% of the forest cover within the local buffer. Increasing forest cover beyond 30–50% results in relatively small increases in thermal buffering capacity in lower Michigan streams (Figure 3). Summing the offsetting effects of air temperature and local forest cover suggests that the effect of a 5°C increase in July air temperature on stream temperature might be ameliorated by restoring the amount of upstream forest cover. Although this example is relatively simplistic, it does illustrate the utility of this type of model. We believe it is possible to generate more realistic predictions for how stream temperatures and their associated fish assemblages will respond to human thermal perturbations and rehabilitation scenarios. A more complex CSA analysis that included all relevant climatic and heat-balance variables could be coupled to a biological response model (e.g., Wehrly et al. 2003) to provide more realistic evaluations of the likely effects of climate change on fish assemblages in Michigan's lower peninsula.

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Importance of Land Use, Streamflow, and Water Quality on Stream Toxicity in the Lake Tahoe and Truckee River Watersheds

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Abstract.—Rapid urbanization in the southwest United States has increased concern about water quality of streams and its impact on aquatic biota. One way to estimate potential toxicity impacts is to deploy passive samplers that accumulate many organic contaminants associated with anthropogenic landscapes. Semipermeable membrane devices (SPMDs) use a lipid to mimic bioaccumulation of hydrophobic organic contaminants (HOCs), including polycyclic aromatic hydrocarbons (PAHs), pesticides, and industrial compounds. We investigated effects of land use and streamflow on the presence of HOCs and potential toxicity in the Truckee River and Lake Tahoe watersheds of Nevada and California. We used SPMDs during August/September 2002 and 2003 base flows and during March 2003 high flows. We employed two complementary toxicity tests to assess potential toxicity to aquatic organisms. The fluoroscan (pyrene index) is designed to assess PAH concentrations. The CYP1A test measures the toxicity of aryl hydrocarbon receptor type compounds, which include PAHs, polychlorinated biphenyls (PCBs), and dioxins. A relatively strong correlation ($r = 0.79$) between the pyrene index and CYP1A in our data indicated that PAHs were the dominant group of organic contaminants sequestered by our SPMDs. Due to its low-density urbanization, SPMD extracts from the Lake Tahoe watershed generally had less toxicity than those deployed in the Truckee River watershed. Samples from the Truckee River and its tributaries near Reno/Sparks had the highest toxicity, owing to dense residential development and light industry. Higher percentages of urban and agricultural land use correlated with increased toxicity of SPMD extracts, although urban land use had a much greater influence. Streamflow was a less important factor than land use, and only flows greater than $5 \text{ m}^3/\text{s}$ correlated with toxicity. Toxicity decreased with higher flows, probably due to dilution. Toxicity of SPMD extracts at all sites during both high and low flows significantly correlated with percent urban land use ($R^2 = 0.32$). Generally, toxicity did not correlate with dissolved oxygen, pH, or temperature, but did with specific conductance ($R^2 = 0.27$) when samples influenced by geothermal water were excluded.

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INTRODUCTION

Water is a precious commodity, particularly in the arid southwestern United States. As population increases, the concern over the quality of this limited resource grows (Gleick 2001). More and timely information is needed to determine the extent of contamination in public water supplies and aquatic environments that affect both human populations and aquatic communities.

Nevada's population has been among the fastest growing in the United States for more than 10 years (Nevada State Demographer's Office 2004), which has caused concern about degrading water quality in urban areas. Bevans et al. (1998) found that the Reno and Sparks, Nevada, metropolitan areas were sources of synthetic organic compounds to streams and rivers. Semivolatile organic compound (SVOC) concentrations in bottom sediments from the Truckee River downstream from Reno/Sparks exceeded the 75th percentile when compared to 19 other U.S. river basins sampled by the U.S. Geological Survey's (USGS) National Water Quality Assessment (NAWQA) Program (Bevans et al. 1998).

Environmental contaminants can produce fish anomalies, chronic and acute toxicity, and endocrine disruption (Birge et al. 1989; Smith et al. 1994; Kime 1998; McLachlan 2001). Fish assemblages in the lower Truckee River, downstream from Reno/Sparks, had higher proportions of nonnative species and 7–13% abnormalities on fish, crayfish, and invertebrates (Bevans et al. 1998; Lawrence and Seiler 2002). These results indicate disturbance of the aquatic ecosystem downstream from Reno/Sparks. However, the driving forces creating this disturbance, such as urbanization scale and natural variations in flow, and water quality have not been investigated in detail. To do so and to determine the roles of organic contaminants and urbanization, we deployed semipermeable membrane devices (SPMDs) along an urbanization gradient under different environmental and streamflow conditions.

Semipermeable membrane devices are polyethylene membrane tubes containing a purified

synthetic lipid (triolein) found in fish tissue. The permeability of the membrane is similar to fish gills in terms of size selectivity for organic contaminants. The SPMD was developed by Huckins et al. (1990) as a passive in situ sampler to concentrate organics for subsequent chemical analyses and other types of analyses like toxicity testing. Accumulation of compounds in SPMDs is related to molecular size and the compound's octanol/water partitioning coefficient (K_{ow}), which measures the solubility of a compound in water versus octanol. The rate-limiting step for uptake of compounds is diffusion across the membrane (Huckins et al. 1996); therefore, water velocity past the membrane should not influence the concentration in the SPMDs.

Semipermeable membrane devices have several advantages over traditional bioassays and chemical analyses. Semipermeable membrane devices have been used for more than a decade and can detect the presence, bioavailability, and bioconcentration potential of many hydrophobic organic compounds (HOCs), including polycyclic aromatic hydrocarbons (PAHs), pesticides, and organic compounds with a K_{ow} greater than 3.0 (Huckins et al. 1990, 1993; Petty et al. 1995, 2000). Semipermeable membrane devices concentrate dissolved neutral hydrophobic organic molecules that are bioavailable to aquatic organisms, give reproducible results, are durable in severe environments, and do not metabolize accumulated compounds unlike aquatic organisms. Furthermore, use of biological tissues as media for analyses is hampered by the lack of a common species at all sites in regional and national surveys. Chemical analyses of bed sediments and water do not address questions related to bioavailability.

Semipermeable membrane devices have been used successfully in a variety of aquatic environments (Lebo et al. 1995; Huckins et al. 1996; Moring and Rose 1997; Echols et al. 2000; Rantalainen et al. 2000; Wang et al. 2001). In Nevada, SPMDs have been used to detect organochlorine pesticides and SVOCs in Las Vegas Wash and Lake Mead (Bevans et al. 1996). In the

Lake Tahoe basin, Lico and Pennington (1999) and Lico (2004) used SPMDs to investigate the occurrence of HOCs. They found organochlorine and PAH compounds in all six tributary streams sampled, and SVOCs and volatile organic compounds (including gasoline components) in all eight lake sites. The highest number and concentration of PAHs found in any of the tributaries was in the upper Truckee River, which has an urban area upstream of the sampling site. Gasoline components were found in the highest concentration at lake sites during the summer boating season, whereas none were found during the midwinter low boating season.

Many toxicity tests have been developed and validated, but microscale testing using bacterial and cellular *in vitro* assays has emerged as an important ecotoxicological screening tool for SPMD extracts (Burton 1991). One microscale test, the P450RGS test (CYP1A), responds to planar PCBs, chlorinated dibenzo-*p*-dioxins, chlorinated dibenzofurans, chlorodiphenylethers, chlorinated naphthalenes, plant flavones, and PAH compounds (Safe 1990). This test offers a simple cost-effective and sensitive alternative to traditional and costly whole animal tests with fish and invertebrates (Ang et al. 2000). The protocols are simple and well defined and have been used successfully in many environmental studies (McFarland et al. 2002). We also used the fluoroscan test (pyrene index) for assessing PAH compounds (Johnson et al. 2004). Thus, the two tests should induce similar, but not necessarily identical, responses in the same SPMD extract from a sample site. This is the first study to assess the tests' usefulness in detecting patterns in toxicity of SPMD extracts from streams influenced by different amounts of urbanization.

We sampled from the same six Lake Tahoe tributary sites as Lico and Pennington (1999), but then compared the results to the degree of urban land use in each watershed and used toxicity tests to assess potential effects to aquatic biota. These results from small exurban watersheds were compared with urban sites along the Truckee River in Nevada.

Our objectives were (1) to describe patterns in toxicity of the CYP1A and fluoroscan toxicity tests on HOCs from SPMD extracts in streams from the Lake Tahoe basin and along the Truckee River, and (2) to examine how urban land use, temporal variations in streamflow, and water quality influenced those patterns.

STUDY AREA

The Truckee River basin of California and Nevada, which includes Lake Tahoe and its watershed (Figure 1), was chosen due to the large amount of urban growth in the Lake Tahoe and Reno/Sparks areas. The greater Reno/Sparks metropolitan area has had an average annual population increase of 3.3% from 1991 to 2003 and now houses more than 373,000 people (Nevada State Demographer's Office 2004). The Lake Tahoe watershed has considerably fewer year round residents, but many tourists visit the area. Urban centers at the southern part of the lake include South Lake Tahoe and Stateline, and urban centers at the north end of the lake include Incline Village and Tahoe City. The Truckee River provides most of the drinking water for Reno/Sparks.

The Lake Tahoe watershed is in the Sierra Nevada ecoregion, and the Truckee River flows from Lake Tahoe into the Central Basin and Range ecoregion (U.S. Environmental Protection Agency 2002). These two ecoregions have contrasting climates; streams in the Lake Tahoe watershed have colder temperatures, colder air temperatures, higher elevations, and smaller catchment areas than those in the Truckee River watershed. Elevations range from 3,300 m in the headwaters to 1,430 m at Reno/Sparks and 1,160 at Pyramid Lake. Annual precipitation ranges from 230 cm in the high Sierra to 76 cm at the outlet of Lake Tahoe, 20 cm in Reno, and 18 cm at Pyramid Lake (Crippen and Pavelka 1970; Smith et al. 2001). Precipitation mostly falls as snow with pronounced snowmelt runoff in March–June. Local summer thundershowers occur, but summers generally are dry in both

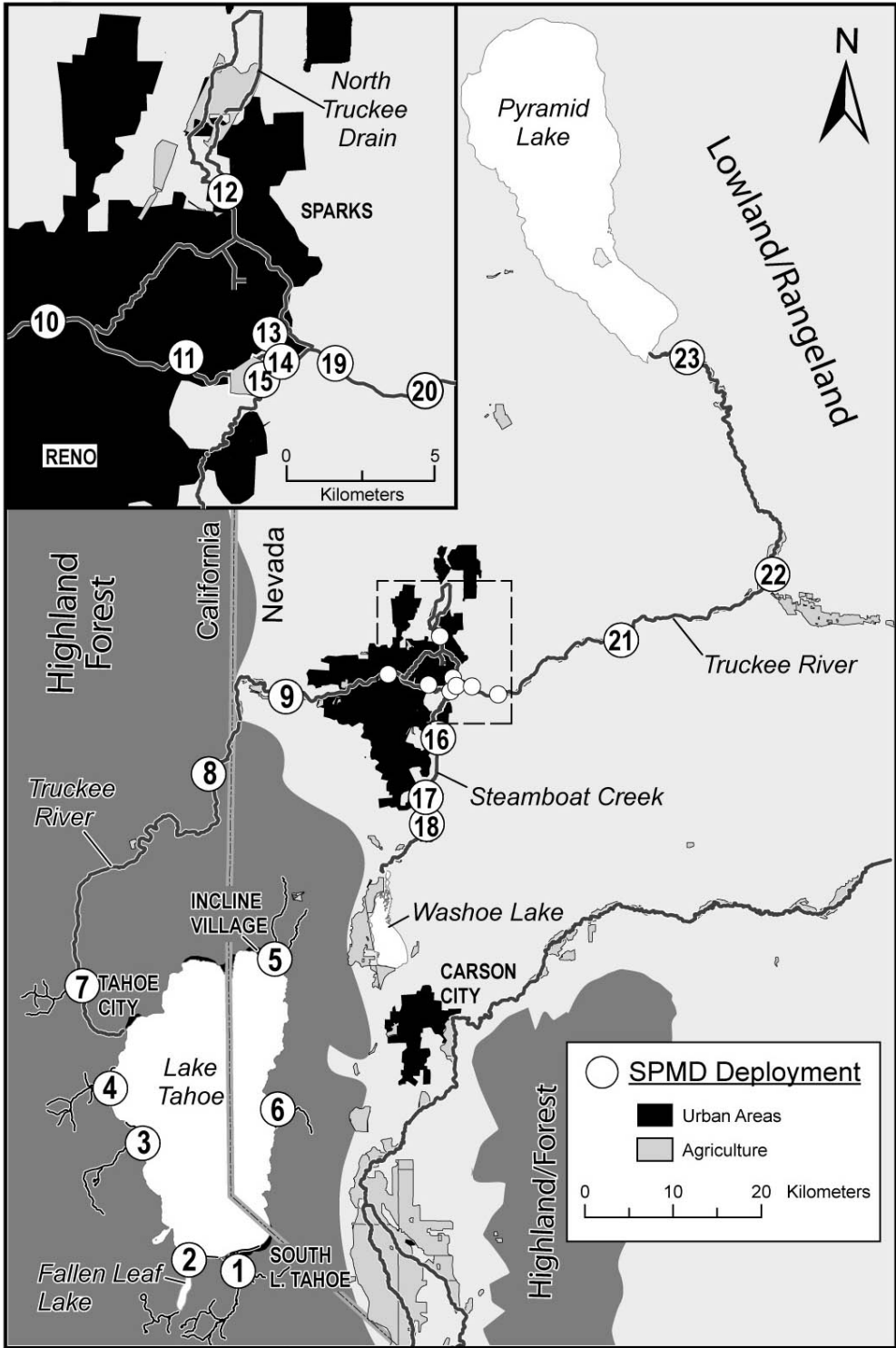


Figure 1. SPMD sampling sites in the Lake Tahoe watershed and along the Truckee River, August 2002–September 2003. See Appendix 1 for numbered site names and deployment times. Inset map shows detail of the site locations around Reno/Sparks.

watersheds. Catchments drain steep, forested land around Lake Tahoe and open, relatively flat-lying scrub land near Reno and Sparks.

Fish assemblages change along the Truckee River, from cool- and coldwater, mostly native species that are more sensitive to pollution in upper reaches, to warmwater species with a higher proportion of nonnatives that are tolerant to pollution in lower reaches. In the upper reaches, speckled dace *Rhinichthys osculus* and Paiute sculpin *Cottus beldingii* are dominant. Lahontan redbside *Richardsonius egregius* and mountain and Tahoe suckers *Catostomus commersoni* and *C. tahoensis*, respectively, are dominant in the warmer lower elevation reaches. Two nonnative salmonids, rainbow trout *Oncorhynchus mykiss* and brown trout *Salmo trutta*, support sport fisheries in the Lake Tahoe watershed and the Truckee River above Farad (Lawrence and Seiler 2002). The federally threatened Lahontan cutthroat trout *O. clarkii henshawi*, which is tolerant of high alkalinity, once supported a world class sport fisheries but was eliminated by impassable dams and excessive water diversions.

METHODS

Land-Use Characterization

We employed a geographic information system (GIS) to classify land uses within a buffer 1 km from each streambank and 6 km upstream of each site (Figure 2). The calculated zone of land use influence could be greater than the expected 12-km² area, due to channel curvature, more than one channel and/or the presence of a lake. Contributing areas around Lake Tahoe were defined in the same way, except that drainage areas were generally smaller to accommodate drainage-basin boundaries that were less than 1 km from small watersheds. We thought these buffers would have the highest and most direct influence on water quality because HOC sources in such buffers have the greatest chance to flow directly from the land surface into streams. Hy-

drophobic organic contaminants sources outside such buffers tend to be absorbed to particulates and not flow directly into streams unless there is a continuous impervious surface leading to the stream (Larson et al. 1997). Base map data for the main river, as well as for contributing drainage basins, were derived from the USGS National Water Information System and local data sources.

To identify urban land use within these buffers, a combination of Washoe County parcel data and aerial imagery were added to the GIS. Digital Ortho Quarter Quadrangle (DOQQ) data from the 1990s formed the foundation for classifying urban land. Land that had been developed since the 1990s was identified from the parcel map, which provided a consistent source for identifying recent land use. After mapping land use within each contribution zone, data were exported for analysis.

SPMD Deployment

The SPMDs were deployed August 2002 (12 sites) and September 2003 (23 sites plus two replicates) to capture summer low-flow conditions, while a March 2003 deployment (15 sites) captured higher spring flow conditions (Figure 3; Appendix 1). The deployment period was 27–34 d. Sites were chosen to represent 0–96% urban development. If possible, sites were near existing USGS gaging stations so that a hydrograph would be available to assess flow conditions during the deployment period. We also selected sites to provide wide geographic coverage of tributaries in the Lake Tahoe watershed and a longitudinal gradient along the Truckee River.

We placed 15-cm SPMDs on a metal carrier, sealed in unused clean paint cans. The cans were frozen until deployment and brought to the field in coolers with sealed ice containers. During deployment, the metal carriers (with the SPMDs inside) were placed in the water within 1–2 min to minimize air contamination. Latex gloves were worn at all times by all handlers during deployment and retrieval. The SPMD membranes and carrier were attached by a nylon tie to steel rebar,

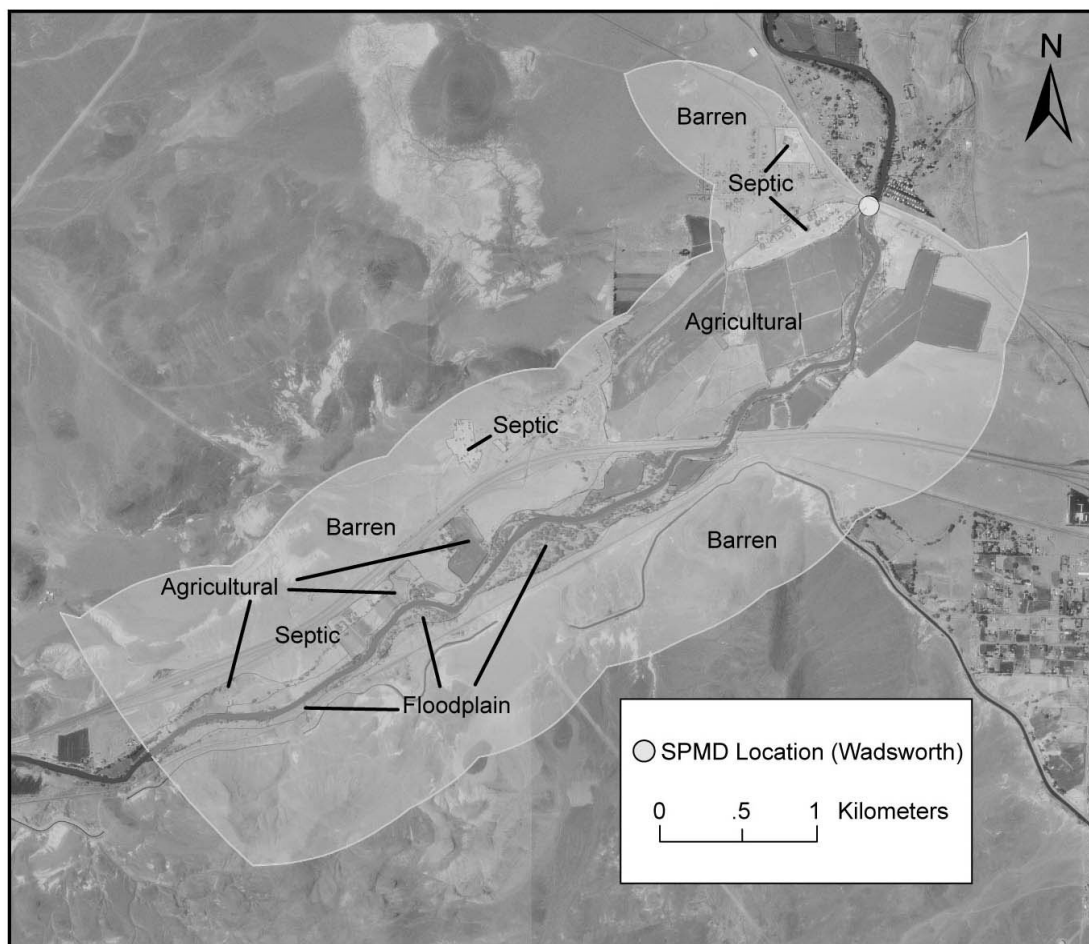


Figure 2. Example of 2 km by 6 km buffer used to define urbanization upstream of each site. The boundary is extended at the northeast portion of the buffer due to curvature in the river and catchment properties.

previously driven into the bottom substrate. The SPMDs were installed where the water was ≥ 0.15 m deep and flowing at ≥ 0.03 m/s, and mounted ≥ 0.06 m above the stream bottom and low enough to stay ≥ 0.05 m below the water surface. One SPMD exposed to the atmosphere at the end of deployment due to low flow (Appendix 1) was not analyzed, but we believe the other SPMDs remained submerged.

Quality Control

To test for consistency of results and ensure that sampling procedures did not influence our re-

sults, two duplicate SPMDs were deployed in September 2003, one at the Incline Creek site in the Lake Tahoe watershed and one at the Clark site in the Truckee River watershed (Appendix 1; Figure 1). In addition, two trip-blank SPMDs were simultaneously exposed at all sites during deployment in August 2002 and March 2003 when the SPMD that was to be placed in the water was exposed to the air. The trip-blank SPMD also was tested for toxicity to determine if there was any significant contamination coming from the air when the SPMDs were deployed. Three trip-blanks were used for the September 2003 sampling period. Only a small amount of

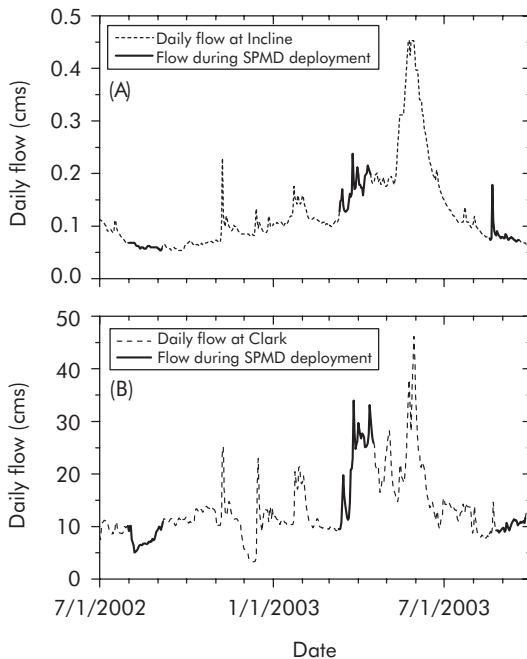


Figure 3. Annual hydrographs for (A) a Lake Tahoe watershed site (Incline Creek), and (B) a Truckee River watershed site (Clark) showing SPMD deployment periods (solid lines). cms = m^3/s .

contamination was found in the blanks during all sampling periods, indicating that almost all of the toxicity reported came from the river and not from the air. The amount of contamination was not subtracted from results because the contamination was a cumulative result of opening the same trip-blank at different sites and it would not represent the amount of contamination at any particular site.

Extraction from SPMDs

Retrieved SPMDs were quickly placed back into the paint cans, iced, and stored frozen. Frozen samples were shipped overnight on ice to Environmental Sampling Technologies (EST), where the SPMDs were removed from the can and carrier, washed with tap water, brushed, cleaned, rinsed in a beaker of hexane, and rinsed with 1 N HCl for 30 s. They were then rinsed with tap water, followed by acetone, and air dried in a

controlled environment. The SPMDs were then put in clean jars with at least 180 mL of hexane in an incubator at 18°C for 24 h. The hexane was decanted into another jar, and the first jar was refilled with hexane and incubated 8 h longer. The extracts from each site were concentrated with a Kuderna-Danish flask, further concentrated with N_2 to approximately 1 mL, and stored in an amber ampoule.

The SPMD extracts were split into two ampoules with different solvents, iso-octane and DMSO. The iso-octane portion was sent to V. McFarland, U.S. Army Corps of Engineers, Vicksburg, Mississippi, for P450RGS assay (Ang et al. 2000). The DMSO portion was sent to B.T. Johnson, USGS, Columbia, Missouri, for PAH assay by ultraviolet (UV) fluorescence scan (Fluoroscan) (Johnson et al. 2004).

Microscale Toxicity Testing

P450RGS (CYP1A) assay.—Organisms can transform xenobiotic organic compounds with a series of proteins called cytochrome P450 monooxygenases (CYP1A system) into metabolites that either activate or inactivate toxicity (Heath 1995). Bioassays are based on the increased content and activity of CYP1A as a result of exposure to HOCs that include PAHs (Payne et al. 1987; Safe 1990). Increases in CYP1A have been associated with changes in physiology, growth, reproduction, and pathology of fish (Spies et al. 1996; Parrott and Tillitt 1997). Use of SPMD extracts to produce CYP1A inducers has also been documented (Huckins et al. 1996; Parrott and Tillitt 1997; Petty et al. 2000).

The specific CYP1A test we used, P450RGS, employs human hepatoma HepG2 (101 L) cells that are stably transfected with a plasmid containing the human CYP1A promoter sequence fused to the firefly luciferase gene as a reporter. The induction of the CYP1A gene results in the production of luciferase, and the light produced responds to the presence of chemicals that bind to the aryl hydrocarbon receptor (AhR) in a

quantitative fashion. Results are reported in toxic equivalents (TEQ), which are the number of picograms (pg) of 2,3,7,8 TCDD dioxin in 1 mL of SPMD extract that would cause the same response as the sample. Details of the protocols can be found in Ang et al. (2000) and at <http://www.wes.army.mil/el/dots/doer/technote.html>. The assay conforms to APHA Standard Method 8070, ASTM Standard E-1853, and EPA Method 4425.

Fluoroscan (pyrene index).—The SPMD extracts in DMSO were exposed to UV light at 280 nm to determine presence of PAH compounds (Johnson et al. 2004). A fluorometer was used to measure the fluorescence of the extract from each site and compare it to a standard pyrene curve. The estimated PAH concentration for each site is reported as the equivalent number of micrograms (μg) of pyrene in 1 mL of SPMD extract that would produce the same fluorescence and therefore is called the pyrene index.

Field Measurements

We measured a number of variables to determine their correlations with toxicity estimates. We estimated velocity with a pygmy meter on a wading rod at each SPMD location, and total water depth and depth of the SPMD also were obtained with the wading rod. Stream discharges were obtained from nearby USGS gaging stations, except for two sites. Daily flows were used to develop a hydrograph during the deployment period at each gauged site and discharge measurements were used to estimate flows at the two ungaged sites. Gaging station discharge data were obtained from the USGS NWIS (National Water Information System) Web site and ADAPS (Automatic Data Analysis and Processing System) databases for each gauge.

Dissolved oxygen, pH, specific conductance, and water temperature were measured with calibrated meters according to USGS field measurement protocols (Wilde and Radtke 2004). These measurements, along with velocity and depth, were made at deployment and when SPMDs were retrieved.

Data Analysis

After testing for normality, we used standard linear regression techniques using S-PLUS (v6.1). Statistical significance was assessed using a P -value of 0.05. Box plots were constructed with S-PLUS and were tested for differences with a two-tailed t -test. We also used nonparametric regression techniques (Spearman's Rho and Kendall's Tau) to examine the variables and found identical results to the t -tests. To examine simple correlations among variables we used Pearson Correlation.

RESULTS

Toxicity Patterns

Lake Tahoe sites had significantly lower toxicity than Truckee River sites (Figure 4A) and measured toxicity was generally lower during spring runoff (Figure 4B). On the Truckee River, toxicity generally increased downstream with a peak just below Reno/Sparks. Toxicity results for CYP1A and pyrene index tests indicated that the two tests were highly correlated ($r = 0.79$; Figure 5). This indicated that PAHs were the most prevalent hydrophobic organic contaminant at most of our sites because the pyrene index test only responds to PAHs.

Land Use Influence on Toxicity

Combined agricultural and urban land use percentages (Appendix 1) explained a moderate amount of the toxicity patterns in the Lake Tahoe and Truckee River watersheds ($R^2 = 0.36$ for CYP1A and $R^2 = 0.33$ for the pyrene index), with urban land use alone explaining 0.32 and 0.33, respectively, of the variability (Figure 6). CYP1A and pyrene index toxicity were greatest in Reno/Sparks, with the North Truckee Drain the highest (Figure 7). Results for Lake Tahoe sites generally were lower except for the predominantly urban Incline Creek site (Figure 7). Toxicities at Truckee River sites were generally lower outside

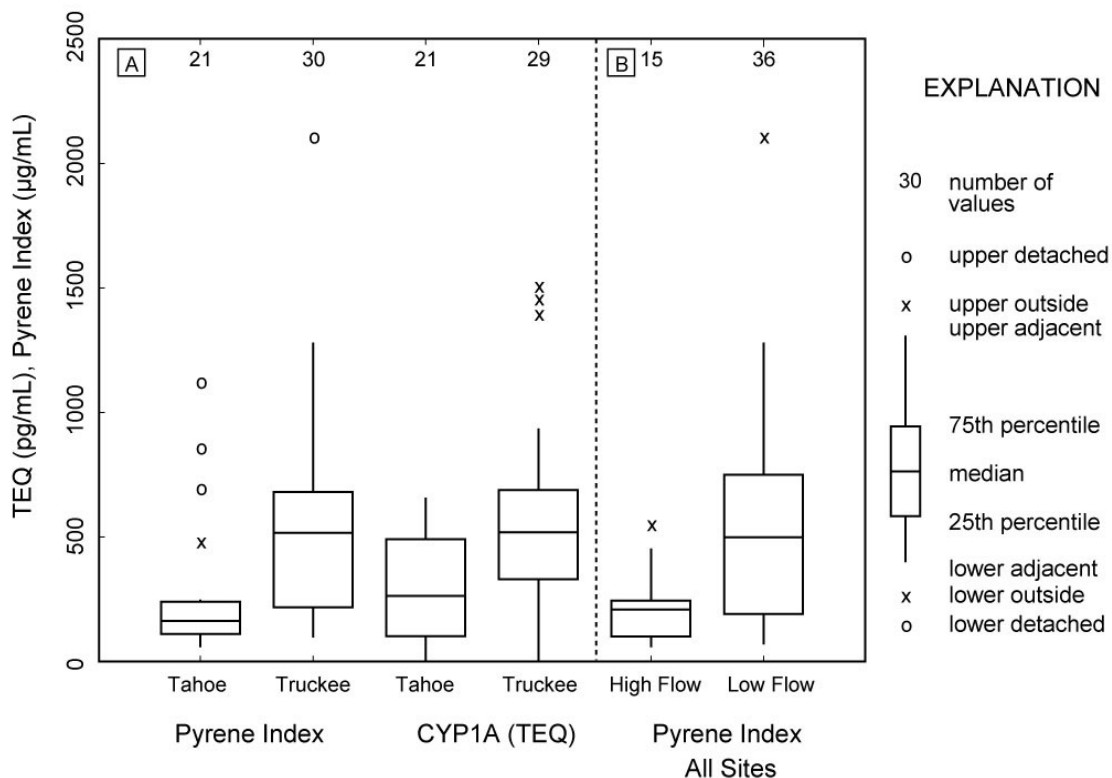


Figure 4. Toxicity tests comparing (A) Lake Tahoe and Truckee River watershed samples, and (B) low flow (August 2002 and September 2003) versus high flow (March 2003) sampling periods for all sites. All comparisons indicate statistically different means ($p < 0.0001$).

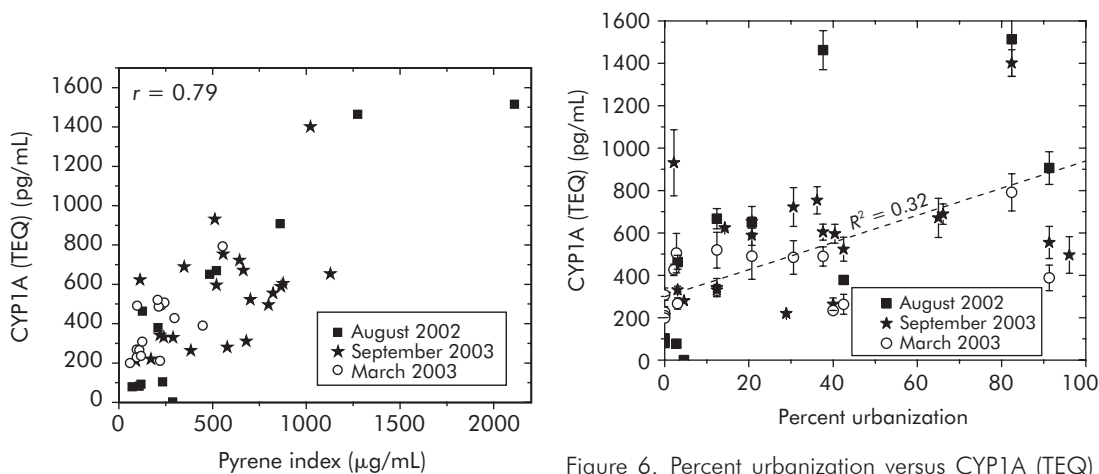


Figure 5. Comparison of CYP1A (TEQ) versus pyrene-index results for all sampling sites and sampling times.

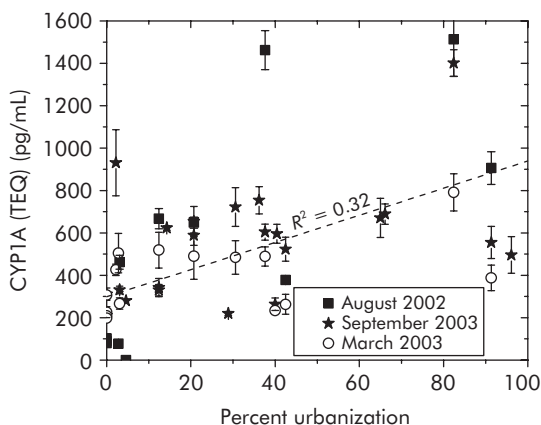


Figure 6. Percent urbanization versus CYP1A (TEQ) toxicity for all samples. Error bars represent one standard deviation. Pyrene-index measurements yielded the same correlations.

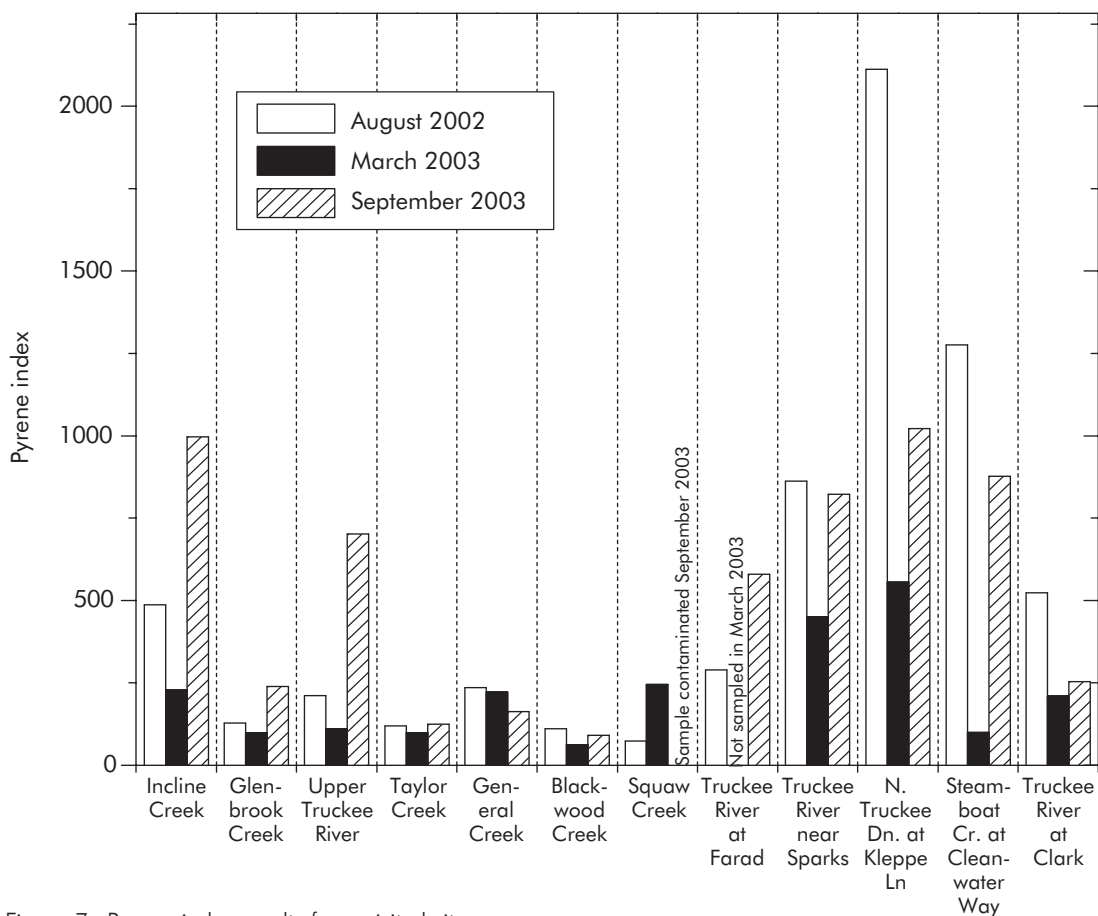


Figure 7. Pyrene-index results for revisited sites.

of Reno/Sparks for the CYP1A and pyrene indices, regardless of season (Figure 8A and 8B). The measured toxicity response at sites on Steamboat Creek showed higher values near more urban areas, with the highest responses occurring just upstream and downstream of the Reno/Sparks water reclamation facility. The high upstream toxicity values indicated that the facility is not a major contributor of hydrophobic organic contaminants found in the creek (Figure 9).

Seasonal Influence on Toxicity

There was no correlation between flow and toxicity with either test for Lake Tahoe watershed samples and low-flow tributaries in the Truckee River watershed. But main-stem Truckee River

sites showed a weak correlation ($R^2 = 0.18$, $p = 0.06$), with higher toxicity occurring at lower base flows during summer. Seasonal differences in streamflow showed that both CYP1A and pyrene index toxicity was lower during spring high flows than during summer low flows at any given site (Figure 4B), indicating that higher flow can dilute toxicity in some places. However, there were 35 measurements taken during summer low flows and only 15 during spring runoff.

Water Quality Influences on Toxicity

There was no observed correlation between water quality variables and toxicity tests with the possible exception of specific conductance. Dissolved oxygen and pH measurements were relatively consistent and most likely were not

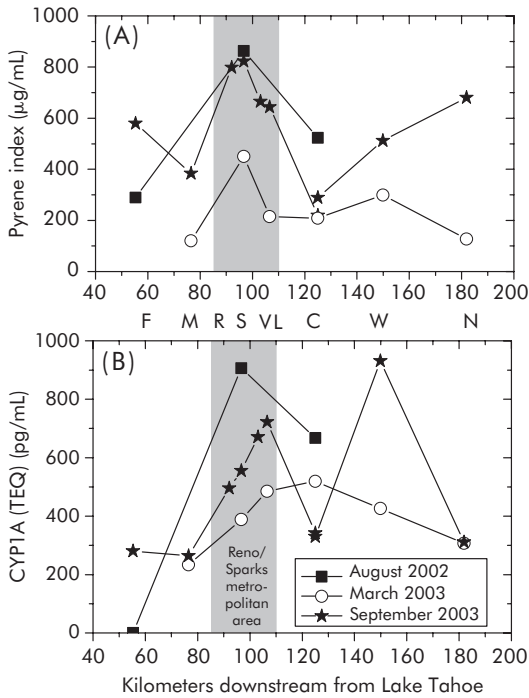


Figure 8. Toxicity from SPMD sites on the Truckee River, shown as kilometers downstream from Lake Tahoe: (A) pyrene index, and (B) CYP1A (TEQ). Letters indicate sites: F = Farad, M = Mogul, R = Reno, S = Sparks, V = Vista, L = Lockwood, C = Clark, W = Wadsworth, N = Nixon (Marble Bluff Dam).

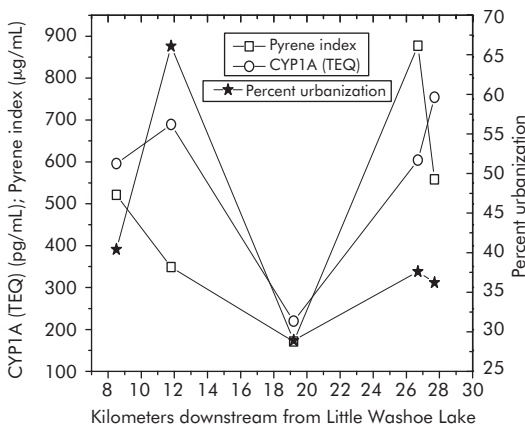


Figure 9. Pyrene and CYP1A (TEQ) toxicity and percent urbanization at SPMD sites on Steamboat Creek versus kilometers downstream of Little Washoe Lake. The Reno/Sparks sewage treatment plant is between the last two points on the right.

associated with any changes in toxicity (Appendices C and D). Specific conductance was more variable. However, higher conductivity generally corresponded to sites with higher toxicity, particularly for the CYP1A test. When two Steamboat Creek sites with naturally high specific conductance and relatively low toxicity for one sampling period were excluded, the R^2 improved to 0.27 (Figure 10).

The greatest temperature difference among sites was 12°C, which is enough to influence organic compound uptake (Huckins et al. 2002). However, plots of temperature versus toxicity test results showed no correlation, indicating that temperature alone could not be responsible for the variations. In addition, water temperature differences between deployment and retrieval times were less than 10°C at all sites each time they were deployed and generally were less than 4°C (Appendices C and D), indicating that this was not an important factor.

DISCUSSION

Toxicity Patterns

Higher toxicity in the Truckee River watershed is influenced by tributary sites (North Truckee

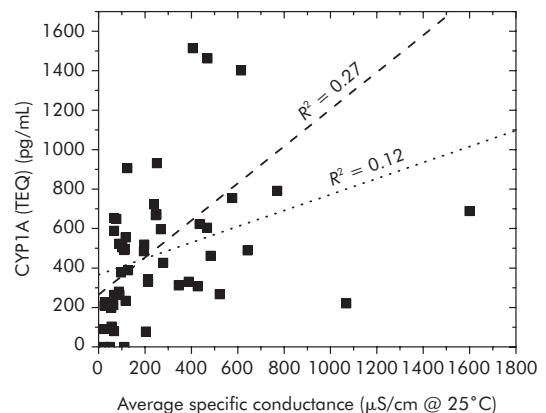


Figure 10. CYP1A (TEQ) versus average specific conductance. The higher correlation excludes two outliers with exceptionally high specific-conductance from natural springs.

Drain and Steamboat Creek), but the toxicity measured at main-stem sites also was statistically higher than Lake Tahoe sites. This is expected because urbanization along the Truckee River is much greater than along streams in the Lake Tahoe watershed. However, some undeveloped Lake Tahoe sites in the Lake Tahoe showed toxicity in both tests. At Taylor Creek, there was no urbanization within the buffer; yet, there was still a small, positive toxicity response in all three deployment periods. One possible source is a main road and bridge near the site. Runoff or atmospheric transport of car exhaust, fuel, oil, or grease from this road may have contributed to the toxicity measured at this site. Alternatively, Fallen Leaf Lake (Figure 1), which is the source of water to Taylor Creek, has summer and year-round residences along its shores and motorized boating that could provide a source of organic contaminants. Significant toxicity also was detected on the upper Truckee River in September 2003 (Appendix 2). The upper Truckee River has a greater percentage of urban land use than any of the other Lake Tahoe watershed sites, indicating that urbanization may be contributing to the measured toxicity.

Comparison of Toxicity Tests

Both the CYP1A and pyrene index toxicity tests proved rapid, inexpensive, and useful for distinguishing HOC concentrations. The strong correlation between these tests ($r = 0.79$) indicates that they were responding to similar types of HOCs, particularly PAHs. The pyrene index specifically detects presence and amount of organic aromatic compounds that fluoresce under UV light. Some of these compounds are higher molecular weight PAHs (4–7 rings) that are fish carcinogens (Black 1983; Kimura et al. 1984; Couch and Harshbarger 1985; Baumann et al. 1987; Eisler 1987). Therefore, the higher the pyrene index, the greater the chance that fish in that stream are exposed to carcinogens, reducing health and fitness. We cannot predict a pyrene index value associated with reduced health in

aquatic biota at this time. However, sites with more than 1,000 $\mu\text{g/mL}$, like North Truckee Drain, are likely to effect fish health.

The CYP1A test responds to a wider variety of HOCs than the pyrene index. Therefore, it is more useful for detecting HOCs in streams where the presence of specific HOCs are unknown. The CYP1A test responds specifically to HOCs that bind to the AhR receptor involved in detoxification (or in some cases actually increasing toxicity) and include some of the most toxic HOCs like PCBs, dioxins/furans, and PAHs. Without analytical chemistry of the SPMD extracts, we cannot specify the HOCs causing the response. However, because there is a strong correlation between CYP1A and the pyrene index, which responds specifically to PAHs, we know the CYP1A response in our study was due mostly to PAHs. Polycyclic aromatic hydrocarbons also are one of the classes of HOCs typically found at higher concentrations in urban streams (Lopes and Furlong 2001).

Land-Use Influences on Toxicity

Percent urban and agricultural land use together explained 36% and 33% of the toxicity in both the Lake Tahoe and Truckee River watersheds for CYP1A and pyrene index tests, respectively. However, agricultural land use only explained up to 4% of the toxicity on its own. This indicates that the organic contaminants likely are derived from discharges or runoff that is within the land-use zone used to calculate urban intensity affecting the SPMD site. This hypothesis is further supported by the relation between HOCs and flow. The relation is weaker during spring runoff when flow is more likely derived from forested areas outside the buffer (Figures 4B and 6). When flows are lower and contaminant sources are more likely local, the correlation was better and statistically more significant (Figure 6).

There are several possible sources of error influencing the correlations: (1) The area influencing the sampling site may be larger or smaller

than the area chosen for our percent urban land use calculation; (2) the types of urban land use at each sampling site differ, as do road densities, industries, and point sources of pollution; (3) there may have been significantly more urban development after the aerial photographs used to derive the percent urban land-use values were taken; and (4) urban land use may not have been interpreted accurately from the aerial photographs. Such sources of error reduce the correlation, but because a statistically significant correlation can still be derived, we are confident that there is a relationship. For the Truckee River and Lake Tahoe watersheds and perhaps for other western basins that have large, mostly rural catchments, dense urban areas, and few tributary streams, local urban land use may be more useful for assessing urbanization effects than the urban index proposed by McMahon and Cuffney (2000). This is because local land use depicts urban influences near sampling sites along a river. Mebane et al. (2003) and Wang et al. (2006, this volume) also concluded that in largely undisturbed catchments, sites are influenced most by local factors. However little of the Truckee River basin is undisturbed, unless disturbed only means intensively farmed or urbanized.

Truckee River toxicity usually peaked in or near the Reno/Sparks metropolitan area (Figure 8). Truckee tributary sites on the North Truckee Drain and Steamboat Creek also had some of the highest toxicities recorded in this study (Appendix 2 sites 13 and 15). Tahoe suckers collected in August 2004 from the Steamboat Creek sites at Cleanwater Way and downstream of the sewage treatment outfall had lesions and fin erosion, indicating highly stressed aquatic biota at these sites (M.R. Rosen and coworkers, unpublished data). Sites at the more urban areas in the Lake Tahoe watershed also showed higher toxicity than more forested sites. The Incline Creek site was sampled during renovation of a large hotel nearby. Sedimentation barriers did not effectively prevent runoff, and HOCs from heavy equipment may have contributed to increased toxicity from August 2002 to September 2003 (Figure 7).

High toxicity measured at the Wadsworth site on the Truckee River (Figure 8B; September 2003) was unexpected due to relatively low urbanization in this area (Figure 2). In addition, the March 2003 sample did not yield a comparable result and the pyrene index was much lower (Figure 8A) than the CYP1A result. The inconsistency of the CYP1A result and the pyrene-index result indicates that PAHs may not be the main contaminants contributing to the high toxicity there. The Wadsworth site has alfalfa farming directly upstream (Appendix 1), indicating that agricultural pesticides may be influencing toxicity at this site more than urban inputs. Other sites with approximately 20% agricultural land use are Steamboat Creek near its mouth and at Cleanwater Way; however, these sites also are approximately 40% urbanized. Further research is needed to confirm an agricultural pesticide hypothesis, but clearly factors other than degree of urbanization must be considered when interpreting SPMD toxicity tests. For example, Mebane et al. (2003) concluded that irrigated agriculture exceeding 15% in the Columbia basin was detrimental to coldwater fish assemblages, and Van Sickle et al. (2004) reported that model coefficients for irrigated agriculture and urbanization in the Willamette Valley were not significantly different.

Seasonal Influence on Toxicity

The lack of correlation of toxicity and flow ($R^2 = 0.003$) when all sites were used in the correlation indicates that toxicity was not greatly affected by flow, particularly when flow was less than $5 \text{ m}^3/\text{s}$. However, the slightly better correlation between flow and toxicity on the main-stem Truckee River sites ($R^2 = 0.18$), particularly at higher flows, indicates that for a larger river system, higher flows may reduce the toxicity measured (Figure 4B; Figure 7). Higher flows may dilute contaminants because flow is derived from cleaner areas much higher in the watershed. In contrast, flows for smaller streams may be more locally derived, even during wet periods, and may

not dilute the toxicity measured by the SPMDs. The variability in toxicity at lower flows may indicate variability in organic contaminant sources that are affecting the streams or at low flows the mechanisms for transporting contaminants to streams are less efficient for certain streams. Thus, for the Lake Tahoe watershed, Steamboat Creek, and the North Truckee Drain samples, which are dominated by smaller streams and lower flows in the spring, there was no correlation between toxicity and flow when compared at different sites. The Truckee River main-stem samples do appear to be affected by dilution. Figure 7 demonstrates that during spring runoff, toxicity at sites sampled on the Truckee River was consistently lower, but toxicity at sites in the Lake Tahoe watershed and tributaries to the Truckee River was not consistent. This indicates that sampling for organic contaminants is best conducted during summer low flows, at least in the Truckee River basin.

Water Quality Influence on Toxicity

The weak correlation between organic contaminants and specific conductance was improved when two points sampled on Steamboat Creek in September 2003 were excluded (Figure 10). These two points had relatively high specific conductance and low toxicity, indicating that the specific conductance values are not consistently related to organic contaminants. These sites (16 and 17, Appendix 1) are influenced by geothermal water high in inorganic ions that enters the stream at Steamboat site 18 (Garside and Schilling 1979). Specific conductance in the Lake Tahoe and Truckee River watersheds is naturally low. Sites in the Lake Tahoe watershed that are minimally altered by human development have low specific-conductance values except on Glenbrook Creek, which is influenced by different catchment geology. Sites upstream from Reno/Sparks also have low specific-conductance values. It is expected that specific conductance near metropolitan areas would be higher than in less disturbed areas of the same watershed because of an increase in

stormwater runoff that includes inorganic contaminants with high conductance as well as HOCs. Therefore, it is not surprising that there is at least some correlation between specific conductance and organic contaminants.

The influence of temperature on contaminant uptake in SPMDs is important over relatively small temperature ranges for HOCs, with a two-fold to fourfold increase over a 16°C temperature rise (Huckins et al. 2002). The maximum temperature difference among our sites was 12°C. There was also a maximum difference of 10°C between deployment and retrieval at any one site. These temperature differences are enough to influence organic compound uptake. However, the lack of a correlation between temperature and toxicity test indicates that temperature alone was not responsible for the variations.

In streams with muddy bottoms, uptake of organic compounds into the SPMD is enhanced by burrowing organisms passing the contaminated material in the mud up to the mud/water interface where it can be redissolved (Thibodeaux and Bierman 2003). However, only Steamboat Creek and North Truckee Drain had muddy bottoms where bioturbation may have influenced the toxicity recorded there.

Management and Research Implications

One of the significant difficulties for fisheries and water quality managers is determining the stressors limiting establishment of sport fisheries and healthy aquatic ecosystems. Stressors may be chemical, physical, or biological. Our results indicate that toxic contaminants may be limiting fisheries in the Truckee basin. This study raises a number of issues worth further study, including (1) defining land use contributions to SPMD toxicity at individual sampling sites, (2) establishing robust correlations between biological condition and the concentration of organic contaminants, (3) identifying types and concentrations of organic contaminants that are entering streams and rivers, and (4) sampling polar (hydrophilic) organic contaminants. This type of

sampling is particularly important near wastewater treatment systems where many potential contaminants are hydrophylic.

Passive sampling devices and microscale testing provide a rapid assessment tool to evaluate areas of risk to aquatic biota and fish consumers and to locate potential sources of toxic contaminants across a watershed. An advantage of using microscale testing to assess potential toxicity in a stream is low cost compared to chemical analysis, whole effluent toxicity testing (WET), or biological monitoring. Cost for the two tests we used, FluorSCAN and P450RGS, including the cost of the SPMD and dialysis, were about \$200 per site. This is considerably less than analytical chemistry for hydrophobic organic compounds of composite water and sediment samples, which can range from \$1,000 to \$2,000, depending on the laboratory and analytes measured, and quite a bit lower than WET tests using an invertebrate and a fish, which are about three times as high (\$700) as microscale tests. Microscale testing costs compared to biological monitoring is similar only when the lowest cost sample and laboratory are used (i.e., \$175–\$400 for processing 100–300 randomly selected invertebrates; \$200–\$400 for a fish assemblage sample, depending on site size). From a cost effectiveness perspective, the use of SPMDs as a screening tool wherever HOCs are expected would be advantageous.

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names are for identification purposes only and do not imply endorsement by the U.S. Geological Survey.

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Appendix 1. SPMD sites, percent land use, and deployment duration listed by map number in Figure 1.

Map no.	Site name	USGS site number	Percent urban land use	Percent agricultural land use	Percent undisturbed land use	Days deployed August 2002	Days deployed March 2003	Days deployed September 2003
1	Upper Truckee River	10336610	43	0	57	34	34	31
2	Taylor Creek	10336628	0	0	100	34	34	31
3	General Creek	10336645	0	0	100	34	33	31
4	Blackwood Creek	10336660	0	0	100	34	33	31
5	Incline Creek	10336700	21	0	79	34	33	31
6	Glenbrook Creek	10336730	3	0	97	34	34	31
7	Squaw Creek	10337855	3	0	97	34	33	31
8	Truckee River at Farad	10346000	5	0	95	34		32
9	Truckee River at Mogul	10347460	40	3	57		30	32
10	Truckee River at Reno	10348000	96	0	4			32
11	Truckee River near Sparks	10348200	91	1	8	34	30	32
12	N Truckee Drain at Spanish Springs Road	10348245	14	15	71			33
13	N Truckee Drain at Kleppe Lane	10348300	82	0	18	34	29	33
14	Steamboat Creek near Mouth	10439989	36	25	39			32
15	Steamboat Creek at Cleanwater Way	10349980	38	19	43	34	29	32
16	Steamboat Creek at Short Lane	10349849	29	8	63			32
17	Steamboat Creek at Gieger Grade	10349495	66	11	23			32
18	Steamboat Creek at Steamboat	10349300	40	11	49			31
19	Truckee River at Vista	10350000	65	10	25			32
20	Truckee River at Lockwood	10350050	31	6	63		27	32
21	Truckee River at Clark	10350500	12	0	88	34	29	31
22	Truckee River at Wadsworth	10351650	2	19	79		29	31
23	Truckee River at Marble Bluff Dam	10351780	0	13	87		30	31

Appendix 2. SPMD toxicity test results for all sampling periods.

Map no.	Pyrene index August 2002 ($\mu\text{g}/\text{mL}$)	TEQ August 2002 (pg/mL)	Pyrene index March 2003 ($\mu\text{g}/\text{mL}$)	TEQ March 2003 (pg/mL)	Pyrene index September 2003 ($\mu\text{g}/\text{mL}$)	TEQ September 2003 (pg/mL)
1	211	378 ± 8^a	111	263 ± 47	702	523 ± 57
2	120	90 ± 16	98	226 ± 26	125	BDL ^b
3	235	103 ± 9	222	208	163	BDL
4	111	80 ± 12	62	198	91	211
5	487	649 ± 26	228	490 ± 109	1129	654 ± 71
5 (replicate)					865	589 ± 48
6	128	462 ± 33	98	267 ± 27	240	331 ± 18
7	73	77 ± 17	245	505 ± 93	Cont. ^c	Cont.
8	289	BDL			579	280
9			120	234	384	264 ± 29
10					799	496 ± 86
11	863	906 ± 77	450	388 ± 60	823	555 ± 76
12					114	623 ± 11
13	2113	1514 ± 176	556	791 ± 88	1023	1401 ± 63
14					558	754 ± 64
15	1276	1462 ± 92	100	489 ± 45	877	604 ± 38
16					171	220 ± 9
17					349	689 ± 48
18					521	596 ± 45
19					665	671 ± 92
20			215	484 ± 79	644	722 ± 91
21	523	668 ± 47	209	519 ± 84	219	342 ± 43
21 (replicate)					289	330 ± 27
22			299	426 ± 27	512	931 ± 156
23			127	307	680	311 ± 29

^a \pm refers to one standard deviation.^b BDL = below detection limit.^c Cont. = contaminated.

Appendix 3. Water quality measurements during the August 2002 and March 2003 SPMD deployments.

Map no.		Water temp (°C)		Specific conductance (μs/cm)		pH (pH units)		Dissolved oxygen (mg/L)		Median ^a flow (m ³ /s)
		begin	end	begin	end	begin	end	begin	end	
August 2002 (Total deployment—02/08/02–05/09/02)										
1	Upper Truckee River	14.0	15.8	88	105	7.6	7.3	8.2	8.3	0.09
2	Taylor Creek	23.0	17.4	22	22	7.0	7.1	6.5	7.7	0.06 ^b
3	General Creek	20.0	14.6	53	59	7.1	7.2	6.8	7.6	0.02
4	Blackwood Creek	22.0	17.0	61	73	7.6	7.6	6.1	7.4	0.06
5	Incline Creek	11.5	12.7	76	77	7.3	7.4	8.5	8.2	0.06
6	Glenbrook Creek	13.0	12.0	466	500	7.2	7.5	7.2	7.4	<0.01
7	Squaw Creek	21.9	20.4	145	263	7.3	7.3	6.6	8.1	0.01 ^b
8	Truckee River at Farad	16.5	15.0	105	118	7.6	7.0	8.4	8.1	11.27
11	Truckee River near Sparks	19.9	17.6	129	119	7.8	7.2	8.6	8.7	4.02
13	N Truckee Drain at Kleppe Lane	21.5	19.1	443	369	7.6	7.4	7.1	8.0	0.71
15	Steamboat Creek at Cleanwater Way	23.5	20.3	327	613	7.2	7.9	3.1	7.2	0.61
21	Truckee River at Clark	23.4	20.8	236	257	8.3	7.7	9.1	7.7	7.05
March 2003 (Total deployment—12/03/03–18/04/03)										
1	Upper Truckee River	4.8	1.5	84	53	7.0	7.0	10	11	3.12
2	Taylor Creek	6.9	5.0	25	30	7.0	7.0	9.2	11	0.28 ^b
3	General Creek	4.4	0.8	31	21	7.1	7.0	10	12	0.59
4	Blackwood Creek	7.3	4.9	59	50	7.4	7.1	9.2	11	1.25
5	Incline Creek	6.2	3.0	111	112	7.7	7.3	9.4	11	0.17
6	Glenbrook Creek	2.9	1.5	553	492	7.6	7.5	9.8	10	0.05
7	Squaw Creek	7.6	5.3	115	90	7.6	7.2	9.3	11	0.45 ^b
9	Truckee River at Mogul	6.8	7.8	129	104	7.5	7.7	12	11	22.23
11	Truckee River near Sparks	9.0	8.2	145	110	7.8	8.0	11	11	22.29
13	N Truckee Drain at Kleppe Lane	11.3	11.7	798	743	7.8	8.0	11	12	0.25
15	Steamboat Creek at Cleanwater Way	13.0	12.7	650	635	8.2	8.2	11	9.4	0.93
20	Truckee River at Lockwood	7.6	8.0	222	168	8.0	7.7	11	11	24.98
21	Truckee River at Clark	7.5	8.0	227	166	8.0	7.8	7.8	11	26.03
22	Truckee River at Wadsworth	7.0	9.0	381	177	8.2	7.8	5.4	11	2.36
23	Truckee River at Marble Bluff Dam	8.4	10.5	563	292	8.1	7.9	10	10	2.97

^a Median flow for SPMD deployment period.^b Estimated value, no gage at this site.

Appendix 4. Water quality measurements during the September 2003 SPMD deployment.

		Water temp (°C)		Specific conductance (μs/cm)		pH (pH units)		Dissolved oxygen (mg/L)		Median ^a flow (m ³ /s)
		begin	end	begin	end	begin	end	begin	end	
Map no.										
September 2003										
(Total deployment—18/08/03–25/09/03)										
1	Upper Truckee River	17.9	10.8	87	90	7.4	7.0	8.4	7.0	0.15
2	Taylor Creek	19.7	12.8	26	23	7.2	7.2	6.8	7.0	0.04 ^b
3	General Creek	16.8	10.8	48	48	7.4	7.2	7.7	7.5	0.03
4	Blackwood Creek	19.7	13.0	64	63	7.7	7.4	7.9	7.9	0.09
5	Incline Creek	14.3	9.0	69	65	7.0	7.2	9.5	8.5	0.08
6	Glenbrook Creek	12.1	7.5	394	384	7.8	7.1	8.4	6.6	<0.01
7	Squaw Creek	21.1	14.7	158	202	7.3	7.5	8.9	8.6	0.02 ^b
8	Truckee River at Farad	17.6	14.0	85	90	7.4	7.4	7.7	8.5	14.53
9	Truckee River at Mogul	18.9	14.0	89	92	7.5	7.5	8.2	9.4	10.85
10	Truckee River at Reno	23.2	15.3	112	113	8.1	7.8	7.8	9.2	8.10
11	Truckee River near Sparks	19.1	15.7	120	113	8.1	7.9	7.5	9.7	6.97
12	N Truckee Drain at Spanish Springs Road	23.5	21.0	452	420	7.7	8.4	7.4	11	0.20
13	N Truckee Drain at Kleppe Lane	21.5	19.3	623	606	8.2	8.2	6.3	11	0.37
14	Steamboat Creek near Mouth	24.7	21.9	533	619	7.7	NM ^c	5.8	NM ^c	2.52
15	Steamboat Creek at Cleanwater Way	24.0	19.3	468	468	7.7	8.2	6.7	13	1.30
16	Steamboat Creek at Short Lane	23.9	15.0	1160	977	7.9	7.9	7.6	10	0.19
17	Steamboat Creek at Gieger Grade	22.1	14.6	1900	1300	7.8	7.8	9.5	8.3	0.01
18	Steamboat Creek at Steamboat	22.6	12.2	248	290	7.1	7.3	6.5	7.8	0.02
19	Truckee River at Vista	21.3	18.2	232	268	7.3	7.4	7.4	8.4	10.11
20	Truckee River at Lockwood	22.8	18.4	241	237	7.8	7.8	8.7	9.8	10.11
21	Truckee River at Clark	22.3	18.7	228	199	8.0	7.8	8.9	8.6	10.29
22	Truckee River at Wadsworth	20.1	18.8	249	254	7.5	8.0	7.4	9.8	5.81
23	Truckee River at Marble Bluff Dam	22.1	19.5	345	347	8.1	8.2	7.8	8.2	5.83

^a Median flow for SPMD deployment period.^b Estimated value, no gage at this site.^c NM = not measured.

Landscape- and Reach-Scale Predictors of Large Wood Abundance in Low-Gradient Streams

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Abstract.—Wood is an important component of small to medium-sized streams in forested regions, but has been poorly studied in agricultural areas. Our goals were to (1) characterize the abundance, size, and distribution of wood in low-gradient streams in two agricultural regions, (2) quantify the influence of reach- and landscape-scale factors on the abundance and distribution of wood in these streams, and (3) compare trends across two study areas. Wood abundance was quantified in stream reaches in two diverse agricultural regions of the Midwestern United States: central Michigan and southeastern Minnesota. Wood abundance was quantified in 71 stream reaches, and an array of channel, riparian zone, and landscape features were characterized. Multiple regressions were conducted to predict abundance from those explanatory variables. We found that large wood was relatively scarce in these low-gradient streams compared to low-gradient streams in forested regions. Mean log size was greater, but total abundance was lower in Minnesota than Michigan. In Minnesota, greatest wood abundance and greatest extent of accumulations were predicted in wide, shallow stream channels with high substrate heterogeneity and woody riparian vegetation overhanging the channel. Models were dominated by reach-scale variables. In Michigan, largest densities of wood and accumulations were associated with catchments in hilly regions containing urban centers, with low soil water capacity, wide, shallow stream channels, low coarse particulate organic matter standing stocks, and woody riparian zones. Models contained both reach- and landscape-scale variables. Difference in the extent of agricultural and forest land use/cover between Michigan and Minnesota may explain the differences in the models predicting wood variables. Patterns in wood abundance and distribution in these Midwestern streams differ from those observed in high gradient regions, and in low-gradient streams within forested regions. This has important implications for ecosystem processes and management of headwater streams in agricultural regions.

INTRODUCTION

Coarse woody debris (herein referred to as large wood) is an important component of small to medium-size streams in forested regions, directly influencing stream morphology and many eco-

system properties and processes (e.g., Harmon et al. 1986; Gurnell et al. 1995; Gregory et al. 2003a). Historically, large wood was a prominent feature in streams across forested regions (Gurnell and Petts 2002). In some cases log jams stretched for kilometers in both small and large streams in the United States (Triska 1984; Maser and Sedell 1994; Bragg 2003). By the mid- to late 19th century, streams were cleared on a large scale to provide unobstructed waterways for

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navigation or transportation of harvested logs. Wood removal from rivers remains an active role of the U.S. Army Corps of Engineers (Harmon et al. 1986), and is still a statutory requirement of landowners and resource agencies in some parts of the world (e.g., England, Ireland, Australia).

Wood abundance in streams is regulated by a complex set of factors that act on the source of the wood itself, its delivery to the channel, and the myriad factors that control its retention and mobility in the channel. Both historic and current land management factors in riparian zones and floodplains influence wood supply (Murphy and Koski 1989; Elosegı and Johnson 2003; Petts and Welcomme 2003). In agricultural and urban areas, sources of wood and the retention capacity of streams are altered by management practices such as grazing, landscaping, riparian vegetation thinning or removal, dredging, and channelization.

The primary sources of wood in streams are derived from natural mortality, fire, disease, insect damage, ice/snow loading, and wind-throw damage to trees in the riparian zone or uplands (Keller and Swanson 1979; Swanson 2003). Processes such as soil mass wasting, bank undercutting and erosion, windthrow, ice storms, post fire toppling, hurricanes, and flooding transport this material into the stream (Benda et al. 2003). In some systems beaver are the primary vector transporting large volumes of wood to the channel (Naiman et al. 1986). Alteration of the hydrologic regime by stream channelization, wetland drainage, or urbanization frequently results in increased bank erosion, one of the primary mechanisms of wood input to low-gradient streams (Keller and Swanson 1979; Davis and Gregory 1994). Erosion processes are themselves regulated by geologic factors (e.g., soil type, topography), vegetation, hydrologic regime, weather/climate (e.g., flooding), and anthropogenic factors such as grazing, forest harvest, construction, urbanization, and agriculture. Thus processes regulating wood abundance range in scale from the local to the landscape.

Because wood fundamentally influences the structure and function of streams in historically

forested regions, identifying the factors that influence its abundance and distribution is essential for understanding how natural stream ecosystems are regulated. Many studies have examined the role of wood in forested catchments, but studies addressing relationships between landscape factors and wood abundance or distribution are less common (exceptions are Wing and Skaugset 2002 and Swanson 2003). There are several models that predict wood input to streams that incorporate local-scale variables such as riparian vegetative composition and structure, soil erosion, decomposition and wind-throw (Gregory et al. 2003b). These models are well suited for use in forested systems, but for the most part, do not account for mixed land-use scenarios (an exception is Downs and Simon 2001). Because many potential stream restoration activities involve increasing wood volume in stream channels, successful restoration efforts require a full appreciation of factors influencing wood abundance at relevant spatial scales. The goals of this paper are to (1) characterize the abundance, size, and distribution of wood in low-gradient streams in landscapes altered by agricultural and urban development, (2) quantify the influence of reach- and landscape-scale factors on the abundance and distribution of wood in these streams, and (3) compare these trends across two Midwestern U.S. regions. While addressing the second objective we tested the hypotheses that wood abundance and distribution are controlled primarily by reach-scale factors (e.g., riparian zone structure and composition, or channel features), and secondarily by landscape features that influence wood in streams through indirect control of reach-scale characteristics.

METHODS

Study Area

We studied in two regions of the upper Midwestern United States—central Michigan and southeastern Minnesota (Figure 1). In Michigan, the

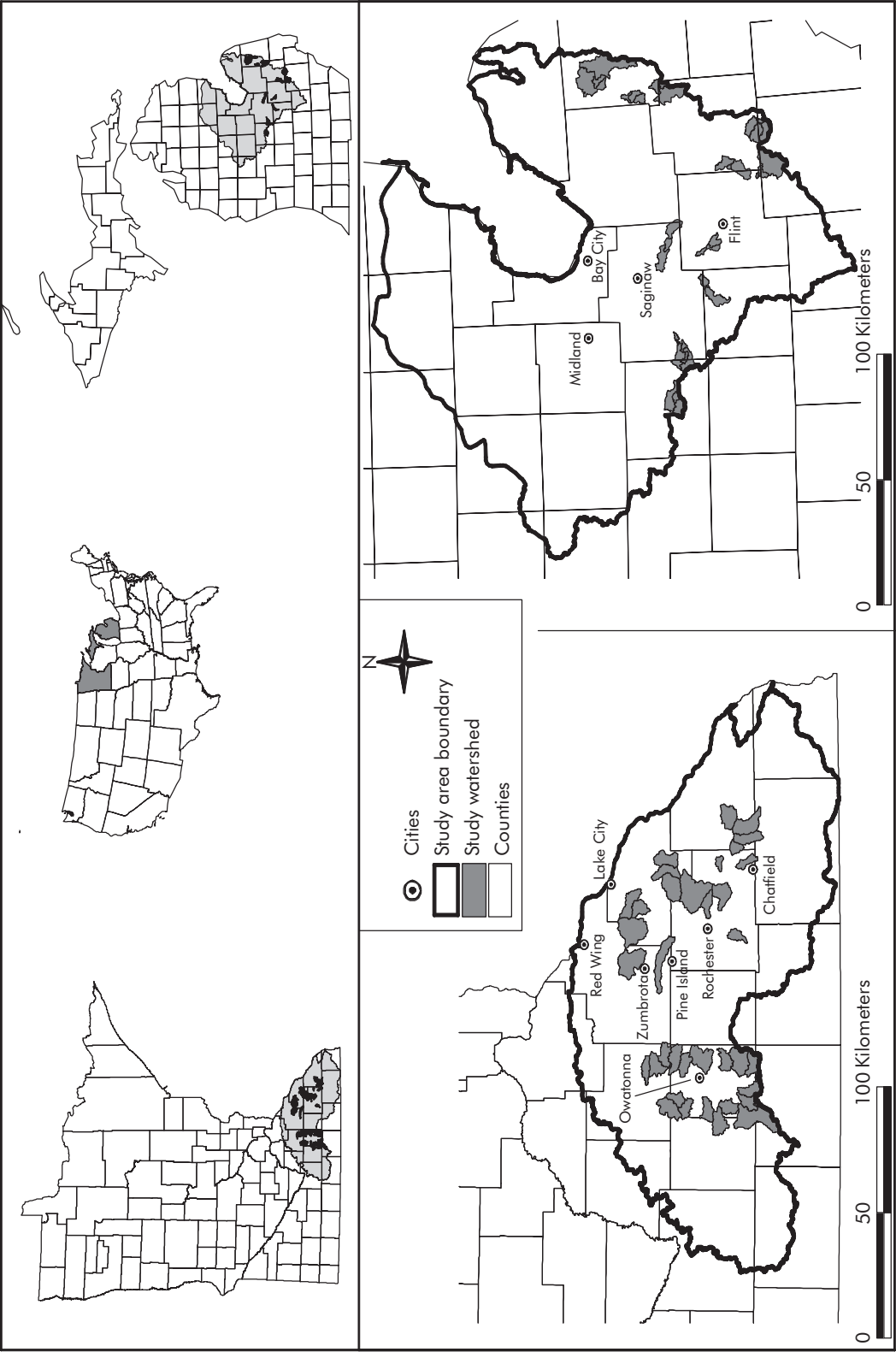


Figure 1. Study areas in southeastern Minnesota (left panel) and central Michigan (right panel), USA.

study area is characterized by sand and clay-dominated lacustrine plains interspersed with end- and ground-moraines and outwash plains. A full description of the study area is in Johnson et al. (1997) and Richards et al. (1997). Expanses of wetlands were present in the historic lakebeds of the Great Lakes, the great majority of which have been drained and are now under agricultural production (Comer et al. 1993). Inland forested regions (composing the majority of the study region) were logged for white pine and eastern hemlock between 1840 and 1900 (Quinlan 1997), and remnant forest patches now consist primarily of second-growth hardwoods. Current land use across the region is dominated by rowcrop agriculture (mean = 54.5%, range = 20–86%). Riparian vegetation includes manicured lawns, grass strips with or without shrubs and small trees, and a few mature second growth floodplain forests. Previous work (Richards et al. 1996, 1997; Johnson et al. 1997) has shown that both land use and Quaternary geology mediate the landscape's response to environmental stress. Our sampling design was chosen to reflect the variation in these factors. In Michigan, we sampled three replicate catchments/streams ($n = 12$ total), randomly chosen from a pool of candidate catchments that reflected the following combinations of land use and geology: lacustrine geology and agricultural land use; lacustrine geology with mixed land use, morainal geology and agricultural land use, and morainal geology with mixed land use. Morainal landforms are characterized by porous soils, are highly connected to the groundwater, and experience more stable flow regimes; lacustrine landforms are dominated by more poorly drained sands and clay soils, and hydrology is dominated by surficial processes that tend to be more flashy (Wiley et al. 1997). Mixed land-use catchments contain 50% or less agricultural land. Three first- to third-order reaches in each stream were studied, resulting in a total of 36 subcatchments ranging from 14.7 to 218.9 km² (Appendix 1). One reach was eliminated after impoundment by beaver flooded the channel to a depth that could not be

sampled without altering our sampling technique, resulting in a total of 35 reaches.

The study region in Minnesota encompassed five river basins in the southeastern part of the state (Figure 1), also chosen to reflect contrasting surficial geology and land use. Quaternary geology in this region is dominated by glacial remnants consisting of moraines, excised valleys in the loess covered plains, and highly eroded streams entrenched in Paleozoic-age bedrock. Historic land cover consisted of hardwood forests. Streams in the Cannon and LeSeur basins drain morainal geology, whereas streams in the Zumbro, Root, and Whitewater basins drain loess geology (Hobbs and Goebel 1982). In Minnesota, the morainal landform is poorly drained and hydrology is dominated by surficial processes, while the loess regions have porous soils with extensive interactions with the groundwater. Karst topography is also a prominent feature within the loess geology, accentuating groundwater–surface water interactions. Agricultural land averaged 73% and ranged from 49% to 92% of the study area (Appendix 1). Land-use patch density was almost half that of the Michigan study catchments, reflecting a landscape with a large number of extensive agricultural patches and fewer remnant forest and wetland patches. Minnesota catchments have lower topographic heterogeneity (Appendix 1). Richards et al. (1997) provided more detailed descriptions of the study region. Riparian vegetation associated with the agricultural areas on morainal landforms consists of grasses and sedges directly adjacent to the stream (2–10 m in width) with expansive areas of row crop beyond the embankment. Canopy cover in this area is provided by overhanging grasses with occasional shrubs or mature tree stands. Riparian vegetation in the loess geology is generally more extensive, including a mixture of grasses, shrubs, and forested buffer strips adjacent to the streams. Like our study catchments in Michigan, Minnesota catchments were selected to capture the variation in geology and land use in the region. In Minnesota, we randomly selected streams from

the pool of catchments fitting our land use and geology criteria, and sampled 36 second- or third-order streams in catchments ranging from 13.8 to 146.5 km² (Appendix 1).

Wood Abundance and Distribution

Wood was quantified during summer base flow conditions in 1996 in Michigan and 1999 in Minnesota. Wood abundance, log size, and wood accumulations were quantified within the bank-full channel. Wood volume was measured at three random transects across the channel at the top, middle, and end of the study reach using the line transect method (De Vries 1974; Wallace and Benke 1984). Volume analyses were performed from logs ≥ 5 cm diameter and ≥ 1.0 m length. Log diameter was measured at the base of the log.

The length of logs ≥ 5 cm diameter and ≥ 1 m in length was quantified across the entire reach. Data were summarized as the total length of wood/m² of stream bottom for a reach (m/m²). The data generated by this technique are referred to as total length density (TLD). The rapid assessment method was developed for this study because quantifying wood via the line transect method was prohibitively time-consuming where wood was abundant and was impractical for a study of 71 stream reaches.

Debris accumulations were broadly defined to include loose accumulations of logs and log dams. Accumulations ≥ 1 m² in area were counted for the entire reach and assigned a size-class based on the dimensions of the accumulation relative to the channel width at the upstream point of the accumulation location (Shields and Smith 1992). Accumulation size was subsequently estimated from stream width and size-class measurements. Data were summarized as total number of accumulations per 100 m reach (hereafter referred to as accumulation density) and accumulation area per 100-m reach (referred to as accumulation area). These measures are not significantly correlated with one another; therefore all are used as dependent variables in subsequent analyses.

Reach Features

In Michigan a stream reach of approximately 100 m was sampled. This usually incorporated more than one riffle-pool sequence and represented 10–20 times the stream width (Richards 1982; Bisson and Montgomery 1996). The downstream point of the reach was located at the first bend or approximately 100 m upstream of a road crossing or bridge. In Minnesota, a stream reach of approximately 30 times the average width was sampled, resulting in reaches of 100–250 m. A comprehensive set of parameters was measured within each reach, representing factors associated with channel morphology, habitat, riparian vegetation, and canopy cover (Table 1). Evidence of historical channelization was determined visually or deduced from channel profiles.

Obtaining detailed information about riparian zone composition and width is extremely challenging in these disturbed landscapes, because the width of the riparian zone is frequently smaller than the minimum resolution of the satellite imagery commonly used to map land use and land cover (Hollenhorst et al., in press). As a result, measurements and observations of riparian width and vegetative composition and height were obtained in the field from each bank at three points (beginning, middle, and end) along the reach (Table 1). Riparian zone width and height of the dominant vegetation community (recorded as one of five height classes) were recorded separately for the left and right banks, and the six values of each measure were averaged to derive mean values for each reach. The maximum width for riparian zones was set at 100 m.

Land use, hydrography, soils, and elevation databases were used to quantify landscape structure (Table 1). Land-use data were obtained from the National Land Cover Database (NLCD; Vogelmann et al. 2001). Land-use classes were aggregated into residential, commercial, row crop agriculture, pasture, forest, wetlands, and open water based on previous work (Johnson et al. 1997; Richards et al. 1997). Land-use values are

Table 1. Environmental variables measured during this study.

Variable	Description	Method/source
<i>Reach</i>		
Boulder*, cobble*, gravel*, sand*, fines*	proportion of substrate particles in each class	Osborne et al. 1991; Platts, et al. 1983; direct observations from 10 transects.
% riffle*	proportion of wetted area with riffles	Hawkins et al. 1993; direct observations from reach
% pool *	proportion of wetted area with pools	Hawkins et al. 1993; direct observations from reach
% run	proportion of wetted area with run	Hawkins et al. 1993; direct observations from reach
Maximum depth in pools*	greatest depth recorded in the reach (m)	Hawkins et al. 1993; direct observations from reach
Bank-full width*	mean bank-full width (m)	Osborne et al. 1991; Platts et al. 1983; direct observations from 10 transects
Bank-full depth	mean bank-full depth (m)	Osborne et al. 1991; Platts et al. 1983; direct observations from 10 transects
Flood height*	maximum bank-full depth (m)	Direct observations from 10 transects
# habitat types*	number of distinct instream habitat types	Direct observations from 10 transects
Manning's N*	index of channel roughness	Gore 1996; calculated from measurements at 10 transects
% open canopy*	proportion of wetted area not shaded by riparian vegetation	Armour et al. 1983; direct measurement from 10 transects
% CPOM*	habitat-weighted coarse particulate organic matter (CPOM) standing crops	mean of three samples per reach
Ditch*	evidence of channelization	visual observation and width:depth values
<i>Riparian</i>		
Riparian zone width*	width of the coverytype immediately adjacent to the river (m)	estimated at wood transect locations
Vegetation height*	vegetation cover type height (m)	estimated on both sides of river at wood transect locations
<i>Landscape</i>		
SD elevation*	elevation (m)	USGS Digital Elevation Model
Land use/cover*	proportion of land use/land cover in catchments (see text for variables used). (~30m resolution)	National Land Cover Database
Stream density*	total length streams/catchment area (km/km ²).	USGS, Digital Line Graph
Depth to bedrock*	mean depth to bedrock (m)	STATSGO; data are mapped by integrating downward through all soil horizons in each pedon and then doing a weighted spatial average over each area component of each soil association polygon.
Water capacity*	mean plant-available soil water capacity	STATSGO; see above
Permeability	mean soil permeability in catchment	STATSGO; see above
K-factor*	mean soil erodibility factor in catchment	STATSGO; see above
% organic matter*	mean soil organic matter in catchment	STATSGO; see above
% sand	mean soil % sand in catchment	STATSGO; see above
% clay	mean soil % clay in catchment	STATSGO; see above
Water yield*	annual water volume exported from catchment	calculated from SWAT model
Patch density	# land use/cover patches/ km ²	National Land Cover Database
Link*	number of first order streams entering above site	Shreve 1966
Stream order	assigned manually	Strahler 1964
Catchment area*	(km ²) from digital elevation (boundaries delineated manually and digitized from 1:24,000 USGS topo)	USGS Digital Line Graph, digital raster graphics
Population density*	individuals/km ²	TIGER census data

* indicates variables used in most analyses; others are omitted due to high correlations with other variables.

reported and analyzed as the proportion of total catchment area.

Soil characteristics were summarized using the STATSGO database obtained from the Natural Resources Conservation Service. We selected soil characteristics that influence catchment hydrology (i.e., depth to bedrock, water capacity, permeability, and proportion of sand and clay in catchment), erosion potential (K-factor from the Universal Soil Loss equation), and productivity (proportion of soils with high organic matter content in catchment). Values were averaged by depth for different soil layers and by area. Catchment water yield was derived from the SWAT model.

Stream orders (Strahler 1964) and link numbers (Shreve 1966) were assigned as an attribute of the stream data file derived from the USGS digital line graphs. The link number (number of first-order segments) in each catchment was counted manually from the digital 1:24,000 topographic maps. The standard deviation of elevation (SD elevation) within the catchment was used to represent topographic heterogeneity. Mean slope and elevation for the entire catchment were obtained from USGS 1° digital elevation models at a scale of 1:250,000. Valley slope was derived from elevation data using ARC/INFO algorithms. Stream length was estimated using TIGER (U.S. Census Bureau) data and converted to drainage density (km/km²). Population (individuals/km²) and road density (km/km²) were also estimated using TIGER census and transportation data respectively.

Data Analysis

We tested our hypotheses by (1) quantifying patterns in wood size, abundance, accumulation density, and area across the two study areas, and (2) predicting these variables from reach- and landscape-scale features. Analyses were performed using SAS v. 8.2 (SAS Institute Inc. 2000).

Distributional properties of all variables were assessed and appropriate transformations applied to nonnormal variables. Variables were

transformed as follows: square root transformations were performed on accumulation density, accumulation area, mean log diameter and length, and any count data; log transformations ($\ln(x + \frac{1}{2} \text{ lowest nonzero value})$) were performed on TLD, catchment area, and road and population density. Arcsine (sqrt) transformations were performed on percentages, including land use and geology data. Pearson correlations were performed for all the variables, and highly correlated variables ($r > 0.7$) with strong linear patterns were not included in the same analyses. Of special note, percent forest and percent residential were not included in the analyses due to high correlations with percent rowcrop and percent commercial, respectively; therefore, negative correlations with rowcrop agriculture should be interpreted as positive correlations with forest land cover, and percent commercial should be interpreted as percent-urban.

Multiple regressions were conducted using uncorrelated reach, riparian, or landscape variables to predict TLD, accumulation density, accumulation area, mean log diameter, and mean log length. Automatic stepwise selection methods in regression have been shown to be problematic (James and McCulloch 1990); therefore, an all subsets regression procedure (PROC REG; SAS Institute Inc. 2000) was used to generate the top models for each wood variable. We then conducted an extensive set of diagnostic tests to select the best model from that group. We examined models containing five or fewer independent variables and ranked them by Akaike Information Criterion (AIC), Mallows' Cp statistic (Draper and Smith 1981), R^2 values, and P -values of independent variables. Variance inflation factors and condition indices were then examined to assess the degree of collinearity among independent variables (Belsley et al. 1980). The best candidate models were further examined using partial regression leverage plots, plots of residuals versus independent variables, and the Wilkes-Shapiro statistic to examine the assumption of a normal distribution of the residuals. Influential outliers were identified using

Cook's Distance (Draper and Smith 1981). Models were evaluated by comparing AIC values. Where AIC values and other diagnostics were similar, the model with the smallest number of variables was selected. To assess the relative importance of the selected variables within a model we examined the standard partial regression coefficients. These measures are free of the original measurement scale, thus, their magnitudes can be compared directly to show the relative strength of the effects of several independent variables on the same dependent variable (Sokal and Rohlf 1995). Standard partial coefficients express the rate of change in the number of standard deviation units of the dependent variable that is caused by one standard deviation of change in an independent variable, with all other independent variables held constant.

To assess whether data from the two study regions could be combined into a single data set, we examined differences in wood measures and independent variables across the two states. We found that the means of all wood variables and many of the independent variables differed across the two regions. In addition, we conducted an all subsets regression, as described above, and inserted a dummy variable for the states. We

found that the majority of the resulting models included "State" as one of the predictor variables. We concluded that these differences did not warrant a combined analysis and, therefore, added a third objective to compare trends across the two study regions.

RESULTS

Abundance, Size, and Distribution

Wood in both sets of study streams was sparse and the mean size of individual logs was small (Table 2). In Michigan only 1 of the 35 reaches (4%) had no wood \geq 5 cm diameter and 1.0 m in length in the study reach; however, 16 of the 34 reaches with wood had no wood \geq 5 cm diameter and 1.0 m in length on the transects. Logs were generally small (mean log diameter was 9.4 cm); 68% of logs on transects were between 5 and 10 cm in diameter, 20% were between 10 and 15 cm. There was a mean of 6 wood accumulations occupying a mean area of 73 m² per 100 m of reach.

Minnesota streams contained less wood on average than Michigan streams, but logs were slightly larger. Wood was absent from 7 of 36

Table 2. Mean \pm 1 SE (range) of wood measures in Michigan and Minnesota streams. See Methods for descriptions of wood variables. Unless otherwise noted, $n = 35$ in Michigan and $n = 36$ in Minnesota.

Wood measure	Michigan		Minnesota	
	All sites	# sites > 0	All sites	# sites > 0
<i>Abundance</i>				
Total length density (m/m ²)	0.25 \pm 0.05 (0–1.17)	34	0.07 \pm 0.01 (0–0.27)	28
Volume (m ³ /m ²)	0.0023 \pm 0.0009 (0–0.0312)	18	0.0017 \pm 0.0005 (0–0.0117)	26
<i>Log Size (from transects)</i>				
Mean diameter (cm)	4.8 \pm 0.9 (0–0.2)	$n = 18$ 9.4 \pm 0.6	8.9 \pm 1.2 (0–0.2)	$n = 26$ 12.3 \pm 1.1
Mean length (m)	1.37 \pm 0.28 (0–5.43)	2.670 \pm 0.33	2.63 \pm 0.40 (0–8.99)	3.65 \pm 0.41
<i>Accumulations</i>				
Number accums/100 m	6.0 \pm 1.0 (0–18.0)	7.9 \pm 0.9	8.0 \pm 1.0 (0–24.0)	10.8 \pm 1.2
Accum area/100 m	72.9 \pm 15.2 (0–306.6)	98 \pm 18	185 \pm 43.4 (0–1184.0)	247 \pm 53

reaches (19%), while 31% of reaches had no logs on the transect. Almost 55% of logs were less than 10 cm in diameter, and about 30% were between 10 and 15 cm (Figure 2). Mean log diameter was 12 cm. There was a mean of 8 accumulations per 100 m reach; accumulations covered a mean of 185 m² per 100 m of reach.

Predicting Wood Abundance

For Michigan streams, models predicting TLD contained variables representing both landscape and reach scales (Tables 3, 4). TLD was best predicted by landscape-scale variables, including percent commercial land, soil water holding capacity, catchment area, and substrate coarse particulate organic matter (CPOM). Commercial land use and soil water holding capacity had the largest standardized coefficients and thus explained the greatest amount of variance in the

model (Table 4). The best model of accumulation density predicted only 58% of the variance, and the best predictors were percent commercial (with the largest standardized coefficient), bank-full width, road density, drainage density, and number of habitat types. Accumulation area was best predicted by bank-full width (with a large standardized coefficient), percent commercial land, and soil water holding capacity. Substrate CPOM, SD elevation, and percent gravel substrate were the best predictors of log diameters while percent sand substrate, riparian vegetation height and maximum depth best predicted mean log length per reach.

In Minnesota, the number of habitat types (highest standardized coefficient), riparian vegetation height, and percent wetland in the catchment were the best predictors of TLD (Tables 3, 4), representing reach and landscape scales. Accumulation density was well predicted (82%)

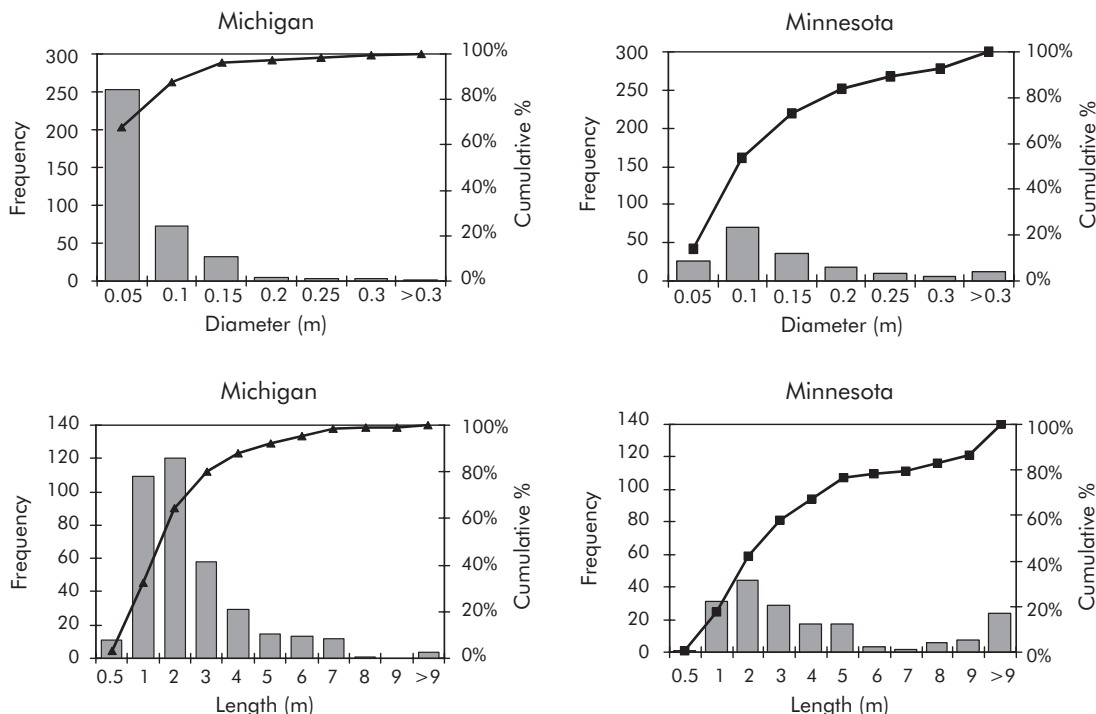


Figure 2. Frequency distribution (bars) and cumulative frequency of diameter and length (curves) of 372 logs measured on transects in 35 Michigan stream reaches and 181 logs from 36 Minnesota streams (minimum diameter ≥ 5 cm and ≥ 1 m length).

Table 3. Regression models for each wood variable. Variables are listed in order of their influence on the model, based on standardized coefficients. Unless otherwise noted, $p < 0.0001$. See Methods for transformations applied to variables. (Abbreviations as follows: riparian veg. ht. = riparian vegetation height; CPOM = coarse particulate organic matter; max depth = maximum depth).

Wood variable	Michigan ($n = 35$)	Minnesota ($n = 36$)
Total length density	adj $r^2 = 0.62$ $-3.81 + 14.11$ (% commercial ^a) $- 0.20$ (H_2O capacity ^a) $+ 1.67$ (catchment area) $+ 0.60$ (CPOM)	adj $r^2 = 0.68$ -7.9 ± 2.9 (# habitat types) ± 0.12 (riparian veg ht) ± 7.59 (% wetland)
Accum density	adj $r^2 = 0.58$ $4.52 + 21.3$ (% commercial ^a) $+ 0.27$ (bank-full width) $- 4.53$ (road density) $-$ 2.88 (drainage density) $- 2.35$ (# habitat types)	adj $r^2 = 0.82$ $6.0 - 3.0$ (% open canopy) $+ 11.2$ (catchment organic matter ^b) $+ 0.32$ (link) $- 3.3$ (% rowcrop ^b)
Accum area	adj $r^2 = 0.77$ $-0.63 + 2.1$ (bank-full width) $+ 59.1$ (% commercial) $- 0.88$ (H_2O capacity ^a)	adj $r^2 = 0.80$ $-3.6 + 1.8$ (bank-full width) $+ 26.7$ (% pasture ^b) $- 8.3$ (% open canopy)
Mean diameter	adj $r^2 = 0.61$ ($n = 26$) $0.38 - 0.05$ (CPOM) $+ 0.01$ (SD elevation) $- 0.08$ (% gravel substrate)	adj $r^2 = 0.54$ ($n = 18$) $0.40 - 0.13$ (ditch) $- 0.14$ (max depth) $+$ 0.14 (Manning's N) $+ 0.01$ (riparian veg. ht.)
Mean length	adj $r^2 = 0.61$ ($n = 26$) $2.3 - 0.82$ (% sand substrate) $+ 0.09$ riparian veg. ht. $- 1.20$ (max. depth)	adj $r^2 = 0.66$ ($n = 18$) $2.1 + 0.17$ (bank-full width) $+ 0.54$ (% cobble substrate) $- 1.03$ (catchment area)

^a In MI, forest land cover is negatively correlated with soil water capacity ($r = -0.59$). Commercial land use is highly correlated with residential land use ($r = 0.79$); therefore, we use urban to reflect the composite land use type, although commercial was the variable used in the analysis.

^b In MN, forest land cover is correlated with rowcrop agriculture ($r = -0.81$); % pasture ($r = 0.65$); catchment organic matter ($r = -0.57$).

variance explained) in Minnesota streams from percent open canopy (highest standardized coefficient), catchment soil organic matter, link number and percent rowcrop. Bank-full width, percent pasture, and percent open canopy were the best predictors of accumulation area. Log diameter models for Minnesota streams contained the ditch variable, along with maximum depth, Manning's N and riparian vegetation height. Mean log length per reach was best predicted by bank-full width (highest standardized coefficient), percent cobble substrate, and catchment area.

Models of wood volume from both study regions had nonnormal residuals that could not be corrected by transforming the data. Logistic regression models all showed a lack of convergence for the maximum likelihood estimate and high overlap between the reaches with and without wood on the transect. As a result, our predictive models focus on TLD as a measure of

wood abundance, and accumulation density and area as measures of wood distribution; wood volume is discussed only in relative terms.

DISCUSSION

Factors operating at both the reach and landscape scales account for the patterns in wood abundance, distribution, and size observed in streams across this Midwestern landscape. These relationships, however, are complicated by current land-use patterns, the underlying structure of the landscape, and the disturbance history of the region.

Patterns of Wood Abundance and Size

The study streams contain a lower abundance of wood (measured as total length of wood per reach) and smaller logs in comparison with forested temperate streams (see reviews by Gurnell

Table 4. Summary of the spatial scales of independent variables predicting wood variables. Standardized coefficients (Sokal and Rohlf 1995) are shown in parentheses. (See Table 3 notes and Methods for further explanation of the independent variables used in the analyses and abbreviations. MI = Michigan; MN = Minnesota).

Wood - variable	State	Scale		
		Reach	Riparian	Landscape
Total length density	MI	CPOM (0.36)		% commercial (0.56) ^a soil water capacity (−0.52) ^b catchment area (0.44)
	MN	# habitat types (0.62)	riparian veg. ht. (0.36)	% wetland (0.36)
Accum density	MI	Bank-full width (0.40) # habitat types (−0.29)		% commercial (0.53) ^a road density (−0.37) drainage density (−0.36) soil organic matter (0.39) link # (0.38) % rowcrop (−0.31) ^a
	MN		% open canopy (−0.73)	
Accum area	MI	Bank-full width (0.77)		% commercial (0.37) ^a soil water capacity (−0.37) ^b
	MN	Bank-full width (0.46)	% open canopy (−0.36)	% pasture (0.43) ^c
Mean diameter	MI	CPOM (−0.76) % gravel (−0.51)		SD elevation (0.74)
	MN	ditch (−0.61) max depth (−0.45) Manning's N (0.44)	riparian veg. ht. (0.33)	
Mean length	MI	% sand (−0.67) max depth (−0.53)	riparian veg. ht. (0.60)	
	MN	bank-full width (0.75) % cobble (0.37)		catchment area (−0.35)

^a Commercial land use is highly correlated with residential land use ($r = 0.79$); therefore, only commercial was included in the models. This variable should be interpreted as urban land use.

^b Soil water capacity is negatively correlated with forest land cover ($r = -0.59$).

^c Pasture is positively correlated with forest land cover ($r = 0.64$); rowcrop agriculture is highly, negatively correlated with forest land cover ($r = -0.81$). Forest land cover was not included in the analyses.

et al. 1995; Eloisegi and Johnson 2003). However, direct comparison among studies is difficult, due to inconsistencies in the minimum size of logs considered and a lack of studies in similar streams or landscape types. The definition of coarse woody debris has varied greatly across studies, ranging from >1 cm diameter (e.g., Diez 2000), ≥ 5 cm diameter (Gregory et al. 1993), ≥ 10 cm diameter and >1 m length (Murphy and Koski 1989; Carlson et al. 1990; Richmond and Fausch 1995), ≥ 10 cm diameter and ≥ 2 m length (Bilby and Ward 1991), to ≥ 20 cm diameter and ≥ 1.5 m long (Robison and Beschta 1989). Logs with diameters ≥ 10 cm (the most common definition of large wood) were rare in

our study streams (Figure 2). Since we were working in a mixed land-use region, we adopted Gregory et al.'s (1993) criteria of log dimensions of ≥ 5 cm diameter as the minimum log size.

The use of widely ranging minimum log lengths makes it difficult to compare wood abundance across regions; however, some generalizations are possible. Large wood in disturbed streams the world over is highly depleted, and remnant logs are small in size (Eloisegi and Johnson 2003). In our study, the volume of wood is similar to recently cleared reaches in an agricultural stream in Tennessee (Shields and Smith 1992), and exceeded that observed in a first-order agricultural reach of a Spanish stream, but not

the second-order reach (Diez 2000). Many streams in agricultural areas of Germany completely lacked wood (Reich 1999; Gerhard and Reich 2000; Hering et al. 2000), or had fewer wood accumulations adjacent to agricultural areas, as observed in the Ain River of France (Piégay 1993). Wood clearing is a common practice in those regions, as it is in the Midwestern United States.

In comparison to forested regions, wood density in these Midwestern streams was much lower (Gurnell et al. 1995). In a typical example, two low-gradient streams with forested floodplains in Georgia had much higher wood volumes (Wallace and Benke 1984) compared to those in the mixed land-use catchments in our Michigan streams. Wood was not scarce in all these Midwestern streams, though. Several of the Michigan streams with forested riparian zones contained wood abundance comparable to some old growth forest streams (Gurnell et al. 1995).

Although wood volume in these Midwestern streams was similar to some disturbed (likely by harvest before 1900) Rocky Mountain streams (Richmond and Fausch 1995), the mean log diameter was smaller. The low abundance of wood and small logs in our study is consistent with the disturbance history of the region. Michigan forests were logged from 1840 to 1900 and then subjected to widespread fires (Quinlan 1997). Minnesota forests also experienced extensive logging during the 19th century; consequently, the potential for input of large logs is very limited.

While wood density is low, the accumulation densities in this study are similar to or greater than those encountered in some forested streams (Gregory et al. 1993), an uncleared agricultural stream in Tennessee (Shields and Smith 1992), a managed stream with mixed land use in England (Gregory et al. 1993), and a third order forested stream in New Hampshire (Bilby and Likens 1980). The low abundance, but similar accumulation densities suggest that accumulation sizes are probably small compared to forested streams; however, because no standard methods exist for

quantifying accumulation size, comparisons across studies are not easy.

Wood enters low-gradient streams through blowdown, bank erosion, and ice loading (Keller and Swanson 1979). In both Michigan and Minnesota, we noted that downed trees resulted predominantly from undercut banks and bank erosion. In addition, numerous new limbs and tree fragments were observed in the streams after intense summer storms. Hillside mass wasting and avalanches typical of montane topography move large volumes of wood into high gradient stream channels in a very short time (Swanson and Lienkaemper 1978; Lienkaemper and Swanson 1987). In contrast, bank erosion and storm damage deliver smaller amounts of wood to the channel in low gradient streams.

Predicting Wood Size, Abundance, and Distribution

We expected that wood size would be a most influenced by riparian conditions (e.g., riparian zone vegetative composition and width) and channel size, whereas wood abundance was expected to be limited by reach, riparian, and landscape-scale features that control the source, input, and retention of wood. We also expected that accumulation density and size would be most influenced by reach-scale features, because the formation of wood accumulations typically requires a physical obstruction such as a boulder, downed tree, point bar, or island in the channel (Gurnell et al. 2002; Abbe and Montgomery 2003). Riparian vegetation did not play as prominent a role in the models predicting log size and abundance as anticipated. (Riparian vegetation height was included in the model of TLD and log diameter in Minnesota but had the lowest standardized coefficient in those models and was not included at all in the Michigan models.) As expected, landscape-scale variables were important predictors of TLD, and both reach- and landscape-scale variables were included in the models of accumulation density and accumulation area. The resulting models for the two study regions

suggest that different factors are influencing wood abundance and distribution.

In Minnesota, the largest logs, greatest wood abundance, and greatest extent of accumulations were predicted in catchments with wide, shallow channels with high substrate heterogeneity, and woody riparian vegetation overhanging the channel. The dominant predictors of wood in these models were reach-scale variables that influence wood retention (number of habitat types) and wood supply (percent open canopy). Landscape-scale variables included in the models were related to channel size (e.g., catchment area, link number), and to a lesser extent, land-use types that influence the wood supply (e.g., presence of forest and pasture land; Table 4).

In Michigan, landscape-scale features played a greater role in predicting wood size, abundance and distribution compared to Minnesota. Largest densities of wood and accumulations were associated with wide, shallow stream channels with low CPOM standing stocks, catchments in hilly regions containing urban centers with low soil water capacity, and woody riparian zones (Tables 3, 4).

Reach-scale features.—Wood size has been well predicted in other studies from channel width alone. For example, Bilby and Ward (1989), in the Pacific Northwest, explained 79% of the variance in wood diameter and length, with those variables increasing with channel width. This pattern is observed repeatedly in the literature (Gurnell et al. 1995). The best predictors of log size in these Midwestern streams were reach-scale variables reflecting substrate characteristics (e.g., bed roughness) and channel morphology (e.g., width, lack of channelization). The strong relationship with channel width found by Bilby and Ward (1989) is likely due to their study's location in old-growth forests, where large wood in the upland and the channel is abundant, logs are very large, and mobility is restricted by the size of the log relative to the channel size. Our Midwestern U.S. study streams have been exposed to numerous large-scale disturbances ranging from forest harvest and fire late

in the 1800s to channelization and other land management practices in modern times. Channelization modifies riparian zones and reduces sources of larger diameter logs; furthermore, the size of the log relative to the size of the channel is small, enhancing the probability that logs will be exported from the reach.

In contrast to the strong log diameter–channel width relationship, observed relations between wood abundance and channel characteristics have varied in the literature. A strong positive relationship between wood volume or frequency and channel width has been reported by several studies (Bilby and Ward 1989; Murphy and Koski 1989; Robison and Beschta 1989), but others have not observed this pattern (Carlson et al. 1990; Richmond and Fausch 1995; Beechie and Sibley 1997). This may be due to differences in the minimum log sizes included, wood-censusing techniques, or how the data were summarized. For example, when Beechie and Sibley (1997) expressed wood frequency on an areal basis, there was a negative correlation with channel width, but no significant relationship was observed when wood frequency was expressed per length of channel.

Riparian factors.—Interestingly, the width of the riparian zone was never a significant element of any of the predictive models. However, riparian vegetation height (reflecting differences between grass, shrub, and woody vegetation) and/or the amount of canopy cover were important predictors of TLD, abundance density and area in Minnesota, where woody vegetation and closed canopy cover were consistently associated with larger wood metrics. Current and historic management practices have altered the composition and width of the riparian zone throughout the Midwestern United States. Modification of riparian vegetation can rapidly influence the characteristics of the wood in a stream, because the source-distance area for wood in a stream is typically less than two tree lengths (about 20–30 m; McDade et al. 1990; Robison and Beschta 1990; Gregory et al. 2003b). The source-distance is dependent upon geomorphic factors such as

slope, soil type, and age and species composition of the riparian vegetation. Disturbances in the riparian zone are detectable within a short time frame and persist for a long time. Bilby and Ward (1991) reported a change in log size in streams and changes in species composition within 5 years of harvest. After 100 years, lower wood volume and log sizes were still evident in some Colorado Rocky Mountain streams (Richmond and Fausch 1995) and Alaska, where recovery to preharvest levels is predicted to take more than 250 years (Murphy and Koski 1989).

In the Midwestern United States, the effects of riparian vegetation harvest and conversion are exacerbated by channelization, which, in addition to enlarging the channel, and disturbing bank-side vegetation, mechanically extracts roughness elements such as boulders and logs to enhance drainage from adjacent farm fields. The result is complete removal of all remnant and modern-day wood from the channel and a functional simplification of the stream channel.

Riparian stewardship practices of individual landowners are important factors controlling the abundance of wood in streams, since both economic and social/ethical issues affect a landowner's choice of management practice (R. L. Ryan, University of Michigan, personal communication). As a result, the factors influencing the absence of wood at a reach are more difficult to predict than those influencing its presence.

Landscape-scale factors.—Agricultural land cover was expected to be associated with lower wood density, and forest land use was expected to be associated with greater wood density. Contrary to expectations, these land use and cover classes, which directly influence wood supply, were not strong predictors in the models (Table 4), especially in Minnesota. Instead, we found that commercial land use (representing "urban land") was a strong predictor in models of TLD and accumulation density in Michigan. Urban land use in Michigan may provide a source area for wood, since it is positively associated with woody riparian vegetation, wider riparian zones,

and more closed canopy cover. The simplistic explanations for the positive relationships between wood and urban land use are that humans prefer to live in areas with trees and water, and development in this region is concentrated along water bodies. Lending support to this explanation is the observation that the mean population density in Michigan watersheds is more than 4 times that in Minnesota. Another landscape variable that was included in TLD and accumulation area models was soil water capacity. This variable is negatively correlated with sandy soils and forest land cover, and therefore may also behave as a land-cover surrogate related to wood supply.

In Minnesota, landscape variables were not as prominent in the models, and when they were included in a model they did not have large standardized coefficients (Table 4). Two land-cover variables that were included (percent pasture and percent rowcrop) in the models (albeit with low standardized coefficients) were related to wood supply. Improved methods for representing land use in a catchment (e.g., flow-weighted distance which accounts for the spatial position of landscape features) would better reflect the reality of wood delivery to streams and would potentially increase the importance of land use in predicting wood abundance in Midwestern streams. These assessments would be most important in catchments with homogeneous landscapes, where proximity of urban or agricultural patches relative to the stream and the size and contiguity of riparian zones could directly or indirectly affect wood supply and retention.

Study area comparison.—Differences in the explanatory models between the two states are likely due to differences in land-use patterns. There are significant differences between Minnesota and Michigan in percent forest in the watershed (averaging 4.4 and 20.1 respectively), as well as percent rowcrop (73% and 54%, respectively). Furthermore, land-use patch density in Minnesota is one-half that of Michigan, because the landscape is dominated by large agricultural

patches with few forest or wetland patches. Overall, the Minnesota study catchments are much more homogeneous in terms of land use, compared to Michigan. In such a homogeneous landscape, local-scale features within the riparian zone and stream channel are most likely to exert an influence over the wood supply and instream retention processes. In ongoing work (J. J. Hutchens, Coastal Carolina University, and co-workers, University of Minnesota Duluth, unpublished data), we have found that macro-invertebrate assemblages and habitat are well predicted by landscape factors in these Michigan and Minnesota streams. However, despite obvious impacts of agricultural land-use practices on the stream ecosystem, land use is not included among the predictor variables in Minnesota, probably due to the small variation in land use across that landscape.

Two additional factors, topography and surficial geology, may also explain some of the differences in the models between the two study regions. Topographic heterogeneity (SD elevation) in Michigan is more than twice that of Minnesota. The hilly regions in Michigan are associated with morainal landforms with very stable flow regimes that are retentive of large wood. Wood accumulations on those landforms are larger and older (data not shown); in some locations, logs and whole accumulations are almost completely encased in marl—strong evidence that the logs have not moved for some time. The hillier regions in Minnesota are associated with morainal landforms that are heavily farmed; wood supplies there are heavily depleted in both the upland and the riparian zones. Furthermore, the hydrology is characterized by flashy flow regimes that tend to be less retentive of wood. Land use and surficial geology are highly correlated in this glaciated landscape (for example, agriculture is not associated with coarse soils); therefore, the regional differences in wood variables between the two study areas are most readily explained by the interactions between land use, geology, and hydrology.

Hierarchical Relationships among Factors Influencing Wood

The abundance of wood in a reach was hypothesized to be controlled by factors operating at reach scales, with these factors being hierarchically influenced by landscape factors. These hypotheses are supported in both states, where models for TLD, accumulation density and area in Michigan included features that incorporated wood supply (percent urban), channel morphology (bank-full width), and landscape features that influence flow regimes (catchment area, soil water capacity, drainage density). In Minnesota, wood supply variables (e.g., riparian vegetation or canopy cover) or stream morphology (e.g., instream habitats or bank-full width) were the most common predictors in the models. Bankfull width, however, is largely controlled by larger-scale features, such as catchment size (Richards 1982) or link number (a predictor of accumulation density). This agrees with our previous findings of strong hierarchical control of reach-scale features by landscape-scale variables, such as catchment size (Richards et al. 1996, 1997).

Role of Wood

Among the most important roles attributed to wood in streams are changes in channel morphology that result in greater physical habitat diversity. Specific roles include formation of plunge pools (e.g., Bilby and Ward 1991; Hilderbrand et al. 1997), changes in the number, location, and volume of pools (e.g., Fausch and Northcote 1992; Richmond and Fausch 1995; Kennard et al. 1998), lateral adjustment in the channel (Gregory et al. 1993; Nakamura and Swanson 1993; Nakamura and Swanson 2003), and changes in the longitudinal profile of a river (Smith et al. 1993; Beechie and Sibley 1997). Morphological changes in the channel that are attributed to wood can influence wood mobility and retention. We found a mild association between wood size (length and/or diameter) and

channel depth, as well as with the total number of instream habitats. However, we found no correlation between wood abundance and the proportion of a reach with pools or with the maximum depth of pools, suggesting that wood does not play a major role in generating habitats in these streams. The low density of wood, small size of logs, and their mobile nature are the most likely reasons that wood abundance does not play a structural role in these Midwestern stream channels.

While wood did not generate stream habitats in these agricultural and developed streams, wood does play a critical role in regulating biotic communities. Increases in biodiversity have been associated with wood as an energy source, a physical substrate, a geomorphic element, a feature creating additional habitat complexity in the channel, and a mechanism retaining sediment and organic matter (Wondzell and Bisson 2003). Specifically, wood habitats in streams are associated with higher macroinvertebrate biodiversity compared to other habitats (Benke and Wallace 2003; Johnson et al. 2003; Wondzell and Bisson 2003). In the Minnesota streams, regional macroinvertebrate biodiversity was found to be heavily dependent on wood, with 95% of total taxa being found in association with wood habitats. Local biodiversity increased by an average of 10 taxa when wood was present in a reach (Johnson et al. 2003). Similar trends in macroinvertebrate biodiversity were found in the Michigan streams, as well as wood in soft bottom lowland streams in New Zealand (Maxted et al. 2003).

The importance of wood for fish assemblages is difficult to discern for Midwestern streams because studies of fish assemblages that implicitly incorporate wood as a habitat element are rare. Contrary to macroinvertebrate assemblages, we found that fish assemblages in our Minnesota streams were not directly associated with the presence of large wood, as were the macroinvertebrates. Rather, the greatest variance in fish assemblage composition was related to maximum stream temperature, substrate CPOM, and

channelization; as noted above, however, channelized streams were associated with lower wood abundance. The width of the riparian zone and the presence of debris dams were only moderately correlated with the dominant fish species in a Redundancy Analysis (RDA) (J. A. Schuldt and coworkers, University of Wisconsin, Superior, unpublished data). Similar trends were observed in the Michigan streams (R. Haro and coworkers, University of Wisconsin, La-crosse, unpublished data). Conversely, a strong relationship between fish growth and wood was found in Kansas prairie streams, in which the amount of large wood was found to influence growth rates of creek chub *Semotilus atromaculatus*, red shiner *Cyprinella lutrensis*, and green sunfish *Lepomis cyanellus* (Quist and Guy 2001). The lack of attention to this area of research in the Midwest is in sharp contrast to forested regions, where strong links between fish and large wood in small streams (Dolloff and Warren 2003) and large rivers (Zalewski et al. 2003) have been observed. More research in Midwestern streams would clarify the patterns to allow similar generalizations.

Control of Wood Abundance and Distribution

The abundance and distribution of wood along the longitudinal gradient in high-gradient streams differs significantly from that in the low-gradient streams of our study areas. In high-gradient streams, wood in the channel is regulated by catchment area, stream width, riparian vegetation age, log decomposition rate, and time since the last transporting floods (Abbe and Montgomery 1996; Nakamura and Swanson 2003; Swanson 2003). Large wood is largely transport-limited in the headwaters, because log movement is restricted by the size of the channel, relative to that of the logs. In intermediate-sized streams, stable structures such as log jams and boulders entrain wood in the channel, and channel morphology (including sinuosity, width and depth, or presence of point bars and islands)

is the most important factor regulating the location of accumulations in larger channels. Wood tends to be supply- rather than transport-limited in those larger reaches (Swanson 2003). In contrast to high-gradient, forested systems, our Midwestern streams are supply-limited in the headwaters but neither supply- nor transport-limited in the intermediate-size channels (Figure 3). Headwater streams in low-gradient regions are highly accessible to development and management practices that deplete wood supplies (e.g., channelization, plowing adjacent to stream bank, conversion of woody vegetation to lawn). Further, due to the small size of the logs, lack of retention structures such as large boulders, and the flashy flow regimes associated with altered hydrology and channel morphology, wood recruited into the channel is rapidly exported downstream. In ten streams in our Michigan study area, 50% of tagged logs were

transported more than 5 m from their original location over one winter (Johnson 1999). In contrast, tagged logs in the Andrews Experimental Forest moved only during extreme flood events (F. J. Swanson, Oregon State University, personal communication). Although Gregory et al. (1993) demonstrated that logs not associated with an accumulation (or not buried) were more likely to be mobilized and transported out of the reach, this was not the case in our Michigan streams, where logs in accumulations were equally as mobile as isolated logs in the channel (Johnson 1999).

In this study we used a minimum log diameter of 5 cm (and > 1.0 m length). We recognize that our methods have overestimated the total abundance of wood compared to forested streams where larger minimum log criteria were used. Our use of a smaller diameter recognizes that wood in these disturbed streams is composed of smaller logs than were present under undisturbed conditions. Had we used the larger diameter logs our models would very likely have shown stronger relationships with instream conditions, particularly bank-full width (as per models of Bilby and Ward 1989). However, patterns of development have fundamentally changed the landscape and channel morphology in the Midwestern United States, breaking down those relationships, especially in headwater streams where development has had the greatest impact.

Where patterns of wood abundance have been quantified across a gradient of stream sizes, wood abundance and accumulation densities are greatest in small streams (e.g., Gurnell 2003). Trends demonstrated in this study, however, show that headwater streams have less wood relative to the larger streams (Figure 3). Because headwater streams represent the majority of river miles and perform many important ecosystem functions (Meyer and Wallace 2001), woody vegetation removal from the riparian zone in these headwater streams represents a permanent loss of wood and other sources of organic matter from the channel. Such losses can result in fundamental changes to the ecosystem; including shifts in the food web from heterotrophy to autotrophy,

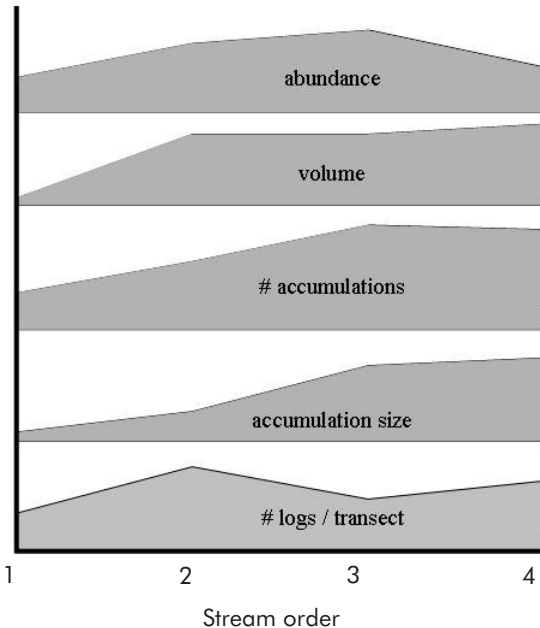


Figure 3. General trends in the amount and size of large wood with respect to increasing stream order. Data are derived from Michigan streams, which ranged from 3 to 13 m in width and from first to fourth order. Patterns are similar in Minnesota streams. The y-axis represents increasing values of each wood measurement.

and reduced potential for downstream colonization from headwater source populations.

The important role of wood in temperate streams is well recognized, and stream managers, along with advocacy organizations, such as Trout Unlimited, continue to support or implement stream improvement projects that either employ large wood or mimic the role of large wood for habitat improvement. Yet few studies have documented the successes of these improvements in rehabilitating or improving biotic communities (Kerschner 1997), but when they do, biological improvements appear to lag behind improvements to the physical habitat (Larson et al. 2001). The benefits of healthy riparian zones, in contrast, have been well documented with respect to moderating temperature extremes, retaining nutrients and sediments, as well as providing large wood and other energy sources (Gregory et al. 1991). Therefore, management goals geared towards conserving and restoring woody riparian vegetation will also provide the added benefit of increasing potential sources of large wood.

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Appendix 1. Descriptive statistics for channel, riparian, and landscape variables for Michigan ($n = 35$) and Minnesota ($n = 36$). Values represent means ± 1 SE (range). (CPOM = coarse particulate organic matter). (* Indicates variables used in most analyses; others are omitted due to high correlations with other variables.)

Variable	Michigan	Minnesota
Channel morphology		
Average width (m)	5.2 \pm 0.3 (1.9–10.2)	5.4 \pm 0.3 (2.9–11.2)
Bank-full width (m)*	6.3 \pm 0.3 (3.7–12.1)	6.8 \pm 0.4 (3.5–13.4)
Flood height (m)*	2.1 \pm 0.2 (0.5–5)	1.7 \pm 0.1 (0.3–4.6)
Maximum depth (m)*	0.6 \pm 0.04 (0.2–1.1)	0.7 \pm 0.4 (0.3–1.3)
Width:depth*	15.2 \pm 1.4 (7.7–55.8)	17 \pm 1.4 (5.9–43.1)
Habitat-weighted CPOM standing crop*	193.3 \pm 49.6 (4–1254.3)	93.8 \pm 16.8 (3.1–384.6)
% open canopy cover in the reach*	67 \pm 6 (2–100)	72 \pm 5 (8–100)
Number of instream habitat types in the reach*	2.6 \pm 0.1 (2–4)	2.9 \pm 0.1 (2–4)
Manning's N value*	0.48 \pm 0.1 (0.05–2.87)	0.22 \pm 0.04 (0.03–1.23)
Channel unit		
% riffle*	11 \pm 2 (0–42)	15 \pm 4 (0–83)
% run	38 \pm 6 (0–100)	63 \pm 7 (0–100)
% pool*	42 \pm 6 (0–99)	17 \pm 4 (0–81)
Substratum		
% boulder*	1 \pm 0.5 (0–14)	2 \pm 0.8 (0–20)
% cobble*	11 \pm 3 (0–64)	26 \pm 5 (0–80)
% gravel*	9 \pm 2 (0–65)	14 \pm 3 (0–74)
% sand*	43 \pm 5 (0–100)	27 \pm 5 (0–100)
% fines*	34 \pm 5 (0–100)	31 \pm 5 (0–100)
Riparian		
Width of riparian zone (m)*	24.2 \pm 2.2 (2–40)	22.6 \pm 2.3 (2–40)
Height of riparian vegetation (m)*	5.2 \pm 0.7 (0.5–10)	3.9 \pm 0.5 (0.5–10)
Landscape		
% open water*	0.7 \pm 0.2 (0.003–4.2)	0.1 \pm 0.06 (0–1.64)
% residential*	2.0 \pm 0.8 (0.001–19.5)	3.7 \pm 0.1 (2.4–8.7)
% commercial*	0.3 \pm 0.06 (0–1.4)	1.1 \pm 0.2 (0.01–4.5)
% forest	20.1 \pm 2.1 (2.7–38.7)	4.4 \pm 0.7 (0.2–16.4)
% hay pasture*	12.1 \pm 1.2 (1.9–28.1)	16.4 \pm 1.8 (2.8–35.6)
% row crop*	54.5 \pm 3.8 (20.3–86.4)	73 \pm 2.2 (49.2–92.2)
% wetland*	9.8 \pm 1.9 (0.6–35.3)	1 \pm 0.2 (0.1–5.2)
Land use patch density (# patches/km ²)	50.4 \pm 3.6 (21.4–98.7)	25.2 \pm 1.6 (9.4–45.2)
Catchment area (km ²)*	58.7 \pm 7.1 (14.7–218.9)	54.5 \pm 4.9 (13.8–146.5)
# of links*	10.8 \pm 2.6 (1–77)	24.4 \pm 3.5 (3–100)
Drainage density (km/km ²)*	0.9 \pm 0.01 (0.14–1.45)	1.1 \pm 0.1 (0.4–1.6)
Average water yield (mm)*	158.1 \pm 14.5 (37.4–415.4)	283.7 \pm 4.9 (234.6–356.3)
Soil water capacity (cm per cm of soil)*	9.15 \pm 0.39 (5.19–15.27)	11.36 \pm 0.24 (7.78–14.39)
K factor*	0.24 \pm 0.01 (0.17–0.32)	0.32 \pm 0.01 (0.24–0.38)
Soil permeability (cm per h)	11.2 \pm 1.5 (2.8–30.7)	4.8 \pm 0.3 (2.4–11.6)
Elevation (m)	235.6 \pm 6.4 (186.5–330.8)	359.4 \pm 3.2 (319.9–386.8)
SD of elevation (m)*	5.1 \pm 0.7 (1.4–17.9)	13.0 \pm 1.0 (3.1–26.2)
Population density (# indiv/km ²)*	44.0 \pm 10.4 (7.4–340.7)	8.8 \pm 1.1 (2.97–32.4)
Road density (km/km ²)*	1.7 \pm 0.1 (0.76–3.5)	1.3 \pm 0.3 (0.96–1.6)
Catchment slope (degrees)	0.9 \pm 0.1 (0.3–2.95)	2.2 \pm 0.2 (0.5–4.7)
% clay soils in catchment	16.9 \pm 0.7 (6.8–23.2)	22.8 \pm 0.4 (17.4–31)
% sand soils in catchment	37.7 \pm 2.5 (19.7–72.2)	19.2 \pm 1.8 (5.02–36.6)
% soil organic matter*	5.1 \pm 1.0 (0.8–29.5)	2.3 \pm 0.3 (0.7–8.3)
Depth to bedrock (cm)*	152.1 \pm 0.8 (151.1–152.4)	146.3 \pm 1.5 (108.9–152.5)

Comparing Riparian and Catchment Influences on Stream Habitat in a Forested, Montane Landscape

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Abstract.—Multiscale analysis of relationships with landscape characteristics can help identify areas and physical processes that affect stream habitats, and thus suggest where and how land management is likely to influence these habitats. Such analysis is rare for mountainous areas where forestry is the primary land use. Consequently, we examined relationships in a forested, montane basin between stream habitat features and landscape characteristics that were summarized at five spatial scales (three riparian and two catchment scales). Spatial scales varied in the area encompassed upstream and upslope of surveyed stream segments and, presumably, in physical processes. For many landscape characteristics, riparian spatial scales, approximated by fixed-width buffers, could be differentiated from catchment spatial scales using forest cover from 30-m satellite imagery and 30-m digital elevation data. In regression with landscape characteristics, more variation in the mean maximum depth and volume of pools was explained by catchment area than by any other landscape characteristic summarized at any spatial scale. In contrast, at each spatial scale except the catchment, variation in the mean density of large wood in pools was positively related to percent area in older forests and negatively related to percent area in sedimentary rock types. The regression model containing these two variables had the greatest explanatory power at an intermediate spatial scale. Finer spatial scales may have omitted important source areas and processes for wood delivery, but coarser spatial scales likely incorporated source areas and processes less tightly coupled to large wood dynamics in surveyed stream segments. Our findings indicate that multiscale assessments can identify areas and suggest processes most closely linked to stream habitat and, thus, can aid in designing land management to protect and restore stream ecosystems in forested landscapes.

INTRODUCTION

The condition of a stream ecosystem is largely a function of landscape characteristics in the surrounding catchment (Hynes 1975; Frissell et

al. 1986; Naiman et al. 2000). A catchment contains a mosaic of patches and interconnected networks (Pickett and White 1985; Swanson et al. 1997; Jones et al. 2000) that control the routing of energy and materials to streams and that ultimately control stream ecosystems (Swanson et al. 1998; Jones et al. 2000; Puth and Wilson

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2001). These patches and networks have characteristics such as size, shape, type (e.g., forest or paved roads) and location (e.g., ridge top or riparian). Direct effects on streams of landscape characteristics in the local riparian area are well established (Osborne and Koviak 1993; Naiman et al. 2000; National Research Council 2002). However, relationships between streams and landscape characteristics are less well understood and agreed upon when landscape characteristics are considered upstream along a riparian network (Weller et al. 1998; Jones et al. 1999) or upslope throughout a catchment (Jones and Grant 1996, 2001; Thomas and Megahan 1998; Gergel 2005).

Influences of riparian and catchment characteristics on stream ecosystems have been examined predominantly in agricultural and urbanized areas. For example, the abundance of adult coho salmon *Oncorhynchus kisutch* in the Snohomish River, Washington was significantly related to land cover (expressed as percent urban, agriculture, or forest) summarized for the local riparian area and for the entire catchment (Pess et al. 2002). Riparian and catchment land cover may explain approximately equal proportions of physical (Richards et al. 1996) and biological (Van Sickle et al. 2004) variation in agricultural or urbanized stream systems.

Conclusions often differ, however, regarding the relative influence of riparian and catchment land cover on streams in agricultural and urban environments. Certain in-channel responses were best explained by land-cover characteristics summarized for the local riparian area (e.g., catch per 100 m of cool- and coldwater fish [Wang et al. 2003a]). Others were best explained by land-cover characteristics summarized for the entire catchment (e.g., total fish and macroinvertebrate species richness [Harding et al. 1998]). For water quality parameters, land-cover characteristics explained more variation when summarized for the riparian network in some studies (Osborne and Wiley 1988) but for

the entire catchment in others (Omernik et al. 1981), or explained a variable degree of variation depending on data resolution, season or location of sampling, and modeling approach (Hunsaker and Levine 1995; Johnson et al. 1997). Even when the same response variable (index of biological integrity) was examined in the same river basin but at different spatial extents, judgments differed about the influences of riparian and catchment land cover (Roth et al. 1996; Lammert and Allan 1999). Given such variability, extrapolating understanding from multiscale studies in more developed landscapes to stream systems in forested landscapes may be ill advised.

Riparian and catchment land cover have seldom been compared for relationships to streams in mountainous areas where forest uses dominate. We are aware of few studies examining riparian and catchment influences on streams that drain forested regions or areas with minimal human development (Hawkins et al. 2000; Wang et al. 2003b; Weigel et al. 2003; Sandin and Johnson 2004). Understanding arising from such studies may contribute to conservation of Pacific salmon and trout, which are widely distributed in North America. Abundances of these fish and conditions of their freshwater habitat have been related to land-cover characteristics at different spatial scales, including the local riparian area (Bilby and Ward 1991), the riparian network (Botkin et al. 1995), and the catchment (e.g., Reeves et al. 1993; Dose and Roper 1994; Dunham and Rieman 1999; Thompson and Lee 2002). Although such studies offered valuable insights, none directly examined relationships between salmon, or their habitats, and land-cover characteristics summarized at more than one spatial scale.

Multiscale assessments may identify riparian and upslope areas that help create and maintain salmon habitats in forested, montane landscapes. Pools and large wood are essential components of salmon habitat in such landscapes, providing living space and cover from predators (Bilby and

Bisson 1998; McIntosh et al. 2000). Pools are areas of local scour caused by fluvial entrainment and transport of bed substrates that persist until sediment inputs to, and outputs from, a pool equilibrate. The creation and morphology (depth, volume, and surface area) of pools are driven by sediment supply, hydraulic discharge, and presence of flow obstructions (e.g., wood and boulders) (Buffington et al. 2002). All three factors are affected by channel-adjacent and hill-slope processes. For example, the amount of sediment and wood supplied to pools can increase with increases in the frequency of channel-adjacent processes, such as bank erosion, or of hill-slope processes, such as landsliding. The relative importance of channel-adjacent and hill-slope processes can vary with channel type (Montgomery and Buffington 1998; Buffington et al. 2002) and land cover (e.g., Bilby and Bisson 1998; Ziemer and Lisle 1998; Montgomery et al. 2000), and thus, the potential for land management to impact pools and large wood varies across the landscape. Consequently, studying relationships at multiple spatial scales can help identify which processes are, and where land management is, likely to alter salmon habitat.

Our goal was to understand relationships between salmon habitat and landscape characteristics, summarized at multiple spatial scales, in a montane basin where forestry is the dominant land use. Targeted habitat features were the mean maximum depth of pools, mean volume of pools, and mean density of large wood in pools. Three riparian scales (segment, subnetwork, and network) and two catchment scales (subcatchment and catchment) were considered for each stream segment where targeted habitat features were evaluated (Figure 1). Spatial scales differed in the area included upslope and upstream of surveyed stream segments, and presumably in vegetative, geomorphic, and fluvial processes that may affect targeted habitat features. Channel-adjacent processes (e.g., tree mortality in riparian stands and streamside landsliding) and in-channel process (e.g., debris flows and fluvial

transport) were assumed to dominate at the riparian scales. Potential for nonchannelized hill slope processes (e.g., surface erosion and landsliding) were added at the two catchment scales. Specific study objectives were to (1) examine differences among spatial scales for landscape characteristics described with relatively coarse-resolution data, and (2) compare the proportion of variation in stream habitat features explained by landscape characteristics summarized within and among different spatial scales.

STUDY AREA

The study was conducted in tributaries of the upper Elk River, located in southwestern Oregon, USA (Figure 2). The main stem of the Elk River flows primarily east to west, entering the Pacific Ocean just south of Cape Blanco (42°5'N latitude and 124°3'W longitude). The Elk River basin (236 km²) is in the Klamath Mountains physiographic province (Franklin and Dyrness 1988) and is similar to other Klamath Mountain coastal basins in climate, landform, vegetation, land use, and salmonid assemblage.

The climate is temperate maritime with restricted diurnal and seasonal temperature fluctuations (USFS 1998). Ninety percent of the annual precipitation occurs between September and May, principally as rainfall. Peak stream flows are flashy following 3–5-d winter rainstorms, and base flows occur between July and October. Elevation ranges from sea level to approximately 1,200 m at the easternmost drainage divide. Recent tectonic uplift produced a highly dissected terrain that is underlain by the complex geologic formations of the Klamath Mountains. Stream densities in these rock types range from 3 to 6 km/km² (FEMAT 1993).

Much of the study area is in mixed conifer and broadleaf forests that include tree species of Douglas fir *Pseudotsuga menziesii*, western hemlock *Tsuga heterophylla*, Port Orford cedar *Chamaecyparis lawsoniana*, tanoak *Lithocarpus*

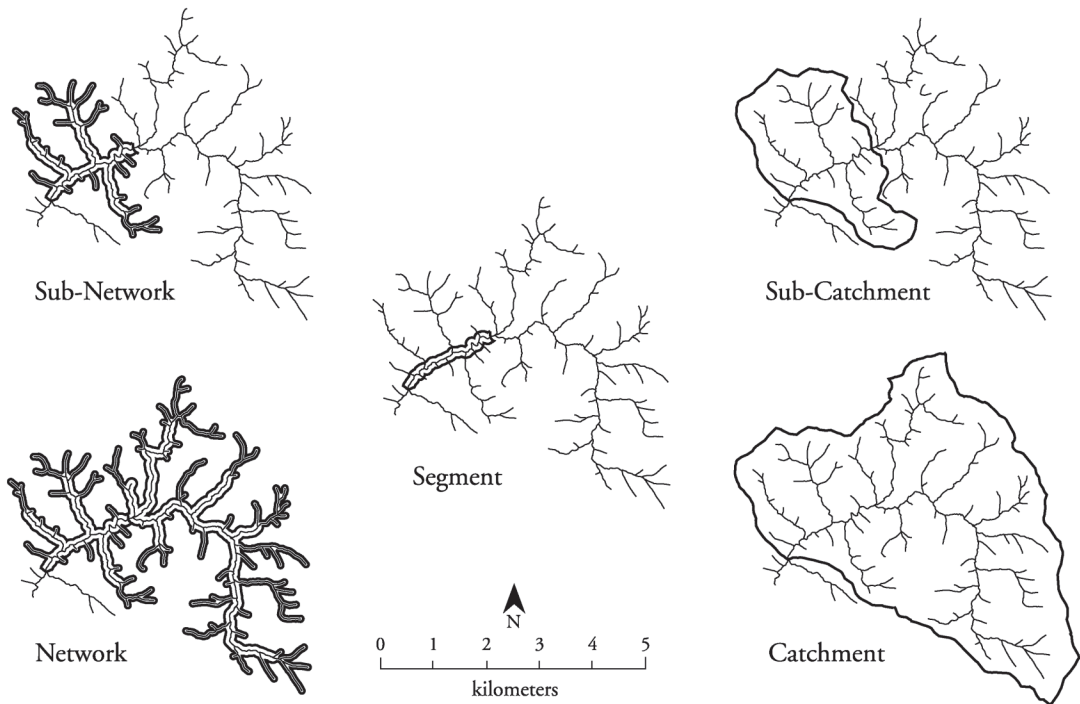


Figure 1. Analytical units used to summarize landscape characteristics at five spatial scales illustrated for a single surveyed stream segment. The segment scale analytical unit includes the area within a buffer extending 100 m on each side of the stream segment. The subnetwork scale analytical unit encompasses the segment-scale analytical unit scale plus the area within a buffer around channels orthogonal to the stream segment. The network scale analytical unit includes the subnetwork scale analytical unit plus the area within a buffer around all mapped channels upstream of the stream segment. Buffers at the subnetwork and network scales extend 100 m on each side of fish-bearing channels and 50 m on each side of nonfish-bearing channels. The subcatchment scale analytical unit contains catchments orthogonal to the stream segment and encompasses the entire area draining into the stream segment from adjacent hill slopes. The catchment scale analytical unit encompasses the subcatchment analytical unit and is the catchment of the stream segment.

densiflorus, Pacific madrone *Arbutus menziesii*, and California bay laurel *Umbellularia californica*. Typical additions in riparian areas are western red cedar *Thuja plicata*, big leaf maple *Acer macrophyllum*, and red alder *Alnus rubra*. Forests span early to late successional/old growth seral stages due to a disturbance regime driven by infrequent, intense wild fires and windstorms and by timber harvest (USFS 1998). The last major fire in the Elk River basin burned approximately 1.3 km² of the Butler Creek drainage in 1961. The next year a windstorm blew down approximately 2.8 km² of forest throughout the basin. Other than these events, timber harvest has been the domi-

nant disturbance mechanism since fire suppression began in the 1930s (USFS 1998).

Ninety percent of the study area is federally owned with the majority of this managed by the U.S. Forest Service. The remainder is in private ownership. Much of the northern and eastern drainage is in the Grassy Knob Wilderness Area, Grassy Knob Roadless Area, and Copper Mountain Roadless Area.

The upper main stem of the Elk River and its tributaries provide spawning and rearing habitat for native ocean-type Chinook salmon *O. tshawytscha*, coho salmon, coastal cutthroat trout *O. clarkii*, and winter-run steelhead *O. mykiss*. The

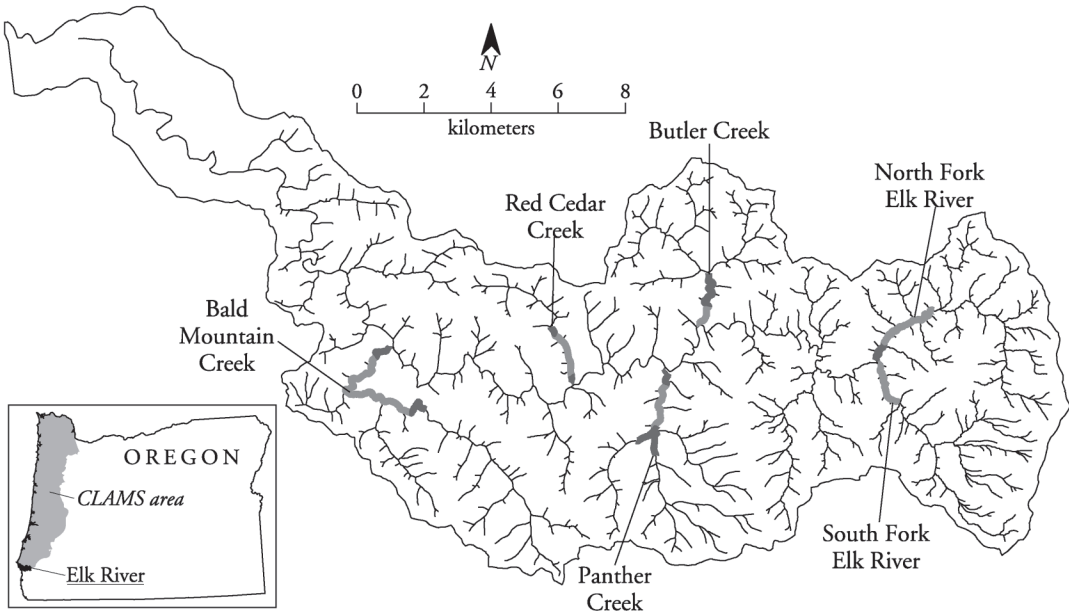


Figure 2. Location and map of the Elk River, Oregon. Stream segments surveyed in this study are shown.

basin is highlighted in both state and federal strategies for protecting and restoring salmonids (USFS and USBLM 1994; State of Oregon 1997).

METHODS

All GIS manipulations of digital coverages were conducted with ARC/INFO (Version 7.1, ESRI, Inc., Redlands, California). All statistical analyses were performed with SAS statistical software (Version 8.2, 2001, SAS Institute Inc., Cary, North Carolina).

Digital Stream Layer and Stream Segment Identification

The UTM projection, Zone 10, Datum NAD 27 was used for digital coverages. A 1:24,000, center-lined, routed, vector-based, digital stream coverage representing all perennially flowing streams within the Elk River basin was obtained from the Siskiyou National Forest. The coverage

identified each stream as either fish-bearing or nonfish-bearing. Surveyed tributaries were either third- or fourth-order channels (Strahler 1957) on this stream coverage.

Fifteen stream segments were delineated that encompassed the entire extent accessible by anadromous salmonids in each surveyed tributary (Table 1; Figure 2). Accessibility was determined in the field based on the absence of barriers to adult fish migrating upstream. In the spatially nested, hierarchical stream classification system of Frissell et al. (1986), stream segments are lengths of stream (10^2 – 10^3 m) that are bounded by abrupt changes in drainage area or gradient and are relatively homogeneous in bed-rock geology, valley gradient, and channel constraint over long time frames (10^3 – 10^4 years). Stream segments subsume reaches, habitats, and microhabitats, which are lower levels in the hierarchy. Boundaries of stream segments used in this study were originally mapped by Frissell (1992) and then adjusted through additional field reconnaissance (Burnett 2001).

Table 1. Characteristics of tributary stream segments in the Elk River, Oregon. Numbers identifying stream segments increase in the upstream direction.

Stream segment	Surveyed Length (m)	Mean Wetted Width (m)	Drainage area (ha)	Mean (SD) % gradient	Mean (SD) maximum depth of pools (m)	Mean (SD) volume of pools (m ³)	Mean (SD) density of wood in pools (no./100m)
Bald Mountain 1	826	7.7	2,715	3.1 (3.8)	1.32 (0.58)	97.3 (97.2)	6(10)
Bald Mountain 2	4,251	7.0	2,679	2.4 (2.7)	0.89 (0.32)	54.5 (50.9)	8(16)
Bald Mountain 3	965	5.6	1,511	2.3 (2.6)	0.94 (0.35)	44.8 (36.7)	9(22)
Butler 1	763	4.8	1,752	3.3 (4.3)	0.78 (0.41)	56.3 (72.8)	4 (8)
Butler 2	1,588	5.1	1,724	1.2 (1.8)	0.83 (0.29)	61.6 (46.9)	1 (2)
North Fork Elk 1	648	9.4	2,456	3.3 (4.9)	1.35 (0.38)	73.0 (36.1)	7(11)
North Fork Elk 2	2,511	7.1	2,303	1.6 (2.9)	1.08 (0.32)	81.6 (70.3)	13(16)
Panther 1	727	7.7	2,347	0.6 (0.8)	0.89 (0.47)	85.5 (73.1)	5(15)
Panther 2	1,697	8.0	2,275	2.3 (2.0)	0.90 (0.34)	71.8 (51.3)	1 (5)
Panther 3	1,165	6.2	929	1.9 (1.9)	0.69 (0.32)	34.2 (30.2)	9(17)
W. Fork Panther	806	4.3	575	2.8 (2.7)	0.51 (0.16)	8.7 (4.0)	12(23)
Red Cedar 1	344	3.2	743	4.7 (3.3)	0.63 (0.13)	13.1 (12.8)	11(19)
Red Cedar 2	1,418	4.4	737	2.1 (1.9)	0.81 (0.55)	19.7 (10.5)	13(20)
Red Cedar 3	419	3.8	565	3.3 (3.4)	0.80 (0.20)	13.1 (6.0)	17(26)
South Fork Elk	1,544	7.6	1,988	5.6 (6.2)	1.17 (0.44)	63.4 (35.2)	9(14)

Landscape Characterization

The three steps in landscape characterization were to (1) delineate analytical units at five spatial scales for each stream segment; (2) overlay analytical units onto digital coverages of lithology, land form, and land cover, then calculate the percent area of each analytical unit occupied by each landscape characteristic; and (3) compare landscape characteristics among the five spatial scales.

Analytical units.—Five analytical units, one for each spatial scale, were delineated for each stream segment. Spatial scales considered ranged from the local riparian area to the entire catchment draining into surveyed stream segments (Figure 1). Analytical units were developed for three riparian scales (segment, subnetwork, and network) and two catchment scales (subcatchment and catchment). Buffers for riparian scales were based on the Riparian Reserve widths in the report of the Forest Ecosystem Management and Assessment Team (FEMAT 1993). Consequently, buffers extended 100 m on either side of fish-bearing channels and 50 m on either side of nonfish-bearing channels. Subcatchment and catchment

boundaries were screen digitized from contour lines generated using U.S. Geological Survey (USGS) 30-m digital elevation models (DEMs).

Segment scale analytical units included the area within a buffer on each side of stream segments (22 ± 19 ha, mean \pm SD; Figure 1). Channel-adjacent processes (e.g., tree mortality in riparian stands and bank erosion) were assumed to dominate at the segment scale. Subnetwork scale analytical units encompassed segment-scale analytical units plus the area within a buffer around mapped channels orthogonal to stream segments (53 ± 82 ha; Figure 1). Channelized processes (e.g., debris flows and fluvial transport of wood and sediment) were assumed to be added to channel-adjacent processes at the subnetwork scale. Network scale analytical units included subnetwork scale analytical units plus the area within a buffer around all mapped channels upstream of stream segments (367 ± 211 ha; Figure 1). This increased the length over which channelized processes could affect stream segments. Subcatchment scale analytical units contained catchments orthogonal to stream segments and encompassed the entire area draining

into stream segments from adjacent hill slopes (190 ± 299 ha; Figure 1). This added unmapped channels capable of transporting debris flows and nonchannelized hill slope processes (e.g., surface erosion and landsliding). Catchment scale analytical units encompassed subcatchment scale analytical units and were the catchments of stream segments ($1,562 \pm 820$ ha; Figure 1), increasing the area over which nonchannelized and channelized hill slope processes could affect a stream segment.

Digital coverages of landscape characteristics.—Lithology, landform, and land-cover data layers were classified as described in Table 2. The lithology coverage was generalized by the FEMAT (1993) from the 1:500,000-scale Quaternary geologic map of Oregon (Walker and MacLeod 1991). The landform layer of percent slope was generated for the basin from USGS 30-m DEMs. Slope classes were similar to those in Lunetta et al. (1997). Road density (km/km^2) was calculated from a vector coverage of roads on all ownerships within the Elk River basin. The Siskiyou National

Forest developed this coverage by augmenting the 1:24,000, 7.5-min USGS quadrangle Digital Line Graph (DLG) data with roads interpreted from Resource Orthophoto Quadrangles.

The forest-cover layer was clipped from a coverage for western Oregon. It was developed by a regression modeling approach with spectral data from 1988 Landsat Thematic Mapper (TM) Satellite imagery and elevation data from USGS 30-m DEMs (Cohen et al. 2001). In areas such as the Elk River basin where forestry-related activities are the primary disturbance mechanism, age and stem diameter of forest cover reflects time since timber harvest. More older, larger trees generally mean less logging. Most researchers relating stream and landscape characteristics in forested areas of the Pacific Northwest used harvest intensity or percent area logged (Reeves et al. 1993; Dose and Roper 1994; Ralph et al. 1994); however, a few researchers (Botkin et al. 1995; Wing and Skaugset 2002; Van Sickle et al. 2004) used forest-cover data similar to that available for the Elk River basin.

Table 2. Description of landscape characteristics for the Elk River, Oregon. All variables except road density were expressed as percent area of analytical units at each spatial scale.

Landscape characteristic	Description
<i>Lithology:</i>	
Sedimentary rock types	Cretaceous - Rocky Point Formation sandstones/siltstones; Humbug Mountain Formation conglomerates
Meta-sedimentary rock types	Jurassic - Galice Formation shales; Colebrook Formation schists
Igneous intrusive rock types	Granite and diorite
<i>Landform:</i>	
Catchment drainage area	
Slope class $\leq 30\%$	
Slope class 31–60%	
Slope class $> 60\%$	
<i>Land cover:</i>	
Road density	(km/km^2)
Open and semi-closed canopy	$< 70\%$ tree cover
Broadleaf	$> 70\%$ deciduous tree and shrub cover
Mixed broadleaf–conifer forests:	$> 70\%$ of deciduous and conifer tree cover
small diameter	≤ 25 cm diameter at breast height (dbh)
medium diameter	26–50 cm dbh
large diameter	51–75 cm dbh
very large diameter	> 75 cm dbh
medium - very large diameter ^a	> 25 cm dbh

^a Encompasses all tree diameters capable of contributing large wood (diameter ≥ 30 cm) to streams.

Differences among spatial scales in landscape characteristics.—To investigate whether or not the five spatial scales differed, we assessed among-scale differences in variances and medians for each landscape characteristic. Among-scale differences in variances were analyzed using Levene's test of homogeneity of variance (Snedecor and Cochran 1980) on the absolute value of residuals from one-way analysis of variance (ANOVA), with scale as the independent variable. Among-scale differences in medians were evaluated with one-way ANOVA (SAS version 8.2; PROC GLM) on the ranked data because parametric assumptions could not be met. Data were blocked by stream segment to address potential correlations among spatial scales for each stream segment. Whenever an ANOVA *F*-test was significant ($\alpha = 0.05$), posthoc pair-wise comparisons of differences between spatial scales were conducted maintaining the overall type I error rate at $\alpha = 0.05$ (SAS version 8.2; option LSMEANS, TUKEY). Although extreme values were observed when landscape characteristics were screened for outliers, all data points were considered valid and were included in analyses.

We recognize that analytical units were not independent; analytical units at coarser scales subsumed those at finer scales. For example, the subcatchment scale completely encompassed the subnetwork scale. Spatial dependence inherent in the design of analytical units could reduce the actual degrees of freedom below the nominal value and inflate the probability of a type I error (Hurlbert 1984; Legendre 1993). All significance values should be evaluated with this in mind, but are presented to indicate the relative strength of differences in ANOVA and posthoc comparisons and of relationships in regressing stream habitat features with landscape characteristics, even though multiple models were considered.

Regression of Stream Habitat Features with Landscape Characteristics

Stream habitat features.—Between July 25 and August 5, 1988, habitat data were collected for every channel unit in the 20 km of stream com-

prising the 15 delineated stream segments, which taken together are the extent of anadromy in the surveyed tributaries. The length of each stream segment was at least 70 times its wetted channel width. Channel-unit habitat data were collected to derive salmonid habitat features (mean maximum depth of pools [m], mean volume of pools [m^3], and mean density of large wood in pools [no. pieces/100 m]) for each stream segment. These habitat features were chosen in part because each helped discriminate between level of use of stream segments by juvenile ocean-type Chinook salmon in Elk River tributaries (Burnett 2001).

Each channel unit was classified by type (pool, fastwater [Hawkins et al. 1993], or side channel [$<10\%$ flow]). The length, mean wetted width, and mean depth of each channel unit were estimated using the method of Hankin and Reeves (1988). Channel units were at least as long as the estimated mean active channel width (1–10 m). The number of wood pieces (≥ 3 m long and ≥ 0.3 m diameter) was counted in each channel unit. Maximum depth of pools was measured to the nearest centimeter using a meter stick for pools ≤ 1 m deep (70% of pools) and was estimated to the best ability of each surveyor for pools deeper than this. Channel unit data were georeferenced to the digital stream network through Dynamic Segmentation in ARC/INFO, then were summarized for each stream segment to obtain stream habitat features for subsequent regression analyses.

Developing regression models.—Three sets of regression models were developed to explain variation in stream habitat features: (1) we regressed each stream habitat feature with catchment area only; (2) we attempted to develop five “best” within-scale linear regression models for each stream habitat feature by selecting from landscape characteristics summarized at each of five spatial scales; and (3) we attempted to develop a single “best” among-scale linear regression model for each stream habitat feature by selecting from among catchment area and landscape characteristics at all spatial scales.

We considered models with no more than two explanatory variables to avoid overfitting because relatively few stream segments ($n = 15$) were available for analyses. This is a more conservative criterion than the 5:1 cases to explanatory variables ratio of Johnston et al. (1990) but still somewhat below ratios identified elsewhere (Flack and Chang 1987). The proportion of variation explained in linear regression was reported as R^2 and calculated as the coefficient of determination for one-variable models and as R^2_{adj} and calculated as the adjusted coefficient of determination for two-variable models. Three landscape characteristics were not considered in any regression procedure. The percent area in metasedimentary rock types was excluded due to significant ($r > 0.7$; $n = 15$; $P \leq 0.005$) negative pair-wise correlations with percent area in sedimentary rock types at each spatial scale. Percent area in igneous intrusive rock types and percent area in forests of small diameter trees were excluded because variation among valley segments was generally low at each spatial scale (Figure 3).

For each within- and among-scale regression procedure, the 10 models with the largest R^2_{adj} were identified using best-subsets procedures (SAS version 8.2, Proc REG, option ADJR SQ, AIC). We further considered models from this set that included, or were within, two Akaike's information criteria (AIC) units of the model with the lowest AIC value. Of this subset, we reported models only if slope estimates for explanatory variables and the overall model were significant ($\alpha = 0.05$) and if variance inflation factors (VIF) were less than four. Larger values of VIF indicate that multivariate multicollinearity has doubled the standard error of regression slopes (Fox 1991). The pair-wise correlation between explanatory variables was not significant ($P > 0.05$) for any of the reported two-variable models, providing further evidence that multicollinearity was of little concern. The reported ΔAIC is the difference in AIC values between the regression model with catchment area alone and the particular regression model for a given stream habitat feature. Small values

of ΔAIC suggest a model is as good as, or better than, the one containing only catchment area. Reported models met parametric assumptions based on evaluation of regression residuals: (1) for normality using the Shapiro-Wilk test and box and normal probability plots (SAS version 8.2, Proc UNIVARIATE), and (2) for constant variance using residual-versus-predicted plots.

We recognize that variable selection procedures cannot guarantee the best-fitting or most relevant model. Thus, the "best" regression model for a stream habitat feature from each within-scale selection process had a larger F -value and generally explained more of the variation than other models at that scale but was reported only if it had a $\Delta\text{AIC} \leq 5$. The "best" among-scale regression model for a stream habitat feature had a larger F -value and generally explained more of the variation than other models, including the one containing only catchment area.

The AIC from Proc REG (SAS version 8.2) is calculated by an earlier method (Akaike 1969) than the method (Akaike 1974) recommended in Burnham and Anderson (1998) and is not corrected for small sample size (AIC_c). Thus, we evaluated the potential for these differences to affect our results. Values of AIC_c were obtained (SAS version 8.2, Proc MIXED, option IC) for the 10 among-scale regression models originally identified for each stream habitat feature. For the mean maximum depth and volume of pools, the models that met our reporting and best-model criteria using AIC_c were identical to those using AIC. For the mean density of large wood in pools, three more models would have been reported using AIC_c than AIC; however, these models had larger AIC_c values and smaller F -values than the models we originally reported. The among-scale regression model for the mean density of large wood in pools that met our best-model criterion would have been the same using either metric. Based on these considerations, we are confident that results from within-scale regressions were also negligibly influenced by the use of AIC (Akaike 1969) instead of AIC_c .

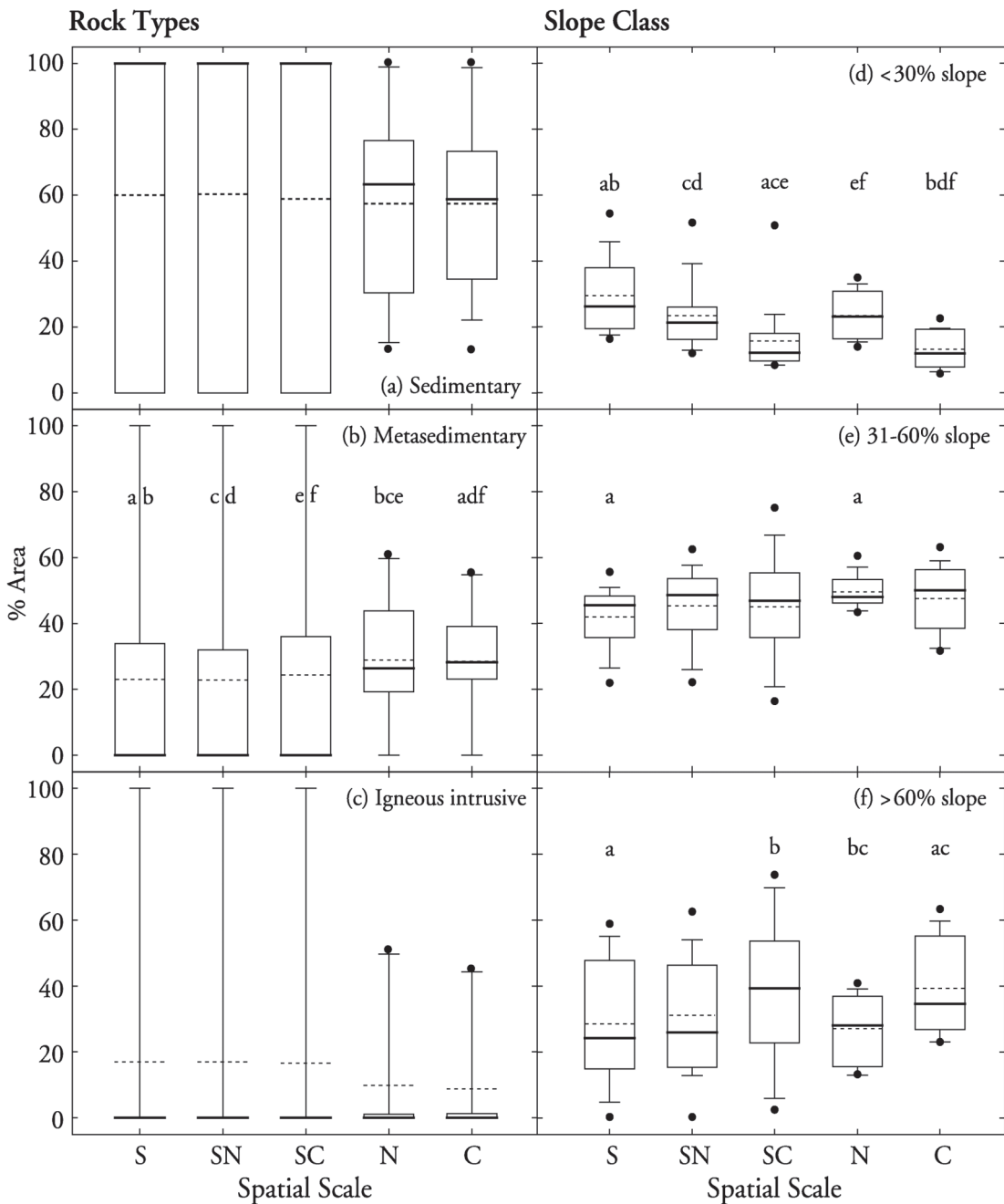


Figure 3. Distribution of landscape characteristics among analytical units at each of the five spatial scales in tributaries of the Elk River, Oregon. Spatial scales were the segment (S), subnetwork (SN), subcatchment (SC), network (N), and catchment (C). Boxes designate the 25th and 75th percentiles, the solid line indicates the median and the dotted line the mean, whiskers denote the nearest data point within 1.5 times the interquartile range, and 5th and 95th percentiles are shown by disconnected points. For a given landscape characteristic, two scales with the same letter label above their box plots have a significant pair-wise difference between medians when the overall type I error rate is controlled at $\alpha = 0.05$.

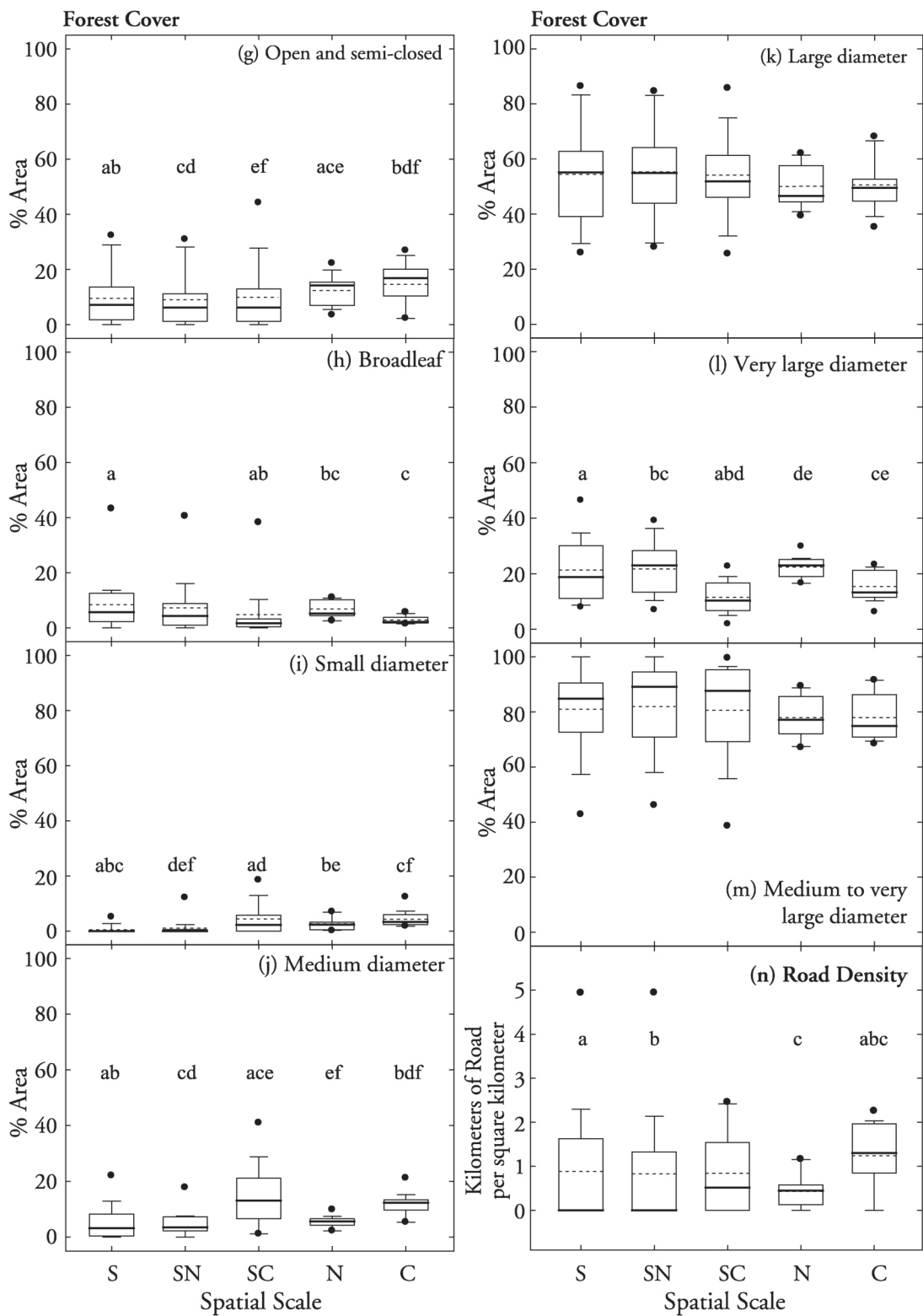


Figure 3. continued

Because stream segments were not selected with a probability sampling design, we assessed regression residuals from each best among-scale model for nonrandom errors that might reflect spatial autocorrelation. For all possible pairs of stream segments, stream distance and the absolute difference between regression residuals were calculated. These two sets of values were regressed to determine the proportion of the variation in the absolute difference between regression residuals explained by the stream distance between stream segments.

RESULTS

Landscape Characterization

Variance across stream segments differed significantly ($df = 4, 70$; $P \leq 0.05$) among spatial scales for all but four landscape characteristics, the percent area in (1) igneous intrusive rock types, (2) slopes $\leq 30\%$, (3) slopes $> 60\%$, and (4) open and semiclosed canopy forest. The smallest variance was observed at either the network or catchment scale for all landscape characteristics except the percent area in forests of small diameter trees.

In one-way ANOVA, the blocking factor, stream segment, was significant ($F_{(4,14)}$; $P \leq 0.0001$) for all landscape characteristics, and medians differed significantly ($F_{(4,14)}$; $P \leq 0.03$) among spatial scales for 10 of 14 landscape characteristics (Figure 3). Pair-wise differences in medians were not significantly ($P > 0.05$) different between the segment and subnetwork scales for any landscape characteristic. For most landscape characteristics, pair-wise differences between medians were significant ($P \leq 0.05$) between a catchment scale (subcatchment or catchment) and one or more of the riparian scales (segment, subnetwork, or network) (Figure 3). To illustrate, for the percent area in slopes $\leq 30\%$ (Figure 3D), the medians of the subcatchment (12.2%) and the catchment (11.9%) scales, although not significantly different from each other, were significantly different from those of the segment (26.2%), subnetwork (21.3%), and

network (23.1%) scales. Pair-wise differences between the riparian scales were not significant for this landscape characteristic.

Regression of Stream Habitat Features with Landscape Characteristics

Mean maximum depth and mean volume of pools.—Both of these stream habitat features were positively related to catchment area (Table 3). In one or more of the within-scale regressions, landscape characteristics explained a significant proportion of the variation in the mean maximum depth of pools ($R^2 \leq 0.29$; $df = 14$; $P \geq 0.04$; $\Delta AIC \geq 7.3$) and in the mean volume of pools ($R^2 \leq 0.48$; $14 < df < 13$; $P \geq 0.008$; $\Delta AIC \geq 20.2$). However, no within-scale model met the reporting criterion of $\Delta AIC \leq 5$ and each explained about half or less of the variation explained by catchment area alone. Therefore, a best within-scale regression model was not identified for either the mean maximum depth or volume of pools.

The best among-scale regression model for the mean maximum depth of pools contained only catchment area (Table 3). This was the only one of seven models for the mean maximum depth of pools, which included or were within two AIC units of the smallest AIC value, to meet the reporting criteria. In among-scale regression for the mean volume of pools, only one model met the reporting criteria (Table 3). However, the F -value of this model was substantially lower than that of the model containing catchment area alone, which was therefore considered the best among-scale regression model for the mean volume of pools (Table 3). Stream distance between each pair of stream segments explained only a small proportion of the variation in the absolute differences between residuals from the best among-scale regression model for the mean maximum depth of pools ($R^2 = 0.04$; $df = 104$; $P = 0.06$) or for the mean volume of pools ($R^2 = 0.01$; $df = 104$; $P = 0.36$).

Mean density of large wood in pools.—Although the mean density of large wood in pools

Table 3. Results from among-scale linear regression to explain variation in stream habitat features among 15 stream segments for tributaries of the Elk River, Oregon. Explanatory variables were catchment area alone and catchment area plus landscape characteristics summarized at the segment (S), subnetwork (SN), subcatchment (SC), network (N), and catchment (C) scales. For among-scale regressions, the number of models that included, or were within two AIC units of the smallest AIC value, is given after the stream habitat feature. Reported models had explanatory variables with significant slope estimates ($\alpha = 0.05$) and little multicollinearity ($VIF < 4$). Methods are fully described in the text for identifying the set of reported models and best among-scale models indicated by *. Direction of relationships with explanatory variables is indicated by +/- . The ΔAIC is relative to the model with catchment area alone for that stream habitat feature.

<i>Stream habitat feature</i>						
Explanatory variable in model	+/- $P > t $	VIF	Model F	$P > F$	R^2 (R^2_{adj})	ΔAIC
<i>Mean maximum depth of pools</i>						
Catchment area			17.1	+0.001*	0.57	
<i>Mean volume of pools</i>						
Catchment area			84.7	+<0.0001*	0.87	
<i>Mean density of large wood in pools</i>						
Catchment area			6.99	-0.02	0.35	
<i>Mean volume of pools (4)</i>						
Catchment area	+<0.0001	1.00	57.9	<0.0001	0.89	-3.2
% very large trees (N)	+0.05					
<i>Mean density of large wood in pools (3)</i>						
% sedimentary rock types (SC)	-0.004	1.07	10.48	0.002*	0.58	-6.8
% medium-very large trees (SC)	+0.003					
% sedimentary rock types (SN)	-0.004	1.08	9.89	0.003	0.56	-6.2
% medium-very large trees (SC)	+0.004					
% sedimentary rock types (S)	-0.005	1.08	9.84	0.003	0.56	-6.2
% medium-very large trees (SC)	+0.004					

was negatively related to catchment area (Table 3), an equal or greater proportion of the variation was explained by other landscape characteristics summarized at each of the five spatial scales (Table 4). The best within-scale regression model at the segment, subnetwork, subcatchment, and network scales contained the percent area in sedimentary rock types and the percent area in forests of medium to very large diameter trees (Table 4). The best catchment-scale model for the mean density of large wood in pools consisted simply of the percent area in open area and semiclosed canopy forests (Table 4).

Two other models for the mean density of large wood in pools met the reporting criteria at the network scale (Table 4). These models contained the percent area in sedimentary rock types along with a land-cover characteristic (road density or percent area in open and semiclosed

canopy forests). The three significant land-cover characteristics for the mean density of large wood in pools were correlated with one another at the network scale. This was true also at each of the other spatial scales. For example, as the density of roads increased, the percent area in forests of medium to very large diameter trees decreased at the network scale ($R^2 = 0.69$; $df = 14$; $F = 28.2$; $P = 0.0001$) (Figure 4) and at each of the other four spatial scales ($R^2 = 0.35$ [segment scale], $R^2 = 0.46$ [subnetwork scale], $R^2 = 0.37$ [subcatchment scale], and $R^2 = 0.85$ [catchment scale]; $df = 14$; $F \leq 72.7$; $P \leq 0.02$).

The best among-scale regression model contained two landscape characteristics, each summarized at the subcatchment scale: the mean density of large wood in pools was negatively related to the percent area of sedimentary rock types and positively related to the percent area

Table 4. Results from within-scale linear regression to explain variation in the mean density of large wood in pools among 15 stream segments in tributaries of the Elk River, Oregon. Explanatory variables are landscape characteristics summarized at five spatial scales. The number of models that included, or were within two AIC units of, the smallest AIC value is listed after the spatial scale. Reported models had explanatory variables with significant slope estimates ($\alpha = 0.05$) and little multicollinearity ($VIF < 4$). Methods are fully described in the text for identifying the set of reported models and the best model for each spatial scale, indicated by *. Direction of relationships with explanatory variables is indicated by +/- . The ΔAIC is relative to the model with catchment area alone for the stream habitat feature.

Spatial scale						
Explanatory variable in model	+/- $P > t $	VIF	Model F	$P > F$	R^2 (R^2_{adj})	ΔAIC
Segment (7)						
% sedimentary rock types	-0.04	1.00	4.55	0.03*	0.34	0.0
% medium-very large trees	+0.05					
Subnetwork (2)						
% sedimentary rock types	-0.01	1.03	7.47	0.008*	0.48	-3.7
% medium-very large trees	+0.01					
Subcatchment (1)						
% sedimentary rock types	-0.004	1.07	10.48	0.002*	0.58	-6.8
% medium-very large trees	+0.003					
Network (4)						
% sedimentary rock types	-0.04	1.09	5.94	0.02*	0.41	-1.9
% medium-very large trees	+0.01					
% sedimentary rock types	-0.04	1.08	5.92	0.02	0.41	-1.9
% open and semi-closed	-0.01					
% sedimentary rock types	-0.02	1.29	5.63	0.02	0.40	-1.5
% road density (km/km ²)	-0.01					
Catchment (10)						
% open and semi-closed			7.31	-0.02*	0.36	-0.2

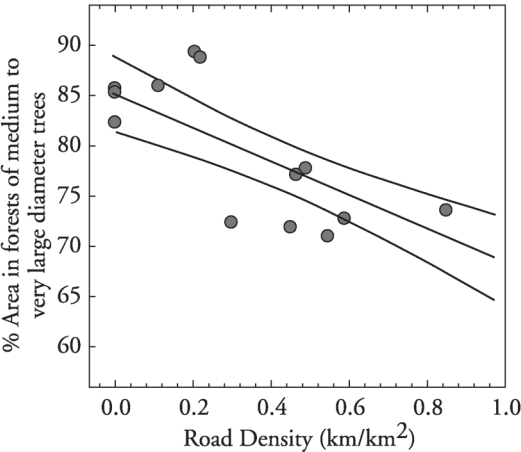


Figure 4. Results of linear regression between the percent area in forests of medium to very large diameter trees and road density at the network scale to explain variation among stream segments for tributaries of the Elk River, Oregon. The linear regression line and 95% mean confidence curves are shown ($y = 85.7 - 16.7x$; $R^2 = 0.69$; $P = 0.0001$).

in forests of medium to very large diameter trees (Table 3). Stream distance between each pair of stream segments explained little of the variation in the absolute difference between residuals from this among-scale regression ($R^2 = 0.01$; $df = 104$; $P = 0.26$).

DISCUSSION

This study illustrated the value of multiscale analysis in relating stream habitat to riparian and catchment characteristics in a landscape dominated by forest uses. Although ecologists acknowledge the importance of matching the scale of inquiry to the questions posed (Wiens 1989, 2002), often the “right scale” is not known at the outset of an investigation. Analysis at multiple scales may be necessary to elucidate linkages among stream organisms, their habitats, and the

surrounding landscape. Indeed, we found that relationships between stream-habitat features and specific landscape characteristics differed depending on spatial scale, enabling us to suggest processes responsible for observed variation. Fausch et al. (2002) emphasized that information most germane to land management decisions will likely stem from research in stream ecology at intermediate temporal and spatial scales. Our finding that the mean density of large wood in pools of mid-order channels was best explained with landscape characteristics summarized at an intermediate spatial scale seems to bolster their case. We recognize that the scale at which stream habitat and landscape characteristics are most tightly coupled is undoubtedly influenced by where examination is focused in the drainage network. Had we targeted low-order, headwater channels instead of mid-order channels, stream habitat features may have been more directly affected by landscape conditions throughout these smaller catchments, increasing the likelihood of more variation being explained at the catchment scale.

Differences among Spatial Scales in Landscape Characteristics

The smallest variance among analytical units for landscape characteristics was generally observed at one of the coarser spatial scales (network or catchment scale). Because the spatial resolution of landscape coverages was typically finer than the area of analytical units, variance declined as the area of analytical units increased. Our results agree with predictions from landscape ecology that variability in landscape characteristics decreases as grain or patch size increases (Forman and Godron 1986; Syms and Jones 1999).

Given that significant pair-wise differences in medians for landscape characteristics were generally between catchment and riparian scales, riparian areas were distinguished when delineated with a fixed width buffer and described by 30-m digital elevation data and 30-m Landsat Thematic Mapper Satellite imagery. This method

detected expected geomorphic and ecological differences between riparian and upslope areas and so appears to be useful for characterizing riparian areas over broad spatial extents in forested systems. For example, our buffer characterization distinguished low-gradient valley bottoms in that segment, subnetwork, and network scales contained greater percentages of the lowest slope class than either of the catchment scales. Furthermore, among-scale differences in percentage area of broadleaf forest apparently reflect the greater likelihood of red alder occurrence in the wetter and more frequently disturbed areas near streams (Pabst and Spies 1999).

Previous studies characterizing riparian areas over a broad region generally used a fixed-width buffer rather than attempting to delineate the actual riparian area. Some of these studies found similarities between riparian and upslope areas in landscape characteristics (e.g., Richards and Host 1994; Wang et al. 1997; Van Sickle et al. 2004), but others did not (e.g., Lammert and Allan 1999). Alternative, and potentially more accurate, methods for delineating and characterizing riparian areas include mapping valley bottoms from finer-resolution digital topographic data (e.g., Hemstrom et al. 2002), classifying digital imagery of higher spectral or spatial resolution, interpreting standard aerial photography, and field mapping. The latter two methods are time and labor intensive, however, and thus may limit the spatial extent reasonably addressed.

Spatial Autocorrelation in Regression of Stream Habitat Features with Landscape Characteristics

Residuals from among-scale regression of the three stream habitat features (mean maximum depth of pools, mean volume of pools, and mean density of large wood in pools) suggested little evidence of spatial autocorrelation, and so we did not attempt to remove or account for it in regression models (Cliff and Ord 1973; Legendre 1993). However, relatively small sample size may have limited our ability to detect spatial autocorrelation.

We are aware of no ideal technique to assess spatial dependence for stream networks when using relatively coarse-grained analytical units that differ in size and spacing. Consequently, we adapted an approach that assesses the degree of relationship for geographic distances between all pairs of locations and corresponding differences between values of variables at those locations (Legendre and Fortin 1989). Geographic distances are usually calculated with x - y coordinates (e.g., Hinch et al. 1994), but we chose stream distance to better reflect potential connectivity between stream segments.

Stream Habitat Features and Catchment Area

Catchment area explained more among-stream segment variation in the mean maximum depth of pools and the mean volume of pools than other landscape characteristics at any of the five spatial scales we examined. Land-cover variables also had less explanatory power for channel morphology than catchment area in agricultural systems (Richards et al. 1996) and in a relatively undegraded forest ecoregion (Wang et al. 2003b). Catchment area is related to stream power through its direct influence on stream discharge. Streams with higher discharge generally have greater stream power, an index of the ability to transport materials, and tend to be deeper and wider than those with lower discharge (Gordon et al. 1992). Accordingly, the mean maximum depth and volume of pools in Elk River tributaries increased as catchment area increased, paralleling results of Buffington et al. (2002).

Although we determined that land cover explained little of the variation in maximum depth or volume of pools, previous studies have demonstrated relationships between channel morphology and land use/cover. Based on correlative studies, stream morphology is thought to be affected by land uses (Roth et al. 1996; Snyder et al. 2003; Wang et al. 2003a, 2003b), including timber harvest (Bilby and Ward 1991; Reeves et al. 1993; Dose and Roper 1994; Wood-Smith and

Buffington 1996). Our ability to discern relationships between land cover and the mean maximum depth of pools may have been hampered because the maximum depths of the deepest pools were estimated and not measured. Given the apparent influence of catchment area, a sample size larger than ours may be necessary to account for catchment area and thus to distinguish relationships between timber harvest and pool morphology. Scaling by catchment area did improve the ability to detect anthropogenic effects on IBI metrics in Pacific Northwest coastal streams (Hughes et al. 2004; Kaufmann and Hughes 2006, this volume).

The mean density of large wood in pools was also related to catchment area. The inverse relationship between these two variables likely arises from an increased ability of larger streams to transport wood. An inverse relationship was found with stream size in other forestry-dominated systems of the Pacific Northwestern United States (Bilby and Ward 1991; Montgomery et al. 1995; Wing and Skaugset 2002) but not in Midwestern agricultural systems (Richards et al. 1996; Johnson et al. 2006, this volume) or when data from mixed-use and silvicultural systems were combined (Wing and Skaugset 2002). A direct relationship was found in midwestern agricultural systems (Richards et al. 1996; Johnson et al. 2006) and in mixed-use silvicultural systems (Wing and Skaugset 2002). As the intensity and duration of human-caused disturbance increases, the presence of large wood in a stream may be determined more by sources of new recruitment than by transport capacity of the stream.

Wood density and an indicator of stream discharge, bank-full stream width, were related in old-growth forests with few human impacts (Bilby and Ward 1989). Bilby and Ward (1989) noted the value of this relationship for determining if wood density at another site was similar to that expected for a "natural" stream of the same size. Regression parameters or proportion of variation explained by such a relationship may be useful benchmarks for assessing whether

wood dynamics at broader spatial scales are operating naturally (within the range of natural variability [Landres et al. 1999]). Deviations from such benchmarks may indicate that anthropogenic disturbances have disrupted wood dynamics and constrained variability of in-channel wood across a landscape.

Density of Large Wood in Pools and Landscape Characteristics

We found that landscape characteristics at each spatial scale generally explained as much or more of the variation in the mean density of large wood in pools as catchment area. The mean density of large wood in pools was negatively related to the percent area of sedimentary rock types summarized at one or more spatial scales when considered in combination with land cover. The importance of mass-wasting processes, such as debris flows, to large wood delivery has been established in the Oregon Coast Range (Reeves et al. 2003) and the Olympic Peninsula, Washington (Benda et al. 2003). Although possibly more prevalent in other systems, debris flows occur in the Elk River basin on all lithologies and deliver to higher order channels (Ryan and Grant 1991). However, less mass-wasting debris reaches streams of the Elk River basin in sedimentary rock types than in other rock types (McHugh 1986), which is consistent with interpretations of results from elsewhere in western Oregon (Scott 2002; Kaufmann and Hughes 2006), and may help explain the negative relationship we found between sedimentary rock types and the mean density of large wood in pools.

The mean density of large wood in pools was positively related to stand age. Age or stem diameter of forest cover reflects time since timber harvest in areas such as the Elk River basin, where logging dominates the disturbance regime. Thus, the positive associations we found between large wood and the percent area in forests of medium to very large diameter trees, for example, corroborate negative associations with percent area logged or harvest intensity in other forested systems

(Bilby and Ward 1991; Reeves et al. 1993; Montgomery et al. 1995; Wood-Smith and Buffington 1996; Lee et al. 1997). Large wood was also positively related to the amount of forested land in systems with more agricultural and urbanized area (Richards et al. 1996; Wang et al. 1997; Snyder et al. 2003). The large wood in the stream and indicators of timber harvest may not always be related (Lisle 1986; Frissell 1992; Ralph et al. 1994), particularly considering time lags in tree mortality as forests age, decay of in-channel wood from the previous stand, and wood delivery following episodic disturbances (fires, storms). Because land cover variables had more explanatory power for the mean density of large wood in pools than for pool morphology, large wood metrics may be the more sensitive indicators of land management effects, especially where logging has been moderate as in the Elk River basin.

Importance of Spatial Scale in Understanding Variation in Large Wood Density

Our use of multiscale analysis suggests areas and processes that are most closely linked to large wood in pools. The relatively low proportion of variation explained with lithology and forest cover summarized at the segment scale implies that wood is delivered from sources in addition to those immediately adjacent to surveyed stream segments. Explanatory power was greater at the subnetwork than at the segment scale, possibly because the subnetwork scale included many of the lower-order tributaries capable of delivering large wood via debris flows to surveyed stream segments. The most variation was explained at the subcatchment scale. This scale incorporates unmapped lower-order tributaries and upslope areas capable of delivering wood from unchanneled hill slope processes. The proportion of variation explained by landscape characteristics decreased at spatial scales beyond the subcatchment, indicating that regression relationships may be less reflective of processes and source areas influencing wood dynamics in surveyed stream segments.

We did not determine the distance upstream from surveyed segments that explanatory power began to decline. Identification of any such upstream threshold may help in comparing the importance of fluvial transport and other wood delivery processes in these higher-order channels and, therefore, in designing riparian protection and timber harvest. To more thoroughly mitigate negative effects of logging on wood in streams, our findings indicate that it may be necessary to modify management practices along low-order tributaries and on hill slopes susceptible to mass wasting, as well as along fish-bearing channels. This is consistent with the conclusion drawn from other multiscale studies that riparian buffers alone may not fully protect streams from land use impacts (Roth et al. 1996; Wang et al. 1997; Snyder et al. 2003).

With landscape characteristics summarized at the network scale, an approximately equal proportion of variation in the mean density of large wood in pools was explained by substituting road density (km/km²) for forest cover in regression with percent area of sedimentary rock types. Dose and Roper (1994) found similar results in the South Umpqua River basin of Oregon where the percent area harvested and road density were highly correlated with each other and were almost equally correlated with change in stream width. Road density and forest cover variables (the percent area in forests of medium to very large diameter trees, the percent area in open and semiclosed canopy forests, and the percent area in large diameter forests) were correlated at all five spatial scales. The degree of correlation, however, generally increased with increasing spatial scale, suggesting that roads and forest disturbances were not always sited together.

Although road density and forest cover can be highly correlated, one variable or the other may have more explanatory power for a particular response (Bradford and Irvine 2000) or at a particular spatial scale, as we found. Roads and timber removal share effects on some processes that shape stream ecosystems (e.g., increasing landsliding and surface runoff rates) but not all

(e.g., increasing direct insolation to streams) (Hicks et al. 1991) and may differ in the quality, timing, or magnitude of those effects shared (e.g., Jones and Grant 1996; Jones 2000). Roads can intercept debris flows that would have otherwise delivered wood to streams (Jones et al. 2000). However, the amount of wood available for delivery in our study was probably influenced more by timber harvest. Two findings suggest this: (1) more variation in large wood density was explained by a model containing forest cover at each scale than by the model containing road density; and (2) the only significant relationship to road density was at the network scale, one of the two spatial scales that road density and forest cover were most strongly related. Before one concludes that conditions of aquatic habitat or biota are unrelated to silvicultural activities, it may be prudent to examine relationships with both forest cover and road density, particularly when these are summarized at finer spatial scales. Additionally, primary influences may be indicated by determining if a response variable is related to road density or forest cover or both and at what scales.

In conclusion, the spatial scales explored can influence interpretations about the importance of particular landscape characteristics, physical processes, or terrestrial areas to stream ecosystems. For example, our finding that variation in the mean density of large wood in pools was best explained with landscape characteristics summarized at an intermediate spatial scale suggested that source areas for important processes were probably not fully encompassed at finer scales, but at coarser scales, source areas were included that were less connected to large wood dynamics in surveyed stream segments. Additionally, had only the catchment scale been examined, we might have incorrectly concluded that the amount of large wood in pools is unrelated to lithology and forest cover. Although multiscale analysis has contributed to exploring land-use effects on stream ecosystems in urbanized and agricultural settings, this study demonstrated its benefits for understanding relationships between

landscape characteristics and stream habitat in a mountainous area where forestry is the primary land use. Among-scale similarities and differences in relationships suggested key processes responsible for those relationships. Consequently, analysis at multiple scales may provide critical knowledge about system function and inform land management decisions to better protect and restore stream ecosystems.

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Effects of Levels of Human Disturbance on the Influence of Catchment, Riparian, and Reach-Scale Factors on Fish Assemblages

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Abstract.—We analyzed data from 287 streams in Wisconsin and northern Michigan to evaluate the relative effects of human disturbance levels on the influence of catchment, network riparian, reach riparian, and instream variables on fish assemblages. The streams were divided into high, medium, and low human disturbance groups based on catchment and network riparian urban and agricultural land uses. We used canonical correspondence analyses to evaluate relations among variables at the four spatial scales and fish assemblage composition, abundance, and presence/absence and to partition the relative importance of spatial scales. Catchment and network riparian land uses were among the dominant variables correlated with fish for high disturbance catchments but not for low disturbance catchments. The variations in fish assemblage composition, abundance, and presence/absence explained by catchment factors were substantially higher for high than for low disturbance catchments, although the variations explained by network riparian factors and reach riparian land uses were similar among disturbance levels. In contrast, the variations in fish variables explained by instream factors and the interaction of the four spatial scale environmental factors were considerably lower for high disturbance than for low disturbance catchments. We concluded that in largely undisturbed catchments, fish assemblages were predominantly influenced by local factors, but as disturbance increased in catchments and riparian areas, the relative importance of local factors declined and that of catchment increased. Hence, instream and riparian habitat improvements would be most effective in catchments that are largely undisturbed and catchment scale land-use management would be more effective for improving stream quality in degraded catchments.

INTRODUCTION

To maintain and improve stream ecosystem health, managers must understand how streams and their biological assemblages are shaped by both natural and human-induced environmental factors that operate at a variety of spatial and

temporal scales. Understanding which environmental factors are most influential, and the spatial scales at which this influence is manifest, is essential for directing conservation and rehabilitation efforts to the factors and scales where management activities are most effective.

Traditionally, stream rehabilitation and conservation efforts have mainly focused on riparian areas and instream physical and chemical

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habitats. This is partly because the structure of fish assemblages is strongly influenced by local factors such as water depth, current velocity, size of substrate particles, cover, bank condition, canopy shading, food sources, temperature, and other physicochemical variables (Rabeni and Jacobson 1993; Wang et al. 1998). While some rehabilitation projects have been successful, others focused on improving local habitat conditions have failed to improve fish assemblages. For example, streambank fencing improved fish assemblages and trout standing crops in a Colorado stream where the catchment was largely rangeland (Stuber 1985). And streambank and channel habitat improvements significantly increased brook trout abundance in a Wisconsin stream draining a largely forested catchment (Hunt 1976). On the other hand, after a 6-year implementation of stream bank fencing to exclude livestock significantly improved instream habitat, the fish assemblage remained degraded in a Wisconsin stream because the catchment was heavily altered by agriculture (Wang et al. 2002). Moerke and Lamberti (2003) also reported that stream rehabilitation, by reconnecting historical meanders to the channelized Potato Creek, Indiana, resulted in low fish densities, altered assemblage structure, and domination by slow-water, silt-tolerant fish species. These successes and failures of local management practices have been attributed to variation in the spatial scale of the dominant influential factors (e.g., Wang et al. 2002, 2003a; Moerke and Lamberti 2003). The more dominant local factors are in influencing biological communities, the more successful local management practices can be. Hence, identifying dominant factors and scales that are most influential to fish assemblages is critical to the success of stream improvement.

Both catchment and local characteristics explained considerable amounts of variation in fish assemblages (e.g., Marsh-Matthews and Matthews 2000; Stauffer et al. 2000; Zorn 2003). Although an increasing number of studies have evaluated the relative importance of different spatial scale factors in influencing biological as-

semblages, conclusions have been inconsistent. Several studies have indicated that catchment factors accounted for more variation in stream biotic integrity than did local conditions (e.g., Roth et al. 1996; Allan et al. 1997; Wang et al. 1997, 2001), whereas others have found just the opposite (e.g., Lammert and Allan 1999; Wang et al. 2003a). The less the catchment is disturbed, the more local factors are believed to determine biological assemblages, and vice versa (DeBano and Schmidt 1989; Wang et al. 2002, 2003a). This hypothesis has not been tested directly (Wang et al. 2003a).

In this study, we tested the hypothesis that in largely undisturbed catchments, fish assemblages are predominantly influenced by local factors (instream habitat and riparian conditions), but as the level of disturbance increases in the catchments, the relative importance of local factors declines and that of catchment increases. We also determined whether the dominant influential factors differed among catchments with different human disturbance levels.

METHODS

Study Areas

Data were collected from 287 sites on 1st- to 4th-order streams across Wisconsin and northern Michigan (Figure 1). Sites were selected to be easily accessible, represent a range of anthropogenic influence, and cover a range of natural variation in stream and catchment characteristics.

The study sites represent the range of catchment surficial geology types, land relief, and stream thermal regimes found across Wisconsin and northern Michigan. In northern Wisconsin and the upper peninsula of Michigan, the landscape characteristics are dominated by undulating till plains, morainal hills, broad lacustrine basins, and extensive sandy outwash plains with low relief. Central Wisconsin and northern lower Michigan are typified by flat to rolling glacial till plains, lacustrine basins, outwash plains, and rolling to hilly moraines and beach ridges. Hilly

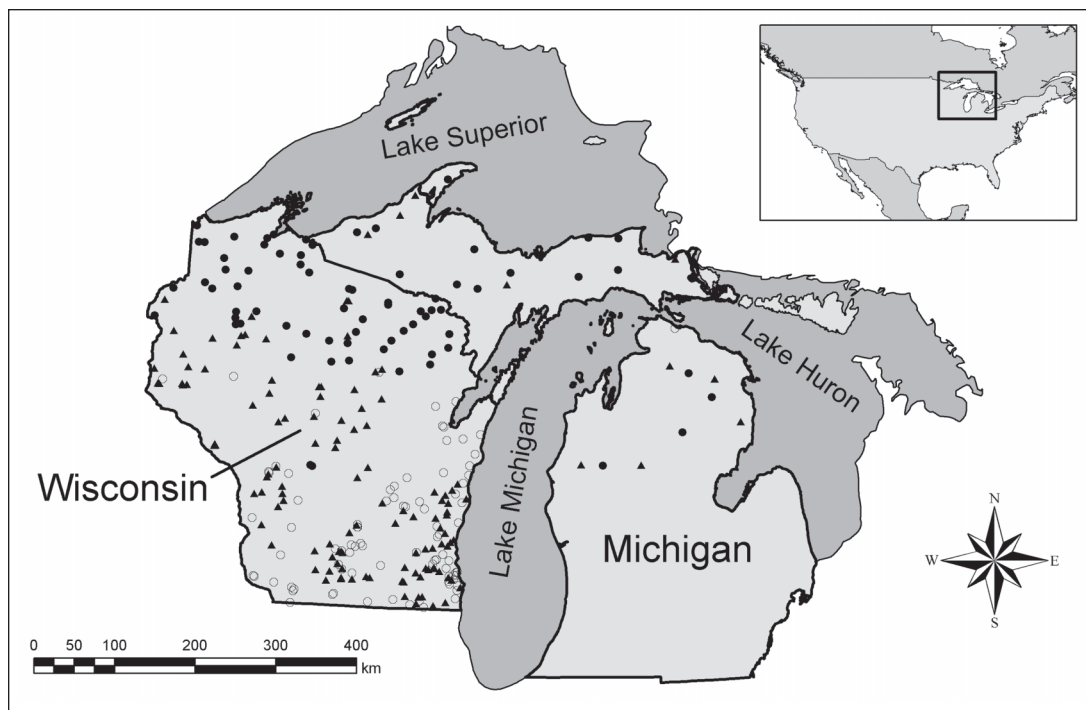


Figure 1. Sampling locations in Michigan and Wisconsin. Open circles are high disturbance sites, filled triangles are medium disturbance sites, and filled circles are low disturbance sites.

uplands dominated by a loess-capped plateau that is deeply dissected by stream valleys are characteristics of southwestern Wisconsin, and outwash plains, lacustrine basins, and flat to rolling till plains were the characteristics of southeastern Wisconsin. The study streams are dominated by cool- and coldwater systems in the north and a mixture of cool-, cold-, and warmwater systems in the southern part of the study area.

The study sites also have a range of catchment sizes, land-cover types, and local instream conditions. Catchment size varies from less than 5 to 1,006 km² (mean = 136). The combination of woodland, wetland, and water ranges from 2% to 100% of the catchment. Agriculture land ranges from 0% to 93% (mean = 36%) and urban land varies from 0% to 52% (mean = 3%). Stream wetted width varies from 2 to 56 m (mean = 9).

Catchment and Buffer Data

Catchment boundaries upstream of each sampling site were delineated using Arc View WATERSHED Avenue Command Procedures (ESRI 2002) and a Digital Elevation model with a 30-m resolution. Catchment surficial geology, soil permeability, bedrock depth and geology, growing degree-days, annual precipitation, land use/-cover, and groundwater delivery potential (Baker et al. 2003) within each catchment were quantified using ARC/INFO software to overlay catchment boundaries on these readily available database layers assembled by an ongoing stream segment modeling and classification project (Brenden et al. 2006, this volume). Stream riparian characteristics within 150 m centered at the stream line for the channel network were also gathered using the same landscape database layers.

Instream Habitat and Fish Sampling

Stream physical habitat, dissolved oxygen, discharge, and fish data were collected once between 1997 and 2002. We assessed physical habitat at a site length of 35 times the mean stream width or a minimum of 100 m. This length was sufficient to encompass about three meander sequences (Simonson et al. 1994; Wang et al. 1996). We sampled physical habitat and fish between late May and late August when low stream flows facilitated effective sampling and large-scale seasonal fish movements were unlikely to occur (Lyons and Kanehl 1993). At each site, 30 habitat variables, including channel morphology, bottom substrates, cover, bank conditions, and riparian vegetation and land cover, were measured or visually estimated along 12 transects using standardized procedures (Simonson et al. 1994). Dissolved oxygen was measured using a YSI oxygen-conductivity meter (model 85) and discharge was measured with a Flow-Mate portable flowmeter (model 2000) at the downstream end of each site before sampling physical habitat. Continuous water temperatures were recorded using Onset Stow-Away temperature loggers between mid-May and late September. The entire length of each site was electrofished once with either two backpack units in tandem or a single tow-barge unit with three anodes (Lyons and Kanehl 1993; Simonson and Lyons 1995). Efforts were made to collect all fish observed, and all captured fish were identified and counted.

Data Summary

The catchment, network riparian, reach riparian land-use, and instream habitat variables were organized into four data sets and summarized before statistical analysis. From the catchment and network riparian data, we summarized surficial geology, bedrock geology, bedrock depth, and land use/cover as percentages of the total surface area of each catchment or riparian zone upstream of the sampling reach. The an-

nual precipitation, number of growing degree-days, soil permeability, bedrock depth, and potential groundwater delivery rates were averaged across each catchment.

From the reach riparian land-use and instream habitat data, we calculated the frequency of occurrence for algae, macrophytes, shading, and fish cover; the percent composition of substrate, embeddedness, riffle/run/pool, bank condition, riparian land-use categories; and the means of thalweg depth, wetted width, and sediment depth. We combined some of these individual variables into additional summary variables. We also calculated the ratio of stream width to depth and coefficients of variation for sediment depth, embeddedness, and water depth. From the continuous water temperature data, we determined the maxima for 7-d means of daily means, daily maxima, and daily ranges; maxima for 21-d means of daily means, maxima, and ranges; maxima for July means of daily means, maxima, and ranges; and maxima for daily means, daily maxima, and daily ranges for June through August.

We created three fish data sets: fish assemblage characteristics, fish abundance (individuals/100 m by species), and species presence/absence. For the abundance and presence/absence data sets, we included only species that occurred at more than 14 sites ($\geq 5\%$ of sites) and had at least one site with five or more individuals per 100 m. This criterion reduced the number of fish variables and minimized the influence of rare species on results. The fish assemblage data set included 14 variables (Table 1). Thermal, feeding, tolerant, and reproduction classifications were based on Lyons (1992) and Lyons et al. (1996), and the Shannon diversity index was calculated based on Magurran (1988). The index of biotic integrity (IBI) score was calculated using the coldwater version for streams that had maximum daily mean water temperatures less than 22°C (Lyons et al. 1996) and the warmwater version for streams with temperatures greater than 24°C (Lyons 1992). For streams with intermediate temperatures, we calculated both versions and

Table 1. Fish assemblage characteristics variables, with variable abbreviation and their summary statistics for the study sites.

Variable	Abbreviation	Mean	Standard deviation	Minimum	Maximum
Fish abundance (individuals/100 m)	Abundance	368.4	442.6	20.0	3,006.0
Number of fish species	Fishsp	11.6	5.7	2.0	33.0
% of top carnivore individuals	Pcarniv	12.7	20.6	0.0	95.9
% of cool- and coldwater individuals	Pclcdiv	25.9	32.1	0.0	100.0
% of cool- and coldwater species	Pclcdsp	24.7	23.3	0.0	100.0
% of invertivore individuals	Pinviv	49.5	23.8	0.7	100.0
% of intolerant individuals	Pintoiv	18.5	25.4	0.0	100.0
% of omnivore individuals	Pomniv	16.1	16.9	0.0	81.1
% of salmonid individuals	Psaiv	10.4	20.6	0.0	95.9
% of salmonid species	Psasp	7.6	12.3	0.0	66.7
% of simple lithophil individuals	Plithiv	30.5	22.5	0.0	88.9
% of tolerant individuals	Ptoliv	42.6	28.8	0.0	100.0
IBI score	IBI	42.1	22.1	0.0	100.0
Shannon diversity index	Shan	1.7	0.5	0.2	2.7

used the higher of the two scores; a coolwater IBI does not yet exist for the study region.

Although our data originated from a 7-year period, the majority of habitat and fish data were collected between 1998 and 2000. A small portion of the study sites were sampled in multiple years, and we used the mean of each variable for each site. Our preliminary analysis on sites with multiple-year data and previous studies (Wang et al. 1996; Hughes et al. 1998; McCormick et al. 2001) indicated minor temporal changes in fish assemblage and habitat measures. Our exclusion of fish that occurred in less than 5% of sites and species that had maximum catch of less than 5 individuals per 100 m minimized the influence of temporal variation in fish abundance and presence/absence. Additionally, no substantial land-use change occurred in the study catchments during the study period (Wang et al. 2002, 2003a, 2003b; Baker et al. 2005).

Data Analysis

We divided the 287 sites into three groups according to urban and agricultural land uses based on previous findings of relationships between fish assemblages, and urban or agricultural land uses in catchments and in riparian areas (Wang

et al. 1997, 2001, 2003b). High disturbance sites (87 sites) had either catchment urban land use greater than 20% or agriculture greater than 70%; or network riparian urban land use greater than 10% or agriculture greater than 50%. Low disturbance sites (72 sites) had either catchment urban land use less than 2% or agriculture land use less than 10%; or network riparian urban land use less than 1% and agriculture land use less than 5%. Although agricultural and urban land uses were minimal in the catchments of this data set, some legacy effects from previous logging or burning might remain (Richards 1976; Harding et al. 1998). Medium disturbance sites (128 sites) had intermediate levels of urban and agricultural land uses.

We conducted two multivariate analyses on the three data sets of different disturbance levels. The first analysis was to test the hypothesis that in largely undisturbed catchments, fish assemblages are predominantly influenced by local factors (instream habitat and reach riparian land uses), but as level of disturbance increases in the catchments, the relative importance of local factors declines and that of catchment increases. We performed a canonical correspondence analysis (CCA) forward selection procedure (ter Braak and Smilauer 1998) to select the environmental

variables that were significantly ($p < 0.05$) correlated with CCA axes in each of the 36 data pairs—fish assemblage characteristics, abundance, and presence/absence data sets paired with each of the high, medium, and low disturbance data sets; and paired with each of the catchment, network riparian, reach riparian land-use, and instream habitat using CANOCO software (ter Braak and Smilauer 1998). We then conducted a CCA partition procedure (Borcard et al. 1992) to estimate the relative importance of catchment, network riparian, reach riparian land-use, or instream habitat in explaining the fish variables at the three-level disturbance data sets using the selected environmental variables.

The second analysis was to evaluate whether the influential factors at the four spatial scales were different among the three data sets that had different disturbance levels. Using CANOCO software (ter Braak and Smilauer 1998), we first performed a CCA forward selection procedure to select the environmental variables that were significantly ($p < 0.05$) correlated with CCA axes in each of the nine data pairs—fish assemblage characteristics, abundance, presence/absence data sets paired with each of the high, medium, and low disturbance data sets. We again used CANOCO software to conduct CCA on each data-set pair using only the retained environmental variables to examine the loadings of both the fish and environmental variables on the resultant CCA axes for each data set pair.

RESULTS

Fish Assemblage Characteristics

We collected 109 fish species during the study period (Appendix 1). Species richness per reach ranged from 2 to 33 with a mean of 12. The most frequently occurring fishes were white sucker *Catostomus commersonii* (81% sites), creek chub *Semotilus atromaculatus* (73% sites), central mudminnow *Umbra limi* (56% sites), Johnny darter *Etheostoma nigrum* (54% sites), and common shiner *Luxilus cornutus* (53% sites). The

catch at sampling sites ranged from 20 to 3,006 fish per 100 m, with a mean of 375 individuals per 100 m. About 78% of the sites supported cool-/coldwater fishes, and 42% of the sites contained salmonids. Species intolerant of environmental degradation occurred at 76% of the study sites and comprised more than 50% of the individuals at 14% of the sites. Forty-two percent of the study sites had IBI scores greater than 50 and 26% had scores less than 30.

Disturbance Level Effect on Scales Influencing Fishes

Fish assemblage characteristics.—For the fish assemblage characteristics-high disturbance data pair, the selected 33 different-scale environmental factors (Appendix 2) explained 77% of the variance in fish variables. Interactions among factors at the four spatial scales explained the most variation (38%); catchment and instream habitat explained moderate amounts (26% and 28%), and network riparian and reach riparian land-use explained the least (each <4%) (Figure 2). For the medium disturbance data set, the selected 33 environmental factors explained 69% of the variance in fish assemblages. Interactions among the four spatial scales explained the most variance (41%), instream habitat explained twice as much variance as catchment factors (30% versus 15%), and network riparian and reach riparian land-use variables explained the least (9% and 5%). For the low disturbance data set, the 23 selected environmental factors explained 72% of the variance in fish assemblages. Instream habitat and interactions among the four spatial scales explained similar amounts of variance (42% and 41%), which was much higher than that explained by catchment factors (9%). Network riparian and reach riparian land-use factors explained the least variance (5% and 4%).

Fish abundance.—For the fish abundance-high disturbance data pair, the selected 49 different-scale environmental factors (Appendix 2) explained 82% of the variance in fish variables. Catchment factors explained the most variance

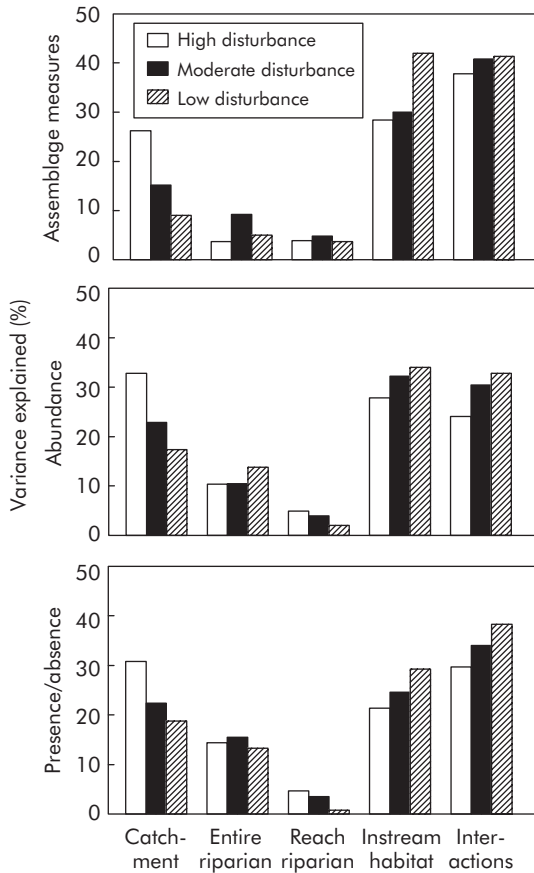


Figure 2. Percentages of variances of fish assemblage composition, abundance, and presence/absence explained by catchment, network riparian, reach riparian land-use, and instream habitat variables at high, medium, and low human disturbance levels.

(33%), instream habitat and interactions among the four spatial scales explained lesser amounts (27% and 25%), and network riparian and reach riparian land-use explained the least variance (10% and 5%) (Figure 2). For the medium disturbance data set, the selected 46 environmental factors explained 66% of the variance in fish abundance. Instream habitat and interactions among the four spatial scales explained the most variance (32% and 30%), catchment explained a lesser amount (23%), and network riparian and reach riparian land use explained the least variance (11% and 4%). For the low disturbance data set, the selected 40 factors explained 79% of the

variance in fish abundance. Of the explained variance, instream habitat and interactions among the four spatial scales explained the most (34% and 33%), catchment and network riparian explained a lesser amount (17% and 14%), and reach riparian land use explained very little variance (2%).

Fish presence/absence.—For the fish presence/absence-high disturbance data pair, the selected 41 different scale environmental factors (Appendix 2) explained 68% of the variance in fish variables. Of the explained variance, catchment factors and interactions among factors at the four spatial scales explained the most (32% and 30%), instream habitat and network riparian factors explained moderate amounts (20% and 14%), and reach riparian land use explained the least (4%) (Figure 2). For the medium disturbance data set, the selected 37 factors explained 54% of the variance in fish presence/absence. Of the explained variance, interactions among the four spatial scales explained the most (34%), instream habitat and catchment factors explained similar amounts (24% and 23%), and network riparian and reach riparian land-use factors explained the least (16% and 3%). For the low disturbance data set, the 42 selected factors explained 76% of the variance in fish variables. Of the explained variance, interactions among factors at the four spatial scales explained the most (38%), instream habitat explained a moderate amount (29%), catchment and network riparian factors explained much less (19% and 13%), and reach riparian land-use explained very little variance (2%).

The variation explained by catchment factors for all three types of fish measurements clearly decreased as levels of anthropogenic disturbance decreased (Figure 2). In contrast, the variations explained by the instream habitat and interaction among the spatial scale factors for all three types of fish measurements consistently increased as human disturbance decreased. The variation explained by network riparian land-use was unclear, although the variation explained by reach riparian land-use for fish abundance and

presence/absence decreased slightly as disturbance levels decreased.

Disturbance Level Influence on the Dominance of Environmental Factors

Fish assemblage characteristics.—The environmental factors at all three levels of disturbance oriented fish assemblages in a similar pattern (Figure 3). The first two CCA axes oriented fish variables from a cold/cool water, intolerant, carnivore, and high IBI-value dominated assemblage to a tolerant, omnivore, and high diversity assemblage. Water temperature variables in all three disturbance levels had similar association patterns with the orientation of fish variables, however the other dominant factors determining fish assemblage orientation differed among disturbance levels.

In the high disturbance data set, both land-use/-cover factors (e.g., catchment forest land, catchment grassland, and network riparian agriculture) and natural landscape factors (e.g., network riparian soil permeability, network riparian carbon and shale bedrock geology) had a strong influence on fish assemblage characteristics. To a lesser degree, instream habitat, such as dissolved oxygen, substrate embeddedness, and coefficient of variation for width/depth ratio, also influenced fish assemblages. In contrast, land-use factors were not strongly associated with fish assemblages in the medium and low disturbance data sets. For the medium disturbance data set, the dominant factors were catchment soil permeability, network riparian shallow bedrock depth, reach bank stability, and substrate embeddedness. For the low disturbance data set, the influential environmental factors were catchment and network riparian groundwater potential delivery rates, catchment medium textured surficial geology, and instream overall habitat and dissolved oxygen conditions. Fish total abundance slightly deviated from the orientation of the other assemblage measures, being associated with variation coefficient of width/depth ratio and network riparian carbonate bedrock in high

disturbance, associated with network riparian shallow bedrock in medium disturbance, and associated with high temperature in low disturbance data sets. No strong association was observed between fish assemblage measures and catchment size for three disturbance levels.

Fish abundance.—Water temperature variables were strongly negatively associated with abundance of coldwater fishes (e.g., brown trout *Salmo trutta*, brook trout *Salvelinus fontinalis*, rainbow trout *Oncorhynchus mykiss*, and American brook lamprey *Lampetra appendix*) at all disturbance levels, but the other dominant environmental factors and their associated fish groups differed among the disturbance levels (Figure 4). For the high disturbance data set, the dominant environmental factors were catchment urban land use, catchment sandstone bedrock, network riparian agricultural land use, and network riparian coarse texture surficial geology. These environmental factors distinguished central mudminnow, pearl dace *Margariscus margarita* (also known as *Semotilus margarita*), northern redbelly dace *Phoxinus eos*, and eastern blacknose dace (also known as blacknose dace) *Rhinichthys atratulus*, which are adapted to slow-moving water with low-dissolved oxygen, from northern hog sucker *Hypentelium nigricans*, banded darter *Etheostoma zonale*, sand shiner *Notropis stramineus*, and shorthead redhorse *Moxostoma macrolepidotum*, which are adapted to fast-moving water.

For the medium disturbance data set, instream factors such as silt substrate and gradient distinguished central mudminnow and northern redbelly dace from sand shiner, logperch *Percina caprodes*, smallmouth bass *Micropterus dolomieu*, and shorthead redhorse. In contrast, for the low disturbance data set, catchment water land cover, soil permeability, and shallow bedrock depth strongly associated with rosyface shiner *Notropis rubellus*, yellow bullhead *Ameiurus natalis*, bluntnose minnow *Pimephales notatus*, and logperch. Water temperature daily variations were also associated with central mudminnow, brassy minnow

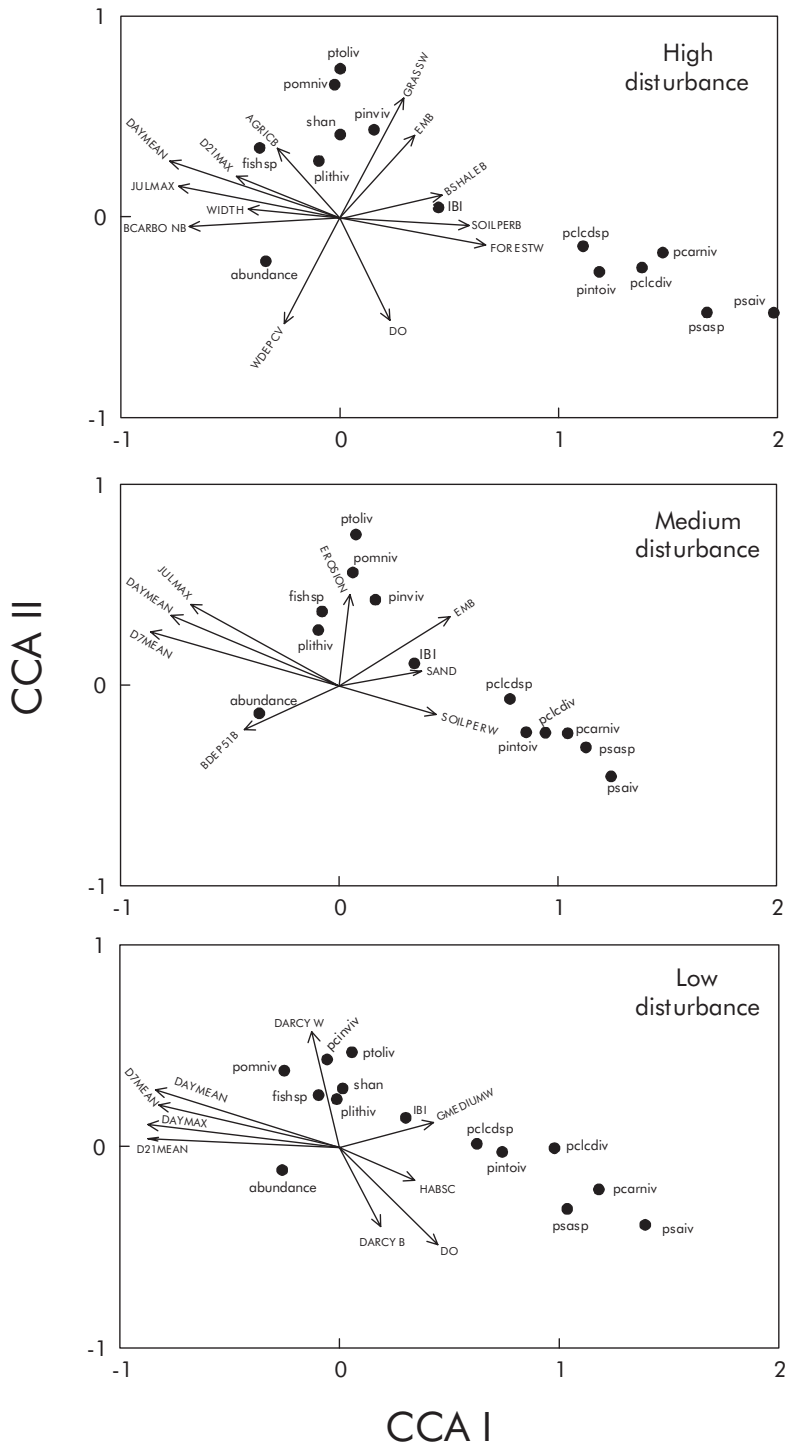


Figure 3. Plots of the first two axes from canonical correspondence analyses with stepwise forward variable selection for the fish assemblage composition and all four spatial scale factors at high, medium, and low human disturbance levels. The dots represent fish assemblage variables (names in Table 1). The arrows represent the environmental factors (names in Appendix 2).

Hybognathus hankinsoni, finescale dace *Phoxinus neogaeus*, and blacknose shiner *Notropis heterolepis*. Catchment size also had stronger influences on medium-large stream fish species, such as logperch, rosyface shiner, and shorthead redhorse, for medium and low disturbance data sets than for high disturbance data set.

Fish presence/absence.— Water temperature measures strongly negatively influenced the occurrence of coldwater fishes at all disturbance levels, but the other environment-fish associations were different among the three disturbance levels (Figure 5). For the high disturbance data set, catchment agricultural land use and substrate embeddedness were associated with a group of tolerant fishes (e.g., pearl dace, brook stickleback *Culaea inconstans*, fathead minnow *Pimephales promelas*, central mudminnow, and creek chub). Catchment forest land cover and network riparian sandstone bedrock were associated with coldwater fishes. And discharge and stream width were associated with a group of fish adapted to medium-large streams (e.g., northern hogsucker, shorthead redhorse, golden redhorse *Moxostoma erythrum*, banded darter, and rosyface shiner).

For the medium disturbance data set, catchment agricultural land use, daily temperature variation, shading, and substrate embeddedness were associated with central mudminnow, northern redbelly dace, brassy minnow, blacknose shiner, and fathead minnow. Stream width, thalweg depth, and embeddedness variation were associated with shorthead redhorse, golden redhorse, black Crappie *Pomoxis nigromaculatus*, smallmouth bass, northern hog sucker, and spotfin shiner *Cyprinella spiloptera* (also known as *Notropis spilopterus*). For the low disturbance data set, in addition to temperature mean measures, percent of deep bedrock and gradient were associated with coldwater fishes. Catchment size and channel width to depth ratio were associated with largescale stoneroller *Camptostoma oligolepis*, smallmouth bass, shorthead redhorse, and northern hog sucker. Associations among environmental factors and

tolerant fishes were not as clear as in the high or medium disturbance data sets.

DISCUSSION

Disturbance Level Effects on Scale Influence on Fish

Our results supported the hypothesis that in largely undisturbed catchments, fish assemblages are predominantly influenced by local factors, but as the level of disturbance increases in the catchment, the relative importance of local factors declines and that of the catchment increases. Our results also demonstrated that dominant factors at different spatial scales were closely linked and interactively influenced fish assemblage composition.

Our results are supported by the theories of hierarchical organization and nested constraining mechanisms of stream and lake systems (e.g., Frissell et al. 1986; Poff 1997; Allen et al. 1999; Parsons et al. 2003). These theories, in principle, state that the array of local instream conditions found within fluvial systems are created and constrained by predictable hydrologic and geomorphologic processes (e.g., Harper and Everard 1998; Parsons et al. 2004; Seelbach et al. 2006, this volume). These processes operate hierarchically; large-scale processes constrain the expression of processes at successively smaller scales, and hence, stream systems can be divided into and viewed as discrete scales that reflect the relationship between geomorphologic processes and local stream features (Parsons et al. 2003). Consequently, the distribution and character of local stream conditions determine the types of biological assemblages found because habitat provides the templet on which evolution acts to forge characteristic life history strategies (Southwood 1977).

In natural or minimally disturbed systems, catchment, riparian, and instream conditions are at a dynamic equilibrium that maintains a level of stability that permits internal adjustment of factors without producing rapid change in the

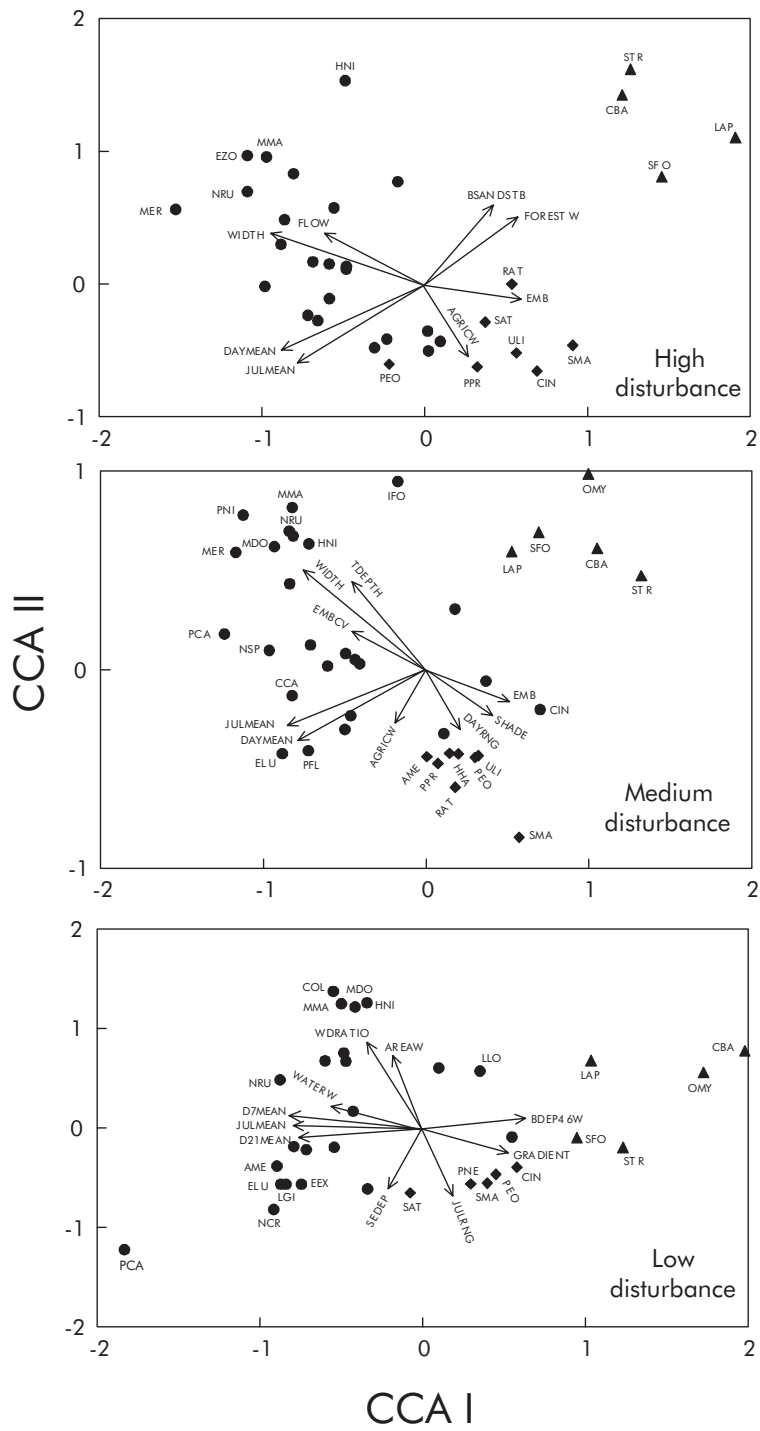


Figure 5. Plots of the first two axes from canonical correspondence analyses with stepwise forward variable selection for the fish presence/absence and all four spatial scale factors at high, medium, and low human disturbance levels. Filled triangles, diamonds, and circles represent coldwater, tolerant, and other fish species groups, and the label by the symbol is the first letter of the genus and the first two letters for that species (also see Appendix 1). The arrows represent the environmental variables (names in Appendix 2).

system. The resilience or ability to maintain the equilibrium results from combined factors acting together across the different scales. Fishes living in such systems are adapted to the dynamic equilibrium conditions. Fish assemblage characteristics are a direct reflection of the instream conditions, and the influences of catchment and riparian conditions on fishes are expressed indirectly through their direct influence on instream factors (Wang et al. 2003a; Kaufmann and Hughes 2006, this volume)

Fish assemblage characteristics cannot be completely reflected by instream conditions in anthropogenically disturbed catchments. When anthropogenic disturbances break the equilibrium among catchment, riparian, and instream conditions, the instream variables tend to reestablish new equilibria with their environments; hence, different and generally degraded fish assemblages occur. Because anthropogenic development does not happen overnight and past disturbances leave a legacy effect, instream variables continuously adjust their conditions and so do the associated fish assemblages. Under such a continuous dynamic status, traditional instream channel habitat measures do not reflect the entire stream conditions in which fish live. For example, the usual habitat sampling does not include temperature and flow extreme measures, pollutant pulses, and their occurrence frequencies because of their associated costs. These hydrologically driven instream factors are critical to fish assemblages and are often influenced by catchment and riparian anthropogenic development. Hence, fish assemblage characteristics tend to be associated more with large-scale and riparian conditions in anthropogenic disturbed catchments than in natural catchments.

Our results are also supported by other studies that have indirectly confirmed our hypothesis. In a review of improving riparian areas through catchment management, DeBano and Schmidt (1989) described two potential catchment scenarios that are directly linked to the scales of influential factors, and that may affect the effectiveness of riparian management prac-

tices. They presented one scenario where much of the catchment remained in reasonably good condition but localized degradation occurred by concentrated livestock overgrazing or other farming activities. In such a situation, they predicted that local riparian management practices alone would be sufficient for improving habitat and, hence, biological assemblages. In their other scenario, both the riparian zone and catchment were damaged by human activities. In this case, they predicted that catchment management alone or catchment plus riparian management practices might improve fish assemblages, but riparian management alone would be inefficient because the linkages between catchment and instream habitat remained altered. In studying effects of various levels of urban land use on cold-water streams in Minnesota and Wisconsin, Wang et al. (2003b) reported that catchment and riparian land uses had stronger associations with fish assemblages than instream physical habitat. However, in studying streams in the Northern Lakes and Forest ecoregion in Minnesota, Michigan, and Wisconsin where the catchments were largely undisturbed by human activities, Wang et al. (2003a) found that instream physical factor had more influence on fish assemblages than did catchment variables.

Disturbance Level Influence on the Dominance of Environmental Factors

Mean water temperature measures were the most important factors explaining fish assemblage compositions in our study region regardless of levels of human disturbance in the catchment or riparian areas. Streams in the study region have varied thermal regimes from warm, cool, to cold, which are determined by natural variation in climate, landscape slope and surficial deposits controlling potential groundwater deliveries, and land cover in the region (Wang et al. 2003a; Wehrly et al. 2003). Catchment and riparian land uses alter stream thermal regimes both directly and indirectly (Wang et al. 2003b).

Such an impact can be well depicted in measured stream mean temperatures (Wang et al. 2003b); however, the levels of human disturbance in our study did not affect the relationship between temperature and fish assemblages.

Unlike mean temperature measures, the other dominant environmental factors associated with fish assemblages were different among the three human disturbance levels in our study region. In general, catchment and riparian land uses were among the dominant factors determining fish assemblage characteristics in highly disturbed streams, while in least disturbed streams, land uses were not dominant factors associated with fish assemblages. Human disturbances in catchment and riparian areas disrupt the connections between water and land (Dunne and Leopold 1978), and alter the natural dynamic equilibrium between instream characteristics and their catchment conditions. Changes in stream conditions resulting from human disturbance are often only partially measured during routine instream habitat assessment because of their cumulative and sporadic nature, which is difficult and expensive to measure (Wang and Lyons 2003). Hence, the influence of human disturbance on fish in supplying excessive amounts of nutrients and sediment and in altering flood peaks and frequencies, thermal extremes, and toxicants are often more easily measured by associating fish assemblages with urban or agriculture land uses (Karr and Chu 1999).

It is interesting to note that daily temperature variations strongly influenced fish abundance and presence/absence only in slightly disturbed streams. It was also reported that distributions of coldwater fishes were influenced by mean maximum summer temperature and daily temperature variations in Michigan and Wisconsin streams (K. Wehrly and L. Wang, Michigan DNR, Ann Arbor, Michigan, unpublished data), which is consistent with our findings. Our results also imply that the other influences of human disturbances override the influence of daily temperature variation in catchments with high levels of human disturbance.

Despite the large number of different scale environmental factors investigated and their strong association with fish assemblages, a considerable amount of variation in emergent fish assemblage properties was unexplained in our study. Several factors may have contributed to the unexplained variations. Our investigation focused on the relative importance of different spatial scale factors at different human disturbance levels. We purposely excluded factors such as latitude and longitude that may obscure our interpretation. These excluded factors are known to influence fish distribution in the Midwestern United States (Wang et al. 2003a) and in other areas of the United States (Angermeier and Winston 1999). Temporal variation in environmental factors on fish assemblage composition could not be detected by our single sample per site design, and it certainly plays an important role in assemblage structuring (Wiley et al. 1997). We investigated only extrinsic factors, but intrinsic factors such as competition and predation may also be important in structuring assemblage richness and complexity (Marsh-Matthews and Matthews 2000). Because our study was designed to evaluate the relative influence of different scale factors on fish assemblages at different human disturbance levels, we selectively examined only factors relevant to our question. By selecting multiple factors at multiple scales over a broad range of environmental conditions, we were able to detect patterns of influence of extrinsic factors at different human disturbance levels on composition, richness, complexity, and other aspects of fish assemblage structure.

Management Implications

Our study has several implications for catchment research and management. First, we found that fish assemblages were predominantly influenced by instream and riparian factors in largely undisturbed catchments, and as level of disturbance increases in the catchments, the relative importance of local factors declines and that of catchment increases. These findings provide more

insightful information on why some conclusions, regarding the relative importance of local versus catchment factors, have been inconsistent in previous studies. Second, our results provide new evidence on how stream environments and their associated fish assemblages were influenced by landscapes through multiple pathways and mechanisms, operating at different spatial scales. Last, our results imply that instream habitat and riparian improvement will be most effective in largely undegraded catchments and minimally effective in degraded catchments. Catchment scale land-use management, in conjunction with instream habitat and riparian rehabilitation, should be emphasized for improving stream quality in degraded catchments.

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Appendix 1. Fish species captured and included in the data analysis, with fish code (the first letter of the genus and the first two letters for that species), percent occurrence at sites, and the mean and maximum catch (individuals \cdot 100 m⁻¹). Minimum catch was zero for all sites since no species occurred in all sites. Fifty-seven additional fish species or hybrids that were caught at less than 5% of the sites or the maximum catch of less than 5 individuals \cdot 100 m⁻¹ were not included. Codes in bold are used in Figures 4 and 5.

Species	Fish code	Percent occurrence	Mean catch	Maximum catch
American brook lamprey <i>Lampetra appendix</i>	LAP	9.1	0.2	10
Northern brook lamprey <i>Ichthyomyzon fossor</i>	IFO	5.2	0.3	13
Rainbow trout <i>Oncorhynchus mykiss</i>	OMY	7.3	0.7	81
Brown trout <i>Salmo trutta</i>	STR	25.4	3.6	134
Brook trout <i>Salvelinus fontinalis</i>	SFO	24.7	6.1	238
Central mudminnow <i>Umbra limi</i>	ULI	55.7	12.9	494
Northern pike <i>Esox lucius</i>	ELU	10.5	0.2	11
Central stoneroller <i>Campostoma anomalum</i>	CAN	17.4	4.2	209
Largescale stoneroller <i>C. oligolepis</i>	COL	8.4	1.3	99
Common carp <i>Cyrinus carpio</i>	CCA	16.7	0.5	15
Brassy minnow <i>Hybognathus hankinsoni</i>	HHA	10.5	1.1	179
Hornyhead chub <i>Nocomis biguttatus</i>	NBI	29.6	5.3	355
Golden shiner <i>Notemigonus crysoleucas</i>	NCR	11.1	0.3	26
Common shiner <i>Luxilus cornutus</i>	LCO	53.3	19.3	810
Bigmouth shiner <i>Notropis dorsalis</i>	NDO	9.8	0.5	43
Blacknose shiner <i>N. heterolepis</i>	NHE	10.8	0.6	44
Rosyface shiner <i>N. rubellus</i>	NRU	8.7	2.2	506
Spotfin shiner <i>Cyprinella spilopterus</i>	NSP	8.7	0.2	16
Sand shiner <i>N. stramineus</i>	NST	7.7	0.9	193
Northern redbelly dace <i>Phoxinus eos</i>	PEO	19.2	1.5	61
Southern redbelly dace <i>P. erythrogaster</i>	PER	8.0	2.3	157
Finescale dace <i>P. neogaeus</i>	PNE	7.0	0.8	163
Bluntnose minnow <i>Pimephales notatus</i>	PNO	27.9	5.7	471
Fathead minnow <i>P. promelas</i>	PPR	33.1	3.1	107
Eastern blacknose dace <i>Rhinichthys atratulus</i>	RAT	46.7	10.2	155
Longnose dace <i>R. cataractae</i>	RCA	26.8	4.8	203
Creek chub <i>Semotilus atromaculatus</i>	SAT	72.8	20.7	318
Pearl dace <i>Margariscus margarita</i>	SMA	17.1	2.7	121
White sucker <i>Catostomus commersonii</i>	CCO	81.2	17.6	512
Northern hog sucker <i>Hypentelium nigricans</i>	HNI	11.1	0.2	8.1
Golden redbreast <i>Moxostoma erythrurum</i>	MER	7.0	0.1	7.8
Shorthead redbreast <i>M. macrolepidotum</i>	MMA	9.4	0.2	14
Black bullhead <i>Ameiurus melas</i>	AME	20.6	0.6	42
Yellow bullhead <i>A. natalis</i>	ANA	12.9	0.3	19
Burbot <i>Lota lota</i>	LLO	7.0	0.2	33
Brook stickleback <i>Culaea inconstans</i>	CIN	40.1	4.2	128
Rock bass <i>Ambloplites rupestris</i>	ARU	18.5	0.6	28
Green sunfish <i>Lepomis cyanellus</i>	LCY	28.6	1.5	86
Pumpkinseed <i>L. gibbosus</i>	LGI	15.7	0.7	37
Bluegill <i>L. macrochirus</i>	LMA	26.5	0.9	49
Smallmouth bass <i>Micropterus dolomieu</i>	MDO	15.3	0.3	8
Largemouth bass <i>M. salmoides</i>	MSA	11.5	0.3	10
Black crappie <i>Pomoxis nigromaculatus</i>	PNI	8.0	0.2	5
Rainbow darter <i>Etheostoma caeruleum</i>	ECA	8.0	1.5	123
Iowa darter <i>E. exile</i>	EEX	5.9	0.3	36
Fantail darter <i>E. flabellare</i>	EFL	20.2	2.7	89
Johnny darter <i>E. nigrum</i>	ENI	54.4	5.7	136
Banded darter <i>E. zonale</i>	EZO	6.3	0.1	5
Yellow perch <i>Perca flavescens</i>	PFL	14.3	0.6	81
Logperch <i>Percina caprodes</i>	PCA	13.6	0.7	58
Blackside darter <i>P. maculata</i>	PMA	18.8	0.9	35
Mottled sculpin <i>Cottus bairdii</i>	CBA	39.7	10.9	37

Appendix 2. Mean and standard error (SE) for catchment, network riparian, reach riparian, and instream variables that were significantly ($P < 0.05$) correlated with fish variables in the forward selection of canonical correspondence analysis (CCA). An "X" indicates the fish variable with which an environmental variable was correlated in high (H), medium (M), and low (L) disturbance data sets. Variables in Figures 3–5 are in bold.

Variable	Description	Mean ± (1 SE)	Presence/ absence			Abundance			Assemblage characteristics		
			H	M	L	H	M	L	H	M	L
Catchment area, land use, and landscape											
AREAW	Catchment area (km ²)	136.4 + 14.4	X	X	X	X	X	X	X	X	X
AGRICW	Agricultural land use (%)	35.5 + 1.7	X	X	–	X	X	–	X	–	–
BARRENW	Barren land (%)	1.5 + 0.1	–	–	–	X	X	–	X	X	–
FORESTW	Forest land (%)	34.7 + 1.6	X	–	–	–	–	–	X	–	–
GRASSW	Grassland (%)	12.1 + 0.6	–	–	X	–	X	–	X	X	–
URBANW	Urban land use (%)	2.9 + 0.5	X	X	–	X	X	–	X	–	–
WATERW	Water (%)	1.5 + 0.2	X	X	X	X	X	X	–	X	X
WETLANDW	Wetland (%)	11.8 + 0.7	–	X	–	X	X	–	–	X	–
DARCYW	Ground water velocity (m/d)	9.4 + 0.5	X	X	X	X	X	X	X	–	X
GDD	Growing degree-days at sample sites	2,290.2 + 23.3	X	X	X	X	X	X	–	–	X
PPT	Precipitation at sample sites (mm)	736.0 + 14.4	–	X	X	–	–	X	–	–	–
Catchment surficial geology											
GCOARSEW	Coarse textured (%)	63.8 + 2.5	–	–	–	X	X	–	–	–	–
GFINW	Fine texture (%)	13.2 + 1.8	–	–	X	–	–	–	–	–	–
GMEDIUMW	Medium texture (%)	5.8 + 1.2	–	–	–	X	X	–	–	–	X
GNOTEXTW	No texture (%)	16.1 + 2.1	X	X	–	X	X	–	–	–	–
GPEATMUW	Peat and muck (%)	1.2 + 0.3	–	–	X	–	–	X	–	–	–
Catchment bedrock depth and geology											
BCARBONW	Carbonate bedrock geology (%)	44.1 + 2.5	X	X	–	–	–	–	X	–	–
BDEP05W	Bedrock depth < 5 ft (%)	40.9 + 2.4	–	–	–	X	–	–	–	–	–
BDEP51W	Bedrock depth 5–10 ft (%)	24.1 + 1.7	–	–	–	–	X	–	–	X	–
BDEP12W	Bedrock depth 10–20 ft (%)	24.2 + 1.9	X	–	X	–	–	X	X	–	–
BDEP24W	Bedrock depth 20–40 ft (%)	7.7 + 1.2	–	–	–	–	–	–	–	X	–
BDEP46W	Bedrock depth > 40 ft (%)	3.1 + 0.9	–	–	X	–	–	–	–	–	–
BDEPMENW	Mean bedrock depth (feet)	102.8 + 5.6	X	X	–	X	X	X	X	X	–
BIGNMETW	Metamorphic/igneous bedrock geology (%)	25.6 + 2.5	–	–	–	–	–	–	–	–	X
BSANDSTW	Sandstone bedrock geology (%)	24.5 + 2.0	–	–	X	X	–	X	–	–	–
Catchment soil permeability											
Q25P150W	Soil permeability < 150 in 100 h ^{–1} (%)	23.1 + 2.1	–	X	–	–	X	–	–	–	–
Q50P265W	Soil permeability < 265 in 100 h ^{–1} (%)	48.8 + 2.5	–	–	–	X	–	–	–	X	–
Q75P500W	Soil permeability < 500 in 100 h ^{–1} (%)	62.1 + 2.4	X	–	–	X	–	–	–	–	–
SOILPERW	Mean soil permeability (in 100 h ^{–1})	381.8 + 17.4	–	X	–	–	X	X	–	X	–
Network riparian variables											
AGRICB	Agricultural land use (%)	27.6 + 1.5	X	–	–	X	X	–	X	–	–
BARRENB	Barren land (%)	0.9 + 0.1	–	X	–	X	–	–	–	X	–
FORESTB	Forest land (%)	28.5 + 1.3	X	X	–	X	–	–	X	–	–
GRASSB	Grass land (%)	10.5 + 0.6	X	–	X	–	–	X	–	–	–
URBANB	Urban land (%)	2.5 + 0.5	X	X	X	X	X	X	X	–	–

(Appendix continues)

Appendix 2 (continued)

Variable	Description	Mean \pm (1 SE)	Presence/ absence			Abundance			Assemblage characteristics		
			H	M	L	H	M	L	H	M	L
WETLANDB	Wetland (%)	30.0 + 1.3	X	X	–	–	X	–	–	X	X
BDEP05B	Bedrock depth < 5 ft (%)	14.0 + 1.3	X	–	X	X	–	X	–	–	X
BDEP51B	Bedrock depth 5–10 ft (%)	18.6 + 1.3	X	–	–	–	X	–	–	X	–
BDEP12B	Bedrock depth 10–20 ft (%)	36.6 + 2.9	X	–	–	–	–	X	–	–	–
BDEP24B	Bedrock depth 20–40 ft (%)	22.2 + 3.6	–	–	–	X	–	–	–	X	–
BDEP46B	Bedrock depth > 40 ft (%)	3.7 + 1.3	–	–	X	–	–	–	–	–	–
BDEPMENB	Mean bedrock depth (feet)	102.2 + 5.5	–	–	X	X	–	X	–	X	–
Q25P150B	Soil permeability < 150 in 100 h ⁻¹ (%)	24.4 + 2.2	–	–	–	–	–	–	–	X	–
Q50P265B	Soil permeability < 265 in 100 h ⁻¹ (%)	47.9 + 2.5	X	–	–	X	X	–	–	X	–
Q75P500B	Soil permeability < 500 in 100 h ⁻¹ (%)	59.1 + 2.5	X	–	–	–	–	–	–	–	–
SOILPERB	Mean soil permeability (in 100 h ⁻¹)	382.6 + 17.8	–	X	X	X	X	X	X	X	–
BCARBONB	Carbonate bedrock geology (%)	33.3 + 2.6	–	X	–	–	–	–	X	–	–
BIGNMETB	Metamorphic/Igneous bedrock geology (%)	25.6 + 2.5	–	–	–	–	–	–	–	–	X
BSANDSTB	Sandstone bedrock geology (%)	24.5 + 2.0	X	–	X	X	–	X	X	–	–
BSHALEB	Shale bedrock geology (%)	14.9 + 1.6	–	X	–	–	–	–	X	–	–
DARCYB	Ground water velocity (m/day)	69.5 + 5.1	–	–	–	–	–	X	–	–	X
GCOARSEB	Coarse textured (%)	62.5 + 2.6	–	–	–	X	X	–	–	–	–
GFINEB	Fine texture (%)	14.1 + 1.8	–	–	X	–	–	–	–	–	–
GMEDIUMB	Medium texture (%)	5.5 + 1.2	–	–	–	–	X	–	–	–	–
GNOTEXTB	No texture (%)	16.7 + 2.1	X	X	X	X	–	–	–	X	–
GPEATMUB	Peat and muck (%)	1.3 + 0.3	–	X	X	–	–	X	–	–	–
<i>Reach riparian land use</i>											
CROPLAND	Reach scale crop land use (%)	0.7 + 0.2	–	–	–	X	–	–	X	–	–
DEVELOP	Reach scale developed land use (%)	5.3 + 0.8	X	X	–	–	X	–	–	X	–
MEADOW	Reach scale meadow land (%)	27.8 + 1.9	–	X	–	–	–	–	X	–	–
PASTURE	Reach scale pasture land (%)	4.8 + 1.1	X	–	–	X	–	–	X	–	–
SHRUB	Reach scale shrub land (%)	15.4 + 1.3	–	–	–	–	X	–	–	X	–
WETLAND	% riparian wetland	6.4 + 1.2	–	–	X	–	X	X	–	–	–
WOODS	Reach scale wood land (%)	38.9 + 2.1	–	–	X	X	–	X	–	–	X
<i>Instream habitat</i>											
CLAY	% stream bottom covered with clay	4.1 + 0.6	–	X	X	–	X	–	–	–	X
DETRTS	% stream bottom covered with detritus	4.6 + 0.5	X	X	–	–	–	X	–	X	–
GRAVRUB	% stream bottom covered with gravel or rubble	21.9 + 0.9	–	–	–	X	–	–	–	–	X
SAND	% stream bottom covered with sand	34.7 + 1.5	X	–	X	X	–	X	–	–	–
SILT	% stream bottom covered with silt	14.8 + 1.0	X	X	–	–	X	–	–	X	–
DO	Dissolved oxygen (mg/L)	8.6 + 0.1	X	X	–	X	X	–	X	X	X
EMB	% rocky substrate covered by silt or sand	58.6 + 1.8	X	X	–	X	–	–	X	X	–
EMBCV	Coefficient of variation for EMB	77.2 + 4.2	–	X	X	X	–	X	–	X	–
EROSION	% stream banks are erodable	16.6 + 1.0	–	X	–	X	–	X	X	X	–
FLOW	Stream discharge (m/s)	0.7 + 0.1	X	–	–	–	–	–	–	–	–
FSCOVER	% stream with fish cover	12.5 + 0.8	X	–	X	X	X	X	X	–	–

Appendix 2 (continued)

Variable	Description	Mean \pm (1 SE)	Presence/ absence			Abundance			Assemblage characteristics		
			H	M	L	H	M	L	H	M	L
GRADIENT	Stream gradient within sampling site (m/1,000 m)	3.1 + 0.2	–	–	X	X	X	X	X	X	X
HABSC	Habitat score	59.9 + 0.7	–	–	–	–	–	–	–	–	X
POOL	% stream reach that is pool	11.0 + 1.0	–	–	–	–	X	–	X	–	X
RIFFLE	% stream reach that is riffle	13.5 + 1.0	–	–	X	–	X	X	–	–	–
SEDEP	Sediment depth (cm)	9.3 + 0.7	–	–	X	X	X	X	–	X	X
SEDEPCV	Coefficient of variation for sediment depth	155.8 + 6.6	–	–	–	–	–	–	X	–	–
SHADE	% stream is shaded by canopy	36.8 + 1.6	–	X	–	–	–	–	X	–	–
SINUOS	Sinuosity of stream reach (ratio)	1.3 + 0.0	X	–	–	X	X	–	–	–	X
TDEPTH	Thalweg depth (m)	0.49 + 0.0	X	X	X	–	–	–	–	–	X
WDEPCV	Coefficient of variation for width to depth ration	43.7 + 0.8	–	–	–	–	X	–	X	–	X
WDRATIO	Width to depth ratio (ratio)	17.6 + 0.7	–	–	X	–	X	X	–	–	X
WIDTH	Stream width (m)	8.7 + 0.5	X	X	X	X	X	–	X	X	X
DAYMEAN	Maximum daily mean temperature (°C)	23.0 + 0.2	X	X	–	X	X	X	X	X	X
DAYMAX	Highest temperature reading during the season (°C)	26.0 + 0.2	X	–	X	–	–	X	–	–	X
DAYRNG	Maximum difference between daily maximum and daily minimum temperature (°C)	8.0 + 0.2	–	X	X	–	X	X	–	X	–
D7MEAN	Maximum 7-d mean of daily mean temperature (°C)	22.1 + 0.2	X	–	X	–	–	X	–	–	X
D7MAX	Maximum 7-d mean of daily maximum temperature (°C)	24.7 + 0.2	–	–	X	–	–	X	–	–	–
D7RNG	Maximum 7-d mean DAYRNG (°C)	8.0 + 0.2	–	–	X	X	X	X	–	–	–
D21MEAN	Maximum 21-d mean of daily mean temperature (°C)	21.1 + 0.2	–	–	X	X	X	X	–	–	X
D21MAX	Maximum 21-d mean of daily maximum temperature (°C)	23.6 + 0.2	–	–	X	X	–	X	X	–	–
JULMEAN	Mean of July daily mean temperature (°C)	19.7 + 0.2	X	X	X	X	X	X	–	–	–
JULMAX	Mean of July daily maximum temperature (°C)	22.0 + 0.2	–	–	–	X	X	–	X	X	–
JULRNG	Mean July daily temperature range (°C)	4.3 + 0.1	X	–	X	X	X	X	–	–	–

Island Biogeography of Native Fish Faunas among Great Plains Drainage Basins: Basin Scale Features Influence Composition

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Abstract.—We reviewed native fish zoogeography in 22 major tributary basins of the Missouri River basin in the Great Plains geomorphic province and used island biogeographical approaches to study the influence of basin area and isolation on faunal composition. Basin area was correlated with elevation range and basin isolation was negatively correlated with annual freeze-free days. Ninety-six species were native to the tributary basins. Ninety-one were of southern (Gulf of Mexico drainage) origin. Fifty were found in four or fewer tributary basins and, except for three mountain species, were only found from the Cheyenne basin downstream. Twenty-five widespread species were either present among tributary basins during glaciation or colonized the region during recession of the continental glaciers. Sixty-six more restricted species presumably colonized more recently. Five species colonized from Pacific Ocean drainages via interdrainage connections in the Rocky Mountains. The hypothesis that variation between some closely related Great Plains fishes reflects the former presence of a prehistoric “Ancient Plains Drainage” is no longer tenable given recent geological findings, but a series of stream captures between the ancient Arkansas and Kansas basins could account for such variation. All analyses indicated that native fish faunal composition among tributary basins was heavily influenced by factors related to basin area and isolation. A presence–absence matrix of fishes by tributary basin had very high nestedness, whether ordered by basin area or basin isolation. Cluster analysis of Wilcoxon two-sample tests of individual species distributions revealed seven species groups with distinct distribution patterns. The three largest groups were most prevalent in less isolated (southern) tributary basins. A nonmetric multidimensional scaling analysis (NMDS) based on Sørensen’s index of similarity indicated that two axes (both correlated with tributary basin isolation, one correlated with tributary basin area) accounted for 95% of variance between distance in the ordination space and distance in the original n -dimensional space. A cluster analysis of NMDS scores identified five tributary basin groups. The five southernmost basins (Kansas to White) composed one group, and the eight basins to the north (Bad to Little Missouri) composed another. The nine northernmost basins were split into three groups, one including small basins isolated from the Rocky Mountains, another including large basins with Rocky Mountain headwaters, and the last including two basins that were mostly within the Rocky Mountains. The influence of tributary basin area on faunal composition was presumably due to increased chance of colonization, higher habitat stability, and higher habitat diversity in larger tributary basins. The influence of tributary basin isolation was presumably due to higher colonization rates and more equitable climate

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in southern tributary basins. Fish faunas of the Missouri River basin in the Great Plains have experienced cyclical geomorphic and climatic instability for roughly 2.8 million years and were assembled like island faunas by variable colonization and extinction rates mediated by tributary basin area and isolation. This contrasts with the highly diverse freshwater fish faunas of the Central Highlands that have differentiated through speciation within regions that have been relatively stable geomorphically and climatically for more than 38 million years.

INTRODUCTION

The equilibrium theory of island biogeography provides a basis for understanding factors that govern the composition of faunas in insular habitats of all kinds (Simberloff 1974; Whittaker 1998). Extinction and colonization are important mechanisms for assembling faunas (MacArthur and Wilson 1963, 1967; Lomolino 1986) but are difficult to study directly (Simberloff and Martin 1991). Indirect assessments of extinction and colonization focus on the relation of insular area and isolation to faunal composition (Simberloff 1976; Lomolino et al. 1989; Taylor 1997). Larger insular areas have more species due to chance, more diverse habitat, more individuals per species, and lower disturbance (McGuinness 1984; Simberloff and Levin 1985). Less isolated insular areas are colonized more frequently (Brown and Kodric-Brown 1977) and are accessible to a wider range of species, including those with low dispersal ability (Darlington 1957; Carlquist 1966, 1974).

Nested faunas may develop in response to the effects of variable insular area and isolation (Patterson 1990; Wright et al. 1998). Nested faunas are organized hierarchically by size. Small faunas of a nested set include only species present in all larger faunas (Patterson and Atmar 1986; Wright and Reeves 1992). In a perfectly nested set, no species is present in a given fauna without being present also in all smaller faunas. Wright et al. (1998) described four filters that cause nestedness: (1) insular isolation and area interact with species colonization rates (Darlington 1957; Cook and Quinn 1995), (2) insular isolation and area interact with species extinction rates (Patterson and Atmar 1986; Cutler 1991), (3) abundance of suitable habitat interacts with spe-

cies habitat requirements (Simberloff and Martin 1991; Cook and Quinn 1995), and (4) more abundant species are more widely distributed by chance (Cutler 1994; Wright et al. 1998). Strong environmental gradients within geographically uniform regions create diversity that also leads to nestedness by influencing colonization and extinction rates (Cook et al. 2004). Nestedness is expected among insular areas that are ecologically similar, have a common biogeographical history, and comprise species that vary hierarchically in their niche requirements (Patterson and Brown 1991; Wright et al. 1998).

Freshwater fish faunas are ideal for zoogeographic study because they are confined to drainage basins and respond more directly to climate than do homeotherms (Darlington 1957). Island biogeography theory should apply to freshwater fishes because they have restricted geographical ranges that are similar to terrestrial species of islands (Eadie et al. 1986; Sheldon 1988; Rosenfield 2002). Smith (1978) concluded that extinction and colonization rates were important determinants of fish faunal composition among drainages of the Great Basin but he did not estimate nestedness. More recent studies have shown that freshwater fish faunas of spring pools (Kodric-Brown and Brown 1993), isolated wetlands (Snodgrass et al. 1996), and stream pools (Taylor 1997; Taylor and Warren 2001) are nested. Nestedness has rarely been investigated for freshwater fishes at spatial scales as large as terrestrial islands, but Cook et al. (2004) found nestedness among freshwater fish faunas at four regional scales and concluded that drainage basin and physiographic region scales were biologically meaningful. This makes sense from a biogeography point of view. Freshwater fish zoogeographers typically analyze distribution patterns

among drainage basins within specific physiographic regions to sample a distinct species pool and control for the effects of environmental variation (Ramsey 1965; Jenkins et al. 1971; Conner and Suttkus 1986; Hocutt et al. 1986).

Our goal was to investigate drainage basin scale influences on fish faunal composition among Missouri River tributary basins of the Great Plains (Thornbury 1965) using the regional-historical viewpoint of Ricklefs (1987), which emphasizes the influence of historical, systematic, and biogeographic information on faunal structure. The Missouri River basin extends from north to south over a large portion of the Great Plains and is composed of tributary basins that each have unique but interwoven geomorphic histories. There is a strong gradient of increasing cold from south to north in this region (Grimm 2001). We (1) conducted a zoogeographical review to determine the native fish fauna of each tributary basin and establish historical context for fish distributions, (2) investigated the relative influence of tributary basin area and isolation on fish faunal composition among basins, (3) determined the strength of relations between individual species distributions and tributary basin area and isolation, and (4) grouped tributary basin faunas by faunal similarity. In a broad sense, this work is applicable to the question of why vertebrate species diversity is negatively correlated with latitude (Pianka 1966). Our expectation, based on the observations of Cross et al. (1986) and references they cited, was that the combined influence of tributary basin isolation and the gradient of increasing cold would explain patterns of faunal composition.

STUDY AREA

The Missouri River Basin

The Missouri River basin, the largest tributary by area of the Mississippi River basin, comprises one sixth of the conterminous United States (1,345,848 km²), including all or parts of 10 states. Another 25,161 km² are in Canada and

include portions of two provinces. The main-stem Missouri River extends 3,725 km and is the longest river in the United States. It is the master river of a drainage network that originates along the eastern front of the Rocky Mountains (Thornbury 1965). The network extends from southern Alberta to central Colorado over more than 10° of latitude. Drainage of this extensive mountain front is accomplished by the Missouri River itself and a series of major tributary rivers that ultimately join the Missouri River after flowing east across the Great Plains. Other major tributary rivers arise on the plains and also flow east to the Missouri River.

The source of the main-stem Missouri River is in the Rocky Mountains of southwest Montana and northwest Wyoming. The river flows northwest to the Great Falls, where it descended approximately 187 m in 16 km over a series of waterfalls (including Rainbow Falls, 11.3 m, and Big Falls, 22.9 m) before the falls were modified by dams (Alden 1932). The Missouri River downstream of the Great Falls turns east across the Great Plains and is joined by nine major tributaries. Four of the tributaries, the Marias, Milk, Poplar, and Big Muddy basins, enter from glaciated regions to the north and five, the Judith, Musselshell, Redwater, Yellowstone, and Little Missouri basins, enter from unglaciated regions to the south. The Missouri River then turns south and is joined from the west by nine more major tributaries: the Knife, Heart, Cannonball, Grand, Moreau, Cheyenne, Bad, White, and Niobrara. The Missouri River flows east from the Niobrara River confluence and enters the Central Lowlands (Thornbury 1965) before turning south again. Three major tributaries join the Missouri River from the west in the Central Lowlands: the Platte, Big Nemaha, and Kansas. At Kansas City, Missouri, the Missouri River turns east and receives no other major tributaries from the Great Plains.

Study Tributary Basins

The study area comprised 22 major western tributaries of the Missouri River basin (Figure 1). The

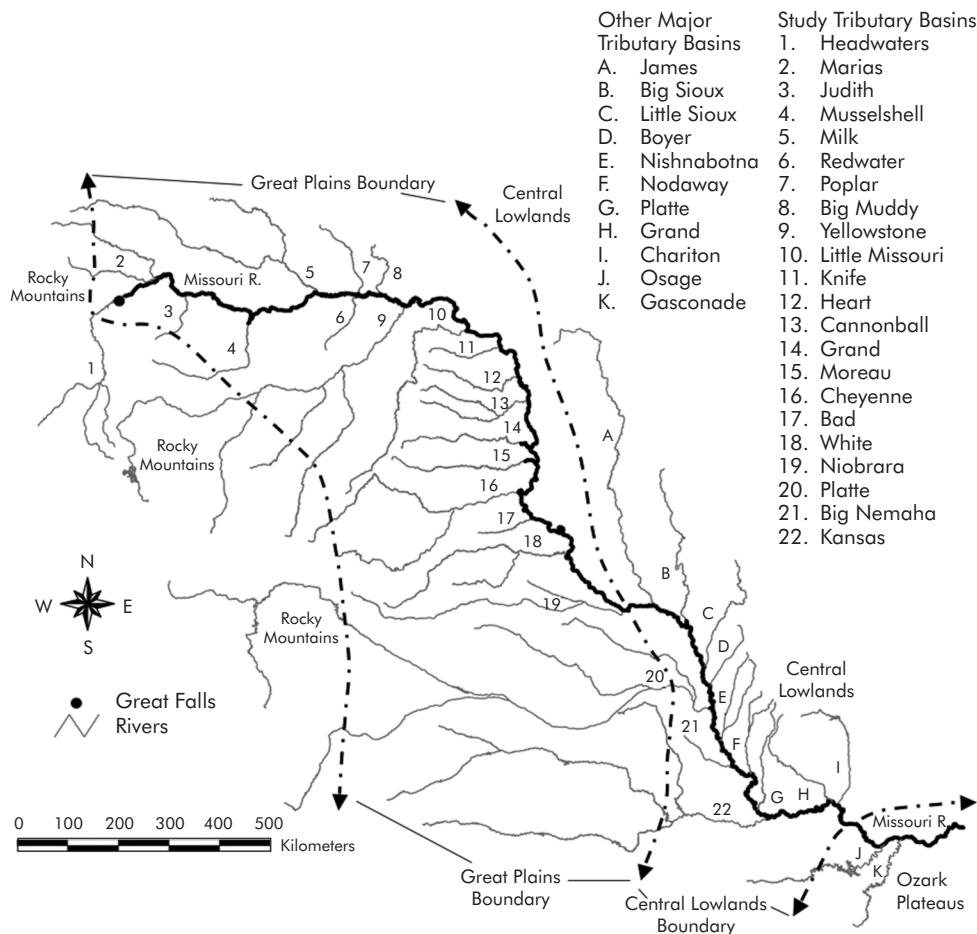


Figure 1. Geographic provinces and major Missouri River tributaries (numbered) used in this study. Lettered tributaries are eastern and southern tributary basins outside the Great Plains and not used in this study.

basis for selecting tributary basins was zoogeographical and had three main components: (1) drainage basins are natural morphological units of rivers (Leopold et al. 1964; Morisawa 1968), (2) streams with similar geomorphic conditions (e.g., those in the same geomorphic province) should exhibit similar fish–habitat relations (Montgomery 1999; Walters et al. 2003), and (3) the main-stem Missouri River connects all 22 tributary basins, making it the principal dispersal corridor among basins and from the lower Missouri basin (Metcalf 1966; Cross et al. 1986; Pflieger and Grace 1987).

The tributary basins we studied were necessarily of a minimum size because not all smaller

tributary basins have been well sampled. Tributary basin area ranged from 4,974 to 233,437 km² (Table 1). Twenty-one of the 22 tributary basins traverse the Great Plains. Thirteen of the tributary basins are entirely within the Great Plains. Six tributary basins, including the Missouri River upstream of the Great Falls (referred to hereafter as the Headwater basin), begin in the Rocky Mountains and then cross the Great Plains to the Missouri River. The Platte basin begins in the Rocky Mountains, crosses the Great Plains, and then enters the Central Lowlands, where it joins the Missouri River. The Kansas basin originates in the Great Plains and enters the Central Lowlands where it joins the Missouri River. The Big

Table 1. Physiographic and ecological diversity (based on geomorphic provinces and ecological regions), climatic variation (based on annual freeze-free days), and physical dimensions (elevation range, position of river mouth along the Missouri River, and basin area) for each tributary basin.

Basin	State(s) and province(s) ^a	Geomorphic region(s) ^b	Ecological region(s) ^c	Average freeze-free period (days) ^d	Approximate elevation range (m)	Mouth position (river km)	Basin area (km ²)
Headwaters	MT, WY	RM, GP	21, 48	30–120	3,473–884	3,411	59,456
Marias	MT	RM, GP	46, 47	30–120	3,103–782	3,302	18,447
Judith	MT	RM, GP	21, 48	60–120	2,797–732	3,192	7,163
Musselshell	MT	RM, GP	21, 48	60–120	2,816–670	3,004	24,688
Milk	AB, MT, SK	RM, GP	46, 47	30–120	2,690–616	2,833	59,572
Redwater	MT	GP	48	90–120	1,105–591	2,705	5,475
Poplar	MT, SK	GP	47	90–120	1,021–591	2,700	9,613
Big Muddy	MT	GP	47	90–120	882–582	2,623	8,939
Yellowstone	MT, ND, WY	RM, GP	21, 22, 48	30–135	3,705–565	2,545	181,537
Little Missouri	MT, ND, SD, WY	GP	48	90–135	1,402–555	2,304	24,462
Knife	ND	GP	48	90–120	847–509	2,211	6,484
Heart	ND	GP	48	90–135	878–494	2,109	8,665
Cannonball	ND	GP	48	90–135	1,069–488	2,042	11,103
Grand	ND, SD	GP	48	90–150	1,098–478	1,928	14,547
Moreau	SD	GP	48	90–150	1,225–468	1,894	13,984
Cheyenne	NE, SD, WY	GP	21, 48	60–150	2,207–458	1,788	65,398
Bad	SD	GP	48	90–150	847–433	1,714	8,227
White	NE, SD	GP	30, 48	90–150	1,516–399	1,537	25,743
Niobrara	NE, SD, WY	GP	30, 47, 48, 49	60–150	1,711–369	1,358	36,454
Platte	CO, NE, WY	RM, GP, CL	22, 25, 30, 31, 32, 49, 51	30–180	4,354–287	957	233,437
Big Nemaha	KS, NE	CL	51	150–180	457–256	795	4,974
Kansas	CO, KS, NE	GP, CL	30, 31, 32, 33, 51	120–210	1,826–219	591	156,269

^a State and province abbreviations follow U.S. and Canadian postal codes: AB = Alberta, CO = Colorado, KS = Kansas, MT = Montana, ND = North Dakota, NE = Nebraska, SD = South Dakota, SK = Saskatchewan, and WY = Wyoming.

^b Geomorphic regions follow Thornbury (1965): RM = Rocky Mountain System, GP = Great Plains Province, and CL = Central Lowlands Province.

^c Ecological regions follow McMahon et al. (2001): 21 = Middle Rockies, 22 = Wyoming Basin, 25 = Southern Rockies, 30 = Western High Plains, 31 = Southwestern Tablelands, 32 = Central Great Plains, 33 = Flint Hills, 46 = Canadian Rockies, 47 = Northwestern Glaciated Plains, 48 = Northwestern Great Plains, 49 = Nebraska Sandhills, and 51 = Western Cornbelt Plains.

^d Average freeze free period summarizes the range of days per year with temperatures below 0°C reported by the Missouri basin Inter-Agency Committee (1971) based on the years 1921 through 1950.

Nemaha basin, which was the smallest basin studied, is entirely within the Central Lowlands. It was included in this study because it is within the sequence of western Missouri basin tributaries.

The Great Plains has distinctive geology, soil, and vegetation. Rocks of the Great Plains are of Mesozoic and Cenozoic age (Thornbury 1965). Rivers and streams are the dominant water bodies except in the Nebraska Sandhills (Winter and Woo 1990). The rivers historically transported a high bedload volume because of erosive soils, high relief, and few natural lakes (Meade et al. 1990). Ustolls comprise the dominant soil sub-

order of the province and are typical of subhumid to semiarid climates (NRCS 1999). Ustolls are freely drained Mollisols that are characteristic of grasslands throughout the world. The Orthents and Psamments are widespread Entisol suborders (NRCS 1999). Orthents (erosional Entisols) are predominant in badlands and Psamments (sandy Entisols) are predominant in the Nebraska Sandhills. Short-grass prairie is the dominant natural vegetation of the Great Plains, but tall-grass prairie is present on the eastern edge and interior montane forest, Rocky Mountain coniferous forest, and western sagebrush

steppe are present in mountainous areas (Saxton and Shiau 1990).

Major Missouri River tributary basins that we excluded from this study are entirely within the Central Lowlands or Ozark Plateaus geomorphic provinces (Ozark Plateaus; Thornbury 1965). These provinces have different surface geology (Thornbury 1965), soil (NRCS 1999), and vegetation (Saxton and Shiau 1990) than the Great Plains. The zoogeographic history of the Central Lowlands and Ozark Plateaus is different from the Great Plains because the Central Lowlands were entirely glaciated (Bailey and Allum 1962) and the Ozark Plateaus are ancient highlands that have been geologically stable for at least 38 million years (Pflieger 1971; Mayden 1987c).

The Missouri basin of the Central Lowlands and Ozark Plateaus forms the eastern and southeastern boundary of the study area. Boundaries on the north, west, and south are the divides between the Missouri basin and neighboring drainage basins. The Saskatchewan and Souris subbasins of the Hudson Bay basin compose the northern boundary. The western boundary is the Continental Divide between Pacific Ocean and Atlantic Ocean drainages. The southern boundary is the Arkansas basin, a major tributary of the Mississippi basin.

Although Great Plains geography appears uniform compared to other geomorphic provinces, a wide range of stream types is present due to variable local geology and climate (Thornbury 1965). Many characteristics vary within tributary basins. Smaller scale characteristics include channel-sediments and stream slopes that are highly variable among stream reaches throughout the study area (Osterkamp and Hedman 1982), and precipitation, which declines from east to west within each river basin but is locally modified by mountains (Lins et al. 1990). Mean annual snowfall also increases from east to west (Meier 1990). Within-basin scale factors are important for determining fish distributions at smaller scales (Duehr 2004) but are not considered in this study.

Each tributary basin is one of a kind because it includes a unique assemblage of stream types that are integrated into a distinctive drainage network. There are two primary tributary basin scale differences among basins: (1) position along the Missouri River, and (2) basin area. Tributary basins further upstream (i.e., farther north) are increasingly cold, as illustrated by the decreasing maximum annual freeze free days per tributary basin (Table 1), which is negatively correlated with tributary basin position (Spearman Rank Correlation (Sokal and Rohlf 1995): $N = 22$, $df = 20$, $r = -0.92$). Tributary basins with greater area extend further west into the mountains or farther east into lowlands, so the elevation range of basins is highly correlated with tributary basin area (Spearman Rank Correlation: $N = 22$, $df = 20$, $r = 0.80$). Larger tributary basins also include more geomorphic regions (Thornbury 1965) and ecological regions (McMahon et al. 2001).

Geomorphological History

Here, we provide a review of geomorphic evolution within the study area. The time period of interest is the middle Pliocene Epoch to the Holocene Epoch, that is, from the end of preglacial times to historical times. Modern fish species have been extant throughout this period (Miller 1965; Mayden 1988).

The Missouri basin as such did not exist prior to glaciations of late Pliocene and early Pleistocene time. Portions of the modern Missouri basin belonged to three different preglacial drainages that existed for at least 38 million years prior to glaciation (Seeland 1985). The preglacial Hudson Bay basin flowed northeast to the Labrador Sea, the preglacial White basin flowed southeast to the preglacial Mississippi River, and the preglacial Osage basin flowed east to the preglacial Missouri River (Wayne et al. 1991; Figure 2). The preglacial divide between the Hudson Bay and Gulf of Mexico drainages was the southern Absaroka Mountains, the Owl Creek Mountains,

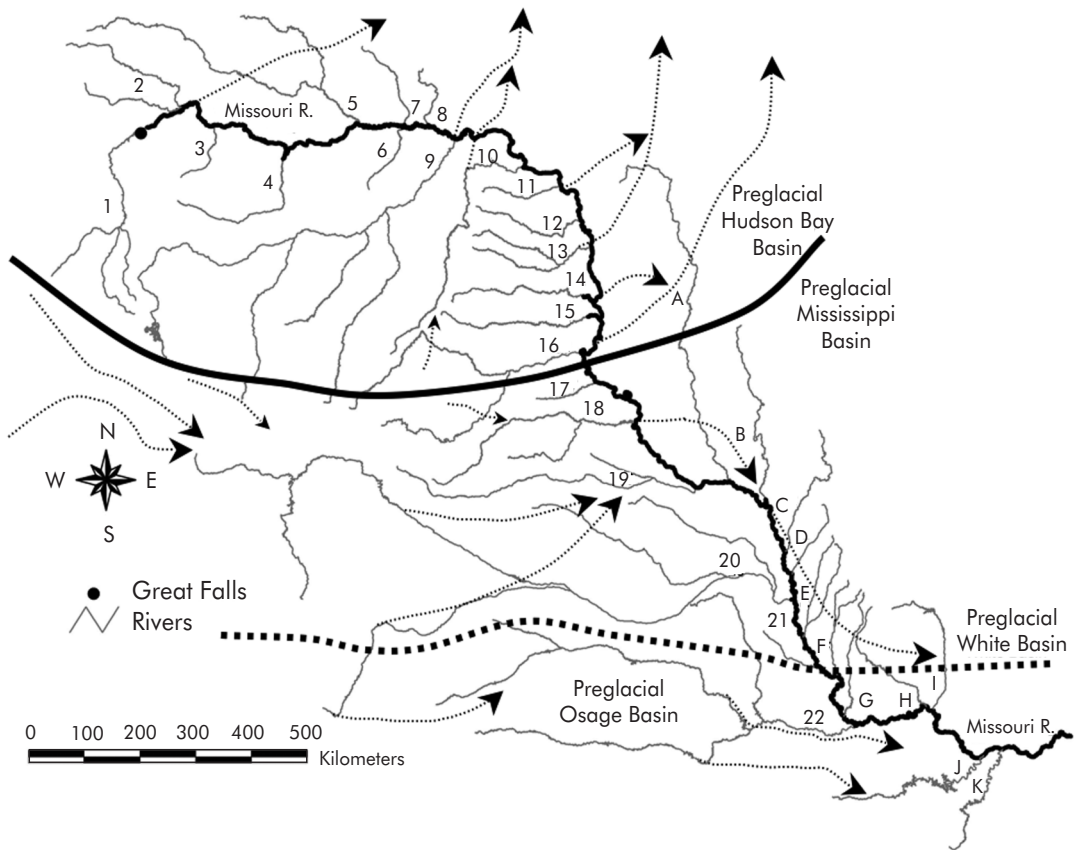


Figure 2. Major Missouri River tributaries in relation to preglacial drainage basins. The preglacial continental divide between the Hudson Bay and Gulf of Mexico (solid line) is estimated from Seeland (1985). The preglacial divide between the White and Osage basins (dotted line) and estimated preglacial drainage patterns (arrows) follow Wayne et al. (1991). Tributary numbers and letters correspond to Figure 1.

the southern Bighorn Mountains, and the northern Black Hills (Seeland 1985).

Preglacial Hudson Bay basin.—The preglacial Hudson Bay basin included major tributary basins between the Missouri River headwaters and the Cheyenne basin except the preglacial Wind River and upper Cheyenne River, which were then part of the preglacial White basin (Seeland 1985; Wayne et al. 1991). Advancing glaciers overrode rivers north of the present-day Missouri River in early Pleistocene time and blocked the north and eastward flowing streams, which caused proglacial lakes to fill major river valleys along the glacial front (Alden 1932; Howard 1960; Lemke et al. 1965). Subsequent overflow

from the proglacial lakes formed connecting channels between lakes that eventually integrated all eastward flowing rivers along the glacial front from North Dakota to Kansas (Howard 1960; Hedges 1975; Duchossois 1993). This connection was intermittent through Pleistocene time and was established in the present form following the most recent glaciation (Bluemle 1972; Duchossois 1993). During early deglaciation, the modern Missouri River was greatly enlarged by continental glacial meltwater discharged via the Milk, Poplar, and Big Muddy basins (Christiansen 1979; Christiansen and Sauer 1988). In addition, alpine glacier meltwater reached the Missouri River via the Headwater, Milk, Marias,

Yellowstone, and Platte basins (Alden 1932; Richmond 1965). The connection between continental glacier meltwater and the Missouri basin was severed roughly 12,000 years ago when meltwater runoff turned east to glacial Lake Agassiz (Clayton and Moran 1982; Teller 1987; Klassen 1994). Alpine deglaciation continues to the present day.

Preglacial White basin.—The preglacial White basin included the modern White, Niobrara, and Platte basins along with the upper Cheyenne River, but not the South Platte River upstream of Denver, which was then part of the preglacial Osage basin (Swinehart et al. 1985; Wayne et al. 1991; Swinehart and Diffendal 1998). The preglacial White basin extended west to the Wyoming Ranges and Uinta Mountains, including the modern Wind River of the Yellowstone basin, upper Green River of the Colorado basin, and the endorheic Great Divide basin of Wyoming (Seeland 1985; Wing and Bown 1985). Glacial advances during early Pleistocene time repeatedly diverted the preglacial White River to the south (Simpson 1960; Hedges 1975). This connected the ancient White basin with the ancient Osage basin during multiple glacial advances and eventually incorporated them both into the modern Missouri basin (Simpson 1960; Wayne 1985; Dort 1987).

Preglacial Osage basin.—The preglacial Osage basin extended from the Rocky Mountain front, across the high plains of western Kansas, through the Flint Hills of eastern Kansas, to the preglacial Missouri River (Aber 1985; Wayne et al. 1991). It included the modern day Kansas basin, the South Platte River upstream of Denver, and the preglacial Osage River of Missouri and Kansas. The preglacial Osage basin included a large portion of the Ozark Plateaus Province, which is an isolated remnant of an ancient highland region (Thornbury 1965; Madole et al. 1991). The preglacial Osage basin was dismembered during Pleistocene time by headward erosion of the ancestral Neosho River and by the southward diversion of the ancestral Smoky Hill River (Aber 1985). Headward erosion by the South Platte and

Arkansas rivers created the Colorado Piedmont and ultimately resulted in the capture of the mountainous headwaters of the preglacial Osage basin by those rivers (Morse 1985; Swinehart et al. 1985; Wayne et al. 1991). The lower Kansas River formed at the margin of early Pleistocene glaciers and captured much of the upper portion of the preglacial Osage basin (Aber 1985; Dort 1985, 1987). The ancestral Kansas River eventually recaptured the ancestral Smoky Hill River as well (Aber 1985; Madole et al. 1991). Rivers along the glacial margin connected the preglacial Osage and White basins via the ancestral Big Blue River (Wayne 1985). Neither glacial ice nor meltwater runoff reached the preglacial Osage basin in middle or late Pleistocene time because the glacial front did not advance that far south (Madole et al. 1991).

Ancient climate patterns.—The northern Great Plains were arid grasslands at the beginning of the Pliocene Epoch, roughly 5.0 million years ago, but the Pliocene climate was milder and warmer than today (Dorf 1959; Wayne et al. 1991). Glaciation began near the end of Pliocene time, roughly 2.8 million years ago (Richmond and Fullerton 1986). There were alternating periods of glacial advance and retreat during Pleistocene time until about 11,000 years ago (Richmond and Fullerton 1986). Climatic zones were shifted to the south and to lower elevations during periods of glacial advance (Dillon 1956; Dorf 1959; Porter et al. 1983). Periglacial conditions with annual average temperature below 0°C and widespread permafrost were prevalent near the ice front at least during the most recent glaciation (Dorf 1959; Péwé 1983) and grasslands were greatly diminished at that time (Fredlund and Jaumann 1987). The climatic gradient among regions of unglaciated North America was steeper during glacial advances than at present (Barry 1983) and climates farther from the glacial front had more stable temperatures and precipitation patterns than analogous climates do today (Wright 1987; Wayne et al. 1991).

Periods of glacial recession were characterized by warming and increased moisture. Tanner

(1985) concluded that interglacial periods lasted for roughly 150,000 years. Klassen and Delorme (1967) concluded that during at least one interglacial period, the climate in southern Alberta, was at least as warm as the present day, but some interglacial stages were apparently even warmer (Dorf 1959). The final retreat of Laurentide continental glaciers from the Missouri basin began 14,000 years ago (Mickelson et al. 1983). Rocky Mountain glaciers were declining by 17,000 years ago (Porter et al. 1983).

Climate change continued after the glacial retreat (Dorf 1959; Newbrey and Ashworth 2004). Alternate warm-dry and cool-moist periods allowed floras and faunas to advance and retreat, but relicts remained where local climates were favorable (Sears 1942; Smith 1957, 1965; Wright 1970). Grasslands invaded the Great Plains after deglaciation and replaced existing boreal forest (Watts and Wright 1966; Wright 1970; Barry 1983). Modern grassland vegetation colonized the province roughly 8,000 years ago (King 1981). Conditions in southern Alberta and Saskatchewan were relatively warm and arid from 7,000 to 5,100 years ago (Sauchyn 1990). The climate of the northeastern Great Plains and the adjacent Central Lowlands was increasingly dry in the middle Holocene Epoch (9,500–5,500 years ago) according to lake levels, but precipitation patterns varied from today, with more moisture during the growing season (Grimm 2001). Mountain glaciers advanced and retreated throughout Holocene time (Burke and Birkeland 1983).

Ancient rivers.—Great Plains river conditions during the Pliocene Epoch may have been similar to those of today because the climate was similar. River conditions were more variable once glaciation began because the climate oscillated from warm to cold every 300,000 years or so (Tanner 1985) and glacial ice dramatically modified drainage patterns (Baker 1983). The ancient Platte River was sometimes much larger than the modern Platte River and carried a heavy sediment load (Stanley and Wayne 1972). The Mississippi River was a major recipient of meltwater

runoff during deglaciation because it received glacial meltwater from the Missouri, Ohio, and upper Mississippi basins (Baker 1983). During deglaciation, the Mississippi and Missouri rivers were braided and aggrading due to large volumes of sediment transported with meltwater (Baker 1983; Schumm and Brakenridge 1987; Wright 1987). Aggradation of the mainstem Missouri and Mississippi rivers blocked tributary inflows and caused lakes to form in the lower tributary valleys until they eventually filled with sediments (Baker 1983; Wayne 1985). Even after deglaciation, rivers experienced alternating episodes of aggradation and degradation because climate and vegetation continued to change (Frye 1973; Knox 1983).

METHODS

Zoogeography Review

We summarized historical native fish distributions at the drainage basin scale for major western tributaries of the Missouri basin. It was necessary to compile each drainage basin fauna from various sources because few of the drainage basins have been summarized in detail before. We conducted an extensive review of fish distribution literature to determine native fish distributions as accurately as possible. We included recognized subspecies because we were interested in distributional histories that are sometimes revealed by intraspecific variation (Crossman and McAllister 1986). Our approach was to seek corroborative evidence for the native distribution of each species among different authors. When authors disagreed, we followed those that provided the most convincing evidence, such as inspection of specimens from known localities.

Former authors interpreted faunal patterns in the Missouri basin as reflective of postglacial dispersal during late Pleistocene and Holocene time (e.g., Bailey and Allum 1962; Metcalf 1966; Pflieger 1971; Cross et al. 1986). We followed suit. McPhail and Lindsey (1970), Stewart and

Lindsey (1983), and Crossman and McAllister (1986), reviewed the distribution of fishes in Canada and postulated which species dispersed into the western Hudson Bay basin from the Missouri basin via glacial meltwater connections with the Milk, Poplar, or Big Muddy tributary basins. In order for those fishes to reach the Hudson Bay basin via this route, they must have been present before the meltwater was diverted to glacial Lake Agassiz 12,000 years ago. Fishes native to the Missouri basin upstream of the Great Falls (Headwater basin) must have been present even earlier, assuming they colonized prior to development of the Great Falls. We used evidence of dispersal from the upper Missouri basin to the Hudson Bay basin or presence above the Great Falls to categorize fish species as early dispersers throughout the study area.

We did not attempt to discern the preglacial origin of fish species based on present day distributions. Metcalf (1966) and Pflieger (1971) proposed that fishes currently restricted to the Missouri basin originated in the preglacial Hudson Bay basin, but interbasin connections during glacial advances allowed fishes to disperse in either direction. Repeated connections between the preglacial Hudson Bay and Mississippi basins and dramatic climate changes during Pleistocene time would have allowed fishes from both preglacial basins to intermingle and disperse widely. It is also likely that fish distributions have changed during the 12,000 years since glaciation, particularly in light of faunal and flora changes that were characteristic of that period (Sears 1942; Smith 1957, 1965; Wright 1970).

It is not certain that any fishes survived the entire Pleistocene Epoch within the preglacial Hudson Bay basin. McAllister et al. (1986) noted reduced fish species density within 3° of latitude from the glacial maxima and concluded that fish extirpations extended at least that far south of the glacial front. This suggests very little of the unglaciated preglacial Hudson Bay basin escaped extinctions, particularly if alpine glaciers to the west also caused extinctions. Periglacial conditions and boreal forest that dominated the region dur-

ing the last glacial advance make it even more doubtful that species currently restricted far south of such environments could have survived.

We categorized species postglacial origin based on our literature review. The main-stem Missouri River was the most important postglacial dispersal route, but a few species entered the region from Pacific Ocean drainages via headwater connections between Rocky Mountain streams (Cross et al. 1986), likely associated with alpine glaciers. It is possible that fishes dispersed between the upper Mississippi basin and Missouri basin via headwater connections in southwestern Minnesota and northwestern Iowa (Bailey and Allum 1962). Species could have dispersed in either direction, from the Mississippi basin to the Missouri basin or vice versa. We characterized all species distributed on both sides of the upper Mississippi basin-Missouri basin divide as potentially using this route in one or both directions.

Fish Distribution Analysis

We tested for nonrandom patterns (*sensu* Connor and Simberloff 1979, 1986; Jackson et al. 1992) among native fish faunas of tributary basins with respect to basin area or basin isolation. We organized presence/absence data into a matrix (1 = present, 0 = absent) with columns representing native fish species and rows representing tributary basins. We tested for nonrandom organization in the matrix using the Nested Temperature Calculator computer program (Atmar and Patterson 1993, 1995). The program estimates nestedness by calculating a temperature (T) that can range from 0° to 100°. Lower temperature indicates more nestedness (i.e., when $T = 0^\circ$, every species present in a given fauna is also present in every larger fauna). Smaller faunas are composed entirely of species present in all larger faunas. When $T = 100^\circ$, there is no relation between faunal size and composition. We determined the probability of deriving a certain T using Monte Carlo simulations that generated null matrices with the same number

of presences as the empirical matrix, but with presences distributed randomly among columns and rows (Atmar and Patterson 1995). We used 500 iterations.

Nested subsets have been documented for many faunas of many taxa at many scales (e.g., mammals of mountain top forests (Patterson and Atmar 1986), birds in isolated woodlands (Blake 1991; Bolger et al. 1991), granivorous rodents of study sites (Patterson and Brown 1991), fishes in individual pools (Kodric-Brown and Brown 1993; Taylor 1997), mammals of the Japanese Islands (Millien-Parra and Jaeger 1999), and forest birds and butterflies among the Andaman islands (Davidar et al. 2002)) but the mere presence of a nested pattern is not necessarily informative (Simberloff and Martin 1991). Nestedness analysis is most useful when it considers relevant temporal as well as spatial and ecological scales (Lomolino and Davis 1997). We focused on habitat at the tributary basin scale, environmental gradients at the landscape scale, fish taxa at the subspecies scale, and geomorphic and climatic history at the less than 2.8 million year scale. We consider these scales complementary.

We used nestedness estimates to examine the relative importance of specific environmental factors (Kadmon 1995; Gotelli and Graves 1996; Lomolino 1996; Worthen 1996; Hecnar et al. 2002; Bruun and Moen 2003). Specifically, we studied the relative importance of tributary basin area versus tributary basin isolation (Missouri River km) by ordering the presence/absence matrix according to each parameter (Lomolino 1996). We used a Pearson product-moment correlation to determine the level of association between tributary basin area and isolation and multiple regression analysis to quantify the overall strength and relative importance of tributary basin area and isolation for explaining species richness patterns (Hamilton et al. 1964; Hecnar et al. 2002).

Species of nested faunas do not necessarily exhibit equal nestedness (Schoener and Schoener 1983; Simberloff and Martin 1991), so we used the Wilcoxon two-sample test, which is equivalent

to the Mann–Whitney *U*-test (Sokal and Rohlf 1995), to determine the randomness of individual species distributions in relation to tributary basin area and isolation (Schoener and Schoener 1983; Patterson 1984; Simberloff and Martin 1991; Hecnar et al. 2002). We calculated *t* values (Sokal and Rohlf 1995), also known as *z* values (Siegel 1956), from *U* to compare the strengths of relations among fish species (Schoener and Schoener 1983; Patterson 1984; Simberloff and Martin 1991). We grouped species according to their *t* values with a hierarchical, agglomerative, polythetic cluster analysis (Legendre and Legendre 1998). Each species was represented by *t* values versus tributary area and isolation. We used Sørensen's coefficient as our distance measure because, unlike Jaccard's coefficient, it gives double weight to double presences that are theoretically more meaningful than double absences (Legendre and Legendre 1998; McCune and Mefford 1999). We used flexible clustering, with $\beta = -0.25$ as our linkage method because it performs similarly to Ward's method, but is compatible with Sørensen's coefficient (Legendre and Legendre 1998; McCune and Grace 2002). We scaled the cluster dendrogram with Wishart's objective function that measures information loss for each step in a hierarchical cluster (Wishart 1969; McCune and Grace 2002). We determined the number of clusters in order to maximize the amount of information conserved and provide a reasonable number of interpretable species groups (sensu McCune et al. 2000). Cluster analysis was performed with PC-ORD version 4.25 software. We plotted 95% confidence intervals for the mean *t* values of each species group to summarize the results of the cluster analysis. The confidence intervals were calculated using the *t*-distribution (Sokal and Rohlf 1995).

We analyzed the relative similarity of native fish faunas among tributary basins with global nonmetric multidimensional scaling (NMDS; Kruskal and Wish 1978; McCune and Grace 2002). This type of ordination creates a depiction from biologically meaningful similarity

coefficients so that the rank order of distances among assemblages is the same as the rank order of dissimilarities among assemblages (Clarke 1993). Data points are placed in ordination space in a manner that portrays their positions relative to each other (Clarke 1993). The accuracy of the portrayal is indicated by a stress value (a dimensionless residual sum of squares expressed as a percentage) that indicates departure from monotonicity between dissimilarities between points and their distances in ordination space (Kruskal 1964a; McCune and Grace 2002). Generally, stress values less than 10% are considered good, values greater than 20% are considered poor, and intermediate values are considered fair (Kruskal 1964b; Clarke 1993; McCune and Grace 2002).

We used Sørensen's coefficient to measure similarity among tributary basin fish faunas (McCune and Mefford 1999; McCune and Grace 2002) and conducted 40 iterations from random starting positions with the empirical data using PC-ORD version 4.25 software that uses the algorithm of Kruskal (1964b) and Mather (1976). Our analysis started with six axes. The number of dimensions was truncated when additional dimensions reduced final stress by 5 or less on a scale of 0–100 (McCune and Mefford 1999). The instability criterion was 0.00001. Fifty Monte Carlo simulations were conducted to compare with the empirical ordination. We calculated the coefficient of determination for correlations between the final ordination distances and the distances in the original n -dimensional space to estimate the proportion of variance represented by each ordination axis. We quantified associations between ordination values for each axis versus tributary basin area and isolation using Pearson product-moment correlations for which $\alpha = 0.05$ (Sokal and Rohlf 1995).

We ranked the Sørensen similarities from the NMDS analysis and converted them to percentages for use in a hierarchical, agglomerative, polythetic cluster analysis that grouped tributary basins by faunal similarity (Clarke 1993). The cluster analysis was conducted in the same man-

ner described above for Wilcoxon two-sample test scores. We summarized the results of the cluster analysis by plotting the ranges of tributary basin area and isolation for each resulting cluster and we also plotted the range of species richness among tributary basins of each cluster. We anticipated that the NMDS results would complement the Wilcoxon two-sample test nestedness analysis results, and facilitate a comprehensive understanding of the relative importance of tributary basin area and habitat diversity versus tributary basin isolation and climatic harshness to structuring native fish faunas.

RESULTS

Zoogeography Review

We found documentation for a total of 96 native fishes (species and subspecies) among the 22 tributary basins (Appendix A). One species, cutthroat trout *Oncorhynchus clarkii*, was represented by three subspecies, none of which were native to the same tributary basin. Twelve other recognized subspecies were present but were sole representatives of their species in the study area, not counting intergrades (see notes in Appendix A). One species, a sculpin *Cottus* cf. sp. *Cottus bairdii*, is undescribed (D.A. Neely, Saint Louis University, personal communication). For simplicity, all taxa are referred to as species, but each cutthroat trout subspecies was treated individually in analyses.

We divided the fish fauna of the study area into three groups based on evidence for time and direction of dispersal (Appendix A). There were 25 species with evidence of widespread presence throughout the study area during late Pleistocene or early Holocene time because they presumably colonized the modern Hudson Bay basin from the Missouri basin or were native upstream of the Great Falls. These species were considered early dispersers and must have either invaded from Gulf of Mexico drainages during deglaciation or survived in situ throughout glaciation. Early dispersing species were widespread

among the 22 tributary basins (Figure 3). Another 66 species showed no evidence of early Holocene time presence in the upper Missouri basin and presumably dispersed into the study area from Gulf of Mexico drainages following deglaciation and subsequent climate change. These late dispersing species were most numerous in the Kansas, Platte, Niobrara, White, and Big Nemaha basins (Figure 3). The remaining five species entered the study area from Pacific Ocean drainages after glaciation, and their contemporary distributions were confined to the Rocky Mountains (Figure 3).

Sixty fish species were historically distributed on both sides of the divide between the Missouri

basin and upper Mississippi basin (Appendix A), suggesting they may have crossed the divide between basins. Historical distribution data are not sufficient to determine whether or not any of these species used this route once, multiple times, in different locations, or in different directions.

Fish Distribution Analysis

Forty-six species were found in five or more basins, and 50 species (52%) were native to four or fewer tributary basins (Figure 4). This latter group was concentrated in southern basins (Figure 5), and all but three (Yellowstone cutthroat trout *O. clarkii bouvieri*, westslope cutthroat

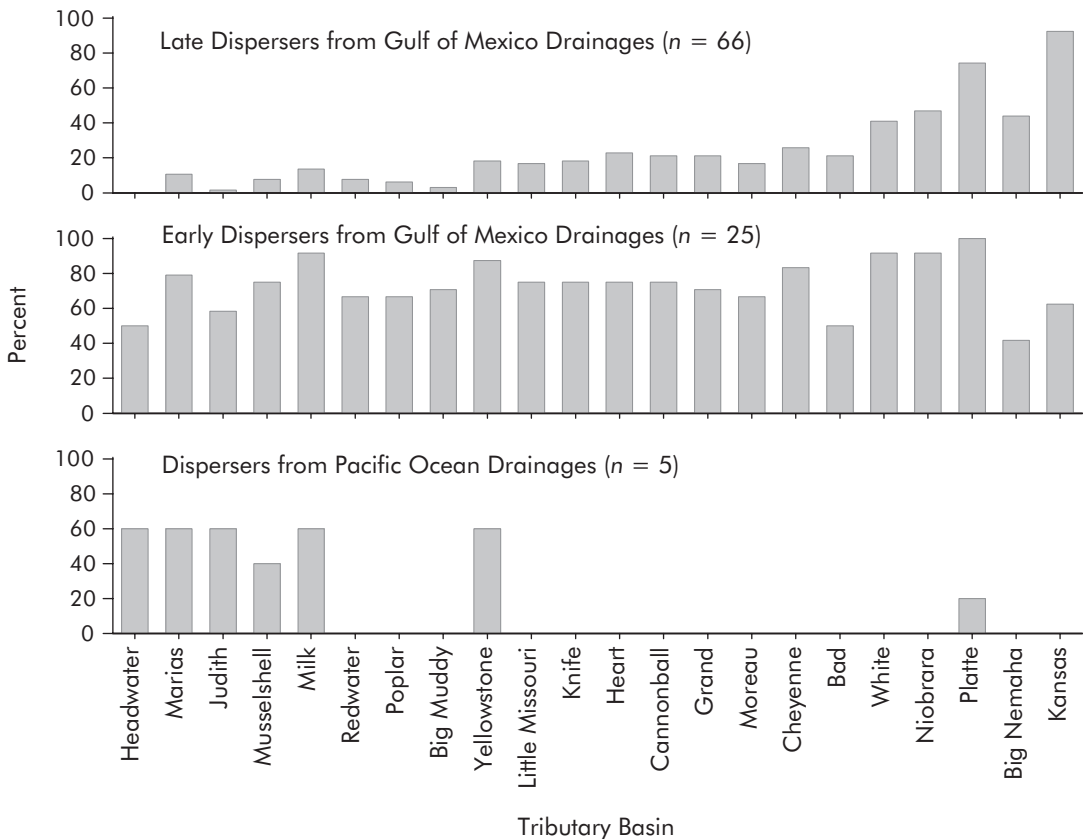


Figure 3. Percent occurrence of each fish dispersal group compared among tributary basins. Late dispersers (top) were absent from the Headwaters basin above the Great Falls and did not colonize the postglacial Hudson Bay basin from the Missouri basin, as opposed to early dispersers (middle). Dispersers from Pacific Ocean drainages (bottom) entered the study area through headwater connections during or after alpine deglaciation.



Figure 4. Number of fish species (includes species and subspecies) present in different numbers of tributary basins.

trout *O. clarkii lewisi*, Arctic grayling *Thymallus arcticus*) were distributed among only the Kansas, Big Nemaha, Platte, Niobrara, White, and Cheyenne basins. All species found in four or fewer tributary basins were relatively close to the source of colonizers, either the lower Missouri basin or the Atlantic–Pacific continental divide.

Multiple regression analysis indicated that tributary basin isolation and area affected species richness although the influence of isolation was somewhat stronger than that of area (partial correlation coefficients $b'_{\text{area}} = 0.49$, $b'_{\text{isolation}} = -0.63$; analysis of variance (ANOVA) $df = 2, 19$, $F = 51.2$, $R^2 = 0.84$). The Kansas, Platte, Niobrara, and White basins accounted for much of the increased richness by basin area (Figure 6). The

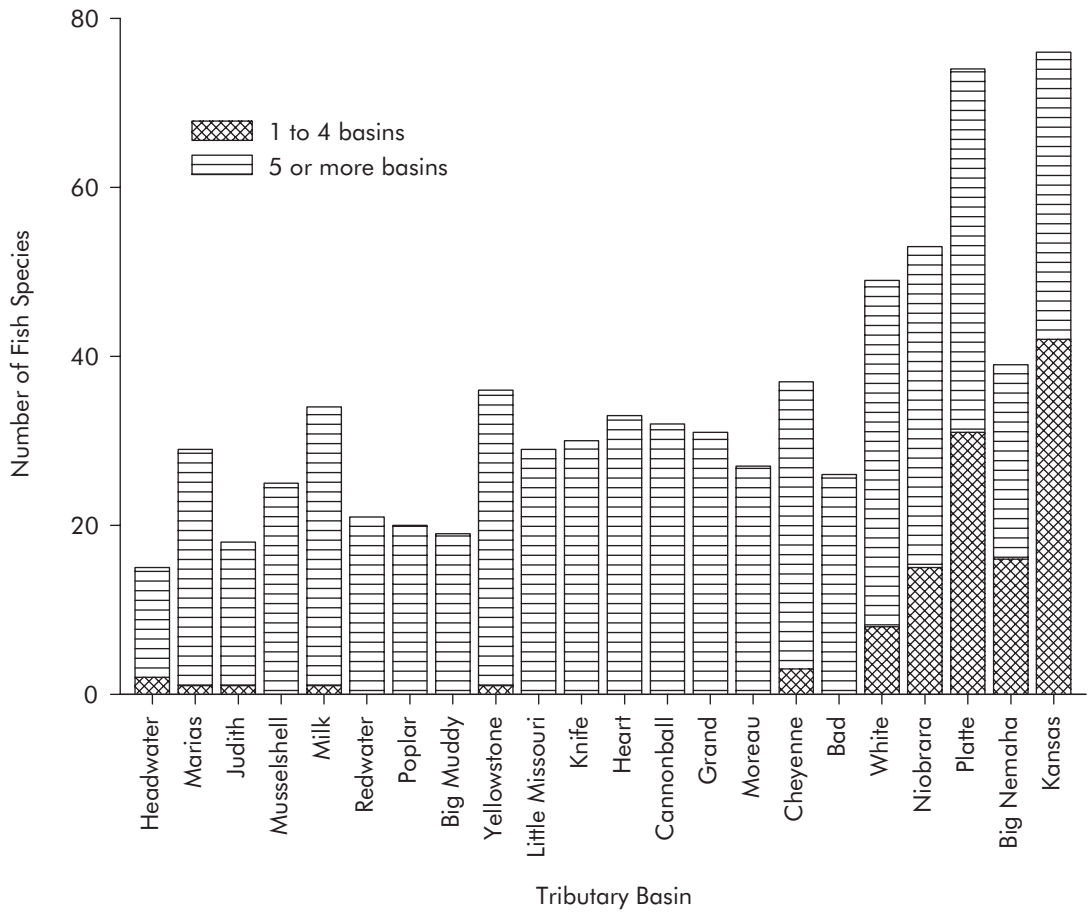


Figure 5. Number of fish species (includes species and subspecies) present in each tributary basin. Species are presented in two groups: those found in between one and four tributary basins and those found in five or more tributary basins.

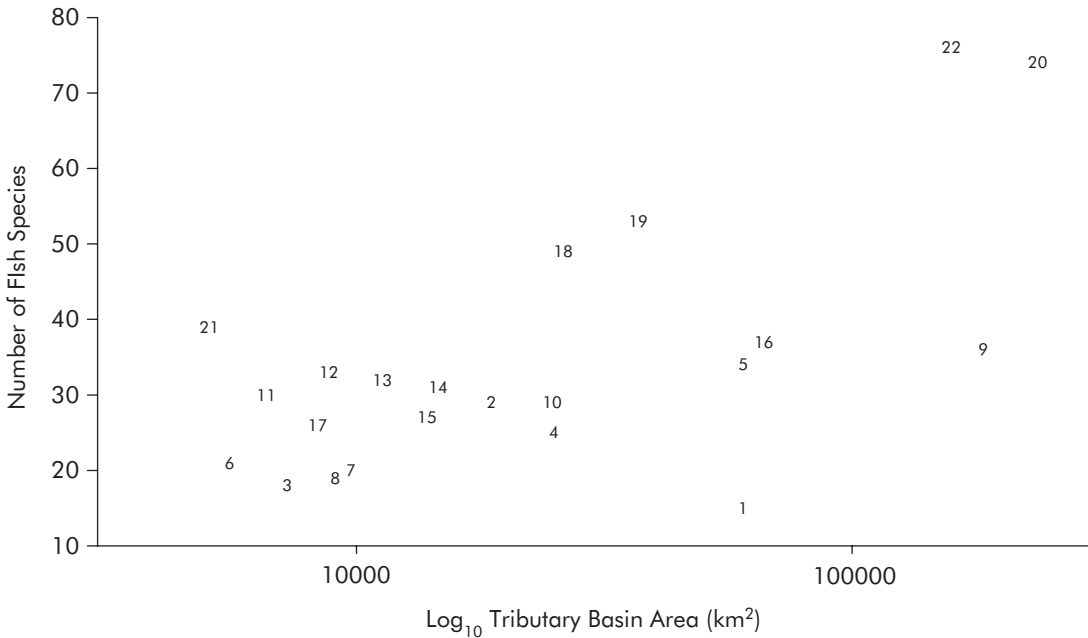


Figure 6. Fish species richness plotted against the log of tributary basin area. Numbers correspond to tributary basin numbers presented on Figure 1.

Big Nemaha basin was the smallest basin but had higher species richness than 17 larger basins. The Headwater basin, isolated by the greatest distance and the Great Falls, had lowest species richness.

Fish faunas of tributary basins were highly nested by tributary basin area ($T = 24.0^\circ$, mean of 500 iterations = $68.7 \pm 2.77^\circ$ SD, probability of observed $T = 5^{-48}$) and by tributary basin isolation ($T = 21.5^\circ$, mean of 500 iterations = $68.8 \pm 2.88^\circ$ SD, probability of observed $T = 3^{-49}$). Tributary basin area was not correlated with tributary basin isolation ($r = -0.35$, $df = 20$). Only fathead minnow *Pimephales promelas*, flathead chub *Platygobio gracilis*, and white sucker *Catostomus commersonii* were native to every tributary basin and thus excluded from nestedness analyses.

Cluster analysis of Wilcoxon two-sample t values sorted species into seven groups at a level that retained 85% of the information. The 95% confidence intervals of mean t values did not overlap between any groups (Figure 7). The largest

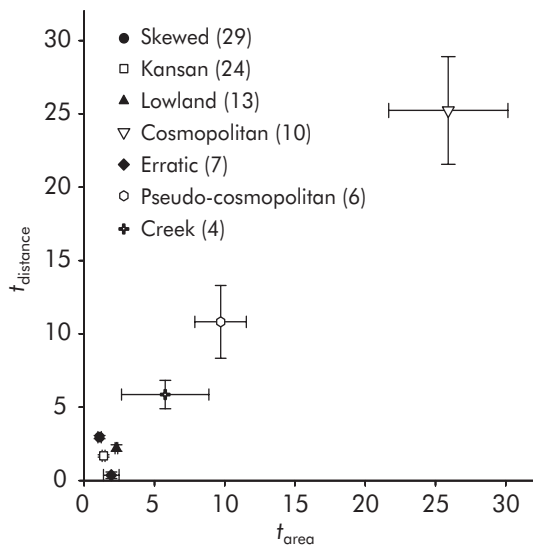


Figure 7. Mean t values, with 95% confidence intervals, for fish species groups based on Wilcoxon two-sample tests of fish species presence versus tributary basin isolation and area and subsequent cluster analysis of species scores. Number of fish species composing each group is given in parentheses.

group (29 species) included species native to between 3 and 12 tributary basins (modally 4) with distributions either in consecutive downstream or upstream basins (Appendix B). This is referred to as the Skewed group because of the distribution patterns of member species (Figure 8). Widespread species of the Skewed group (>4 basins occupied) were similar in being absent (one exception) upstream of the Yellowstone basin. All species were absent from the Big Muddy, Poplar, and Redwater basins.

The second largest group (24 species) included primarily species native only to southern basins (Appendix C). Nineteen (79%) of the species inhabited only one tributary basin with 15 of those in the Kansas basin, so this group is referred to as the Kansan group. Widespread Kansan species (>3 basins occupied) were large river forms (pallid sturgeon *Scaphirhynchus albus*, sicklefin chub *Macrhybopsis meeki*, blue sucker *Cycleptus elongatus*) that were only found sporadically within tributary basins. No Kansan species were found in the Big Nemaha, Big Muddy, Poplar, Redwater, Musselshell, Judith, or Marias basins (Figure 8).

Another cluster included 13 species that were also primarily native to southern basins. They differed from Kansan species by being more widespread, found in between 2 and 10 basins each (modally 2, Appendix D). They were mostly typical of lowland rivers and wetlands and thus referred to as the Lowland group. Sturgeon chub *M. gelida*, bigmouth buffalo *Ictiobus cyprinus*, and mountain sucker *Catostomus platyrhynchus* were atypical members of the Lowland group because they were more widespread (>4 basins). Species of the Lowland group were all absent from the Big Nemaha, Bad, Moreau, Cannonball, Knife, Big Muddy, Poplar, and Redwater basins (Figure 8).

Ten species composed a cluster of fishes native to 20 or more tributary basins (modally 20, Appendix E). We assigned the three omnipresent species to this group, which raised the total to 13 species. These species were present in all tributary basins (Figure 8) and referred to as the Cosmopolitan group.

Seven species grouped into a cluster that was difficult to interpret because member species ranged widely among tributary basins and occupied between 1 and 13 basins (Appendix F). This group was absent from only the Headwater and Judith basins (Figure 8). These species were presumably grouped due to their erratic distribution among tributary basins, so they are collectively referred to as the Erratic group.

Six widespread species composed another cluster (Appendix G). Two species were native to 16 tributary basins, two to 17, and two to 18. This cluster is referred to as the Pseudo-cosmopolitan group because the species were widespread, but less so than members of the Cosmopolitan group. The Pseudo-cosmopolitan group was present in every tributary basin (Figure 8).

The smallest cluster included four species native to between 14 and 16 tributary basins (modally 15, Appendix H). Each species was typical of clear, cool streams, so this cluster is referred to as the Creek group. The group distribution was centered within the study area. Only the longnose sucker *C. catostomus* was native upstream of the Milk basin and only the creek chub *Semotilus atromaculatus* was native downstream of the Platte basin (Figure 8).

The final NMDS solution was two-dimensional (Figure 9). The two axes accounted for 95% of the variance between the distance in the original n -dimensional space and the distance in the final ordination space. The final ordination required 400 iterations and had a final mean stress of 10% that indicated a good ordination. This mean stress was significantly better than that of 50 Monte Carlo simulations (mean stress = 28%, $P = 0.02$). The first ordination axis accounted for 67% of the variation and was negatively correlated with tributary basin isolation ($r = -0.95$, $df = 20$) and uncorrelated with tributary basin area ($r = 0.28$, $df = 20$). The second axis accounted for 28% of the variation and was negatively correlated with tributary basin area ($r = -0.55$, $df = 20$) and positively correlated with tributary basin isolation ($r = 0.42$, $df = 20$).

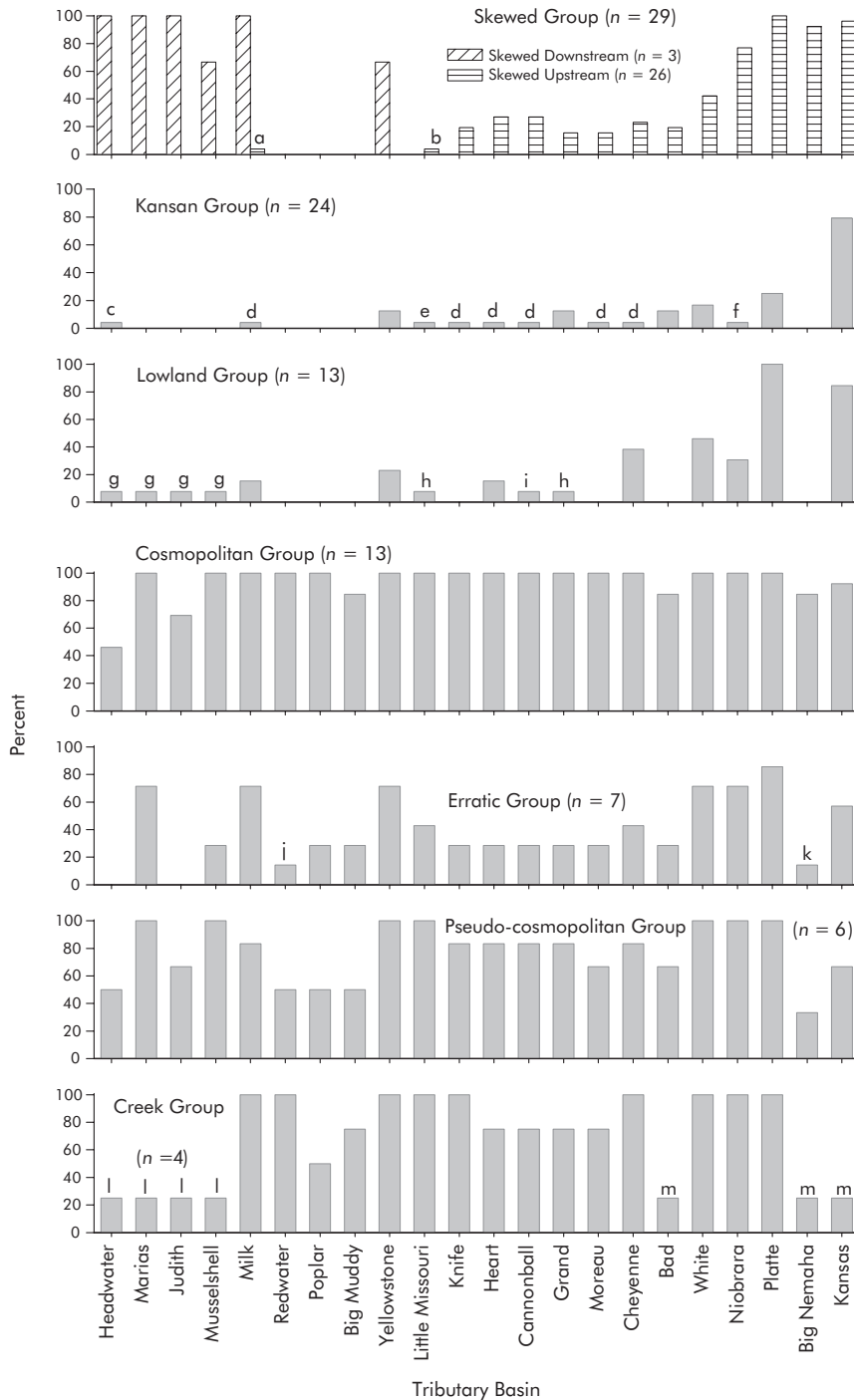


Figure 8. Percent of native fish species group membership by tributary basin. The skewed group is divided into groups based on upstream or downstream distributions (e.g., skewed upstream indicates the tail of the distribution of group members is extended in the upstream direction; Sokal and Rohlf 1995). Letters indicate tributary basins that were occupied by a single fish species of a group: a = shortnose gar, b = common shiner, c = Arctic grayling, d = blue sucker, e = sicklefin chub, f = grass pickerel, g = mountain sucker, h = bigmouth buffalo, i = sturgeon chub, j = finescale dace, k = black bullhead, l = longnose sucker, and m = creek chub.

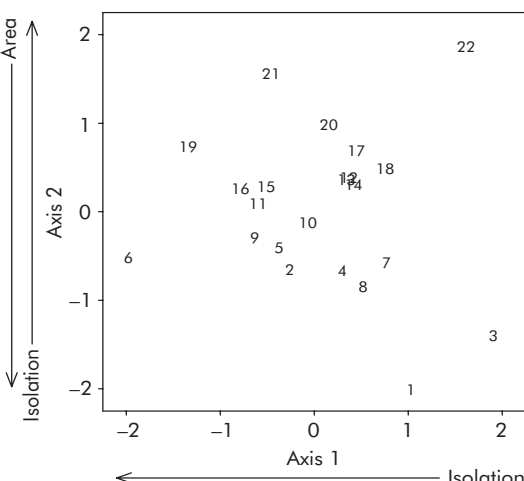


Figure 9. Ordination plot derived from nonmetric multidimensional scaling analysis based on fish faunal similarity (Sørensen index). Vectors along each axis indicate significantly correlated parameters and the direction of each relation. Numbers correspond to tributary basin numbers provided on Figure 1.

Cluster analysis of NMDS scores grouped tributary basins into five clusters at a level that retained 85% of the information (Figure 10). The largest tributary basin group included eight consecutive basins. The Bad basin was the southernmost of this group and the Little Missouri basin was the northernmost. These basins were primarily in western South Dakota and North Dakota and were named the Dakota basins. The second largest group included five consecutive basins from the Kansas basin on the south to the White basin on the north. These were the southernmost basins of the study area and named the Southern basins. The third largest group included four basins, the Yellowstone, Milk, Musselshell, and Marias. These were named large northern basins. The fourth largest group included three consecutive basins, the Big Muddy, Poplar, and Redwater, which were named small northern

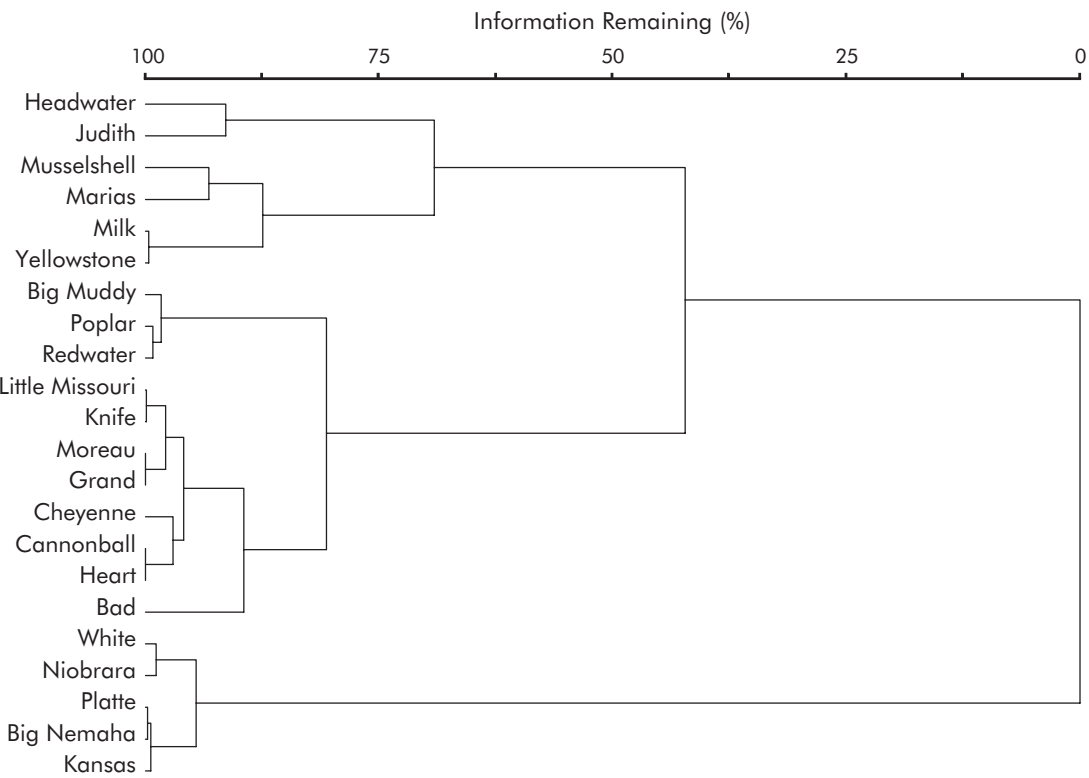


Figure 10. Dendrogram of tributary basin fish faunal similarity from hierarchical, agglomerative, polythetic cluster analysis of nonmetric multidimensional scaling analysis scores. Dendrogram scale is by Wishart's objective function converted to a percentage of information remaining.

basins. Finally, the smallest group included only the Headwater and Judith basins. These basins were relatively mountainous and had relatively low species richness and thus named the mountain basins. Tributary basin groups were segregated by distance along the Missouri River, that is, by isolation, but there was overlap in isolation among large and small northern basins and mountain basins (Figure 11). As expected, species richness of tributary basin groups declined from downstream to upstream and was higher for groups that included larger tributary basins (Figure 12).

DISCUSSION

The strong relation of native fish fauna composition to tributary basin isolation and the associated coldness gradient was consistent with the observations of Cross et al. (1986) and our expectations. Excepting mountain fishes with distributions skewed downstream, fishes of the three largest groups identified by cluster analysis of Wilcoxon two-sample scores (66% of all

species) were increasingly abundant to the south. This suggests that distance and environmental harshness historically interacted with variable species dispersal, establishment, and persistence capabilities to influence the faunal composition of each tributary basin. In other words, fish species that were more cold tolerant, had higher dispersal ability, and were better at establishing populations successfully colonized tributary basins farther upstream than other species.

The influence of tributary basin area and associated habitat diversity was less evident in our analyses of species distributions, but the multiple regression and nestedness results indicated that it was also important. This relation was pervasive in our analyses because the majority of species contributed to this trend by each having more absences from smaller basins than larger

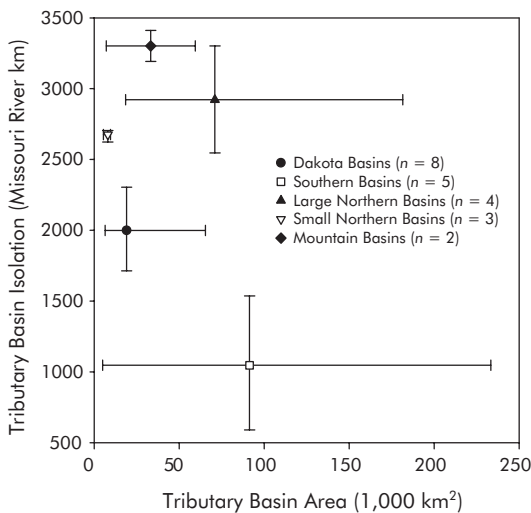


Figure 11. Plot showing the mean and range of tributary basin isolation and area for each tributary basin group. Groups were determined using a cluster analysis of ranked scores from a nonmetric multidimensional scaling analysis of faunal resemblance.

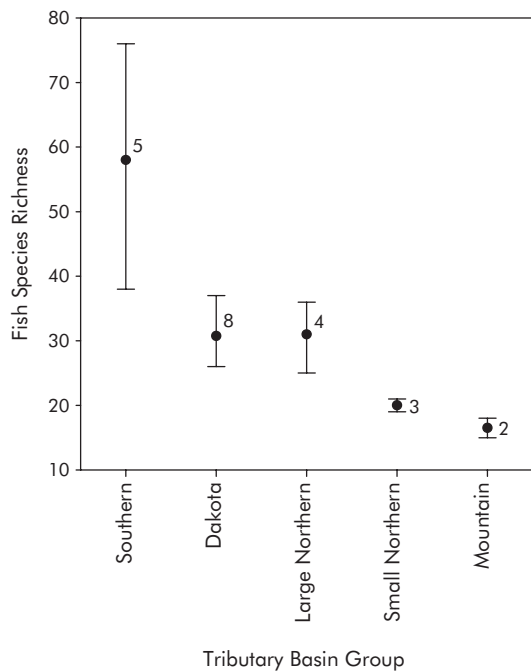


Figure 12. Plot showing the mean and range of native fish species richness for each tributary basin group. Groups were determined using a cluster analysis of ranked scores from a nonmetric multidimensional scaling analysis of faunal resemblance. The number of tributary basins in each group is provided next to each group mean.

basins. Higher species richness in larger tributary basins suggests that greater environmental stability and habitat diversity along with potential for larger populations and increased chance for successful colonization, factors presumably associated with larger tributary basins, did affect faunal composition.

When geomorphic and climatic history are also considered, it appears that the gradient of distance and cold has restricted the upstream establishment of more than half of the native species, but this gradient was dynamic throughout Holocene time and allowed some species to expand their range to the north during warmer periods and other species to expanded their range to the south during colder periods. Van Devender (1986) described a similar phenomenon for plant communities of the Chihuahuan Desert. Larger tributary basins buffered the effects of the coldness gradient more effectively than smaller tributary basins and provided additional niche space and, thus over time, accumulated and retained more species as their distributions oscillated back and forth, but southern tributary basins always maintained the most species because of their more equitable climate and proximity to regions of higher species richness (e.g., the Central Lowlands and Ozark Plateaus).

Zoogeography Review

Two geological findings reviewed in this study have important implications for zoogeographic interpretations. First, the apparent severity of climatic conditions within the preglacial Hudson Bay basin suggests fishes did not survive there throughout Pleistocene time, as has been previously postulated. Aquatic habitat present during the height of glacial advances included relatively short rivers that flowed across frozen terrain into proglacial lakes. Fishes preferring big rivers and high sediment loads, such as pallid sturgeon, shovelnose sturgeon *Scaphirhynchus platyrhynchus*, western silvery minnow *Hybognathus argyritis*, sturgeon chub, and sicklefin chub, seem unsuited for such an environment, even if they could have

withstood the cold, which is questionable based on their modern distributions. Geologic (Stanley and Wayne 1972) and fossil (Cross 1970) evidence suggest that the preglacial White, Osage, and Arkansas basins were more suitable for big river fishes during Pleistocene time. In situ persistence in the preglacial Hudson Bay basins is most likely for fishes native to the Headwater basin (15 species) because the Great Falls were presumably a barrier to fish dispersal after early glaciations. Even this evidence is not conclusive because early glaciations connected all preglacial basins and fishes from all sources could have dispersed northward as early glaciers receded.

Second, western extension of the preglacial Osage basin through the Flint Hills to the Rocky Mountains necessitates changes in hypotheses of the origins of some closely related Missouri River basin fishes. Plains orangethroat darter *Etheostoma spectabile pulchellum* is proposed to have differentiated via isolation in the "Ancient Plains Drainage" of Metcalf (1966) that included the ancient Kansas basin. This subspecies presumably later came into contact with northern orangethroat darter *E. spectabile spectabile* when the Kansas and Missouri basins joined (Distler 1968; Wiseman et al. 1978). This hypothesis is not possible if the Kansas basin was always connected to the lower Missouri River via the ancient Osage River, but the plains orangethroat darter could have been isolated from the northern orangethroat darter in a southern Great Plains basin (e.g., the ancestral Arkansas River). If so, early Pleistocene capture of the Smoky Hill subbasin by the ancient Arkansas basin likely allowed plains orangethroat darter access to that river. Later, when the Kansas basin recaptured the Smoky Hill subbasin, the plains orangethroat darter could have entered the lower Kansas River and encountered the northern orangethroat darter. This scenario could also apply to the plains sand shiner *Notropis stramineus missouriensis*, which exhibits similar intraspecific distribution to the plains orangethroat darter (Metcalf 1966), the northern plains killifish *Fundulus kansae*, which colonized to the north of the Arkansas

basin in the middle Pleistocene (Kreiser et al. 2001), the plains minnow *Hybognathus placitus*, which shows similar geographic variation to plains killifish species (Al-Rawi and Cross 1964; Kreiser et al. 2001), and the pealip redhorse *Moxostoma pisolabrum*, which intergrades with shorthead redhorse *M. macrolepidotum* in the Kansas basin (Minckley and Cross 1960; Jenkins 1980). Shoal chub *Macrhybopsis hyostoma* potentially used this route in the reverse direction, which allowed it to intermingle with the closely related peppered chub *Macrhybopsis tetranema* (Eisenhour 1997; Underwood et al. 2003). Pleistocene connections between the Kansas and Platte basins such as the ancient Big Blue and Missouri rivers presumably allowed plains minnow, shoal chub, plains sand shiner, northern plains killifish, and plains orangethroat darter to disperse into the Platte basin.

Although ichthyologists have composed lists of species presumed to have originated in different preglacial drainages (Bailey and Allum 1962; Metcalf 1966), we believe these lists are premature. The high likelihood of preglacial faunas being intermixed during early glacial advances makes it difficult if not impossible to determine preglacial distributions solely from modern distributions. Some species never recolonized regions they formerly inhabited (Pflieger 1971; Cross et al. 1986). Phylogeographic analysis is a promising method for revealing the location of species origins and directions of subsequent dispersal (Mayden 1988). Metcalf (1966) and Pflieger (1971) suggested that red shiner *Cyprinella lutrensis* was present in the Ancient Plains Drainage, but Richardson and Gold (1995) presented phylogeographic evidence that red shiner entered the Mississippi basin from the Trinity River of Texas in mid to late Pleistocene time, after which it dispersed north and eventually reached the Missouri basin. Substantial range expansion to the north during and after deglaciation (a period of > 11,000 years) is not surprising because red shiners have dramatically increased their range even within historic time (Page and Smith 1970). There is no reason to

believe that other fishes, particularly more mobile species, could not also have dispersed widely during the Holocene Epoch, especially because terrestrial animals and plants have done so (Davis 1986; Graham 1986). Relict (southern) populations of cold adapted fish species have typically been referred to as "preglacial relicts" (Bailey and Allum 1962) but more likely are relicts from more recent climatic fluctuations. For example, pearl dace *Margariscus margarita nachtriebi*, northern redbelly dace *Phoxinus eos*, and finescale dace *P. neogaeus* must have been more widespread at some time during the middle or late Holocene Epoch because relict populations are present in the Nebraska Sandhills that formed between 8,000 and 1,500 years ago (Swinehart 1998), 4,000 or more years after glaciers receded.

Fish Distribution Analysis

Of the four filters that cause nestedness (Wright et al. 1998), three (passive sampling, habitat nestedness, and reduced extinction rates) could potentially explain the influence of tributary basin area on faunal composition. Passive sampling (sensu Connor and McCoy 1979; Cutler 1994) provides a partial explanation because large downstream basins such as the Kansas and Platte contained more species with restricted distributions than smaller downstream basins such as the Big Nemaha and Bad. This suggests that less tolerant or more specialized species were more likely to colonize and persist within larger tributary basins. However Eadie et al. (1986) believed passive sampling was unimportant for freshwater fishes because colonization is not normally passive, but requires deliberate movements via dispersal corridors. Habitat nestedness may be a more important determinant of distributional patterns because larger tributary basins span more ecological regions and a larger elevation range, which indicates they contain higher habitat diversity (Eadie et al. 1986). A wider variety of habitats supposedly would support a wider variety of fishes. Reduced extinction rates due to higher habitat stability and higher population sizes in larger

basins may also be important (Diamond 1984a, 1984b) because larger streams normally support more fish species (Sheldon 1968; Horwitz 1978; Schlosser 1987) and larger basins with higher discharge presumably provide more stable long-term refugia (Livingstone et al. 1982). It is possible that all three of these filters reinforce each other to influence faunal nestedness by tributary basin area.

The filters of variable colonization and extinction rates (Wright et al. 1998) best explain nestedness by distance isolation and are certainly influenced by a gradient of increasing climatic harshness (Cook et al. 2004). Extinction rates may be lower for tributary basins closer to sources of colonists because of the rescue effect (Brown and Kodric-Brown 1977) and colonization rates may be higher for closer basins because more species are capable of dispersal over shorter distances (Darlington 1957; Carlquist 1974). This presumably explains the relatively high species richness of the small Big Nemaha basin. Aside from the Great Falls, there are no known dispersal barriers along the Missouri River and thus southern species had opportunity to disperse further upstream throughout Holocene time. Colonization rates may have been reduced by sheer distance between tributary basins, while establishment and persistence rates may have been reduced by increased cold. Increasing flow variability upstream might also increase environmental harshness (Horwitz 1978) and thus reduce colonization. The combined influence of increasing cold, increasing flow variability, and increasing distance on extinction and colonization rates may be sufficient to explain nestedness by isolation.

The characteristic habitat conditions of the Great Plains may also reduce establishment and persistence of some colonizing (or invading) species (Gido et al. 2004). The Great Plains is a region of high sediment transport (Osterkamp and Hedman 1982), and many of the main rivers are dominated by shifting sand substrates. Streams with stable gravel and cobble substrates are generally isolated in spring fed tributaries or mountain headwater streams (Cross and Moss 1987;

Fausch and Bestgen 1997). The scarcity of such habitats could reduce colonization and establishment rates of fish species that require stable substrates, such as highland stream fishes of the Ozark Plateaus (Pflieger 1971; Mayden 1985; 1987b, 1987c).

Faunal variation within tributary basins may be similar to that among tributary basins. The Platte basin has the second highest native species richness of the study area, but not all of its subbasins have high native species richness. The Salt Creek subbasin is 4,198 km², 2% of the Platte basin, and supported 35 native species (Maret and Peters 1980). The much larger South Platte subbasin in Colorado is 59,927 km², 26% of the Platte basin, and supported only 31 native species (Propst and Carlson 1986). Finally, the North Platte subbasin in Colorado at 3,706 km², 2% of the Platte basin, is only 492 km² smaller than the Salt Creek subbasin, but supported only seven native species (Propst and Carlson 1986). Native species composition among Platte subbasins was likely influenced by the combination of subbasin area, subbasin isolation, and strong environmental gradients. Subbasins farther west are environmentally harsher because upstream subbasins have higher flow variability, higher elevation subbasins are colder, and subbasins in the Rocky Mountain rain shadow are more arid.

Faunal variation within tributary basins may also be affected by smaller scale factors. Duehr (2004) found similar native species richness between two Cheyenne basin subbasins that join the main-stem Cheyenne River within a few kilometers of each other. Cherry Creek subbasin comprises 7% of the Cheyenne basin (4,745 km²) and supported 12 native species. The nearby Plum Creek Subbasin comprises only 2% (1,292 km²) but supported 13 native species. The much smaller Plum Creek basin has perennial spring inflows, while Cherry Creek is commonly reduced to intermittent pools. Higher stability of Plum Creek habitats could explain why the faunas are equally diverse.

The tributary basin faunal groups defined from NMDS analysis illustrated the importance

of isolation and increasing cold because tributary basins grouped from upstream to downstream. Southern basins from the Kansas to the White constituted the most distinct group because of their high species richness and the prevalence of species with restricted distributions. The presence of mountainous headwaters also appeared to be important because the mountain and large northern basin faunas were relatively similar compared to faunas of small northern basins, which were isolated from mountains.

Influences of Landscape and Climate on Indigenous Fish Faunas

Nestedness is a result of processes that act on at least three dimensions: spatial, ecological, and temporal (Lomolino and Davis 1997). Strong gradients in fish faunal composition among major western tributary basins of the Missouri River support the hypothesis of Cook et al. (2004) that strong nestedness will be present in regions with strong environmental gradients. However, the harshness gradient of the Great Plains is not fixed, but has advanced and retreated for roughly 2.8 million years. This has complicated fish distribution patterns by bringing the variable size of tributary basins into play. As fish faunas advanced and retreated, populations that inhabited relatively stable regions persisted even when adjacent areas became unsuitable. Stable regions were more frequently present in larger tributary basins. Large tributary basins retained more species over time because they also sustained larger species populations and included more habitat types.

The zoogeography of Missouri basin fishes in the Great Plains is strikingly different from the zoogeography of fishes in the adjacent Central Highlands. Our results indicate ecological processes such as dispersal ability and environmental tolerance were important for assembling faunas among Missouri River tributary basins in the Great Plains, while Gorman (1992) and Strange and Burr (1997) found that Central Highland faunas were heavily influenced by spe-

cific historical events. The fauna of the Central Highlands has greatly diversified over millions of years through dispersal, vicariance, and peripheral isolation events that took place within an environmentally stable region (Mayden 1985, 1987c; Strange and Burr 1997). The fauna of the Missouri basin in the Great Plains has escaped diversification through frequent dispersal and extinction events facilitated by dramatic, cyclical geomorphic and climatic change. The contrast between these two faunas reflects the dominance of different processes that operate on different time scales. The Central Highland fauna was affected most by geological isolation that maintained fish distributions over millions of years, but the distributions of Great Plains fishes in the Missouri basin were periodically altered by climate cycles of roughly 300,000 years.

Tributary basins of the Missouri River in the Great Plains are analogous to islands. Extinction and colonization rates were high because the Great Plains was subject to dramatic climatic cycles for a period of 2.8 million years. This interacted with the size and location of each tributary basin to ultimately determine faunal composition. Human developments such as dams have disrupted (or eliminated) dispersal corridors (Hesse et al. 1989; Pegg and Pierce 2002) and have degraded habitat conditions (Dodds et al. 2004). As a result, it is likely that extinction and colonization rates have changed as they did in the Great Basin after human settlement (Smith 1978). Quantification of this change could help explain recent changes in native fish faunas and help predict their future.

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Appendix A. Native presence (+) or absence (–) of fish species from Great Plains tributary basins of the Missouri River. Species names follow Nelson et al. (2004) except where noted.

Tributary basin																								
Headwaters ^a	Marías ^a	Judith ^a	Musselshell ^a	Milk ^b	Redwater ^a	Poplar ^a	Big Muddy ^a	Yellowstone ^c	Little Missouri ^d	Knife ^e	Heart ^e	Cannonball ^e	Grand ^f	Moreau ^g	Cheyenne ^h	Bad ⁱ	White ^j	Niobrara ^k	Platte ^l	Big Nemaha ^m	Kansas ⁿ	Total basins	Dispersal group ^o	Typical habitat ^a
Chestnut lamprey <i>Ichthyomyzon castaneus</i> Girard	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	LG ^a	BSL
Lake sturgeon <i>Acipenser fulvescens</i> Rafinesque	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	EG ^a	B
Pallid sturgeon <i>Scaphirhynchus albus</i> (Forbes and Richardson)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5	LG	B
Shovelnose sturgeon <i>S. platyrhynchus</i> (Rafinesque)	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	12	LG ^a	B
Paddlefish <i>Polyodon spathula</i> (Walbaum)	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	7	LG ^b	BL
Longnose gar <i>Lepisosteus osseus</i> (Linnaeus)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	LG ^a	BSL
Shortnose gar <i>L. platostomus</i> Rafinesque	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	11	LG ^a	BS
Goldeye <i>Hiodon alosoides</i> (Rafinesque)	–	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	20	EG ^a	BS
Mooneye <i>H. tergisus</i> Lesueur	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	LG ^a	BS
American eel <i>Anguilla rostrata</i> (Lesueur)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	LG ^a	BS
Gizzard shad <i>Dorosoma cepedianum</i> (Lesueur)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4	LG ^a	BSL
Central stoneroller ^r <i>Campostoma anomalum pullum</i> (Agassiz)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5	LG ^a	SC
Lake chub <i>Couesius plumbeus</i> (Agassiz)	+	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	16	EG	SCL
Red shiner ^s <i>Cyprinella lutrensis lutrensis</i> (Baird & Girard)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	9	LG ^a	BSCL
Western silvery minnow <i>Hybognathus argyritis</i> Girard	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	20	EG	BS
Brassy minnow ^r <i>H. hankinsoni</i> Hubbs	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	20	EG ^a	C
Plains minnow <i>H. placitus</i> Girard	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	20	LG	BS
Common shiner ^v <i>Luxilus cornutus</i> (Mitchill)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	9	LG ^a	SC
Redfin shiner ^r <i>Lythrurus umbratilis umbratilis</i> (Girard)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	LG	SC
Sturgeon chub <i>Macrhybopsis gelida</i> (Girard)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	8	LG	BS
Shoal chub <i>M. hyostoma</i> (Gilbert)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	LG ^a	BS
Sicklefin chub <i>M. meeki</i> (Jordan & Evermann)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	7	LG	B
Silver chub <i>M. storeriana</i> (Kirtland)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4	LG ^a	B
Pearl dace [™] <i>Margariscus margarita nachtriebi</i> (Cox)	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	8	EG	CL
Hornyhead chub ^r <i>Nocomis biguttatus</i> (Kirtland)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	LG ^a	SC
Golden shiner <i>Notemigonus crysoleucas</i> (Mitchill)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4	LG ^a	SCL
Emerald shiner <i>Notropis atherinoides</i> Rafinesque	–	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	21	EG ^a	BSL
River shiner <i>N. blennioides</i> (Girard)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4	LG ^a	BS
Ghost shiner <i>N. buchanani</i> Meek	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	LG	BS
Bigmouth shiner <i>N. dorsalis</i> (Agassiz)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5	LG ^a	BSC

Appendix A (continued)

Species	Tributary basin															Total basins	Dispersal group ^o	Typical habitat ^p						
	Headwaters ^a	Marias ^a	Judith ^a	Musselshell ^a	Milk ^b	Redwater ^a	Poplar ^a	Big Muddy ^a	Yellowstone ^c	Little Missouri ^d	Knife ^e	Heart ^e	Cannonball ^e	Grand ^f	Moreau ^g				Cheyenne ^h	Bad ⁱ	White ⁱ	Niobrara ^k	Platte ⁱ	Big Nemaha ^m
Yellowstone cutthroat trout ^{q28} <i>Oncorhynchus clarkii bouvieri</i> (Bendire)	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	1	P	CL
Westslope cutthroat trout ^{q29} <i>O. c. lewisi</i> (Girard)	+	+	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	P	CL
Greenback cutthroat trout ^{q30} <i>O. c. stomias</i> (Cope)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	P	CL
Mountain whitefish <i>Prosopium williamsi</i> (Girard)	+	+	+	+	+	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	6	P	L
Arctic grayling <i>Thymallus arcticus</i> (Pallas)	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	EG	SCL
Burbot <i>Lota lota</i> (Linnaeus)	+	+	+	+	+	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	18	EG	L
Northern plains killifish th <i>Fundulus kansae</i> Garman	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	LG	BSC
Plains topminnow <i>F. sciadicus</i> Cope	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	LG	C
Brook stickleback ⁱ <i>Culaea inconstans</i> (Kirtland)	-	-	-	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	15	EG ^a	CL
Cottus sp. ⁱⁱ	+	+	+	+	+	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	6	P	SC
White bass <i>Morone chrysops</i> (Rafinesque)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	LG ^a	BL
Green sunfish <i>Lepomis cyanellus</i> Rafinesque	-	-	-	-	-	-	-	-	-	-	+	+	+	+	+	+	+	+	+	+	+	12	LG ^a	BSCL
Warmouth <i>L. gulosus</i> (Cuvier)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	LG	CL
Orangespotted sunfish <i>L. humilis</i> (Girard)	-	-	-	-	-	-	-	-	-	-	+	+	+	+	+	+	+	+	+	+	+	12	LG ^a	BSCL
Bluegill ^{lll} <i>L. macrochirus macrochirus</i> Rafinesque	-	-	-	-	-	-	-	-	-	-	+	+	+	+	+	+	+	+	+	+	+	4	LG ^a	BSCL
Longear sunfish ^{kk} <i>L. megalotis</i> (Rafinesque)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	LG	SCL
Largemouth bass ^l <i>Micropterus salmoides salmoides</i> (Lacepède)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	LG ^a	BSCL
White crappie <i>Pomoxis annularis</i> Rafinesque	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	LG ^a	BSL
Greenside darter ^{mmm} <i>Etheostoma blennioides</i> <i>pholidotum</i> Miller	-	-	-	-	-	-	-	-	-	+	+	+	+	+	+	+	+	+	+	+	+	1	LG	SC
Iowa darter <i>E. exile</i> (Girard)	-	-	-	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	15	EG ^a	SL
Johnny darter <i>E. nigrum</i> Rafinesque	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	LG ^a	SC
Plains orangefthroat darter ⁿⁿ <i>E. spectabile pulchellum</i> (Girard)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	LG	SC
Ozark logperch <i>Percina fulviraenia</i> Morris & Page	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	LG	SCL
Blackside darter <i>P. maculata</i> (Girard)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	LG ^a	SC
Sauger <i>Sander canadensis</i> (Griffith & Smith)	-	+	+	+	+	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	18	EG ^a	BSL
Walleye <i>S. vitreus</i> (Mitchill)	-	-	-	-	-	-	-	-	-	+	+	+	+	+	+	+	+	+	+	+	+	12	EG ^a	BSL
Freshwater drum <i>Aplodinotus grunniens</i> Rafinesque	-	+	-	+	+	-	-	-	+	+	+	+	+	+	+	+	+	+	+	+	+	17	EG ^a	BSL

^aPrimary sources for determining native fishes of the Missouri basin upstream from the Great Falls, as well as the Marias, Judith, Musselshell, Redwater, Poplar, and Big Muddy basins were Brown (1971), Scott and Crossman (1973), Lee et al. (1980), and Holton and Johnson (2003).

^bPrimary sources for determining native fishes of the Milk basin were Brown (1971), Scott and Crossman (1973), Lee et al. (1980), Nelson and Paetz (1992), Stash (2001), and Holton and Johnson (2003).

- ^cPrimary sources for determining native fishes of the Yellowstone basin were Simon (1951), Baxter and Simon (1970), Brown (1971), Lee et al. (1980), Hubert (1993), White and Bramblett (1993), Baxter and Stone (1995), Patton (1997), and Halton and Johnson (2003).
- ^dPrimary sources for determining native fishes of the Little Missouri basin were Hankinson (1929), Simon (1951), Personius and Eddy (1955), Bailey and Allum (1962), Baxter and Simon (1970), Bich and Scalet (1977), Reigh and Owen (1978), Lee et al. (1980), Ryckman (1981), Kelsch (1994), Baxter and Stone (1995), and Patton (1997).
- ^ePrimary sources for determining native fishes of the Knife, Heart, and Cannonball basins were Hankinson (1929), Reigh and Owen (1978), Lee et al. (1980), and Ryckman (1981).
- ^fPrimary sources for determining native fishes of the Grand basin were Bailey and Allum (1962), Lee et al. (1980), and Ruelle et al. (1993).
- ^gPrimary sources for determining native fishes of the Moreau basin were Bailey and Allum (1962), Lee et al. (1980), Ruelle et al. (1993), and Loomis et al. (1999).
- ^hPrimary sources for determining native fishes of the Cheyenne basin were Simon (1951), Bailey and Allum (1962), Baxter and Simon (1970), Lee et al. (1980), Ruelle et al. (1993), Cunningham et al. (1995), Hampton and Berry (1997), Patton (1997), Doorenbos (1998), and Duehr (2004).
- ⁱPrimary sources for determining native fishes of the Bad basin were Bailey and Allum (1962), Lee et al. (1980), Ruelle et al. (1993), Milewski (2001), and Harland (2003).
- ^jPrimary sources for determining native fishes of the White basin were Bailey and Allum (1962), Lee et al. (1980), Mayden (1987a), Ruelle et al. (1993), Cunningham et al. (1995), Fryda (2001), and Harland (2003).
- ^kPrimary sources for determining native fishes of the Niobrara basin were Johnson (1942), Simon (1951), Morris et al. (1974), Hesse et al. (1979), Lee et al. (1980), Stewart (1985), Mayden (1987a), Cunningham et al. (1995), and Harland and Berry (2004).
- ^lPrimary sources for determining native fishes of the Platte basin were Ellis (1914), Johnson (1942), Simon (1951), Morris (1960), Baxter and Simon (1970), Beckman (1970), Morris et al. (1974), Lee et al. (1980), Maret and Peters (1980), Propst and Carlson (1986), Baxter and Stone (1995), Lynch and Roh (1996), Chadwick et al. (1997), and Patton (1997).
- ^mPrimary sources for determining native fishes of the Big Nemaha basin were Johnson (1942), Cross (1967), Morris et al. (1974), Lee et al. (1980), and Cross and Collins (1995).
- ⁿPrimary sources for determining native fishes of the Kansas basin were Metcalf (1966), Cross (1967), Lee et al. (1980), Sanders et al. (1993), and Cross and Collins (1995).
- ^oPostglacial dispersal group designations were based on Bailey and Allum (1962), McPhail and Lindsey (1970), Stewart and Lindsey (1983), and Crossman and McAllister (1986) and native fishes present upstream of the Great Falls. Group labels were E = early, dispersed to Canada during deglaciation; L = late, did not disperse to Canada during deglaciation; G = invaded from Gulf of Mexico basin waters; and P = invaded from Pacific waters.
- ^pTypical habitat categories were from Cross et al. (1986). Habitat categories were B = big river, S = small river, C = creek, and L = lake.
- ^qBased on historical distributions reported by Underhill (1957), Cleary (1956), Bailey and Allum (1962), and Lee et al. (1980), these species potentially dispersed in one or more directions via headwater connections between Missouri River tributaries (Big Sioux, Little Sioux, and Boyer basins) and upper Mississippi River tributaries (Minnesota and Des Moines basins).
- ^rCentral stoneroller *Campestris anomalum* of northwestern Missouri River tributary basins is normally referred to as *C. a. pullum*, the western subspecies (Metcalf 1966; Cross 1967; Pflieger 1971; Cross and Collins 1995), which Pflieger (1997) considered a valid species.
- ^sThe nominal red shiner *Cyprinella lutrensis* subspecies is widespread throughout the central United States (Richardson and Gold 1995).
- ^tJack Erickson, South Dakota Department of Game, Fish, and Parks (personal communication), reports that *H. hankinsoni* and *C. inconstans* from small streams in the Belle Fourche River portion of the Cheyenne basin.
- ^uSimon and Simon (1939) and Simon (1951) listed *L. cornutus* as abundant in the Belle Fourche River of the Cheyenne basin in Wyoming, but Baxter and Simon (1970) considered this "doubtful" (reason not stated), presumably because the species was absent from more recent collections. Given the fact that *L. cornutus* was present in early collections from the western Kansas basin, disappearing by 1961 (Cross and Moss 1987) and that *L. cornutus* is native to the Little Missouri, Knife, Heart, and Cannonball basins, it is considered native to the Cheyenne basin here. Stream piracy between the Belle Fourche and Little Missouri rivers (Darton 1905; Rankl and Lowry 1990) that may have allowed fish faunal exchange between the Cheyenne and Little Missouri basins (Bailey and Allum 1962) also supports this view. Finally, this interpretation potentially supports Gilbert (1964) who hypothesized from morphometric analysis that *L. cornutus* originally inhabited the preglacial Hudson Bay basin.
- ^vSnelson and Pflieger (1975) described subspecies of redbell shiner *L. umbratilus*, with the nominal subspecies present in the Kansas basin.
- ^wBailey and Allum (1962) provided a description of *M. margarita* subspecies with a map of their distributions.
- ^xSimon and Simon (1939), Simon (1951), Baxter and Simon (1970), and Lachner and Jenkins (1971) reported *N. biguttatus* to be native in the Cheyenne basin in Wyoming.

(continued)

Appendix A (continued)

^v Johnson (1942), Bailey and Allum (1962), Metcalf (1966), Tanyolac (1973), and Cross and Collins (1995) considered the subspecies *N. stramineus missouriensis* to be typical of the Great Plains Missouri River tributaries, despite the presence of intergrades with *N. stramineus stramineus* in the Platte, Big Nemaha, and Kansas basins. The nominal subspecies is present in eastern, Central Lowland Missouri River tributaries, which it presumably reached via headwater connections with the upper Mississippi basin (Bailey and Allum 1962).

^w Morey and Berry (2004) documented a previously unknown population of *P. eos* in the Grand basin.

^{xx} In some cases, *Phoxinus eos* × *P. neogaeus* hybrids persist where pure *P. neogaeus* are absent (Dawley et al. 1987; Bestgen 1989; Cunningham et al. 1995). For this study, presence of hybrids was treated as presence of both species.

^{xb} River carpsucker *Carpiodes carpio* is divisible into two distinct subspecies, *C. c. carpio* of the Mississippi basin and *C. c. elongatus* of western Gulf of Mexico basins (Hubbs and Black 1940; Suttkus and Bart 2002).

^{xc} Quillback *Carpiodes cyprinus* is divisible into two distinct subspecies, *C. c. cyprinus* of the Great Lakes, Hudson Bay, and Atlantic Coast basins and *C. c. hinei* of the Gulf of Mexico basins and portions of the Great Lakes basin (Trautman, 1981).

^{xd} *Catostomus platyrhynchus* colonized the preglacial Missouri River basin and postglacial dispersal was from Gulf of Mexico waters (Smith 1966, 1992). *Catostomus platyrhynchus* was known from late Pleistocene fossils beds in the state of Kansas (Cross et al. 1986). This species was also reported from the Niobrara basin, but Bailey and Allum (1962) believed the specimen was mislabeled.

^{ee} *Moxostoma macrolepidotum* intergrades with pealip redbhorse *M. pisolabrum* in the Kansas basin (Minckley and Cross 1960; Jenkins 1980).

^{ff} *Esox americanus vermiculatus* is the Mississippi basin and Great Lakes basin form of grass pickerel *E. americanus* (Crossman 1966, 1978; Reist and Crossman 1987).

^{gg} Names and native ranges of cutthroat trout *O. clarkii* subspecies follow Behnke (1992, 2002).

^{hh} *Fundulus kansae* of the Cheyenne basin is considered nonnative based on circumstantial evidence reported by Miller (1955). Baxter and Simon (1970) reported *F. kansae* as introduced into the Yellowstone basin as well. Bait bucket introductions were presumed. However, if it was present in the preglacial White basin, it could have reached the Cheyenne and Yellowstone basins via stream captures.

ⁱ Recent research by David A. Neely of Saint Louis University (personal communication) indicates that the undescribed *Cottus* species of the Missouri basin in the Rocky Mountains is neither mottled sculpin *C. bairdii* as commonly considered (Baxter and Stone 1995; Holton and Johnson 2003) nor shorthead sculpin *C. confusus* as reported for populations in the Milk basin of Alberta (Nelson and Poetz 1992). Additional work is necessary to describe this form.

^j Bluegill *Lepomis macrochirus* native to the Great Plains tributaries of the Missouri River basin are of the widespread northern form, *L. m. macrochirus*, distinguished from *L. m. purperescens* of the Atlantic coast (Avisé and Smith 1974; Felley 1980).

^{kk} Several *L. megalotis* subspecies are commonly recognized, but relations among populations are not resolved (Jennings and Philipp 1992), so the subspecies that is native to the northwestern Missouri basin is undetermined.

^{ll} Two largemouth bass *M. salmoides* subspecies are recognized, the widespread northern form, *M. s. salmoides*, which is native to the Great Plains tributaries of the Missouri basin, and the southeastern form, *M. s. floridanus*, which some consider to be a distinct species (Kassler et al. 2002; Near et al. 2003).

^{mmm} Metcalf (1966) reported scale counts (59 in lateral line, 19 around caudal peduncle) for the single greenside darter *E. blennioides* specimen known from the Kansas basin. He noted that these counts were closest to *E. blennioides* found in the Missouri basin of the state of Missouri, which was later described by Miller (1968) as *E. b. pholidotum*.

ⁿⁿ Distler (1968) described the subspecies of orangefthroat darter *E. spectabile* with *E. s. pulchellum* present in the Great Plains tributaries of the Missouri River basin, although intergrades with *E. s. spectabile* were found in the lower Kansas basin. His results were upheld by the electrophoretic analysis of Wiseman et al. (1978).

Appendix B. Average drainage basin area and position occupied by each fish species of the Skewed group. Confidence limits (95%) are provided in parentheses. Number of basins occupied is also provided.

Species	Basins	Mean basin area (km ²)		Mean basin position (river km)	
<i>Lepisosteus platostomus</i>	11	57,582	(48,874)	1,705	(403)
<i>Dorosoma cepedianum</i>	4	105,106	(172,855)	970	(647)
<i>Camptostoma anomalum pullum</i>	5	91,376	(122,870)	1,047	(487)
<i>Cyprinella lutrensis lutrensis</i>	9	61,141	(61,869)	1,432	(420)
<i>Luxilus cornutus</i>	9	63,113	(60,872)	1,655	(457)
<i>Macrhybopsis hyostoma</i>	3	131,560	(288,726)	781	(457)
<i>M. storeriana</i>	4	107,784	(168,870)	925	(517)
<i>Notemigonus crysoleucas</i>	4	107,784	(168,870)	925	(517)
<i>Notropis blennius</i>	4	107,784	(168,870)	925	(517)
<i>N. dorsalis</i>	5	91,376	(122,870)	1,047	(487)
<i>N. topeka</i>	3	131,560	(288,726)	781	(457)
<i>Phenacobius mirabilis</i>	4	107,784	(168,870)	925	(517)
<i>Rhinichthys obtusus</i>	7	46,694	(76,907)	1,573	(527)
<i>Carpionodes cyprinus hinei</i>	4	107,784	(168,870)	925	(517)
<i>C. velifer</i>	4	107,784	(168,870)	925	(517)
<i>Ameiurus natalis</i>	4	107,784	(168,870)	925	(517)
<i>Noturus gyrinus</i>	3	131,560	(288,726)	781	(457)
<i>Pylodictis olivaris</i>	4	105,106	(172,855)	970	(647)
<i>Oncorhynchus clarkii lewisi</i>	4	36,160	(43,527)	3,185	(399)
<i>Prosopium williamsoni</i>	6	58,477	(67,245)	3,048	(338)
<i>Fundulus kansae</i>	4	107,784	(168,870)	925	(517)
<i>Cottus</i> sp.	6	58,477	(67,245)	3,048	(338)
<i>Lepomis cyanellus</i>	12	48,774	(45,887)	1,577	(343)
<i>L. humilis</i>	12	48,774	(45,887)	1,577	(343)
<i>L. macrochirus macrochirus</i>	4	107,784	(168,870)	925	(517)
<i>Micropterus salmoides salmoides</i>	4	107,784	(168,870)	925	(517)
<i>Pomoxis annularis</i>	3	131,560	(288,726)	781	(457)
<i>Etheostoma nigrum</i>	4	107,784	(168,870)	925	(517)
<i>Sander vitreus</i>	12	48,774	(45,887)	1,577	(343)

Appendix C. Average drainage basin area and position occupied by each fish species of the Kansan group. Confidence limits (95%) are provided in parentheses. Number of basins occupied is also provided.

Species	Basins	Mean basin area (km ²)		Mean basin position (river km)	
<i>Ichthyomyzon castaneus</i>	1	156,269		591	
<i>Scaphirhynchus albus</i>	5	118,804	(126,569)	1,547	(968)
<i>Hiodon tergisus</i>	1	233,437		957	
<i>Lythrurus umbratilis umbratilis</i>	1	156,269		591	
<i>Macrhybopsis meeki</i>	7	92,032	(87,839)	1,654	(646)
<i>Notropis buchani</i>	1	156,269		591	
<i>N. percobromus</i>	1	156,269		591	
<i>N. shumardi</i>	2	91,006	(829,233)	1,064	(6,011)
<i>Phoxinus erythrogaster</i>	1	156,269		591	
<i>Cycleptus elongatus</i>	11	50,139	(41,912)	1,926	(388)
<i>Ictiobus niger</i>	1	156,269		591	
<i>Minytrema melanops</i>	1	156,269		591	
<i>Moxostoma carinatum</i>	1	156,269		591	
<i>M. erythrurum</i>	1	156,269		591	
<i>Noturus exilis</i>	1	156,269		591	
<i>Esox americanus vermiculatus</i>	3	98,545	(290,526)	1,284	(737)
<i>E. lucius</i>	1	233,437		957	
<i>Oncorhynchus clarkii stomias</i>	1	233,437		957	
<i>Thymallus arcticus</i>	1	59,456		3,411	
<i>Morone chrysops</i>	1	156,269		591	
<i>Lepomis gulosus</i>	1	156,269		591	
<i>L. megalotis</i>	1	156,269		591	
<i>Etheostoma blennioides pholidotum</i>	1	156,269		591	
<i>Percina fulvitaenia</i>	1	156,269		591	

Appendix D. Average drainage basin area and position occupied by each fish species of the Lowland group. Confidence limits (95%) are provided in parentheses. Number of basins occupied is also provided.

Species	Basins	Mean basin area (km ²)		Mean basin position (river km)	
<i>Acipenser fulvescens</i>	2	194,853	(166,027)	774	(789)
<i>Lepisosteus osseus</i>	3	142,054	(246,590)	969	(954)
<i>Anguilla rostrata</i>	3	138,483	(260,814)	1,028	(1,185)
<i>Macrhybopsis gelida</i>	8	88,757	(73,895)	1,720	(558)
<i>Nocomis biguttatus</i>	3	151,702	(208,964)	1,112	(1,524)
<i>Notropis heterolepis</i>	4	112,976	(158,703)	1,111	(673)
<i>Pimephales notatus</i>	2	194,853	(490,248)	774	(2,331)
<i>Catostomus platyrhynchus</i>	10	75,049	(60,636)	2,508	(673)
<i>Ictiobus cyprinellus</i>	7	98,148	(84,017)	1,777	(768)
<i>Ictalurus furcatus</i>	4	120,212	(148,254)	1,218	(865)
<i>Fundulus sciadicus</i>	4	90,258	(154,186)	1,410	(556)
<i>Etheostoma spectabile pulchellum</i>	2	194,853	(490,248)	774	(2,331)
<i>Percina maculata</i>	2	194,853	(490,248)	774	(2,331)

Appendix E. Average drainage basin area and position occupied by each fish species of the Cosmopolitan group. Confidence limits (95%) are provided in parentheses. Number of basins occupied is also provided. Species present in all 22 drainage basins were included in this cluster although they were not used in the cluster analysis.

Species	Basins	Mean basin area (km ²)		Mean basin position (river km)	
<i>Hiodon alosoides</i>	20	46,010	(30,720)	2,167	(338)
<i>Hybognathus argyritis</i>	20	45,901	(30,753)	2,047	(347)
<i>H. hankinsoni</i>	20	48,462	(30,496)	2,132	(373)
<i>H. placitus</i>	20	45,901	(30,753)	2,047	(347)
<i>Notropis atherinoides</i>	21	44,056	(29,407)	2,101	(348)
<i>Pimephales promelas</i> ^a	22	44,756	(27,996)	2,161	(354)
<i>Platygobio gracilis</i> ^a	22	44,756	(27,996)	2,161	(354)
<i>Rhinichthys cataractae</i>	20	41,170	(28,289)	2,308	(315)
<i>Carpionotus carpio carpio</i>	20	45,901	(30,753)	2,047	(347)
<i>Catostomus commersonii</i> ^a	22	44,756	(27,996)	2,161	(354)
<i>Moxostoma macrolepidotum</i>	21	44,056	(29,407)	2,101	(348)
<i>Ictalurus punctatus</i>	20	45,812	(30,778)	2,075	(363)
<i>Noturus flavus</i>	20	48,374	(30,523)	2,160	(386)

^aSpecies present in every drainage basin.

Appendix F. Average drainage basin area and position occupied by each fish species of the Erratic group. Confidence limits (95%) are provided in parentheses. Number of basins occupied is also provided.

Species	Basins	Mean basin area (km ²)		Mean basin position (river km)	
<i>Scaphirhynchus platyrhynchus</i>	12	69,840	(48,679)	1,896	(488)
<i>Polyodon spathula</i>	7	97,803	(84,053)	2,066	(958)
<i>Margariscus margarita nachtriebi</i>	8	71,718	(72,312)	2,232	(696)
<i>Phoxinus neogaeus</i>	9	53,128	(54,330)	2,234	(640)
<i>Ictiobus bubalus</i>	11	69,193	(54,521)	2,114	(570)
<i>Ameiurus melas</i>	13	46,904	(41,987)	1,633	(335)
<i>Oncorhynchus clarkii bouvieri</i>	1	181,537		2,545	

Appendix G. Average drainage basin area and position occupied by each fish species of the Pseudo-Cosmopolitan group. Confidence limits (95%) are provided in parentheses. Number of basins occupied is also provided.

Species	Basins	Mean basin area (km ²)		Mean basin position (river km)	
<i>Couesius plumbeus</i>	16	48,471	(35,105)	2,411	(381)
<i>Notropis stramineus missouriensis</i>	17	49,406	(36,121)	1,928	(383)
<i>Phoxinus eos</i>	16	45,386	(35,266)	2,379	(378)
<i>Lota lota</i>	18	53,280	(33,361)	2,207	(403)
<i>Sander canadensis</i>	18	50,322	(33,798)	2,122	(369)
<i>Aplodinotus grunniens</i>	17	52,588	(35,660)	1,936	(387)

Appendix H. Average drainage basin area and position occupied by each fish species of the Creek group. Confidence limits (95%) are provided in parentheses. Number of basins occupied is also provided.

Species	Basins	Mean basin area (km ²)		Mean basin position (river km)	
<i>Semotilus atromaculatus</i>	16	53,521	(38,225)	1,832	(350)
<i>Catostomus catostomus</i>	14	54,090	(39,736)	2,412	(439)
<i>Culaea inconstans</i>	15	47,027	(37,894)	2,102	(301)
<i>Etheostoma exile</i>	15	47,027	(37,894)	2,102	(301)

Fish–Habitat Relations across Spatial Scales in Prairie Streams

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Abstract.—Habitat data collected at three spatial scales (catchments, reaches, and sites) were used to predict individual fish species occurrences and assemblage structure at 150 sites in the Kansas River basin. Habitat measurements for the catchments and reaches of each sample site were derived from available geographic information system (GIS) data layers. Habitat measurements at the sample sites were collected at the time of fish sampling. Because habitat measurements are typically more difficult to collect as the spatial scale of sampling decreases (i.e., field measurement versus a GIS analysis), our objective was to quantify the relative increase in predictive ability as we added habitat measurements from increasingly finer spatial scales. Although the addition of site-scale habitat variables increased the predictive performance of models, the relative magnitude of these increases was small. This was largely due to the general association of species occurrences with measurements of catchment area and soil factors, both of which could be quantified with a GIS. Habitat measurements taken at different spatial scales were often correlated; however, a partial canonical correspondence analysis showed that catchment-scale habitat measurements accounted for a slightly higher percent of the variation in fish-assemblage structure across the 150 sample sites than reach- or site-scale habitat measurements. We concluded that field habitat measurements were less informative for predicting species occurrences within the Kansas River basin than catchment data. However, because of the hierarchical nature of the geomorphological processes that form stream habitats, a refined understanding of the relationship between catchment-, reach- and site-scale habitats provides a mechanistic understanding of fish–habitat relations across spatial scales.

INTRODUCTION

Understanding species–environment relations is an important step toward the conservation of aquatic communities. This is particularly important in regions such as the Great Plains, which have a highly endangered fauna as a result of ex-

tensive human alterations to aquatic systems (Cross et al. 1985; Cross and Moss 1987; Fausch and Bestgen 1997; Dodds et al. 2004). However, identifying the appropriate scale at which to measure these relations is complicated. Both natural and human factors work across multiple spatial scales to constrain species distributions. At broad spatial scales, natural factors such as basin geology and stream network configurations influence

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fish assemblage structure (e.g., Benda et al. 2004) and food web interactions (Power and Dietrich 2002). At finer spatial scales, fish species partition habitats based on stream substrate size, depth, and current velocity (e.g., Gorman 1988; Aadland 1993; Gido and Propst 1999). Human impacts at broad spatial scales, such as groundwater mining or impoundment, have reduced and fragmented Great Plains river systems. Although these factors have left many local habitats intact, some species have clearly been affected by these disturbances (Cross and Moss 1987; Fausch and Bestgen 1997). In addition, local-scale alterations to habitat (e.g., gravel mining or bridge construction) can also affect local fish-assemblage structure (Burns 1972; Kondolf 1997).

Understanding of aquatic species distributions and ecosystem processes vary widely with the spatial scale of analysis (Allan et al. 1997). Several studies have previously reported species-habitat relationships across spatial scales, but these findings suggest reach and site habitats are primarily important in studies with a limited spatial extent (i.e., 100–10,000 km²). For example, Bond and Lake (2003; spatial extent 225 km²) evaluated habitat associations across three spatial scales (among streams, among sites, and within sites). They found that three of four species showed significant habitat associations at local spatial scales and that differences in habitat availability among sites and streams were less influential. Walters et al. (2003; spatial extent 300–400 km²) found that species composition in Piedmont streams was best predicted by reach-level geomorphic variables, including stream slope, bed texture, bed mobility, and tractive forces. However, species richness and density were best predicted by stream size. Joy and Death (2003; spatial extent 5,000 km²) successfully predicted the occurrences of 12 fish and invertebrate species in New Zealand streams based on reach-scale habitat features and two spatial variables (elevation and distance from the coast). Rich et al. (2003; spatial extent 7,900 km²), found that predictive models with both local-habitat and biotic variables (proximity to source popula-

tions) best explained the occurrence of bull trout *Salvelinus fontinalis* in 112 Montana streams.

Across broader spatial scales, quantifying catchment habitats may become more important in predicting local fish-assemblage structure. Because of the hierarchical structuring of streams, catchment landscapes can be closely linked to a stream's hydrologic regime, chemistry, and physical structure (Ritter et al. 1995). In addition, interactions between the catchment landscapes and stream organisms can change predictably with longitudinal position (Power and Dietrich 2002). Thus, because fish assemblages are tightly linked to hydrologic variability (e.g., Poff and Allan 1995), catchment area and geology are predicted to be closely associated with fish-assemblage structure. Santoul et al. (2004; spatial extent 57,000 km²) provide an example of this association, as they were able to explain 87.2% of the variation in fish species composition across 329 sites in southwestern France with the variables altitude, slope, and catchment area. The studies listed above indicate that stream fish assemblages are influenced by factors that occur at multiple spatial scales, but catchment or stream segment habitat measurements may be the best predictors of assemblage structure across broad spatial scales.

Broad-scale patterns of land use have been linked to aquatic community structure, but these effects also can be scale dependent. For example, Rashleigh (2004) found that land use associated with agriculture and urban development was associated with fish-assemblage structure, primarily by shifting trophic composition. Wang et al. (2001) found that the amount of connected impervious surface in a catchment influenced stream fish assemblages, instream habitat, and base flow in 47 small Wisconsin streams. Roth et al. (1996) found that land use quantified at the catchment scale was more reflective of stream biotic integrity (index of biotic integrity) than local scale habitat measurements. These results also are consistent with studies of macro-invertebrate assemblage structure, which has been associated with differences in land use (e.g.,

native versus nonnative land cover; Townsend et al. 2004).

Correlations between fish-assemblage structure and broad-scale habitat measurements such as land use and geology are due to the response of individuals to local conditions that are partly influenced by broader-scale factors. That is, major driving factors that structure assemblages may be correlated with measurements taken at different spatial scales due to the hierarchical organization of lotic systems (Frissell et al. 1986). For example, Richards et al. (1996) found a strong association between land-use and geologic variables, both of which were associated with macroinvertebrate assemblage structure. Despite the potential influence of broad-scale factors, these coarse landscape filters typically cannot explain all levels of variation in species distributions because they only represent an average of variability in finer scale habitat features that are relevant to the biota (Poff 1997). Thus, we would predict that fine-scale characterization of habitat would increase our ability to predict assemblage structure at fine to intermediate spatial scales because they more adequately reflect macro- and microhabitats used by fishes.

Given that fish assemblages are structured by factors that operate across multiple spatial scales, an understanding of these species-habitat relationships should provide information to help manage and predict the consequences of habitat changes that occur at different spatial scales. In addition, identifying the scales at which species respond to habitat will allow managers to estimate the scale at which to apply conservation efforts. For example, the scale of conservation is likely dependent on dispersal ability of organisms, and reach- or segment-level conservation may only be appropriate for those organisms with poor dispersal ability (Fausch et al. 2002; Wishart and Davies 2003). Species that require moderate to high levels of dispersal may require larger, regional conservation efforts.

Our objective was to evaluate the association between local fish-assemblage structure and habitat characteristics of 150 sample sites quan-

tified at three spatial scales. Habitat measurements from field sites (~ 0.1 km) were taken in conjunction with fish assemblage sampling. Reach (~ 1.0 km) and catchment (>5 km²) habitat characteristics were measured using a GIS. This partitioning of our habitat measurements allowed us to compare the relative predictive ability of field versus GIS methods of quantifying habitat. In addition, our approach was to first explain variability of assemblage structure with catchment variables and then quantify how much additional variation could be explained by adding habitat variables from finer spatial scales. This nested sequence of analyses was used because of the hierarchical structuring of stream habitats and the relative effort required in gathering habitat information as opposed to quantifying landscape-level factors. In addition, important processes in lotic systems typically occur in a downstream direction (i.e., from catchment to sites). Based on the broad spatial extent of our study (67,000 km²), we predicted that catchment-scale habitats that can be quantified by GIS are the best predictors of fish-assemblage structure, and little additional variability will be explained by adding habitat information taken at finer spatial scales (i.e., field measurements).

METHODS AND MATERIALS

Study Area

Fishes were collected at 150 sites in the lower Kansas River basin (Figure 1). This area falls within four EPA level III ecoregions: Central Irregular Plains (13.0%), Flint Hills (17.0%), Western Corn Belt Plains (19.5%), and Central Great Plains (50.5%; Omernik 1987). Primary land uses within the lower Kansas River basin were row crop agriculture (53%), seminatural herbaceous vegetation (20%), and pasture/hay (13%). Urban and wetland land uses combined composed $\sim 3\%$ of land use in the basin (USGS 1992). Stream order at the collection sites ranged from first to fifth order (Strahler 1957) and catchment

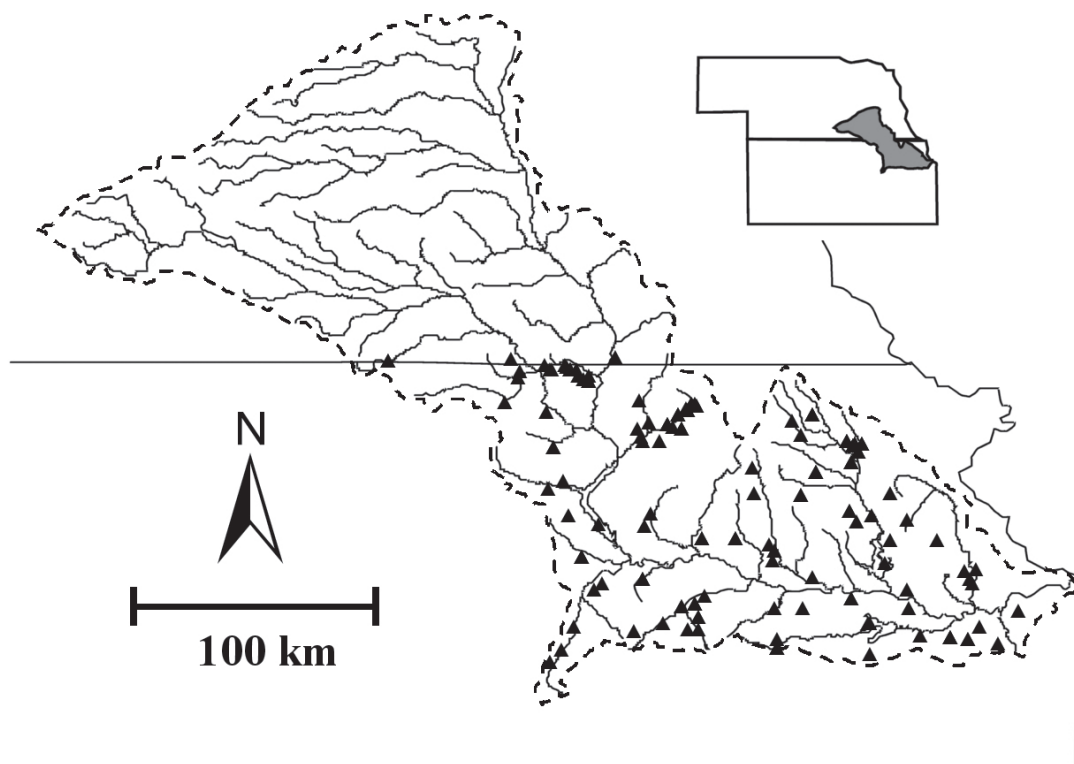


Figure 1. Location of sample sites in the Kansas River basin. Major rivers and major impoundments are provided for spatial reference.

area of study reaches ranged from 5 to 33,775 km². Three major impoundments (4,734–6,257-ha surface area) and numerous small impoundments are spread throughout this region.

Fish Data

Our analysis was based on 150 fish collections taken by the Kansas Department of Wildlife and Parks (KDWP) between September 1995 and August 2000. Fifty-three fish species were captured, 41 of which occurred at six or more sites. The frequency of occurrence across sites for these species ranged from less than 1.0% to 96% (mean 36%; Table 1). Included in these collections were four species that have been identified as being of special conservation concern in Kansas: Topeka shiner *Notropis topeka*, southern redbelly dace *Phoxinus erythrogaster*, common shiner *Luxilus cornutus*, and Johnny darter *Etheostoma nigrum*

(Haslouer et al. 2005). The KDWP sampling followed the protocol of Lazorchak et al. (1998); at each site a reach that was 40 times the average wetted width of the stream (minimum 150 m, maximum 300 m) was sampled using a combination of straight and bag seines (4.7-mm mesh) and DC-pulsed backpack electrofishing.

Environmental Variables

Predictive modeling was conducted using habitat measurements taken at three spatial scales (sites, reaches, and catchments; Table 2). Habitat variables included in our analysis were those that were available for the entire region and that we considered to potentially influence stream fish assemblages, based on a review of pertinent literature and personal observations. Habitat measured at field sites included the length of stream from which fish were sampled (i.e., between

Table 1. Common and scientific names of fishes, species codes, and number of sample sites occupied by each species in the Kansas River basin.

Species	Scientific name	Species code	Number of sites occupied
Black bullhead	<i>Ameiurus melas</i>	AMEMEL	54
Yellow bullhead	<i>A. natalis</i>	AMENAT	78
Freshwater drum	<i>Aplodinotus grunniens</i>	APLGRU	17
Central stoneroller	<i>Campostoma anomalum</i>	CAMANO	124
River carpsucker	<i>Carpionodes carpio</i>	CARCAR	54
White sucker	<i>Catostomus commersonii</i>	CATCOM	61
Red shiner	<i>Cyprinella lutrensis</i>	CYPLUT	144
Common carp	<i>Cyprinus carpio</i>	CYPCAR	54
Gizzard shad	<i>Dorosoma cepedianum</i>	DORCEP	22
Johnny darter	<i>Etheostoma nigrum</i>	ETHNIG	32
Orangethroat darter	<i>E. spectabilis</i>	ETHSPE	91
Western mosquitofish	<i>Gambusia affinis</i>	GAMAFF	10
Channel catfish	<i>Ictalurus punctatus</i>	ICTPUN	88
Smallmouth buffalo	<i>Ictiobus bubalus</i>	ICTBUB	8
Longnose gar	<i>Lepisosteus osseus</i>	LEPOSS	21
Green sunfish	<i>Lepomis cyanellus</i>	LEPCYA	138
Orangespotted sunfish	<i>L. humilis</i>	LEPHUM	48
Bluegill	<i>L. macrochirus</i>	LEPMAC	67
Longear sunfish	<i>L. megalotis</i>	LEPMEG	34
Common shiner	<i>Luxilus cornutus</i>	LUXCOR	50
Redfin shiner	<i>Lythrurus umbratilis</i>	LYTUMB	38
Largemouth bass	<i>Micropterus salmoides</i>	MICSAL	86
White bass	<i>Morone chrysops</i>	MORCHR	6
Golden redhorse	<i>Moxostoma erythrum</i>	MOXERY	12
Shortnose redhorse	<i>M. macrolepidotum</i>	MOXMAC	28
Golden shiner	<i>Notemigonus crysoleucas</i>	NOTCRY	19
Bigmouth shiner	<i>Notropis dorsalis</i>	NOTDOR	15
Rosyface shiner	<i>N. rubellus</i>	NOTRUB	16
Sand shiner	<i>N. stramineus</i>	NOTSTR	110
Topeka shiner	<i>N. topeka</i>	NOTTOP	8
Slender madtom	<i>Noturus exilis</i>	NOTEXI	46
Stonecat	<i>N. flavus</i>	NOTFLA	57
Logperch	<i>Percina caprodes</i>	PERCAP	27
Suckermouth minnow	<i>Phenacobius mirabilis</i>	PHEMIR	111
Southern redbelly dace	<i>Phoxinus erythrogaster</i>	PHOERY	14
Bluntnose minnow	<i>Pimephales notatus</i>	PIMNOT	120
Fathead minnow	<i>P. promelas</i>	PIMPRO	105
Bullhead minnow	<i>P. vigilax</i>	PIMVIG	13
White crappie	<i>Pomoxis annularis</i>	POMANN	27
Flathead catfish	<i>Pylodictis olivaris</i>	PYLOLI	30
Creek chub	<i>Semotilus atromaculatus</i>	SEMATR	119

150 m and 300 m). Channel width, bank angle, and canopy cover (based on densiometer reading) were measured at 11 equally spaced transects along the site. Depth and substrate size were measured at 5 points along each of these transects. All values were averaged for each site. In addition, we measured discharge, specific con-

ductance, turbidity, total dissolved solids, nitrate, ammonia, and phosphorus.

A stream reach was defined as a stream course from its upstream confluence to its downstream confluence with other tributaries (mean length = 1.6 km). Landscape-scale habitat variables were quantified for each reach and were chosen to

Table 2. Reference codes and descriptions of habitat variables measured at three different spatial scales (catchment, reach, and site) in the Kansas River basin. Variable loadings and percent variance explained is given for the first four axes of principal component analyses to summarize variation in measurements across sites.

Reference code	Variable description	PCA1	PCA2	PCA3	PCA4
Catchment		28.4%	22.5%	12.6%	9.1%
CmtAREA	Catchment area (km ²)	0.026	-0.127	0.351	0.367
Density	Stream density (km/km ²)	0.072	-0.321	-0.187	-0.004
Slope	Field slope (%)	-0.375	0.138	0.008	0.127
WTDEP	Water table depth (m)	-0.339	-0.215	0.277	0.161
KFACT	Soil erodibility factor (tons/unit of rainfall erosion index)	0.363	-0.156	-0.062	-0.121
PERM	Soil permeability (cm/h)	-0.032	-0.209	0.584	0.162
BD	Bulk density of soils (g/cm ³)	0.072	0.388	-0.299	0.260
OM	Organic matter content of soils (% by weight)	-0.291	0.252	-0.173	0.284
TFACT	Soil loss tolerance factor (tons/acre/year)	0.370	-0.056	0.155	0.256
WEG	Wind erosion group	-0.164	-0.060	0.056	-0.654
Urban	Urban land	0.132	0.132	0.275	-0.210
Forest_u	Forested land	0.104	0.389	0.298	-0.124
Grasslan	Grassland	-0.435	-0.085	-0.070	0.107
Pasture	Pasture	0.198	0.358	0.050	0.128
Sm_grain	Small grain	0.302	-0.271	-0.198	0.228
Wetlands	Wetlands	0.069	0.386	0.251	-0.050
Reach		21.1%	14.3%	11.0%	9.9%
Res_dist	Downstream distance to the nearest reservoir (km)	0.052	0.244	-0.260	0.341
STRAHLER	Strahler order of stream segment	0.401	0.129	0.168	0.007
DOWNORD	Strahler order of downstream segment	0.384	0.224	-0.030	-0.212
MAX_ELEV	Maximum elevation of the stream segment (m)	-0.132	0.419	-0.049	0.361
Clay_loa	NRCS soil texture class clay loam in the stream segment	-0.241	0.218	-0.318	-0.234
Silty_cl	NRCS soil texture class silty clay in the stream segment	0.162	-0.483	-0.222	0.088
Siltyclo	NRCS soil texture class silty clay loam in the stream segment	-0.145	0.113	0.502	0.199
Silt_loa	NRCS soil texture class silty loam in the stream segment	0.232	0.255	-0.060	0.129
Sandy_lo	NRCS soil texture class sandy loam in the stream segment	0.072	-0.012	-0.015	-0.402
Loam	NRCS soil texture class loam in the stream segment	-0.041	-0.061	0.108	-0.308
Loamy_up	NRCS range site information, loamy upland	-0.113	0.124	0.274	-0.329
Loamy_lo	NRCS range site information, loamy lowland	0.308	-0.302	-0.205	0.300
Clay_up	NRCS range site information, clay upland	-0.243	0.254	-0.331	-0.016
Limy_up	NRCS range site information, limy upland	-0.099	0.001	0.381	0.158
Clay_lo	NRCS range site information, clay lowland	0.036	0.061	0.105	-0.025
Cenozoic	Presence of Cenozoic soils in the segment	0.150	0.339	-0.045	0.035
Sinuosity	Sinuosity (km/km)	0.047	-0.066	0.271	0.172
Site		20.1%	18.2%	12.7%	9.7%
Mean_sub	Mean substrate size	-0.342	0.161	0.021	0.339
Brk_angl	Bank angle (degrees)	-0.011	0.306	0.130	0.312
Canopy	Percent canopy cover (%)	-0.178	0.215	-0.063	0.591
Mean_dep	Mean depth (m)	-0.074	0.520	0.084	-0.047
Mean_wid	Mean width (m)	-0.041	0.534	-0.068	-0.272
Discharge	Discharge (L/s)	0.160	0.470	0.084	-0.306
Cond	Conductivity (isiemens/cm)	-0.146	0.043	0.636	-0.064
Turb	Turbidity (NTU)	0.473	0.144	-0.105	0.157
Alkil	Alkalinity (mg/L)	-0.194	-0.084	0.550	0.108
Chlor	Chlorides (mg/L)	0.332	0.060	0.105	-0.117
Ammonia	Ammonia (mg/L)	0.391	-0.113	0.227	0.102
Nitrate	Nitrate (mg/L)	0.368	0.106	-0.107	0.444
Phos	Phosphorous (mg/L)	0.371	-0.030	0.411	0.085

represent factors linked to fish-assemblage structure, including stream size and position in the watershed (Sheldon 1968; Osborne and Wiley 1992; Zorn et al. 2002) and surface geology of the reach (Matthews and Robison 1988; Nelson et al. 1992; Mandrak 1995). Measures of stream size and position were calculated from a modified version of the national hydrography data set (USGS 1997). Surficial geology of the reach was based on soil measurements obtained from the STATSGO database (NRCS 1994). Environmental variables were classified at the stream-reach scale for use in modeling with ArcMap version 8.2 software and methods described in Maidment (2002).

Catchment area was calculated using a GIS. Catchment-scale soil factors, land use, stream density, and basin slope were extracted from available data layers for the region. As above, soil variables were obtained from the STATSGO database (NRCS 1994) and land use was calculated from the national land cover data set (USGS 1992), which contains 21 categories at a resolution of 30 m².

Statistical Analyses

Concordance of habitat measurements across spatial scales.—Prior to analysis, all habitat measurements were evaluated for normality, and appropriate transformations were applied to reduce heterogeneity of variances and the effects of outliers. Associations among variables were evaluated prior to modeling and those exhibiting a high degree of concordance (i.e., Pearson correlation, $r > 0.70$) were eliminated to reduce multicollinearity in the data set. Of the highly correlated variables, we retained those expected to be most closely associated with assemblage structure based on previous research in this system (Oakes et al. 2005). To evaluate correlations of the remaining habitat measurements across spatial scales we first conducted a principal components analyses (PCA) to summarize variation in habitat measurements across sites for each of the three spatial scales. For these analyses, all vari-

ables were centered and standardized to a standard deviation of one and mean of zero. Next, to characterize the association of environmental variables across spatial scales, we used a Procrustean analysis (PROTEST) to test for congruence among PCA scores from the analysis of habitat measurements from different scales. PROTEST is similar to the Mantel test and is equal in power for comparing matrices with no correlation between or within them and more powerful in comparing correlated matrices (Peres-Neto and Jackson 2001). The PROTEST analysis provided a graphical relationship of two matrices and a residual error value between paired observations. The matrices were matched by translating both matrices to a common centroid and then rotating and dilating one configuration to match the other configuration and minimize the sum of the squared deviations between landmarks (the deviations between landmarks were vector residuals). A small vector residual indicates a close agreement between the corresponding landmarks. The measure of fit (m^2) was based on the sum of the squared deviations (Gower 1971). To test if the original m^2 was smaller than expected due to chance, the observed m^2 was compared to 9,999 permutations using PROTEST. To test for correlations in habitat measurements across spatial scales, we used PROTEST to perform pair-wise comparisons of PCA scores for habitat measurements taken at the scale of catchments, reaches, and field sites. All comparisons were based on the first four axes of the PCA.

Predicting individual species occurrences.—We used discriminant function analysis (DFA), which uses linear combinations of predictor variables to maximize the separation between groups (i.e., presence and absence) to test the association between habitat variables and species occurrences. Discriminant function analysis is expected to perform similar to logistic regression when parametric assumptions are met (Efron 1975) and therefore is representative of traditional, parametric approaches in general. Discriminant function analysis has been used in

ecological studies of fishes (e.g., Joy and Death 2002) but is constrained by the assumptions of linear relationships among variables (e.g., Olden and Jackson 2002). Nevertheless, previous comparisons of several modeling techniques, including DFA, classification trees, and artificial neural networks, revealed only slight differences among these approaches (Olden and Jackson 2002; K.B. Gido, Kansas State University, unpublished data). Thus, we chose DFA because of the availability of a stepwise selection procedure to eliminate variables that were redundant or explained a small amount of variation in species occurrences. For these analyses, variables with partial correlation coefficients with P -values greater than 0.05 were entered and those with P less than 0.10 were removed. Because this stepwise procedure requires multiple tests, it is likely to include superfluous variables in the model (Legendre and Legendre 1998). However, because we were primarily interested in forecasting species occurrences, and secondarily interested in variable importance, we did not correct for this error (e.g., with a Bonferroni correction) in order to maximize the predictive ability of our models. Within-group covariance matrices were used and prior probabilities were computed from group sizes (i.e., species prevalence). Model effectiveness was assessed by our ability to correctly classify species presence or absence across the 150 sites. All error rates were expressed as percentages. For all model predictions a decision threshold of 0.5 was used to classify a species as present or absent. All models were generated using SPSS, version 11.0. To evaluate the predictive power of independent variables, we tallied the number of individual species models that included each habitat variable.

Individual species models were evaluated using a jackknife procedure, in which one site was excluded, a model was constructed using $n - 1$ sites, and the excluded site was predicted using this model. This procedure was repeated for each of the 150 sites to give a prediction matrix that was compared to the actual occurrences of each species to give error rates across sites.

Predicting assemblages.—Fish-assemblage structure was characterized by both indirect and direct gradient analysis. Correspondence analysis (CA) is an indirect gradient analysis that was used to characterize the variation among fish samples without the constraint of measured environmental gradients. Canonical correspondence analysis (CCA) also ordinales samples and species, but under the constraint of the measured habitat features at the different spatial scales. These methods were chosen over linear-based approaches (e.g., principle components analysis and redundancy analysis) because of the large environmental gradients across our study area and predicted monotonic relationships between species occurrences and habitat measurements (Legendre and Legendre 1998). Because these two methods use the same algorithm to ordinate samples, the total inertia (variance) from both approaches can be directly compared to evaluate how well our environmental variables explained variability in the fish assemblage across sample sites. In addition, we were able to partition variation based on habitat measures at the three spatial scales by including different subsets of our data as covariables and evaluating the residual variation explained by the remaining data (Borcard et al. 1992). Thus, we estimated the percent variability explained by habitat variables taken at each of the three spatial scales and the interactions among these variables following the method of Anderson and Gribble (1998). Eigenvalues and site scores for CCA were calculated using CANOCO software, version 4.5 (ter Braak and Smilauer 2002). A forward selection procedure was used to select a subset of variables that significantly contributed to the variation in the species data for each scale of analysis. In sequential steps, each variable that explained the greatest amount of added variation to the model was included in a Monte Carlo permutation test (1,000 iterations) to evaluate if that variable explained a significant proportion of the species data. To correct for the inflated type I error rate associated with this multiple selection procedure, a Bonferroni adjusted alpha was used to select

variables for inclusion in the CCA. Once a variable failed to explain a significant proportion of the variation, no additional variables were added to the model.

RESULTS

Concordance of Habitat Measurements across Spatial Scales

Several highly correlated ($r > 0.70$) variables were removed from the analysis; 16 of 23, 17 of 21, and 13 of 13 variables were retained for catchment-, reach-, and site-scale habitat measurements. Principal component analyses of the remaining habitat measurements at the three spatial scales summarized the majority of variation (between 56% and 73%) across sites on the first four axes (Table 2). Variation in habitat measurements among sites at the catchment scale was primarily attributed to soil variables (soil loss tolerance factor [TFACT], soil erodibility factor [KFACT], and catchment slope), and secondarily to land use and stream density. Variation in habitat measurements across sites at the reach scale was primarily due to variables associated with stream size (stream order) and secondarily by soil factors and elevation. Of the variables measured at the field sites, water quality parameters (turbidity, ammonia, and phosphorus) were negatively associated with mean substrate size, and a secondary axis was weighted by measures of stream size (mean width, depth, and discharge).

Procrustean analysis revealed highly significant concordance in the relative position of sample scores on the first four PCA axes based on habitat measurements taken at the three different scales. The strongest association occurred between ordinations of reach and site habitat variables ($m^2 = 0.803$, $P < 0.001$) and the weakest between ordination of catchment and reach variables ($m^2 = 0.634$, $P < 0.001$). The association between ordinations based on catchment and site habitat measurements also was quite high ($m^2 = 0.799$, $P < 0.001$).

Predicting Individual Species Occurrences

As expected, total classification error across species generally declined as habitat measurements from finer spatial scales were introduced into DFA models (Figure 2). However, these differences were minor, as classification error only decreased, on average, approximately 1% for each added group of habitat variables; 26.6%, 25.1%, and 24.0% for catchment, catchment + reach, and catchment + reach + site models, respectively.

An analysis of variable importance from DFA models showed that variables representing geology and stream size were generally important in predicting the occurrences of fish species in the Kansas River basin. KFACT was selected in 13 of the 41 species models, regardless of whether reach or site variables were included in individual DFA models (Figure 3). Catchment area, however, was notably more important when only catchment variables were included in individual species DFA models (included in 25 of 41 models) than when combined with reach (13 of 41 models) or reach and site (6 of 41 models) variables. This was likely because habitat variables at finer spatial scales (e.g., stream order and mean width) were correlated with catchment area and were selected to replace catchment area in the stepwise selection. No single variable was selected for more than one-third of the species models, when habitat information from all three spatial scales was included. Of the reach habitat variables, stream order (of the downstream reach), sinuosity, and geology (percent sandy loam and Cenozoic) were most frequently included in the species models. Mean width was the most commonly selected site variable but was only selected for 10 of 41 species models.

Predicting Assemblages

Correspondence analysis explained approximately 40% of the variation in species composition on the first four axes. The first axis, which explained 16% of the variation in fish-assemblage structure across sites contrasted sites with

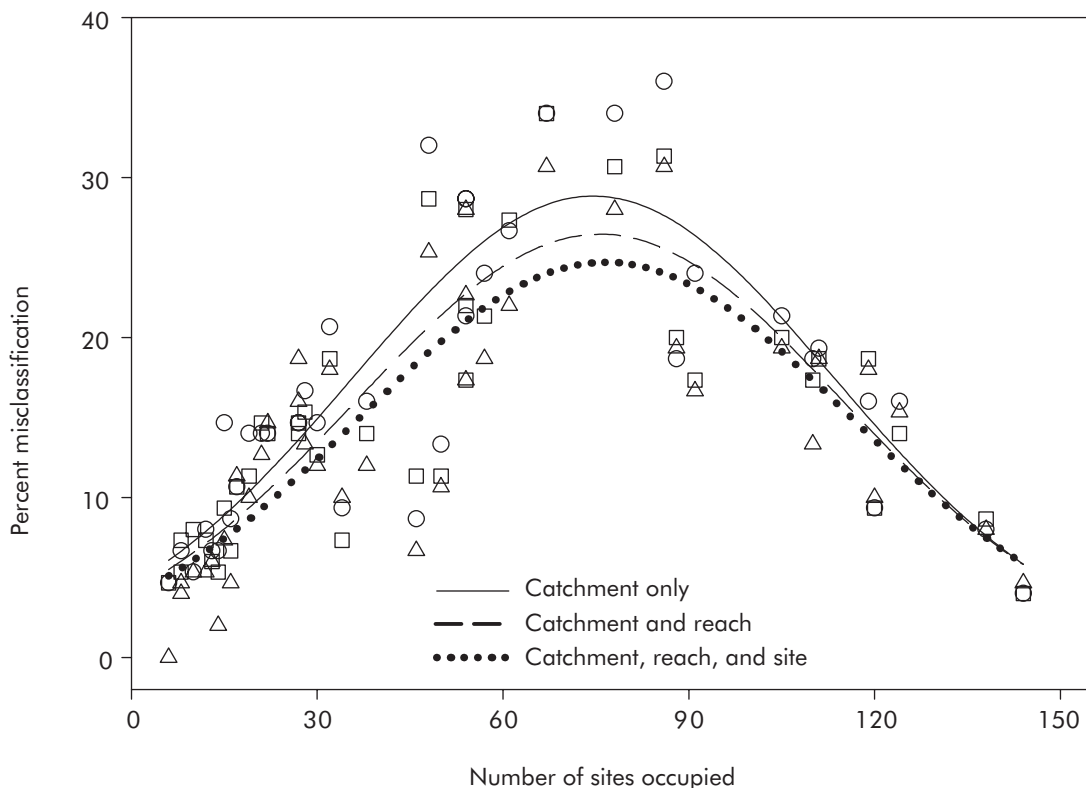


Figure 2. Cross-validated total error rates for discriminant function models that predicted the occurrence of 41 fish species in the Kansas River basin. Each regression line was fit to a three-parameter Gaussian curve to compare the relationship between model error rate and abundance among models that include habitat measurements from increasingly finer spatial scales (catchment, reach, and site, respectively). Circles are models with only catchment variables, squares are models with catchment and reach variables, and triangles are models with catchment, reach, and site variables.

species typical of small, clear-water streams (e.g., southern redbelly dace) with those typical of mid-sized streams to large rivers (Figure 4). The second axis appeared to separate species that occur in mid-sized streams (bullheads *Amiurus* spp.) with those that typically occur in large, sand-bottom rivers (e.g., white bass *Morone chrysops* and longnose gar *Lepisosteus osseus*).

Canonical correspondence analysis, constrained by environmental variables, explained over half the variability in fish-assemblage structure that was explained by the unconstrained ordination (CA). Percent variation explained by the first four axes of the CCA increased as variables from finer spatial scales were included in the analysis. The CCA explained 27.4%, 29.5%,

and 31.6% of the variation in fish-assemblage structure based on the inclusion of catchment, catchment + reach, and catchment + reach + site variables, respectively. Thus, less than 3% of the variation in fish-assemblage structure was explained with the addition of habitat measurements from field sites. Fish-assemblage structure along the first axis of the CCA, which only included catchment-scale habitat measurements, was primarily associated with catchment geology (KFACT) and organic content of soils (OM) (Figure 5), whereas the second axis was related to catchment area and catchment geology (TFACT). When habitat measurements from reaches were included in the analysis, several soil factors (Cenozoic and Clay upland) and

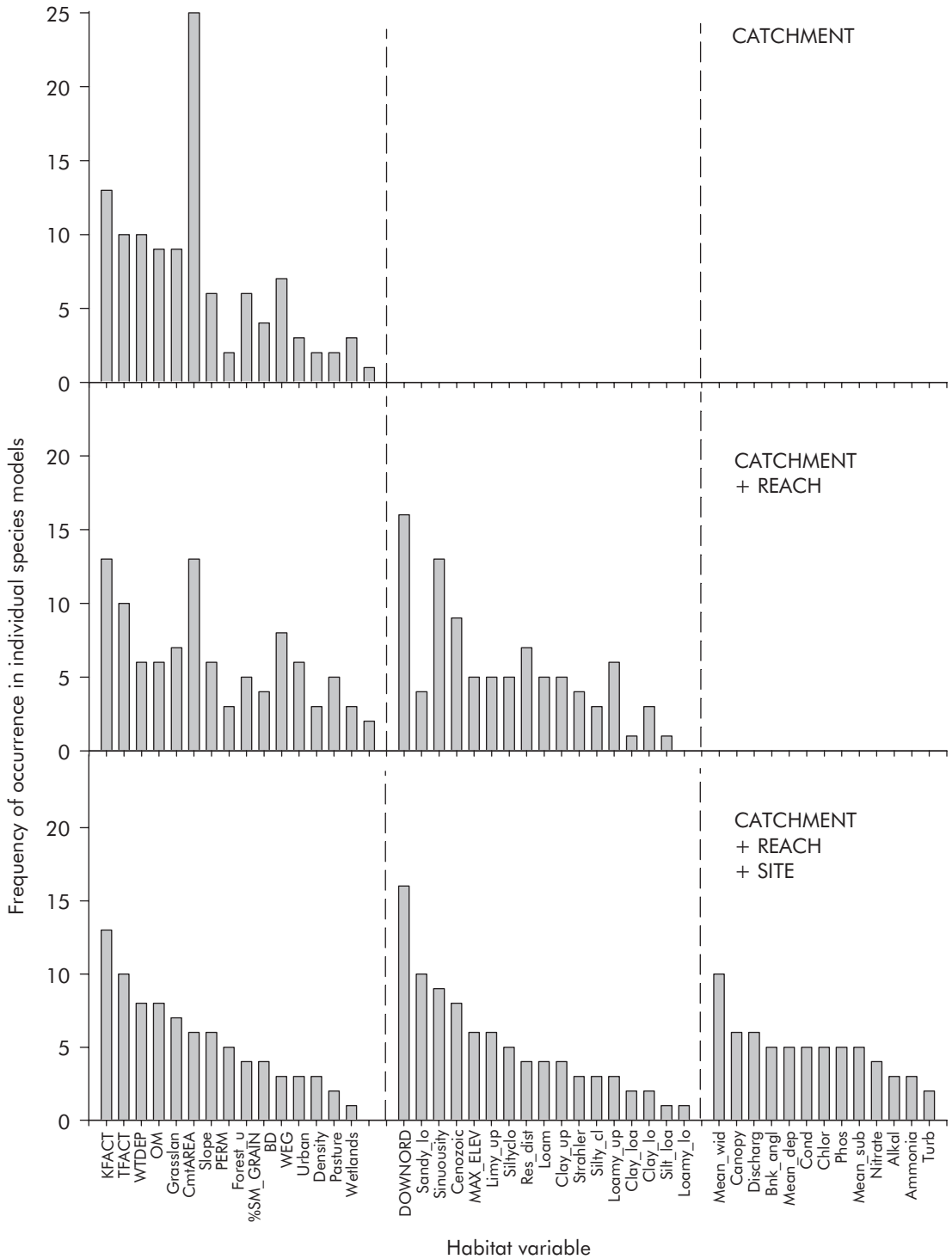


Figure 3. Number of species models for which each habitat variable was selected in a stepwise discriminant function analysis to predict its occurrence across the 150 sample locations in the Kansas River basin. Reference codes as in Table 2.

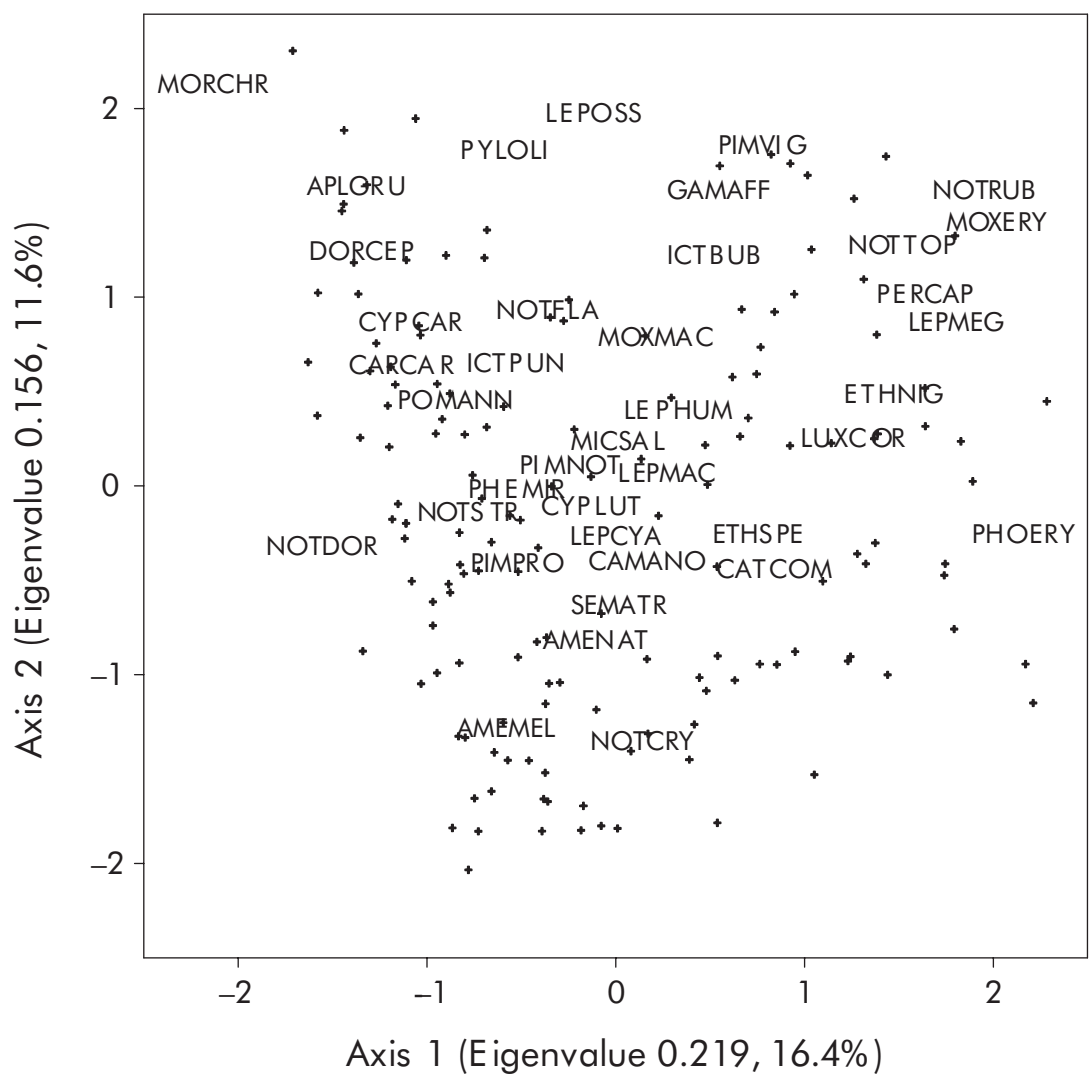


Figure 4. Site and species scores from the first two axes of a correspondence analysis that summarized variation in the fish assemblage structure across 150 sample sites in the Kansas River basin. Eigenvalues and percent variance in fish assemblage structure explained are given for each axis. Species codes as in Table 1.

sinuosity were included in the ordination (Figure 6) without the loss of major variables from the ordination of catchment-only variables. When habitat measurements from all spatial scales were added, the importance of water table depth along the first axis declined, and mean width and depth were included with catchment area as an important gradient along the second axis (Figure 7).

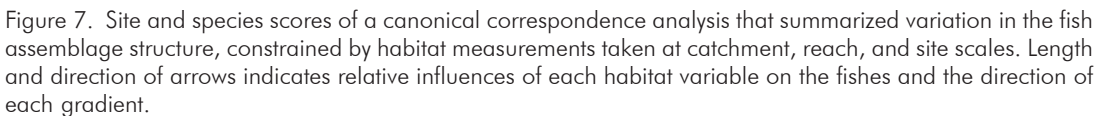
A partial CCA that evaluated residual variation attributed to “pure” effects of variables from the three spatial scales illustrated the strong interaction among habitats measured at different scales (Figure 8). When using reach- and site-scale habitat variables as covariates, catchment variables explained 8.8% and reach-scale variables explained 6.4% of the variability in the CCA



that included habitat variables from all spatial scales. Variables measured at field sites explained 6.2% of the variation in fish-assemblage structure explained by the full CCA. The percent variation attributed to the interaction of all three variables (10.2%) was also quite large because of the high degree of correlation among habitat measurements taken at different spatial scales.

DISCUSSION

Most of the variation in fish-assemblage structure and in individual species occurrences could be explained by environmental factors that were quantified using GIS-derived habitat measurements at the scale of catchments and reaches. However, because of the hierarchical nature of



in species occurrences that was explained by variables measured at field sites.

Variables associated with stream size were important predictors of individual species as well as assemblage structure. This was not surprising given the tendency for fish assemblages (Huet 1959; Schlosser 1987; Edds 1993) and ecosystem processes (Vannote et al. 1980) to change longitudinally in river systems. Also, this study included a wide range of stream sizes across sample sites. Because habitat variables

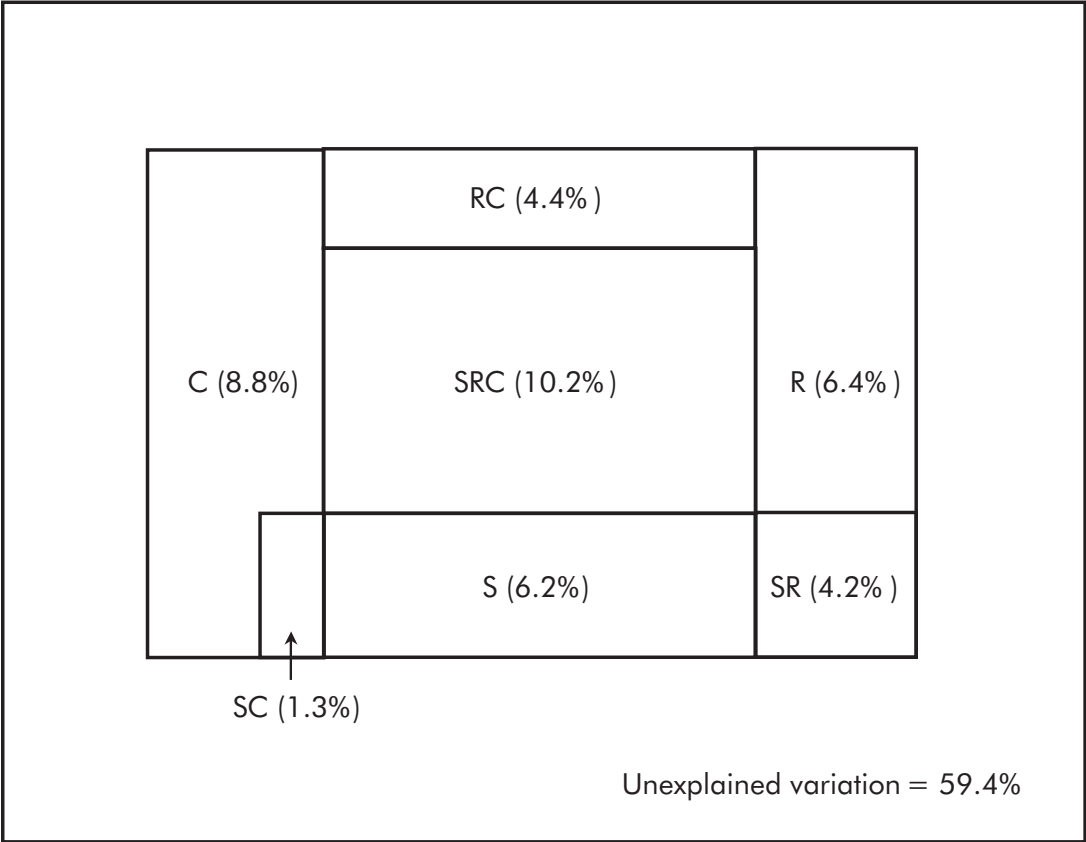


Figure 8. Venn diagram illustrating variance partitioning in a CCA of habitat measurements that explain fish-assemblage structure across 150 sample sites in the Kansas River basin. Block sizes are proportional to the percent variation explained by site (S), reach (R), and catchment (C) scale habitat measurements as well as all possible interactions among those variables.

that were representative of stream size occurred at all three spatial scales (e.g., catchment area, stream order, and stream width), it was hard to evaluate the relative predictive ability of the different measurements. Whereas large rivers have unique reach-scale habitats, such as braided channels, turbid water, fine substrates, and reduced variability in flows, catchment-scale habitats of large rivers also contain complex stream networks and a greater degree of habitat heterogeneity than small catchments. Reach habitats in large rivers should favor generalist, water column, and predatory species (e.g., red shiner and channel catfish) that may require a diversity of habitats throughout their life cycles. Alterna-

tively, smaller tributary streams with flashy flows and reduced turbidity were dominated by benthic-feeding herbivorous and insectivorous fish such as central stoneroller *Campestris anomalum* and orangethroat darter *Etheostoma spectabile*. An evaluation of how individual species with different life history traits respond to habitat measurements taken at different spatial scales would help partition the relative influence of stream size in determining species distributions.

Although stream size was an important predictor of fish-assemblage structure, soil factors were of equal or greater importance for many species. For example, KFACT, which is a measure of

soil erodeability, averaged over each catchment was of considerable importance for both individual species and assemblage modeling. In our study area, such soil variables separated high gradient streams flowing through terraced limestone and shale layers from streams with low gradient, high turbidity that flowed through highly erodible soils. This is consistent with previous studies in the Big Blue River basin that show fish assemblages are separated based on three dominant substrate types (mud, gravel, and sand; Minckley 1959; Gido et al. 2002). In addition, catchments with porous soils and steep slopes should also have a higher degree of groundwater input and less variable flow regimes (e.g., Baker et al. 2003). Thus, species that typically occupy spring-fed stream reaches with stable hydrologic regimes should respond to these geologic factors. This is illustrated by the inverse relationship between KFACT and the occurrences of southern redbelly dace, which typically occupy headwater springs (Cross 1967; Figures 6 and 7).

It is informative to learn that adding site habitat measurements to models with habitat measurements from broader spatial scales adds little to our ability to predict species occurrences, particularly because broad-scale habitat measurements are relatively easy to capture using data layers from a GIS. However, because landscape features may be surrogates for local-scale phenomena (Wall et al. 2004), it is often necessary to identify local-scale habitat conditions to understand the mechanistic response of fish assemblages along these gradients. For example, feeding and reproduction of two darter species evaluated in this study (orangethroat darter and Johnny darter) are closely linked to coarse substrates (Cross 1967). However, in our DFA models, geologic (KFACT) and landcover (percent grassland) variables were selected as important predictors of their occurrences, rather than substrate size. Thus, even though coarse substrates are required for the survival of this species, other habitat variables that may covary with substrate

size or that reflect other important habitat features appear to be equally important.

Alternatively, habitat data averaged across a field site may be poor predictors of fish-assemblage composition. In particular, averaging habitat measurements such as substrate size and stream depth may not adequately reflect important meso- or microhabitats required by particular fish species. Rather, fishes may respond to smaller habitat patches, such as deep pools or riffle characteristics. There are also a number of habitat features that were not quantified in our sampling such as the occurrence of large woody debris, which is known to influence the abundance of stream fishes (Angermeier and Karr 1984). Perhaps a more thorough quantification of mesohabitats would have increased our predictive ability. Nevertheless, to identify the utility of habitat measurements at finer spatial scales, it would be necessary to divide field sites into smaller spatial units (i.e., local habitat units) in order to partition variation attributed to variables measured at these fine spatial scales.

Spatial extent of sampling influences the relative importance of variables measured at different spatial scales (Roth et al. 1996). Because of the large spatial extent of this study, it is possible the inclusion of soil factors simply reflected zoogeographic barriers among catchments. For example, bigmouth shiner *Notropis dorsalis* was primarily captured in the Delaware River basin, and results from both the CCA and DFA indicated that soil erodibility (KFACT) was an important predictor of its occurrence. Although there is potentially unique habitat in the Delaware River basin, bigmouth shiner may simply be isolated in this system and have not dispersed to other regions within our study area. Thus, the relatively high importance of catchment-scale habitat measurements could be due to the characterization of zoogeographic boundaries.

In conclusion, our ability to predict fish-assemblage structure in the Kansas River basin did not notably improve with the addition of site-scale habitat measurements. These findings are consistent with recent studies (e.g., Roth et al.

1996; Poff 1997; Wang et al. 2001; Joy and Death 2004) that indicate landscape features exhibit important constraints on the distribution of fishes. Moreover, predictive modeling for conservation of aquatic systems, such as in Gap Analysis (e.g., Sowa et al. 2004; Wall et al. 2004), may not require intensive site-scale habitat quantification. Nevertheless, field habitat measurements provide a mechanistic understanding of species–habitat relationships that contribute to a better understanding of large-scale problems (Poff 1997; Park et al. 2003). We suggest that further research on the linkages between habitats across spatial scales will likely improve our understanding of species–environment relationships across spatial scales.

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Habitat, Land Use, and Fish Assemblage Relationships in Iowa Streams: Preliminary Assessment in an Agricultural Landscape

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Abstract.—Iowa leads the nation in percentage of land area converted to cropland, with a resulting negative impact on streams. We examined physical habitat, land use, and fish assemblage data from 37 second- to sixth-order stream sites, representing 7 of the 10 ecoregions within Iowa. Physical habitat conditions varied widely among sites, with sand dominating substrate composition. A nonmetric multidimensional scaling ordination of physical habitat variables suggested a pattern of among-site similarities defined by a stream size axis, an axis contrasting sites dominated by either woody or rocky fish cover, and an axis characterizing degree of riparian canopy coverage. Bluntnose minnow *Pimephales notatus* and sand shiner *Notropis stramineus* were the most abundant fish species, followed by green sunfish *Lepomis cyanellus* and common carp *Cyprinus carpio*. These four species were collected in more than 80% of the sites. Fish species richness at sites averaged 22, ranging from 6 to 38, and fish index of biotic integrity (IBI) at sites averaged 47 (fair), ranging from 21 (poor) to 96 (excellent). Species richness and IBI were highest at sites characterized by rocky fish cover and relatively coarse substrates. Values for several physical habitat and land use variables were significantly different between sites with $IBI \leq 30$ (fair) and sites with $IBI \geq 50$ (good). We found a general pattern of IBI, species richness, total fish abundance, and width-to-depth ratio decreasing from the northeast to the southwest ecoregions, and percentage of unvegetated banks and bank slope increasing from northeast to southwest. Stable and vegetated banks, wide stream channels with coarse substrates, and rocky fish cover were associated with high biotic condition; while unvegetated and eroding banks, and deep channels with predominantly fine substrates were associated with lower biotic condition. Land use was calculated at three spatial scales: catchment, network riparian buffer, and local riparian buffer. We found few relationships of fish assemblages with land use, potentially due to sampling design and the pervasiveness of agriculture across Iowa. There is substantial variation among physical habitat, land use, and fish assemblage conditions across Iowa, due to a combination of geology, climate, zoogeography, and human alteration.

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INTRODUCTION

Iowa streams have been drastically altered, primarily due to land use changes associated with agriculture (Bulkley 1975; Menzel 1981, 1983). Iowa leads the nation, with 72% of land area converted to cropland (Natural Resources Conservation Service 2000). Combined with pastureland (10%) and developed land (5%), 87% of Iowa's land area is altered by either agriculture or urban development. Comparable figures for surrounding states are slightly lower for Illinois (84%) and much lower for Missouri (63%), Wisconsin (57%), Minnesota (53%), Nebraska (46%), and South Dakota (41%) (Natural Resources Conservation Service 2000). Agricultural impacts to streams are known to include modification of: habitat structure, water quality, flow regimes, energy patterns, and biotic community structure (Menzel 1983; Karr et al. 1985; Wang et al. 1997). Fish can be affected through reductions in feeding efficiency, growth, reproduction, and recruitment (Waters 1995; Stevenson and Mills 1999).

Sedimentation is one way agriculture has negatively affected Iowa streams (Waters 1995). Sedimentation is a direct consequence of pervasive agricultural land use in Iowa. Approximately 12,000 kg/ha/year of soil is eroded from one-third of Iowa's land, (Natural Resources Conservation Service 2000) and much of this eroded material enters streams (Menzel 1983; Waters 1995). Sedimentation often results in naturally diverse habitats being replaced with wider, shallower channels, decreased substrate size, decreased water velocity, and steep eroding streambanks, negatively affecting fish assemblages (Schumm 1977; Rosgen 1994; Waters 1995).

Efforts to drain land for agriculture have also altered Iowa streams (Menzel 1983). Within the last 150 years, tiling and ditching were used to drain 95% of Iowa's wetlands (Whitney 1994), resulting in the creation of artificial stream channels (Anderson 2000). In contrast, more than 4,800 km of streams have been lost due to channelization (Bulkley 1975), which results in

decreased habitat area and diversity (Waters 1995). Studies have linked channelization with increased gradient, current velocity, bank erosion, and sediment bedload (Bulkley 1975; Rosgen 1994), as well as decreased depth variation, velocity variation, and numbers and biomass of drifting invertebrates (Zimmer and Bachman 1976). Studies of fish assemblages in Iowa streams have linked habitat degradation and channelization to reduced abundance and diversity of fish species (Paragamian 1987, 1990a, 1990b; Wilton 2004). Low-head dams, removal of vegetative land cover, and point and nonpoint pollution have also altered Iowa's streams and fish assemblages (Menzel 1981; Paragamian 1987).

Landscape conditions are intimately related to stream conditions across a range of spatial scales from local to regional. At a local scale, well-vegetated banks with diverse plant assemblages provide erosion resistance, shade, allochthonous carbon inputs, woody debris, nutrient removal, reduction of overland flow, and fish refuge during flooding (Simonson et al. 1994a; Mills and Stevenson 1999; Stevenson and Mills 1999). At an intermediate scale forested riparian buffers have been positively related to habitat and fish index of biotic integrity (IBI; Wang et al. 1997; Lammert and Allan 1999). Catchment scale land uses have also been shown to influence habitat and biotic condition (Wang et al. 1997; Meixler 1999; Wang et al. 2003). In Midwestern streams, instream physical habitat quality and IBI scores were positively related to the amount of forest and negatively related to the amount of agriculture within a catchment (Roth et al. 1996; Allan et al. 1997; Wang et al. 1997). At a larger scale, agriculture and other alterations can lead to regional fish and physical habitat characteristics becoming less distinctive (Li and Reynolds 1994).

The question of which spatial scale reveals the strongest relationships among physical habitat, land use, and fish assemblages has attracted considerable interest. Of the studies that directly addressed this question, four reported stronger relationships at local scales (Lammert and Allan 1999; Stauffer et al. 2000; Nerbonne and

Vondracek 2001; Wang et al. 2003) and six reported stronger relationships at catchment-level scales (Steedman 1988; Roth et al. 1996; Wang et al. 1997; Fitzpatrick et al. 2001; Snyder et al. 2003; Van Sickle et al. 2004). The question of how landscapes are related to stream conditions across a range of land uses and geographical settings has profound implications for stream management and restoration.

Although Iowa is often perceived as having a flat, homogeneous landscape, terrestrial features and stream habitat conditions differ among Iowa's ecoregions (Menzel 1987; Paragamian 1990b; Griffith et al. 1994; Wilton 2004). Ecoregions are areas of relatively homogeneous soils, vegetation, climate, geology, physiography, and responses to degradation (Omernik 1987; Griffith et al. 1994). Most of Iowa falls within seven ecoregions: the Central Irregular Plains (CP), Des Moines Lobe (DL), Iowan Surface (IS), Loess Hills and Rolling Prairies (LH) Northwest Iowa Loess Prairies (NW), the Paleozoic Plateau (PP), and Southern Iowa Rolling Loess Prairies (SI). Previous research suggests there is an increase in percent fine substrates and decrease in percent forested riparian land cover and fish IBI scores from northeast Iowa to southern and western Iowa (Menzel 1987; Paragamian 1990b; Griffith et al. 1994; Wilton 2004). The PP region in northeast Iowa is described as having highest IBI scores, most topographical relief, most riparian forests, narrowest stream channels, and highest percentages of coarse substrates. The LH ecoregion in southwest Iowa is described as having lowest average IBI scores, silty substrates, highly eroding banks, turbid water, straightened channels, and numerous low-head dams and streambed stabilization structures. Compared with the PP and LH ecoregions, IBI scores and physical habitat conditions are intermediate in the rest of the state.

Our overall goal was a preliminary assessment of relationships among physical habitat, land use, and fish assemblages in streams throughout Iowa. We addressed this goal with three specific objectives. First, because Iowa's streams are of-

ten thought of as homogeneous, we sought to determine how physical habitat conditions varied among sites using a multivariate ordination. Second, we explored differences among ecoregions. We hypothesized that physical habitat, land use, and fish assemblage conditions would vary among ecoregions, along a gradient from northeastern Iowa to the southwest. Third, we determined which physical habitat and land use variables could distinguish sites with good or excellent IBI scores (≥ 50) from those with poor or fair scores (≤ 30). We hypothesized that this test would contrast less degraded landscape and physical habitat conditions typical of northeast Iowa with more degraded conditions in the southwest. We also hypothesized that regardless of ecoregion, sites with high amounts of agricultural land uses would be associated with lower IBI scores.

STUDY SITES

The physical habitat and fish assemblage data we examined for this study were collected by the Iowa Department of Natural Resources between July and September 1995–2001 as part of an ongoing inventory of Iowa's interior streams (Siegwarth 1998; Gelwicks 1999, 2000). Data were available from 37 sites on 32 second- to sixth-order streams, representing 7 of the 10 ecoregions in Iowa (Figure 1). Each site was sampled once. The number of sites within each ecoregion was variable, ranging from 1 in the PP to 12 in the IS. Most sites were at locations sampled during an earlier statewide fish inventory (Paragamian 1990b). Sites ranged from 145 to 2,566 m long, depending on width. Sampling occurred under base flow conditions.

METHODS

Data Collection

Physical habitat.—Instream and riparian physical habitat features were measured or visually estimated at sites (Table 1). Transect habitat

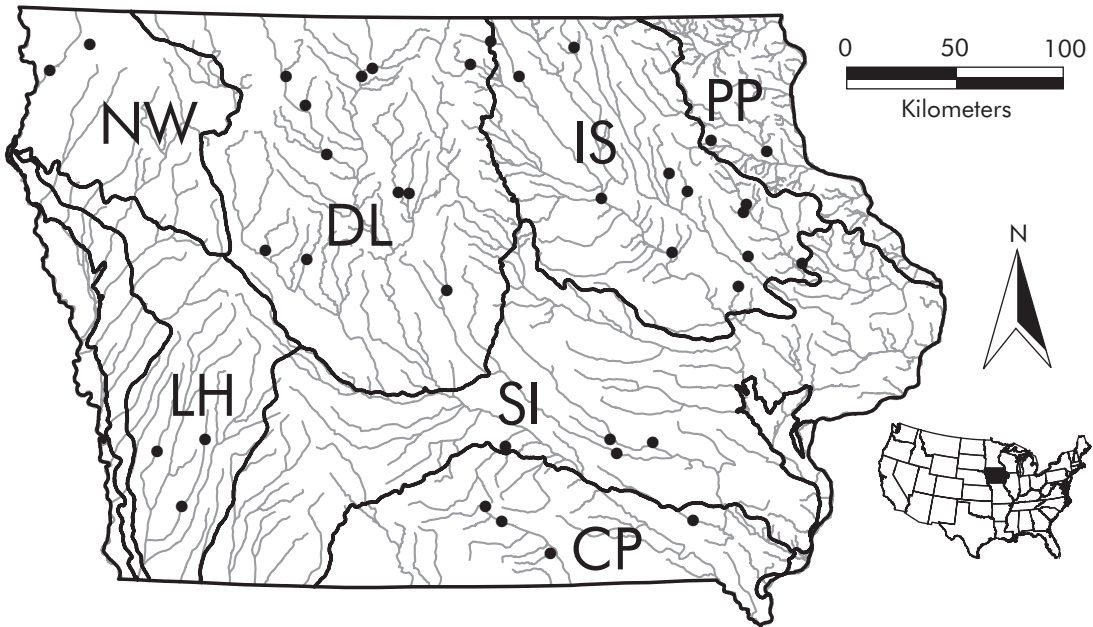


Figure 1. Locations of sampling sites within ecoregions in Iowa. Ecoregions are Central Irregular Plains (CP), Des Moines Lobe (DL), Iowa Surface (IS), Loess Hills and Rolling Prairies (LH), Northwest Iowa Loess Prairies (NW), Paleozoic Plateau (PP), and Southern Iowa Rolling Loess Prairies (SI). The number of sites in each ecoregion is PP (1), IS (12), NW (2), DL (11), SI (4), CP (4), and LH (3).

assessment procedures developed in adjacent states (Bovee 1982; Illinois EPA 1987; Simonson et al. 1994a, 1994b) were modified to accommodate both wadeable and unwadeable conditions, and available personnel and resources in Iowa. Instream physical habitat features were surveyed at transects, including depth, wetted width, current velocity, types and abundance of fish cover, and substrate (Table 1). Riparian features surveyed included bank type (e.g., cut eroding, sloping, undercut), slope, vegetation, canopy, and high water cover (from the water's edge to two vertical meters above the water level). Riparian and instream physical habitats were sampled along transects spaced two average stream widths apart (Simonson et al. 1994a). The number of transects ranged from 15 to 30; most sites had 20. Sites with 20 transects had a minimum of 420 measurements or visual estimates. Details of physical habitat assessment methods are given in Heitke (2002).

Fish assemblages.—Fish were collected using a single upstream electrofishing pass through the entire length of sites. A DC tow-barge electrofisher was used for most sites. A DC boat electrofisher was used for unwadeable habitats at six sites and a DC backpack shocker was used at one site too small for the tow-barge. An effort was made to collect all fish observed. Species, and wet weight (nearest 0.1 g) and length of captured fish (nearest millimeter) were recorded in the field. Most fish were returned to the stream alive. In nearly all cases fish sampling occurred the same day as physical habitat sampling.

Land use.—A GIS was used to determine land use percentages upstream of each site. Land use was calculated at three spatial scales: catchment, network buffer, and local buffer. Catchment land use included use percentages in entire catchments of sampling sites. Network-buffer land use included use percentages within 60 m riparian buffers of entire drainage networks

Table 1. Station descriptors and physical habitat variables used to characterize Iowa streams.

Variable	Average	SE	Description
Station descriptors			
Stream order	3.81	0.15	Strahler ranking of channel size
Drainage area	876.89	208.46	Drainage area (km ²)
Sinuosity	1.5	0.05	Ratio of 5,000-m segment of stream (centered on station) to the straight line distance between the start and end of the segment
Stream morphology			
Average stream width	17.3	1.63	Station average of stream width measurements taken at each transect (m)
Average stream width CV	23.08	1.16	Coefficient of variation of stream width measurements
Average depth	0.49	0.05	Average of depth measurements (m)
Average depth CV	52.96	2.02	Coefficient of variation of depth measurements
Width to depth ratio	50.09	4.38	Stream width divided by average depth for each transect, then averaged for station
Width to depth ratio CV	57.03	4.66	Coefficient of variation of width to depth ratios
Average velocity	0.22	0.03	Average of velocity measurements taken 0.4 of depth from the stream bottom (m/s)
Average velocity CV	79.09	9.8	Coefficient of variation of average velocity measurements
Substrate			
% clay	6.09	1.98	Substrate particles < 0.004 mm
% silt	13.72	2.34	Substrate particles 0.004–0.062 mm
% sand	54.22	3.97	Substrate particles 0.062–0.25 mm
% gravel	54.22	3.97	Substrate particles 2.0–64 mm
% cobble	12.3	2.01	Substrate particles 65–256 mm
% boulder	6.03	1.65	Substrate particles > 256 mm
% CPOM (coarse particulate organic matter)	2.75	0.58	Substrate of partially decayed coarse organic matter such as leaves, dead macrophytes, sticks, and so forth.
In-stream fish cover^a			
Cover types ^a	0.32	0.02	Average number of fish cover types per transect
Cover abundance ^a	2.04	0.22	Average number of fish cover units per transect
Rock cover ^b	1.06	0.23	Average number of rock fish cover units per transect
Wood cover ^c	0.82	0.13	Average number of wood fish cover units per transect
Riparian vegetation, bank condition and high water fish cover^d			
Vegetation types	2.72	0.1	Average number of vegetation types (trees, shrubs, forbs, grasses, etc.) per bank
% banks open	32.38	0.03	Percent of bank area with no vegetation
% banks with trees	28.08	0.04	Percent of transects with standing trees
% cut eroding banks	20.94	0.02	Percent of bank area classified as “eroding cutbank”: near vertical slope, no vegetation and evidence of erosion
Bank slope	37.11	1.5	Average bank slope (°)
% banks with canopy	33.63	0.04	Proportion of banks that shade stream channel when the sun is directly overhead
Average canopy	1.61	0.24	Average canopy per bank (m)
High water cover types ^d	0.42	0.03	Average number of high water fish cover types per transect
High water cover abundance ^d	2.46	0.28	Average number of high water fish cover units per transect
High water rock cover ^{b,c}	0.26	0.06	Average number of high water rock fish cover units per transect
High water wood cover ^{c,d}	1.85	0.26	Average number of high water wood fish cover units per transect

^a fish cover: Any object, channel feature, or bank feature that provides shelter from the current or visual isolation was considered to be fish cover (Simonson et al. 1994a). Instream cover categories included tree falls, submerged trees, root balls, log piles, debris dams, stumps, boulders, boulder fields, and rip rap fields.

^b rock cover: Bedrock outcropping, single boulders, and boulder aggregates; concrete, rip-rap were excluded.

^c wood cover: Logs, tree falls, partially submerged trees, submerged trees, standing trees in stream channel, overhanging trees, root balls, protruding bank roots, brush piles, debris dams, stumps.

^d high water fish cover: Fish cover that was above the water's surface but would have been submerged or partially submerged if the water level rose 2 m.

upstream of sites. Local buffer included 60 m riparian buffer land use located within a 1-km-diameter radius centered on sampling sites. The amount of land included in local buffer calculations was variable and depended on channel sinuosity; more sinuous stream segments had more buffer area included in radii than straighter segments. Shapefiles of the three land use scales were generated for each site and used to extract land use data. Land use data were clipped from the Iowa Land Cover 2000, Minnesota's 1990 Land Use and Cover, and South Dakota's National Land Cover Data (portions of some catchments extended into Minnesota and South Dakota). Four categories were used to summarize land uses: agriculture, grass (pasture and prairie), forest, and other.

DATA ANALYSIS

All variables were analyzed untransformed. The *P*-values of Shapiro-Wilk normality tests ranged from less than 0.0001 to 0.9448, while skewness ranged from -1.24 to 4.07. No single transformation applied to all variables yielded consistent improvements in normality and skewness. Since a mixture of transformations would have hindered interpretation, we left all variables untransformed for analysis. We believe that departures from normality were primarily due to small sample sizes rather than nonnormal distributions of physical habitat, land use, and fish conditions we measured. When summarized for 58 physical habitat sites (Heitke 2002) the normality and skewness of physical habitat variables improved. These additional physical habitat sites were not included in this analysis because they were not accompanied by fish samples.

Physical habitat.—Thirty-three variables were used to characterize physical habitat features of sites (Table 1). Instream physical habitat was characterized using stream morphology, substrate, and fish cover variables. Riparian physical habitat was characterized using bank vegetation, classification, slope, and canopy cover. Prior research suggested that these 33 vari-

ables characterized most of the variability, and encompassed the range of physical habitat conditions, among sites (Heitke 2002).

A nonmetric multidimensional scaling (MDS) ordination was used to examine physical habitat similarities among sites. Ordinations are commonly used in studies of this type to visualize physical habitat similarity based on a large number of variables (James and McCullach 1990; Paukert and Wittig 2002). Sites with similar values for physical habitat variables were plotted closer together, while sites with dissimilar values were plotted further apart. To generate the ordination we calculated pair-wise similarities between all physical habitat sites using normalized Euclidean distances of standardized variables (average of zero, standard deviation of one). Next, the resultant 37×37 similarity matrix was used as input for an MDS ordination. To assign axis labels to the ordination, we calculated Pearson correlations of MDS dimension scores with the original physical habitat variables. The strongest correlations revealed variables most associated with overall habitat similarities and differences among sites. The similarity matrix, MDS ordination, and dimension scores were generated using PRIMER (Clarke and Warwick 1994). Correlations were examined using SAS (SAS Institute Inc. 1999).

Fish assemblages.—Fish assemblages were characterized using IBI scores, number of species, number of individuals, trophic and tolerance guilds, catch rates (number of fish captured per 100 m), and percent occurrence. The IBI was based on Karr's (Karr et al. 1986) original index, but was calculated using the program developed and calibrated in Iowa (Wilton 2004). Scores could range from 0 to 100, with higher scores indicating healthier fish assemblages. Fish species were identified as being tolerant, intermediate, or sensitive to degradation. Species were also grouped into one of 7 trophic guilds: benthic invertivore, filter feeder, invertivore/carnivore, herbivore, invertivore, omnivore, or top carnivore.

Physical habitat, land use and fish assemblage relationships.—We examined relationships

between stream physical habitat, land use, and fish assemblage data using analysis of variances and *t*-tests. ANOVAs were used to determine ecoregional differences of physical habitat, land use, and fish assemblages. If the main effect (ecoregion) was significant, pair-wise comparisons among ecoregions were performed using the Tukey-Kramer test. *T*-tests were used to determine which of the 33 physical habitat and 12 land use variables could distinguish sites with poor or fair biotic condition (IBI scores ≤ 30) from those with good to excellent biotic condition (IBI scores ≥ 50). Results of statistical analyses were considered significant if $P < 0.5$. All analyses were performed in SAS (SAS 1999).

RESULTS

Physical Habitat

Channel sizes and proportions varied widely; average wetted widths ranged from 3.8 to 44.5 m, average depths ranged from 0.12 to 1.35 m, and width-to-depth ratios ranged from 7.3 to 110.8 (Table 2). Average velocity was slow (0.22 m/s), but highly variable. Substrate was dominated by fine substrates (74%), particularly sand, which ranged from 11% to 92%. There were nearly equal amounts of instream rock and wood fish cover, while high water fish cover was dominated by wood (75%). Riparian habitat conditions varied widely, between 4% and 90% of banks were unvegetated, between 0% and 52% of banks were "cut eroding banks" and site averages of bank slope ranged from 20° to 59°. The average percent of banks with canopy cover ranged from 0% to 88%.

The stress value of the MDS ordination was low (0.09), which indicated that similarities among sites were sufficiently represented (Clarke and Warwick 1994). No distinct grouping of sites was evident, rather, sites were scattered throughout the ordination space, indicating gradual variation in physical habitat characteristics among ecoregions (Figure 2). Dimension one of the ordination depicted differences in stream size

and was most correlated with drainage area ($r = 0.71$), average stream width ($r = 0.62$), and stream order ($r = 0.61$). Dimension two contrasted sites dominated by wood habitat ($r = -0.43$) (toward the left of the plot) from sites with rock cover ($r = 0.71$), cobble ($r = 0.61$), or boulder ($r = 0.64$) substrates (toward the right of the plot) (Figure 2). The latter habitat characteristics were strongly correlated with IBI score ($r = 0.53$), number of fish ($r = 0.58$), and number of species sampled at sites ($r = 0.53$). Width to depth ratio was positively correlated ($r = 0.54$), and bank slope was negatively correlated ($r = -0.63$) to Dimension 2. Dimension three of the ordination was most correlated with proportion of canopy cover ($r = -0.63$) (Figure 2).

Fish Assemblages

The average IBI score was 47 (SE = 3.0). Four sites had poor scores, 18 had fair scores, 12 had good scores, and 3 sites rated as excellent. From 138 to 3,626 (average = 1,031, SE = 132.9) individuals and from 6 to 38 (average = 22, SE = 1.2) species were captured at sites. On average, 56% (SE = 3.1) of sampled fish had intermediate sensitivity to degradation, 38% (SE = 3.4) were tolerant, and 6% (SE = 1.1) were sensitive. Invertivores (35%) (SE = 3.8) and omnivores (31%) (SE = 3.2) were the most common trophic guilds. Bluntnose minnow *Pimephales notatus* had the highest catch rates per 100 m, followed by sand shiner *Notropis stramineus*, green sunfish *Lepomis cyanellus*, fathead minnow *Pimephales promelas*, and spotfin shiner *Cyprinella spilopterus*. Green sunfish and common carp *Cyprinus carpio* occurred at the most sites, followed by sand shiner, bluntnose minnow and white sucker *Catostomus commersonii*.

Land Use

Agriculture in study catchments consisted of cultivated row crops. Average amount of agriculture was 69% (SE = 3.3) in catchments, 50% (SE = 24) in network buffers, but only 11%

Table 2. Summary of ANOVAs testing the effect of ecoregion on physical habitat, fish assemblage and land use variables in Iowa streams. Only significant ($P < 0.05$) main effects are shown. Significant ($P < 0.05$) Tukey-Kramer pairwise comparisons between regions^a are shown.

	ANOVA				Significant Tukey-Kramer pairwise contrasts					
Variable	df	MS	F	P						
Habitat										
Average depth CV	6	316.79	2.7	0.0326	PP>LH					
Average velocity CV	6	7298.50	2.6	0.0376	CP>DL	CP>IS				
Width to depth ratio	6	1743.83	3.79	0.0049	NW>CP	NW>LH				
% clay	6	451.86	6.4	0.0001	CP>DL	CP>IS	CP>NW	CP>PP	CP>SI	
% banks open	6	0.09	3.78	0.0049	CP>IS	NW>IS	SI>IS			
Average bank slope	6	315.19	11.6	<.0001	CP>DL	CP>IS	CP>NW	LH>DL	LH>IS	
					LH>NW	SI>IS				
Fish assemblage										
IBI	6	1021.59	5.81	0.0003	PP>CP	PP>LH	IS>SI	IS>CP	IS>LH	
Number of species	6	164.58	7.03	<0.0001	PP>CP	PP>DL	PP>LH	PP>SI	IS>CP	
					IS>LH					
% sensitive species	6	134.36	5.11	0.0007	IS>CP	IS>LH	IS>SI	PP>CP	PP>DL	
					PP>LH	PP>SI	PP>NW			
% filter feeder	6	0.26	3.64	0.0062	PP>CP	PP>DL	PP>IS	PP>LH	PP>NW	
					PP>SI					
% herbivores	6	132.16	2.91	0.0196	PP>CP	PP>DL	PP>LH			
Land Use										
% local buffer ag.	6	614.90	4.56	0.0021	LH>CP	LH>DL	LH>IS			
% network buffer ag.	6	865.18	10.04	<.0001	NW>SI	NW>CP	LH>IS	LH>CP	DL>CP	
					IS>CP					
% network buffer for.	6	411.18	12.00	<.0001	CP>IS	CP>DL	CP>LH	CP>NW	SI>DL	
					SI>LH	SI>NW				
% catchment ag.	6	955.84	3.36	0.0119	DL>CP					
% catchment other	6	570.69	11.76	<.0001	CP>IS	CP>DL	CP>LH	CP>NW	SI>IS	
					SI>DL	SI>NW				

^aEcoregions abbreviated as follows: CP= Central Irregular Plains; DL = Des Moines Lobe; IS = Iowan Surface; LH = Loess Hills and Rolling Prairies; NW = Northwest Iowa Loess Prairies; PP = Paleozoic Plateau; and SI = Southern Iowa Rolling Loess Prairies.

(SE = 2.4) in local buffers. Percentages of forest were highly variable across spatial scales, with average amounts ranging from 5% (SE = 1.3) in catchments to 46% (SE = 4.0) in local buffers. Network buffers and local buffers had similar average percentages of grasses (35%, 21%, respectively) and “other” (2.3%, 4.5%, respectively) land uses. Average percentages of “other” land uses were low across scales, ranging from 2.3% (SE = 0.45) in network buffers to 5.2% (SE = 1.6) in catchments. Percentages of agriculture in local buffers, buffers, and catchments differed among regions, but a northeast to southwest gradient was not evident (Figure 3). Regions also differed in percentages of forest in buffers and other land uses in catchments.

Relationships among Physical Habitats, Land Uses, and Fish Assemblages

Fish IBI, species richness, percentage of sensitive species, width-to-depth ratios, percentage open banks, and average bank slope exhibited a northeast to southwest gradient among ecoregions (Figure 4). Other physical habitat variables that distinguished some regions were depth CV, velocity CV, and percent clay (CP had significantly more clay than all other regions except loess hills) (Table 2). Most of the significant pair-wise differences involved the CP ecoregion, which had more clay substrate than five other regions, higher velocity CV than two regions, and steeper banks than three regions.

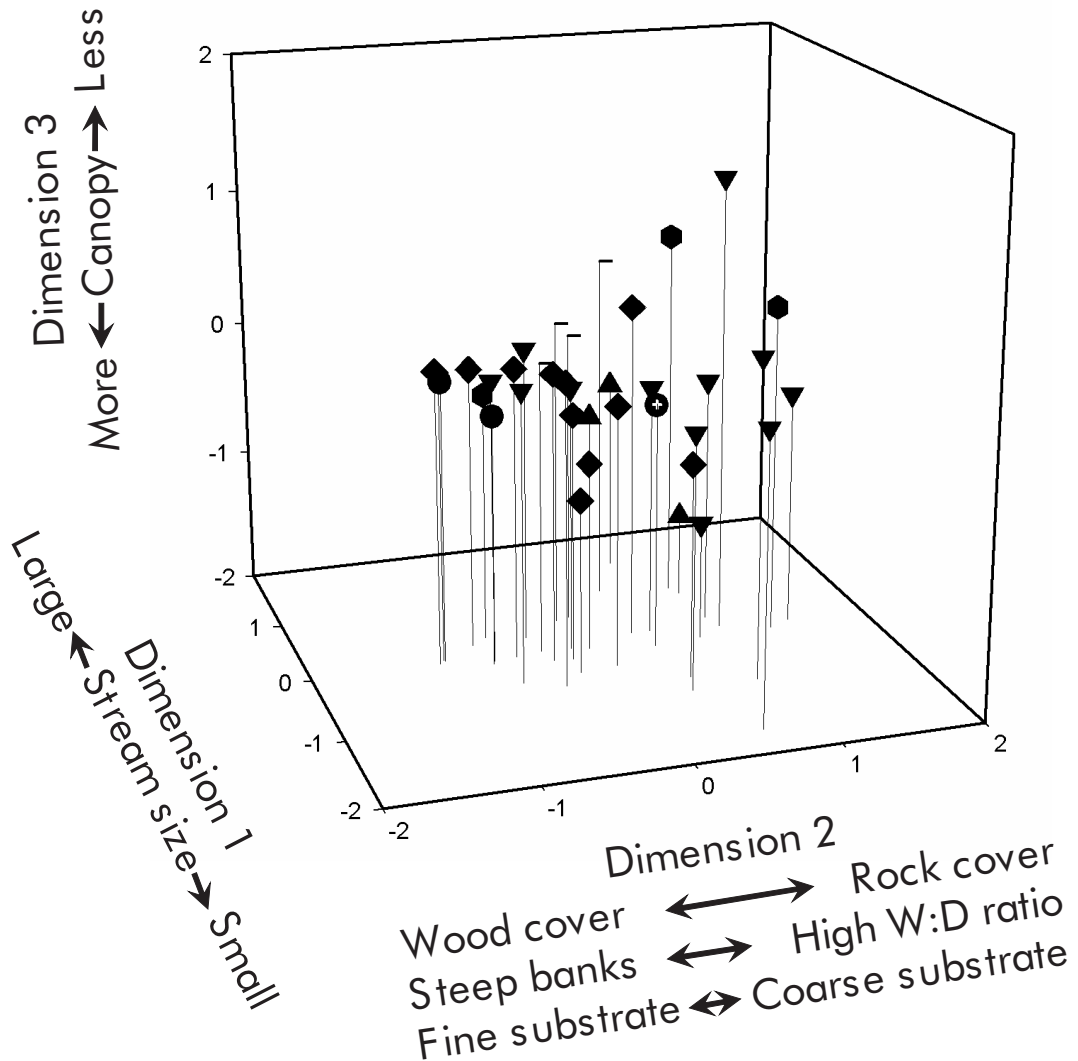


Figure 2. MDS ordination showing physical habitat similarities among 37 Iowa stream sites. Three dimensions characterized most similarities and differences among sampling sites. Ecoregions are represented by symbols as follows: PP (circle with cross), IS (triangle down), NW (circle), DL (diamond), SI (hexagon), CP (horizontal dash), and LH (triangle up).

Percent filter feeders and percent herbivores also differed among ecoregions. The only filter feeder sampled was the American brook lamprey *Lampetra appendix*, which was only found in the PP region.

Sites with good IBI (≥ 50) had shallower and more variable depths than sites with poor IBI (≤ 30 ; Table 3). Higher IBI scores were associated with higher percentages of boulder and

gravel substrates, more rock cover, and more total fish cover. Lower IBI scores were associated with higher percentages of silt and clay substrates and steeper, more erodeable banks with less vegetative coverage. Seven land use variables were able to differentiate the IBI groups (Table 3; Figure 3). Sites with good or excellent IBI scores had lower percentages of agriculture in local buffers but higher percentages in network buffers and

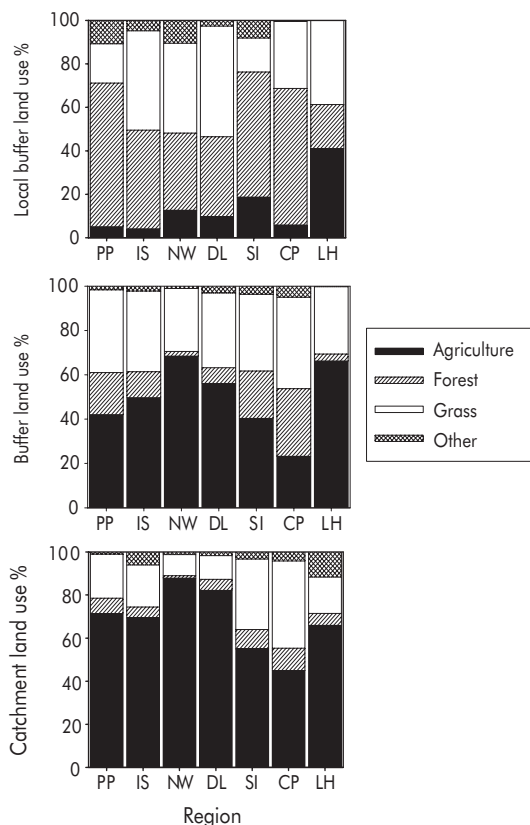


Figure 3. Land-use percentages in catchments, network buffers and local buffers upstream of sampling sites. Catchment land use included use percentages in catchments upstream of sampling sites. Network buffer land use included use percentages in 60-m riparian buffers of drainage networks upstream of sites. Local buffer included 60-m riparian buffer land uses located within 1-km-diameter circles centered on sampling sites.

catchments. Lower percentages of network buffer and catchment forests were also associated with higher IBI. Lower amounts of other land uses in buffers and catchments also distinguished sites with higher IBI scores.

DISCUSSION

Physical habitat conditions in Iowa streams reflect attributes characteristic of Midwestern prairie streams, overlain with attributes characteristic of agricultural land use alteration. Fine substrates

were common, even at our least-altered sites, which is consistent with previous research in Iowa (Griffith et al. 1994; Wilton 2004). Iowa sites had much higher percentages of sand and lower percentages of gravel and cobble than catchments with less agriculture in other Midwestern states (Goldstein et al. 2002; Putman et al. 1995), Nevada (Nelson et al. 1992), and Oregon (Whittier et al. 1988). Substrate composition at Iowa sites was similar to 27 streams in northwestern Mississippi (Shields et al. 1995), that were described as degraded due to deforestation, channel straightening, gully erosion, and sedimentation. In our study, degraded stream-bank conditions were common; roughly one-third of banks were devoid of vegetation and one-fifth of banks were eroding cut banks. In contrast to physical habitat conditions in Iowa streams, bank conditions in the Northern Lakes and Forests ecoregion, which includes northern portions of Minnesota, Wisconsin, and Michigan, were much better; 96% of banks were undisturbed and only 8% of banks were eroded (Wang et al. 2003). That ecoregion is dominated by forest (87.7%) and has low amounts of agricultural (5.7%) and urban (0.5%) land uses (Wang et al. 2003). The high percentage of fine substrates and eroding banks at Iowa sites is likely due in part to prairie physiography (Matthews 1988), but clearly has been intensified by agricultural land use (Menzel 1981, 1983; Waters 1995).

Physical habitat conditions in Iowa streams varied along three broad axes. The most dominant axis reflected differences in stream size. Average stream width, depth, and velocity all increased with stream size, as shown for many other rivers and streams (Leopold 1994). The next most important physical habitat axis contrasted sites with woody cover, fine substrates, and steep banks from sites with rocky cover, coarse substrates, and relatively wide and shallow channels. The other important physical habitat axis contrasted sites based on the prevalence of riparian canopy; some sites were completely barren of riparian trees shading the channel while other sites had shading trees at nearly every

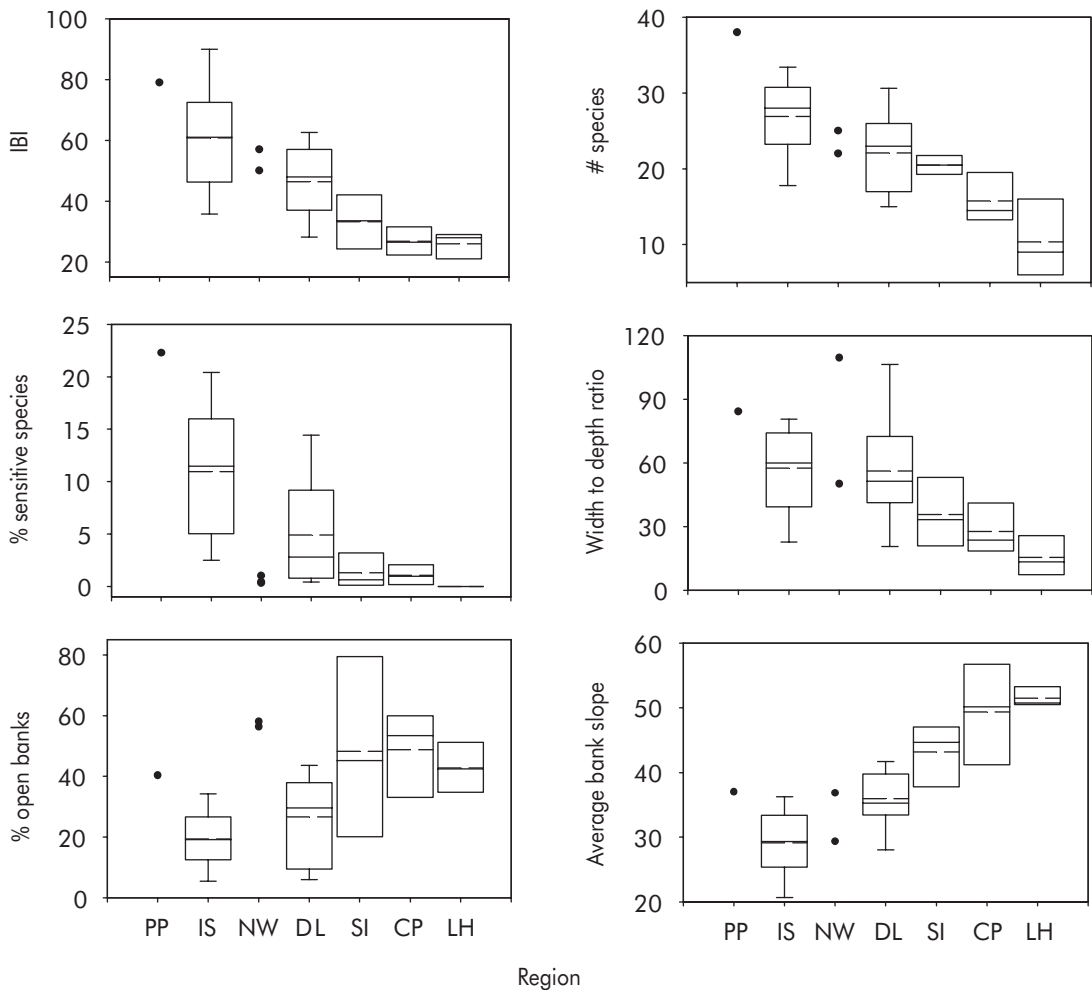


Figure 4. Fish and physical habitat variables with significant differences among ecological regions. Boxes encompass interquartile ranges; solid lines within boxes represent medians; dashed lines within boxes represent averages; vertical lines above and below boxes extend to the 95th and 5th percentiles, respectively. Dots represent individual values in ecoregions with fewer than three sites.

transect. Portions of the last two axes reflect symptoms of agricultural degradation. Severe erosion and channel down-cutting as a result of poor agricultural land use practices, most notable in southwestern Iowa (Menzel 1981, 1983), have resulted in sediment-laden streambeds, steep eroding banks, and trees falling into channels as large portions of streambanks are undermined. Riparian trees have been cleared from the banks of many rivers and streams in Iowa to allow cultivation as close to the channel as pos-

sible. A physical habitat ordination from a study of stream sites in an agriculturally dominated region just to the north of Iowa identified similar patterns (Talmage et al. 2002); boulders, woody debris, canopy cover, and stream size were among the variables that best characterized variation among those sites.

We found that fish IBI, species richness, and percentage of sensitive species were highest in northeast Iowa and decreased to the south and west, which agrees with previous findings in Iowa

Table 3. Significant differences ($P < 0.05$) among sites with IBI scores ≤ 30 ($N = 8$) and sites with IBI scores ≥ 50 ($N = 17$) in Iowa streams.

Variable	IBI ≤ 30 average	IBI ≥ 50 average	P
Width to depth ratio	26.54	61.72	0.0016
Average depth	0.74	0.38	0.0011
Average depth CV	42.73	58.63	0.0047
% clay	19.49	0.49	0.0003
% silt	20.51	8.19	0.0378
% gravel	4.70	17.19	0.014
% boulder	0.59	3.95	0.0489
Cover abundance	1.23	2.52	0.019
Rock cover	0.16	1.47	0.0197
% banks open	0.48	0.29	0.0113
% cut eroding banks	0.29	0.19	0.0355
Bank slope	48.03	31.78	<0.0001
Local buffer % agriculture	22.24	5.49	0.0094
Network buffer % ag.	39.68	54.22	0.0369
Network buffer % forest	19.71	9.66	0.0287
Network buffer % other	4.38	1.36	0.0045
Catchment % agriculture	52.24	76.18	0.0084
Catchment % forest	9.25	3.25	0.0061

(Menzel 1987; Paragamian 1990b; Wilton 2004). An underlying cause of this pattern is greater numbers of native sensitive and total species in the Mississippi River basin (eastern and central Iowa) than the Missouri River basin (portions of western Iowa) (Hocutt and Wiley 1986). Even though several IBI metrics have been calibrated separately for the Mississippi and Missouri drainages in Iowa (Wilton 2004), IBI scores exhibited a marked decline from northeast (PP average IBI = 79) to southern and western Iowa (LH average IBI = 45). The statewide gradient in fish assemblage characteristics appears to reflect differences in the native species pool, geology, and climate, as well as more degraded stream conditions in portions of southern and western Iowa (Wilton 2004). We found that lower width to depth ratios, higher percentages of open banks, and higher average bank slopes exhibited the same statewide gradient and distinguished sites with poor or fair IBI scores from those with good or excellent scores.

Based on previous studies in Iowa, we hypothesized that land use differences among regions were a driving factor in the statewide IBI gradi-

ent. We did not find a northeast to southwest increase in percent agriculture and decrease in percent forest as had been reported in other studies (Menzel 1987; Paragamian 1990b; Griffith et al. 1994; Wilton 2004). Rather, we found a contradictory pattern; higher percentages of forests at all scales were associated with poor to fair IBI scores, while higher percentages of agriculture in catchments were associated with good to excellent scores. Combining grazed pasture and native prairie into the land use category "grass" may have masked different effects of grass cover of different type. Both the SI and CP regions had relatively low percentages of agriculture, but high percentages of grass. Grass land uses in these regions were primarily grazed pastures, which degrade streams (Menzel 1987; Griffith et al. 1994). We conclude that although agricultural land uses may diminish the natural distinction of ecoregions (Li and Reynolds 1994), ecoregions in Iowa have distinctive underlying landscape-stream relationships that should be examined both within ecoregions and across ecoregions. However, McCormick et al. (2000), Van Sickle and Hughes (2000), and Herlihy et al. (2006, this volume) reported that ecoregions and other spatial classification approaches explain less than half the variability possible with a biologically-based landscape classification. Future analyses will require more sites per ecoregion to adequately represent within-ecoregion variation. Even with more sites, we may find the same pattern as Stauffer et al. (2000), who examined an agriculturally dominated area of southern Minnesota. Stauffer et al. (2000) speculated that in areas like southern Minnesota and Iowa, where the percentage of agricultural land use is uniformly high, there may not be sufficient variation in land use to see its effects. The question of whether pervasive row-crop agriculture throughout Iowa may have essentially eliminated land use as a factor to explain variation in physical habitat and fish assemblages needs to be addressed at the within-ecoregion scale.

Our relationships of IBI and other fish assemblage variables with physical habitat conditions

were similar to relationships reported in other studies from agriculturally dominated areas in the Midwest. An Illinois study reported that bank vegetation and width-to-depth ratio were positive predictors of IBI (Holtrop and Fischer 2002). Nerbonne and Vondracek (2001) found positive correlation of width-to-depth ratio and negative correlation of fine substrates with IBI in an agriculturally dominated landscape of southeastern Minnesota. In a statewide study for IBI calibration and development of other stream biological assessment tools for Iowa, Wilton (2004) found several relationships when comparing IBI scores with physical habitat variables. As in our study, IBI was positively correlated with coarse substrates and boulders, and negatively correlated with fine substrates and unvegetated banks. Although our findings on physical habitat agreed with Talmage et al. (2002), agreement on physical habitat and fish relationships was mixed. They found positive relationships of boulders with species richness and other fish assemblage variables. These relationships were comparable to our positive relationships of IBI, fish abundance, and species richness with habitat dimension 2, which was primarily defined by boulders and in-stream rock cover. However, their positive relationships of woody debris with IBI and other fish assemblage variables were not evident in Iowa streams. In a portion of the same area studied by Talmage et al. (2002), Stauffer et al. (2000) found a similar relationship; higher IBI at sites with wooded riparian zones than with nonwooded riparian zones. A possible difference between our findings and those of Stauffer et al. (2000) and Talmage et al. (2002) is that in some Iowa streams, woody debris is a consequence of poor bank conditions and severe bank erosion rather than a reflection of naturally forested riparian zones. Although there were differences in methodology and some details of findings, the collective evidence from studies of physical habitat and fish assemblages in agriculturally degraded upper-Midwestern streams is remarkably consistent. Stable, vegetated banks, wide stream channels with abundant coarse substrates and

boulder-sized cover favor high IBI scores, while unvegetated, eroding banks and deep channels with predominantly fine substrates are associated with lower IBI scores. Presence of a wooded riparian zone and associated woody debris apparently enhances biotic integrity in some areas, as has been demonstrated in other regions (Gregory et al. 1991), while being symptomatic of stream habitat degradation in portions of Iowa.

Because of several shortcomings, we consider our study a preliminary assessment. Low sample sizes in some ecoregions limited our ability to characterize the range of stream conditions in these ecoregions. A clearer picture of within- and among-ecoregion variation would emerge with larger sample sizes, and the northeast to southwest trends in natural stream conditions would be better defined. Sites were sampled only once within a seven-year period, so it is possible that seasonal and annual variation may have further confounded comparisons. Three different gear types were used to sample fish, which may have introduced additional variation to the fish data. Several statistical tests were run, increasing the probability of type I error. Perhaps the greatest shortcoming was in the nonrandom selection of sites, which were subjectively chosen based on locations from a previous survey and ease of access. This significantly biased the local buffer land use towards artificially high percentages of forest. A study currently underway in Iowa was designed to avoid (or at least minimize) these problems, by greatly increasing within-ecoregion sample sizes and randomly choosing sites. Although these shortcomings limit conclusions based on our data alone, we believe that the congruence of many of our findings with previous studies allows broader interpretation and adds significantly to an emerging picture of streams in the agriculturally dominated Midwestern landscape.

Our results demonstrated that there is substantial variation among physical habitat, land use, and fish assemblage conditions across Iowa. Some of this variation is due to geology, climate, and zoogeographic patterns, which are depicted

by ecoregion classifications. Future studies should address these natural patterns of ecoregions, particularly those aimed at identifying land use influences. Because of the dominance of agriculture, future management and restoration efforts targeting riparian zones and stream reaches will play an important role in improving biotic condition. Restored riparian buffers have been shown to improve many aspects of stream ecosystem structure and function in Iowa and elsewhere (Schultz et al. 2004). Instream and channel restoration techniques, such as those described by Newbury and Gaboury (1993), have proven effective at enhancing streams for fish by restoring natural habitat structure and the hydraulic functions that sustain them. Reducing upland and bank soil erosion, and mitigating channel sedimentation (Waters 1995) are perhaps the most important keys to improving physical habitat and biotic condition in Iowa streams.

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The Importance of Multiscale Habitat Relations and Biotic Associations to the Conservation of an Endangered Fish Species, the Topeka Shiner

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Abstract.—The Topeka shiner *Notropis topeka* is a small cyprinid listed as endangered in 1999 due to an 80% reduction in its former range across six Great Plains states. Conservation and recovery plans require information on structural indices of existing populations, distribution, and habitat relations at several spatial scales. We examined physical habitat associations of Topeka shiners at the valley segment and reach scales, and associations with fish species using stepwise logistic regression. Fish and habitat data were collected at 52 sites. Habitat features at the valley segment scale were acquired using data from a geographic information system. At the valley segment scale, Topeka shiners were associated with stream condition variables (stream size, groundwater potential, channel slope, streamflow, network position) and land-cover variables (% pasture, % trees). At the reach scale, Topeka shiners were associated with low grazing and small trees in riparian zones, low bank height, less submerged vegetation, and coarse substrates. Topeka shiners were associated with five fishes that inhabit small, intermittent, warmwater streams. Evidence of greater abundance of Topeka shiner populations in our region compared to other regions may be a result of the natural character of the streams and associated wetlands, which can influence the habitat variables associated with Topeka shiners at both scales. We identified management strategies that would be effective at conserving habitat of Topeka shiners at large and local scales.

INTRODUCTION

Stream ecology studies increasingly demonstrate the importance of assessing habitats at several scales because processes that influence aquatic biota differ temporally and spatially. Spatial scales vary from microhabitats to ecoregions, as studies compare large-scale and local-scale effects on various taxa or indices (Roth et al. 1996; Wiley et al. 1997; Weigel et al. 2003; Willson and Dorcas 2003). Effects of large-scale features like climate, geology, and water quality may dominate

(Meador and Goldstein 2003; Harrison et al. 2004), but local-scale factors may also be important (Crossman et al. 1998; Wang et al. 2003). Biotic factors, usually competition or predation, are sometimes important in shaping aquatic communities locally (Moyle and Li 1979), but abiotic factors are often more important (Angermeier et al. 2002), especially in harsh environments (Poff and Ward 1990). Great Plains streams are considered harsh environments where abiotic controls are usually more important than biotic controls (Braaten and Berry 1997; Marsh-Matthews and Matthews 2000; Milewski 2001).

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The decline of the fish fauna in Great Plains streams may not be as severe as in other parts of North America (Warren and Burr 1994; Rahel 2000; Shearer and Berry 2003), but there are species of concern (Echelle et al. 1995; Patton et al. 1998). An example is the Topeka shiner *Notropis topeka*, which was recently listed as a federally endangered species. Topeka shiner populations may be affected by large-scale land use changes and by biotic interactions such as the distributions of predators and nest-building centrarchids and cyprinids (Wall and Berry 2004). Understanding abiotic and biotic controls at several scales could assist in prioritizing the scale for conservation activities that include stream rehabilitation, population management, and policy making (Maddock 1999; Bond and Lake 2003; Weigel et al. 2003).

The Topeka shiner had been recorded in 24 streams in South Dakota before 1999, so the species was more common in our area than in most other parts of its range. However, previous studies reported only species presence, and we had little information of population metrics or habitat associations. Our objectives were to determine (1) the status of Topeka shiner populations, (2) associations with other fishes, and (3) habitat associations at two scales.

METHODS

Topeka Shiner

The Topeka shiner is a small (<55 mm long), stout minnow found in small streams in six Great Plains states (Iowa, Kansas, Minnesota, Missouri, Nebraska, and South Dakota). The habitat requirements of the Topeka shiner vary across its range and appear dependent on large-scale geological factors (Dahle 2001; Kuitunen 2001; Kerns and Bonneau 2002; Stark et al. 2002; Wall and Berry 2004). A working description of habitat at the landscape scale is low-order, shallow, low-flow streams in agricultural landscapes with pastures and row crops. Streams may be intermittent, but subsurface geology provides

groundwater connections. Vegetated off-channel habitats of natural and artificial origin sometimes contain fish (Dahle 2001), but there is a negative effect of main channel impoundments on populations (Layher 1993; Schrank et al. 2001; Mammoliti 2002).

At the reach scale, substrates can range in size from silt to cobble. Alluvium glacial outwash and groundwater inputs characterize some sites. Water may be clear or turbid. Submergent vegetation may be present or absent. Riparian areas usually have grasses and shrubs but few trees (occasionally willows), and livestock use can be low, moderate, or heavy (Kerns 1983; Barber 1986; Clark 2000). The negative relation between pool size and Topeka shiner population size may be related to an increased predator niche.

Biotic controls probably influence the presence and abundance of Topeka shiners. Topeka shiners are usually found with nest-building sunfishes because Topeka shiners spawn in sunfish nests (Kerns and Bonneau 2002). But piscivorous largemouth bass *Micropterus salmoides* may be detrimental (USFWS 1998; Schrank et al. 2001).

Study Location

This study was conducted in 1999 and 2000 on tributaries of the James, Vermillion, and Big Sioux rivers in eastern South Dakota. These rivers drain the Central Lowlands physiographic region in eastern South Dakota, before joining the Missouri River (Figure 1). Flow varied annually; most tributaries contained water throughout 1999 when conditions were similar to past normal water years, but low precipitation in 2000 caused intermittency in some streams. Fish assemblages are well known for the main channel of the James (Walsh 1992; Schumacher 1995), Vermillion (Underhill 1959; Braaten 1993), and Big Sioux rivers (Nickum and Sinning 1971; Diertman 1995), where species richness ranges from 50 to 70 species. Less information on fish assemblages is available for tributaries, where most Topeka shiners have been found. Agriculture dominates land use around

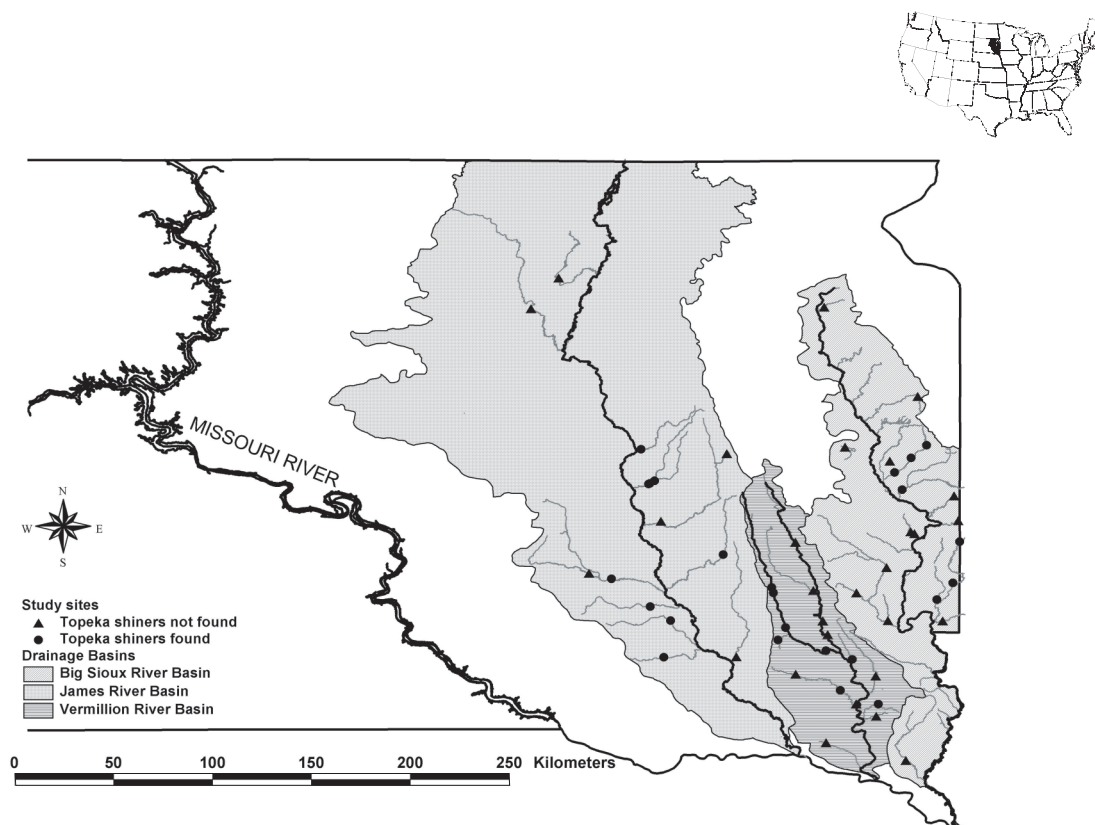


Figure 1. Study area showing location of reaches in eastern South Dakota streams sampled for Topeka shiner.

Topeka shiner streams where pastures border many streams and row crops cover uplands.

Fifty-two sites were sampled in 1999 and 2000 on 43 tributaries of the James, Vermillion, and Big Sioux rivers (Figure 1). Sites in 1999 were selected based on historical records from the South Dakota Natural Heritage Database and from Cunningham and Hickey (1997) and Cunningham (1999). In 2000, sampling was done at new sites predicted from preliminary geographical information systems (GIS) analysis of 1999 data (Wall et al. 2001). We studied both the valley segment scale and the reach scale. The valley segment scale included landscape use, hydrological, and geological factors whereas the reach scale included instream, bank, and riparian zone physical factors.

Fish Sampling Methods

Block nets consisting of 4.7-mm (bar-measure) mesh were placed at the first and last transect. A bag seine with 4.7-mm mesh (bar-measure) was pulled downstream with periodic stops to count captured fish until the reach was covered. Length of seine haul and stream width were recorded to determine area sampled (m^2) for each site to allow calculation of species density as number of fish/100 m^2 . We used stepwise logistic regression to test for the association between Topeka shiner presence and two fish assemblage measures—abundance and presence of other species considered individually.

All fish were collected with seines, and those accumulated in the downstream block net were

retained in a holding pen in the stream while Topeka shiners were counted and individual Topeka shiners measured for total length and weighed. Individuals of other species were then identified, counted, and released. Length-frequency and condition (Fulton's K) was summed for Topeka shiners by major river basin because patterns for fish from each tributary were meaningless due to low sample size.

Valley Segment Scale Variables

River Reach 3 files (RF3) at a scale of 1:100 000 (USEPA 1999) formed the base hydrography layer for valley segment analysis. Lake and large river valley segments were not considered in analysis because of their lack of association with Topeka shiners (USFWS 1998). Nine stream condition variables (Appendix A) were used to classify valley segments within a GIS according to a standard aquatic classification system (Lammert et al. 1996). We chose variables considered important for shaping the distribution of aquatic communities at the valley segment scale based upon literature review and expert opinion (Wall et al. 2001). Valley segments were buffered by 30 m and the percent area of 11 cover types (Table 1) within the buffered riparian zone was determined using a 30-m² grid map of land cover interpreted from 1992 Landsat imagery (Smith et al. 2002).

To determine stream conditions associated with Topeka shiner presence, Topeka shiner locations recorded from 1934 to 2000 were used to attribute valley segments. Segments with the shiner present were termed "events," whereas segments with no record of Topeka shiners were termed "nonevents." We considered stream conditions (e.g., geology, stream size) to be stable during this time period (Frissell et al. 1986). We randomly chose three times as many nonevents as events to account for differences in variance resulting from the difference in the number of nonevents to events as recommended for analysis (Pereira and Itami 1991; Sperduto and Congalton 1996). Stepwise logistic regression

(significance level entry of $\alpha = 0.5$ and a significance level stay of $\alpha = 0.05$ based on Wald's test) was used to identify significant variables.

We compared percent land cover within 30-m buffers of valley segments with and without events between 1989 and 2000. The random sample of nonevents had the same proportion of segments classified as headwaters, creeks, small rivers, and large rivers, as did the sample of events to eliminate bias (Vannote et al. 1980; Wiley et al. 1990). A two-tailed t -test was used to compare land cover surrounding events to land cover surrounding nonevents. Instances of unequal variances were accounted for using the Satterthwaite method (SAS Institute 1994). Variables significant ($\alpha = 0.05$) to Topeka shiner presence were used in a stepwise logistic regression model.

Reach Scale Variables

At each site, we sampled 13 transects placed three mean stream widths apart (Simonson et al. 1993). Variables describing channel morphology and riparian zone were measured or visually estimated at each transect (Table 2). Visually scored features included dominant stream bank vegetation type, surrounding land use practices, animal vegetation use, instream habitat types (pools, riffles, runs), and bank slumpage. Substrate composition was characterized by taking three samples from each bank (upper, mid, and lower), and eight samples of bottom sediment across the wetted portion of each transect. Substrate samples were categorized as silt, sand, very fine to coarse gravels, cobbles, and boulders, based upon Wolman (1954).

The association between events and habitat variables was examined using stepwise logistic regression for left and right banks separately because of categorical variables for which means cannot be calculated. Continuous variables from right and left banks were summarized together, and means were used in both right and left bank analyses.

We looked at several statistics to validate the logistic regression models (Wall et al. 2004), but

Table 1. Land-cover variables and results of two-tailed *t* test with 95% confidence intervals (CI), showing percent land cover comparisons between 30-m riparian buffers surrounding valley segments where Topeka shiners had been found between 1982 and 1999 (events) to those where the shiner had not been found (nonevents) in eastern South Dakota.

Land-cover class	<i>n</i>	Topeka shiners found	mean	CI	<i>p</i>
Cultivated land (row-crop)	171	nonevent	22.18	18.62–25.73	0.0591
	56	event	17.04	13.00–21.08	
Hay land	171	nonevent	4.84	3.69–6.00	0.7369
	56	event	4.51	2.98–6.05	
Idle grass	171	nonevent	6.61	5.33–7.88	0.6485
	56	event	7.18	5.30–9.05	
Pasture	171	nonevent	30.54	27.67–33.41	0.0011
	56	event	38.63	34.75–42.51	
Trees	171	nonevent	3.32	2.61–4.02	0.0387
	56	event	4.77	3.64–5.91	
Semi-permanent wetland	171	nonevent	6.06	4.23–7.89	0.3060
	56	event	4.47	1.97–6.96	
Seasonal wetland	171	nonevent	5.73	4.36–7.11	0.4259
	56	event	4.81	2.94–6.67	
Temporary wetland	171	nonevent	2.24	1.55–2.94	0.1723
	56	event	1.41	0.42–2.40	
Riverine wetland	171	nonevent	17.92	14.87–20.98	0.3259
	56	event	15.89	13.16–18.62	
Permanent wetland	171	nonevent	0.27	–0.08–0.62	0.8191
	56	event	0.35	–0.26–0.96	
Urban	171	nonevent	0.29	0.01–0.57	0.3617
	56	event	0.94	–0.45–2.33	
Wetlands (semi-permanent + seasonal + temporary + riverine + permanent wetlands)	171	nonevent	32.22	29.03–35.42	0.0157
	56	event	26.92	24.01–29.83	
Grasses (hay land + idle grass + pasture)	171	nonevent	41.99	38.77–45.20	0.0015
	56	event	50.33	46.33–54.32	
(Cultivated land ^a) · (wetlands) ^{–1}	170	nonevent	4.641	1.055–8.227	0.0330
	56	event	0.736	0.533–0.938	
(Cultivated land) · (uncultivated land ^b) ^{–1}	171	nonevent	1.118	0.405–1.833	0.0215
	56	event	0.271	0.169–0.374	

^aCultivated land = row crop, ^buncultivated land = wetlands + grasses + trees

report here concordance, discordance, and tie values (SAS Institute 1994). Percent concordance indicates the percent pairs (present and absent) for which the model predicts high probability of Topeka shiner presence where the shiner was found, whereas percent discordance indicates the percent pairs predicted as having a high probability for presence where the Topeka shiner was not found. The percent ties indicates pairs with the same probabilities and do not correctly or incorrectly predict Topeka shiner presence. High concordance, low discordance, and low ties point

to a greater ability of the model to correctly compute outcome (Kohont 1974).

RESULTS

We captured 39,685 fishes from 52 sites on 36 creeks (Appendix B). Topeka shiners comprised 0.4–5.4% of the cyprinids and had a maximum density of 46/100 m² at one site in the Big Sioux basin, but relative abundance and catch per unit effort (CPUE) varied yearly and by basin (Blausey 2001). In the James River basin, mean

Table 2. Stream reach scale habitat variables measured at sites sampled for Topeka shiner in eastern South Dakota.

Habitat variable and (code)	Category or measurement	
Bank height (BH)	m	
Bank angle (BA)	degrees	
Streambank length (STRB)	m	
Vegetated streambank (STRBV)	m	
Eroded streambank (STRBE)	m	
Deposited streambank (STRBD)	m	
Streambank vegetation type (VEG)	1 = grasses and forbes 3 = shrubs 5 = trees	2 = sedges and rushes 4 = small willows
Age-class of trees (AGE)	1 = seedling 3 = mature 5 = dead	2 = sapling 4 = decadent 6 = other
Riparian land use (LNDU)	1 = wetland 3 = forested 5 = crop land	2 = shrubs 4 = pasture 6 = developed
Animal vegetation use (ANVG)	0 = prairie 0 = none 2 = medium 1 = present	8 = other 1 = low 3 = high 0 = absent
Bank slumpage (BS)	m	
Overhanging vegetation (OVG)	m	
Undercut bank (UB)	m	
Submerged macrophytes (SUB)	m	
Emerged macrophytes (EMER)	m	
Habitat type (HABTYP)	1 = pool; 2 = run; 3 = riffle	
Substrate (after Wolman 1954)	CL = clay (<0.004 mm – slick) SI = silt (0.001–0.062 mm) SA = sand (>0.062–2mm - gritty) VFG = very fine gravel (>2–4 mm) FG = fine gravel (>4–8 mm) MG = medium gravel (>8–16 mm) CG = coarse gravel (>16–32 mm) VCG = very coarse gravel (>32–64 mm) CO = cobble (>64–128 mm) LC = large cobble (>128–256 mm) BO = boulder (>256–512 mm) LB = boulder (>512 mm)	

Measurements to nearest 0.1 m or nearest degree, means for continuous data were calculated for all transects per reach, % substrate was calculated for each reach.

CPUE was 9.1 ± 4.3 fish/100 m² in 1999 and 4.0 ± 2.5 fish/100 m² in 2000. In the Vermillion River basin, mean CPUE was 6.0 ± 1.6 fish/100 m² in 1999 and 4.8 ± 2.7 fish/100 m² in 2000. In the Big Sioux River basin, mean CPUE was 8.0 ± 6.4 fish/100 m² in 1999 and 11.3 ± 8.8 fish/100 m² in 2000. The length-frequency distributions indicated that two age-classes dominated Topeka shiner populations in the Vermillion and James River basins, whereas three age-classes were apparent in the Big Sioux River basin population (Figure 2).

Streams with and without Topeka shiners had about the same assemblage of other species, but abundances differed. Species richness ranged from 2 to 17 at James River sites, from 7 to 16 at Vermillion River sites, and from 4 to 21 at Big Sioux River sites. Cyprinids were represented by 12–15 species depending on basin, and usually made up 70–90% of the catch. Ictalurids dominated (44%) the catch in the James River basin in 2000 but were less abundant in other samples. Other families present were Centrarchidae (five species),

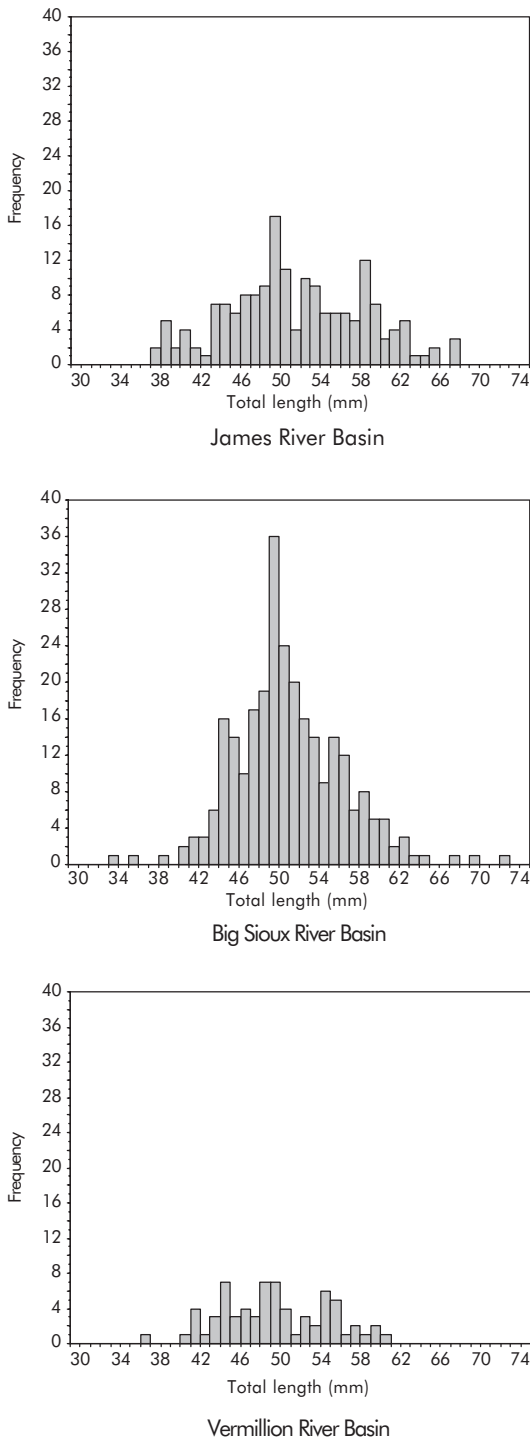


Figure 2. Length-frequency graphs for Topeka shiners found in the James, Vermillion, and Big Sioux River basins.

Catostomidae (three species), Clupeidae (one species), Percidae (two species), Cyprinodontidae (one species), Esocidae (one species), and Hiodontidae (one species).

The Topeka shiner was associated with five species (Table 3): orangespotted sunfish *Lepomis humilis*, bigmouth shiner *Notropis dorsalis*, black bullhead *Ameiurus melas*, red shiner *Cyprinella lutrensis*, and tadpole madtom *Noturus gyrinus*. Stepwise logistic regression comparing abundance of other species to presence of Topeka shiners indicated that Topeka shiner presence depended positively on the abundance of orangespotted sunfish and tadpole madtom. Stepwise logistic regression comparing the presence of other species to the presence of Topeka shiners indicated that the probability of Topeka shiner presence was dependent on the presence of bigmouth shiner, black bullhead, red shiner, and tadpole madtom.

Fish/Habitat Associations: Segment Scale Variables

Stepwise logistic regression indicated that stream size, groundwater potential, streamflow, channel slope, and network position were significant to Topeka shiner presence (Table 3). Estimated coefficients of variables (Table 3) indicated that increases in stream size, groundwater potential, and stream network position were associated with an increase in the probability of Topeka shiner presence. As stream flow values increased, which indicated more intermittent (from perennial to temporary) streams, and as channel slope values increased, the probability for Topeka shiner presence decreased.

The 30-m riparian buffers around segments with events had more pasture, trees, and grasses than did nonevent segments (Table 1). The cultivated:uncultivated land ratios and cultivated lands:wetlands ratios were less in 30-m buffers surrounding event segments than in buffers around nonevent segments. Stepwise logistic regression using variables identified by

Table 3. Logistic regression models for fish and habitat associations with Topeka shiner presence at the valley segment and reach scales.

Variable	β	Wald (<i>P</i>)	% concordance	% discordance	% ties
Fish abundance			74.0	18.8	7.2
<i>Lepomis humilis</i>	0.02	0.054			
<i>Noturus gyrinus</i>	1.7	0.048			
Intercept	-1.04				
Fish presence			83.5	7.5	9.0
<i>Notropis dorsalis</i>	1.7	0.034			
<i>Ameiurus melas</i>	2.55	0.004			
<i>Cyprinella lutrensis</i>	4.15	0.006			
<i>Noturus gyrinus</i>	2.55	0.021			
Intercept	-7.10				
Segment scale					
stream condition			88.0	10.1	1.9
stream size	1.03	0.003			
groundwater	0.90	0.0001			
flow	-0.91	0.010			
stream gradient	-0.68	0.030			
network position	0.46	0.015			
intercept	-1.26				
land use			67.3	32.2	0.5
% pasture	0.03	0.003			
% trees	0.07	0.025			
intercept	-2.35				
Reach scale					
left bank			69.5	28.9	1.6
AGE(L)	-0.31	0.008			
ANVG(L)	-0.39	0.001			
BH	-1.73	<0.001			
SUB	-0.72	0.001			
Intercept	2.18				
right bank			67.8	30.4	1.8
ANVG(R)	-0.29	0.014			
BH	-1.71	<0.001			
SUB	-0.69	0.001			
Intercept	1.98				
substrate			70.2	28.4	1.4
VFG	0.08	<0.001			
CO	0.09	0.001			
Intercept	-1.06				

β = estimated coefficients, Wald (*P*) = *p*-value of Wald's test. Abbreviations for variables can be found in Table 2.

the two-tailed *t*-test showed that increase in percentage of pasture and trees in 30-m buffers were related to higher probability of Topeka shiner presence (Table 3).

Fish/Habitat Associations:
Reach Scale Variables

Stepwise logistic regression models were similar for left and right banks with estimated coef-

ficients of variables showing lower bank height, less animal vegetation use (i.e., less grazing), and less submerged vegetation in the reach associated with Topeka shiner presence (Table 3). Smaller trees (i.e., younger trees) were associated with Topeka shiner presence for the left bank. Two variables for the substrate composition (very fine gravel and cobble) were shown to be significant indicating that Topeka shiners in streams are associated with somewhat

coarse substrates rather than with silt and sand (Table 3).

DISCUSSION

Between 1997 and 2000, we and others found the Topeka shiner at 71% (50 of 70) of sites and 80% (35 of 44) of tributaries where it had been previously documented in South Dakota. The persistence, wide distribution, occasionally common occurrence (about 5% of the cyprinids), and presence of several year-classes indicating successful natural reproduction, suggests that the species is more secure in the James, Vermillion, and Big Sioux river drainages (including headwaters in Minnesota, Hatch 2001) than in other parts of its range.

The fish assemblage at sites with Topeka shiners includes many native species and few introduced predators, and assemblages have not changed temporally (Shearer and Berry 2003). Introduced predators have been suggested as one cause for the decline of the Topeka shiner (Schrank et al. 2001). Our fish species association models suggested a positive association between the Topeka shiner and five other native fishes (orange spotted sunfish, bigmouth shiner, black bullhead, red shiner, and tadpole madtom). All five species are classified as tolerant or intermediately tolerant of turbid, warm waters, and hypoxic conditions sometimes found in small prairie streams (reviewed by Blausey 2001). Other researchers have also associated one or more of these species with the Topeka shiner (Pflieger 1997; Winston 2002). The Topeka shiner spawns with red shiner and two other shiners in sunfish nests, such as those of the orange spotted sunfish (Pflieger 1997). Four of the associated species spawn in clean gravel. Black bullheads sometimes excavate nests in gravel and we speculate that the Topeka shiner could possibly also be using nests created by black bullheads and nest-building cyprinids in the absence of sunfish species. Fishes that we found associated with the Topeka shiner occur in small streams with low to moderate flow, and some are associated

with intermittency. Likewise, we associated the Topeka shiner with streams classified as creeks and small rivers.

Endangered fishes are indicator organisms, frequently indicating stream habitat deterioration by the decline of the species, but their persistence can also indicate relatively intact stream systems. Declines in the Topeka shiner may be indicating large-scale patterns in landscape change driven by climate, geology, and agriculture over its native range of six Great Plains states. Agricultural activities such as drainage, irrigation, cultivation, chemical applications, and livestock watering and grazing are stressors to wetlands, surface waters, and aquatic biota. Some of these practices alone or cumulatively are suggested as causative factors in the decline of the Topeka shiner (USFWS 1998).

The relatively high abundance of the Topeka shiner and other native fishes in the northern portion of its range in South Dakota and Minnesota may correspond with fewer impoundments, introduced species, channelized streams, or drained wetlands compared to other drainages in its historic range. For example, in the James, Vermillion, and Big Sioux river basins, few streams have been impounded (Johnson and Higgins 1997), only 3% of the stream channels have been dredged (Johnson and Higgins 1997), only about 35% of the wetlands have been drained (Dahl 1990), and about 40% of the native prairie remains (Higgins et al. 2002). Stream and land cover changes are more extensive in basins in the southern portion of the range (Menzel et al. 1984; Cross and Moss 1987; Higgins et al. 2002; Mammoliti 2002; Heitke et al. 2006, this volume). The Topeka shiner uses floodplain wetlands where available (Dahle 2001). In the southern part of the Topeka shiner's range, the number of small impoundments per watershed area was the only significant variable at this scale (Schrank et al. 2001). We did not include small impoundments because they are scarce in our study area.

In a landscape where the wetlands and grasslands have been conserved, large-scale patterns and processes should be reflected in the habitat

conditions at the segment and reach scales (Poole 2002). The seven factors associated with Topeka shiner presence at the segment scale (stream flow, groundwater input, stream size and network position, pasture, wetlands, and uncultivated lands) represent the general landscape well. For example, water infiltration from grasslands, pastures, and wetlands recharges groundwater and enhances and attenuates groundwater inputs to streams (Hubbard 1988; Mitsch and Gosselink 1993), which were all conditions we found associated with Topeka shiner presence. Where groundwater inputs occur, stream segments tend to be perennial and more stable than the “flashy” segments that receive only overland runoff. Topeka shiner was associated with segments receiving groundwater, but the segments were nested within the larger-scale pattern of network position (more upstream from confluences than downstream from confluences) and stream size (more perennial than intermittent, but sometimes intermittent).

The Topeka shiner often occurred in segments classed as intermittent with a high potential for groundwater delivery, which might be recognized as persistent isolated pools. This finding agrees with the suggested association between Topeka shiner presence and intermittent section length and isolated pool size (USFWS 1998). Our identification of segments that are both intermittent and have a high potential for groundwater input seems contradictory, but might be explained by temporal and spatial patterns of water in the shallow aquifer. Intersection of the streambed with the water table should occur in segments with low channel slope, and our data suggested that the probability of Topeka shiner presence increased as channel slope decreased. Low channel slopes foster low water velocities (i.e., <0.5 m/s), which have also been associated with Topeka shiner presence (Kerns 1983; Barber 1986; Adams et al. 2000). Our identification of important segments within the river continuum may be an example of patch dynamics (Naiman et al. 1988).

Segment-scale land cover variables (pasture, uncultivated lands, wetlands) were also represented at the reach scale by livestock use and tree age variables. There were five factors associated with Topeka shiner presence at the reach scale: three bank and riparian zone variables (bank height, animal use, small trees) and two instream habitat variables (substrates, submerged vegetation). Several of these features are linked as reach-scale processes and several are probably influenced by segment-scale processes. For example, livestock grazing and riparian tree regeneration are inversely related (Smith and Flake 1983). Low bank height indicates that a stream is not incised; stream incision occurs because of altered hydrology from wetland drainage (Leopold et al. 1964), channelization (Menzel 1983; Pringle 1997), or other watershed disturbances (Jacobson et al. 2000). Topeka shiner presence was negatively associated with variables indicating livestock grazing, but only at heavy grazing levels. The impacts of heavy livestock use on streams are well known (Platts 1981; Hauer and Lamberti 1996; Schramm and Hubert 1999).

Two instream habitat variables (less submerged vegetation, coarse substrates) were associated with Topeka shiner presence. Both are linked to land cover (e.g., riparian grasslands and floodplain wetlands) and instream flow conditions (groundwater inputs, stream flow) that limit siltation, substrate embeddedness, and submergent rooted plants in the main channel (Waters 1995). Submerged plants (e.g., *Potamogeton* sp.) were occasionally present in our study streams, but usually in areas of reduced flow over silt substrates. Others have also associated the Topeka shiner with coarse substrates, which may be silt covered or not (Barber 1986; Hatch 2001; Kuitunen 2001). The disagreement among studies about Topeka shiner habitat associations might be expected for this generalist, pioneering species. Kuitunen (2001) called the Topeka shiner a “specialist for prairie streams,” which are usually described as harsh environments (Poff 1996) with basic differences from

streams in other biomes (Wiley et al. 1990). The differences relate to the reversed organization of grassland and forested riparian zones along the river continuum.

Our study results were more important in showing linkages among habitat variables and biotic controls at several scales that influence overall stream health than in identifying habitat needs of the Topeka shiner. However, our work has several pragmatic applications. We found several year-classes in each watershed and provide the first quantitative measures of population abundance that can be used as benchmarks for future monitoring programs (Shearer 2003). This new information on the status of the species and the comprehensive nature of the state conservation plan (Shearer 2003) were reasons for exempting South Dakota from critical habitat designation under the Endangered Species Act (U.S. Office of the Federal Register 2004).

To improve the efficiency of future surveys, we developed models that showed the likelihood of Topeka shiner presence in stream segments, thus identifying streams and watersheds in need of conservation and aiding in finding new populations (Wall et al. 2004). We developed biological insight about where to sample within a reach, which are partially supported by the statistical models. We would sample in low gradient, low-order streams, and pools or runs of moderate depth, low bank height, and water velocity over coarse substrates (Blausey 2001). We would also sample backwater macrohabitats and nearby floodplain wetlands where we have since documented Topeka shiners, as have others (Hatch 2001). Additionally, we would be attentive to the presence of nest-building stream fishes and introduced species such as largemouth bass, which may have positive and negative impacts, respectively, on the Topeka shiner (Schrunk et al. 2001).

In conclusion, we attempted to identify controls on Topeka shiner populations at different spatial scales as recommended (Storch 1997; Hooper et al. 2001; Schneider 2001). The Topeka shiner is distributed across the landscape accord-

ing to a nested hierarchy of spatial levels from broad ecoregions and drainage units (Wall et al. 2004); to local watersheds, valley segments, reaches (this study); to macro and microhabitats (Blausey 2001). We show that the Topeka shiner is related to valley segment and reach scale variables that indicate intact hydrological processes (i.e., groundwater input, wetlands, riparian zones, low bank height, etc.). Our results indicate that watershed scale conservation efforts such as wetland conservation and maintaining riparian buffers are beneficial to Topeka shiner habitat at several scales. In the historic range of the Topeka shiner, conservation should be focused on areas of species occurrence where reproduction and age structure are greatest, stressors are least, and land use and dominant biological processes are relatively intact (Groves et al. 2002).

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Appendix A. Valley segment habitat variables, GIS data source, and method used to derive variables. Percent occurrence of variables in valley segments with Topeka shiner events, and in all available valley segments in three rivers in South Dakota.

Habitat variable and numeric code	Available valley segments (%) (n = 8693)	Valley segments with events (%) (n = 64)	GIS data source	Method (Wall et al. 2004)
Stream size class			EPA River Reach	Shreve link
1 = headwater (link = 0 to 9)	79.5	29.3	3 files	
2 = creek (link = 10 to 75)	12.6	46.1	(USEPA 1999)	
3 = small river (link = 76 to 1500)	5.8	23.1		
4 = large river (link > 1500)	2.2	1.5		
Channel slope class			Digital elevation model (DEM)	elevation change between valley segment t-node and f-node relative to stream size and EDU
1 = low (headwater < 0.0043; creek < 0.0009; small river < 0.0004; large river < 0.0004)	57.1	63.1		
2 = medium (headwater 0.0043 to 0.0087; creek 0.0009 to 0.0019; small river 0.0004 to 0.0022; large river 0.0004 to 0.0005)	21.8	33.8		
3 = high (headwater > 0.0087; creek > 0.0019; small river > 0.0022; large river > 0.0005)	21.1	3.1		
Network position class			EPA River Reach	downstream Shreve link
0 = none (no discrepancy – e.g., headwater to headwater)	81.8	80.0	3 files	
1 = headwater to creek (link = 0 to 9 and d-link = 10 to 75)	11.9	9.3	(USEPA 1999)	
2 = headwater to small river (link = 0 to 9 and d-link = 76 to 1500)	3.3	1.5		
3 = headwater to large river (link = 0 to 9 and d-link = 10 to 75)	2.2	1.5		
4 = creek to small river (link = 10 to 75 and d-link = 76 to 1500)	0.7	4.6		
5 = creek to large river (link = 10 to 75 and d-link > 1500)	0.3	3.1		
6 = small river to large river (link = 76 to 1500 and d-link > 1500)	0.05	0.0		
Parent material class			Soil Survey Geographic (SSURGO)	dominant parent materials by soil map units
1 = alluvium	47.6	92.3	database; State	
4 = glacial till	25.9	3.1	Soil Geographic (STATSGO)	intersecting majority of valley segment
9 = outwash	17.0	3.1	database	
8 = loess	3.2	1.5	(USDA 1991, 1995)	
6 = Sioux quartzite	1.1	0.0		
14 = shale	0.5	4.7		
other (i.e., eolian sands [3], silty glacial till [5], lacustrine [7], ponded soils [13])	0.0	0.0		

Habitat variable and numeric code	Available valley segments (%) (n = 8693)	Valley segments with events (%) (n = 64)	GIS data source	Method (Wall et al. 2004)
Stream flow			National wetland inventory (NWI) (USFWS 1993)	classified valley segments according to NWI flow regime classifications (Cowardin et al. 1979) and system, subsystem and water regime modifier codes of NWI polygons intersecting majority of valley segment
1 = perennial (has surface water throughout the year in all years except during extreme drought, approximately once every 100 years)	8.3	12.3		
2 = intermittent (has surface water for most of the year)	19.0	69.2		
3 = seasonal (has surface water during growing season, but is absent by the end of the season in most years)	50.3	18.5		
4 = temporary (has surface water for brief periods during the growing season)	22.6	0.0		
Groundwater potential			DEM and parent material classification	MRI-DARCY model (Baker et al. 2003) groundwater velocity to segments derived from hydraulic conductivity of parent materials and slope
1 = low (groundwater velocity 0–0.35 m/d)	74.0	23		
2 = medium (groundwater velocity 0.36 – 0.15 m/d)	15.5	29		
3 = high (>0.15 m/d)	10.5	48		
Downstream connectivity			EPA River Reach 3 files	Valley segments connected downstream to water body polygons > 1 ha
0 = no	96.4	98.5		
1 = yes	3.6	1.5		
Upstream connectivity			EPA River Reach 3 files	Valley segments connected upstream to water body polygons > 1 ha
0 = no	96.4	98.5		
1 = yes	3.6	1.5		
Floodplain influence			DEM	slope from DEM to determine valley wall. Valley segments > 249 m within valley wall of small-large rivers classed as 1
1 = yes	3.3	4.6		
2 = no	96.7	95.4		

Appendix B. Relative abundance of fishes found by seining in streams with and without Topeka shiners in the James, Vermillion, and Big Sioux River basins in South Dakota, 1999 and 2000. Empty cell indicates no fish captured.

Family and scientific name	Basin: Topeka shiner: No. streams:	James River		Vermillion River		Big Sioux River	
		Absent 9	Present 8	Absent 9	Present 5	Absent 12	Present 8
Cyprinidae							
<i>Campostoma anomalum</i>	Central stoneroller	0.00	1.60	0.21	0.14	0.62	1.32
<i>Cyprinella lutrensis</i>	Red shiner	17.00	4.71	4.52	12.44	11.04	14.80
<i>Cyprinus carpio</i>	Common carp	1.71	0.98	0.20	0.57	7.44	2.19
<i>Hybognathus hankinsoni</i>	Brassy minnow	0.65	9.33	1.61	1.82	0.17	0.21
<i>Luxilus cornutus</i>	Common shiner	0.03	5.14	2.32	7.01	12.40	10.30
<i>Notropis atherinoides</i>	Emerald shiner	0.32			0.02		
<i>N. dorsalis</i>	Bigmouth shiner	0.22	1.60	8.28	1.37	18.62	12.74
<i>N. stramineus</i>	Sand shiner	22.57	2.98	36.34	31.29	23.36	22.55
<i>Pimephales notatus</i>	Bluntnose minnow		0.33			1.38	1.98
<i>P. promelas</i>	Fathead minnow	2.90	24.64	18.17	14.64	10.37	7.55
<i>Rhinichthys obtusus</i>	Western blacknose dace			0.01		0.86	0.15
<i>Semotilus atromaculatus</i>	Creek chub	1.33	9.13	10.15	6.12	6.66	10.35
Cyprinodontidae							
<i>Fundulus sciadicus</i>	Plains topminnow	0.19					
Catostomidae							
<i>Carioides carpio</i>	River carpsucker		0.43	0.03			0.54
<i>Catostomus commersonii</i>	White sucker	1.35	6.64	1.41	1.70	3.51	8.18
<i>Moxostoma macrolepidotum</i>	Shorthead redhorse	0.14	1.01	0.04	0.08	0.10	0.27
Ictaluridae							
<i>Ameiurus melas</i>	Black bullhead	24.95	22.81	5.10	12.10	1.78	2.80
<i>Ictalurus punctatus</i>	Channel catfish	2.52	0.26	0.20		0.02	0.01
<i>Noturus flavus</i>	Stonecat	0.03		0.13		0.14	0.16
<i>N. gyrinus</i>	Tadpole madtom	0.11			0.04	0.09	0.11
Centrarchidae							
<i>Lepomis cyanellus</i>	Green sunfish	2.08	4.16	1.11	3.33	0.06	0.41
<i>L. humilis</i>	Orangespotted sunfish	13.75	3.83	0.94	6.73	0.54	1.72
<i>L. macrochirus</i>	Bluegill			5.88	0.12		
<i>Micropterus salmoides</i>	Largemouth bass	2.03		0.51	0.06		0.01
<i>Pomoxis nigromaculatus</i>	Black crappie	4.57	0.16	2.19		0.05	0.00
<i>P. annularis</i>	White crappie	0.11		0.40	0.02		
Percidae							
<i>Etheostoma exile</i>	Iowa darter	0.00	0.00	0.00	0.00	0.03	0.00
<i>E. nigrum</i>	Johnny darter	0.22	0.16	0.22	0.30	0.62	1.29
<i>Perca flavescens</i>	Yellow perch			0.03		0.10	0.15
<i>Percina maculata</i>	Blackside darter						0.01
<i>Sander vitreus</i>	Walleye	0.03					
Clupeidae							
<i>Dorosoma cepedianum</i>	Gizzard shad	0.84					
Hiodontidae							
<i>Hiodon alosoides</i>	Goldeye			0.01			
Esocidae							
<i>Esox lucius</i>	Northern pike		0.10	0.01	0.10	0.04	0.20

Relationships between Land Use and Stream Ecosystems: A Multistream Assessment in Southwestern Michigan

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Abstract.—Ecologists recognize that surrounding land use can influence the structure and function of aquatic ecosystems, but few studies have explicitly examined the relative effects of different types of land use on stream ecosystems. We quantified the relationships between different land uses (forested, urban, agricultural with or without riparian buffers) and stream physicochemical variables and resident fish assemblages in 21 southwestern Michigan streams. These streams were located within a single basin (Kalamazoo River) and ecoregion to minimize differences in natural landscape conditions. Streams responded to a gradient of land use, with forested streams having the least degraded water quality, physical habitat, and fish assemblages, and agricultural streams lacking buffers being the most degraded. Urban and agricultural streams with buffers displayed characteristics intermediate to forested and agricultural streams lacking buffers. In general, habitat complexity and water quality declined across this land-use gradient from forested to agricultural streams, whereas fish density, richness, and dominance by tolerant species increased along the land-use gradient. Although urban streams had lower percentages of altered land use (i.e., <40% urban) in their catchments compared to agricultural streams (i.e., >50% agriculture), both land uses appeared to have similar detrimental effects on streams suggesting higher per unit area impacts of urbanization on streams. The presence of forested riparian buffers along agricultural streams increased the complexity of instream habitat, but resulted in few benefits to fish assemblages, suggesting that stream water quality in altered landscapes may be constraining fish assemblages more than physical habitat.

INTRODUCTION

In the Midwestern United States, land has been rapidly transformed from wetlands, forests, and prairies to agriculture and urban areas beginning in the 1800s. These dramatic and continuing changes in land use have been linked to surface water degradation, including poor water quality, reduced ecological function, and loss of bio-

logical diversity (Allan 1995). For example, by the end of the 20th century, more than 200,000 km of streams and rivers in the United States were designated as “impaired” from activities associated with agricultural and urban land uses (USEPA 2000). Earlier, Judy et al. (1984) inferred that water quality adversely affected fish assemblages in 56% of U.S. waters, and 29% were adversely affected by agriculture. A key to understanding the effects of land use on aquatic ecosystems is to relate their present ecological condition to the extent of landscape alteration.

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Scientists have long suspected that land use plays a major role in determining the condition of aquatic ecosystems. Hynes (1975) theorized that the catchment had primary control over the overall ecological condition of a stream. This perspective evolved into a widely accepted hierarchical view of stream ecosystems, which holds that processes at smaller scales are controlled in part by processes operating at larger scales (Frissell et al. 1986; Gregory et al. 1991). Recent research on Midwestern stream fish assemblages has illustrated these hierarchical patterns. In statewide studies of Michigan streams, temperature and flow regime emerged as major natural controls on fishes at broad spatial scales (Zorn et al. 2002; Wehrly et al. 2003). At local scales (e.g., within a watershed), however, variability in natural temperature and flow regimes is reduced, and land use may emerge as an important factor structuring stream assemblages by altering temperature, hydrology, and instream habitat. Viewing streams in this hierarchical context can help to clarify how land use alters stream ecosystems. For example, changes in land use can negatively affect local instream structure (e.g., biological communities) via alteration of landscape processes (e.g., hydrology; Paul and Meyer 2001). Studies on urban or suburban areas generally have found that urbanization increases surface runoff, channel incision, and nutrient and metal concentrations, which can lead to declines in algal, invertebrate, and fish diversity (Paul and Meyer 2001). Recent studies also suggest a strong relationship between catchment land use and stream water chemistry and various indices of biotic integrity (e.g., Richards et al. 1996; Allan et al. 1997; Scott et al. 2002; Snyder et al. 2003).

While ecologists generally agree that intensive land use affects stream ecosystems, the relative influence of different land-use types on streams is poorly understood. Different types of land use may influence the structure and function of aquatic ecosystems differently. For example, the type and timing of nutrients delivered to a stream can vary greatly among streams draining agricultural, urban, and forested catchments. In ag-

ricultural land, overapplication of fertilizers to agricultural fields and rapid water removal by drainage tiles often result in pulsed inputs of nitrogen and phosphorus to adjacent streams (Omernik 1977; Cole et al. 1993). In urban areas, inputs from non-point sources (e.g., fertilizer application to residential areas, failing septic systems) and point discharge (e.g., wastewater treatment plants) result in more continuous inputs of phosphorus to streams (Omernik 1977; Paul and Meyer 2001). In contrast, in forested areas, nutrient retention and uptake by vegetation in the catchment result in lower inputs of both nitrogen and phosphorus to streams (Likens et al. 1970). Consequently, variation in nutrient inputs, hydrology, and other catchment characteristics, related to differences in land use, are likely to translate into differences in water chemistry and biological characteristics in receiving streams.

In this study, we investigated the relative effects of different land uses on stream physicochemical variables and fish assemblage structure in 21 Michigan streams located in a single basin. The specific objectives of this study were to (1) quantify the relationships between different land uses and physical, chemical, and fish assemblage characteristics within these 21 streams, and (2) determine if distinctive stream fish assemblages were associated with specific land uses. We sampled catchments within a single basin and ecoregion that had relatively homogeneous physiographic characteristics, but differed in their dominant land use: forested, urban, agricultural with a riparian buffer, or agricultural without a riparian buffer. We then used a combination of univariate and multivariate statistical approaches to compare the response variables of interest among land uses.

METHODS

Site Description

This study was conducted during summer 2002 in the Kalamazoo River Basin (KRB) in south-

western Michigan (Figure 1), which is located within the Southern Michigan-Northern Indiana Till Plain ecoregion (Omernik and Gallant 1988). Twenty-one second- to third-order streams were selected in the KRB to represent four land-use types: forested ($N = 5$), low-intensity urban ($N = 4$), agricultural with riparian buffer ($N = 6$), and agricultural without riparian buffer ($N = 6$) (Table 1). Streams draining watersheds dominated by agricultural land use but retaining a 1-km forested riparian buffer upstream of the selected site will be referred to hereafter as “buffered.” Agricultural streams that did not possess any forested riparian buffer within a 1-km reach upstream of the site will be referred to as “unbuffered.” All streams were low-gradient ($<1\%$), sand-bed streams (d_{50} range 1–2), and located in separate catchments less than or equal to 52 km² in size. Streamwater tempera-

tures and low-flow yields were similar among sites and indicated that all streams were cool- or coldwater (Zorn et al. 2002). Basin surficial geology was dominated by end moraines of medium texture, glacial outwash sand and gravel, and lacustrine sand and gravel.

Land Use

ArcGIS 8 was used to delineate catchments and quantify land use for each site. Catchments were delineated from digital elevation models using a watershed and stream delineation tool (<http://ceprofs.tamu.edu/folivera/GISTools/wsdtd/home.htm>). Delineated catchments were verified by comparing them to USGS topographic and 12-digit HUC layers. Percent land use/land cover (i.e., forested, urban, agricultural, wetland) was calculated for each catchment using Landsat

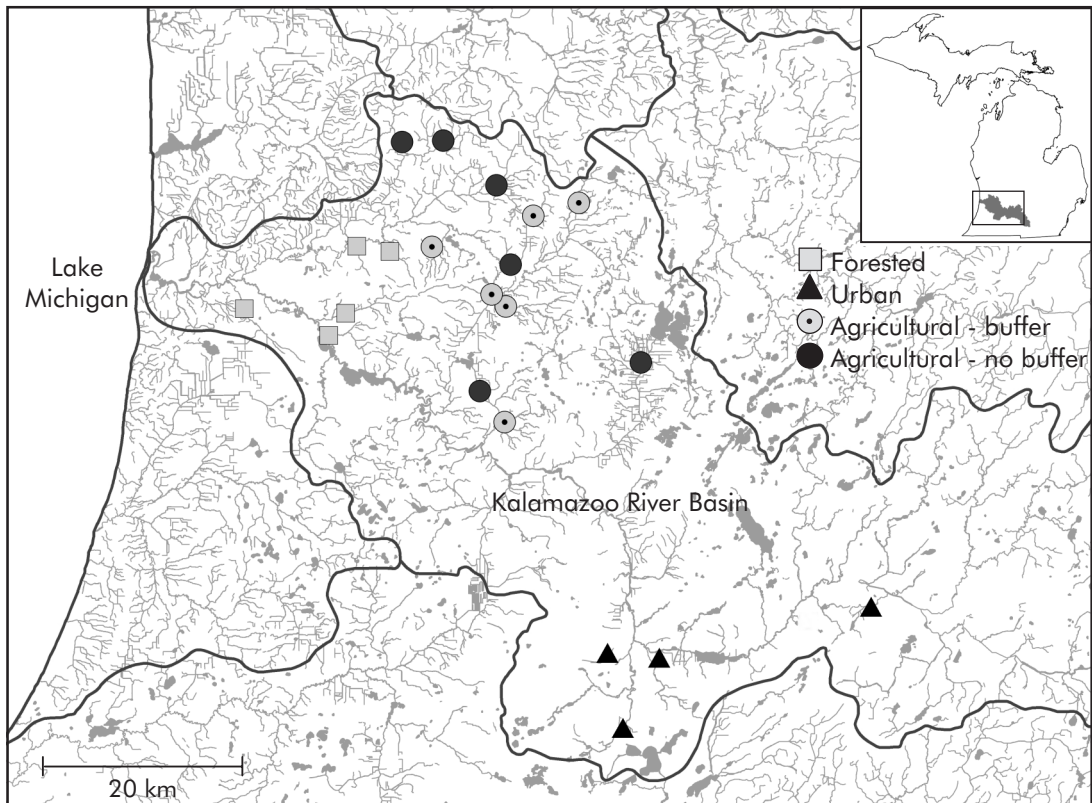


Figure 1. Locations of the 21 study streams sampled in the Kalamazoo River basin, southwestern Michigan, 2002.

Table 1. Range of percent land use and drainage area of catchments within each land-use category for streams sampled in the Kalamazoo River basin, Michigan, in 2002. Bold indicates basis for catchment designation. NA = not applicable.

Parameter	Forested (N = 5)	Urban (N = 4)	Agricultural- buffer (N = 6)	Agricultural- no buffer (N = 6)
Forest (%)	50–67	19–44	9–33	4–26
Urban (%)	4–9	29–40	5–12	4–7
Agriculture (%)	7–29	1–36	48–76	54–89
Drainage area (km ²)	16–39	12–40	5–52	13–30

Thematic Mapper imagery data from 1997 to 2000. Michigan Resource Information System (MIRIS) (1:24,000 scale) and Tiger Census 1995 hydrography were used to display stream layers. Data are available online at Michigan's Geographic Data Library (<http://www.mcgi.state.mi.us/mgdl/>).

Physical Habitat

At each site, local habitat condition was characterized using quantitative and qualitative metrics in June 2002. Quantitative measurements, including cross-sectional channel dimensions, substrate characteristics, and canopy cover, were made along five transects at 50-m intervals over a 200-m reach. Substrate was quantified using the Wolman pebble count technique (Wolman 1954) and particles were classified into size categories using a gravelometer. Canopy cover was measured using a concave hemispherical densiometer. Length of overhanging vegetation, length of undercut bank, and width of the riparian zone (up to 50 m) also were measured at each transect. Embeddedness and bank stability were assessed visually at each transect. Embeddedness values were ranked from 1 to 4 (1 = extremely embedded, >80%; 4 = little or no embeddedness, <20%) and bank stability also was ranked from 1 to 4 (1 = bare, sloughing banks, 4 = vegetated banks). Additional parameters were measured over the entire reach such as volume of woody debris (Lamberti and Gregory 1996) and the qualitative habitat evaluation index (QHEI; Rankin 1989). Finally, current velocity and cross-sectional area were measured three

to four times during the summer to calculate stream discharge. Base flow discharge measurements were then divided by watershed area to calculate low-flow yield, an index of groundwater input (Zorn et al. 2002).

Water Quality

Instantaneous water quality measurements were taken 14 July 2002 and 9 September 2002 at base flow and during mid-day hours. To avoid variability due to precipitation events, samples were taken at least 2 weeks after a rainfall. Dissolved oxygen, temperature, and specific conductance were measured using a YSI meter (model 85, YSI, Yellow Springs, Ohio). Turbidity was measured using a turbidimeter (DRT-15CE, HF Scientific Inc., Ft. Myers, Florida).

Water samples ($N = 3$ per site) were collected at base flow from each stream during July and September 2002 for analysis of nitrate (NO_3^- -N), ammonium (NH_4^+ -N), soluble reactive phosphorus (SRP), dissolved organic carbon (DOC), and specific ultraviolet absorbance (SUVA). Streamwater was filtered in the field through a Whatman GF/F filter (0.7 μm) and stored on ice. In the laboratory, samples for NH_4^+ -N, NO_3^- -N, and SRP were stored at -20°C , and samples for DOC and SUVA were acidified with 100 μL of concentrated HCl and stored at 4°C until analyzed. Ammonium was analyzed using the phenol-hypochlorite method (Solorzano 1969), NO_3^- -N using a Dionex ion chromatograph (USEPA 1993), SRP using the ammonium molybdate spectrophotometric method (Murphy and Riley

1962), and DOC using a Shimadzu 5000 TOC Analyzer (APHA 1995). Specific ultraviolet absorbance (SUVA), a surrogate of organic carbon quality, was determined by dividing the ultraviolet absorbance at 254 nm by its DOC concentration (Ravichandran et al. 1998; Strauss and Lamberti 2002).

Fishes

Within each 200-m study reach, a representative 100-m reach was blocked upstream and downstream with seines (mesh diameter = 5 mm) and sampled with a Smith-Root model 12 backpack electrofisher. All reaches were sampled using triple-pass removal (Li and Li 1996) at base flow in July–August 2002. All individuals were identified to species and measured for mass and total length. Individuals that could not be identified in the field were preserved in 10% formalin and identified in the laboratory. Species were assigned to tolerance classes according to published designations (Becker 1983; Simon 1997; Mundahl and Simon 1999). Tolerant fishes typically are those that can tolerate degraded habitat and water quality, whereas intolerant fishes are sensitive to declines in habitat or water quality. Index of biotic integrity (IBI) scores were calculated using modified indices for the Southern Michigan–Northern Indiana Till Plain (MITP) ecoregion (Simon 1997) and midwestern coldwater streams (Mundahl and Simon 1999). The MITP IBI was modified to categorize salmonid species as sensitive species in the KRB. Both indices were used because many of the streams bordered the coolwater category. The highest IBI score from either the MITP or coldwater IBI was assigned as the final value for each site. Patterns in IBI scores among land uses were similar, regardless of the IBI employed in the analysis (A. H. Moerke, unpublished data).

Statistical Analyses

Differences in nutrient concentrations and fish metrics among land-use categories were assessed

using analysis of variance (ANOVA). Variables were transformed when necessary to meet assumptions of ANOVA, and nonnormal and ranked data were analyzed using the nonparametric Kruskal–Wallis test. Statistical analyses were conducted using SYSTAT v.10.2 (SPSS Inc., Chicago). Fish species composition was related to catchment land use using nonmetric multidimensional scaling (NMS) in PC-ORD v. 4.25 (McCune and Mefford 1999). McCune and Grace (2002) suggest that NMS generally is the most effective ordination method for assemblage data. NMS was conducted on the abundances of fish species at each site. Rare species (i.e., occurring at only one site or comprising less than 5% of the total catch) were excluded from the analyses. Thirty-seven fish species were captured, but only 23 species were used in the ordination (Table 2). Abundances were log-transformed prior to the analysis. NMS analysis was carried out using the autopilot mode (i.e., 400 iterations, Sorensen's distance, instability criterion of 0.00001, and a step length of 0.20). A Monte Carlo test was run on the final stress to determine the best dimensional solution. Individual fish species were correlated with the ordination axes to determine which species best accounted for the separation of streams in the ordination. The percent catchment land use (i.e., percent forest, percent urban, percent agriculture, percent wetland) also was correlated with the ordination axes to determine how much of the separation in the streams could be explained by land use.

RESULTS

Relationships between Land Use and Stream Habitat

Stream geomorphology differed significantly between forested versus agricultural catchments (Table 3). Sinuosity and width:depth ratios were highest in forested streams and lowest in unbuffered agricultural streams. Discharge or low-flow yield did not differ significantly among land uses,

Table 2. List of common and scientific names of fish species collected in the Kalamazoo River basin, Michigan, in 2002.

Common name	Scientific name
American brook lamprey	<i>Lampetra appendix</i>
Bigmouth shiner	<i>Notropis dorsalis</i>
Black bullhead*	<i>Ameiurus melas</i>
Black crappie*	<i>Pomoxis nigromaculatus</i>
Eastern blacknose dace	<i>Rhinichthys atratulus</i>
Blackside darter	<i>Percina maculata</i>
Bluegill	<i>Lepomis macrochirus</i>
Bluntnose minnow	<i>Pimephales notatus</i>
Brook silverside*	<i>Labidesthes sicculus</i>
Brook stickleback	<i>Culaea inconstans</i>
Brook trout	<i>Salvelinus fontinalis</i>
Brown trout*	<i>Salmo trutta</i>
Central mudminnow	<i>Umbra limi</i>
Central stoneroller	<i>Campostoma anomalum</i>
Common carp	<i>Cyprinus carpio</i>
Common shiner	<i>Luxilus cornutus</i>
Creek chub	<i>Semotilus atromaculatus</i>
Fathead minnow*	<i>Pimephales promelas</i>
Golden shiner*	<i>Notemigonus crysoleucas</i>
Goldfish*	<i>Carassius auratus auratus</i>
Green sunfish	<i>Lepomis cyanellus</i>
Hornyhead chub*	<i>Nocomis biguttatus</i>
Johnny darter	<i>Etheostoma nigrum</i>
Lake chubsucker*	<i>Erimyzon sucetta</i>
Largemouth bass	<i>Micropterus salmoides</i>
Mottled sculpin	<i>Cottus bairdii</i>
Northern hog sucker*	<i>Hypentelium nigricans</i>
Pirate perch	<i>Aphredoderus sayanus</i>
Pumpkinseed*	<i>Lepomis gibbosus</i>
Rainbow darter*	<i>Etheostoma caeruleum</i>
Rainbow trout	<i>Oncorhynchus mykiss</i>
Redfin pickerel	<i>Esox americanus</i>
(also known as grass pickerel)	
Rock bass*	<i>Ambloplites rupestris</i>
Stonecat	<i>Noturus flavus</i>
White sucker	<i>Catostomus commersonii</i>
Yellow bullhead	<i>Ameiurus natalis</i>
Yellow perch*	<i>Perca flavescens</i>

* = rare species excluded from the ordination.

but we observed a trend toward lower and less variable discharge and low-flow yield in forested streams than in urban streams.

Mean scores for the qualitative habitat evaluation index (QHEI) were highest in forested streams and lowest in agricultural streams, but QHEI scores did not differ significantly among land-use types (Table 3). Bank stability, percent overhanging vegetation, and percent undercut

banks also did not differ significantly among land uses. In contrast, LWD volume, embeddedness, canopy cover, and riparian width differed among land-use types. Volume of LWD was highest in forested streams and buffered agricultural streams, but it was nearly absent in unbuffered agricultural streams. Embeddedness ranks were highest (i.e., lower embeddedness) in urban streams and lowest in forested and unbuffered agricultural streams. Canopy cover was similar in forested, urban, and buffered agricultural streams, but significantly lower in unbuffered agricultural streams. Riparian width was significantly greater in forested and buffered agricultural streams than in urban and unbuffered agricultural streams.

Relationships between Land Use and Water Quality

Water quality varied substantially both within and among land-use types (Table 4). Dissolved oxygen (percent saturation) was on average lowest in urban and buffered agricultural streams, but varied most in unbuffered agricultural streams. Mean temperature was significantly lower in forested streams compared to urban streams and unbuffered agricultural streams. Turbidity was significantly lower in forested and urban streams than in agricultural streams. Specific conductivity was significantly lower in forested streams than in urban streams and unbuffered agricultural streams. Dissolved organic carbon concentrations and SUVA did not differ significantly among land-use types.

Streamwater concentrations of NO_3^- -N, NH_4^+ -N, and SRP differed significantly among land uses (Figure 2). Nitrate concentrations were significantly lower in forested streams than in unbuffered agricultural streams during both July and September. Ammonium concentrations were significantly lower in forested streams than in agricultural streams, and SRP concentrations were significantly lower in forested and urban streams than in unbuffered agricultural streams. Ammonium and especially SRP concentrations generally were higher in July than in September.

Table 3. Mean (range) of habitat characteristics of streams within each land-use category for streams sampled in the Kalamazoo River basin, Michigan, in 2002. Values with the same lowercase letter are not significantly different ($P > 0.05$).

Characteristic	Forested	Urban	Agricultural-buffer	Agricultural-no buffer
<i>Channel characteristics</i>				
Sinuosity rank*	2.6 (2.0–3.0) ^a	1.5 (0–3.0) ^{ab}	1.8 (0–3.0) ^{ab}	0.2 (0–1.0) ^b
Width:depth [†]	37.7 (26.7–51.8) ^a	33.0 (17.9–53.8) ^{ab}	30.1 (12.4–54.0) ^{ab}	18.3 (1.4–29.5) ^b
Discharge (m ³ /s)	0.08 (0.06–0.12) ^a	0.17 (0.05–0.46) ^a	0.15 (0.05–0.33) ^a	0.09 (0.03–0.14) ^a
Low flow yield	0.004 (0.003–0.005) ^a	0.006 (0.001–0.010) ^a	0.006 (0.003–0.015) ^a	0.005 (0.002–0.008) ^a
<i>Instream and riparian habitat</i>				
QHEI*	50 (47–57) ^a	46 (26–62) ^a	45 (36–56) ^a	32 (27–40) ^a
LWD volume (m ³ /100m ²) [†]	0.57 (0.21–1.28) ^a	0.26 (0.01–0.63) ^{ab}	0.31 (0.10–0.75) ^{ab}	0.02 (0–0.08) ^b
Embeddedness rank*	1.0 (1.0) ^a	2.6 (2.3–2.8) ^b	1.2 (1.0–2.4) ^{ab}	1.0 (1.0) ^a
Bank stability rank*	3.5 (2.9–4.0) ^a	2.7 (2.4–2.9) ^a	3.0 (2.3–3.5) ^a	3.5 (1.4–4.0) ^a
Overhanging vegetation (%) [†]	10.0 (2.5–19.3) ^a	22.8 (10.0–39.2) ^a	17.9 (8.3–32.5) ^a	23.1 (4.2–63.4) ^a
Undercut bank (%) [†]	3.2 (2.0–6.5) ^a	2.1 (0–6.2) ^a	3.0 (0.8–8.8) ^a	2.5 (0.1–6.4) ^a
Canopy cover (%) [†]	76.1 (61.7–83.8) ^a	65.1 (51.2–82.9) ^a	73.2 (49.5–84.3) ^a	23.9 (1.2–67.7) ^b
Riparian width (m) [†]	50.0 (50.0) ^a	16.1 (2.8–50.0) ^b	39.8 (11.5–50.0) ^a	6.7 (4.1–8.3) ^b

* = statistical significance among groups determined using a Kruskal-Wallis test. [†] = arc-sin square root transformed prior to statistical analysis. [†] = $\log(x + 1)$ transformed prior to statistical analysis.

Relationships between Land Use and Fish Assemblage Structure

Fish metrics including fish density, species richness, percent tolerant individuals, percent intolerant individuals, and IBI scores appeared to respond to differences in catchment land use (Table 5). Mean fish densities were lowest in forested streams and highest in unbuffered agricultural streams. Fish species richness also was significantly lower in forested streams than in agricultural streams. The percentage of tolerant fishes was significantly lower in forested streams than in urban streams or buffered or unbuffered

agricultural streams. Accordingly, the mean percentage of intolerant fishes was 8–15 times higher in forested streams than in streams of other land-use types. Index of biotic integrity scores also were significantly higher in forested streams compared to other streams. Forested streams had a mean IBI score of 50 out of 60, which suggests good to excellent biological condition, whereas streams in other land uses scored about 35, which indicates poor to fair biological condition. Total fish biomass and mean individual mass did not differ significantly among land-use types. However, total and individual biomass tended to be higher in urban streams and unbuffered agricultural

Table 4. Mean (range) of water quality parameters of streams within each land-use category for streams sampled in the Kalamazoo River basin, Michigan, in 2002. Values with the same lowercase letter are not significantly different ($P > 0.05$).

Parameter	Forested	Urban	Agricultural-buffer	Agricultural-no buffer
DO (% saturation)	118 (101–135) ^{ab}	98 (82–109) ^a	99 (90–121) ^a	134 (97–155) ^b
Mean summer temperature (°C)	14.5 (13.2–16.0) ^a	18.7 (17.2–20.3) ^b	17.0 (14.5–19.4) ^{ab}	18.6 (17.2–20.3) ^b
Turbidity (NTU) [†]	3.42 (1.49–4.21) ^a	2.90 (1.29–3.97) ^a	12.86 (7.58–27.35) ^b	12.96 (3.88–36.25) ^b
Specific conductivity (μs/cm)	383 (285–460) ^a	771 (533–1164) ^b	529 (391–675) ^{ab}	618 (503–785) ^b
DOC (mg/L)	4.87 (1.65–8.60) ^a	5.52 (1.65–7.71) ^a	4.23 (2.14–7.15) ^a	4.35 (1.66–6.71) ^a
SUVA (Abs ₂₅₄ /DOC)	0.020 (0.004–0.057) ^a	0.033 (0.006–0.036) ^a	0.026 (0.011–0.047) ^a	0.032 (0.017–0.122) ^a

[†] = $\log(x + 1)$ transformed prior to statistical analysis.

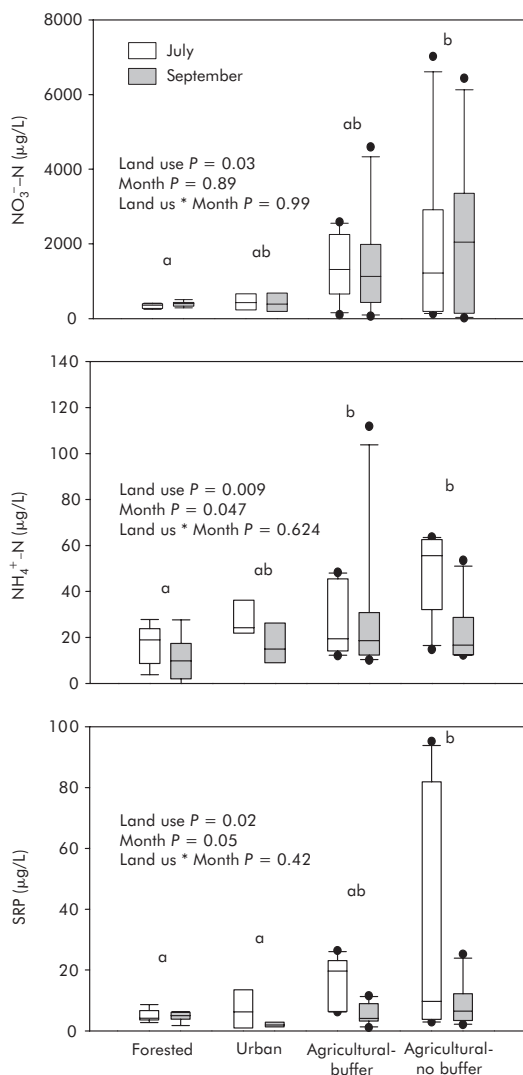


Figure 2. Dissolved $\text{NO}_3^- \text{-N}$, $\text{NH}_4^+ \text{-N}$, and SRP concentrations for streams draining catchments dominated by different land uses in the Kalamazoo River basin, Michigan. Nutrient concentrations shown are for samples collected in July and September, 2002. Values with the same lowercase letter are not significantly different ($P > 0.05$). The box bottom and top represent the 25th and 75th percentiles, the box midline is the median, whiskers are 10th and 90th percentiles, and the dots represent outliers.

streams compared to forested and buffered agricultural streams.

Nonmetric multidimensional scaling (NMS) analysis of fish abundance was optimized with a two-dimensional solution (Monte Carlo test, 50

runs, $P = 0.02$; final stress = 13.4%), that explained 87.7% of the variation in the fish assemblage (excluding rare species). The first NMS axis accounted for 31.6% of the variation among streams, while the second axis accounted for 56.1%. Separation in sites along both NMS axes was highly influenced (Pearson's $r > 0.50$, $P < 0.05$) by two groups of fishes: (1) species typical of a coolwater fish assemblage, such as American brook lamprey *Lampetra appendix*, brook trout *Salvelinus fontinalis*, and mottled sculpin *Cottus bairdii*; and (2) tolerant fishes, such as bluntnose minnow *Pimephales notatus*, creek chub *Semotilus atromaculatus*, and white sucker *Catostomus commersonii* (Figure 3). The two NMS axes were related significantly to catchment land use ($r > 0.45$, $P < 0.05$; Figure 3). Axis 1 was related to the percent of forest cover and percent of agricultural cover within a catchment. Streams with a lower percentage of forest and a higher percentage of agriculture in their catchment corresponded to sites on the right side of the ordination, whereas streams with a higher percentage of forest and a lower percentage of agriculture corresponded to streams on the left side of the ordination. Axis 2 was related to the percent of forest cover and percent of urban cover, where streams with a higher percentage of urban cover and lower percentage of forest cover corresponded to sites near the bottom of the ordination.

DISCUSSION

Although broad relationships between land use and stream characteristics have been described previously (e.g., Osborne and Wiley 1988; Hunsaker and Levine 1995; Wang et al. 2001), few studies have explicitly addressed the relative effects of different land uses on stream ecosystems. To the best of our knowledge, only one other study (Van Sickle et al. 2004) has evaluated stream responses to multiple land uses (i.e., forested, agricultural, and urban) using a replicated, basin-wide design as we have conducted. Most previous studies that have assessed land-use effects on streams

Table 5. Mean (range) of fish metrics for streams within each land-use category for streams sampled in the Kalamazoo River basin, Michigan, in 2002. Values with the same lowercase letter are not significantly different ($P > 0.05$).

Metric	Forested	Urban	Agricultural-buffer	Agricultural-no buffer
Density (fish/100m ²)	47 (19–85) ^a	60 (49–81) ^{ab}	78 (29–190) ^{ab}	222 (53–441) ^b
Species richness	7 (6–7) ^a	8 (5–11) ^{ab}	11 (6–15) ^b	11 (8–12) ^b
Tolerant individuals (%) [†]	28.9 (1.2–77.9) ^a	86.7 (71.6–97.8) ^b	65.5 (51.2–74.2) ^b	56.3 (19.9–79.6) ^b
Intolerant individuals (%) [†]	59.5 (44.8–96.5) ^a	5.2 (0–20.4) ^b	8.6 (0–26.4) ^b	4.7 (0–14.1) ^b
Index of biotic integrity*	50 (42–54) ^a	34 (30–38) ^b	36 (30–42) ^b	36 (30–42) ^b
Total biomass (kg) [‡]	2.2 (1.0–4.8) ^a	5.2 (1.1–9.5) ^a	3.4 (0.5–7.1) ^a	5.6 (1.8–11.9) ^a
Mean individual mass (g) [‡]	10.5 (3.1–24.6) ^a	19.9 (6.2–33.2) ^a	10.0 (3.5–21.6) ^a	27.6 (2.1–133.2) ^a

[†] = arc-sin square root transformed. [‡] = log($x + 1$) transformed. *value < 40 = poor; values of 40–44 = fair; values > 44 = good to excellent.

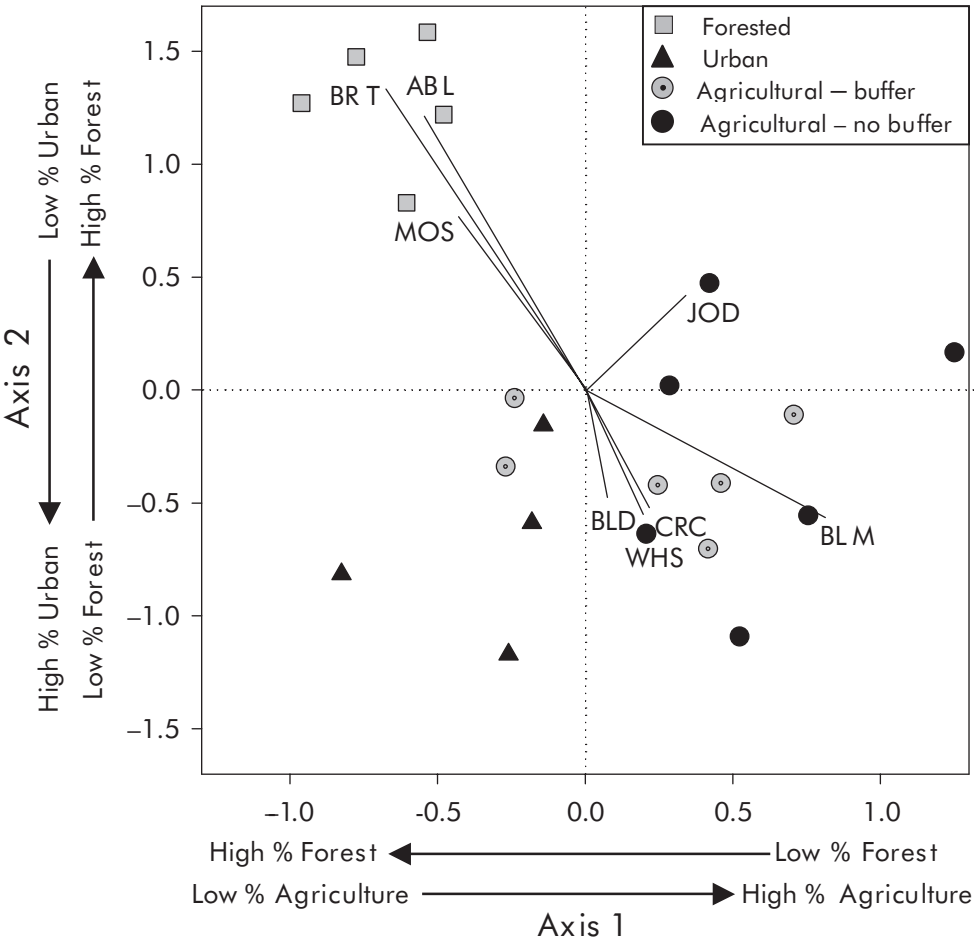


Figure 3. Nonmetric multidimensional scaling (NMS) ordination using axes 1 and 2 for all but rare fish species (occurring at only one site or $\leq 5\%$ of total catch). Symbols represent sites and vectors represent fish species that were significantly correlated ($r > 0.5$) with either axis. Catchment land uses having significant relationships ($r > 0.45$) with an axis are noted alongside the corresponding axis. ABL = American brook lamprey, BLD = blacknose dace, BLM = bluntnose minnow, BRT = brook trout, CRC = creek chub, JOD = johnny darter, MOS = mottled sculpin, WHS = white sucker.

were conducted at very broad scales (e.g., multiple basins), focused on only one or two land-use types, or lacked stream replication. For example, Lenat and Crawford (1994) evaluated the effects of forested, agricultural, and urban land uses on stream water quality and biota in a single stream per land use, which limited their ability to draw broader conclusions from their study. However, findings from land-use studies conducted at very broad scales often are confounded by natural spatial variability (e.g., physiography). Therefore, our study within a single basin and ecoregion minimized differences in background stream conditions and maximized detection of differences due to land use. Such studies are still vulnerable to natural confounding factors, and the analytical challenge is to separate natural landscape patterns and processes from those that have been altered by anthropogenic activities (Richards et al. 1996; Allan and Johnson 1997). In our study, surficial geology varied among our study catchments but catchment area and hydrology (i.e., low-flow yield) were similar among sites and temperature varied in a pattern consistent with effects of land use (e.g., canopy removal).

Overall, southwestern Michigan streams appeared to respond to a gradient of land use, with forested streams having the least degraded water quality, physical habitat, and fish assemblages and unbuffered agricultural streams having the most degraded. Urban streams and buffered agricultural streams generally were intermediate to forested and unbuffered agricultural streams. In general, habitat complexity and water quality declined, and fish density, richness, and tolerance increased across the land-use gradient from forested to agricultural.

Relationships between Land Use and Physical Habitat, Water Quality, and Fishes

Changes in land use can alter large-scale catchment processes, including infiltration, surface runoff, nutrient mobility, and sediment routing (Paul and Meyer 2001). However, the degree to

which these processes are altered varies with the type of land use, which can dictate the changes to stream habitat, water quality, and biota. Previous studies have found negative relationships between gradients of human land use (i.e., low to high altered land use) and stream habitat quality (e.g., Roth et al. 1996; Allan et al. 1997; Wang et al. 1997; Meador and Goldstein 2003), but the relative differences in habitat structure among different land-use types have not been quantified. In our study, geomorphic measurements and habitat heterogeneity generally declined across a land-use gradient (from forested to unbuffered agricultural land use) in streams of the Kalamazoo River basin. Forested, urban, and buffered agricultural streams tended to have similar or higher sinuosity and width:depth ratio compared to unbuffered agricultural streams. Many studies have found that urbanization results in channel widening (i.e., higher width:depth ratio; Paul and Meyer 2001), but we found no significant differences in geomorphology between urban and forested streams. However, we did find significant differences in large wood volume, embeddedness, and canopy cover among land uses. Streams with intact riparian zones, such as forested and buffered agricultural streams, generally possessed greater volumes of wood and denser canopies as expected. In general, unbuffered agricultural streams had the most degraded stream habitat when compared to the other land uses. This result is not surprising because activities associated with agricultural land use (e.g., dredging, channelization, removal of riparian vegetation) act as a physical press disturbance that can severely alter stream habitat and biota and impede stream recovery (Niemi et al. 1990).

Altered land use can also contribute to degraded water quality in streams by increasing fine sediment and nutrient inputs. Increased suspended sediment, turbidity, and nutrient levels often are observed with increasing agriculture (Gove et al. 2001) and urbanization (Lenat and Crawford 1994; Paul and Meyer 2001) in the catchment. However, in our study, only streams

draining agricultural catchments had elevated suspended sediment and turbidity levels, whereas urban streams had low turbidity levels similar to forested streams. We measured turbidity only at base flow, however, which may account for the low turbidity levels observed in urban streams. In streams draining urbanized catchments, floods often are more frequent and lead to increased sediment erosion and export from within the stream channel (Paul and Meyer 2001). We also observed elevated nutrient concentrations and specific conductivity in streams draining agricultural and urban catchments, which is consistent with patterns found in previous studies (Osborne and Wiley 1988; Lenat and Crawford 1994; Dow and Zampella 2000; Gove et al. 2001). For example, Omernik (1977) found higher nutrient concentrations in streams draining agricultural catchments than in forested catchments, and a positive relationship between the amount of agricultural land use and streamwater nitrogen and phosphorus concentrations. Dow and Zampella (2000) reported a positive relationship between specific conductivity and the percent of altered land (i.e., urban and agriculture) in the catchment of New Jersey pineland streams. In our study, the increased specific conductivity in agricultural streams likely was best explained by elevated nutrient concentrations. In urban streams, high specific conductivity may have resulted from the presence of other ions, such as Cl^- (Paul and Meyer 2001). We also measured DOC quantity and quality, but did not observe any differences among streams of different land uses because of high variation within a land use. Gergel et al. (1999) found that DOC concentrations in Wisconsin rivers were strongly related to the proportion of wetlands in the landscape. We did not find a similar relationship between DOC concentrations and wetland area in our smaller study streams (Moerke, unpublished data), which suggests that factors other than land use or proportion of wetlands in the catchment may control DOC in these small streams.

Many studies have used biological indices to assess the relationships between land use and

biological communities. Low fish assemblage condition often is related to high agricultural or urban land use (Roth et al. 1996; Allan et al. 1997; Wang et al. 1997; Meador and Goldstein 2003). For example, Fitzpatrick et al. (2001) found that fish IBI scores exhibited a threshold response to agriculture, with IBI scores tending to decline once agricultural land use in the catchment exceeded 30%. A similar threshold response to urban land use has been reported, but IBI scores declined when urban land use in the catchment exceeded 20% (Wang et al. 1997). In contrast, only a few studies have compared fish assemblage attributes among land uses. Harding et al. (1998) reported that fish abundance, species richness, and Margalef's diversity were higher in agricultural streams than in forested streams of two North Carolina river basins. Lenat and Crawford (1994) compared fish assemblage metrics in three North Carolina streams draining different catchment land uses. They found that the fish assemblage of an agricultural stream generally was similar to that of a forested stream, except that fish biomass and abundance were higher in the agricultural stream. In contrast, an urban stream had dramatically lower species richness, fewer intolerant taxa, and reduced fish biomass compared to the agricultural and forested streams. Regression models developed from 129 Willamette Valley, Oregon, sites indicated that urban and agriculture coefficients did not differ significantly (Van Sickle et al. 2004); however in that ecoregion most agriculture is irrigated. We found that forested streams in southern Michigan tended to have lower fish species richness and densities, but higher IBI scores and proportionally more intolerant individuals compared to urban and agricultural streams. We did not find a significant difference in fish biomass among land uses, although forested streams tended to have lower biomass than other streams. We used multivariate analyses to identify distinct fish assemblages associated with each land use, but we were only successful in distinguishing between forested and other altered land-use types. In general, sensitive fish species typical of

coolwater streams, such as brook trout, mottled sculpin, and American brook lamprey, were associated with higher percentages of forest in the catchment. In contrast, more tolerant fishes, such as minnows (Cyprinidae), were associated with streams of other land uses (i.e., agriculture and urban). Although tolerant fishes in our study sites appear to be related to anthropogenic activities associated with agricultural and urban land uses, tolerant fishes also can be characteristic of natural Midwestern streams draining wetland-dominated catchments with low groundwater inputs (Wang et al. 2003).

Our results suggest that unbuffered agricultural land use is more detrimental to stream ecosystems than urban land use in the Kalamazoo River basin, but the proportion of each catchment land-use type should be considered in more detail. Agricultural streams contained 54–89% agricultural land use in their catchments, whereas urban streams possessed only 29–40% urban land use in their catchments. Past studies have found that streams exhibit a threshold response at 10–20% impervious surfaces or urban land use (Klein 1979; Wang et al. 1997; Yoder et al. 1999) and 30–50% agricultural land use (Roth et al. 1996; Wang et al. 1997). Still others have observed no threshold response with urbanization (Karr and Chu 2000; Van Sickle et al. 2004; Cuffney et al. 2005). Other studies also have suggested that urban land use may be more damaging to streams than agricultural land use on a per unit area basis (Wang et al. 2000; Paul and Meyer 2001). We did not compare streams draining catchments with equal proportions of the different land uses, but we did find reduced water quality and degraded fish assemblages in urban streams at relatively low percentages of urban land use. Our study therefore suggests that even low percentages of urban land use (i.e., <40%) can have a similar impact on streams as higher percentages of agricultural land use (i.e., >50%). However, the type of urban land use likely will influence the degree of degradation. For example, large-lot residential development has less effect on stream fishes

than extensive industrial or commercial development (Yoder et al. 1999). Although the mechanisms involved have not been clearly identified, the different biological impact may be related to greater perviousness and higher quality riparian habitat found in low-intensity urban areas. In addition, local hydrology may affect a stream's response to a given land-use type. In our study streams, groundwater inputs may have lessened the overall impact of both agricultural and urban land uses by moderating stream water temperature increases that often are associated with agricultural and urban activities.

Are Forested Buffers Mediators of Catchment Disturbance?

Forested riparian zones often are viewed as a key to stream protection and rehabilitation because they buffer against changes in catchment land use that may alter water temperature, flow, wood recruitment, and nutrient and sediment supplies to streams (Gregory et al. 1991). Our study provided further insights into the importance of riparian zones to the condition of Midwestern streams because we assessed streams draining agricultural catchments with forested buffers (mean forested buffer width = 25 m) and without forested buffers (mean forested buffer width = 0 m). Although the agricultural streams had highly altered catchments, the preservation of even a limited forested riparian zone seemed important for maintaining local habitat conditions and reducing nutrient inputs. For instance, canopy cover was higher and woody debris more abundant in buffered streams compared to unbuffered streams. However, the forested riparian habitat did not appear to benefit fish assemblages probably because the most abundant fishes in both buffered and unbuffered streams were largely tolerant to silt and pollutants. Our findings suggest that water quality may be controlling fish assemblage condition more than physical habitat quality in agricultural streams in our study area.

Most of the urban streams possessed relatively narrow (<15 m) forested buffers that resulted in instream habitat quality intermediate to forested and unbuffered agricultural streams. However, the fish assemblage was typical of a degraded assemblage, which provides further evidence that water quality may be more influential on fishes than the physical habitat. Other studies also have indicated that fish assemblages in urban streams may be more affected by poor water quality and urban-induced hydrologic changes (e.g., increased floods) than by degraded habitat structure (Wang et al. 1997, 2000).

Land-use alteration represents a major global change that has serious implications for the planet's flora and fauna (Sala et al. 2000). Therefore, it is essential that we understand how different types of land use affect aquatic ecosystems in order to predict and counteract damage. Additional replicated, catchment-level studies in other geographic areas will enhance our knowledge of how different land uses affect stream ecosystems, and help identify characteristics that make streams more or less sensitive to land-use change. Information gained from such studies will assist resource managers and land use planners in limiting the detrimental effects of land-use change and in rehabilitating degraded catchments and stream ecosystems.

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Relationships among Channel Shape, Catchment Characteristics, and Fish in Lower Michigan Streams

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Abstract.—We investigated the effects of channel shape on the fish assemblages of 51 streams in Michigan's Lower Peninsula. We considered three measures of stream channel shape: the low-flow hydraulic radius, channel incision, and a measure of channel fit (bank-full over low-flow stream width). Covariance structure analysis (CSA) was used to quantify relationships among fish assemblage properties, channel shape variables, and a number of other reach and catchment scale measures, including stream slope, catchment area, and the proportions of agriculture and coarse surficial geology in stream catchments. Our analyses showed that with increasing channel incision, total fish biomass decreased and that decreasing low flow hydraulic radius led to a reduction in the biomass of intolerant fishes. Our analyses emphasized the ways that catchment and reach scale measures affected fish assemblages through their effects on catchment hydrology, stream hydraulics, and stream channel shape. Catchment area was positively related to species richness and the average weight of fish; coarse geology was positively related to the biomass of the intolerant assemblage and to the average weight of intolerant fishes; and stream slope was negatively related to species richness and the average weight of individuals. Catchment agriculture had negative effects on the average weight of fish, yet species richness was found to increase with this measure, possibly due to the positive relationship between catchment agriculture and stream temperature. By investigating the effects of large scale factors on measures of channel shape and stream fishes with CSA, this study provides insights into the mechanisms by which the landscape influences stream fish assemblages.

INTRODUCTION

In alluvial environments, a stream channel's cross-sectional shape is a reflection of its hydrologic and sediment loading regimes (Schumm 1963; Knighton 1998). Channel shape constrains

how water moves through the channel, influencing local hydraulics through effects on velocity distributions, depth, and the frictional surface to which flows are exposed. At the same time, local hydraulics shape the channel through erosion and deposition. Because flow and sediment regimes are determined by catchment properties that affect the quantity and delivery rates of

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water and sediment, channel shape is a sensitive integrator of many complex catchment processes (Rosgen 1994; Richards et al. 1996). Natural variations in catchment water budgets, physiography, land cover, and downstream hydraulic controls lead to large variations in channel cross-sectional shape both within and between rivers (Schumm 1963; Whiting and Bradley 1993; Wiley et al. 1997), and systemic variations in channel shape and size within river systems were first described by Leopold and Maddock (1953) in terms of the quantitative set of relationships between width, depth, velocity, and cross-sectional area known as river hydraulic geometry.

Fisheries ecologists have long emphasized the importance of local channel hydraulics in shaping fish habitat, and the importance of stream depth and velocity is emphasized in literature describing instream incremental flow methodology (IFIM) (Bovee 1982) and the habitat suitability index (HSI) (U.S. Fish and Wildlife Service 1981). However, little direct investigation of the channel shape itself has occurred. Likewise, recent interest in relating hydrologic regimes to the structure of stream fish communities (Poff and Ward 1989; Rabeni and Jacobson 1993; Poff and Allan 1995; Wiley et al. 1997) has proceeded with little explicit acknowledgment that channel shape is a primary linkage between river catchment hydrology and the hydraulics of local habitats.

Human activities can have dramatic effects on channel shape (Galay 1983; Shields 1995; Shields et al. 1997). Channels may be directly modified to enhance drainage of the landscape (dredging) and/or to prevent channel wall erosion (channel widening or hardening). Also, by changing land cover or water routing through the landscape, we often indirectly influence channel shape by altering the water yields and rates of water delivery to the channel system. Erosive widening and vertical channel incision are common channel responses associated with both urban and agricultural activities. In either case, human activities ultimately change both habitat hydraulics and channel shape, resulting in changes in

fish habitat quality. While fish assemblages found in highly developed catchments are often degraded (Gorman and Karr 1978; Karr et al. 1986), the covariance of hydrologic alteration, water quality deterioration, increased sediment loading, and changes in channel shape make it difficult to isolate the causal effects of any single perturbation (Gorman and Karr 1978).

In this study, we employ a covariance structure analysis (CSA) to examine the role that channel cross-sectional shape plays in structuring stream fish assemblages in systems not strongly influenced by degraded water quality. We seek to understand how three channel shape parameters (low-flow hydraulic radius, vertical channel incision, and a measure of low-flow channel fit) are related to several fish assemblage descriptors. Our primary objective was to examine how variations in these channel shape parameters influence the structure of fish assemblages. A secondary objective was to investigate the effects of several important landscape characteristics (agricultural land use, hydraulically conductive glacial drift geology, and catchment size) on channel shape and on other important site variables and therefore, indirectly, on stream fishes.

METHODS

Study Region

We sampled 51 stream sites across Michigan's Lower Peninsula (Figure 1). The streams represented a sample of relatively natural systems with good but variable water quality selected from the Michigan Rivers Inventory (MRI) (Seelbach and Wiley 1997). Catchment areas ranged from 2 to 480 km² (Table 1) and encompassed a wide variety of hydrologic and sediment loading regimes. The percentage of land use within catchments varied from systems dominated by natural landscape features to those dominated by agriculture (Table 1). Urban land use also varied, but systems with catchments that had extensive commercial or industrial development were excluded from

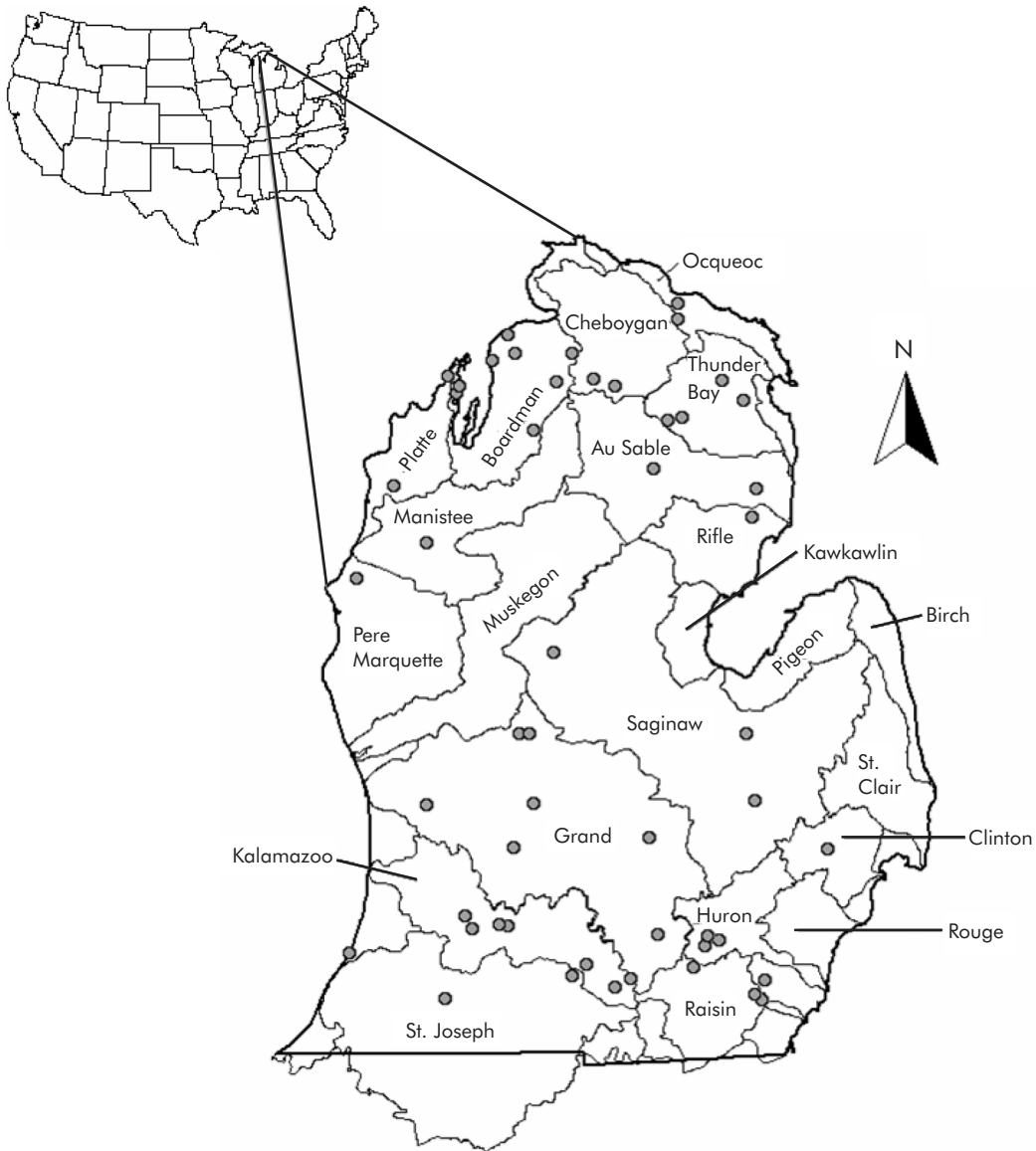


Figure 1. Locations of 51 study sites and major hydrologic units in Michigan's lower peninsula.

study to minimize the potential for seriously altered stream chemistry or thermal regimes to mask relationships among fish assemblages and measures of channel shape.

Fish Assemblages

We sampled fish assemblages during summer low-flow conditions between 1982 and 1997. Six

of the largest sites were sampled with rotenone, and the remaining 45 were sampled using three-pass electrofishing depletion surveys in blocked reaches. Both methods provided comparable data for the purposes of this study (Seelbach et al. 1994). All fish captured, except for some young-of-year minnows and native lamprey, were identified to species and weighed. For this investigation, we evaluated only typical stream

Table 1. Average, maximum, and minimum values of measures describing the study sites, including catchment and reach scale variables, fish assemblage properties, and measures of channel shape.

	Average	Maximum	Minimum	Abbreviation
<i>Catchment and reach scale properties</i>				
Drainage area (km ²)	124.10	479.99	2.00	Area
Agricultural land use (proportion)	0.50	1.00	0.00	Ag
Urban land use (proportion)	0.02	0.23	0.00	
Coarse geology (proportion)	0.68	1.00	0.00	Coarse
Fine geology (proportion)	0.17	1.00	0.00	
Temperature estimate (1 = cold; 0 = warm)	0.39	1.00	0.00	Temp
Slope	0.00662	0.05119	0.00009	
10/90 ratio	14.89	149.34	1.12	10/90
<i>Fish assemblage properties</i>				
Total number of species	9.67	26.00	2.00	Species
Number of game species	4.45	14.00	1.00	Species
Number of intolerant species	3.53	10.00	0.00	Species
Total fish biomass (kg/ha)	106.18	403.17	22.12	Biomass
Game fish biomass (kg/ha)	78.78	382.52	0.26	Biomass
Intolerant fish biomass (kg/ha)	51.66	227.76	0.00	Biomass
Total number of fish (num/ha)	10019.05	166395.52	599.53	
Number of game fish (num/ha)	2300.52	10500.55	296.77	
Number of intolerant fish (num/ha)	6716.87	166395.52	0.00	
All fish average weight (g/fish)	30.58	667.47	0.51	Weight
Game fish average weight (g/fish)	64.96	885.24	0.45	Weight
Intolerant fish average weight (g/fish)	19.16	89.55	0.00	Weight
<i>Measures of channel shape</i>				
Bank-full area (m ²)	6.58	29.04	0.28	
Bank-full average depth (m)	0.60	1.25	0.14	
Low-flow area (m ²)	2.26	10.36	0.03	
Low-flow average depth (m)	0.23	0.63	0.03	
Low-flow hydraulic radius (m)	0.22	0.61	0.03	LF radius
High-flow hydraulic radius (m)	0.55	1.24	0.12	HF radius
Channel incision (m)	0.36	1.04	0.09	Incision
Channel fit (higher values = wider bank-full/low-flow widths)	1.31	2.47	1.03	Fit

fish; those more common to lakes were excluded from analysis (Appendix 1).

Abundances for species collected by electro-fishing were estimated using Zippen's theories on population estimation (Zippen 1958) following Seelbach and Wiley (1997). Total number of stream species, estimates of total biomass per area sampled, and average weight per fish were calculated for each site. From the fish data, we also estimated the number of game and intolerant species (Appendix 1), their assemblage biomass, and the average weight of individuals. Game and intolerant species were defined according to Rakoczy (1992) and the Michigan Department of Environmental Quality (MDEQ) (1997), respectively.

Channel Shape Measures

We collected channel shape data from 51 stream reaches during summer low-flow conditions in 1998. Cross-sectional profiles were characterized through use of a rangefinder and clinometer (Bowler 1999; Minn 2000). Preliminary data analysis showed that this methodology provided results similar to level/transit and rod surveys of stream channels for the purposes of this study. Cross-sectional profiles were taken perpendicular to streamflow, and features of interest noted in each profile included bank-full points, water surface edges, channel thalweg, and inflection points. Standing on each feature, data collectors

recorded their distance and angle to a reference point located above the elevation of bank-full on one of the stream banks. These data, collected in polar coordinates, were converted to Cartesian coordinates. In cases when the collector could not stand directly on a point of interest (for example, when water surface occurred below an undercut), vertical and/or horizontal corrections were taken and applied to the resulting distance and depth from the reference. Each profile consisted of 10–20 points, which were used to calculate descriptors of channel shape, including width, depth, and area of bank-full and low-flow stream channels. Four to six cross-sectional profiles were measured at uniform intervals through 100 m of each stream, and results were averaged to characterize the reach.

Three channel shape descriptors were calculated from the cross-sectional profiles: low-flow hydraulic radius, vertical channel incision, and a measure of the fit of the low flow to the available channel. Low-flow hydraulic radius, which is the ratio of stream bed cross-sectional area to wetted perimeter, provided a measure of the length of the frictional resistance in the channel cross section. Vertical channel incision, calculated as the difference between mean bank-full and low-flow stream depths, described the distance of the low flow from the surrounding floodplain. This measure differs from the index used by Rosgen (1994) (the ratio of flood-prone to low-flow width) in that it focuses on the purely vertical component of incision. This allowed us to examine the issue of changes in wetted width separately in terms of our third measure, low-flow channel fit. This measure, calculated as the ratio of bank-full to low-flow width, provided an estimate of the fit of the low flow hydraulics to the available channel cross section. Stream channels are formed by large, erosive flows, and the bank-full area may be much greater than the area required to transport low flows (Schumm 1977; Knighton 1998). Therefore, large width ratios may indicate streams with highly variable water budgets, which might result from declining hydrologic storage in the upstream channel and

catchment, or from highly variable precipitation seasons. For clarity, this measure is referred to as “channel fit,” and higher values indicate relatively greater bank-full versus low-flow stream widths.

Reach-Scale Variables

We used three reach-scale variables in our analyses. The slope of each study site was estimated using 1:24,000 U.S. Geological Survey (USGS) topographic maps. Annual flow variability, a ratio of flows exceeded 10% of the time to those exceeded 90% of the time (10/90 ratio), was estimated using models developed for the MRI incorporating annual rainfall data, catchment land use, geology, and topography (Wiley et al. 1997). The third reach-scale measure was an estimate of stream temperature. Our study sites included both cold- and warmwater streams, and many fewer fish species are adapted to cold- versus warmwater environments (Diana 1995). In order for our models (described below) to successfully associate variation in fish assemblages with measures of channel shape, it was first necessary to account for obvious differences resulting from differing temperature regimes. Because no quantitative temperature measures were available for our study streams, we used a categorical “dummy variable” (Bollen 1989; Riseng et al. 2004) to characterize these broad differences by considering each site’s fish assemblage. Streams that clearly supported cold water assemblages, including brook trout *Salvelinus fontinalis* and slimy sculpin *Cottus cognatus* were coded as “1,” and all other systems were coded as “0.”

Catchment-Scale Variables

For each of the study sites, catchment boundaries were determined from digital elevation maps (DEMs) using a geographic information system (GIS). Surficial geology of each catchment was determined from data from Farrand and Bell (1982). Within each of the catchments, we considered the proportions of various geologic categories that most readily allow water

infiltration, reducing surface runoff and providing a stable supply of groundwater to streams. These included dune sand, outwash sand and gravel, ice contact sand and gravel, coarse till, and coarse end moraine. The sum of the proportions of each of these categories within each of the catchments is referred to as "coarse geology." Land uses within the catchments were estimated with data from the Michigan Resource Information System (MIRIS) (MIRIS 1978). In our analyses, we used only the proportion of land devoted to agriculture in each study catchment because land devoted to agriculture could most likely result in an unnatural or altered basin hydrology. While urban land also has the potential to alter basin hydrology, we did not consider this measure because the study catchments generally contained relatively small amounts of urban land (average = 2%) (Table 1).

Data Analysis

Covariance structure analysis (CSA, sometimes referred to as structural equation modeling) was used to investigate relationships among fish assemblage properties, measures of channel shape, and the remaining physical variables. Covariance structure analysis is a statistical technique that uses a series of linear equations to describe causal hypotheses about complex systems (Bollen 1989; Asher 1993; Wootton 1994). While CSA cannot be used to prove causality, it can be used to compare models and falsify various hypotheses regarding causal relationships among measures of interest (Sheldon and Meffe 1995; Riseng et al. 2004). Further, it has been used successfully to address multivariate questions in many investigations (Sheldon and Meffe 1995; Pugsek and Grace 1998; Riseng et al. 2004; and Riseng et al. 2006; Wehrly et al. 2006; Zorn and Wiley 2006; all this volume).

To perform CSA, a model hypothesizing the relationships among all variables of interest must be specified. Linear equations in the model are then parameterized by iterative solution and used to map the causal relationships among variables

via path analysis (Asher 1993). CSA results include estimates of the overall fit of the model to the data as well as estimations of the strengths of all hypothesized relationships among variables. These estimates provide information on the direct effects of one variable on another and on the indirect effects of a variable on another as it acts through one or more variables (Maruyama 1998). The sum of direct and indirect effects of one variable on another are the total effects, and were given primary consideration in this investigation.

The model developed for this analysis generally depicts catchment scale variables working through smaller scale variables including slope, the 10/90 ratio, and channel shape to influence fish (Figure 2). Regarding specific relationships among channel shape measures and fish, we hypothesized that low flow hydraulic radius would have positive effects and that both channel incision and an increasing channel fit ratio would have negative effects on fish assemblages. The model structure reflects the notion that stream systems are hierarchies of habitat subsystems, with large-scale features influencing the instream environment (Hynes 1975; Vannote et al. 1980; Frissell et al. 1986; Gregory et al. 1991). One exception to this structure in our models is a direct relationship between catchment area and number of species, included to account for the established relationship of increasing number of fish species with greater catchment area (Fausch et al. 1984; Watters 1992). Further, this model explicitly accounts for observed but noncausal (i.e., spurious) correlations among related measures, including catchment scale variables and measures of channel shape, which may be related, for example, by measurement error (Maruyama 1998). Because the model attempts to assign all variance in a system to one or more measures, we included residual error terms for all predicted variables.

With AMOS 4.0 (Arbuckle and Wothke 1999) software, we fit the data to the model hypothesizing relationships among measures via maximum likelihood estimation. Model fitting was an iterative process. We began by modeling all

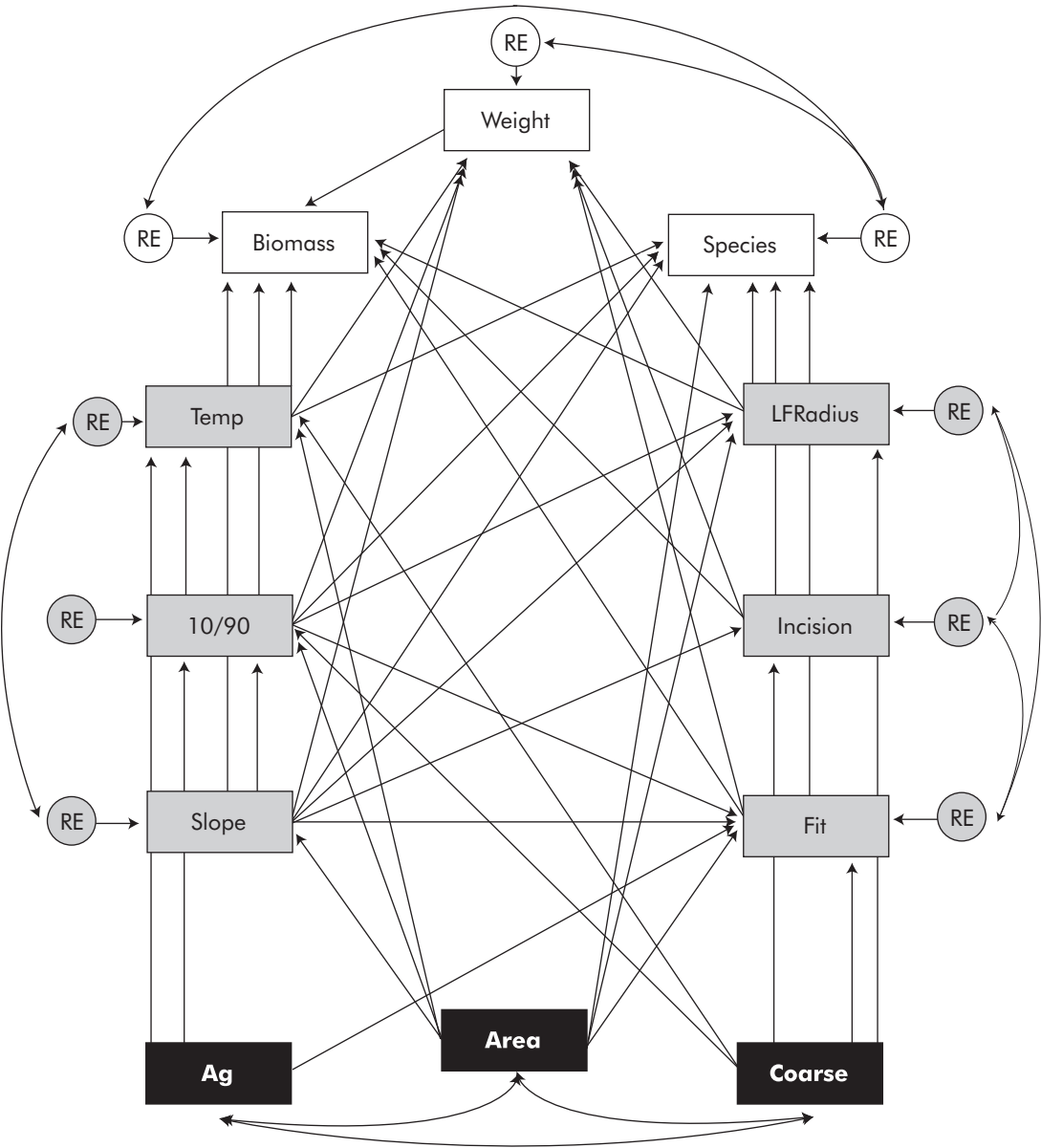


Figure 2. Model relating number of species, assemblage biomass, and average fish size; three measures of channel shape; and remaining physical variables for 51 sites in Michigan’s lower peninsula. Straight lines indicate hypothesized effects, curved lines indicate correlations, and error terms associated with measures account for unexplained variance. The model was run for all stream fish, game fish, and intolerant fish. Variable abbreviations are listed in Table 1.

interactions supported by theory and removed two insignificant relationships that reduced the fit of the model, including a direct effect of catchment area on channel incision and a direct effect of slope on the temperature estimate. We

considered all fish, game fish, and intolerant fish separately, running the model three times with the same set of physical variables to describe variation in these fish assemblage measures. Model fit was evaluated by considering the chi-squared and

its associated probability, the root mean square error of approximation (RMSEA), the Tucker Lewis index (TLI), and the normed fit index. The amount of variability in fish assemblage properties explained by the models was evaluated with squared multiple correlation coefficients, and the significance of effects were assessed with 95% bias-corrected confidence intervals generated from a Monte Carlo bootstrap procedure and t -distribution based on the degrees of freedom for the models following Arbuckle and Wothke (1999). Before analysis, all variables except coarse geology, agriculture, and the temperature estimate were natural-log transformed to meet the assumptions of normality.

RESULTS

Variability in Biological Assemblages and Channel Shape

The fish assemblages of the study sites were diverse in terms of their total number of species and biomass, and in the average weight of fish comprising the assemblages. Sites ranged from coldwater trout streams that supported only two species, brook trout and slimy sculpin, to warmwater systems that supported 20 or more species, including central stoneroller *Camptostoma anomalum*, northern hog sucker *Hypentelium nigricans*, green sunfish *Lepomis cyanellus*, white sucker *Catostomus commersonii*, and rainbow darter *Etheostoma caeruleum*. Total fish biomass varied from 22 to 403 kg/ha, and average weight of fish found at the study sites ranged from 1 to 667 g/fish (Table 1).

Sites also differed in their numbers of game and intolerant species. Both Thunder Bay and Kalamazoo rivers had more than 10 species of game fish, including smallmouth bass *Micropterus dolomieu*, northern pike *Esox lucius*, and white sucker. The Raisin River had 10 intolerant species, including stonecat *Noturus flavus*, rosyface shiner *Notropis rubellus*, river chub *Nocomis micropogon*, and black redhorse *Moxostoma duquesnei*. However, Cole Creek (a

tributary of the Saginaw River) had no intolerant fish.

The size and shape of the channels at the study sites also varied. Measures of bank-full and low-flow cross-sectional area ranged from 0.28 to 29.04 m² and from 0.03 to 10.36 m², respectively, and average bank-full depth was more than twice as great as average stream depth (Table 1). The low flow hydraulic radius ranged from 0.03 to 0.61 m, and channel incision ranged by an order of magnitude (0.09–1.04 m) (Table 1). Variation in the measure of channel fit was relatively small, ranging from 1.03 to 2.47 with an average of 1.31 (Table 1).

Correlations among measures of stream channel shape considered in the models were low ($r < 0.40$) but significant ($p < 0.05$), providing insights into stream channel morphology. The strongest correlation existed between channel incision and the measure of channel fit ($r = 0.39$) (Table 2), implying that with greater channel incision, the fit of the low flow to the available channel also decreased. Channel fit was also negatively correlated with the low-flow hydraulic radius, indicating that in channels with a high ratio of bank-full to low-flow stream width, flows were exposed to relatively greater frictional surface drag. The low flow hydraulic radius was positively correlated with channel incision, leading to the notion that incised channels expose flows to a relatively smaller frictional surface than less incised streams.

CSA Results

Goodness of fit and predictions.—The fits of the three causal models for all stream fish, game fish, and intolerant fish were good, indicating that the models implied a structure consistent with the data (Table 3). Squared multiple correlation coefficients were calculated for the fish assemblage properties from the measures of channel shape and other physical variables (Table 3). The models explained most variance in numbers of all, game, and intolerant species (0.83, 0.71, and 0.83, respectively), and they adequately explained

Table 2. Pearson-pairwise correlations among measures. Bold values indicate significant correlations ($p \leq 0.05$). Variable abbreviations are listed in Table 1.

	All fish			Game fish			Intolerant fish		
	Species	Biomass	Weight	Species	Biomass	Weight	Species	Biomass	Weight
<i>All fish</i>									
Number of species	1.00								
Biomass	0.17	1.00							
Average weight	0.26	0.62	1.00						
<i>Game fish</i>									
Number of species	0.82	0.30	0.46	1.00					
Biomass	0.01	0.83	0.60	0.20	1.00				
Average weight	0.44	0.66	0.69	0.49	0.69	1.00			
<i>Intolerant fish</i>									
Number of species	0.19	-0.09	-0.21	0.13	0.20	0.11	1.00		
Biomass	-0.31	0.05	-0.18	-0.19	0.35	-0.01	0.79	1.00	
Average weight	0.06	0.05	0.02	0.07	0.36	0.22	0.87	0.78	1.00
<i>Reach scale measures</i>									
Temperature estimate	-0.81	-0.18	-0.16	-0.61	0.09	-0.31	0.07	0.44	0.10
10/90 ratio	0.29	0.07	-0.14	0.07	-0.23	-0.06	-0.32	-0.49	-0.34
Slope	-0.84	-0.26	-0.50	-0.78	-0.04	-0.53	0.07	0.43	0.10
<i>Catchment scale measures</i>									
Drainage area	0.75	0.13	0.35	0.73	0.07	0.44	0.14	-0.19	0.07
Coarse geology	-0.05	0.16	0.16	0.10	0.29	0.19	0.19	0.29	0.18
Agricultural land use	0.40	0.23	-0.03	0.23	0.07	0.24	0.02	-0.10	-0.03
<i>Channel shape</i>									
Low-flow hydraulic radius	0.68	0.24	0.45	0.75	0.18	0.44	0.19	-0.04	0.10
Channel incision	0.49	-0.17	0.09	0.37	-0.34	0.12	-0.20	-0.54	-0.26
Poor channel fit	-0.04	0.02	-0.22	-0.19	-0.23	-0.30	-0.35	-0.35	-0.36
High-flow hydraulic radius	0.68	0.07	0.32	0.63	-0.10	0.38	-0.11	-0.43	-0.20
	Reach			Catchment			Channel shape		
	Temp	10/90	Slope	Area	Coarse	Ag	Low-flow radius	Incision	High-flow radius
<i>Reach scale measures</i>									
Temperature estimate	1.00								
10/90 ratio	-0.41	1.00							
Slope	0.68	-0.24	1.00						
<i>Catchment scale measures</i>									
Drainage area	-0.57	0.14	-0.81	1.00					
Coarse geology	0.14	-0.74	-0.03	0.04	1.00				
Agricultural land use	-0.44	0.47	-0.21	0.19	-0.24	1.00			
<i>Channel shape</i>									
Low-flow hydraulic radius	-0.51	0.00	-0.72	0.79	0.04	0.15	1.00		
Channel incision	-0.48	0.48	-0.49	0.39	-0.51	0.27	0.30	1.00	
Poor channel fit	-0.08	0.65	0.12	-0.28	-0.62	0.29	-0.35	0.39	1.00
High-flow hydraulic radius	-0.59	0.34	-0.74	0.69	-0.30	0.26	0.71	0.83	0.12

Table 3. Goodness of fit measures for models of all, game, and intolerant stream fish. Rules for good fit are described in more detail in Riseng et al. (2004). Also included are squared multiple correlation coefficients describing variance explained in number of species, assemblage biomass, and average weight of fish for all models.

	All stream fish model	Game fish model	Intolerant fish model	Rule for good fit
<i>Goodness of fit measures</i>				
Chi-squared	18.812	13.244	13.556	
Probability	0.339	0.720	0.698	>0.05
Root mean square error of approximation	0.046	0.000	0.000	<0.05
Tucker-Lewis index	0.983	1.035	1.030	>0.9
Normed fit index	0.961	0.972	0.973	>0.9
<i>Squared multiple correlation coefficients</i>				
Number of species	0.83	0.71	0.83	
Biomass	0.59	0.76	0.20	
Average weight	0.36	0.34	0.18	

measures of all, game, and intolerant fish biomass (0.59, 0.76, and 0.20, respectively) (Table 3). The models generally explained less of the variance in the average weights of all, game, and intolerant fish (0.36, 0.34, and 0.18, respectively) (Table 3).

Effects of catchment and reach measures on channel shape.—The low flow hydraulic radius increased with catchment area (0.81) (Table 4). Radius was also negatively affected by both flow variability and by catchment agriculture. In contrast, channel incision was strongly, negatively affected by coarse geology in the catchment (−0.53) and by stream slope (−0.51); it also increased with catchment area to a lesser degree (0.42). Channel fit was strongly influenced by coarse geology (−0.57) and by the estimate of flow variability (the 10/90 ratio) (0.53); the ratio also increased with catchment agriculture and decreased with catchment area.

Effects of channel shape on fish assemblages.—Channel incision had strong, negative direct and total effects on all measures of fish biomass but did not significantly influence species richness or weight of individuals (Tables 4 and 5). The low flow hydraulic radius had significant, positive direct effects on the biomass of the intolerant and game fish assemblages. When indirect effects were accounted for, the low flow hydrau-

lic radius significantly affected only intolerant fish biomass (0.46), indicating that the biomass of the intolerant fish assemblage increased with hydraulic radius. While channel fit had a significant direct effect on game fish biomass, its total effects on all aspects of the fish assemblages were statistically insignificant.

Effects of catchment features on fish assemblages through channel shape and other measures.—Significant effects of catchment agriculture were pervasive in our fitted model. Agriculture affected both the 10/90 ratio and the temperature estimate (0.27 and −0.29) (Table 4). Agriculture had a negative total effect on the low flow hydraulic radius (−0.09) and a larger positive effect on channel fit (0.14) (Table 4). Agriculture negatively affected the average weight of fish indirectly (−0.12), primarily via changes in hydrology. Agriculture also had a positive effect on total species richness, mediated by agriculture's positive effect on stream temperature which, in Michigan streams, is a correlate of increasing fish diversity (Wehrly et al. 2003).

The effects of coarse surficial geology were also widespread in the model, and its strongest total effect was on the 10/90 ratio (−0.68) (Table 4). Coarse geology had an indirect negative effect on intolerant fish biomass due primarily to its negative effects on channel incision (described

Table 4. Standardized total effects of measures on predicted variables. Values in bold are significant ($p \leq 0.05$); values in italics are close to significant ($0.1 > p > 0.05$). Variable abbreviations are listed in Table 1.

Standardized total effects of:	Low-flow									
	Weight	radius	Incision	Fit	Temp	10/90	Slope	Ag	Coarse	Area
<i>Variables affected</i>										
Total number of species		0.24	0.00	0.07	-0.44	0.03	-0.46	0.11	-0.05	0.73
Total fish biomass	0.69	0.10	-0.62	0.40	-0.04	0.18	-0.28	0.06	0.10	0.18
All fish average weight		0.18	-0.12	0.14	0.23	-0.25	-0.60	-0.12	0.16	0.44
Number of game species		0.34	-0.01	0.12	-0.18	-0.20	-0.46	-0.01	0.04	0.73
Game fish biomass	0.91	0.31	-0.48	0.17	0.09	-0.11	0.00	-0.05	0.24	0.07
Game fish average weight		0.01	-0.06	-0.18	0.01	-0.13	-0.46	-0.04	0.16	0.46
Number of intolerant species		0.32	-0.06	-0.12	-0.07	-0.33	0.40	-0.07	0.21	0.09
Intolerant fish biomass	0.65	0.46	-0.29	-0.02	0.13	-0.34	0.58	-0.12	0.29	-0.23
Intolerant fish average weight		0.20	-0.10	-0.21	-0.08	-0.28	0.34	-0.06	0.25	0.00
Temperature estimate						-0.17	0.06	-0.29	0.10	-0.52
10/90 ratio							-0.32	0.27	-0.68	0.12
Slope										-0.81
Low-flow hydraulic radius						-0.35	-0.26	-0.09	-0.01	0.81
Channel incision						-0.08	-0.51	-0.02	-0.53	0.42
Channel fit						0.53	-0.28	0.14	-0.57	-0.29

Table 5. Standardized direct effects of measures on predicted variables. Values in bold are significant ($p \leq 0.05$); values in italics are close to significant ($0.1 > p > 0.05$). Variable abbreviations are listed in Table 1.

Standardized direct effects of:	Low-flow									
	Weight	radius	Incision	Fit	Temp	10/90	Slope	Ag	Coarse	Area
<i>Variables affected</i>										
Total number of species		0.10	0.00	0.07	-0.44	-0.05	-0.40			0.12
Total fish biomass	0.69	0.12	-0.54	0.30	-0.20	0.15	0.04			
All fish average weight		0.18	-0.12	0.14	0.23	-0.23	-0.66			
Number of game species		0.34	-0.01	0.12	-0.18	-0.18	-0.39			0.11
Game fish biomass	0.91	0.31	-0.42	0.33	0.07	-0.09	0.35			
Game fish average weight		0.01	-0.06	-0.18	0.01	-0.03	-0.55			
Number of intolerant species		0.32	-0.06	-0.12	-0.07	-0.17	0.37			0.11
Intolerant fish biomass	0.65	0.34	-0.22	0.12	0.18	-0.09	0.33			
Intolerant fish average weight		0.20	-0.10	-0.21	-0.08	-0.13	0.25			
Temperature estimate						-0.17		-0.24	-0.02	-0.50
10/90 ratio							-0.32	0.27	-0.68	-0.14
Slope										-0.81
Low-flow hydraulic radius						-0.35	-0.37		-0.25	0.55
Channel incision						-0.08	-0.53		-0.59	
Channel fit						0.53	-0.11		-0.21	-0.44

previously). Coarse geology also indirectly affected the average weight of fish, due to a host of weaker effects on the 10/90 ratio, the temperature estimate, and measures of channel shape.

Catchment area had significant indirect effects on the fish assemblages; number of species and average weight of total and game fish increased

with area. Catchment area, however, did not significantly affect any measures of the intolerant fish assemblage; instead, intolerant fish richness and biomass decreased with increasing flow variability. Also worth noting, direct effects of catchment area on richness of the assemblages were insignificant (Table 5), emphasizing that, for our

study streams, catchment area influences fish as it influences intermediate measures, including channel shape, temperature, and reach slope.

DISCUSSION

Effects of Channel Shape on Fish Assemblages

Our results from Michigan's Lower Peninsula are consistent with the hypothesis that stream channel shape is an important mechanism structuring the region's fish assemblages. Both decreasing low flow hydraulic radius and increasing channel incision had negative effects on species composition and biomass.

The impact of low-flow hydraulic radius on assemblage structure likely results from at least two different types of proximal mechanisms: depth restriction and velocity restriction. Increasing hydraulic radius implies increasing cross-sectional area relative to the channel perimeter and typically a greater stream depth. Greater average depth in turn implies more habitat available to fish. During periods of low flow, a small radius may be associated with depths so shallow as to prohibit certain species or older age-classes (Statzner et al. 1988). Based on Manning's equation (Knighton 1998), we should also expect that for a given reach slope, reduced hydraulic radius will result in reduced flow velocities and discharge rate. This can lead to shallow riffles that impound extremely slow pools, restricting longitudinal movements and trapping fish in deteriorating pooled habitats. Reduced velocity can also lower stream oxygen, creating an inhospitable environment for some fish (Smale and Rabeni 1995). Slowed flows may also indirectly affect fish by adversely affecting benthic invertebrate prey by lowering velocity dependent metabolic rates (Ambuhl 1959; Hynes 1970; Wiley and Kohler 1980), by reducing rates of invertebrate drift (Riseng et al. 2004), or both (Fausch and White 1986).

Negative effects of channel incision on fish may result from several factors. Channels that

have incised significantly may lose their connectivity with their floodplains; as a result, high flows may be confined within the channel and prevented from spilling onto the floodplain. This can eliminate spawning and rearing habitat for some species or refuges during high flows (Turner et al. 1994; Kwak 1988). Without floodplain access, juveniles and small fish may perish or be displaced, eliminating a significant portion of a site's biomass but not necessarily the number of species (Paragamian and Wiley 1987). Furthermore, incised channels are associated with a large high flow hydraulic radius (in our data set they are highly correlated, $r = 0.83$ (Table 2), resulting in lower frictional resistance to flow during freshets. This, in turn, causes storm flows to be even faster and more disruptive, resulting in additional hydraulic stress to nonrheophilic fish, their benthic prey, and the channel itself.

Our measure of channel fit had a significant, direct effect only on game fish biomass, but this effect was positive. Further, channel fit's total effects on this measure and on all other fish properties were insignificant. These results contradict our initial hypothesis that relatively higher bank-full to low-flow width ratios should negatively affect fish. We did find that the value of channel fit significantly increased with flashy hydrology (higher 10/90 ratio), enforcing the notion that this measure may result from variable flow regimes. Because width changes more rapidly than depth as flows increase in streams with higher channel fit ratios, shear stress may remain more constant and lower over the variable range of streamflows. During high flows through channels with high fit ratios, fish may consequently have greater opportunity to seek refuge in slow velocity habitat that develops along channel margins or in backwaters than in streams with lower fit ratios but larger radii. This would be particularly true for streams with incised channels. If this is so, then the expectation of a linear response between our fit index and fish assemblage properties is unreasonable and the coefficient estimates would be noisy as we observed.

Links among Catchment Features and Fish Assemblages through Channel Shape and Other Measures

The mechanisms by which the landscape influences stream features and ultimately, stream biota are complex (Karr 1991). Our analyses support this notion by illustrating how the indirect effects of catchment-scale variables can be traced through channel shape measures and other variables to indirectly affect fish. The results strongly implicate both catchment hydrology and instream hydraulics as key proximal mechanisms by which landscape factors affect stream fish assemblages.

Catchment area.—Stream channels of large catchments carry more flow than those draining smaller catchments due to the fact that more water is delivered to the channel from the landscape. Both the low flow hydraulic radius and channel incision increased with increasing catchment area, emphasizing their dependence on the volume of streamflow generated by the catchment. This also implies greater depths within the channels of larger catchments, which is consistent with the work of Leopold and Maddock (1953) who describe these relationships as the “hydraulic geometry” of river channels.

Catchment area also affects the time distribution of water delivery to stream channels. Accumulating upstream hydrologic storage in larger catchments not only moderates the rate that storm flows are delivered to streams but ensures higher rates of water yield during low-flow conditions. The moderating effect of greater catchment area on streamflow variability may explain the negative relationship between channel fit and catchment area. Flows are generally less variable in larger streams than in smaller streams, resulting in a better fit of the low flow to the available channel. Evidence supporting this notion can be found in the direct relationship between channel fit and the 10/90 ratio; as flow variability increased, the channel fit ratio increased.

With increasing catchment area, number of fish species and the average size of individuals increased. The generality of this observation is supported by the work of many others (e.g., Fausch et al. 1984; Karr et al. 1986; Watters 1992; Oberdorff et al. 1995) who reported a positive relationship between species richness and the area drained by streams. It is also in agreement with aspects of the more general theory of island biogeography (i.e., larger areas support more species; MacArthur and Wilson 1967), if we allow that fish species may be maintained largely by demographic processes.

Surficial geology.—The Michigan landscape is dominated by glacial drift deposits of varying hydraulic conductivity, which exert a strong controlling influence on local hydrology (Wiley et al. 1997). Coarser deposits (glacio-fluvial outwash, alluvium, sand dunes, etc.) allow rapid infiltration and subsurface routing of precipitation. Catchments with a high percentage of their landscape comprised of coarser drift have a greater capacity for hydrologic storage and generally experience less temporally variable flows than streams with more impervious catchments. Because storage reduces peak discharge per unit precipitation, sites with more conductive landscapes are associated with less incision and a smaller channel fit ratio at low flow.

Our models suggest that the indirect effects of a coarser geology include reduced temperature and therefore lower species richness. On the other hand, the higher base flows resulting from greater hydrologic storage provide better hydraulic habitat (hydraulic radius) in terms of useable depth and increased velocity. Consequently, we saw that coarse geology had a strong positive effect on intolerant fish biomass and average weight. By definition, intolerant fish are considered more sensitive to stressors than are other species, and the moderating effects of coarse geology on channel shape and flow variability lead to an instream environment that is more hospitable to these fish. This result is consistent with a study by Poff and Allan (1995) who found that streams

with highly variable flow regimes were less favorable to some fish than streams with more stable flows. This result is also consistent with a study that showed that fish assemblages of northern Michigan ecoregions dominated by outwash were less sensitive to agriculture and urbanization (Wiley et al. 2002). However, worth noting is the fact that stabilized flows in southwestern U.S. rivers have been detrimental to endemic fish species adapted to highly fluctuating flows (Hughes et al. 2005).

Agricultural land use.—Impacts on stream ecosystems from large-scale agricultural activity are well documented, but in most cases are associated with declines in water quality or increases in sediment loading (Lenat 1984; Karr et al. 1986; Osborne and Wiley 1988; Cooper 1993; Waters 1995; Johnson et al. 1997). Ours is one of a few studies that we are aware of that documents the potentially widespread indirect impact of agricultural land use on fish assemblages through modification of channel shape (but see Richards and Host 1994; Shields et al. 1994; Wang et al. 2002). Our data are consistent with our causal model in which agricultural land use causes decreased low flow hydraulic radii, increased stream temperatures, and increased hydrologic flashiness. Together, these changes significantly affect fish assemblage structure. Across our study sites, we found that increasing agriculture was associated with increased total species richness, and decreased average weights of individuals comprising those fish assemblages.

Management Implications

Channel shape of Michigan rivers is affected by human activity both directly (through dredging and channel design) and indirectly (through landscape and climate alteration). In either case, the close linkage between channel shape, hydrology, and local hydraulic habitat ensures that fish assemblages will be affected. Our analysis suggests that low flow hydraulic radius and vertical channel incision are particularly potent

shape parameters that are likely to have strong effects on the composition of a local fish assemblage.

Engineered modifications of channels often affect both parameters simultaneously. Dredging, which may be performed either to improve drainage of the landscape or to reduce the potential for streams to flood, typically results in an increase in channel incision and may also change the general shape of the stream's cross-sectional profile from a V-shape to a U-shape, decreasing the low flow hydraulic radius. Our models indicate that these changes will result in large decreases in the biomass of game and intolerant fishes.

Widening stream channels is a second common practice that directly affects stream channel shape. It is usually performed to prevent erosion by forcing flows to come in contact with a greater frictional surface by reducing the high flow radius. As this occurs, the channel fit ratio will increase and the low flow hydraulic radius will decrease. Our models again indicate that this would change fish assemblage structure primarily by affecting the biomass of game and intolerant fishes. To minimize the impacts of these kinds of direct channel modifications to fish assemblages, the degree of channel incision should be minimized and the shape of the channel profile should be structured to maximize the low-flow hydraulic radius.

Sedimentation resulting from land use practices may also alter channel shape in a way that damages fish assemblages. Aggrading channels and channels transporting large amounts of bedload are typically overly wide and shallow (i.e., a small hydraulic radius) (Schumm 1977; Whiting and Bradley 1993). According to our models, this may affect intolerant fish biomass. At the same time, aggradation is essentially the reverse of incision (degradation), and our results imply that a tension may exist between the effects of channel filling (reducing hydraulic radius) and cross-sectional elevation (relieving effects of incision). Certainly, severe sedimentation has the potential to affect assemblage structure in a strong but complex fashion.

Finally, the strong effect of low flow hydraulic radius in our models suggests that at least some of the potential detrimental effects of engineered channel shape modification might be mitigated by designs that directly address this issue. So-called two-stage channel designs which place a smaller low flow channel inside a larger flood flow channel maintain larger radii at both high and low flows. Hydraulically, this is often desirable because it maintains higher flow rates across a wide range of water surface elevations. Ecologically, our analysis suggests that this type of design should be better for fish as well. By maintaining a larger two-stage channel, necessary drainage modifications may be possible that avoid much of the negative impact they would otherwise have on fish.

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Appendix 1. Fish collected from the study sites with their designations as a stream versus lake species, game fish, or intolerant fish (1 = yes, 0 = no).

Common name	Family	Species	Stream species	Game fish	Intolerant fish
Bowfin	Amiidae	<i>Amia calva</i>	1	0	0
Pirate perch	Aphredoderidae	<i>Aphredoderus sayanus</i>	1	0	0
White sucker	Catostomidae	<i>Catostomus commersonii</i>	1	1	0
Lake chubsucker	Catostomidae	<i>Erimyzon sucetta</i>	0	0	0
Northern hog sucker	Catostomidae	<i>Hypentelium nigricans</i>	1	0	1
Black redhorse	Catostomidae	<i>Moxostoma duquesnei</i>	1	1	1
Golden redhorse	Catostomidae	<i>M. erythrurum</i>	1	1	0
Shorthead redhorse	Catostomidae	<i>M. macrolepidotum</i>	1	1	1
Greater redhorse	Catostomidae	<i>M. valenciennesi</i>	1	1	1
Rock bass	Centrarchidae	<i>Ambloplites rupestris</i>	1	1	1
Green sunfish	Centrarchidae	<i>Lepomis cyanellus</i>	1	1	0
Pumpkinseed	Centrarchidae	<i>L. gibbosus</i>	0	1	0
Warmouth	Centrarchidae	<i>L. gulosus</i>	0	1	0
Bluegill	Centrarchidae	<i>L. macrochirus</i>	0	1	0
Longear sunfish	Centrarchidae	<i>L. megalotis</i>	1	1	0
Smallmouth bass	Centrarchidae	<i>Micropterus dolomieu</i>	1	1	1
Largemouth bass	Centrarchidae	<i>M. salmoides</i>	0	1	0
Black crappie	Centrarchidae	<i>Pomoxis nigromaculatus</i>	0	1	0
Hybrid sunfish	Centrarchidae		1	1	0
Mottled sculpin	Cottidae	<i>Cottus bairdii</i>	1	0	1
Slimy sculpin	Cottidae	<i>C. cognatus</i>	1	0	1
Central stoneroller	Cyprinidae	<i>Camptostoma anomalum</i>	1	0	0
Goldfish	Cyprinidae	<i>Carassius auratus</i>	0	0	0
Spotfin shiner	Cyprinidae	<i>Cyprinella spiloptera</i>	1	0	0
Common carp	Cyprinidae	<i>Cyprinus carpio</i>	1	1	0
Striped shiner	Cyprinidae	<i>Luxilus chrysocephalus</i>	1	0	0
Common shiner	Cyprinidae	<i>L. cornutus</i>	1	0	0
Hornyhead chub	Cyprinidae	<i>Nocomis biguttatus</i>	1	0	0
River chub	Cyprinidae	<i>N. micropogon</i>	1	0	1
Golden shiner	Cyprinidae	<i>Notemigonus crysoleucas</i>	0	0	0
Emerald shiner	Cyprinidae	<i>Notropis atherinoides</i>	0	0	0
Silverjaw minnow	Cyprinidae	<i>N. buccatus</i>	1	0	0
Rosyface shiner	Cyprinidae	<i>N. rubellus</i>	1	0	1
Sand shiner	Cyprinidae	<i>N. stramineus</i>	1	0	0

Common name	Family	Species	Stream species	Game fish	Intolerant fish
Mimic shiner	Cyprinidae	<i>N. volucellus</i>	1	0	0
Northern redbelly dace	Cyprinidae	<i>Phoxinus eos</i>	1	0	0
Bluntnose minnow	Cyprinidae	<i>Pimephales notatus</i>	1	0	0
Fathead minnow	Cyprinidae	<i>P. promelas</i>	1	0	0
Blacknose dace	Cyprinidae	<i>Rhinichthys atratulus</i>	1	0	0
Longnose dace	Cyprinidae	<i>R. cataractae</i>	1	0	1
Creek chub	Cyprinidae	<i>Semotilus atromaculatus</i>	1	0	0
Minnow	Cyprinidae		1	0	0
Grass pickerel	Esocidae	<i>Esox americanus</i>	1	0	0
Northern pike	Esocidae	<i>E. lucius</i>	1	1	0
Burbot	Gadidae	<i>Lota lota</i>	1	1	0
Brook stickleback	Gasterosteidae	<i>Culaea inconstans</i>	1	0	0
Black bullhead	Ictaluridae	<i>Ameiurus melas</i>	1	1	0
Yellow bullhead	Ictaluridae	<i>A. natalis</i>	0	1	0
Brown bullhead	Ictaluridae	<i>Ictalurus nebulosus</i>	1	1	0
Stonecat	Ictaluridae	<i>Noturus flavus</i>	1	0	1
Brindled madtom	Ictaluridae	<i>N. miurus</i>	1	0	0
Greenside darter	Percidae	<i>Etheostoma blennioides</i>	1	0	0
Rainbow darter	Percidae	<i>E. caeruleum</i>	1	0	1
Iowa darter	Percidae	<i>E. exile</i>	0	0	1
Fantail darter	Percidae	<i>E. flabellare</i>	1	0	0
Johnny darter	Percidae	<i>E. nigrum</i>	1	0	0
Yellow perch	Percidae	<i>Perca flavescens</i>	0	1	0
Logperch	Percidae	<i>Percina caprodes</i>	1	0	0
Blackside darter	Percidae	<i>P. maculata</i>	1	0	0
Trout-perch	Percopsidae	<i>Percopsis omiscomaycus</i>	1	0	0
Chestnut lamprey	Petromyzontidae	<i>Ichthyomyzon castaneus</i>	1	0	1
Northern brook lamprey	Petromyzontidae	<i>I. fossor</i>	1	0	1
Lamprey	Petromyzontidae		1	0	1
Rainbow trout, steelhead	Salmonidae	<i>Oncorhynchus mykiss</i>	1	1	1
Chinook salmon	Salmonidae	<i>O. tshawytscha</i>	1	1	1
Brown trout	Salmonidae	<i>Salmo trutta</i>	1	1	1
Brook trout	Salmonidae	<i>Salvelinus fontinalis</i>	1	1	1
Central mudminnow	Umbridae	<i>Umbra limi</i>	1	0	0

The Influence of Physical Habitat and Land Use on Stream Fish Assemblages in Southeastern Michigan

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Abstract.—The influence of land use and instream physical habitat on biotic condition of fish assemblages was investigated for 48 stream reaches in the Huron and Raisin rivers. The amount of agriculture and wetland in the catchment and 100-m stream buffers had the strongest relationships with instream physical habitat, and these two categories of land use/cover were negatively correlated with each other ($r = -0.70$, $p < 0.01$). Agriculture was associated with high levels of sedimentation and reduced flow stability, while wetland was associated with low sedimentation and stable flows. The index of biotic integrity (IBI) was positively related to low sedimentation, stable flows, and the presence of fine gravel (2–8 mm). It was not significantly correlated with agricultural land use, but was positively related to natural land cover (forest + wetland combined) in the buffer. The best linear regression model using physical habitat and land-use variables from all sites adequately predicted IBI scores (adjusted $R^2 = 0.52$). However, when the Huron and Raisin basins were treated separately, some of the included variables differed, and model fit increased (Huron adjusted $R^2 = 0.76$, Raisin adj. $R^2 = 0.79$), indicating that relations of fish assemblages to physical habitat and land use differed between basins. The Raisin model included land cover variables, while the Huron model included only variables related to physical habitat. Thus instream habitat and land cover may play different roles in these basins, suggesting the benefit of forming separate models for individual basins when sufficient data are available.

INTRODUCTION

Land-use change has major influences on stream ecosystems. Agriculture is one of the main factors responsible for stream degradation in the United States (Judy et al. 1984; U.S. Environmental Protection Agency 1996). Urban land use also has adverse effects on stream and water quality,

especially when present in critical amounts and close to the stream channel (Wang et al. 1997, 2000, 2001). Agriculture is the dominant land-use feature of many southern Michigan basins, including the Raisin, while others, including the Huron, are in areas of high urban sprawl (Hay-Chmielewski et al. 1995). In addition, wetlands have been reduced to half or less of presettlement estimates (Mitsch and Gosselink 2000), leading to changes in flow stability and aquatic habitat.

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Human activities reflected in altered land use have resulted in high levels of degradation in stream ecosystems in many areas (Allan 2004).

Land use throughout catchments and along stream margins can substantially influence instream physical, chemical, and biological habitat. Physical habitat for fish includes substrate, extent of pools versus riffles, vegetation, undercut banks, flow amount and variability, and any other stream feature whose presence and quality can be important to the presence and abundance of fish species in a stream segment (Gorman and Karr 1978; Milner et al. 1985). Physical habitat degradation can therefore have large effects on the fish assemblages present in a stream.

Numerous studies report agriculture to have a strong influence on fish assemblages (Trautman 1981; Harding et al. 1998; Walser and Bart 1999; Brown 2000). Agriculture increases run-off and sediment transfer to a stream (Waters 1995; Walser and Bart 1999) through the clearing of vegetation and the installation of structures such as drainage tiles (Alexander et al. 1995). Increased sediment loads limit fish habitat and are associated with poor biotic condition (Berkman and Rabeni 1987), due to sediment deposition covering gravel, filling interstitial spaces, and burying logs (Alexander and Hansen 1986). Many fish require stream substrate relatively free of fine sediments for reproduction (Waters 1995). The increased sedimentation associated with agricultural practices decreases survival of eggs and larvae of fish, and the availability of food for fish (Berkman and Rabeni 1987; Chapman 1988). Walser and Bart (1999) observed a reduction in substrate complexity in tributaries to the Chatahoochie River as a result of the sediment deposited in agricultural streams, and Roth et al. (1996) reported a negative correlation between habitat metrics and fish biotic condition for sites within the Raisin River basin.

Urbanization also has well-documented effects on fish assemblages (Wang et al. 2000, 2001). Runoff delivered to a stream increases markedly due to greater imperviousness of the basin (Klein 1979; Wang et al. 2001), causing

increased flow variability and reduced base flows, which in turn alter the erosion and temperature in a stream. Wetlands are important because they trap sediments and other materials in surface flow that would normally reach the stream (Patten 1998), and wetlands help to stabilize streamflows because they hold water during storm events. Thus the presence of wetlands in a catchment may reduce the rate of runoff delivery and levels of sedimentation in a stream.

Our objectives were to identify the major factors, including land use and instream habitat, influencing variation in biotic condition of headwater streams in southeastern Michigan. Fish assemblage structure was assessed using the index of biotic integrity (IBI), a biomonitoring technique that uses fish assemblages to assess biotic condition and environmental quality of a stream (Karr et al. 1986; Karr 1991; Karr and Chu 1997). The main strength of the IBI is its ability to integrate information from several levels of assemblage structure and function into a single, ecologically based index (Hlasek et al. 1998). We identified major causes of variation in the IBI through its correlation with land-use and physical habitat variables. Land-use and physical habitat variables have been shown to be strongly related to biological metrics in other studies of the Raisin River (Roth et al. 1996; Lammert and Allan 1999). We examined small headwater streams throughout the Raisin and Huron basins to identify trends in subcatchments and to explore the relative contributions of land-use versus instream physical habitat variables in explaining variation in biotic condition among stream reaches.

METHODS

Study Area

The Huron (2,350 km²; mean Q = 18.3 m³/s) and Raisin (2,700 km²; mean Q = 22.1 m³/s) basins are located in southeastern Michigan and drain east into the western basin of Lake Erie (Figure 1). The Huron basin includes a mixture of agricultural and relatively undisturbed (forest,

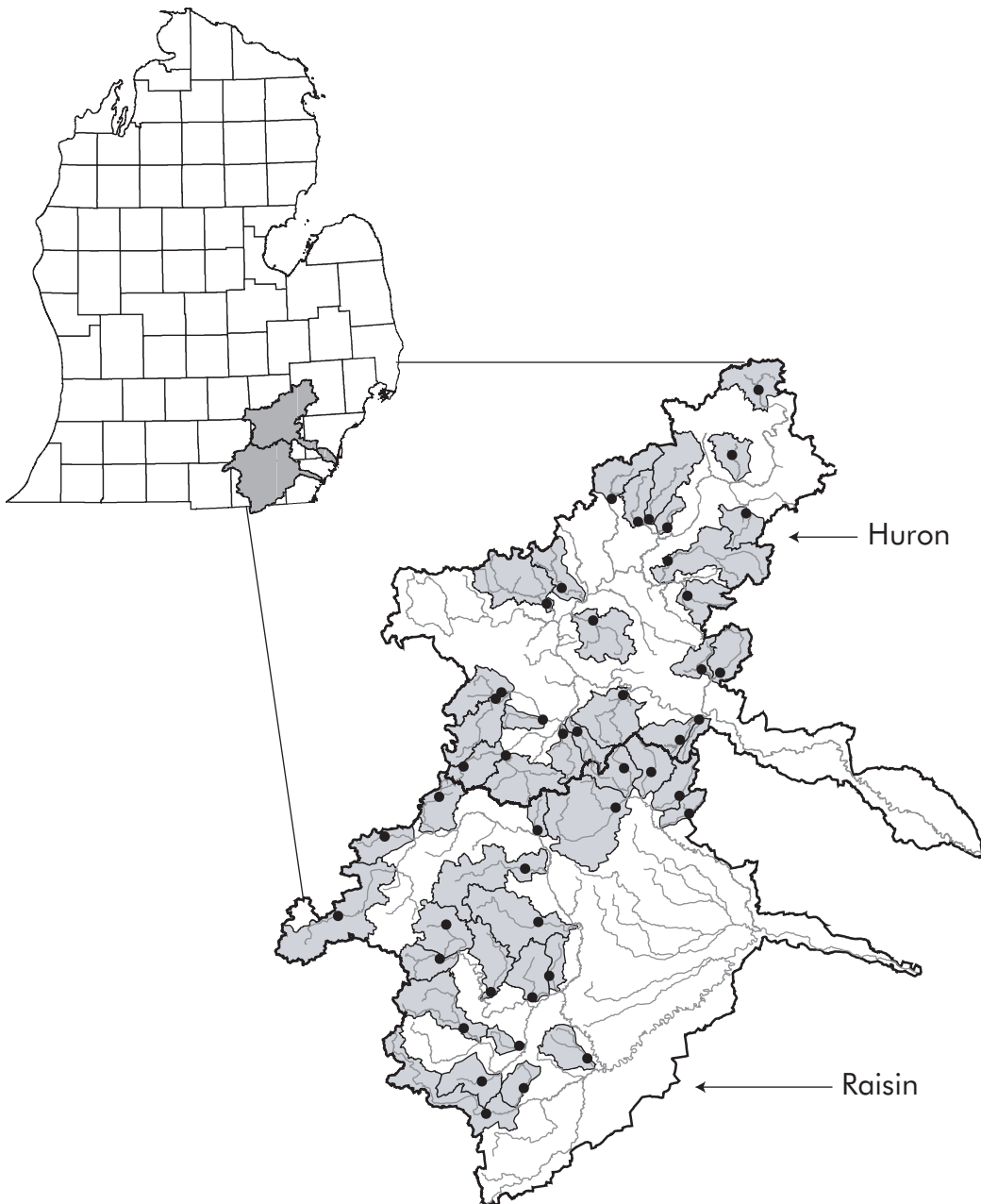


Figure 1. Locations of the Huron and Raisin basins in southeastern Michigan. The study catchments are shown in gray.

wetland, and some herbaceous areas) land uses, with large urban areas interspersed (Hay-Chmielewski et al. 1995). The Southeast Michigan Council of Governments projects population to increase by 6% and urban land-use area to increase by 40% over the next one to two decades,

with most growth occurring in the Huron basin (Hay-Chmielewski et al. 1995). By comparison, the Raisin River basin has higher levels of agricultural land, which is considered to be an important factor causing water quality declines in this basin (Dodge 1998). Fish species richness is

high, with at least 90 species recorded from each basin. See Cifaldi et al. (2003) and Roth et al. (1996) for further description of the region.

Site Selection

The Huron and the Raisin basins were subdivided into smaller catchments to select a set of distinct tributaries and catchments. We delineated 48 catchments from the tributary junction with the main stem or a larger branch of the Huron River or Raisin River. We sampled 25 catchments in 1999 and 23 in 2000. Because catchments differed in their extent of urban and agricultural land (see below), sampling effort was distributed over the 2 years to ensure that a broad range of land cover/use (hereafter, cover) was sampled each year.

Each sample site was at least 1 km above the tributary's confluence with the main stem and at least 1 km from any lake connection to reduce the presence of main-stem and lake fishes (Osborne and Wiley 1992). Sites were located as close to the downstream terminus of the catchment as feasible. All sites were classified as warmwater streams.

Fish Sampling and Analysis

Fish were sampled during midsummer, under low-flow conditions using three-pass depletion electrofishing within a 100-m reach blocked with nets at each end. Due to the small size of the sample sites (mean width = 3.72 m; range 1.47–6.76 m), a stream reach of 100 m was chosen because it was thought to exceed 20 times the stream width and removed the need for reach measurements prior to sampling. Stream segments exceeded 20 times the mean wetted width in 40 of the 48 sites. We used a Wisconsin ABP backpack electrofisher or a Smith-Root SR-6 Tow-Barge and model 2.5 GPP electrofisher, depending on stream size and accessibility. All fish collected were identified to species, measured (total length in millimeters), and weighed (wet weight in grams). Total numbers of fish as well as total biomass were recorded for each site.

To evaluate stream condition from fish collections, we used an IBI developed for warm Wisconsin streams (Lyons 1992), which have similar geology, climate, and fish species as southeastern Michigan. The IBI scores fish assemblages based on the numbers and types of fish species sampled at a site (Karr 1991). All fish species collected in the Raisin and Huron River basins in this study were listed in the classification of Wisconsin fishes (Lyons 1992). Maximum species richness plots used in calculating the Wisconsin IBI described similar numbers of potential fish species for each IBI metric as the Raisin and Huron basins. Maximum species richness plots created using data from the Raisin and Huron basins yielded similar scores, and all metrics were significantly correlated ($p < 0.01$) to Wisconsin IBI scores. Because of the high level of correlation between metric scores and the similar number of potential species used in maximum species richness plots between southern Wisconsin and southern Michigan, we believe the Wisconsin IBI adequately scores biotic condition in southern Michigan streams. Ten metrics were scored based on the abundance of different guilds or taxonomic groups and then summed and reported as a total score (maximum 100).

Physical Habitat Sampling

Physical habitat quality of the 100-m reach was evaluated using the Michigan Department of Environmental Quality's (M-DEQ) Procedure 51 (M-DEQ 1997). This nine-metric index estimates physical habitat quality from visual estimates at a site. The metrics are bottom cover/available substrate, embeddedness/siltation, velocity/depth variation, flow stability, bottom deposition/sedimentation, variety of pools-riffles-runs-bends, bank stability, bank vegetative stability, and streamside cover. Scores were assigned for each metric based on observed condition of each physical habitat feature. We used guidelines defined by the M-DEQ Procedure 51 (MDEQ 1997) to categorize each metric as poor, marginal, suboptimal, or optimal. Scores from individual

metrics were summed to estimate physical habitat quality at each site (maximum 135).

Additional measures of physical habitat supplemented the visually assessed metrics. Substrate size composition was estimated using a pebble count based on 100 particles chosen from the thalweg at meter intervals of the 100-m reach. Pebble counts were used to calculate the proportion of fines and sand (<2 mm), fine gravel (2–8 mm), medium gravel (8–16 mm), coarse gravel (16–32 mm), pebble (32–64 mm), cobble (64–256 mm), and boulder (>256 mm) at each site. We also measured the ratio of fines to the volume of total substrate at the 0, 50, and 100-m point of each reach by recording the volume of substrate that passed through a 2-mm sieve. At 5-m intervals, we also visually estimated habitat type (pool, riffle, or run) and proportion of substrate types (fines and sand, gravel, cobble, boulder, claypan), maximum depth, and number of snags, to estimate habitat condition as a percent of the 100-m stream reach. Slope was measured as the change in elevation between the site and 5 km upstream of the site using 1:100,000 topographic maps.

Data Analysis

We examined scatter plots and simple correlations among physical habitat variables, the IBI, and percent land use to explore relationships, followed by multiple linear regression (MLR) to determine the variables best predicting IBI score. Variables used in MLR model formation included MDEQ habitat metrics and their sum, percent substrate in various size categories, percent habitat type, and percent land cover in the catchment and the 100-m buffer. These variables were examined for collinearity using a Pearson correlation matrix and a partial collinearity correlation γ statistic. Variables that were redundant or highly correlated to other variables were not included in modeling. Forward stepwise regression was used to produce MLR models that predicted IBI scores from land cover and stream physical habitat variables. This analysis was performed on all 48 catchments and on the Raisin and Huron basins separately.

RESULTS

Fish Assemblages

A total of 12,587 individuals and 43 species were collected from 48 sites throughout the Huron and Raisin basins (Figure 2). Of these, the common carp *Cyprinus carpio* was the only nonnative fish. The average number of species caught at a site was 9.5 (range: 2–20), and the average number of fish caught at a site was 262 (range: 18–1,353). Fish assemblages were dominated by cyprinids and centrarchids, including several species that were abundant across most habitats, such as creek chub *Semotilus atromaculatus*, bluegill *Lepomis macrochirus*, white sucker *Catostomus commersonii*, and eastern blacknose dace *Rhinichthys atratulus*. Seven darter species were found in streams with substantial gravel, including the relatively abundant johnny darter *Etheostoma nigrum*, and rainbow darter *E. caeruleum*, as well as the less abundant blackside darter *Percina maculata*, fantail darter *E. flabellare*, greenside darter *E. blennioides*, and logperch *Percina caprodes*. Sites also varied widely in biological condition. The IBI ranged from 5 to 77, with an average score of 37.7 and a median score of 38.5. (Figure 3).

Physical Habitat

Physical habitat quality varied widely across sample sites. Michigan Department of Environmental Quality's habitat scores ranged from 45 to 107. Substrate composition of study reaches ranged from fine sediments to large gravels and cobbles. Pebble counts showed few sites with a high proportion of large cobbles and boulders, and most sites were dominated by fine sediments (<2 mm). Glides comprised more than 85% of all observed habitat types.

Michigan Department of Environmental Quality's metrics were significantly correlated with substrate measurements (Diana 2002). Gravel and larger substrate size categories were negatively correlated to the percent fine substrate

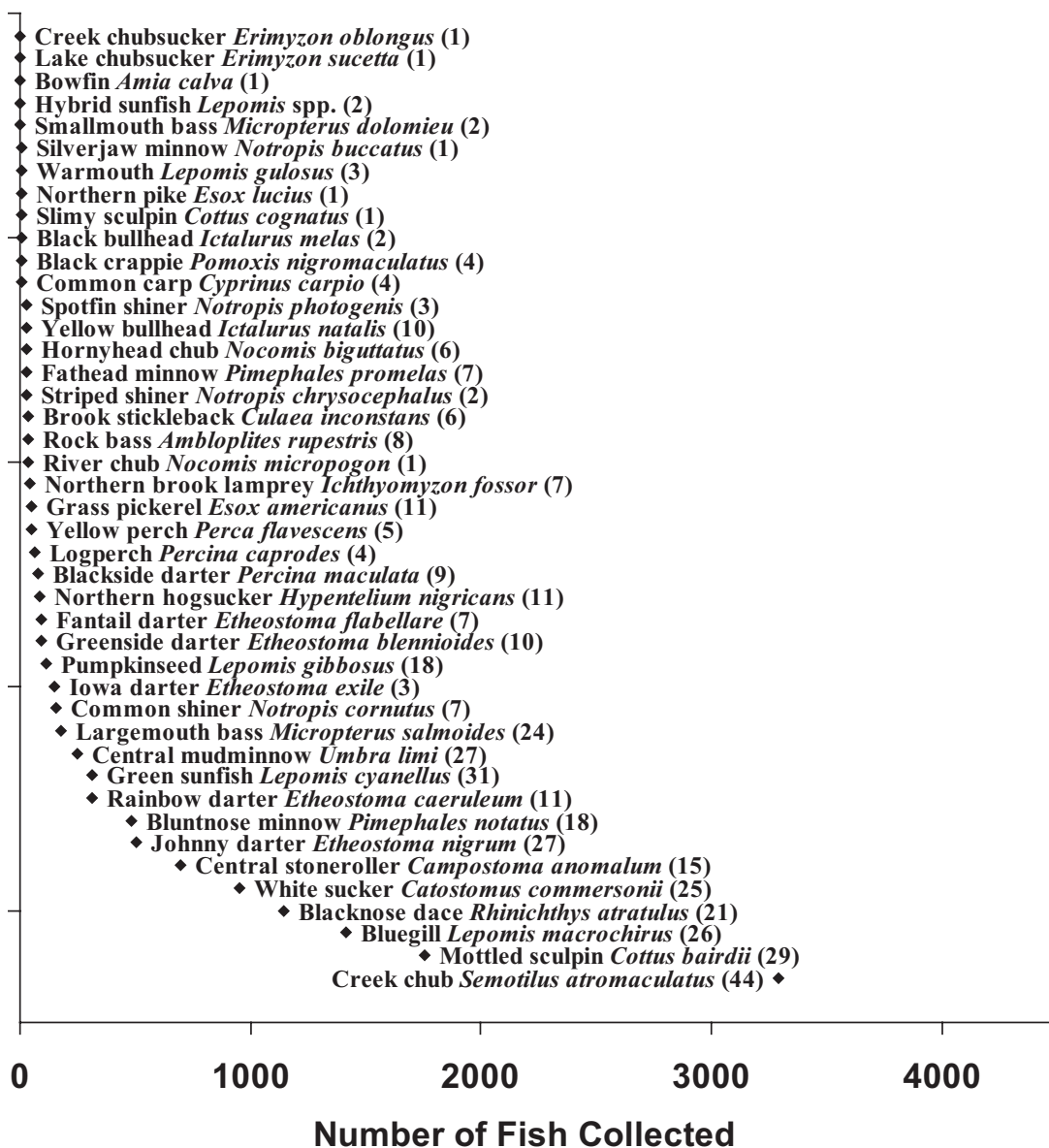


Figure 2. Fish species caught throughout the 48 sample sites and the number of individuals for each species. The number of sites a species was collected in is shown in parentheses.

category. The MDEQ total habitat score, bottom cover/substrate, velocity/depth, bottom deposition, and pools-riffles-runs-bends were negatively correlated with glide habitats and substrate measurements of fine material (proportion ≤ 2 mm, and average fines), and positively correlated with riffle habitat and substrate measurements of medium and large size gravel

(proportion of substrate as boulder, cobble, coarse gravel). Slope for the stream segment was not significantly correlated with proportion of boulder, cobble, coarse gravel, fine gravel, sand, or fines ($P > 0.01$). Slope was correlated with MDEQ habitat metrics that were associated with channel and sedimentation (bottom cover/available substrate [$r = 0.40$, $p = 0.005$], velocity/depth

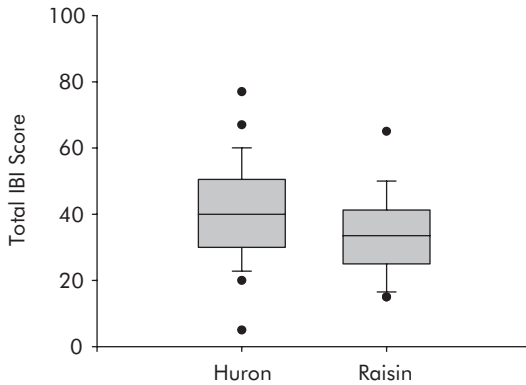


Figure 3. IBI scores for sites sampled in the Raisin and Huron basins.

variation [$r = 0.40$, $p = 0.004$], bottom deposition/sedimentation, [$r = 0.43$, $p = 0.002$], stream-side cover [$r = 0.40$, $p = 0.005$]).

Land Cover

The sampled catchments of the Raisin River basin included a higher percentage of agricultural land and a lower percentage of urban land than observed in Huron catchments (Table 1). Percentage of forest was similar between Huron and Raisin catchments, and percentage of wetland was somewhat greater in the Huron. Percent agricultural land was negatively correlated with percent urban land across the catchments (Figure 4). Land use in the catchment was signifi-

cantly correlated with land use in the 100-m stream buffer for all land-use categories (urban, $r = 0.96$; agriculture, $r = 0.94$; grassland, $r = 0.75$; forest, $r = 0.66$; wetland, $r = 0.89$; for all $p < 0.001$) and both were similarly correlated with physical habitat and IBI variables (Diana 2002). In the small headwater streams of this study, land use in the buffer and catchment appears to influence instream physical habitat and fish assemblage structure in similar ways.

Surficial geology was also related to the land use in a catchment. Agricultural land use in a catchment was negatively correlated with proportion of coarse end moraine ($r = -0.48$, $p = 0.001$) and outwash ($r = -0.56$, $p < 0.001$) and positively correlated with fine end moraine ($r = 0.627$, $p < 0.001$) (Diana 2002). Lake plain geology was not significantly correlated with any land-use components.

Relationships between Instream Habitat and Land Use

Correlations among land cover of the catchments and instream physical habitat suggest that the relative amounts of disturbed (agriculture + urban) and undeveloped land were important factors affecting stream physical habitat. Physical habitat quality was higher in catchments that contained less disturbed land. Total MDEQ habitat scores were negatively correlated with agriculture in the

Table 1. Land use (%) in the Huron and Raisin basins and study catchments and buffers. The Huron catchments are generally composed of a higher proportion of urban land while the Raisin has higher levels of agricultural land.

	Urban	Agriculture	Forest	Wetland	Grassland
<i>Huron</i>					
Basin	28	25	12	19	16
Catchment median	17.8	30.4	11.4	11.0	21.2
Catchment range	1.8–65.4	8.1–70.0	2.2–21.4	2.7–25.0	5.0–28.7
Buffer median	14.0	23.9	8.1	19.1	22.9
Buffer range	1.1–64.4	1.3–70.7	0.0–19.6	0.7–71.0	6.0–40.2
<i>Raisin</i>					
Basin	12	63	10	10	6
Catchment median	6.9	68.5	10.2	2.6	8.0
Catchment range	0.1–27.0	39.7–88.2	3.1–29.1	0.2–10.0	1.8–19.0
Buffer median	3.2	60.2	15.3	3.8	10.9
Buffer range	0.0–18.2	13.8–91.6	0.6–36.1	0.0–35.7	2.2–37.4

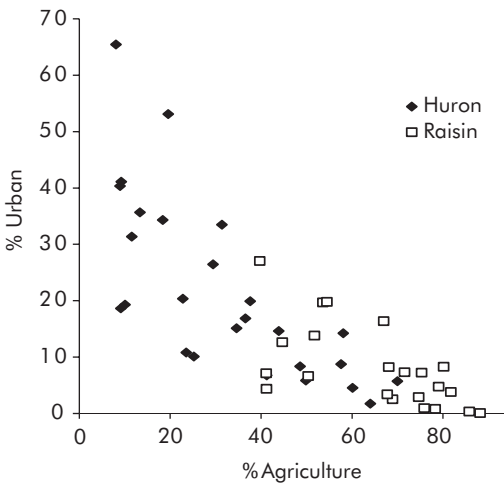


Figure 4. Land use within handpicked catchments ranged from high urban and low agriculture to the opposite extreme. Huron sites tended to have higher percentage of urban land, while Raisin sites generally had higher percentages of agriculture.

scores. Specific physical habitat metrics tended to receive low scores in areas of high agriculture, and higher scores in catchments with high forest and wetland components. Flow stability, bank stability, and bank vegetative stability were positively correlated with wetland and natural land, and negatively correlated with agriculture at the buffer and catchment scales (Table 2; Figure 5). Land cover variables were also examined for correlations with measures of physical habitat. Agricultural land was associated with sites that contained high amounts of fine substrate, while natural land was associated with greater abundance of gravel at a site (Table 2). Although geology was correlated with land use, we observed no significant correlations of geology with proportion of boulder, cobble, coarse gravel, fine gravel, sand, or fines ($P > 0.01$).

Relationship of the IBI to Land Cover and Instream Habitat

catchment (Table 2), while catchments with greater amounts of natural land (forest, wetland) were associated with higher physical habitat

No significant correlations were found between the abundance or biomass of any fish species and

Table 2. Pearson correlation coefficients between land use variables, M-DEQ total and metric scores, IBI scores, and substrate measurements. Urban, agricultural, grassland, forested, and wetland refers to the land cover in the catchment. Disturbed land is the sum of urban and agricultural land in the catchment, and natural land is the sum of grassland, forested, and wetland in the catchment. Bold numbers are significant at $p < 0.05$, and bold and underlined numbers are significant at $p < 0.01$.

	Urban	Agri-cultural	Disturbed land	Grass-land	Forested	Wetland	Natural	IBI
<i>M-DEQ metric scores</i>								
Bottom cover/ available substrate	0.16	-0.20	-0.15	0.19	0.08	0.05	0.15	0.03
Embeddedness/ siltation	-0.01	-0.15	-0.23	0.11	0.22	0.16	0.20	<u>0.40</u>
Velocity/depth variation	0.20	-0.26	-0.22	0.20	0.17	0.06	0.19	0.14
Flow stability	0.06	<u>-0.44</u>	<u>-0.60</u>	<u>0.42</u>	<u>0.42</u>	<u>0.49</u>	<u>0.59</u>	<u>0.49</u>
Bottom deposition /sedimentation	0.12	0.03	0.16	-0.08	-0.06	-0.20	-0.15	0.02
Pools-riffles-runs-bends	0.16	-0.28	-0.28	0.24	0.15	0.13	0.24	0.14
Bank stability	0.10	<u>-0.38</u>	<u>-0.47</u>	0.25	<u>0.32</u>	<u>0.48</u>	<u>0.46</u>	<u>0.36</u>
Bank vegetative stability	0.23	<u>-0.42</u>	<u>-0.43</u>	<u>0.30</u>	0.22	<u>0.41</u>	<u>0.42</u>	0.12
Streamside cover	0.10	-0.15	-0.14	0.07	0.28	0.00	0.34	-0.16
Total M-DEQ score	0.18	<u>-0.37</u>	<u>-0.38</u>	<u>0.29</u>	<u>0.29</u>	0.23	<u>0.36</u>	<u>0.29</u>
<i>Substrate measures</i>								
% fine substrate	<u>-0.41</u>	<u>0.36</u>	0.18	-0.25	0.18	-0.23	0.18	-0.11
% gravel	<u>0.29</u>	<u>-0.41</u>	<u>-0.35</u>	<u>0.36</u>	-0.11	<u>0.43</u>	<u>0.35</u>	<u>0.33</u>
% large substrate	<u>0.34</u>	-0.11	0.14	0.00	-0.19	-0.16	-0.36	-0.23
<i>Total IBI score</i>								
IBI	-0.01	-0.22	<u>-0.34</u>	0.24	0.09	<u>0.40</u>	<u>0.34</u>	<u>1.00</u>

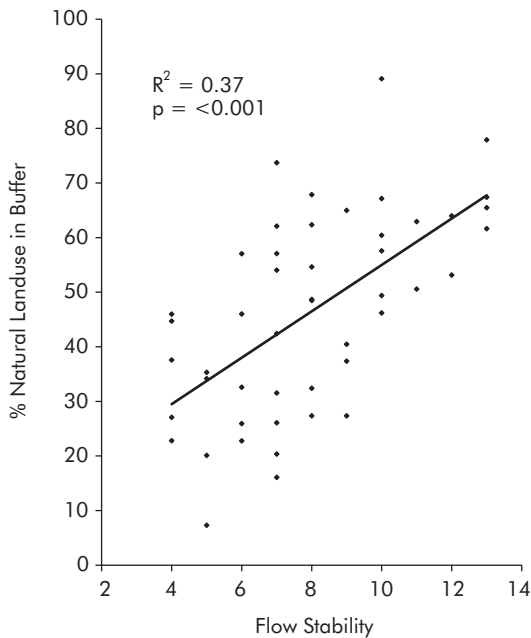


Figure 5. Flow stability versus percent natural land (sum of forest and wetland) increases in the buffer zone.

instream physical habitat features. Total biomass was also not significantly correlated to any instream physical habitat variable. Individual IBI metrics were also examined for correlations with physical habitat and land use, and few significant correlations were found. The IBI total score had stronger correlations with physical habitat and land-use variables than individual IBI metrics or species abundance. Because of this, we focused on IBI as the main indicator of fish assemblage condition in the remaining analyses.

We examined the IBI for correlations with a number of habitat variables. The correlation between the IBI and the MDEQ total habitat score was weaker than the correlation of the IBI with MDEQ physical habitat metrics, including embeddedness/siltation, flow stability and bank stability (Table 2). Flow stability, which was significantly correlated with all land cover categories but urban, exhibited the strongest correlation with the IBI ($r = 0.49$, Table 2; Figure 6). The IBI score was not significantly correlated to bank

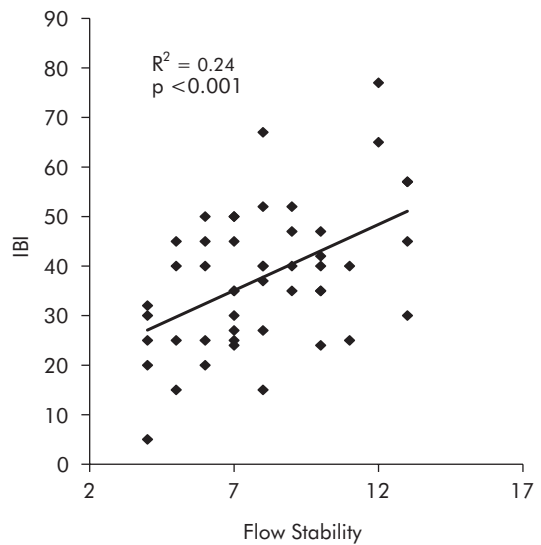


Figure 6. The IBI versus visually assessed flow stability.

vegetative stability, streamside cover, or percent fine substrates, but it was correlated with percent gravel (Table 2).

Among land cover variables, the IBI was positively correlated with percent wetland in the catchment (Table 2) and with the percent natural land in the stream buffer (Figure 7). When summed to create a measure of natural (forest + wetland) and disturbed (agricultural + urban) land, the IBI correlated positively with natural land and negatively with disturbed land (Table 2).

Relationships between the IBI and environmental variables were similar between the two basins for some variables but not others. Flow stability showed a similar relationship in both basins (Huron: $R^2 = 0.25$, Raisin, $R^2 = 0.13$, combined $R^2 = 0.24$) (Figure 8a). Siltation was much more clearly related to the IBI in the Huron ($R^2 = 0.35$) than in the Raisin ($R^2 = 0.07$, combined $R^2 = 0.16$) (Figure 8b). The IBI was significantly related to percent of the buffer as disturbed (agriculture + urban) land for the Huron ($R^2 = 0.35$) but not the Raisin ($R^2 = 0.00$) (Figure 8c), and for the combined data set ($R^2 = 0.15$) (Figure 8d).

Multiple linear regression analysis was used to produce a predictive model for the IBI and to

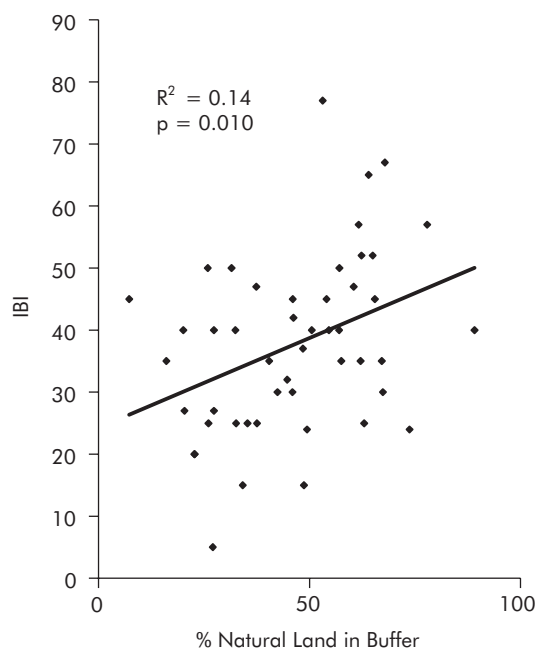


Figure 7. The IBI versus natural land (sum of forest and wetland) covers in the 100-m buffer.

examine all potential factors that may influence variation in IBI scores. All variables entered this model at the 0.05 level of significance, resulting in an overall model with an adjusted $R^2 = 0.52$ (Table 3). This model included the percents of fine gravel and sand, embeddedness/siltation, flow stability, and percent of riffles. No land cover variables were retained in this model.

Based on differences in land cover (Table 1) and environmental variables and IBI (Figure 8), we considered models for each basin. The best model for the Raisin basin had an adjusted R^2 of 0.79 and included wetland buffer, and urban and agricultural land in the catchment in predicting IBI scores. In addition, MDEQ metrics representing flow stability, bank vegetative stability, and streamside cover were included as predictive variables (Table 3). The best model for the Huron basin had an adjusted R^2 of 0.76 and included multiple physical habitat variables, but did not include land cover/use.

DISCUSSION

Human alteration of landscapes through conversion of natural land to agriculture and urban lands is an important and widespread contributor to loss of integrity of aquatic ecosystems (Allan 2004). Throughout the Huron and Raisin basins, land cover/use varies greatly and appears to influence stream condition. In general, reach-scale habitat variables were included in regression models describing variation in biotic condition more frequently than were landscape variables. However, a number of physical habitat variables correlated with land use, wetlands, and the amount of relatively undisturbed versus disturbed land, showing strongest relationships with measures of flow stability, substrate, and riparian vegetation. These results suggest that land use and instream physical habitat both can influence the biotic condition of a stream.

Michigan Department of Environmental Quality's habitat scores documented a wide range of physical habitat quality across sample sites. Physical habitat metrics also were significantly correlated with field measures of physical habitat and substrate (Diana 2002). Performing visual assessment and using quantitative measurements of habitat may be redundant; however, some differences in correlations with the IBI were observed, and the use of both proved useful in predicting IBI scores. Nonetheless, Platts et al. (1983) and Kaufmann et al. (1999) found that the imprecision of qualitative physical habitat metrics made them highly suspect for general monitoring.

The IBI is expected to correlate with habitat indexes, which often are used together to provide a more comprehensive assessment of stream condition or to validate an IBI or habitat assessment protocol (Fausch et al. 1984; Berkman et al. 1986; Schleiger 2000). However, several MDEQ metrics formed stronger bivariate correlations with the IBI than did the MDEQ total habitat scores. Visually assessed flow stability was especially consistent in forming significant relationships with the IBI and with land cover/use.

Table 3. Multiple linear regression models that predict the IBI for all sites combined, and separately for the Huron and Raisin sites. Variables are listed in the order entered in a stepwise forward multiple regression.

Basin	Variables selected	N	R ²	Adjusted R ²
Combined	flow stability fine gravel (%) embeddedness /siltation riffle (%) sand (%)	48	0.58	0.52
Huron	fine gravel (%) bank stability embeddedness / siltation fine sediment (%) pools:riffles:runs:bends	26	0.81	0.76
Raisin	catchment agriculture bank vegetative stability streamside cover catchment urban flow stability buffer wetland	22	0.85	0.79

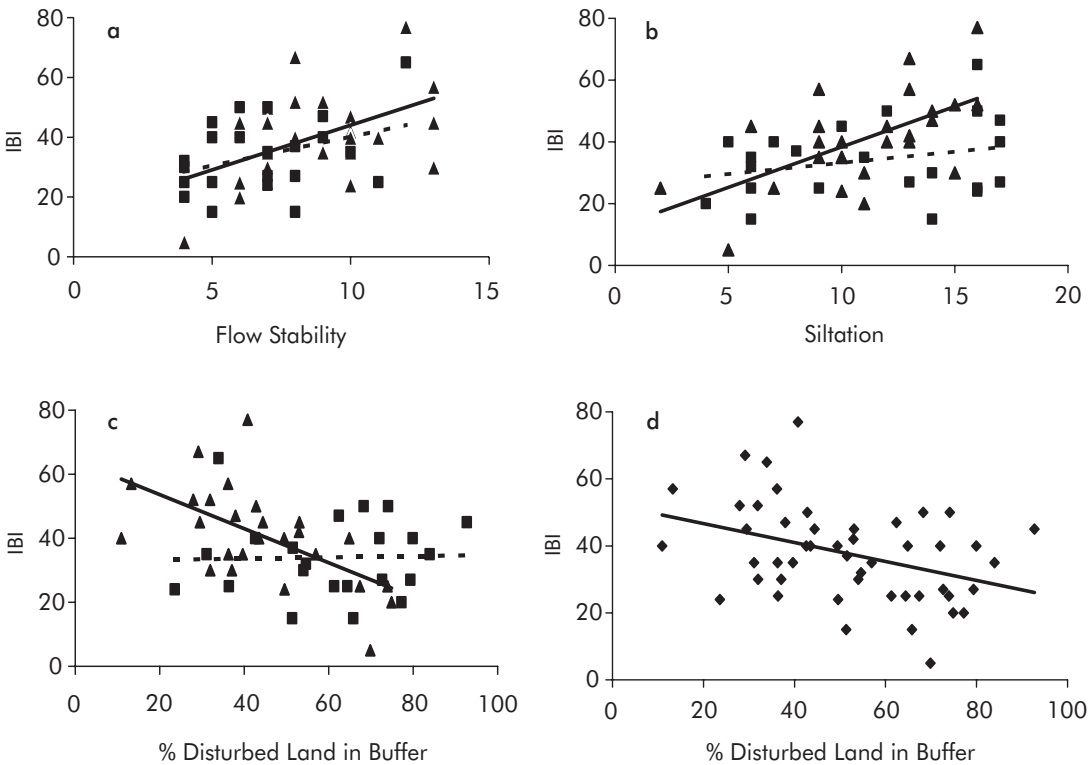


Figure 8. Relationships between the IBI and environmental variables. Huron basin: triangles, solid line; Raisin basin: squares, dashed line, combined: diamonds, solid line.

Agricultural land use was expected to alter stream physical habitat quality, and in this study, agricultural land was negatively correlated with a number of physical habitat variables. Fine substrates increased and gravel substrate decreased as agriculture increased. Agriculture has been shown to increase sedimentation rates in other basins (Waters 1995; Walser and Bart 1999). Agriculture was also negatively correlated with flow stability, leading to decreased bank and bank vegetation stability. Richards et al. (1996) identified variables highly correlated to row-crop agriculture as having the strongest influence on flood ratio in the Saginaw basin of east-central Michigan. Catchments with a high proportion of agriculture were associated with fine geology, and relatively undisturbed lands were associated with catchments with coarser geology (Diana 2002).

Urban land was associated with greater amounts of gravel and large substrate and a decrease in fine substrate. Urbanization of a basin has been shown to increase the imperviousness of the basin and therefore to increase the magnitude of high flows, the flashiness of the stream, and channel erosion (Klein 1979; Paul and Meyer 2001). However, urban land was not strongly correlated with flow stability or other measures of flashiness in our study. To minimize the potential for streams with severely altered stream chemistry or thermal regimes to interfere with our ability to detect links among the landscape, stream habitat, and the IBI, we eliminated sites with catchments containing large amounts of commercially or industrially developed areas. Consequently, the weak relationship between urban land and flow regimes may be due to the fact that variation in urbanized areas in this study is due primarily to residential developments.

The proportion of wetland in the sub-catchments was the only individual land cover component significantly correlated to the IBI. The amount of wetland in a catchment has a direct influence on stream water quality and flow variability and may affect fish assemblages. Roth et al. (1996) found higher IBI scores in areas of

higher wetland and forest and lower agriculture within the Raisin River basin. Richards et al. (1996) showed that agriculture and the presence of wetlands were the most important land cover variables influencing instream habitat features. Roth et al. (1996) also reported that higher habitat index scores were associated with streams located in areas of less agriculture and higher wetland. Correlations in the present study indicate that the relative amount of wetland influences the physical habitat quality of streams.

While individual land cover categories were weakly correlated with the IBI, when they were combined as relatively undisturbed versus disturbed land, the relationships were much stronger. This was also seen with a number of physical habitat variables. This implies that the biotic condition of fish assemblages is affected by whether land is altered for human use or left as relatively undisturbed forest and wetland. Agricultural and urban land have each been shown to have negative effects on fish assemblages (Walser et al. 1999; Brown 2000; Schleiger 2000; Wang et al. 2000, 2001) and there may not be major differences in their negative influence, at least in the present study. Although Wang et al. (1997, 2000) reported much more negative effects of urbanization than agriculture on IBI scores, Mebane et al. (2003) and Van Sickle et al. (2004) projected similar effects of urbanization and irrigated agriculture on the IBI.

The IBI was associated with physical habitat variables that were negatively correlated with disturbed land and positively correlated with wetland in a catchment. Higher IBI scores were observed in streams with a high proportion of gravel, low sedimentation, and low flow variability. High levels of sedimentation and the lack of exposed gravel have been shown to negatively affect stream fish in other studies. Nerbonne and Vondracek (2001) reported a negative correlation between IBI and embeddedness in the Whitewater River in Minnesota. Belliard et al. (1999) also found the IBI to be significantly related to substrate clogging in headwater streams

of the Seine. Substrate was identified as a major factor influencing fish assemblages in a north-east Missouri stream where Berkman and Rabeni (1987) found that exposed gravel substrate was important to certain fish species and, as silt covered gravel, fish species that use gravel for feeding and reproduction were negatively affected. This supports the interpretations that exposed gravel substrate associated with lower levels of embeddedness promotes higher IBI scores in the Huron and Raisin basins. However, because substrate size is naturally affected by stream power and geology, such evaluations must be tempered pending evaluation of relative bed stability (Kaufmann and Hughes 2006, this volume). In addition, flow stability was significantly correlated with IBI score and the amounts of disturbed and natural land in a catchment.

The multiple linear regression model for combined basins identified the variables just discussed as best able to explain a large proportion of the variance in IBI. Flow stability and the relative amounts of fine sediment and gravel in a stream were selected, and no land-use variables remained in the model created for both basins. However, the instream physical habitat variables selected were related to land use, as discussed earlier, lending support to the idea that land cover/use may alter physical habitat features that are important to fish assemblages. When models were developed to predict the IBI separately for the Raisin and Huron rivers, different factors were related to biotic condition in the two basins and model explanatory power was increased. The Raisin model included land cover variables, while the Huron model included only variables related to physical habitat. In basins such as the Raisin, with large amounts of altered land, the negative effects of land cover/use on stream fish assemblages may be more apparent. Because the Huron basin has more relatively undisturbed land and a smaller extent of agriculture in the study subcatchments, land cover/use may be less likely to be identified as a primary factor. Thus instream habitat and land cover may play differ-

ent roles in these basins, suggesting the benefit of forming separate models for individual basins when sufficient data are available.

Instream physical habitat metrics were better predictors of IBI than land use. Substrate conditions, especially sedimentation, and flow stability were important correlates of biotic condition in two watersheds of southeastern Michigan. High IBI scores were associated with exposed gravel substrate and low levels of embeddedness as well as more stable flows. Sedimentation and flow stability were also closely related to land use in a watershed. High levels of sedimentation and decreased flow stability were found in watersheds with low wetland and high agricultural land. A disturbed land-use category combining agriculture and urban land was more closely associated with IBI scores and physical habitat components, suggesting that the relative amount of land that is altered for human use may have a greater effect on stream assemblages than do specific types of land use. In addition, percent disturbed land had higher correlations with IBI score than did most physical habitat variables (Table 2). Specific land uses were not highly correlated with IBI score, but were related to physical habitat metrics that were closely related with IBI score. Like Richards et al. (1996), this study provides evidence that some instream physical habitat scores are more directly related to the IBI than is specific land cover, but that land cover in turn influences instream physical habitat.

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Influence of Landscape Characteristics on Local Habitat and Fish Biomass in Streams of Michigan's Lower Peninsula

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Abstract.—Biologists need to understand causal relations among key habitat elements and fishes to effectively protect and manage stream systems. Though much groundwork has been laid, development of an analytic framework that incorporates spatial hierarchy of stream characteristics to predict instream habitat and fish assemblages has been challenging. A key issue is the complex web of direct and indirect effects that arise when one attempts to include all pertinent habitat parameters in analyses. Covariance structure analysis (CSA) was specifically developed for untangling such webs. We used CSA to quantitatively describe relations between catchment- and local-scale habitat variables and fish biomass in streams of Michigan's Lower Peninsula. Catchment-scale variables characterizing stream size, land use, and surficial geology had significant direct and indirect effects on, and explained 50–83% of spatial variation in, mean depth, velocity, July mean temperature, 90% exceedence flow yield, and total phosphorus values in streams. These variables also had significant direct effects on substrate composition at sites, accounting for up to 30% of the spatial variation in individual substrate classes. Local-scale variables—mean depth, total phosphorus, and percent cobble—had significant direct effects on total fish biomass, explaining 26% of spatial variation among sites. Catchment area and percent of agricultural and urban land uses in the catchment had significant indirect effects on fish biomass. Our findings clearly demonstrated the ecological complexity and multiscale nature of fish habitat in stream ecosystems.

INTRODUCTION

Faced with rapid changes to watersheds and competing demands placed on streams, biologists need to understand relations among key habitat elements and fishes to effectively protect and manage stream systems. Describing these relations seems deceptively simple at first because many physical and biotic characteristics often covary in a downstream direction. Observed changes

formed the basis for the many longitudinal zonation studies (e.g., Huet 1959; Hawkes 1975; Vannote et al. 1980) that represent early general models for stream ecosystems. While all streams may change abruptly at confluences with comparably sized tributaries or at boundaries of major landscape discontinuities such as glacial landforms, bedrock outcrops, impoundments, and lakes (Seelbach et al. 2006, this volume), the direction and degree of change are not always predictable. For example, a stream may warm or cool varying amounts at a confluence depending on

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the relative thermal regime and size of the tributary. Variability between stream systems is great enough that no single descriptive model seems possible (Balon and Stewart 1983; Wiley et al. 1990; Zorn et al. 1998). Nevertheless, development of a general framework is desirable, and seems feasible, since the specific responses of fish to a common suite of local factors (e.g., current velocity, temperature, and predators) are often fairly consistent across each species' geographic range. These consistent relations between local factors and fish distribution and biomass are the basis for widely used Habitat Suitability Index (HSI) models (Terrell et al. 1982).

Work by many authors has led to development of mechanistic-based models for describing physical habitat in stream systems and explaining contemporary patterns in fish assemblages. Early studies (e.g., Lotspeich and Platts 1982; Frissell et al. 1986) provided impetus for thinking about hierarchical influences of landscapes on stream habitats. These concepts have been applied by others (e.g., Wiley et al. 1990) to quantitatively model stream habitat conditions. Contemporary stream fish assemblages can also be thought of as resulting from extinction processes or filters selecting individual populations from a regional species pool (Mahon 1983; Tonn 1990). Filters represent local conditions that may be influenced by site-, reach-, catchment-, and regional-scale habitat characteristics, drainage network characteristics (e.g., wetlands, lakes, and barrier waterfalls), biotic factors, or human activities such as species introduction and habitat modification (Poff 1997). Models incorporating these filters could conceptually be linked to information on species habitat needs (mechanisms) to predict fish assemblage structure or identify habitat attributes limiting fish populations (Imhof et al. 1996).

Previous analyses of habitat and fish assemblages in Michigan streams have also demonstrated the utility of information from various spatial scales. Landscape-based models have been developed for streams in Michigan's Lower Peninsula (lower Michigan) to predict habitat vari-

ables measured at the site, such as water temperature (Wehrly et al. 1997) and nutrient levels (Kleiman 1995; Baker et al. 2001). Variables characterizing stream size and hydrology have provided a macrohabitat template for characterizing individual survey sites and making coarse-scale predictions of fish assemblage structure (Zorn et al. 1998). Use of multiscale data in species-specific modeling of stream fishes in Michigan has helped identify key predictive variables for individual fishes, and collectively for fish assemblages (Zorn 2003).

What is lacking, however, is a quantitative model describing causal (mechanistic) interplay among key habitat variables operating at different hierarchical levels and between these variables and fish biomass. With such a tool, we could demonstrate the relative influence of stream macrohabitat characteristics, measured at different spatial scales, on local habitat parameters directly important to stream fishes. It would also allow a more complete assessment of the direct and indirect effects of landscape and habitat alteration on stream fish assemblages. This would help in answering a variety of complex questions regarding conservation and management of fishes and their habitats. For example, to what extent does increased urban land use affect streamflow, stream temperatures, and substrate conditions, and ultimately fish biomass? If urbanization affects fish by multiple causal pathways, which is the most important to mitigate?

There is a need for synthesis of relations among key aspects of aquatic habitat and fishes, but development of an analytic framework to predict characteristics of habitat and fish assemblages has been challenging for several reasons. A key issue is the complex web of direct and indirect effects that arises when one attempts to include all pertinent habitat parameters in analyses (Zorn 2003). This complexity and the multicollinearity that arises from spatial covariance obscures the meanings of observed correlations and can violate the assumption of independence required by statistical procedures, such as multiple linear regression. Multivariate

analysis techniques (e.g., Lyons 1996; Maret et al. 1997; Waite and Carpenter 2000) can perhaps accommodate these data in a more statistically appropriate manner, but provide little basis for understanding causal relations among habitat variables. In addition, regional differences in mechanisms behind site-scale habitat characteristics will cause empirical relations to vary regionally and may limit broad application of any correlation-based model built from limited regional data. For example, altitude is closely associated with stream temperature variation in the mountain states (Keleher and Rahel 1996) but not in glaciated states, such as Michigan where groundwater is key (Wehrly et al. 1997). Such issues have hindered development of a comprehensive framework for lotic systems.

Covariance structure analysis (CSA; also known as structural equation modeling) was specifically developed for untangling webs of direct and indirect effects and can provide a useful analytic framework for studying interrelations between physical and biotic features of stream systems across multiple scales. In CSA, the researcher uses existing knowledge to generate hypotheses of how the system functions. These hypotheses are explicitly stated in the form of a causal model that depicts pathways, both direct and indirect, by which variables can influence each other. The researcher's theoretical model can be evaluated by assessing the extent to which implied covariances among variables in the model (whose structure was constrained by the researcher's theory) are consistent with those occurring in the actual data. Thus, a CSA model could be developed for streams to depict and quantify the many linkages among intercorrelated habitat parameters. A CSA showing relations for key habitat variables such as HSI parameters (Terrell et al. 1982) could serve as a common analytic framework for models tailored to individual fishes. Use of CSA (which includes path analysis) in studies of fish habitat has been fairly rare to date, but its popularity is increasing (e.g., Sheldon and Meffe 1995; Hinz and Wiley 1998; Isaak and Hubert 2001; Infante 2001).

In this study, our objective was to use CSA to quantitatively describe the many relations between landscape-scale stream habitat attributes, local-scale variables commonly used to predict fish biomass (Zorn 2003), and total fish biomass at sites on lower Michigan streams.

METHODS

Data Sources

This study occurred in lower Michigan, which, except for a few isolated areas, is entirely covered by glacial drifts ranging from glacial till and outwash deposits of sand and gravel to former glacial lakebeds dominated by silt and clay. Streams draining the coarse-textured glacial deposits have very stable, groundwater-dominated flows, whereas those draining finer-textured deposits are fed almost entirely by runoff. We obtained data for this study from sites included in the Michigan Rivers Inventory database for lower Michigan (Seelbach and Wiley 1997). The basic units of the database are sites, 120–450-m stream reaches where population estimates of entire fish assemblages were made (site length increased with stream width). Sites were chosen and sampled by Michigan Department of Natural Resources, Fisheries Division personnel and researchers at The University of Michigan. The desire to choose sample sites for addressing both local management and statewide data needs resulted in a dispersed sample of 245 sites that included most wadeable stream types found in lower Michigan (Figure 1). This sample also included some nonwadeable and seasonally wadeable rivers.

Stream habitat variables included in this study were hypothesized to directly or indirectly influence fish assemblage structure and have been identified in other studies as important correlates with fish assemblages (e.g., Hynes 1972; Lyons 1996; Richards et al. 1996; Zorn et al. 1998). The following data associated with each Michigan Rivers Inventory site were used in this study: (1) geographic information system-based

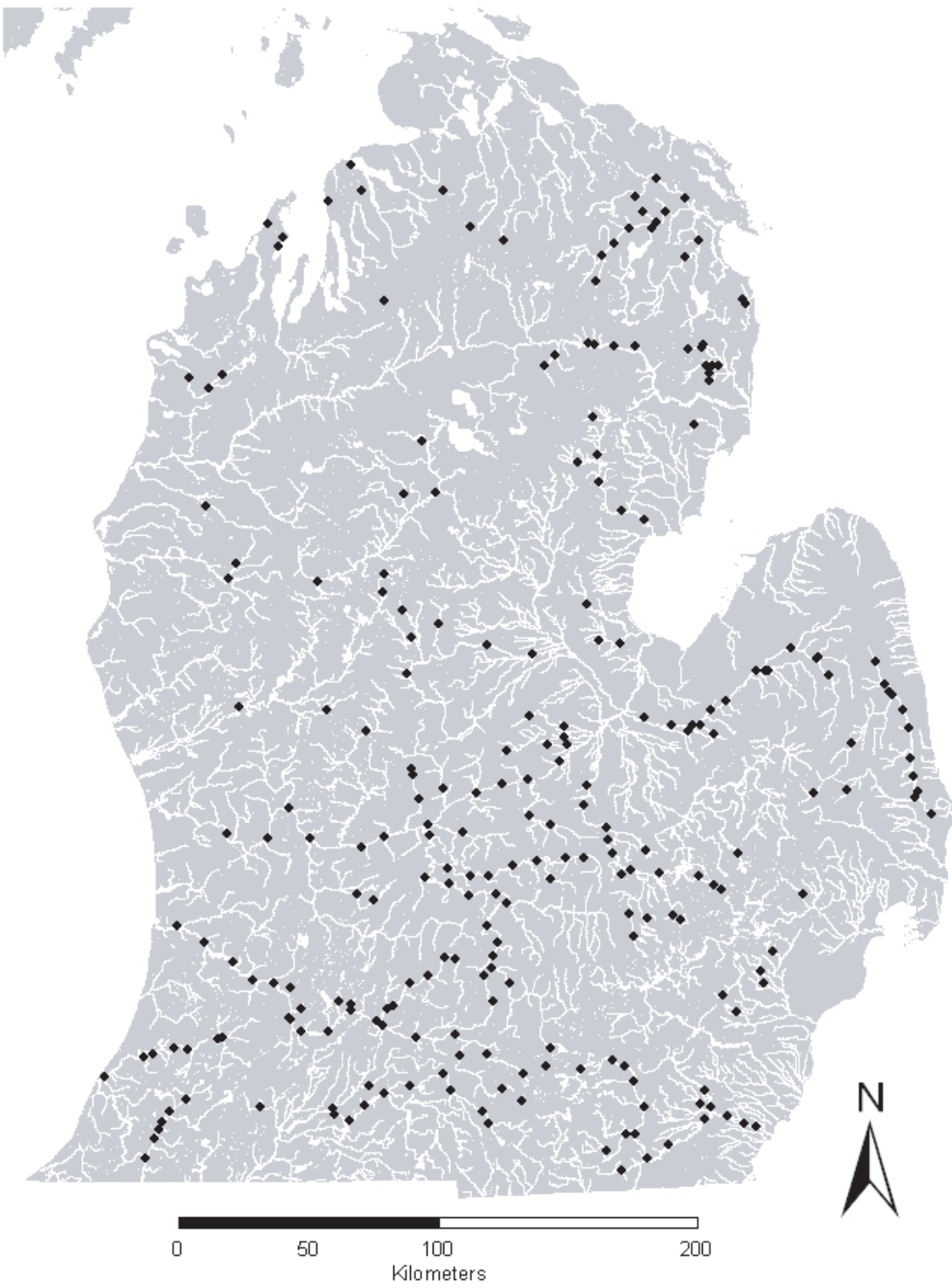


Figure 1. Michigan’s Lower Peninsula showing sites included in this study.

characterizations of surficial geology and land use at the catchment scale; (2) stream gradient measured from topographic maps for the reach bounded by contour lines upstream and downstream of the site; (3) site-scale measurements of instream habitat conditions such as mean depth and percent composition by substrate type; (4) measurements, or predictions when measurements were unavailable, of 90% exceedence streamflows, mean July temperature (hereafter referred to as temperature), and total phosphorus (e.g., Kleiman 1995; Wehrly et al. 1997; Seelbach and Wiley 1997); and (5) biomass estimates for occurring fishes based upon electrofishing depletion samples and rotenone surveys (Table 1). A detailed description of field sampling methods occurs elsewhere (Seelbach and Wiley 1997; Zorn et al. 1998).

Data Analysis

We analyzed causal relations among variables using CSA. Covariance structure analysis has been discussed in detail by other authors (e.g., Mitchell 1992; Wootton 1994a, 1994b; Klem 1995) so only a brief overview is given here. Covariance structure analysis allows correlation coefficients among variables in models to be decomposed into direct, indirect, and spurious effects (Bollen 1989). The sets of causal relations being studied in a CSA are explicitly defined by a path diagram (e.g., Figure 2). Here, each effect is denoted by an arrow whose tail is at the cause and whose head points to its direct effect. A direct effect is represented by a single arrow between cause and effect variables. An indirect effect involves the cause and effect variables being related via paths of two or more

Table 1. Description of variables used in this study, their spatial scale of measurement, and sample mean and standard deviation values prior to transformation. Type indicates both source of the data (M = measured, P = predicted, C = combination of measured and predicted) and transformation used. Transformations were (1) $\log_{10}(x + 0.001)$; (2) $\log_{10}x$; and (3) $\log_{10}(x + 0.01)$. Low-flow yield (LFY) represents a combination of site- and catchment-scale data.

Variable name	Variable description (units)	Type	Mean	Standard deviation
Site-scale data				
JulyTemp	July mean temperature (°C)	C	21.1	3.0
Total P	Total phosphorus (mg/L)	C-1	0.075	0.040
Velocity	Velocity at 90% exceedence flow (m/s)	P-2	0.32	1.90
Depth	Depth at 90% exceedence flow (m)	C	0.48	0.28
Silt	Percent of substrate as silt (%)	M	16.5	19.3
Sand	Percent of substrate as sand (%)	M	37.9	25.7
Gravel	Percent of substrate as gravel (%)	M	22.9	18.9
Cobble	Percent of substrate as cobble (%)	M	12.5	14.3
FishBiom	Total fish biomass (kg/ha)	M-1	218.3	206.0
Reach-scale data				
Gradient	Percent channel gradient (%)	M-1	0.18	0.49
LFY	90% exceedence flow yield ($\text{m}^3 \cdot \text{s}^{-1} \cdot \text{km}^{-2}$)	C-2	0.0032	0.0037
Catchment-scale data				
CA	Catchment area (km^2)	M-2	1000	1926
Urban	Proportion of urban land use in catchment	M-3	0.064	0.084
Agric	Proportion of agricultural land use in catchment	M-3	0.480	0.251
CoarseGeo	Proportion of coarse-textured till and outwash geologic deposits in catchment	M-3	0.558	0.356

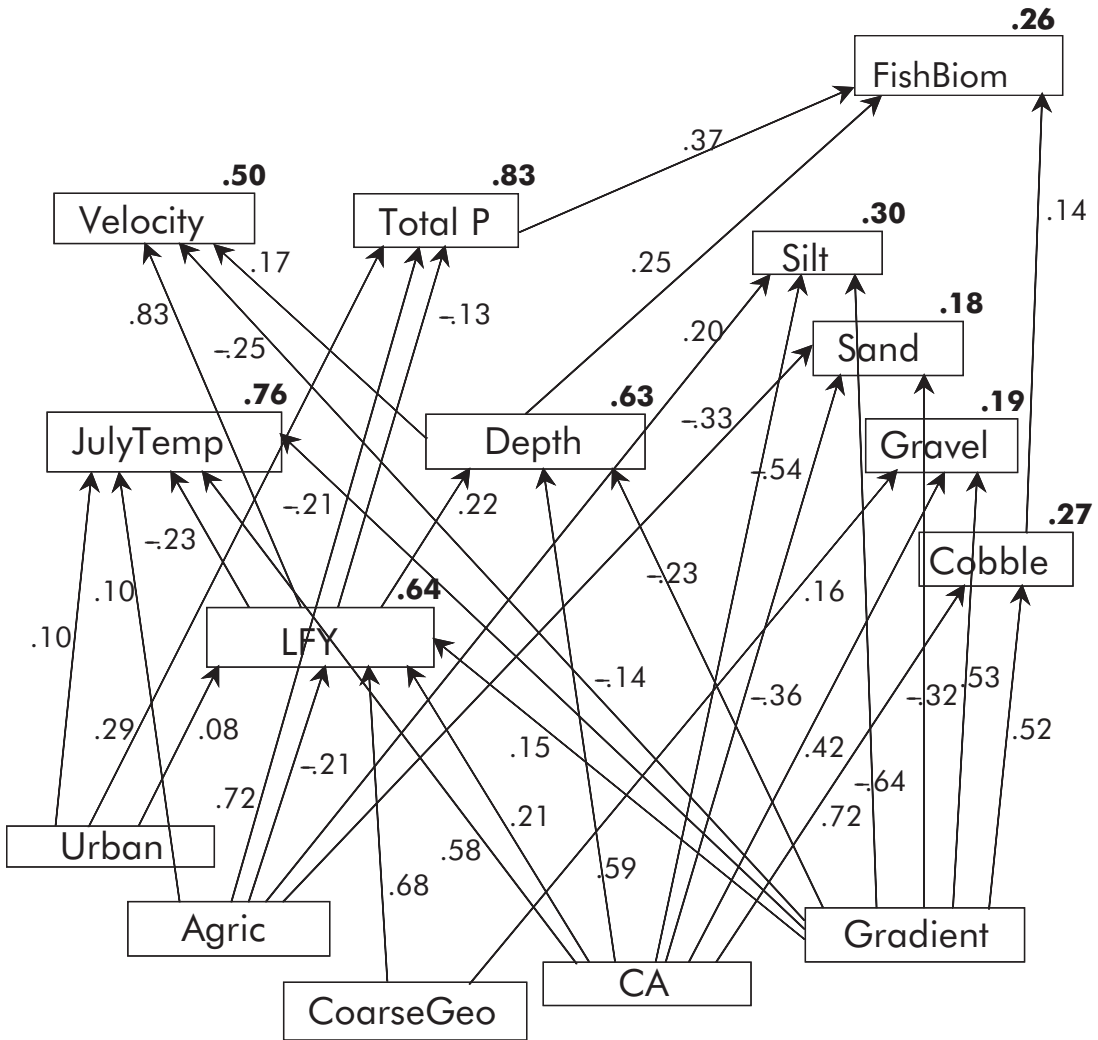


Figure 2. Simplified path diagram for catchment-, reach-, and site-scale habitat attributes and total fish biomass in lower Michigan streams. Standardized direct effects (in regular type) from the covariance structure analysis are shown for each path along with squared multiple correlations for response variables (bold type). Covariances and error terms associated with response variables are omitted from the diagram for clarity.

direct effects with mediating variables in between. For example, in Figure 2, gradient has a direct effect on percent cobble substrate and an indirect effect on fish biomass via its influence on cobble substrate. Spurious effects (noncausal correlations) between variables are indicated by double-headed arrows. The relative strength or magnitude of effects is assessed by comparing standardized effect coefficients; the strength of a path is pro-

portional to the absolute value of its direct effect coefficient. The standardized effect coefficient for an indirect effect is the product of the direct effect estimates along its path, or difference between the total and direct effect estimates for the two variables at each end of the path.

As an explicit hypothesis on how a system functions, a covariance structure (causal) model and its path diagram identify constraints on expected

patterns of covariance in the study system (Wootton 1994a, 1994b). The causal model is evaluated by comparing the covariance matrix of observed data to the covariance matrix implied by the constraints of the causal model. Thus, the utility of CSA is its ability to allow researchers to assess the extent to which theoretical models for complex systems are consistent with the covariance structure of the observed data (Bollen 1989).

We constructed a CSA model for assessing relations among catchment- and reach-scale variables (e.g., surficial geology, land use, and gradient), traditional habitat suitability index variables (i.e., depth, substrate, velocity, and temperature), and total fish biomass (Figure 2). Total phosphorus, a correlate of fish production (Johnston et al. 1990; Hoyer and Canfield 1991; Waite and Carpenter 2000), was also included. The vertical position of the variables in Figure 2 generally represents the spatial scale at which each is measured, with site-scale (proximal) variables at the top and catchment-scale (landscape driver) variables at the bottom. Direct and indirect effects of catchment- and reach-scale variables on stream habitat characteristics were hypothesized based on findings from previous studies. For example, substrate conditions were hypothesized to be influenced by both the availability of different-sized particles (Farrand and Bell 1982) and the stream's power (competency) to transport them (Leopold et al. 1964; Gordon et al. 1992). Stream power is a function of discharge and gradient, being calculated as per the stream power equation ($\text{power loss}_{\text{kw/m}} = 10 * \text{discharge}_{\text{cms}} * \text{gradient}$). Catchments with coarse-textured geology and high slopes provide increased groundwater contribution to streams, producing higher 90% exceedence flow (low-flow) yield values (Hendrickson and Doonan 1972; Wiley et al. 1997). July water temperatures of Michigan streams are influenced by groundwater inputs, channel width, travel time, and incision of the water table in high-gradient reaches (Hendrickson and Doonan 1972; Wehrly et al. 1997; Wiley et al. 1997; Zorn et al. 1998). Flow-related variables influence each other as per hy-

draulic geometry relations (Leopold et al. 1964). In addition, we included variables quantifying urban and agricultural land use in each catchment due to their demonstrated effects on physical, hydrologic, and chemical characteristics of streams (Osborne and Wiley 1988; Wiley et al. 1990; Allan 1995; Kleiman 1995; Richards et al. 1996; Baker et al. 2001). Error terms for response variables in the model were allowed to freely correlate with predictor variables, in part to account for noncausal correlations due to characteristics of the sample (e.g., a lack of data from large catchments dominated by urban land use). Finally, we rejected some hypothesized paths and eliminated them from the final model because they were not supported by our data. Examples of rejected paths included the direct effect of temperature on fish biomass, direct effects of urban land use on percent silt and sand, and direct effect of coarse geology on percent cobble.

The CSA model was analyzed using Amos 4.0 software (Arbuckle and Wothke 1999). We used asymptotic distribution-free (ADF) estimation procedures because significant departures from normality occurred for some variables, such as those characterizing substrate composition (Arbuckle and Wothke 1999). We also used maximum likelihood estimation because ADF estimation is most effective on sample sizes of at least 1,000 (Muthén 1993). Both methods produced similar results for all runs, suggesting that model results were robust. We used a Monte-Carlo parametric bootstrap procedure to estimate direct, indirect, and total effects (Grace and Pugesek 1997). Bootstrap-estimated, unstandardized regression coefficients, and implied and observed (sample) correlation matrices are shown in Appendices A and B.

We evaluated the CSA models in several regards. Squared multiple correlations indicated the amount of variance explained for each dependent variable. The theoretical soundness and statistical significance of total and direct effects were assessed using the 90% bias-corrected confidence interval and *t* distribution based on the degrees of freedom for each model (Arbuckle and Wothke

1999). We assessed fit of the overall model for each run with a variety of fit statistics that measure the discrepancy between the implied covariance structure (as constrained by the model) and the covariance structure of the sample data. Statistics included chi-square (χ^2), Goodness of Fit Index (GFI), Tucker-Lewis Index, and root mean square error of approximation (RMSEA).

RESULTS

Habitat Relations

Covariance structure analysis of habitat variables demonstrated the importance of landscape-scale (i.e., catchment- and reach-scale) variables to site-scale habitat characteristics of lower Michigan streams. Retaining only statistically significant pathways, catchment area, gradient, low-flow yield, and agricultural land use had the highest sums of direct effects (Table 2), implying strong causal controls on other habitat variables. Catchment area had the highest number of significant direct effects on habitat variables (seven), followed by gradient with six (Table 2). The sum of the total effects on habitat variables (Table 3) was highest for catchment area, followed by channel gradient, agricultural land use, and coarse-textured till, outwash geologic deposits, and low-flow yield implying that

these were the most pervasive landscape-scale organizers of fish habitat.

Landscape-scale variables had significant direct and indirect effects on all local habitat variables (Tables 2 and 4). Variables significant at a *P*-value less than 0.05 are discussed below, with standardized coefficients of their direct effects shown in parentheses. Strong effects have highly positive or negative values. Coarse-textured till and outwash geologic deposits (0.68) had the strongest direct effect on low-flow yield, followed by those of catchment area (0.21) and agricultural land use (−0.21). Depth was directly affected by catchment area (0.59), gradient (−0.23), and low-flow yield (0.22). Depth was also indirectly affected by coarse-textured till and outwash geologic deposits, agricultural land use, urban land use, gradient, and catchment area via their influence on low-flow yield (Tables 2 and 4; Figure 2). Velocity was directly affected by low-flow yield (0.83) and depth (0.17) and indirectly affected by coarse-textured till and outwash geologic deposits, catchment area, and agricultural land use (Tables 2 and 4). Some effect values on velocity should be interpreted with caution (e.g., positive direct effect of depth) because velocity was initially predicted from flow values and hydraulic geometry equations. Temperature was directly influenced by catchment area (0.58), low-flow

Table 2. Standardized direct effect estimates from the habitat model for lower Michigan streams (Figure 2). Bold and underlined values are significant at *P*-values of 0.05 and 0.10, respectively. Sums are for absolute values of all effects significant at *P* = 0.05. See Table 1 for variable descriptions.

Dependent variable	Urban	Agric	CA	Gradient	Coarse Geo	LFY	Total P	Depth	Cobble
LFY	<u>0.08</u>	−0.21	0.21	0.15	0.68				
Total P	0.29	0.72				−0.13			
Depth			0.59	−0.23		0.22			
Cobble			0.72	0.52					
FishBiom							0.37	0.25	0.14
Sand		<u>−0.33</u>	−0.36	−0.32					
Gravel			0.42	0.53	0.16				
Velocity				−0.14		0.83		0.17	
JulyTemp	0.10	0.14	0.58	−0.21		−0.23			
Silt		0.20	−0.54	−0.64					
Sum	0.00	1.27	3.42	2.45	0.84	1.40	0.37	0.42	0.14

Table 3. Standardized total effects estimates from the habitat model for lower Michigan streams (Figure 2). Bold and underlined values are significant at P -values of 0.05 and 0.10, respectively. Sums are for absolute values of all effects significant at $P = 0.05$. See Table 1 for variable descriptions.

Dependent variable	Urban	Agric	CA	Gradient	Coarse Geo	LFY	Total P	Depth	Cobble
LFY	<u>0.08</u>	-0.21	0.21	0.15	0.68				
Total P	0.28	0.74	-0.03	<u>-0.02</u>	-0.09	-0.13			
Depth	0.02	-0.05	0.63	-0.19	0.15	0.22			
Cobble			0.72	0.52					
FishBiom	0.11	0.26	0.24	0.02	0.01	0.01	0.37	0.25	0.14
Sand		<u>-0.33</u>	-0.36	-0.32					
Gravel			0.42	0.53	0.16				
Velocity	<u>0.07</u>	-0.18	0.28	-0.05	0.59	0.86		0.17	
JulyTemp	0.08	0.19	0.53	-0.25	-0.16	-0.23			
Silt	0.00	0.20	-0.54	-0.64					
Sum	0.13	1.84	3.97	2.45	1.83	1.44	0.37	0.42	0.14

yield (-0.23), gradient (-0.21), and agricultural land use (0.14) and indirectly affected by coarse-textured till and outwash geologic deposits, agricultural land use, and catchment area (Table 4). Catchment area and gradient, the two components of stream power, had significant direct effects on all four substrate variables. Significant direct effects also occurred for agricultural land use on percent silt (0.20) and coarse-textured till and outwash geologic deposits on percent gravel (0.16). Agricultural land use (0.72) and low flow yield (-0.13) had direct effects on total phosphorus (Table 2), while coarse-textured till and outwash geologic

deposits, agricultural land use, and catchment area had significant indirect effects (Table 4).

Landscape-scale variables explained a significant portion of variance in many variables measured at the site. In this analysis, the amount of variation explained in low-flow yield, depth, velocity, total phosphorus, and temperature variables ranged from 50% to 83% (Table 5). The percent coverage of each substrate type was more difficult to explain, with only 18–30% of the variation being explained for each substrate category (Table 5).

Landscape- and local-scale variables collectively explained 26% of spatial variation in total

Table 4. Standardized indirect effects estimates from the habitat model for lower Michigan streams (Figure 2). Bold and underlined values are significant at P -values of 0.05 and 0.10, respectively. Sums are for absolute values of all effects significant at $P = 0.05$. See Table 1 for variable descriptions.

Dependent variable	Urban	Agric	CA	Gradient	Coarse Geo	LFY	Total P	Depth	Cobble
LFY									
Total P	<u>-0.01</u>	0.03	-0.03	<u>-0.02</u>	-0.09				
Depth	0.02	-0.05	0.05	0.03	0.15				
Cobble									
FishBiom	0.11	0.26	0.24	0.02	0.01	0.01			
Sand									
Gravel									
Velocity	0.07	-0.18	0.28	0.09	0.59	0.04			
JulyTemp	-0.02	0.05	-0.05	<u>-0.04</u>	-0.16				
Silt									
Sum	0.13	0.57	0.65	0.03	0.99	0.04			

Table 5. Squared multiple correlations for response variables and fit statistics from the habitat model for lower Michigan streams (Figure 2).

Dependent variable	Squared multiple correlation	Model fit statistic	Value
LFY	0.64	χ^2	47.75
Total P	0.83	χ^2 Degrees of freedom	44
Depth	0.63	χ^2 p value	0.323
Cobble	0.27	GFI	0.987
FishBiom	0.26	Tucker-Lewis index	0.995
Sand	0.18	RMSEA	0.019
Gravel	0.19	P for test of close fit	0.964
Velocity	0.50	Multivariate kurtosis	52.624
JulyTemp	0.76		
Silt	0.30		

fish biomass at lower Michigan stream sites (Table 5). Of all the local-scale variables available in the model, only total phosphorus (0.37), depth (0.25), and percent cobble substrate (0.14) had significant direct effects on fish biomass (Table 2). However, catchment area, agricultural land use, and urban land use had significant indirect effects on fish biomass (Table 4).

Overall fit measures for the model indicated good correspondence between the predicted and observed covariance structure (Table 5). The χ^2 value of 47.8 ($df = 44$, $p = 0.323$) suggested no significant difference between the covariance matrix of the sample data and the covariance matrix implied by the model. The RMSEA, a measure of the average of the fitted residuals interpreted in relation to observed variances and covariances (Joreskog and Sorbom 1984), was 0.019. The chi-square and RMSEA statistics suggest a close fit of the model to the observed data as do Tucker-Lewis Index and GFI values of 0.995 and 0.987. The multivariate kurtosis value (52.6) indicated the occurrence of nonnormality (mostly due to natural distribution of stream types and conditions in Michigan) that could not be resolved without modifying hypotheses. However, other discrepancy estimation methods (i.e., maximum-likelihood) and bootstrapping efforts produced similar results, suggesting that the model was generally robust.

DISCUSSION

The importance of landscape-scale features as hierarchical constraints on local habitat and the influence of landscape- and local-scale habitat to total fish biomass were both demonstrated using CSA. While other studies have identified landscape-scale variables (e.g., stream size and gradient) as important correlates with fish assemblage structure (Zalewski and Naiman 1985; Degerman and Sers 1993; Lyons 1996), this study quantified the extent to which these variables affect key aspects of local habitat. Of the independent variables in this study, catchment area had the strongest total effect on depth, temperature, sand, and cobble (Table 3). Catchment area is undoubtedly a key force shaping these local habitat conditions (Zorn et al. 1998) because it indexes stream discharge volume, which is the primary determinant of both habitat volume and stream power (Leopold et al. 1964). Gradient, the other key variable in the stream power equation, had the strongest total effect on silt and gravel. As an index of permeability of glacial deposits in the basin, coarse-textured till and outwash geologic deposits had the strongest direct effect on low-flow yield. Low-flow yield, in turn, had the strongest effect on velocity and significant direct effects on temperature, depth, and total phosphorus (Table 2). Temperature, depth, velocity, substrate, and total phosphorus have been identified as key correlates with biomass of stream fishes in Michigan (Zorn 2003) and other regions (e.g., Fausch et al. 1988; Lyons 1996; Maret et al. 1997; Angermeier and Winston 1999; Waite and Carpenter 2000). In lower Michigan, stream size, catchment geology, and gradient are clearly the major driving variables influencing site-level aspects of habitat important to stream fishes.

The habitat model also provided a first-cut look at the complex web of relations among the spatial scales used to characterize stream habitat (Figure 2). Though data from several spatial scales could be added to provide more realistic predictive models for each habitat variable, this analysis plainly showed that features of the site's

catchment shape and constrain local habitat conditions. For example, geology and land-use variables acting together influenced many site-scale aspects of stream habitat (Tables 2 and 3). Coarse-textured till and outwash geologic deposits are highly permeable, and in combination with sloping landscapes, produce groundwater-dominated streams with relatively high low-flow yields (Hendrickson and Doonan 1972; Wiley et al. 1997). Direct effect coefficients of low-flow yield support observations of these streams generally being colder, more gravelly, and having higher mean depths and velocities in summer (Table 2). In addition, landscapes dominated by coarse-textured till and outwash geologic deposits are often ill-suited to agriculture, so streams draining these sandy landscapes also tend to be relatively poor in phosphorus and less silty than streams in agricultural areas (Table 2). This model provides an overview of some key linkages between the landscape and microhabitat conditions and demonstrates the utility of CSA in quantifying them. Future research could focus on more detailed exploration of mechanisms for these and other paths between the landscape and local stream habitat.

The ability to distinguish the relative strength of different paths by which one aspect of stream habitat can influence others is a highly attractive feature of CSA. For example, agricultural land use had significant direct and indirect effects on total phosphorus (Tables 2 and 4; Figure 2). Its direct effect is by far stronger, most likely relating to fertilizer application and enriched runoff associated with farming activity. The more subtle indirect effect however, may be due to agriculture-related drainage activities that reduce streamflows during periods of low flow, further concentrating phosphorus in streams. In this case, the two pathways each contribute to higher phosphorus levels (Table 3), but this is not always the case. For instance, the positive total effect of catchment area on temperature consists of a strong positive direct effect and a weak, but significant, negative indirect effect via its influence on low flow yield (Tables 2, 3, and 4; Figure

2). Here, the hydrologically buffering influence of additional tributaries that feed streams as they increase in size has little influence in comparison to warming that naturally occurs as streams flow across the landscape and widen (Wehrly et al. 1997). The ability to quantify the magnitude and direction of multiple, often competing causal paths (i.e., to incorporate realism) is clearly a major strength of CSA approaches to stream habitat studies.

Variation in some habitat variables was difficult to explain from stream size, catchment geology, and gradient variables alone. For example, little variation in total phosphorus could be explained without the catchment-scale variable, percent agricultural land use, in the model. This was expected because human activities are major contributors of nutrients to stream systems (Osborne and Wiley 1988; Wiley et al. 1990; Allan 1995; Baker et al. 2001). The positive direct effect of agricultural land use on silty substrates is a source of stream degradation documented in other studies (Waters 1995).

As hypothesized, higher stream power (associated with higher gradient or larger catchments) favored coarser substrates. Catchment area and gradient, the two components of stream power (Leopold et al. 1964), had significant direct effects on each substrate category (Table 2). Surprisingly, these variables, along with geology and land-use variables, explained no more than 30% of variation in the spatial distribution of any substrate type (Figure 2). Instream sediment transport processes and local geologic features (e.g., where the stream cuts through a moraine) may add variation in substrate characteristics that is difficult to predict from catchment- and reach-scale variables alone. However, preliminary analyses suggest that use of local-scale geology variables may add little predictive power, since in lower Michigan, these variables are often correlated with reach gradient (T. G. Zorn, unpublished data). Up to 40% of spatial variation in composite substrate percentages (e.g., percent gravel and coarser substrates) could be explained for the sites in this study (Zorn, unpublished

data), but we used individual categories of substrate because fishes often show preferences for distinct substrate types.

Limitations

Covariance structure analysis provided a powerful tool for evaluating hypotheses about complex interactions in multivariate systems where covariance was common and collinearity high (Wootton 1994b). Despite its usefulness, there are limitations that affect both the use and interpretation of CSA results. Covariance structure analysis can only evaluate whether or not the theory and constraints of the specified model correspond to the structure of the sample data. Covariance structure analysis requires the user to supply a theoretically sound causal model (Wootton 1994b). Where theory on system function is sufficient, application of CSA to observed data may provide new insights into system processes by elucidating direct and indirect effects or by falsifying theoretical assumptions. When theory is inadequate, as often occurs in ecological studies, CSA can contribute to evaluation of competing models. Since it is only a confirmatory statistical technique, CSA should not be used to propose direct causal linkages without clear mechanistic justification. Despite the causal implications of structured models, CSA only provides a measurement of the fit of a causal theory to the data and does not prove causality.

Conclusions from CSA (and other analyses) regarding mechanism are limited by the variables included in the analysis. Inadequate theory, or omission of key variables, may lead to misguided conclusions regarding mechanisms. Some variables included in this study, though informative, do not necessarily point to a particular mechanism. For example, this study suggested the importance of cobble substrate to fish biomass (Table 2). Cobble may influence fish populations by providing spawning habitat for certain species, stable substrate for instream forage production, interstitial spaces for fish cover, or through other means. Numerous abiotic or biotic vari-

ables could potentially be added to models to explore mechanisms and account for additional unexplained variance.

Characteristics of the data used in this analysis (Table 1) suggest the need for some caution when interpreting results. It was not possible to obtain all the data needed for these comprehensive analyses of stream systems due to the number of sites studied and types of data needed; for example, 90% exceedence flow yield measurements would require continuous data from streamflow gauges at each site. As a result, several of the variables used in this study (Table 1) represented a combination of values that were measured or predicted from statistical models developed in other studies (e.g., Kleiman 1995; Seelbach and Wiley 1997; Wehrly et al. 1997). Models predicting these variables used some of the parameters in this study as inputs (e.g., catchment area and agricultural land use), along with numerous additional variables. Consequently, multiple correlation coefficient and path coefficient values for these variables may differ from what might be obtained from an analysis based strictly on measured values.

Assumptions of normality could not be met for some variables in this analysis. Some variables important to fishes, such as percent cobble substrate or percent urban land use, have a patchy distribution throughout Michigan and tend to occur with moderate to high levels or not at all. Thus, data transformations were unable to produce an entirely normal distribution for those variables. We used computational procedures (e.g., bootstrapping, ADF estimation, and bias-corrected confidence intervals) to help prevent nonnormally distributed variables from erroneously influencing study results (Arbuckle and Wothke 1999). This may explain why some direct effects with modest-sized coefficients (e.g., urban land use on total phosphorus) were not statistically significant (Table 2). Maximum likelihood estimation was also used because ADF estimation is most effective on large sample sizes (Muthén 1993). Both methods produced similar results in all cases, suggesting that the models

were robust. In addition, comparable analyses using larger (Zorn 2003) and smaller (Zorn, unpublished data) samples of data from Michigan streams showed similar results. Further statistical exploration and modified sampling designs may help alleviate normality issues in future studies.

Research and Management Implications

Several authors have discussed conceptual frameworks whereby aquatic assemblages are seen as products of a series of filters, operating at different temporal and spatial scales, through which each species in the assemblage must pass (Tonn 1990; Poff 1997). The need to explicitly incorporate hierarchical relations among spatial scale and habitat conditions into such a model has been stressed by many (e.g., Imhof et al. 1996; Rabeni and Sowa 1996; Poff 1997). Path diagrams (e.g., Figure 2) provide an analytic framework for studying influences of hierarchically nested habitat variables on aquatic assemblages in streams. Variables can be portrayed at the appropriate spatial scale, and hypothesized relations among them explicitly represented via causal paths. Direct and indirect relations among variables can be evaluated in terms of significance and magnitude of effect. Allowing multiple paths to and from individual variables alleviates statistical issues of collinearity and the conceptual problem of assigning a filter (e.g., temperature) to a single spatial scale (Poff 1997).

Our analyses demonstrated the ecological complexity and multiscale nature of fish habitat in stream ecosystems (Figure 2). One could easily envision other habitat attributes (and associated paths) that could be included to add realism. Path diagrams and associated outputs plainly showed, and quantitatively demonstrated, the importance of large-scale variables in terms of their direct and indirect effects on more proximal habitat attributes. For example, catchment area and 90% exceedence flow yield had significant total effects on depth, temperature, total phosphorus, and velocity (Table 3). These vari-

ables, in turn, are important predictors of biomass for many common stream fishes in lower Michigan (Zorn 2003). These findings also support the use of catchment area and 90% exceedence flow yield as primary habitat axes for Michigan streams (Zorn et al. 2002). By quantifying linkages among habitat elements, managers can more readily show how changes to the landscape would likely influence particular local habitats and fishes. For example, based on total effects observed in this study (Table 3), increasing agricultural land use in Michigan watersheds could be expected to result in decreased 90% exceedence flow yields, reduced depth, slower current velocity, increased total phosphorus concentration, higher summer temperatures, and increased silt substrate. Such effects could be quantitatively described using the equations developed in this study (Table 5; Appendices A and B). The quantitative effects described here, however, reflect patterns of variation observed in the collection of streams included in this study and may not apply to other streams or regions.

The CSA approach to modeling stream systems may provide a general habitat framework that is useful for a variety of purposes. For example, the habitat CSA model developed in this study served as the basis for subsequent models developed for individual fishes (Zorn 2003). These species models consisted of statistically significant paths from the base habitat model plus additional variables that were significant just for the species of interest. Another interesting application would be to use a common path model to compare regional differences in the relative influence of different factors on habitat parameters. For example, a hypothetical model for stream temperature in North American streams may likely include many measures (e.g., groundwater input, latitude, altitude, shading, stream size, etc.), but the relative importance of each path would likely vary from region to region.

By allowing intercorrelations to be accounted for, CSA provided a more appropriate forum for exploring mechanistic relations than linear regression. Still, a single CSA should not be considered

the definitive test of how a system works, nor a substitute for development of a sound understanding of a particular study system. Characteristics of the study system and sample sites must be considered. For example, covariance structure analyses with brook trout *Salvelinus fontinalis*, brown trout *Salmo trutta*, and smallmouth bass *Micropterus dolomieu* demonstrated that the sample of streams (or sites) has an overriding effect on the detection and relative influence of abiotic and biotic factors on fish biomass (Zorn 2003). Thus, issues of sampling scale should always provide the context for interpreting CSA results, or those from any data analysis (Levin 1992).

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Appendix A. Observed (sample) and implied correlation matrices coefficients for the habitat model for lower Michigan streams.

	Urban	Agric	CA	Gradient	CoarseGeo	LFY	Total P	Depth	Cobble	FishBiom	Sand	Gravel	Velocity	JulyTemp	Silt
Sample															
Urban	1	0.277	0.275	-0.227	0.074	0.125	0.529	0.292	0.07	0.268	-0.249	0.238	0.116	0.326	0.043
Agric	0.277	1	0.31	-0.418	-0.225	-0.312	0.83	0.149	0.1	0.316	-0.39	-0.02	-0.334	0.518	0.262
CA	0.275	0.31	1	-0.695	0.038	0.086	0.24	0.739	0.369	0.308	-0.243	0.082	0.313	0.768	-0.047
Gradient	-0.227	-0.418	-0.695	1	0.08	0.125	-0.381	-0.583	-0.005	-0.288	0.127	0.201	-0.116	-0.729	-0.313
CoarseGeo	0.074	-0.225	0.038	0.08	1	0.754	-0.26	0.15	0.034	-0.229	0.084	0.184	0.646	-0.218	-0.034
LFY	0.125	-0.312	0.086	0.125	0.754	1	-0.301	0.227	0.112	-0.141	0.066	0.232	0.678	-0.207	-0.119
Total P	0.529	0.83	0.24	-0.381	-0.26	-0.301	1	0.103	0.057	0.385	-0.352	0.04	-0.353	0.521	0.233
Depth	0.292	0.149	0.739	-0.583	0.15	0.227	0.103	1	0.141	0.236	-0.164	0.003	0.404	0.508	0.093
Cobble	0.07	0.1	0.369	-0.005	0.034	0.112	0.057	0.141	1	0.179	-0.453	0.237	0.103	0.238	-0.347
FishBiom	0.268	0.316	0.308	-0.288	-0.229	-0.141	0.385	0.236	0.179	1	-0.178	-0.013	-0.088	0.349	0.095
Sand	-0.249	-0.39	-0.243	0.127	0.084	0.066	-0.352	-0.164	-0.453	-0.178	1	-0.399	0.11	-0.292	-0.184
Gravel	0.238	-0.02	0.082	0.201	0.184	0.232	0.04	0.003	0.237	-0.013	-0.399	1	0.094	-0.024	-0.409
Velocity	0.116	-0.334	0.313	-0.116	0.646	0.678	-0.353	0.404	0.103	-0.088	0.11	0.094	1	0.01	-0.099
JulyTemp	0.326	0.518	0.768	-0.729	-0.218	-0.207	0.521	0.508	0.238	0.349	-0.292	-0.024	0.01	1	0.112
Silt	0.043	0.262	-0.047	-0.313	-0.034	-0.119	0.233	0.093	-0.347	0.095	-0.184	-0.409	-0.099	0.112	1
Implied															
Urban	1	0.358	0.354	-0.252	0	0.039	0.545	0.361	0.121	0.307	-0.282	0.18	0.128	0.398	0.041
Agric	0.358	1	0.308	-0.395	-0.303	-0.386	0.869	0.184	0.096	0.379	-0.316	-0.129	-0.353	0.53	0.288
CA	0.354	0.308	1	-0.689	0	0.071	0.284	0.757	0.356	0.34	-0.244	0.054	0.281	0.786	-0.042
Gradient	-0.252	-0.395	-0.689	1	0.095	0.134	-0.373	-0.599	0.03	-0.282	0.059	0.258	-0.129	-0.721	-0.343
CoarseGeo	0	-0.303	0	0.095	1	0.762	-0.312	0.148	0.049	-0.284	0.07	0.209	0.641	-0.239	-0.122
LFY	0.039	-0.386	0.071	0.134	0.762	1	-0.396	0.241	0.103	-0.218	0.05	0.234	0.68	-0.224	-0.202
Total P	0.545	0.869	0.284	-0.373	-0.312	-0.396	1	0.151	0.069	0.434	-0.304	-0.082	-0.348	0.552	0.26
Depth	0.361	0.184	0.757	-0.599	0.148	0.241	0.151	1	0.13	0.288	-0.146	0.026	0.413	0.552	0.091
Cobble	0.121	0.096	0.356	0.03	0.049	0.103	0.069	0.13	1	0.194	-0.474	0.174	0.103	0.201	-0.367
FishBiom	0.307	0.379	0.34	-0.282	-0.284	-0.218	0.434	0.288	0.194	1	-0.213	-0.034	-0.137	0.401	0.069
Sand	-0.282	-0.316	-0.244	0.059	0.07	0.05	-0.304	-0.146	-0.474	-0.213	1	-0.412	0.048	-0.238	-0.129
Gravel	0.18	-0.129	0.054	0.258	0.209	0.234	-0.082	0.026	0.174	-0.034	-0.412	1	0.162	-0.078	-0.428
Velocity	0.128	-0.353	0.281	-0.129	0.641	0.68	-0.348	0.413	0.103	-0.137	0.048	0.162	1	0.029	-0.129
JulyTemp	0.398	0.53	0.786	-0.721	-0.239	-0.224	0.552	0.552	0.201	0.401	-0.238	-0.078	0.029	1	0.14
Silt	0.041	0.288	-0.042	-0.343	-0.122	-0.202	0.26	0.091	-0.367	0.069	-0.129	-0.428	-0.129	0.14	1

Appendix B. Bootstrap-estimated, nonstandardized regression coefficients (significance based on bias-corrected 90% confidence intervals) from the habitat model for lower Michigan streams. All predictor variable coefficients were significant at $P = 0.05$ prior to bias correction.

Response	Predictor	Coefficient	BC P -value
LFY	CoarseGeo	1.098	0.059
LFY	Gradient	0.169	0.154
LFY	CA	0.151	0.064
LFY	Agric	-0.264	0.001
LFY	Urban	0.132	0.084
Cobble	Gradient	14.506	0.002
Cobble	CA	12.638	0.021
Depth	CA	0.205	0.004
Depth	LFY	0.110	0.000
Depth	Gradient	-0.124	0.002
Total P	Urban	0.265	0.532
Total P	Agric	0.475	0.000
Total P	LFY	-0.067	0.004
JulyTemp	LFY	-1.246	0.001
Silt	CA	-12.250	0.010
Velocity	LFY	0.738	0.001
Velocity	Gradient	-0.138	0.106
JulyTemp	Gradient	-1.275	0.015
Velocity	Depth	0.306	0.007
JulyTemp	CA	2.218	0.000
Gravel	CoarseGeo	8.798	0.009
Gravel	Gradient	20.511	0.000
Gravel	CA	10.322	0.003
Silt	Gradient	-22.543	0.004
Sand	Gradient	-15.667	0.000
Sand	CA	-11.278	0.000
JulyTemp	Urban	0.898	0.036
JulyTemp	Agric	0.974	0.003
Silt	Agric	8.053	0.053
Sand	Agric	-18.013	0.064
FishBiom	Total P	0.459	0.000
FishBiom	Depth	0.332	0.000
FishBiom	Cobble	0.004	0.023
LFY	CoarseGeo	1.171	0.098
LFY	Gradient	0.194	0.119
LFY	CA	0.173	0.191
LFY	Agric	-0.248	0.000
LFY	Urban	0.049	0.309
Depth	CA	0.212	0.002
Depth	LFY	0.086	0.000
Depth	Gradient	-0.096	0.020
Cobble	Gradient	11.963	0.003
JulyTemp	LFY	-1.268	0.000
Silt	CA	-11.380	0.003
Cobble	CA	11.389	0.017
Velocity	LFY	0.667	0.003
Velocity	Gradient	-0.129	0.002
JulyTemp	Gradient	-1.616	0.025
Velocity	Depth	0.211	0.017
JulyTemp	CA	1.996	0.000
Gravel	CoarseGeo	11.397	0.002
Gravel	Gradient	17.512	0.000
Gravel	CA	10.101	0.000

Appendix B (continued)

Response	Predictor	Coefficient	BC P-value
Silt	Gradient	-21.441	0.003
Sand	Gradient	-11.372	0.000
Sand	CA	-10.071	0.000
JulyTemp	Urban	0.893	0.010
JulyTemp	Agric	0.873	0.009
Total P	Urban	0.339	...
Total P	Agric	0.448	0.000
Silt	Agric	7.417	0.008
Sand	Agric	-17.224	0.071
Total P	LFY	-0.102	0.002

Land-Use Effects on Catchment- and Patch-Scale Habitat and Macroinvertebrate Responses in the Adirondack Uplands

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Abstract.—Catchment characteristics and land-use practices can affect stream habitats at a variety of spatial scales. A suite of variables describing catchment geomorphology (area, circularity, slope, elevation, soil depth, surficial geology), surface water hydrology (drainage density, water velocity, Froude number), and patch (channel) habitat (slope, bank-full width, water depth, substrate particle size, stored and transported organic matter, transported inorganic sediment) were determined using a geographic information systems and field surveys in 19 upland Adirondack catchments (New York, USA) with differing land uses (New York Forest Preserve [Preserve] versus logging). Surber samples of macroinvertebrate assemblages and stored organic matter were collected in July 2003. Catchment geomorphology was similar between land-use types. However, Preserve streams tended to have deeper and wider channels, despite steeper channel slopes, while logged streams had more stored organic matter and finer substrate particles. We collected 177 macroinvertebrate taxa from the streams, and taxa richness was significantly reduced in logged catchments ($p = 0.006$). Twenty-seven taxa occurred more frequently in Preserve sites, while nine taxa occurred more commonly in logged streams (chi-square, $p < 0.10$). Distributions of these taxa were related to water quantity, channel geomorphology, and particle size at the patch scale and circularity, drainage patterns, and sediment load at the reach scale. The presence and absence of invertebrate taxa across the Adirondack landscape was controlled mainly by a combination of catchment-scale geomorphic and anthropogenic (forest management) factors. Patch-scale factors, although influenced by their catchments, had less effect on distributions.

INTRODUCTION

There is a close relationship between headwater mountain streams and their catchments (Hynes 1975; Vannote et al. 1980; Isaak and Hubert 2001). Catchment land use, together with such factors as geology, geomorphology, and vegeta-

tion affect channel hydrology, morphology, temperature, light, and sedimentation (Beschta and Platts 1986; Allan et al. 1997; Poff and Huryin 1998; Church 2002). This, in turn, may have ecological consequences for populations of organisms using the stream and adjacent riparian habitats (Carlson et al. 1990; Benfield et al. 1991, 2001; Davies and Nelson 1994; Stone and Wallace 1998; Kedzierski and Smock 2001; Dieterich et al., in press). Historically, the integrity of small (ephemeral to third-order) streams has been overlooked when developing land management plans (Beschta and Platts 1986). Small streams

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are numerous (Naiman and Decamps 1997) and would greatly reduce the land area available for harvest if riparian buffer strips were enforced for all channels in logged areas. Nevertheless, these small streams and their riparian areas are important habitats for flora and fauna and important in maintaining function in upland forested ecosystems in general (Beschta and Platts 1986; Naiman and Decamps 1997).

The relative importance of habitat factors affecting ecological phenomena, such as the distribution and abundance of organisms, varies with spatial and temporal scale (Wiens 1989; Menge and Olson 1990; Cullinan and Thomas 1992; Hildrew 1996; Poff 1997; Vinson and Hawkins 1998; Poiani et al. 2000; Lamouroux et al. 2004; Wang et al. 2006, this volume). Small-scale factors, including hydraulic habitat, substrate characteristics, and storage of organic food resources, are important in determining the distribution of benthic invertebrates within a stream (Ulfstrand 1967; Reice 1980; Vannote et al. 1980; Huryn and Wallace 1987; Vinson and Hawkins 1998; Lamouroux et al. 2004). However, the composition of stream assemblages is also a response to broader-scale characteristics, determined both by the pool of potential assemblage members and by regional- or catchment-scale characteristics (filters) that directly or indirectly affect the habitat scale at which individual organisms respond (Frissell et al. 1986; Tonn 1990; Poff 1997; Vinson and Hawkins 1998; Lamouroux et al. 2004). Thus, populations can respond to factors at a scale that is several orders of magnitude greater, such as the reach or catchment, than those experienced by individuals at the patch scale (Hildrew 1996; Poff 1997). For example, investigations of leaf litter decomposition across multiple catchments have demonstrated that reach- or catchment-scale factors affect ecosystem functions mediated by organisms at small scales (Sponseller and Benfield 2001; Sponseller et al. 2001; Huryn et al. 2002).

There are several commonly used scales of investigation in stream ecology, including catchment/basin, valley/reach, patch, and microhabitat

(Allan et al. 1997; Poff 1997). However, the manner in which organisms are distributed among and within semi-isolated landscape units such as upland catchments and how various scales of investigation relate to one another are still poorly known. In this paper, we focus on the catchment- and patch-scale differences that may affect distributions of macroinvertebrates in the Adirondack uplands. First, we identify physical and hydrological differences related to catchment land use at these two scales and quantify how the characteristics of the patch-scale habitat may be predicted by catchment-scale variables. Second, we identify macroinvertebrate taxa that show distributional differences related to land use. Finally, we identify and compare the relative importance of catchment- and patch-scale variables that affect the distributions of those macroinvertebrates under the two land-use regimes.

METHODS

Study Sites

The Adirondack Park in upstate New York (USA) was established in 1894 by the "Forever Wild" provision of the New York State Constitution (Article XIV, Section 1) and is a unique mosaic of public and private lands. Today, state-owned lands in the New York Forest Preserve (Preserve) comprise approximately 42% of the 2.4 million hectare park. The remainder of the land supports various private uses, the largest of which is timber production. In recent decades, there have been widespread acute and chronic disturbances in the region, including acid deposition, pest and disease outbreaks, forest-damaging blow downs, and ice storms. In addition, many areas of the Preserve are managed for outdoor activities, including hiking and vehicle trails, sportfishing, and black fly control. We selected 19 second- and third-order catchments (10 Preserve and 9 logged, Figure 1) that were entirely forested with the exception of some small wetlands (NYS-APA 2001). Preserve catchments had not been logged in at least 85 years prior to this study, and forests in some are old-growth with stand ages approaching 400 years

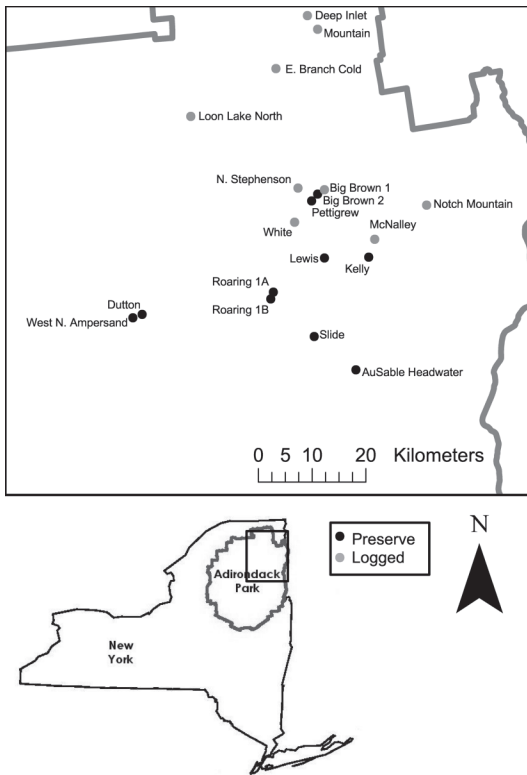


Figure 1. Locations of study catchments within the Adirondack Park, New York.

(Ziegler 2000). Logged catchments were defined as currently used for timber production and/or having had ~30% or greater forest removal within the previous 25 years. A concurrent survey of forest vegetation in the study catchments indicates decreased mean tree size and increased sapling densities in logged catchments (Table 1), indicating that logging has significantly altered some forest cover characteristics when compared to Preserve catchments (T. Woodcock, J. Allen, C. Evans, R. Tucker, T. Mihuc, C. Laxson, J. Mihuc, and E. Allen, Lake Champlain Research Institute, Plattsburgh State University, unpublished data).

Catchment Geomorphology and Hydrology

The study catchments were delineated by hand on 1:24000 U.S. Geological Survey topographic quadrangles and then digitized into a geographi-

cal information systems (GIS) coverage using ArcInfo. Area, aspect, and perimeter were determined for each catchment, and circularity was calculated as the ratio of the catchment area to the area of a circle with the same perimeter. Mean values of slope and elevation were calculated for each catchment using the “Zonal Statistics” function in Spatial Analyst, ArcGIS 8.3. Proportional coverages of soil depth classes (bedrock outcrop, shallow <20 cm, medium 20–60 cm, and deep >60 cm) and surficial geologic features were calculated for each catchment, using public domain GIS data supplied by the Adirondack Park Agency (NYS-APA 2001) and the “Tabulate Areas” function in ArcView 3.3.

Drainage density was estimated for each catchment from digital elevation data (NYS-APA 2001) using the ArcHydro extension for ArcGIS 8.3 (Maidment 2002). The drainage threshold was set at 75, meaning that each pixel flows into only one other pixel along the steepest descent path, and a minimum of 75 pixels must accumulate into an area to indicate a channel. This drainage threshold value was chosen to approximate observed densities of snowmelt channels, ephemeral channels, and first- to third-order permanent streams in the catchments (Figure 2). Some ground-truthing was performed on channels by marking several points of different channel types on a GPS unit in the field and checking that those points were reasonably consistent with the GIS estimates.

Water level and temperature were recorded hourly during the entire year at each catchment pour point (outlet) using capacitance rods (TruTrack WT-HR, www.trutrack.com/WT-HR.html) in streamside stilling wells. Four-liter grab samples of water were collected six times over 2 years, approximating three important points in the hydrologic year (spring snowmelt, summer base flow, autumn following leaf fall). Samples were filtered in the laboratory through preashed and preweighed 0.7- μm glass fiber filters. Filters were dried, weighed, ashed for 1 h at 550°C, moistened with de-ionized water, dried, and reweighed, and quantities of suspended organic and inorganic matter were calculated

Table 1. Summary of sampling locations, forest characteristics, and water temperature at the time of sampling. Forest data summarized from T. Woodcock, J. Allen, C. Evans, R. Tucker, T. Mihuc, C. Laxson, J. Mihuc, and E. Allen (unpublished data). *T*-tests compare characteristics of logged versus Preserve catchments.

	NAD 1983 sampling coordinates		Aspect	Sampling elevation (m)	Total overstory basal area (m ² /ha)	Mean overstory tree size (DBH in cm)	Sapling density (stems/ha)	Mean herb/shrub Cover (%)	Mean July water temp. (°C)
	18T	UTM							
<i>Preserve</i>									
Lewis	596092	4909090	NE	280	—	—	—	—	16.0
Roaring Brook #1A	585066	4902367	W	551	35.5	15.7	3218	13.7	13.6
Roaring Brook #1B	585062	4902356	W	551	28.9	13.4	3015	18.0	13.5
West N. Ampersand	559651	4899403	N	511	26.8	15.2	2604	3.4	14.5
Big Brown Brook 2	595600	4920791	E	401	30.0	15.2	3877	5.0	14.0
Pettigrew	595317	4920587	E	396	34.2	14.0	5026	21.3	14.4
Dutton	560841	4899801	N	500	27.3	17.0	1988	14.0	14.6
Slide	594577	4893747	E	563	32.4	14.3	2482	34.1	14.7
AuSable Headwater	600657	4887807	SW	609	22.6	14.4	2384	35.7	13.4
Kelly Basin	604644	4910421	N	431	21.6	12.9	6468	13.7	14.4
Mean	—	—	—	—	28.8	14.7	3451	17.7	14.31
SE	—	—	—	—	0.9	0.2	280	3.8	1.0
<i>Logged</i>									
Deep Inlet	592152	4954717	NE	493	30.6	13.8	5893	19.1	13.4
McNalley	604860	4911613	SW	414	20.8	15.3	5707	1.1	14.7
Mountain	593863	4951060	W	487	28.7	14.3	6280	14.6	13.6
North Stephenson	590020	4921945	NW	495	27.4	13.2	4414	23.8	13.4
White	590911	4916008	NE	544	29.8	11.8	3547	12.2	13.1
Big Brown Brook 1	595463	4921070	E	406	23.9	13.8	5695	12.7	14.0
Notch Mountain	614024	4917921	W	266	18.3	13.7	8759	8.5	16.0
East Branch Cold	586312	4943523	S	488	21.9	12.4	6683	12.4	16.3
Loon Lake North	571298	4935640	NE	539	27.3	12.1	7615	6.1	14.1
Mean	—	—	—	—	25.4	13.4	6066	12.3	14.29
SE	—	—	—	—	0.8	0.2	300	2.2	1.0
<i>T</i> -test <i>p</i> -value	—	—	—	—	0.14	0.03	0.002	0.24	0.96

(Wallace and Grubaugh 1996). To account for temporal variation in suspended organic and inorganic material, minima, mean, and maxima of these variables were used as predictor variables in the multiple linear regressions (MLRs) of reach-scale invertebrate densities.

Patch Habitat and Aquatic Biota

Ten separate Surber samples (0.09 m², 250 mm mesh size) were taken near the pour point in each of the 19 study sites in July 2003. Samples were taken in the thalweg, beginning at the pour point and moving upstream at randomly determined 5–25-m intervals (Figure 2). At each sampling

point, bank-full width, water depth, and water velocity were measured, and channel slope was measured between the sampling point and the next sampling point upstream using a clinometer. Froude number (*F*) was calculated as

$$F = V/(Dg)^{1/2},$$

where *V* is water velocity, *D* is water depth, and *g* is acceleration due to gravity. Proportional coverages of each particle size (boulder, cobble, pebble, gravel, sand) within each Surber frame were estimated visually, using the modified Wentworth scale (Cummins 1962). Benthic samples were preserved in 10% formalin in the

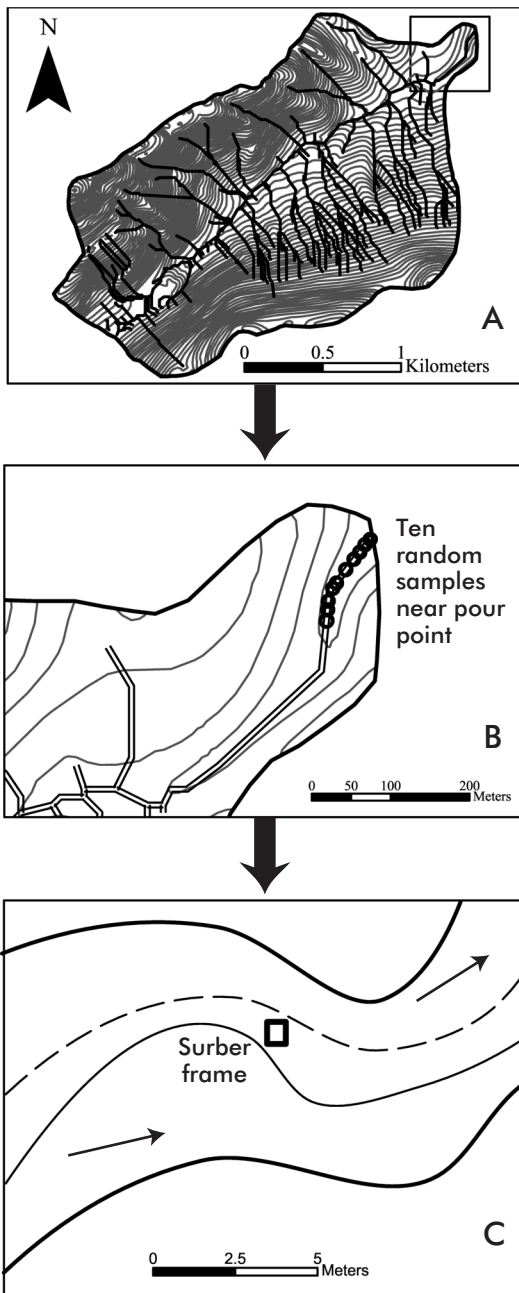


Figure 2. A sample catchment (Loon Lake North), illustrating the decreasing scales of sampling. Variables calculated at the catchment scale (A) are related to habitat variables and invertebrate community characteristics calculated at the reach scale (B). Reach scale variables are the mean values from individual samples taken at the patch scale (C), with the Surber frame placed in the thalweg. In panels A and B, the contour interval is 6.7 m, and the stream network illustrates calculated drainage densities (threshold = 75).

field. All invertebrates retained on a 250-mm sieve were enumerated in the laboratory and identified to the lowest practical taxonomic level (typically genus) using appropriate taxonomic references (Thorp and Covich 1991; Merritt and Cummins 1996). Chironomids were morphotyped, and specimens from each morphotype (at least five individuals or 10% of the morphotype, whichever was greater) were slide-mounted to allow generic identification (Wiederholm 1983). Organic material in the sample was separated into categories (leaves, moss, wood, particulate matter), dried, and weighed. Ash-free dry mass was determined for fine particulate organic matter (FPOM), following ashing in a muffle furnace for 24 h at 550°C, moistening with de-ionized water, redrying, and reweighing (Wallace and Grubaugh 1996).

Statistical Analyses

In addition to catchment-scale variables (Figure 2A), we report mean values of habitat variables or invertebrate densities from the 10 patch-scale samples in a reach (hereafter referred to as reach-scale variables) (Figure 2B), and habitat variables or invertebrate densities from individual Surber samples (hereafter referred to as patch-scale variables) (Figure 2C). Catchment- and patch-scale habitat variables were compared between land uses with a simple *t*-test. Several variables were $\ln(x + 1)$ -transformed to satisfy normality assumptions (Neter et al. 1996). It was not expected that logging would affect catchment-scale geomorphology, but rather that logging may have preferentially occurred on certain topography that would be reflected in catchment-scale differences. Each macroinvertebrate taxon was tested for a skewed distribution (logged versus Preserve) based on a chi-square test of independence between land use and each taxon's occurrence (Neter et al. 1996), with a null hypothesis of a random distribution with respect to land use. Taxa were considered skewed toward a particular land use if they occurred in a minimum of 5% of the 190 Surber samples *and* the chi-square

significance level was $p < 0.10$. Differences in total abundance and richness were compared between land uses with a simple t -test ($\alpha = 0.05$, Neter et al. 1996).

Total abundance, richness, and abundance of taxa showing skewed distributions were related separately to catchment- and patch-scale variables using forward stepwise MLR. Abundance was used for the regression models rather than occurrence because it accounts for the success of a taxon related to smaller-scale habitat conditions (Poff 1997). Three separate series of forward stepwise MLR models (Neter et al. 1996) were used to elucidate relationships between habitat characteristics and macroinvertebrate distributions,

1. The reach-scale habitat variables from each catchment were regressed on catchment-scale predictors ($n = 19$).
2. The reach-scale invertebrate densities from each catchment were regressed on catchment-scale predictors ($n = 19$). Richness was the total number of different taxa collected in the reach.
3. Patch-scale invertebrate densities from each Surber sample were regressed on patch-scale predictors ($n = 190$). Patch-scale richness was the total number of taxa collected in each Surber sample.

Prior to each catchment-scale MLR (analyses 1 and 2, above), correlations between all predictor variables and each response variable were calculated, and poorly correlated predictors (Pearson's $r < 0.25$) were excluded from the MLR, in an effort to prevent overfitting due to small sample size ($n = 19$, Kaufmann and Hughes 2006, this volume). Catchment-scale predictor variables are summarized in Table 2; patch-scale predictor variables are summarized in Table 3.

RESULTS

Habitat Relationships

Only tree size and sapling density differed significantly between land-use categories in any of

the catchment-scale variables (Tables 1 and 2), showing that the logged catchment characteristics were encompassed by our catchment-scale reference condition. However, several patch-scale predictor variables showed significant ($p < 0.05$) or marginal ($p < 0.10$) differences between land uses (Table 3). Channel slope was less in logged catchments and positively related to mean catchment elevation, although mean catchment elevation and slope were not different between land uses (Table 2). Depth and bank-full width were both significantly higher in Preserve streams and positively related to mean elevation and catchment area. In the MLR analyses, reach-scale geomorphology and hydrology (slope, bank-full width, depth, water velocity, Froude number) were related to catchment-scale predictors, including catchment area, mean elevation, drainage density, and surficial geology (Table 3). Of the substrate characteristics, only sand showed a (marginally) significant difference between land uses. Percent sand habitat was negatively related to elevation and percent shallow soil in the catchment (Table 3). While this difference may represent erosion and sedimentation associated with logging practices in some catchments (T. Woodcock, personal observation), sand habitat was dominant at only a few sites, including East Branch Cold and Big Brown 1 (logged) and West N. Ampersand (Preserve), and thus may represent local conditions apart from land use. Percent gravel was related to soil depth at the catchment scale. All three categories of stored organic matter (leaves, wood, FPOM) were higher in the logged catchments and showed weak or no relationships with catchment-scale predictors (Table 3).

Reach-Scale Macroinvertebrate Response

A total of 177 macroinvertebrate taxa were collected from the study streams. Occurrences of 27 taxa were significantly skewed toward Preserve catchments and 9 toward logged catchments (Table 4). Total macroinvertebrate abundance was not significantly different between land uses.

Table 2. Comparisons of catchment-scale variables (logged vs. Preserve, simple *t*-test) used in the stepwise MLR analyses of reach-scale habitat characteristics and invertebrate densities. Circularity is the ratio between the catchment area and the area of a circle with the same perimeter; higher values indicate a more circular catchment shape and a shorter length.

	Mean elevation (m)	Drainage density (km/km ²)	Area (ha)	Circu- larity	Mean slope (%)	Soil depth (% coverage)				Glacial till coverage (%)
						Deep ^a	Medium ^b	Shallow ^c	Bed- rock	
<i>Preserve</i>										
Lewis	664	9.35	898	0.54	13.9	14.7	18.0	18.8	48.4	83.3
Roaring Brook #1A	714	11.88	412	0.55	8.2	71.9	18.1	0.0	10.1	96.0
Roaring Brook #1B	774	9.91	749	0.45	8.2	72.0	3.7	14.5	9.8	88.4
West N. Ampersand	658	8.03	331	0.55	11.3	30.0	0.0	0.0	70.0	94.7
Big Brown Brook #2	578	9.07	301	0.63	11.0	30.3	46.6	0.0	23.1	72.2
Pettigrew	746	11.72	248	0.27	13.7	6.0	16.7	14.4	62.8	31.2
Dutton	644	11.07	329	0.51	9.6	45.5	0.0	0.0	54.5	94.7
Slide	927	7.03	483	0.38	13.7	28.2	14.6	14.7	42.5	70.0
AuSable Headwater	895	6.22	341	0.53	18.4	0.4	15.1	25.4	59.2	30.0
Kelly Basin	752	7.63	433	0.81	15.1	31.9	7.4	17.2	43.4	29.2
Mean	735	9.19	453	0.52	12.3	33.1	14.0	10.5	42.4	69.0
SE	35	0.62	66	0.05	1.0	7.7	4.3	3.0	6.8	8.9
<i>Logged</i>										
Deep Inlet	758	11.00	554	0.45	9.7	4.1	6.1	4.1	85.8	100.0
McNalley	552	6.71	208	0.52	8.8	44.0	26.7	14.0	15.4	84.6
Mountain	635	7.37	483	0.48	6.4	20.3	24.6	3.2	52.0	58.6
North Stephenson	821	11.76	364	0.80	14.1	0.8	26.0	25.7	47.5	9.1
White Brook	884	12.03	306	0.74	16.9	0.0	0.0	6.7	93.3	77.8
Big Brown Brook #1	596	10.41	177	0.46	12.3	16.8	6.8	0.0	76.5	63.6
Notch Mountain	429	8.47	238	0.59	12.1	57.8	2.7	23.3	16.2	33.3
East Branch Cold	589	10.01	334	0.52	7.7	31.1	21.2	5.1	42.6	100.0
Loon Lake North	731	9.80	384	0.67	13.4	4.4	0.0	0.0	95.6	93.8
Mean	666	9.73	339	0.58	11.3	19.9	12.7	9.1	58.3	69.0
SE	48	0.62	42	0.04	1.1	6.9	3.9	3.2	10.4	10.4
<i>T-test p-value</i>	0.25	0.55	0.18	0.36	0.50	0.22	0.82	0.76	0.22	0.99

^a Deep = > 60 cm soil depth, ^b medium = 20–60 cm, ^c shallow = < 20 cm (NYS-APA 2001).

Macroinvertebrate richness was significantly higher in Preserve catchments (79.4 versus 69.4 taxa/reach, *p* = 0.038), and higher richness was negatively associated with mean elevation, circularity, and shallow soils (Table 4).

In the individual MLRs, skewed taxa consistently responded more strongly to catchment-scale variables (mean model *r*² = 0.27, calculated from Table 4) than patch-scale models (mean *r*² = 0.15, calculated from Table 4). Drainage density affected more skewed taxa than any other catchment-scale variable (Figure 3A). Drainage density, circularity, catchment area, and percent glacial till had similar effects on taxa skewed to-

ward either land use. Mean slope and percent deep soil tended to show a more positive affect on the abundance of logged-skewed taxa than on Preserve-skewed taxa. Percent bedrock, mean elevation, and minimum suspended inorganics affected Preserve-skewed taxa but had no effect on logged-skewed taxa (Figure 3A).

Patch-Scale Macroinvertebrate Response

At the patch scale, total macroinvertebrate abundance was not significantly different between land uses. Richness was higher in Preserve catchments (27.4 taxa/sample) than in logged

Table 3. Summary of differences between land uses in patch-scale habitat variables. Catchment-scale predictors significant in the stepwise MLR models are listed in order of the strength of their influence, measured by partial correlation coefficient *r* (included in parentheses). *T*-tests compare characteristics of logged versus Preserve catchments. Particle size nomenclature according to the modified Wentworth scale (Cummins 1962).

Patch variable	Units	Mean ± 1 SE		<i>t</i> -test (<i>p</i> -value)	Model <i>r</i> ²	Catchment-scale predictors	
		Preserve	Logged			positive	negative
Channel slope	%	8.2 ± 0.3	6.5 ± 0.4	0.001	0.36	Mean elevation (0.60)	–
Bank-full width	m	6.5 ± 0.3	4.7 ± 0.2	<0.001	0.68	Mean elevation (0.69), catchment area (0.48)	Drainage density (–0.28)
Depth	m	0.19 ± 0.01	0.14 ± 0.01	0.002	0.67	Catchment area (0.61), mean elevation (0.59)	% bedrock outcrop (–0.26)
Velocity	m/s	0.20 ± 0.02	0.20 ± 0.02	0.96	0.54	Drainage density (0.28)	% glacial till (–0.63)
Froude number	–	0.18 ± 0.02	0.20 ± 0.02	0.58	0.43	–	% glacial till (–0.65)
Boulder ^a	%	19.0 ± 2.8	19.5 ± 2.3	0.90	0.34	Drainage density (0.48), % shallow soil ^d (0.27)	–
Cobble ^a	%	31.4 ± 2.6	28.8 ± 2.8	0.51	0.27	Catchment area (0.52)	–
Pebble ^a	%	19.1 ± 2.4	19.8 ± 2.5	0.84	–	–	–
Gravel ^a	%	16.9 ± 2.3	13.3 ± 2.0	0.24	0.27	% medium soil ^d (0.52)	–
Sand ^a	%	11.6 ± 2.3	18.6 ± 3.3	0.079	0.43	–	% shallow soil ^d (–0.57), Mean Elevation (–0.45)
Leaves ^b	g/m ²	0.2 ± 0.1	8.3 ± 4.2	0.059	0.24	% bedrock outcrop (0.49)	–
Wood ^b	g/m ²	34.9 ± 13	148 ± 58	0.060	0.12	–	Catchment area (–0.35)
FPOM >250µm ^c	g/m ²	22.0 ± 3	103 ± 37	0.027	–	–	–

^a Estimated percent coverage of benthic habitat.

^b Dry mass.

^c Ash-free dry mass.

^d Shallow = < 20 cm, medium = 20–60 cm, deep = > 60 cm soil depth (NYS-APA 2001).

catchments (24.1 taxa/sample, *p* = 0.006). Most taxa had weak relationships with patch-scale habitat descriptors, generally related to substrate particle or channel dimension characteristics (Table 4). Cobble substrate affected more skewed taxa than any other patch-scale variable, and most taxa responded positively to increases in benthic cobble regardless of land use (Figure 3B). The strongest differences were seen for water depth and gravel habitat, both of which had a positive effect on all Preserve-skewed taxa and a negative effect on all logged-skewed taxa for which it was a significant variable. Water velocity, channel slope, and bank-full width had similar effects on both logged- and Preserve-skewed taxa, while other substrate variables (pebble, sand, stored wood) showed inconsistent effects across land uses, affecting various skewed taxa differently. Moss had a positive effect on abun-

dance of all taxa for which it was admitted to the model. Only abundance of Hydracarina and *Remenus* showed strong patch-scale control, almost entirely accounted for by the positive effect of moss habitat (Table 4). However, extensive moss habitat was mostly confined to three Preserve streams (Dutton, Roaring #1B, and Kelly, Figure 1).

DISCUSSION

Selection of an appropriate scale of investigation has been approached several ways in landscape ecology, including empirical determinations using continuous data sets (Cullinan and Thomas 1992) and identification of landscape filters at several discrete scales (Tonn 1990; Poff 1997). In our study, logging represents a broad-scale anthropogenic filter that was related to forest

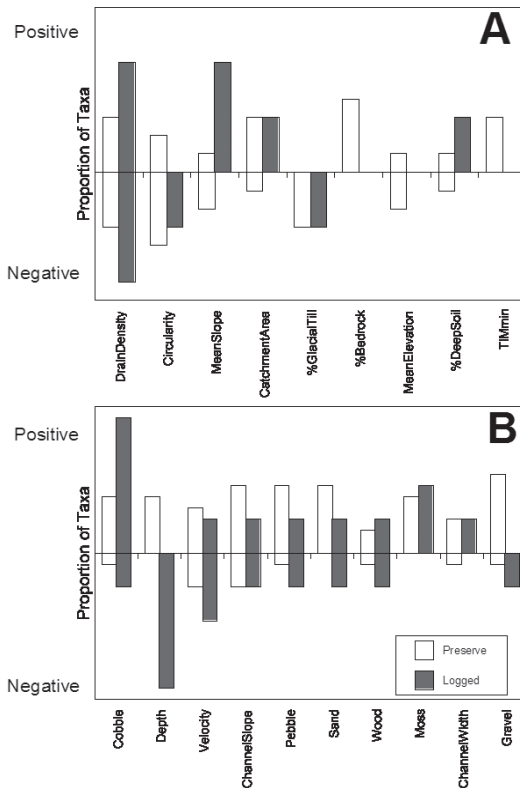


Figure 3. Proportions of all taxa with land use skew showing effects of catchment- (A) and patch-scale (B) habitat characteristics. Only those variables with significant correlations with skewed taxa are included. TIMmin = transported inorganic matter minima.

characteristics at the catchment scale (Table 1) and had some effect on patch-scale habitat in streams that drain logged catchments (Table 3). The level of control on these habitat characteristics varied; hydrology and slope were more strongly correlated than particle size distribution, and organic matter showed only weak correlations with catchment-scale variables (Table 3). Although lower-elevation portions of the catchments where patch-scale data were collected were likely closer to logged areas than were the generally steeper, higher-elevation areas (Figure 2), the distributions and population success of invertebrates responding to land use were better predicted by catchment-scale variables, even though those variables may not have been directly related to the land-use filter.

Hydrologic and Geomorphologic Differences

The quantity and movement of water in the catchment is important to the stream as a physically structuring force on the channel, as a habitat characteristic affecting macroinvertebrate distributions (Statzner et al. 1988; Church 2002; Brooks et al. 2003), and as a medium affecting ecosystem processes such as forest productivity and catchment nutrient dynamics (Allan et al. 1997; Post and Jones 2001). Although catchment-scale descriptors were not significantly different between logged and Preserve study sites (Table 2), a relationship to land use was evident in patch-scale differences (Table 3). Water depth and bank-full width were significantly higher in Preserve channels, in spite of greater mean channel slope in Preserve streams (Table 3), suggesting a decrease in total water availability in the logged catchments. Both width and depth increased with catchment area and mean elevation. This was expected, as a larger catchment typically exports more water than a smaller catchment, and a low-elevation catchment should have less water and less variable flows than a similarly sized catchment with a higher mean elevation due to greater precipitation (Isaak and Hubert 2001; Brooks et al. 2003). Unlike water depth, however, bank-full width in this study represented high flow events rather than current conditions. Future studies making similar hydrologic comparisons must also include wetted width measured at the time of sampling.

At their Rocky Mountain study sites, Isaak and Hubert (2001) investigated the relationship of stream width to nine catchment-scale variables, five of which were considered in our study (drainage density, forest characteristics, basin size, basin elevation, and basin slope). These relationships can be examined at both the catchment-scale (i.e., higher-order or larger catchments have wider streams) and patch-scale (i.e., width decreases for hydrologic reasons related to catchment land use/forest seral stage). They found that although watershed area was

Table 4. Macroinvertebrate taxa showing a significant (χ^2 p -value < 0.10) land use skew and habitat factors affecting their distribution from the stepwise MLR models. For each model, variables with strongest partial correlation are listed first. Occurrence frequency (out of 190 samples) and feeding and habitat guild information for insect taxa (Merritt and Cummins 1996) follow in parentheses. Codes are D = depositional, E = erosional, C = collector, G = gatherer, F = filterer, P = predator, Sc = scraper, and Sh = shredder.

	Catchment scale				Patch scale		
	Model r^2	Positive factors	Negative factors	Model r^2	Positive factors	Negative factors	
Total abundance	0.29	Mean slope	Circularity	0.30	Moss, woody debris, channel width, gravel, pebble	Water depth	
Taxa richness	0.56	–	Mean elevation, circularity, % shallow soil ^a	0.09	Moss	Woody debris	
Logging-skewed taxa							
<i>Tvetenia</i> (64,E,D,G)	–	–	–	0.17	Moss, cobble, pebble, channel width	water depth	
<i>Dolophilodes</i> (50,E,F)	0.28	Maximum suspended inorganics	–	0.12	Cobble, water velocity	Water depth	
<i>Collembola</i> (49,G)	0.21	–	% glacial till	0.05	–	Gravel, sand	
<i>Microtendipes</i> (32,D,F)	0.39	Mean slope	Drainage density	0.05	Cobble	Water velocity	
<i>Krenosmittia</i> (16,E,G)	0.35	Drainage density	–	0.31	Leaves, woody debris, channel slope	–	
<i>Acerpenna</i> (15,E,G)	0.33	Catchment area, % deep soil ^a	–	0.11	–	Cobble, pebble, water depth, woody debris, channel slope	
<i>Hemerodromia</i> (13,E,D,P,G)	0.47	Drainage density	Circularity	0.02	–	Water depth	
<i>Ablabesmyia</i> (12,E,D,P)	0.37	Mean slope	Drainage density	0.04	Cobble	Water velocity	
<i>Microvelia</i> (9,D,P)	–	–	–	0.01	Sand	–	
Preserve-skewed taxa							
<i>Sweltsa</i> (130,P)	–	–	–	0.08	Pebble, gravel, channel slope	–	
<i>Paraleptophlebia</i> (121,E,G,Sh)	0.20	Catchment area	–	0.13	Water depth	Channel slope	
<i>Tanytarsus</i> (98,E,C)	0.54	Drainage density	Circularity, % glacial till	0.09	Pebble, gravel, channel slope	–	

<i>Baetis brunneicolor</i> McDunnough (97,E,D,G,Sc)	0.12	–	Circularity	0.14	Channel slope, pebble, gravel	Gravel
<i>Hydracarina</i> (79)	0.82	Minimum suspended inorganics	–	0.87	Moss	–
<i>Rhyacophila</i> (72,E,P)	0.17	–	Mean slope	0.06	Water velocity, sand	Water velocity, channel slope
<i>Zavrelimyia</i> (71,E,P)	0.55	Mean slope, catchment area	Drainage density	0.13	Leaves, water depth, cobble	Water velocity
<i>Stempellinella</i> (71,E)	0.26	Mean elevation	–	0.06	Gravel	–
<i>Probezzia</i> (55,D,P)	–	–	–	0.29	Woody debris, sand, gravel	–
<i>Apatania</i> (53,E,Sc,G)	–	–	–	0.04	Gravel, pebble	–
<i>Rheotanytarsus</i> (46,E,F)	0.32	Catchment area, % deep soil ^a	–	0.39	Moss	Pebble
<i>Drunella</i> (45,E,Sc,P)	0.38	% bedrock outcrop	–	0.11	Water velocity, channel slope, bank-full width	Boulder
<i>Trissopelopia</i> (33,E,P)	0.36	–	Mean slope, drainage density	0.17	Sand, bank-full width, pebble	Channel slope, leaves, water velocity
<i>Nematoda</i> (32)	–	–	–	0.08	Woody debris, sand	–
<i>Agapetus</i> (27,E,Sc,G)	0.29	% bedrock outcrop	Circularity	0.09	Water velocity	Channel width
<i>Chelifera</i> (26,D,P)	0.54	% bedrock outcrop	Circularity, catchment area	0.28	Channel slope, moss	Cobble, boulder
<i>Rhithrogena</i> (24,E,G,Sc)	0.13	–	Mean elevation	0.04	Cobble	–
<i>Polycentropus</i> (23,E,FP)	0.18	–	% glacial fill	0.06	Cobble, water depth	–
<i>Neophylax</i> (20,E,Sc)	0.18	Minimum suspended inorganics	–	–	–	–
<i>Nymphomyia walkeri</i> Ide (17,E,Sc,G)	0.52	Minimum suspended inorganics	–	0.21	Moss, Cobble	–
<i>Remenus</i> (9,P)	–	–	–	0.71	Moss	–
<i>Lype</i> (9,E,Sc)	0.64	Drainage density, circularity	% deep soil ^a	–	–	Woody debris
<i>Stenonema</i> (9,E,D,Sc,G)	–	–	–	0.04	Sand	–
<i>Onocosmaecus</i> (9,D,Sh)	0.12	–	Mean elevation	0.06	Water depth, gravel	–
<i>Cambarus</i> (9)	0.66	Circularity, drainage density	% glacial fill	0.03	Cobble, gravel	–
<i>Paratrichocladius</i> (9, E, G)	0.26	% bedrock outcrop	–	0.09	Channel slope, water velocity	–
<i>Psychoglypha</i> (9,E,D,Sh,G)	0.12	–	Drainage density	0.22	Channel width, sand, boulder, water depth	–

^aShallow = < 20 cm, medium = 20–60 cm, deep = > 60 cm soil depth (NYS-APA 2001).

the largest single influence on width, higher elevation and tree abundance were also significant. In their study, no effect of drainage density on stream width was found, but Isaak and Hubert (2001) hypothesized that drainage densities are several times greater and likely more important in mountains of eastern North America. We found that drainage density accounted for only 8% of the variation in bank-full width and had a negative relationship with that variable (Table 3).

Vegetational changes related to logging, such as increased forest productivity due to increased densities of actively-growing saplings, could lead to increased evapotranspiration of soil water, which in turn could cause an overall decrease in water volume in logged channels (Mackay and Band 1997). Dieterich et al. (in press) found greater sapling densities in the riparian zones and decreased riparian zone widths (saturated soil adjacent to the channel) in a subset of logged catchments. In addition, we observed greater sapling densities at the catchment scale when all 19 study sites were compared (T. Woodcock, J. Allen, C. Evans, R. Tucker, T. Mihuc, C. Laxson, J. Mihuc, and E. Allen, unpublished data; Table 1). Hydrologic variables were important in the MLR models (Figure 3A), and decreased water volume may also be responsible for the decrease in benthic particle size distribution in logged channels. Headwater channels that are sufficiently steep (i.e., >4.7%) would be unlikely to accumulate sediment under normal discharges (Church 2002). However, increased erosion (bed material supply), together with a reduction in sediment transport competence due to reduced water levels in the channel, could lead to increased accumulation and decreased export of fine particles (sand) in the logged catchments. It is important to remember that while habitat differences may be related to land use, it is also possible that land with lower elevation and slope was preferentially logged over the less accessible land in the New York Forest Preserve. If logging was more likely to occur at lower elevation and relief, however, then the decrease in channel water may actually have been greater than it appeared

because width and depth are expected to increase as stream order increases (Beschta and Platts 1986; Isaak and Hubert 2001; Brooks et al. 2003).

Macroinvertebrate Response to Land Use

Land use represents a powerful landscape filter (*sensu* Poff 1997), potentially affecting invertebrate occurrence and population success by altering physical, chemical, and hydrologic stream characteristics. Because many northeastern stream invertebrate populations are exposed to fairly frequent, if temporally predictable, disturbances and are capable of relatively quick dispersal to other habitats, their distributions will be controlled by broad-scale (i.e., regional) factors rather than local habitat characteristics (Palmer et al. 1996; Vinson and Hawkins 1998). Poff and Huryn (1998) expected that catchment-scale factors such as land use would exert control over patch-scale habitat and thus have a stronger effect on stream-dwelling populations (measured as invertebrate and Atlantic salmon secondary production) than factors operating at smaller scales. Allan et al. (1997) found that instream habitat structure (i.e., organic matter inputs and storage) is determined primarily by local conditions such as vegetative cover, while nutrients, hydrology, sediment, and channel characteristics are influenced by much broader-scale (catchment, regional) factors and that catchment-scale land use was the most important scale for predicting stream invertebrate community characteristics. However, it is possible that land-use choices can affect both the role of important predictors and alter the scale at which they act (Wang et al. 2006).

Macroinvertebrate assemblage characteristics were related to hydrologic variables at both the catchment and patch scales (Figure 3). Gage et al. (2004) found that insect diversity and the distribution of sensitive (family-level) taxa were negatively affected by logging and land development causing sedimentation in headwater catchments. However, they also found a significant difference in total abundance related to land

use, which was not evident in our study. Danehy et al. (1999) found that invertebrate distributions in a central New York basin were related to stream width, Froude number, and (water surface) slope, two of which were patch-scale factors related to land use in our study. Mean catchment slope was important in determining distributions of logging-skewed taxa at the reach scale (Figure 3A), and channel slope was a common predictor of macroinvertebrate taxa at the patch scale (Figure 3B). Froude number was not an important variable in patch-scale MLR models, although both individual hydraulic components (water velocity and depth) were. This suggests that invertebrate taxa skewed for a land use were responding more strongly to one characteristic or the other, rather than to the overall hydraulic microhabitat.

Aside from water depth, particle size (proportions of boulder, cobble, pebble, gravel, sand) had the strongest effects on invertebrates with skewed distributions. It is expected that decreasing habitat heterogeneity would decrease richness (Vinson and Hawkins 1998). Although mean particle size of mineral substrate was reduced in logged streams, there was significantly more stored organic matter in those streams (Table 2). Thus, while the patch-scale habitat was different in the logged catchments, there is no evidence of decreased habitat heterogeneity. Also, a greater proportion of Preserve-skewed taxa responded positively to sand habitat and transported matter than did logged-skewed taxa (Figure 3), implying that these characteristics of logged sites were not responsible for loss of Preserve-skewed populations. Richness was negatively related to elevation, circularity, and shallow soils at the catchment scale and to organic matter characteristics (moss) at the patch scale (Table 3).

A study of riparian organic matter inputs and coarse-matter detritivore populations (shredders, Cummins 1974) carried out in a subset of seven study sites during autumn 2003–spring 2004 (L. Myers, Paul Smith's College, personal communication) found that while the total input of coarse organic matter (leaf litter) was not

different between land uses, instream leaf pack composition did vary, with logged catchments dominated by leaf species that are processed faster when compared to Preserve streams. However, among the 19 sites included in this study, the quantities of stored organic matter were significantly greater in logged streams (Table 2) despite the dominance of faster-processed leaf species. A combination of lower abundances of shredders and reduced transport competence due to decreased water levels could explain the greater quantities of stored organic matter in logged streams. All three categories of stored organic detritus (leaves, wood, FPOM) showed weak or nonexistent relationships with catchment-scale predictors (Table 3), which may suggest that logging plays a strong role in stream organic matter dynamics (see also Stone and Wallace 1998). However, many shredders complete most of their life cycles during the winter and early spring, and future studies characterizing relationships between abundances of these taxa and habitat characteristics would need to be carried out during the winter months. Mihuc et al. (in press) showed an increase in detritivorous benthic invertebrates in Preserve sites during the fall season, suggesting that logged headwater systems contain fewer detritus-adapted consumers, at least seasonally. Further research on seasonal patterns among benthic consumers in logged and reference systems, and the influence of patch and catchment-scale processes on seasonal patterns, is needed.

At a landscape scale of a few hundred hectares (the size of the study catchments), members of a macroinvertebrate assemblage likely interact with one another and with assemblages in nearby catchments, at least in adult (aerial) forms. Thus, at long temporal scales, movement between habitat patches at the catchment and reach scales is likely fairly frequent. The range of habitats used by a given taxon will depend on factors such as the strength of its niche affinity and the use of refugia during disturbances (Hildrew 1996; Palmer et al. 1996; Townsend et al. 1997). However, landscape characteristics,

while controlling smaller-scale habitat to some degree (Table 3), could be more important in determining success of a cohort or even longer-term persistence of a population in a catchment. Our study shows that while individual distributions are related to patch-scale habitat characteristics, distribution across the landscape is more closely related to catchment-scale characteristics (i.e., 10^2 – 10^3 ha).

In our Adirondack study catchments, assemblage richness and invertebrate populations affected by land use showed a stronger response to catchment-scale than to patch-scale habitat variables. However, the relationship between catchment characteristics, patch-scale variables, and land use as it affects stream biota requires further investigation. Channel dimensions, substrate particle size, and organic matter dynamics in these streams were all identified as factors affecting invertebrate distributions at the patch scale and were potentially linked to the changes in vegetation related to logging activity. Thus, it appears that the presence and absence of invertebrate populations across the Adirondack landscape are controlled mainly by a combination of broad-scale geomorphologic and land-use factors. The smaller-scale factors that control the success of individuals and subpopulations, while having some relationship to the landscape in which they are embedded, had less effect on invertebrate distributions. Thus, conservation of streams may be best accomplished by implementing measures at the catchment scale, rather than simply increasing buffer strip width for small streams.

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Local and Landscape Effects of Past Forest Harvest on Stream Habitat and Fish Assemblages

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Abstract.—Forest harvests have been shown to have negative effects on stream fish and habitat; however, the relationship between these factors, and the magnitude of these effects, has received little study. We investigated the influence that various land-cover types (including recent forest harvest) have on fish assemblages at multiple spatial scales and compared these results to the influences of local instream habitat variables. Satellite land-cover data and land management harvest maps were used to characterize the land-cover types throughout the Knife River basin in northeast Minnesota. Eleven spatial scales (with 30-m and 100-m buffer widths), including site, reach, stream corridor, and catchment, were evaluated. Forward stepwise regression was used to relate land cover to coldwater index of biotic integrity scores and metrics. Land-cover relationships varied with spatial scale, but land cover at the catchment and corridor scales explained the most variation in fish and habitat variables. Generally, increases in forest cover and decreases in water/wetland were associated with higher quality fish assemblages and instream habitat. No negative effects of forest harvest were found at the site or reach scales. Forest harvest 5–8 years old was negatively related to fish assemblage quality at the stream corridor and catchment scales, possibly related to changes in temperature and substrate at the corridor scale, and increases in fine sediments and unstable banks at the catchment scale. The cumulative effect of increasing forest harvest from 0 to 8 years old throughout the catchment was associated with lower quality fish assemblages and instream habitat, indicating that large increases in similar timed forest harvests throughout a catchment (not just in the riparian zone) can have negative effects on stream fish and habitat.

INTRODUCTION

The biotic community associated with stream systems is highly dependent on the physical and chemical environment (Karr and Schlosser 1978; Minshall 1988; Poff and Allan 1995). The physical and chemical environment is in turn influenced by terrestrial factors occurring across different spatial and temporal scales (Frissel et al. 1986; Richards et al. 1996). Anthropogenic disturbances to the terrestrial environment can have deleterious effects on stream organisms across multiple scales (Ward 1998).

Many studies have investigated how land use/cover at various scales influences stream habitat and biota (Richards et al. 1996; Roth et al. 1996; Wang et al. 1997; Harding et al. 1998; Lammert and Allan 1999; Jones et al. 1999; Stauffer et al. 2000; Williams et al. 2002; Strayer et al. 2003; Wang et al. 2003). Many of these have had a majority of their study sites located in catchments with more than 35% agricultural land use/cover (Richards et al. 1996; Roth et al. 1996; Wang et al. 1997; Lammert and Allan 1999; Stauffer et al. 2000). Studies in regions with a high amount of agricultural land use/cover are not representative of basins dominated by forest cover, where most land use/cover is associated with past and present forest management practices.

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A few landscape-scale studies have taken place in catchments with an average forest cover greater than 64% (Jones et al. 1999; Williams et al. 2002; Strayer et al. 2003; Wang et al. 2003). Jones et al. (1999) found that increased length of deforested upstream riparian patches was related to poorer fish and habitat quality. Most of these deforested patches were converted to pasture and agriculture land types and not managed for forest harvest. Strayer et al. (2003) and Wang et al. (2003) both assessed the influence land use/cover had on stream biota at multiple scales. Strayer et al. (2003) found that predictive power of land use/cover on fish species richness was similar across catchment, stream corridor, and local scales, while Wang et al. (2003) found that most variation in fish variables was explained directly by reach habitat variables, while less variation was explained by catchment and riparian land use/cover. The variation explained by catchment and riparian land use/cover was likely due to indirect effects on the reach habitat variables (Wang et al. 2003). Both Strayer et al. (2003) and Wang et al. (2003) treated forest cover generically and did not differentiate between age of forest stands; therefore, the influence of past forest harvests was not assessed, but other studies have shown that past land use/cover (Harding et al. 1998), including forest harvest (Stone and Wallace 1998), can influence present-day stream biota.

The effects of forest harvest practices on stream biotic communities are well documented (Campbell and Doeg 1989; Meehan 1991). Harvesting operations and the resulting removal of trees can alter the thermal regime (Rishel et al. 1982; Bowlby and Roff 1986), hydrology (Verry et al. 2000), sediment characteristics (Eaglin and Hubert 1993), and quantity of organic inputs to streams (Murphy and Koski 1989; Bilby and Ward 1991). These changes can have both direct and indirect effects on stream biotic communities and can occur at multiple scales.

Historically, studies of the effects of forest harvest on stream habitat and biota have been con-

cerned with the effects of either basin-wide harvest (e.g., Hartman et al. 1996) or of local forest harvest and protection provided by riparian buffer strips (e.g., Clinnick 1985). With the advent of geographic information systems (GIS) and availability of satellite data, it is now possible to explore the influence that land use/cover (including forest harvests) throughout the catchment has on stream systems at multiple spatial and temporal scales. Studies of this nature can help assess the potential cumulative effects of regular forest harvest throughout large catchments. Williams et al. (2002) found that timber harvesting activities had little influence on fish at the catchment scale, but they did not examine influences at local, reach, or corridor scales. The purpose of our study was to investigate the influence that land cover, especially past forest harvest (0–15 years), has on stream fish assemblages and instream habitat across multiple scales. Information from this study should help forest managers assess the relative importance of local versus landscape effects of forest harvest and predict the cumulative effects of recent forest harvest operations at multiple scales within the same catchment.

STUDY AREA

The Knife River basin is located in the Northern Lakes and Forests ecoregion (Omernik and Galant 1988) in northeast Minnesota. The Knife River and its numerous tributaries drain approximately 22,000 ha before emptying into Lake Superior. The dominant vegetative cover is northern hardwoods, and there is an extensive history of forest harvest throughout the basin (Randy Roff, St Louis County Land Department, personal communication). The Knife River contains brook trout *Salvelinus fontinalis*, rainbow trout *Oncorhynchus mykiss*, and brown trout *Salmo trutta* throughout most of the system. Most underlying geology is superior lobe, high-land type.

METHODS

Study Design

Twenty seven sample sites were selected in three catchments within the Knife River basin (Figure 1). The unofficial names of these catchments are (1) West Branch, (2) McCarthy, and (3) Bergstad.

The majority (19) of the sample sites were within the West Branch (Table 1) and were part of a related study that was designed to evaluate the local effects of riparian harvest on instream habitat and fish assemblages. Three of the remaining sites were in the Bergstad catchment and five were in the McCarthy catchment. The study sites from the Bergstad and McCarthy were chosen

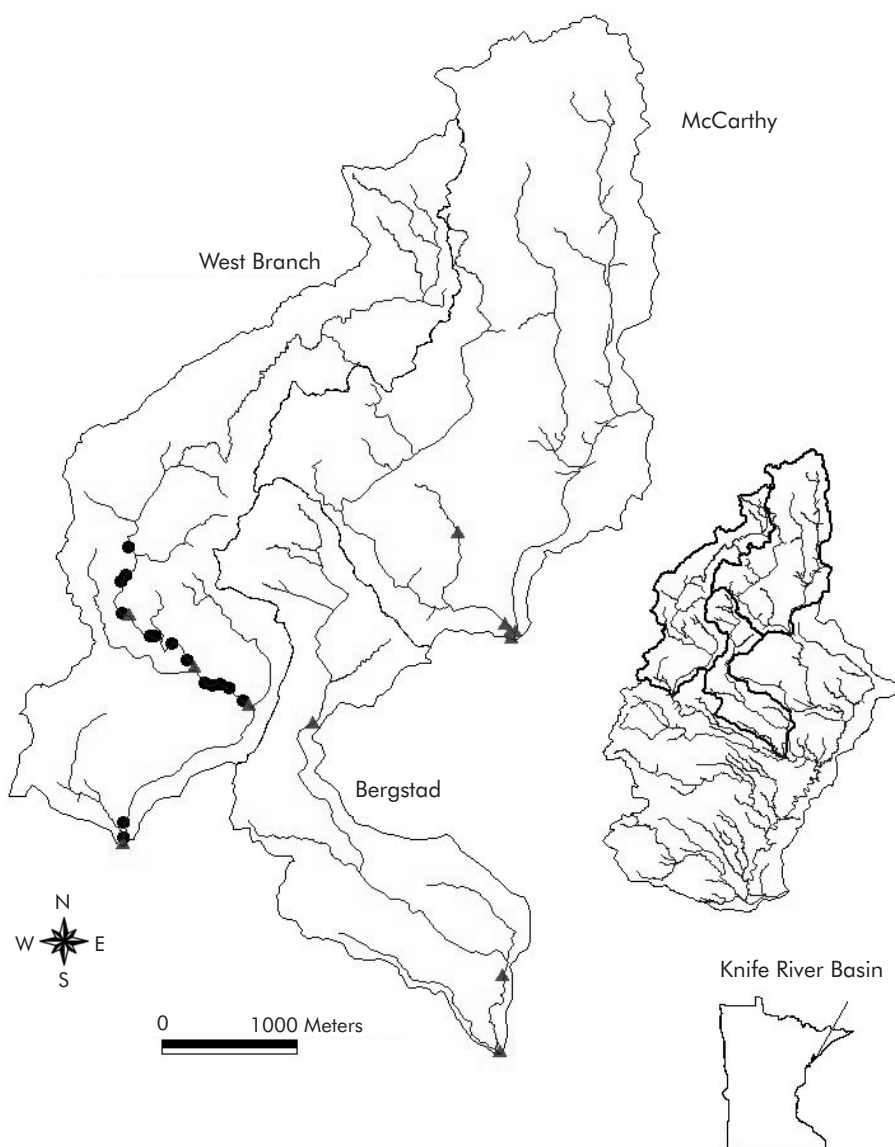


Figure 1. Locations of three catchments within the Knife River basin. Triangles represent sample sites used only at reach, corridor and catchment scale. Circles in addition to triangles represent sample sites used at site scales.

Table 1. Land area and number of study sites for the three study catchments used for each scale.

Catchment	Area (km ²)	Number of study sites at site-level scale	Number of sample sites at reach, stream corridor, and catchment scales
West Branch	28.8	19	4
McCarthy	34.9	5	5
Bergstad	17.3	3	3

based on their proximity to past forest harvests (forest harvest occurred 1–15 years ago). Five of the reaches were within 100 m from a previous harvest. All reaches were located on first- to third-order streams. The influence that land cover has on fish assemblages and instream habitat was measured across 11 spatial scales, including site, reach, stream corridor, and catchment scales (see Land-Cover Characterization below).

Fish Sampling

Fish were sampled in June 2001 at all study sites with a Wisconsin AbP-3 backpack electrofisher. At each site, fish were collected from a 50-m reach. Fish were identified to species, counted, and returned to the stream.

Coldwater index of biotic integrity (IBI) values were calculated according to Mundahl and Simon (1998). This index assesses the environmental health of coldwater streams using fish assemblages. Each reach was assigned a score from 0 to 120 based on 12 metrics. The metrics are based on fish relative abundances, species richness, indicator species, and trophic function. Higher scores are indicative of higher quality reaches. Fish abundance values (number captured) from the 50-m reaches were all standardized to a 150-m reach by multiplying by three, as recommended by Mundahl and Simon (1998).

Instream Habitat Evaluations

Stream habitat measurements were obtained during July 2001. Habitat was assessed with a modified version of the protocol developed by the Minnesota Pollution Control Agency (Bailey

et al. 1993). This protocol develops a habitat index (HI) based on stream cover, physical habitat, and substrate properties. Higher HI scores indicate better quality habitat. Habitat assessments were conducted along the 50-m reaches, usually at three 17-m intervals in each reach. Percent canopy cover was estimated using a spherical concave forest densiometer in four directions in each 17-m section (Lemmon 1957). Overhanging vegetation was estimated as the percentage of stream channel shaded by vegetation within 1 m of the water. Percentage boulder pocket cover was estimated as the amount of stream channel occupied by boulders and the disturbed flow produced from them. Percentage unstable bank was estimated as the percentage of both banks with fine bare soil. Banks covered with roots or larger stable substrates were not considered unstable. Percentage woody cover (WC) was estimated as the amount of bank-full channel containing woody material of any size (including twigs and branches) that could provide cover for fish.

Stream substrates were characterized by visually estimating the percentages of each substrate size-class (clay, silt, sand, gravel, cobble, and boulder) and by ranking the top three substrates present. In each reach, 35 circular (28-cm diameter) quadrats (7 within each 10-m interval) were randomly placed for substrate characterization. Depth was recorded at each quadrat to obtain mean depth for the entire reach. Substrates were summarized into two categories: percentage fine substrate and percentage coarse substrate. Percentage fine substrate was calculated by summing the average percentage of clay, silt, and sand in the 35 quadrats. Percentage coarse substrate

was calculated by summing the average percentage of cobble and boulder in the quadrats.

Land-Cover Characterization

All sample site locations were recorded with a handheld global positioning unit and transferred into a geographic information system (GIS). Eleven different scales were delineated using 30-m elevation models (Table 2). Four site-level scales were created using a 50-m and 150-m upstream segment from the base of all (27) sample sites with a 30-m and 100-m buffer on each side of the stream. At all other spatial scales (reach, corridor, and catchment), only four sample sites from the West Branch catchment were used for a total of 12 sample sites. In addition to the eight sites in the other two watersheds, only four sites were used in order to reduce the amount of overlap in land cover that would occur at different scales for the same sample reach. The sample sites on the West Branch were far enough apart so this overlap in land cover did not occur at the site-level scale, but would at larger scales, which could lead to large independence violations. Land cover at the reach scale was determined for a 1-km and 2-km segment upstream from the remaining 12

study sites and including all land cover within 30 m and 100 m of each side of the stream. Land cover at the corridor scale was determined by including all land cover within 30 and 100 m of either side of the stream along the entire segment upstream from the base of the sample sites, and land cover at the catchment scale was determined by including all land cover within the watershed of each sample site. These scales were similar to the ones used in a study by Harding et al. (1998) to evaluate effects of past land use/cover on biota.

Thematic mapper satellite imagery with a resolution of 30 m was used to obtain land-cover types. These data were from 1995 and were divided into 15 land-cover types. Not all cover types were found in the study catchment. The satellite imagery was obtained from the Minnesota Department of Natural Resources GIS data deli Web site (<http://deli.dnr.state.mn.us>). The percent land-cover type was calculated for each sample site across the 11 spatial scales. Four modifications were made to the land-cover types. A recent harvest land cover was created that included the regeneration/young forest cover from the satellite data and also included manually delineated forest harvests known to occur from 1987 to 2001. These were delineated from the

Table 2. Description of 11 land-use spatial scales. All upstream distances begin at downstream boundary of the study site.

Scale	Description
<i>Site scale</i>	
30-m buffer 50 m upstream	30-m buffer on either side of the stream for an upstream distance of 50 m
30-m buffer 150 m upstream	30-m buffer on either side of the stream for an upstream distance of 150 m
100-m buffer 50 m upstream	100-m buffer on either side of the stream for an upstream distance of 50 m
100-m buffer 150 m upstream	100-m buffer on either side of the stream for an upstream distance of 150 m
<i>Reach scale</i>	
30-m buffer 1 km upstream	30-m buffer on either side of the stream for an upstream distance of 1 km
30-m buffer 2 km upstream	30-m buffer on either side of the stream for an upstream distance of 2 km
100-m buffer 1 km upstream	100-m buffer on either side of the stream for an upstream distance of 1 km
100-m buffer 2 km upstream	100-m buffer on either side of the stream for an upstream distance of 2 km
<i>Stream corridor scale</i>	
30-m corridor	30-m buffer on either side of the stream for the entire upstream corridor
100-m corridor	100-m buffer on either side of the stream for the entire upstream corridor
<i>Catchment scale</i>	
Catchment	Entire catchment upstream of the sample site

harvest sale reports available from local land offices. Recent harvests were divided into four time frames: (1) 0–2 years old, (2) 3–4 years old, (3) 5–8 years old, and (4) 9–15 years old. In this way, the most recent harvest activity could be included in the analyses and exact harvest age was known. Other modifications included (1) combining the open water, marsh and fens, and bogs cover types into one “water/wetland” type; (2) combining the mixwood, deciduous, and conifer forest into one “forest cover” type; and (3) combining the shrub/grass and open cover types into a “shrub/open” type. These combinations reduced the number of variables and allowed cover types with small percentages of land cover (e.g., conifer forest) to be included in analyses at all scales. Tables 3–5 provide a summary of all land-cover types across all spatial scales.

Statistical Analysis

To determine which fish metrics explained significant variation in IBI scores, IBI metrics were regressed on IBI scores. Only IBI metrics that explained a significant portion of the total IBI score were included in further analyses. These

significant metrics were determined from the data set, including all 27 sample sites.

Three sets of forward stepwise regression ($P = 0.10$ from t -test to enter or remove variables) analyses were used in this study to (1) determine the influence that instream habitat variables had on IBI scores and metrics, (2) determine the influence that land-cover types across all 11 spatial scales had on IBI scores and metrics, and (3) for those instream habitat variables that explained significant variation in IBI scores and metrics, determine the influence that land-cover types across all 11 spatial scales had on instream habitat. The criteria for inclusion of land-cover predictor variables in the initial models was an average of greater than 1% coverage and occurrence of the specific land-cover type in at least one-third of the sample sites for each scale. All R^2 values reported represent adjusted R^2 due to the different number of predictors used across scales. The statistical package JMP IN (Sall et al. 2001) was used for analyses. All relationships were visually examined and likely spurious relationships are indicated in the results. Due to overlapping cover areas at larger scales, the independence assumption of regression was

Table 3. Mean percent, range, and occurrence (N) of each land cover type at the local scale. Asterisks denote no range available because of only one occurrence, and numbers after harvest land cover refer to age of harvest in years. Forest cover is composed of mixwood, deciduous, and conifer cover types, and shrub/open is composed of open and shrub/grass cover types.

Land cover	30-m buffer						100-m buffer					
	50 m upstream			150 m upstream			50 m upstream			150 m upstream		
	Mean	Range	N	Mean	Range	N	Mean	Range	N	Mean	Range	N
Forest cover	64.0	0–100	22	59.3	0–100	24	55.7	0–100	26	56.0	1.0–100	27
Mixwood	64.0	0–100	22	59.2	0–100	23	53.4	0–100	24	53.4	1.0–100	25
Deciduous	0.1	*	1	0.0	*	1	0.1	0–1.6	2	0.1	0–1.5	2
Conifer	0.0	0	0	0.0	0–0.5	2	2.2	0–23.2	5	2.5	0–23.4	6
Shrub/open	4.0	0–66.9	2	4.1	0–59.6	3	3.6	0–47.5	4	4.2	0–50.1	5
Shrub/grass	1.5	*	1	2.2	0–59.6	2	2.1	0–47.5	3	2.8	0–50.1	4
Open	2.5	*	1	1.8	*	1	1.6	*	1	1.4	*	1
Water/wetland	21.2	0–100	11	23.8	0–100	12	20.0	0–74.0	13	19.4	0–72.8	14
Harvest 0–2	7.6	0–88.6	9	10.3	0–78.6	11	13.6	0–61.4	11	14.7	0–56.8	11
Harvest 3–4	2.9	0–39.1	4	2.4	0–36.3	4	4.0	0–32.8	5	2.9	0–24.8	5
Harvest 5–8	0.3	*	1	0.2	*	1	1.9	0–33.0	4	1.4	0–30.6	3
Harvest 9–15	0.0	0	0	0.0	0	0	1.2	0–22.8	2	1.2	0–25.5	2

Table 4. Mean percent, range, and occurrence (N) of each land cover type at the reach scale. Asterisks denote no range available because of only one occurrence, and numbers after harvest land cover refer to age of harvest in years. Forest cover is composed of mixwood, deciduous, and conifer cover types, and shrub/open is composed of open and shrub/grass cover types.

Land cover	30-m buffer						100-m buffer					
	1 km upstream			2 km upstream			1 km upstream			2 km upstream		
	Mean	Range	N	Mean	Range	N	Mean	Range	N	Mean	Range	N
Forest cover	67.5	1.0–100	12	61.3	11.9–96.9	12	62.9	1.0–96.1	12	57.7	13.2–86.2	12
Mixwood	67.1	1.0–100	12	60.9	8.9–96.9	12	61.3	1.0–96.1	12	56.0	12.8–86.2	12
Deciduous	0.0	*	1	0.1	0–0.5	3	0.2	0–1.3	3	0.6	0–5.5	4
Conifer	0.4	0–4.8	2	0.3	0–2.7	7	1.5	0–9.3	2	1.2	0–5.9	7
Shrub/open	5.0	0–32.5	2	3.9	0–25.8	5	5.9	0–42.7	2	4.8	0–34.2	5
Shrub/grass	2.3	*	1	1.3	0–14.7	3	2.3	*	1	1.5	0–16.2	3
Open	2.7	*	1	2.6	0–25.8	2	3.6	*	1	3.4	0–34.2	2
Water/wetland	23.0	0–97.0	6	28.7	0–86.4	9	17.1	0–81.2	6	22.6	0–74.3	9
Harvest 0–2	2.4	0–17.2	2	2.4	0–15.0	2	6.1	0–41.1	2	5.7	0–37.7	2
Harvest 3–4	0.9	*	1	0.5	0–5.5	4	1.1	*	1	2.2	0–9.2	6
Harvest 5–8	1.1	0–9.3	4	2.9	0–15.7	5	4.8	0–17.8	6	4.6	0–14.9	7
Harvest 9–15	0.0	*	1	0.3	*	1	2.1	0–14.4	6	2.3	0–11.9	6

somewhat violated. Some caution must be used when interpreting these results, but they should still show broad relationships (Roth et al. 1996).

RESULTS

IBI Scores

Four of the 12 IBI metrics explained 72.7% of the variation in IBI scores across the 27 sample

sites. These significant metrics were (1) number of benthic species (correlates with a decrease in quality), (2) number of tolerant species (correlates with a decrease in quality), (3) percent intolerants (correlates with an increase in quality), and (4) number of coldwater individuals per reach (correlates with an increase in quality). These significant metrics were used in further analyses at all 11 spatial scales.

Table 5. Mean percent, range, and occurrence (N) of each land cover type at the stream corridor and catchment scales. Numbers after harvest land cover refer to age of harvest in years. Forest cover is composed of mixwood, deciduous, and conifer cover types, and shrub/open is composed of open and shrub/grass cover types.

Land cover	30-m stream corridor			100-m stream corridor			Catchment		
	Mean	Range	N	Mean	Range	N	Mean	Range	N
Forest cover	47.9	21.8–90.3	12	50.2	28.2–88.1	12	65.7	53.3–80.8	12
Mixwood	46.6	20.7–87.4	12	48.0	27.1–82.1	12	56.7	42.4–64.4	12
Deciduous	0.7	0–2.1	7	0.9	0–2.3	8	8.0	2.0–14.8	12
Conifer	0.1	0–0.3	7	0.2	0–0.4	7	1.0	0.2–2.0	12
Shrub/open	5.2	0–21.1	11	6.0	0–24.2	11	3.3	0–13.5	11
Shrub/grass	2.0	0–7.5	10	2.0	0–6.7	10	0.9	0–3.4	10
Open	3.2	0–13.5	10	4.0	0–17.6	11	2.4	0–10.3	11
Water/wetland	42.8	8.9–74.5	12	34.4	6.1–66.8	12	15.8	4.7–27.7	12
Harvest 0–2	3.2	0–13.5	6	4.0	0–17.6	10	2.0	0–6.9	11
Harvest 3–4	0.7	0–3.3	3	1.5	0–7.5	5	4.1	0–12.1	9
Harvest 5–8	0.5	0–1.2	7	1.2	0–2.8	8	4.5	1.2–7.1	12
Harvest 9–15	2.7	0–15.7	9	4.5	0–14.9	9	4.4	0.6–17.7	12

IBI and Instream Habitat Relationships

Instream habitat variables explained a significant portion of the variance in IBI scores and metrics (Table 6). Number of benthic species was positively related to unstable bank and percent riffles. Percent intolerant individuals was negatively related to overhanging vegetation and positively related to HI score. The number of coldwater individuals per reach was positively related to depth and negatively related to percent fine sediments. No significant habitat relationships were found with overall IBI scores or number of tolerant species.

IBI and Landscape Relationships

The amount of variation in IBI metrics and scores explained by land cover tended to increase with spatial scale. No significant landscape effects were found for either 50-m or 150-m segments within the 30-m buffer. Number of tolerant species within both 100-m buffers was positively related to harvest 0–2 years old (Table 7). The West Branch was the only catchment that contained harvest 0–2 years old at the site scale. The significant effect of harvest 0–2 years old on tolerant species dropped out when only the sites within the West Branch were used, indicating a catchment rather than a local land-cover effect.

No relationships of fish to landscape were found at the reach scale (1 or 2 km) for the 30-m buffer; however, there were significant land-

scape relationships within the 100-m buffers. IBI scores were positively related to harvest 5–8 years old, and number of coldwater individuals per reach was negatively related to water/wetland and positively related to harvest 5–8 years at 1-km upstream reaches with the 100-m buffers (Table 7). Within the 100-m buffer and 2-km upstream reaches, IBI scores and number of coldwater individuals per reach were both positively related to harvest 5–8 and 3–4 years old, while number of coldwater individuals per reach was also negatively related to water/wetland.

Land cover along the 30-m stream corridor buffer was significantly related to IBI score, number of tolerant species, and number of coldwater individuals per reach (Table 7). IBI scores were positively related to forest cover and negatively related to shrub/open cover. The number of tolerant species was negatively related to forest cover and positively related to shrub/open cover and harvest 5–8 years old. The number of coldwater individuals per reach was negatively related to shrub/open cover and positively related forest cover. At the stream corridors with 100-m buffers scale, IBI scores were positively related to forest cover and negatively related to shrub/open cover. Number of coldwater individuals per reach was positively related to forest cover.

At the catchment scale, IBI scores were negatively related to shrub/open cover, harvest 5–8 years old, and water/wetland (Table 7). Number of coldwater individuals was positively related to forest cover. The number of tolerant species had

Table 6. Significant ($P < 0.10$) regression coefficients, corresponding t -test P values, and cumulative model R^2 values for regression of index of biotic integrity scores and metrics on instream habitat variables.

Response variable	Significant variables	Regression coefficient	t -test P value	Model R^2
Index of biotic integrity score	None			
Number of tolerant species	None			
Number of benthic species	% unstable bank	+0.01	0.013	0.09
	% riffle	+0.01	0.065	0.18
Percent intolerants	% overhanging veg.	−0.48	0.020	0.09
	Habitat index score	+0.005	0.065	0.18
Coldwater individuals per reach	Depth	+55.7	0.012	0.05
	% fine sediments	−1.0	0.020	0.21

Table 7. Significant ($P < 0.10$) regression coefficients, corresponding t -test P values, and cumulative model R^2 values for regression of index of biotic integrity (IBI) scores and metrics on percentage land cover types.

Scale	Significant response variables	Significant predictors	Regression coefficient	t-test P value	Model R ²	
Site scale						
30-m buffer 50 m upstream	None					
30-m buffer 150 m upstream	None					
100-m buffer 50 m upstream	# tolerant species*	Harvest 0–2	+0.018	0.070	0.09	
100-m buffer 150 m upstream	# tolerant species*	Harvest 0–2	+0.018	0.059	0.10	
Reach scale						
30-m buffer 1 km upstream	None					
30-m buffer 2 km upstream	None					
100-m buffer 1 km upstream	IBI score	Harvest 5–8	+1.57	0.043	0.28	
		Coldwater indiv/reach	Harvest 5–8	+3.00	0.007	0.29
		Water/wetland	–0.48	0.028	0.53	
	IBI score	Harvest 5–8	+2.32	0.013	0.28	
		Harvest 3–4	+2.81	0.097	0.42	
	Coldwater indiv/reach	Harvest 5–8	+4.06	0.002	0.31	
		Water/wetland	–0.53	0.035	0.50	
		Harvest 3–4	+0.37	0.080	0.62	
Stream corridor scale						
30-m buffer	IBI score	Shrub/open	–1.66	0.002	0.32	
		Forest cover	+0.50	0.003	0.73	
	# tolerant species	Shrub/open	+0.08	0.008	0.18	
		Forest cover	–0.03	0.011	0.37	
		Harvest 5–8	+0.10	0.032	0.61	
	Coldwater indiv/reach	Forest cover	+0.74	0.027	0.25	
		Shrub/open	–1.64	0.086	0.41	
	100-m buffer	IBI score	Shrub/open	–1.33	0.006	0.32
Forest cover			+0.54	0.007	0.67	
Coldwater indiv/reach		Forest cover	+0.79	0.043	0.28	
Catchment scale						
	IBI score	Shrub/open	–3.18	< 0.001	0.28	
		Water/wetland	–2.54	0.002	0.59	
		Harvest 5–8	–5.10	0.032	0.75	
	# tolerant species	Forest cover	–1.22	0.004	0.46	
		Harvest 5–8	+0.16	0.083	0.59	
	Coldwater indiv/reach	Forest cover	+2.07	0.011	0.48	

* Significant relationship is due to confounding with catchment.

a positive relationship to harvest 5–8 years old and a negative relationship to forest cover.

Habitat and Landscape Relationships

Site scale landscape influences on habitat variables only occurred within the 100-m buffers. Percent riffles and percent fine sediments were negatively related to harvest 0–2 years old at the 50-m and 150-m upstream segments (Table 8). Depth was positively related to forest cover and negatively related to harvest 0–2 years old at the

150-m upstream segments. The significant effect of harvest 0–2 years old on percentage fine sediments and percentage riffle dropped out at the 50-m upstream segment when only the sites within the West Branch were used, indicating a catchment, rather than a local land cover, effect. The effect at the 150-m segment on percentage fines remained. No landscape influences were found with percentage unstable bank, overhanging vegetation, or HI score at the site scale.

Many landscape relationships were found at the reach scale. Percent riffle was negatively related to

Table 8. Significant ($P < 0.10$) regression coefficients, corresponding t -test P values, and cumulative model R^2 values for regression of instream habitat variables on percentage land-cover types.

Scale	Significant response variables	Significant predictors	Regression coefficient	t -test P value	Model R^2
<i>Site scale</i>					
30-m buffer 50 m upstream	None				
30-m buffer 150 m upstream	None				
100-m buffer 50 m upstream	% fine sediments*	Harvest 0–2	–0.22	0.050	0.11
	% riffle*	Harvest 0–2	–0.375	0.040	0.12
100-m buffer 150 m upstream	% fine sediments	Harvest 0–2	–0.26	0.014	0.19
	% riffle*	Harvest 0–2	–0.327	0.072	0.09
	Depth	Forest cover	+0.003	0.042	0.16
		Harvest 0–2	–0.003	0.071	0.24
<i>Reach scale</i>					
30-m buffer 1 km upstream	% riffle	Water/wetland	–0.29	0.057	0.25
	% fine sediments	Water/wetland	+0.22	0.008	0.47
30-m buffer 2 km upstream	% fine sediments	Water/wetland	+0.26	0.012	0.44
	Depth	Forest cover	+0.003	0.088	0.18
100-m buffer 1 km upstream	% riffle	Forest cover	+0.35	0.041	0.29
	% fine sediments	Water/wetland	+0.28	0.003	0.56
100-m buffer 2 km upstream	% fine sediments	Water/wetland	+0.32	0.008	0.48
	Depth	Forest cover	+0.007	0.007	0.22
		Harvest 5–8	+0.020	0.016	0.47
		Harvest 9–16	–0.17	0.098	0.59
<i>Stream corridor scale</i>					
30-m buffer	Depth	Forest cover	+0.008	<0.001	0.72
100-m buffer	% riffle	Harvest 0–2	–5.1	0.006	0.29
		Harvest 3–4	+9.2	0.028	0.55
	Depth	Forest cover	+0.008	<0.001	0.70
<i>Catchment scale</i>					
	% unstable bank	Harvest 0–2	+1.10	0.049	0.27
	% riffle	Harvest 5–8	+4.94	0.041	0.29
	% fine sediments	Harvest 0–2	+4.36	<0.001	0.67
	Depth	Water/wetland	–0.012	0.033	0.55

* Significant relationship is due to confounding with catchment.

water/wetland at the 30-m buffer 1-km upstream segment and positively related to forest cover at the 100-m buffer 1-km upstream segment (Table 8). Percentage fine sediments were positively related to water/wetland at the 30-m and 100-m buffer 1-km segments and the 30-m buffer 2-km segment. At the 100-m buffer 2-km segment, percentage fine sediments was positively related to water/wetland. Depth was positively related to forest cover at both 2-km reach segments and also positively related to harvest 5–8 years old and negatively related to harvest 9–16 years old at the 100-m buffer. No landscape influences were found with percentage unstable bank, overhanging vegetation, or HI score at the reach scale.

Two habitat variables were significantly related to some land-cover categories at the stream corridor scale. Percentage riffle was positively related to harvest 3–4 years old and negatively related to harvest 0–2 years old within the 100-m buffer stream corridor (Table 8). Depth was positively related to forest cover at both the 30-m and 100-m buffer stream corridors. No landscape relationships were found with percentage unstable bank, overhanging vegetation, percentage fine sediments, or HI score at the corridor scale.

Four habitat variables were significantly related to some land-cover categories at the catchment scale. Percentage unstable bank and percentage fine sediments were positively related

to harvest 0–2 years, and percent riffles were positively related to harvest 5–8 years (Table 8). Depth was negatively related to water/wetland. No landscape relationships were found with overhanging vegetation or HI score at the catchment scale.

Comparison of Scales

Comparison of significant average R^2 values shows that more variation in IBI metrics and scores was explained by land cover at the catchment and corridor scale. The amount of variation explained, as well as average number of significant relationships, decreased as scale decreased (Figure 2). The same analysis on instream habitat revealed that land cover at the stream corridor scale explained the highest amount of variation, while the reach and catchment scales explained less (Figure 3). The average number

of significant relationships was highest at the catchment scale.

DISCUSSION

Regression analysis showed relationships among fish assemblages, instream habitat variables, and land cover in the Knife River basin. Land cover at most scales (site, reach, stream corridor, and catchment) explained significant variation in fish and habitat variables.

The primary goal of this study was to determine if recent forest harvests influenced instream habitat and fish assemblages, and at what scale. The three catchments of the Knife River used in this study were relatively unmodified. Most land-cover types were forested with dispersed wetlands and standing water. This presented a unique opportunity because agricultural, rural, and urban development was low

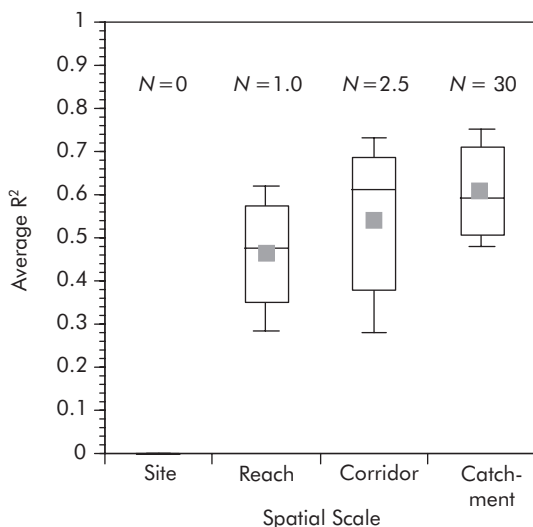


Figure 2. Box plots showing average R^2 (full model) values for regressions of index of biotic integrity metrics and scores on land-cover types across all scales. N = mean number of significant relationships at each scale (total number of significant relationships/number of subscales). The middle line represents the median, the square represents the mean, while the top and bottom of the box represent the 25th and 75th percentiles, respectively. Whiskers show the 10th and 90th percentiles.

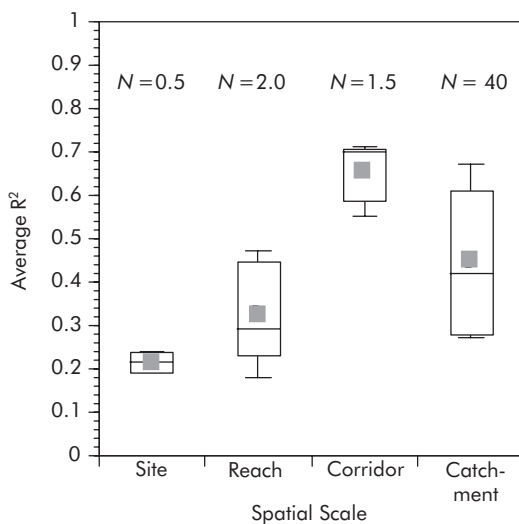


Figure 3. Box plots showing average R^2 (full model) values for regressions of instream habitat variables on land-cover types across all scales. N = mean number of significant relationships at each scale (total number of significant relationships/number of subscales). The middle line represents the median, the square represents the mean, while the top and bottom of the box represent the 25th and 75th percentiles, respectively. Whiskers show the 10th and 90th percentiles.

and forest harvest represented the primary anthropogenic disturbance.

The lack of effects within the 30-m buffers at the reach scale and 50-m and 100-m buffers at the site scale were likely due to several reasons. The resolution of the land-cover data was only 30 m, so there was not much physical area for a diverse set of land-cover predictors. Due to the regression criteria, only three or four land-cover types were allowed as predictors into the model for the site-scale and reach-scale buffers. Also, in many cases there was not a significant amount of harvest within the 30-m buffer (i.e., not much harvesting right next to the stream), but there was more within the 100-m buffer, which seemed to influence some fish variables. Strayer et al. (2003) found that predictive power tended to decrease in small catchments. The small size of our site-scale and reach-scale buffers, and lack of heterogeneous cover types, could be a factor in the low R^2 values observed at these scales.

The influence that forest harvest had on fish assemblages appeared to change with scale. Intermediate age harvests (3–8 years) were correlated with higher fish assemblage quality within 100-m buffers at the reach scale. Regeneration of this age likely provided adequate shade, increasing allochthonous inputs, and stable habitat in the riparian area, but might still have elevated levels of autochthonous production, thus offering an increased and diverse macroinvertebrate energy supply (Hawkins et al. 1983; Stone and Wallace 1998).

The positive effect of forest harvest 5–8 years old on fish assemblages that was observed at the reach scale was reversed at the broader scales. At the catchment scale and 30-m stream corridor, fish assemblage quality was positively correlated with forest cover and negatively correlated with open areas and recent harvests 5–8 years old, indicating a negative cumulative effect of intermediate age forest harvest. Whereas intermediate aged riparian forest harvest had positive influences on fish at scales of 1–2 km upstream, greatly increasing forest harvest throughout a catchment (not just in ripar-

ian areas) in a short period of time (i.e., more land cover as 5–8 year old harvests) could have negative effects on fish assemblages. These cumulative effects could be due to larger scale changes in physical attributes such as hydrology, sediments, and temperature that take a longer time to influence fish assemblages.

Instream habitat variables explained little variation in fish assemblage composition. Generally fish assemblage quality decreased with increases in fine substrates and unstable banks and increased with depth and large substrates. It is possible that instream variables not measured in this study, such as temperature and invertebrate quantity and composition, also had a significant role in fish distribution. Merten (1999) found that IBI scores along the West Branch increased with decreased temperature.

Land-cover types across all scales primarily influenced channel physical characteristics (substrates and dimensions) and did not influence canopy cover or woody cover inputs. Water/wetland was usually related to decreased instream habitat quality, while forest cover was related to increased quality. Few negative effects of harvest were found at the site, reach, and stream corridor scales, while harvests 0–2 years decreased habitat quality at catchment scales.

At the catchment scale, harvests 0–2 years old were positively related to percent unstable bank and percent fine sediments. Basin-wide increases in fine sediments one year after a forest harvest were also observed by Merten (1999) in a central Minnesota stream system. The increased use of forest and logging roads by heavy equipment is one possible explanation for the increases in fine sediments. Furthermore, basin-wide increases in harvest can result in increased runoff and erosion (Campbell and Doeg 1989; Moring et al. 1994; Hartman et al. 1996), resulting in increased fines and decreased bank stability. These reductions in habitat quality may translate to reduced fish assemblage quality seen with harvests 5–8 years old.

Overall, local (riparian) forest harvest appeared to have no negative effect on instream

habitat or fish assemblages at site or reach scales. Lengths of stream subjected to harvest may have been too short to be significantly altered by harvest or the management practices were sufficient to protect adjacent stream fish and habitat. Reductions in fish assemblage and habitat quality at the corridor and catchment scales suggest that cumulative effects of harvest are more important than direct local effects.

Unfortunately it is very difficult to analyze multiscale landscape studies (Strayer et al. 2003). In a statistical sense, the assumption of independence is violated regularly. For example, an increase in a recent harvest cover type will lead to a decrease in a forest cover type (autocorrelation), and also, two study sites on the same stream segment will have overlapping corridor and catchment land-cover types. Increases in cover types can lead to spurious correlations. Examination of the correlations among cover types within the same scale revealed few patterns across scales, with the exception that mixwood cover was usually negatively related to water/wetland (these were the two predominant cover types at most scales). The patterns observed in this study showed relationships among fish, habitat, and land-cover variables, with more relationships appearing at broader scales. While this could in part be due to low cover type representation at the site scale, there was substantial variation of water/wetland and forest cover at the site scale, and few habitat and fish correlations. This, along with the few fish assemblage relationships to instream habitat variables indicates that fish assemblages were influenced more by factors at broader scales within the Knife River basin. Working in higher gradient forested streams in the Pacific Northwest, Burnett et al. (2006, this volume) and Kaufmann and Hughes (2006, this volume) also found catchment scale variables important for explaining habitat and IBI variability, respectively. However, the latter also determined that site scale variables were often important. This information provides more information about how land-cover change affects streams ecosystems (Strayer et al. 2003).

Our study showed some significant trends that occur with recent forest harvests in a fairly undisturbed catchment. Large-scale increases in harvest 0–2 years old seem to decrease quality of instream habitat, of which the cumulative effect on fish populations is not immediate and appears as the harvests reach 5–8 years. Harding et al. (1998) found that historic land cover, especially agricultural cover, approximately 50 years old influenced present-day stream biota. Our study indicates that the influence of past harvests throughout the catchment can last at least 8 years. Forest managers should be concerned with entire stream corridor and catchment management because cumulative recent forest harvests appear just as important, if not more important, than what takes place at the site scale in similar catchments typical of the north shore of Lake Superior.

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Geomorphic and Anthropogenic Influences on Fish and Amphibians in Pacific Northwest Coastal Streams

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Abstract.—Physical habitat degradation has been implicated as a major contributor to the historic decline of salmonids in Pacific Northwest streams. Native aquatic vertebrate assemblages in the Oregon and Washington Coast Range consist primarily of coldwater salmonids, cottids, and amphibians. This region has a dynamic natural disturbance regime, in which mass failures, debris torrents, fire, and tree-fall are driven by weather but are subject to human alteration. The major land uses in the region are logging, dairy farming, and roads, but there is disagreement concerning the effects of those activities on habitat and fish assemblages. To evaluate those effects, we examined associations among physical and chemical habitat, land use, geomorphology, and aquatic vertebrate assemblage data from a regional survey. In general, those data showed that most variation in aquatic vertebrate assemblage composition and habitat characteristics is predetermined by drainage area, channel slope, and basin lithology. To reveal anthropogenic influences, we first modeled the dominant geomorphic influences on aquatic biotic assemblages and physical habitat in the region. Once those geomorphic controls were factored out, associations with human activities were clarified. Streambed instability and excess fines were associated with riparian disturbance and road density, as was a vertebrate assemblage index of biotic integrity (IBI). Low stream IBI values, reflecting lower abundances of salmonids and other sediment-intolerant and coldwater fish and amphibian taxa, were associated with excess streambed fines, bed instability, higher water temperature, higher dissolved nutrient concentrations, and lack of deep pools and cover complexity. Anthropogenic effects were more pronounced in streams draining erodible sedimentary bedrock than in those draining more resistant volcanic terrain. Our findings suggest that the condition of fish and amphibian assemblages in Coast Range streams would be improved by reducing watershed activities that exacerbate erosion and mass-wasting of sediment; protecting and restoring multilayered structure and large, old trees in riparian zones; and managing landscapes so that large wood is delivered along with sediment in both natural and anthropogenic mass-wasting events. These three measures are likely to increase relative bed stability and decrease excess fines by decreasing sediment inputs and increasing energy-dissipating roughness from in-channel large wood and deep residual pools. Reducing sediment supply and transport to sustainable rates should also ensure adequate future supplies of sediment. In addition, these measures would provide more shade, bankside cover, pool volume, colder water, and more complex habitat structure.

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INTRODUCTION

The forested Oregon and Washington Coast Range ecoregion has a cool, wet temperate climate (Omernik and Gallant 1986), with a dynamic natural disturbance regime in which landslides, debris torrents, wildfire and wind-driven tree-fall are important in shaping the landscape and its streams (Dietrich and Dunne 1978; Benda et al. 1998, 2003; Bisson et al. 2003). These disturbances are essential for forming and maintaining complex and productive habitat for biota in the region (Reeves et al. 1995). Native aquatic vertebrates in wadeable streams of this ecoregion consist largely of coldwater fish and amphibian assemblages that are species-depauperate compared with those in many parts of the United States. Common species include resident and anadromous salmonids and lampreys, sculpins, minnows, and amphibians (Herger and Hayslip 2000; Hughes et al. 2004). Stream habitat degradation has been implicated as a major factor contributing to the historic decline of salmonids and the integrity of the food webs supporting them in the Pacific Northwest (Nehlsen et al. 1991). Land disturbances and native vegetation removal increase sediment delivery rates from natural processes in stream catchments (Waters 1995; Jones et al. 2001). Human land uses in the Coast Range consist primarily of silviculture, dairy farming, and roads. These activities can increase erosion rates and sediment supply to streams above those in the absence of human activities (Beschta 1978; Reid et al. 1981; Waters 1995; May 2002). In riparian areas, these activities reduce the effectiveness of riparian corridors in trapping sediment and stabilizing long-term sediment storage in streambanks and valley bottoms (Gregory et al. 1991).

The landscape setting, however, is an influential context underlying human effects in this region (Figure 1). Geoclimatic factors and landscape position exert strong controls on the vigor of geologic weathering, sediment delivery, transport and deposition processes, and on the flow

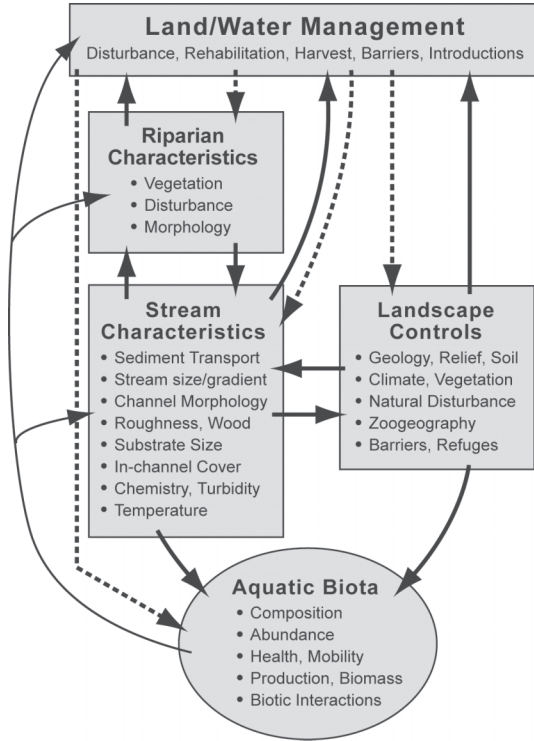


Figure 1. Conceptual diagram of natural and anthropogenic influences on aquatic biota and the physical-chemical habitat supporting it. Solid and dashed arrows represent natural and anthropogenic influences, respectively.

and morphology of streams (Leopold et al. 1964). Furthermore, landscape characteristics, including topography and geology, constrain the types of land and water management activities that are possible and profitable. Finally, many of these same landscape characteristics can exacerbate or ameliorate the degree to which human activities alter the sediment and water delivery processes that in turn influence substrate size, stability, and channel form. It is not surprising, then, that researchers have reported that stream ecosystems in the Coast Range ecoregion vary in their sensitivity to human disturbances, depending upon stream drainage area, channel slopes, and basin geology (e.g., Beschta et al. 1995; Spence et al. 1996).

There is considerable debate concerning the effects of human activities on habitat and aquatic

vertebrate assemblages in the Coast Range ecoregion, but increased sedimentation of streambeds has been identified as a likely cause of impairment (Nehlsen et al. 1991; Waters 1995; Spence et al. 1996). The recent experimental work of Suttle et al. (2004) demonstrated mechanisms through which bedded fine sediments reduce juvenile salmonid growth and survival, and earlier research (e.g., Chapman 1988) demonstrated mechanisms by which fine sediments reduced survival of embryos and emerging salmon fry. However, much of the uncertainty in demonstrating anthropogenic causes of sediment effects on stream biota on a regional scale stems from the fact that human land-use activities covary with strong geomorphic gradients that control aquatic biota through their influence on sediment supply, transport, and channel morphology.

Our objective was to evaluate geomorphic and anthropogenic influences on aquatic vertebrates in this region, separating the most important of these influences to the full extent possible with our survey data. To do so, we examined associations among physical and chemical habitat, land use, geomorphology, and biotic assemblages.

METHODS

Sampling Design

Aquatic vertebrate assemblage composition, chemical and physical habitat, and riparian vegetation structure were measured in a survey of the Coast Range ecoregion conducted by the Oregon Department of Environmental Quality and the Washington Department of Ecology in cooperation with the U.S. Environmental Protection Agency (Herger and Hayslip 2000). Stream sample reaches were selected as a probability sample using the U.S. Environmental Protection Agency's Environmental Monitoring and Assessment Program (EMAP) sampling protocols (Stevens and Olsen 1999; Herlihy et al. 2000). The sample (Figure 2) is representative of the population of 23,700 km of first- through third-

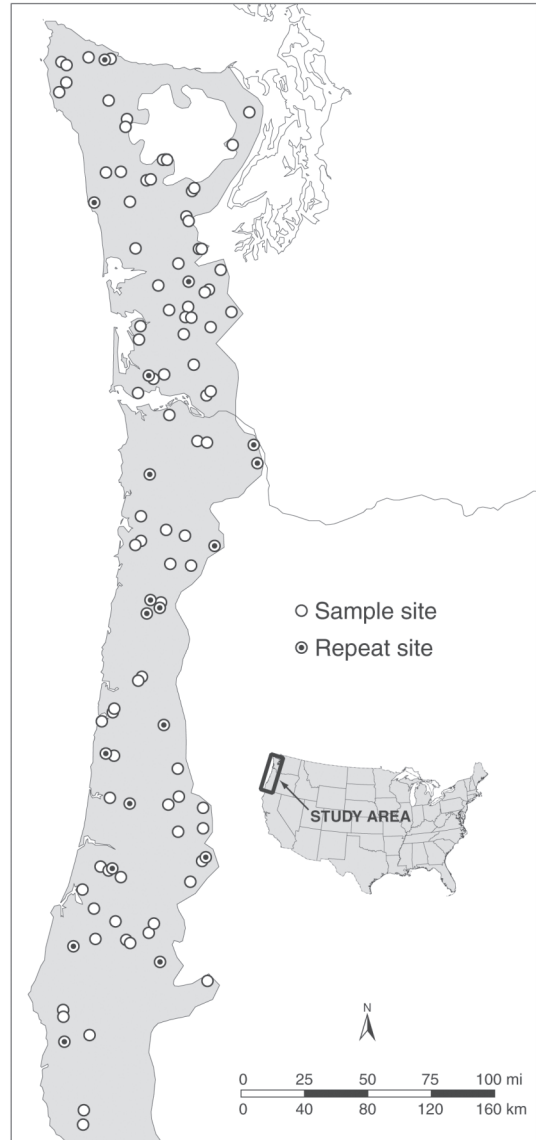


Figure 2. Locations of Coast Range sample sites in Oregon and Washington.

order streams (Strahler 1957) delineated on 1:100,000-scale U.S. Geologic Survey topographic maps of the region. The survey included one or more visits to 104 stream reaches in Oregon ($n = 57$) and Washington ($n = 47$), during the summer low-flow seasons of 1994 and 1995. To evaluate measurement and short-term temporal variability during the sample season, 19 sample reaches were revisited in the same season,

and the 57 Oregon sites were revisited in the summer of 1996 following a 50-year storm. Sample lengths were 40 times their summer season wetted width, but no less than 150 m (Lazorchak et al. 1998)

Aquatic Vertebrates

Stream fish and amphibians were sampled by one-pass electrofishing over the entire length of each sample reach (Lazorchak et al. 1998), a level of effort that Reynolds et al. (2003) found adequate for collecting all but the rarest species in upland and lowland Wadeable streams in Western Oregon. Field crews used Smith-Root backpack electrofishers set at pulsed DC, 300 volt-amperes, 900–1,100 V, and a frequency of 60–70 Hz. A crew of two to three persons typically fished the reach in 1–3 h. Taxa were identified in the field, and specimens were vouchered at the Oregon State University Ichthyology Museum. The concepts and procedures for calculating an IBI for aquatic vertebrate assemblages (including fish and amphibians) in these streams were described by Hughes et al. (2004). Their IBI contains eight assemblage metrics: percent alien species, percent coolwater species, percent anadromous species, percent coldwater species, number of size-classes, number of tolerant individuals, number of native coldwater species, and number of native coldwater individuals. The last three IBI metrics were scaled for watershed area, a procedure that adjusts for the expectation of greater taxa richness in larger streams. Because of the relationships among gradient, elevation and catchment area in this region, this procedure also eliminated most of the dependence of taxa richness on stream gradient and elevation among our sample sites (Hughes et al. 2004).

Chemical and Physical Habitat

Water temperature was measured upon arriving at the stream in the morning. A 4-L grab-sample and two 60-mL syringes of stream water were collected midstream at each sample reach

(Lazorchak et al. 1998). The syringes were sealed with Luer-lock valves to prevent gas exchange. All samples were iced and sent to the analytical laboratory within 24 h. Syringe samples were analyzed for pH and dissolved inorganic carbon (DIC), and the 4 l sample was split into aliquots and preserved within 48–72 h of collection. Detailed information on the analytical procedures is published by USEPA (1987). In brief, Fe, Mn, and base cations were determined by atomic absorption, anions (SO_4^{2-} , NO_3^- , Cl^-) by ion chromatography, dissolved organic carbon (DOC) by a carbon analyzer, total N and P by persulfate oxidation and colorimetry, electrical conductivity by standard methods, and turbidity by nephelometry.

Physical habitat data were collected from longitudinal profiles and from 11 cross-sectional transects evenly spaced along the sampled stream reach (Kaufmann and Robison 1998). Maximum (thalweg) depth was measured at 100 evenly spaced points along the stream reach (150 points for streams less than 2.5 m wide). The location and amount of woody debris, and habitat unit classification (e.g., riffle, pool) were recorded while measuring the thalweg. Data collected along transects included channel dimensions (width, depth, bank angle), systematic “pebble counts,” channel gradient, bearing (for calculating sinuosity), areal cover of fish concealment features (e.g., brush, undercut banks, large wood), riparian vegetation cover and structure, and the occurrence and proximity of riparian human disturbances (e.g., roads, buildings, stumps, agriculture). See Kaufmann et al. (1999) for calculations of reach-scale summary metrics from field data, including mean channel dimensions, residual pool depth, geometric mean substrate diameter, wood volume, bed shear stress, relative bed stability (RBS), riparian vegetation cover and complexity, and proximity-weighted indices of riparian human disturbances. Contributing drainage areas were delineated and measured on 1:24,000-scale U.S. Geological Survey topographic maps using geographical information systems techniques.

Disturbance Indices

We calculated a composite riparian condition index (RCond) from the reach summary data describing the cover and structure of riparian vegetation and a proximity-weighted tally of streamside human activities. RCond was defined as follows:

$$\text{RCond} = \{(\text{XCL})(\text{XCMGW})[1/(1+\text{W1_HALL})]\}^{(1/3)}$$

The index increases with decreases in streamside human activities (W1_HALL), and increases in large-diameter tree cover (XCL) and riparian vegetation complexity (XCMGW, the sum of woody vegetation cover in the tree, shrub, and ground cover layers). The riparian measures contributing to this index are detailed by Kaufmann et al. (1999).

We used digital road data (TIGER 1990) as a surrogate measure of catchment disturbance. The TIGER data were compared with updated forest road data and found adequate for our purposes. We scaled catchment road density (Rd_DenKM) by the highest value we observed among our sample reach catchments (6 km/km²) and combined it with RCond to define an index of watershed + riparian condition as

$$\text{WRCond} = [1/(1+(\text{Rd_DenKM}/6))] \text{RCond}$$

Anthropogenic Sedimentation

To reveal the influence of anthropogenic sedimentation on biota, we needed measures of streambed particle size and the percentage of silt-size particles that reasonably scaled these stream characteristics by their major natural controls. Because stream power for transporting progressively larger sediment particles increases in direct proportion to the product of flow depth and slope, steep streams tend to have coarser substrates than similar size streams on gentle slopes. Similarly, the larger of two streams flowing at the same slope will tend to have coarser substrate, because its deeper flow has more power to scour

and transport fine substrates downstream (Leopold et al. 1964; Morisawa 1968). Many researchers have scaled observed stream reach or riffle substrate size (e.g., median diameter D_{50} , or geometric mean diameter D_{gm}) by the calculated mobile, or “critical” substrate diameter (D_{cbf}) in the stream channel. The scaled median streambed particle size is expressed as relative bed stability (RBS), calculated as the ratio D_{50}/D_{cbf} (Dingman 1984; Gordon et al. 1992), where D_{50} is based on systematic streambed particle sampling (“pebble counts”) and D_{cbf} is based on the estimated streambed shear stress at bank-full flows. Kaufmann et al. (1999) modified the calculation of D_{cbf} to incorporate large wood and pools, which can greatly reduce shear stress in complex natural streams. They formulated both D_{gm} and D_{cbf} so that RBS could be estimated from physical habitat data obtained from large-scale regional ecological surveys. In interpreting RBS on a regional scale, they argued that, over time, streams adjust sediment transport to match supply from natural weathering and delivery mechanisms driven by the natural disturbance regime, so that RBS in appropriately stratified regional reference sites should tend towards a range characteristic of the climate, lithology, and natural disturbance regime. Earlier researchers demonstrated reductions in D_{50} relative to D_{cbf} as a result of increases in sediment supply containing a mix of particle sizes, and had investigated the processes causing these reductions (Lisle 1982; Dietrich et al. 1989; Buffington 1998). We hypothesized that large positive (armoring) or negative (fining) deviations from this size were anthropogenic if they were associated with measures of human disturbances and not other natural gradients, and could be explained by these plausible mechanisms. In streams with low RBS, bed materials are easily moved by floods smaller than bank-full, so may be rapidly transported downstream. The persistence of fine surficial streambed particles is made possible under these circumstances by high rates of sediment supply (including fines) that continue to replenish the streambed.

We used log-transformed relative bed stability (LRBS) as an independent variable in regression analyses to interpret the likely influence of anthropogenic alteration of bed sediment size on aquatic vertebrate assemblages. However, percentages of fine particles might be elevated to levels that are potentially deleterious to biota in some streams without substantially affecting the central tendency of substrate diameter or the general stability of the streambed. As an alternate estimate of excess fine sediments in these streams, we also calculated the deviation of surficial fine sediments (<0.06 mm) from a regression on D_{cbf} (a function of streambed shear stress). We previously applied this approach to Appalachian streams to assess the effects of land use on aquatic macroinvertebrates (Bryce et al. 1999) and the percentage of sand and silt in streambeds (USEPA 2000).

Data Analysis

We took an analytical approach conceptually different from covariance structure analysis (Riseng et al. 2006; Zorn and Wiley 2006; both this volume) or multiple linear regression (Burnett et al. 2006, this volume). Our approach was similar to covariance structure analysis (CSA) in that it includes some intention in attributing portions of variance to one predictor or another when they covary. Like CSA, our approach was motivated by the desire to describe likely functional relationships among controls and responses and to reduce ambiguity in the interpretation of multiple linear regression (MLR) when collinearity among predictor variables was substantial. Similar to the “normalization” approaches described by Wiley et al. (2002) and Baker et al. (2005), we intentionally asserted some dominant functional relationships between natural forcing functions and their responses, based on deterministic modeling of relationships that can be confidently theorized. Specifically, we scaled stream bed particle size data by bed shear stress as described by Kaufmann et al. (1999) and we

examined aquatic vertebrate assemblages after transforming species-abundance data into an index of biotic integrity (IBI; Hughes et al. 2004). We then employed correlation analysis and sequentially withheld certain categories of data in MLR to examine the relationships between anthropogenic disturbances and aquatic biota in the Coast Range, particularly aiming to clarify the influence of anthropogenic sedimentation. This approach was warranted because we have considerable confidence in modeling expected aquatic vertebrate taxa richness and substrate size in streams, and because the magnitude of deviation from those expectations can be reasonably attributed to human activities. Our analytical strategy followed seven steps:

- 1) We assembled a database of potential explanatory variables (Table 1), including landscape variables that could act as natural controls on aquatic vertebrate assemblages, human disturbance (stressor) variables, and in-stream measures of habitat volume, hydraulic energy, substrate size composition, channel complexity, cover, temperature, ionic strength, and nutrients. We eliminated many variables that showed no appreciable or biologically relevant variation in the region (e.g., pH), or that were highly correlated or redundant with other variables in the data set (e.g., sum of base cations was redundant with ANC).

- 2) We divided potential explanatory variables into three groups: landscape variables that are relatively unaffected by human activities in this region, landscape and riparian variables that are measures of human disturbance or are reasonable surrogates of human disturbance, and instream measures of physical and chemical habitat, most of which are subject to direct or indirect alteration by humans (Table 1).

- 3) We used univariate correlation (Spearman rank order correlation, SAS 2004) to explore associations between IBI and potential controlling variables to determine which variables were probably *not* important in explaining regional

Table 1. Variables used in multiple linear regression and correlation analysis

Variable code	Definition
Response variable	
IBI	Index of biotic integrity based on stream fish and amphibians (Hughes et al. 2004)
Landscape setting:	
LAreaKM	$\text{Log}_{10}(\text{drainage area—km}^2)$
LS	Log_{10} (mean % slope of sample reach)
Elev	Elevation at sample reach (m)
LQsp	Log_{10} (areal discharge at summer sample time ($\text{m}^3\text{s}^{-1}\text{km}^{-2}$))
LITH	Basin lithology (0 = Volcanic, 1 = Sedimentary)
Human disturb./condition:	
Rd_DenKM	Basin road density from TIGER data (km/km^2)
W1_HALL	Proximity weighted tally of riparian/streamside disturbances
RCond (see text)	Riparian condition: veg. cover, structure, and human disturbances
WRCond (see text)	Watershed + riparian condition index
RDxRCond	Interaction of Rd_DenKM and RCond
RDx(1-RCond)	Interaction of Rd_DenKM and (1-RCond)
In-channel habitat ————— Water quality:	
TEMPSTRM	Stream water temperature at time of sampling ($^{\circ}\text{C}$)
NNTL	Log_{10} (total nitrogen $\mu\text{g}/\text{L}$ as N) in stream water
LPTL	Log_{10} (total phosphorus $\mu\text{g}/\text{L}$ as P) in stream water
CONDUCT	Electrical conductivity ($\mu\text{S}/\text{cm}$) of stream water
In-channel habitat ————— Physical habitat:	
RP100	Mean residual depth at thalweg (m)
RPQT75	Number of pools with residual depth $\geq 0.75\text{m}$ in reach
SDD	Std deviation of depth at thalweg (m)
LV1W_msq	Log_{10} (large wood volume [m^3 wood/ m^2 bank-full channel])
XFC_BRS	Proportion areal cover of in-channel brush and small woody debris
XFC_UCB	Proportion areal cover of undercut banks
%BDRK	Bedrock (percent of streambed area)
EX_FN (see text)	Excess % streambed silt (deviation % < 0.06 mm diameter)
LRBS (see text)	Log_{10} of relative bed stability = $\text{Log}_{10}(D_{gm}/D_{cbl})$
Used in correlations only:	
XCMGW	Mean riparian tree + shrub + ground woody cover (%)
%FN	Streambed fines (% < 0.6 mm diameter)
%SAFN	Streambed sand + fines (% < 2 mm diameter)
D_{gm}	Streambed particle geometric mean diameter (mm)

IBI variation and to describe similar covarying patterns of association. These associations were the basis for stratifying sample sites into classes with apparently similar major controls on assemblages and physical-chemical habitat. As a result of these analyses, we stratified by catchment lithology (sedimentary and volcanic) and by catchment area (large $\geq 15 \text{ km}^2$, and small $< 15 \text{ km}^2$).

4) Where possible and supported by plausible mechanisms, we scaled the in-channel predictor variables most strongly associated with IBI to factor out natural geomorphic controls, redefining variables to be interpreted as anthropogenic deviations from natural expectations (Wiley et al. 2002; Baker et al. 2005). Geometric mean streambed particle diameter was scaled by critical diameter to define relative bed stability

(RBS, log transformed as LRBS), and percent bed surface silt (%FN) was scaled by critical diameter to define excess percent silt (EX_FN).

5) We carried out three rounds of MLR analysis on each strata, first modeling IBI based on instream physical and chemical variables and natural landscape controls; second, on natural landscape controls and measures of human land use measured at catchment and local riparian scales (riparian measures at catchment scale were not available); and third, on variables from all categories in Table 1.

6) Local influences on IBI were interpreted from the first round of MLR, human stressors from round two, and likely mechanisms of anthropogenic effects from round three. Natural landscape variables were available in all three rounds of MLR, allowing us to factor out or interpret remaining unscaled natural variation in the IBI.

7) The MLR predictor variable selection procedure was stepwise (forward-backward), including and retaining only variables with $p < 0.15$ (SAS 2004), and confirming best-model selection by examining all possible MLR models with less than or equal the number of resultant predictor variables. Only three of the predictor variables actually selected in the various MLR models using these variable selection criteria had $p > 0.05$, and most had $p < 0.01$. All final models were significant at $p < 0.01$; most at $p < 0.0001$. To avoid overfitting (overparameterization), we attempted to build models with fewer than $n/(5-10)$ predictor variables, where n is the number of sample sites in a particular modeled stratum. To further avoid overfitting, we also constrained the number of predictor variables so that the root mean square error (RMSE) of the regression model was generally larger than 7.0, which was the RMSE reported by Hughes et al. (2004) for same-stream repeat measurements of IBI. The RMSE reported by Hughes et al. is equivalent to the pooled standard deviation of site revisits (Kaufmann et al. 1999), representing a practical limit of a MLR model to associate variation of IBI in sites across the region with

ancillary site data (Kaufmann et al. 1999). A regression model with RMSE substantially less than the RMSE for measurement variation would be suspected of overfitting.

RESULTS

Coast Range Stream Characteristics

The Coast Range survey yielded a sample of wadeable small to medium size, dilute, coldwater streams diverse in slope, bed substrate size, large dead wood loadings, canopy cover, and riparian vegetation structural complexity (Table 2). Areal discharge (discharge per unit drainage area), elevation, and channel slope tended to be higher, and water temperature and various measures of human disturbance tended to be lower, in streams draining volcanic basins. Though stream temperatures at the time of summer sampling ranged from 7.3°C to 25.3°C, only one site had a temperature in excess of 18°, and only several had temperatures less than 10°. There were no distinct temperature classes of streams, and most of the summertime stream temperature variation was associated with stream size, elevation, areal discharge, canopy cover and human disturbances. The survey captured 38 aquatic vertebrate species, but typically there were only 3–5 species in a given sample reach. Common or cosmopolitan aquatic vertebrates species included three salmonids, five cottids, two cyprinids, one petromyzontid, and four amphibians (Table 3). Tailed frog and coast range sculpin were the only two species that were strongly associated with volcanic lithology, whereas cutthroat trout, rainbow trout, torrent sculpin, riffle sculpin, and Pacific giant salamander were not strongly associated with either lithology. Red-legged frog, speckled dace, rough-skinned newt, reddsideshiner, prickly sculpin, and threespine stickleback were 3–4 times as likely to be found in streams draining sedimentary basins as in volcanic.

The IBI, summarizing the deviation of fish and amphibian taxa richness and composition

Table 2. Sample distributions of selected basin, channel, and riparian characteristics of 104 Coast Range stream reaches.

Variable	Overall median (range)	Sedimentary sites median (range)	Volcanic sites median (range)
Drainage area (km ²)	14 (0.09–160)	15 (0.09–160)	14 (0.41–119)
Discharge at summer sample time (m ³ s ⁻¹)	0.067 (0–2.12)	0.033 (0–2.12)	0.013 (0.0003–1.16)
Areal discharge at summer sample time (m ³ s ⁻¹ km ⁻²)	0.0033 (0–0.047)	0.0025 (0–0.047)	0.0095 (0.0002–0.020)
Elevation at sample reach (m)	121 (3–673)	105 (3–622)	251 (43–673)
Mean slope of reach water surface (%)	1.2 (0.08–22)	1.1 (0.08–9.4)	2.0 (0.40–22)
Mean wetted width (m)	5.6 (0–23)	4.9 (0–23)	6.1 (1.6–23)
Mean depth at thalweg (m)	0.36 (0–1.4)	0.35 (0–1.40)	0.41 (0.06–0.93)
Mean residual depth at thalweg (m)	0.17 (0.01–0.74)	0.17 (0.02–0.72)	0.15 (0.01–0.38)
Mean canopy cover—mid-channel (densiometer %)	78 (13–100)	78 (13–100)	76 (19–100)
Mean riparian tree + shrub + ground woody cover (%)	100 (1.7–181)	102 (1.7–181)	95 (37–181)
Mean riparian tree canopy cover (%)	40 (0.8–89)	34 (0.8–89)	44 (11–81)
Mean riparian tree canopy cover—trees > 0.3 m dbh (%)	22 (0–67)	22 (0–67)	24 (0.4–67)
Riparian human disturb.—(Prox-wr'd. obs per plot)	1.2 (0–5.2)	1.2 (0–5.2)	0.43 (0–2.6)
Road density in basin (km/km ²)	1.6 (0–5.9)	1.6 (0–5.9)	1.5 (0–3.5)
Large wood vol. (m ³ wood / m ² bank-full channel area)	0.022 (0–1.9)	0.023 (0–1.9)	0.017 (0.0006–0.57)
Substrate fines (% < 0.6 mm diameter)	7 (0–100)	18 (0–100)	0 (0–32)
Substrate sand + fines (% < 2 mm diameter)	29 (0–100)	38 (0–100)	9.1 (0–58)
Substrate % bedrock	3.6 (0–69)	1.8 (0–60)	5.2 (0–69)
Substrate D_{gm} —geom mean diameter (mm)	10 (0.008–1,040)	3.8 (0.008–1,040)	57 (0.75–950)
LRBS = \log_{10} of relative bed stability = $\log(D_{gm}/D_{crit})$	-0.67 (-4.1–+1.23)	-1.1 (-4.1–+1.23)	-0.26 (-1.50–+1.06)
Conductivity (μS/cm)	77 (29–493)	77 (29–493)	76 (45–139)
Water temp. at summer sample time (degrees C)	13 (7–25)	14 (7–25)	12 (7–14)
pH	7.2 (5.5–8.1)	7.2 (5.5–8.1)	7.2 (6.4–7.8)
Acid neutralizing capacity (μeq/L)	498 (79–1,680)	440 (79–1,680)	579 (240–1,180)
Dissolved organic carbon (mg/L)	1.6 (0.5–13)	2.8 (0.5–13)	1.0 (0.5–1.9)
Dissolved oxygen (mg/L)	9.6 (1–12)	9.3 (1–11)	10 (8.6–12)
Chloride (μeq/L)	116 (0.8–2,820)	124 (0.8–2,820)	85 (20–240)
Total nitrogen (μg/L as N)	260 (38–3,200)	316 (60–3,200)	158 (38–1,200)
Total phosphorus (μg/L as P)	20 (5–580)	30 (5–580)	10 (5–50)
Turbidity (NTU)	2.0 (0.5–178)	3.0 (0.5–178)	1.0 (0.5–6.0)

Table 3. The 19 most cosmopolitan fish and amphibian species found in Wadeable Coast Range streams. Note species with apparent affinity for sedimentary^a versus volcanic^b lithology or their correlates.

Common name	Genus-species	% of sample reaches			Mean Count/site
		Overall	Sed.	Volc.	
Cutthroat trout	<i>Oncorhynchus clarkii</i>	61	65	52	23
Rainbow trout	<i>O. mykiss</i>	55	52	62	62
Reticulate sculpin ^a	<i>Cottus perplexus</i>	49	58	28	63
Coho salmon ^a	<i>O. kisutch</i>	48	52	38	38
Pacific lamprey ^a	<i>Lampetra tridentata</i>	46	52	31	15
Torrent sculpin	<i>C. rhotheus</i>	24	25	24	65
Pacific giant salamander	<i>Dicamptodon tenebrosus</i>	24	28	17	10
Riffle sculpin	<i>C. gulosus</i>	20	22	17	68
Red-legged frog ^a	<i>Rana aurora</i>	18	23	07	4
Speckled dace ^a	<i>Rhinichthys osculus</i>	17	22	07	36
Rough-skinned newt ^a	<i>Taricha granulosa</i>	17	20	07	11
Tailed frog ^b	<i>Ascaphus truei</i>	16	09	34	14
Redside shiner ^a	<i>Richardsonius balteatus</i>	12	16	03	36
Coastrange sculpin ^b	<i>C. aleuticus</i>	12	09	21	32
Prickly sculpin	<i>C. asper</i>	12	16	03	24
Threespine stickleback ^a	<i>Gasterosteus aculeatus</i>	09	12	03	13

compared with reference values, ranged from 13 to 94 (interquartile range = 43–66) in the whole region. Low values were more prevalent in streams draining sedimentary versus volcanic terrain (Figure 3A). Streams with low disturbance (high riparian condition, high watershed + riparian condition, and low catchment road densities) were found in both lithologies, but high anthropogenic disturbance was more common in sedimentary terrain (Figures 3B, C, D). Human activities on the gentler, more biologically productive sedimentary terrain began earlier, and have been more intensive and widespread than those on the steeper, less productive volcanic terrain.

Pattern of IBI Association with Individual Landscape, Disturbance, and Habitat Variables

Scaling the index of biotic integrity metrics by catchment area and using percentage metrics virtually eliminated correlations with catchment area, as well as stream slope, elevation and bed shear stress (Hughes et al. 2004). Consequently, we did not show IBI correlations with those vari-

ables in Table 4, but did make them available to MLR models. Considering the natural landscape control variables, IBI was negatively associated with catchment lithology regionally and within both catchment size strata, indicating a pattern of lower IBI values in streams draining sedimentary lithology. Lithology was represented by LITH, an indicator variable with values of 0 for volcanic and 1 for sedimentary rock. In this region, volcanic rock is more resistant to weathering than the softer sedimentary sandstones and siltstones (Pater et al. 1998). In addition, IBI was positively associated with low-flow areal discharge, LQsp, which gives a rough indication of groundwater contribution to low flow. LQsp tended to be higher in volcanic streams, and was also positively correlated with LRBS ($r = 0.42$, $p < 0.0001$) and negatively correlated with W1_HALL ($r = -0.40$, $p < 0.0001$), the measure of local riparian disturbances across the region (Table 2). (The negative correlation between LQsp and W1_HALL was strongest in small volcanic streams, with $r = -0.70$, $p = 0.002$).

In the whole region, IBI was positively correlated with WRCond and RCond, indicators of basin and riparian condition, and negatively related to Rd_DenKM and W1_HALL, indicators

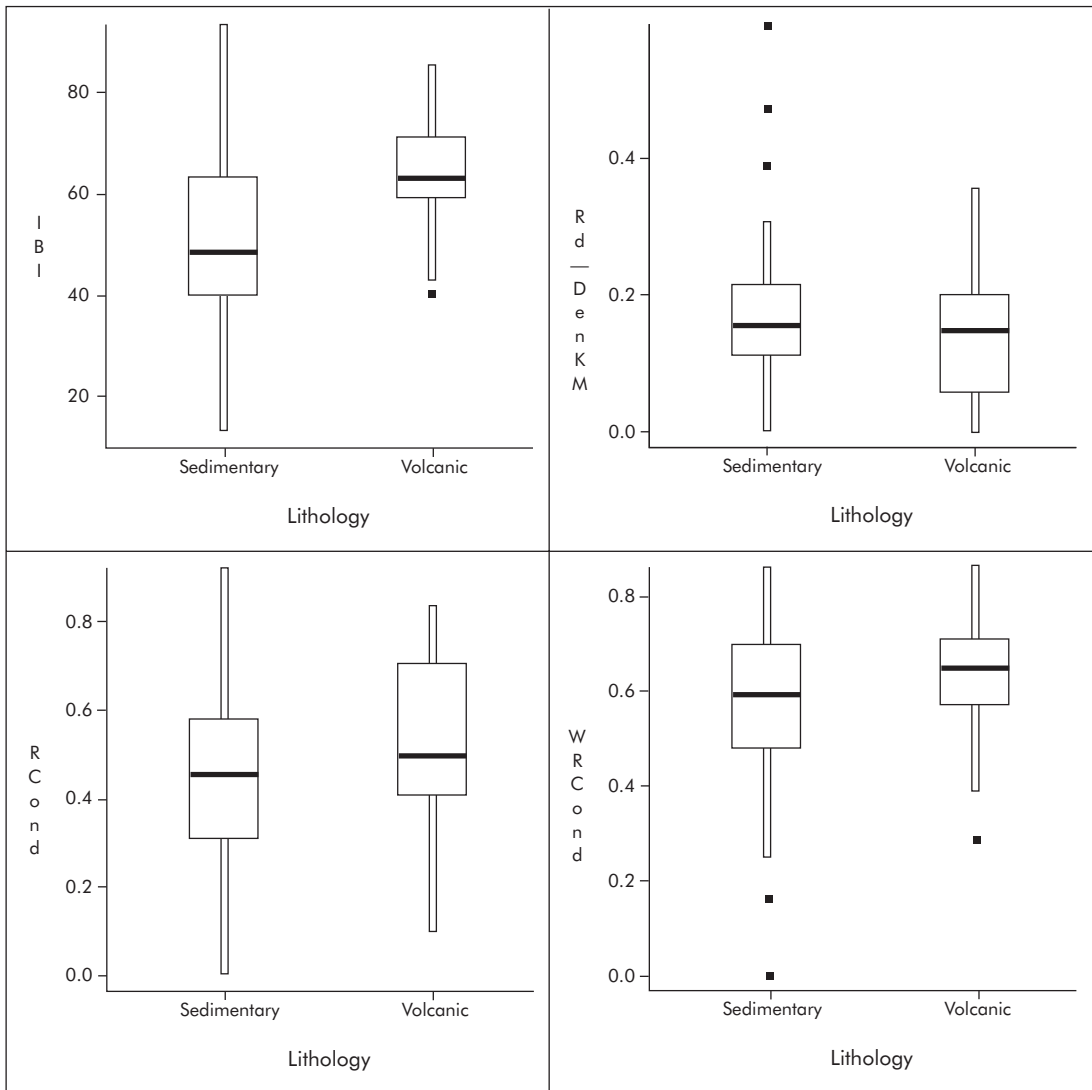


Figure 3. Ecological condition of Pacific Northwest Coast Range streams, and indicators of human disturbance versus watershed lithology: (a) index of biotic integrity of stream fish and amphibians (IBI), (b) catchment road density (Rd_DenKM), (c) riparian condition (RCond), and (d) watershed+riparian condition (WRCond). Boxes depict medians and quartiles; whiskers denote ranges; points are outliers deviating more than 2 SD from the mean.

of basin and riparian disturbance (Table 4). Correlations with these measures of human disturbance tended to be higher within the smaller streams and the volcanic lithology strata. However, the negative association between IBI and the product (interaction) of basin road density and riparian disturbances reveals IBI declined with human disturbance in each lithology, but

generally IBI was lower and more variable in sedimentary streams (Figure 4).

In the region overall, the strongest associations between IBI and in-channel physical-chemical habitat were with measures of streambed particle size (Table 4), represented by the percentage of silt (%FN) and the index of median particle size deviation from reference

Table 4. Spearman rank-order correlations (*r*) of fish/amphibian stream IBI with potential controlling variables in Coast Range streams (bold denotes *r*-values ≥ 0.40 ; asterisk denotes Bonferroni-corrected $p < 0.05$). Drainage area strata were small = $0.09\text{--} < 15 \text{ km}^2$ and large = $15\text{--}160 \text{ km}^2$.

Variables	Whole region (<i>n</i> = 98)	Drainage area		Lithology		Sedimentary		Volcanic	
		Large (<i>n</i> = 48)	Small (<i>n</i> = 50)	Sedi. (<i>n</i> = 69)	Volc. (<i>n</i> = 29)	Large (<i>n</i> = 35)	Small (<i>n</i> = 34)	Large (<i>n</i> = 13)	Small (<i>n</i> = 16)
%FN	−0.67*	−0.56*	−0.73*	−0.55*	−0.40	−0.47	−0.58*	−0.09	−0.53
%BDRK	0.28	0.12	0.46*	0.40*	−0.44	0.24	0.55*	−0.52	−0.40
LRBS	0.58*	0.48*	0.71*	0.53*	0.11	0.43	0.62*	−0.13	0.21
EX_FN	−0.28	−0.08	−0.43*	−0.39*	−0.30	−0.27	−0.44	−0.29	−0.43
RPGT75	0.16	0.26	0.08	0.18	−0.05	0.33	−0.04	−0.34	0.18
LVTW_msq	−0.12	0.06	−0.25	−0.14	−0.08	0.04	−0.24	0.45	−0.43
XFC_UCB	−0.42*	−0.48*	−0.37	−0.37*	−0.08	−0.52*	−0.22	0.15	−0.21
XFC_BRS	−0.40*	−0.36	−0.41	−0.33	−0.19	−0.41	−0.23	0.32	−0.55
LNTL	−0.34*	−0.41	−0.32	−0.21	−0.26	−0.47	0.00	0.07	−0.58
LP TL	−0.47*	−0.43*	−0.50*	−0.32	−0.13	−0.35	−0.29	0.44	−0.40
TEMPSTRM	−0.30*	−0.39	−0.24	−0.15	−0.33	−0.36	0.04	0.02	−0.44
CONDUCT	−0.04	−0.08	−0.03	−0.18	0.45	−0.22	−0.16	0.53	0.42
RCond	0.31*	0.33	0.29	0.30	0.12	0.38	0.19	0.39	−0.02
W1_Hall	−0.39*	−0.35	−0.43	−0.28	−0.41	−0.32	−0.28	−0.06	−0.63
XCMGW	0.15	0.27	0.07	0.22	−0.08	0.40	0.06	0.35	−0.36
Rd_DenKM	−0.35*	0.02	−0.54*	−0.25	−0.72*	0.15	−0.51*	−0.73*	−0.70*
WRCond	0.34*	0.30	0.35	0.29	0.32	0.32	0.24	0.55	0.15
LQsp	0.47*	0.35	0.56*	0.41*	0.19	0.29	0.51	−0.21	0.37
Elev	0.32	0.38	0.31	0.18	0.19	0.31	0.11	0.10	0.07
LITH	−0.42*	−0.42*	−0.42*	na	na	na	na	na	na

conditions (LRBS). These correlations were stronger in small streams than in large ones, and stronger in sedimentary than in volcanic lithology. Correlation of IBI with LRBS was low in the volcanic strata, where bedrock and excess silt were both negatively correlated with IBI (explaining in part the lack of association with LRBS, which increases with %BDRK and decreases with EX_FN). In contrast, IBI showed strong positive correlation with %BDRK and strong negative correlation with EX_FN, and therefore strong positive correlation with LRBS, in small sedimentary streams.

IBI was negatively associated with stream-water phosphorus and nitrogen concentrations, undercut banks, and brush cover in the whole region. This pattern was true of all strata except large volcanic streams, where correlations with these variables were weaker or reversed. Total phosphorus was uncorrelated with catchment area or road density, but was negatively correlated (Spearman $r = -0.43$, $p < 0.0001$) with local

riparian condition (RCond). These phosphorus correlations were consistent with dominant anthropogenic sources, or anthropogenic mobilization of natural sources. IBI also showed a weak to moderate negative correlation with water temperature in the entire region and all strata, with the strongest correlation in small volcanic streams ($r = -0.44$, $p > 0.05$).

Regression Modeling of IBI
from Landscape, Disturbance,
and Habitat Variables

Whole region.—The best MLR model predicting IBI from in-channel physical-chemical habitat variables and landscape controls was dominated by a strong positive association with relative bed stability (LRBS), our inverse indicator of anthropogenic sedimentation (Table 5A). It included a moderately strong positive association with areal discharge, and moderate amounts of variance explained by elevation (positive term)

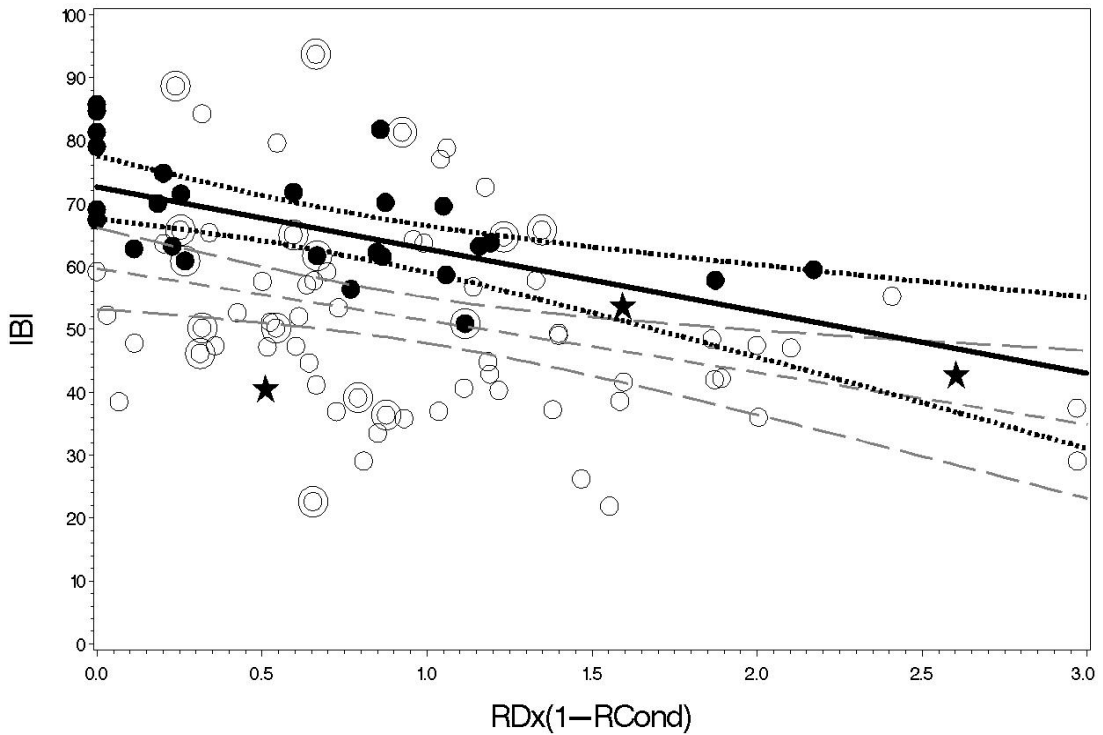


Figure 4. Stream reach IBI versus the interaction between watershed and riparian disturbance, represented by $RDx(1-RCond)$. Open circles denote sedimentary catchments; black dots and stars are volcanic catchments. Circled black dots and double circles denote reaches with bed surface greater than 25% bedrock, and black stars are volcanic reaches with more than 5% excess silt (EX_FN). The regression line and its 95% confidence limits about the mean are shown separately for volcanic reaches: ($IBI = 72.6 - 9.84 \text{ RDx}(1-RCond)$), with $R^2 = 0.37$, $RMSE = 9.0$, and $p < 0.0005$ and sedimentary reaches: ($IBI = 59.7 - 8.27 \text{ RDx}(1-RCond)$), with $R^2 = 0.12$, $RMSE = 14.9$, and $p < 0.0039$.

and the areal percent of undercut banks (negative). When basin and riparian human disturbance variables were substituted for physical-chemical habitat variables, the model R^2 declined slightly, but the terms were similar—the LRBS term in the first model was replaced by the interaction of basin and riparian disturbances and the indicator variable for lithology (Table 5B). When all three types of variables were available as potential predictors, the resultant best model was the same as the first model, but included a negative term for the interaction between basin and riparian disturbance (Table 5C).

All three whole-region models explained about half the regional variance in IBI. Not surprisingly, the RMSE's of these models (11.6–12.5

IBI units) did not suggest that they were overfit, as they were considerably larger than the RMSE of repeat sampling (7.0) reported by Hughes et al. (2004). We suspected that other undefined variables may have accounted for patterned variation across the region, or that disturbance processes were not homogeneous in various classes of streams in the region. Therefore, we subsequently modeled small and large sedimentary streams and volcanic streams as separate strata to describe possibly different patterns of association of IBI with explanatory variables. The small sample size of the volcanic lithology stratum (29) precluded substratification by basin size; as regression models with more than one or two predictor variables would not be advisable for

Table 5. Results of multiple linear regression predicting IBI in all Coast Range Wadeable streams.

Variable	Estimate	Std. error	Indep. R^2	Partial R^2	Model R^2	Prob > F
a) IBI = f (in-channel physical-chemical habitat and landscape controls):						
Intercept	+74.7	5.25	—	—	—	<0.0001
LRBS	+5.72	1.28	0.335	0.335	0.335	<0.0001
LQsp	+6.13	2.08	0.246	0.098	0.433	0.0043
Elev	+0.025	0.009	0.106	0.040	0.474	0.0185
X_UCB	-58.0	29.48	0.159	0.024	0.498	0.0527
Summary of fit: total df = 85 RMSE = 12.2 Prob > F < 0.0001						
b) IBI = f (basin-riparian anthropogenic influences and landscape controls):						
Intercept	+80.22	5.52	—	—	—	<0.0001
RDx(1-RCond)	-8.60	2.04	0.201	0.201	0.201	<0.0001
LQsp	+6.78	2.13	0.198	0.133	0.334	0.0020
Elev	+0.0235	0.0103	0.097	0.071	0.404	0.0243
LITH	-5.67	3.41	0.172	0.019	0.423	0.1004
Summary of fit: total df = 88 RMSE = 12.5 Prob > F < 0.0001						
c) IBI = f (physical-chemical habitat, landscape controls, basin-riparian anthropogenic influences):						
Intercept	+76.45	5.16	—	—	—	<0.0001
LRBS	+3.92	1.35	0.296	0.296	0.296	0.0047
LQsp	+5.22	2.04	0.209	0.095	0.391	0.0124
RDx(1-RCond)	-6.30	2.03	0.205	0.054	0.444	0.0026
Elev	+0.026	0.009	0.094	0.046	0.491	0.0046
X_UCB	-62.81	28.37	0.170	0.030	0.521	0.0297
Summary of fit: total df = 84 RMSE = 11.6 Prob > F < 0.0001						

the resultant substrata, each containing about half of the sample sites.

Streams draining small catchments with sedimentary lithology.—When we considered in-channel physical-chemical habitat and natural landscape variables (no human disturbance variables) as potential predictors, LRBS dominated the model (partial $R^2 = 0.52$) and, combined with %BDRK, these two variables alone explained almost 60% of the variance in IBI (Table 6A). When basin and riparian human disturbance variables were substituted for physical-chemical habitat variables, the model R^2 declined greatly (0.27), and only the negative basin-riparian interaction term RDx(1-RCond) was significant (Table 6B). When we included all three types of variables as potential predictors, MLR yielded a strong three variable model ($R^2 = 0.74$) in which the interaction of road density and riparian condition replaced LRBS, and a strong positive term

remained for %BDRK (Table 6C). As did the first model (Table 6A), this model also included a positive term for areal discharge. The model RMSEs (10.2–16.4) were well above 7.0, so did not suggest overfitting.

Streams draining large catchments with sedimentary lithology.—As observed for small streams in sedimentary lithology, a positive association with LRBS was the major term in the best model built from in-channel physical-chemical habitat and natural landscape variables alone (Table 7A). Additional moderate negative association with water temperature, moderate positive association with the frequency of deep residual pools, and weak association with elevation yielded a final model explaining 61% of the regional variance of IBI in large streams draining sedimentary lithology. When basin and riparian human disturbance variables were substituted for physical-chemical habitat variables (Table

Table 6. Results of multiple linear regression predicting IBI in Coast Range wadeable streams with sedimentary lithology and drainage areas less than 15 km².

Variable	Estimate	Std. error	Indep. R^2	Partial R^2	Model R^2	Prob > F
a) IBI = f (in-channel physical-chemical habitat and landscape controls):						
Intercept	+78.77	9.72	—	—	—	<0.0001
LRBS	+6.60	3.25	0.518	0.518	0.518	0.0542
%BDRK	+0.96	0.37	0.415	0.064	0.582	0.0168
LQsp	+8.06	3.69	0.187	0.072	0.654	0.0393
Summary of fit: total df = 26 RMSE = 12.4 Prob > F < 0.0001						
b) IBI = f (basin-riparian anthropogenic influences and landscape controls):						
Intercept	+62.65	5.10	—	—	—	<0.0001
RDx(1-RCond)	-11.4	3.87	0.268	0.268	0.268	0.0068
Summary of fit: total df = 25 RMSE = 16.4 Prob > F = 0.0068						
c) IBI = f (physical-chemical habitat, landscape controls, basin-riparian anthropogenic influences):						
Intercept	+78.74	8.60	—	—	—	<0.0001
%BDRK	+1.65	0.24	0.429	0.429	0.429	<0.0001
RDxRCond	-11.83	2.94	0.064	0.182	0.611	0.0006
LQsp*	+9.98	3.03	0.106	0.129	0.740	0.0033
Summary of fit: total df = 25 RMSE = 10.2 Prob > F < 0.0001						

*LQsp replaced LRBS in Stepwise MLR (LRBS was first entry with Partial R^2 = 0.45 and P = 0.0002).

7B), the R^2 of the best model was considerably reduced (0.40). About half of the explained variance was attributed to the interaction of catchment disturbance and riparian condition (positive term), and the other half to the combination of areal discharge and elevation (both positive terms). When all three types of variables were available as potential predictors, the resultant best model was identical to that without the human disturbance variables, suggesting that the first model was not missing habitat variables correlated with human disturbances (compare Tables 7C and 7A). The model RMSE of 9.4 IBI units for the most complex model in this stratum was greater than the RMSE of sampling variability (7.0), giving no suggestion of overfitting.

Streams draining catchments with volcanic lithology.—When we considered only in-channel physical-chemical habitat and natural landscape variables as potential predictors, volcanic streams differed from the sedimentary streams in having excess silt (EX_FN), rather than LRBS, as the first predictor variable. Additional moderate as-

sociations with conductivity and areal discharge (both positive), and percent bedrock (negative) produced a best model explaining 60% of the variance in IBI across streams draining volcanic lithology in the region (Table 8A). When basin and riparian human disturbance variables were substituted for physical-chemical habitat variables, the best model was dominated by a strong negative association with catchment road density, with a minor positive term for areal discharge (Table 8B). When all three types of variables were available as potential predictors, the resultant best model was identical to the first model but with an additional strong negative association with catchment road density (compare Tables 8A and 8C). Road density explained 47% of the IBI variance, reducing the partial R^2 values of all the other predictor variables from the levels they had contributed to explaining IBI variation in the absence of road density. The RMSE values of the two more complex models were 6.3 and 5.8 IBI units (Tables 8A and 8C). Even though the tests for inclusion of all predictor variables (P -values

= 0.0001–0.0420) and the final models themselves ($p < 0.0001$) were highly significant, the model RMSE values were lower than the RMSE of repeat measurement variance (7.0), and the ratio of parameters to sample size was 5–7, suggesting marginal overfitting. We therefore suggest interpreting the minor contributors to these models in the volcanic stratum with caution.

IBI, Bed Stability, and Disturbance Relationships

In contrast to the plot of IBI versus human disturbance (Figure 4), a plot of IBI versus LRBS (Figure 5) shows no clear distinction in the response to disturbance between lithologies, ex-

cept that both IBI and LRBS were higher in volcanic streams. The contrasting relationship of IBI to %BDRK is also illustrated in Figure 5, where all volcanic sites with more than 25% bedrock or EX_FN greater than 5% have lower than expected IBI values, given their LRBS. However, the relationship of LRBS to the product (interaction) of basin road density and riparian disturbances (Figure 6) reveals LRBS declined with human disturbance in each lithology, with lower values for sedimentary streams, just as was observed for IBI in Figure 4. Most of the least disturbed streams (by this measure) had LRBS ± 0.5 , and LRBS generally declined more steeply in sedimentary streams (more erodible lithology) than in volcanic streams (more resistant to erosion

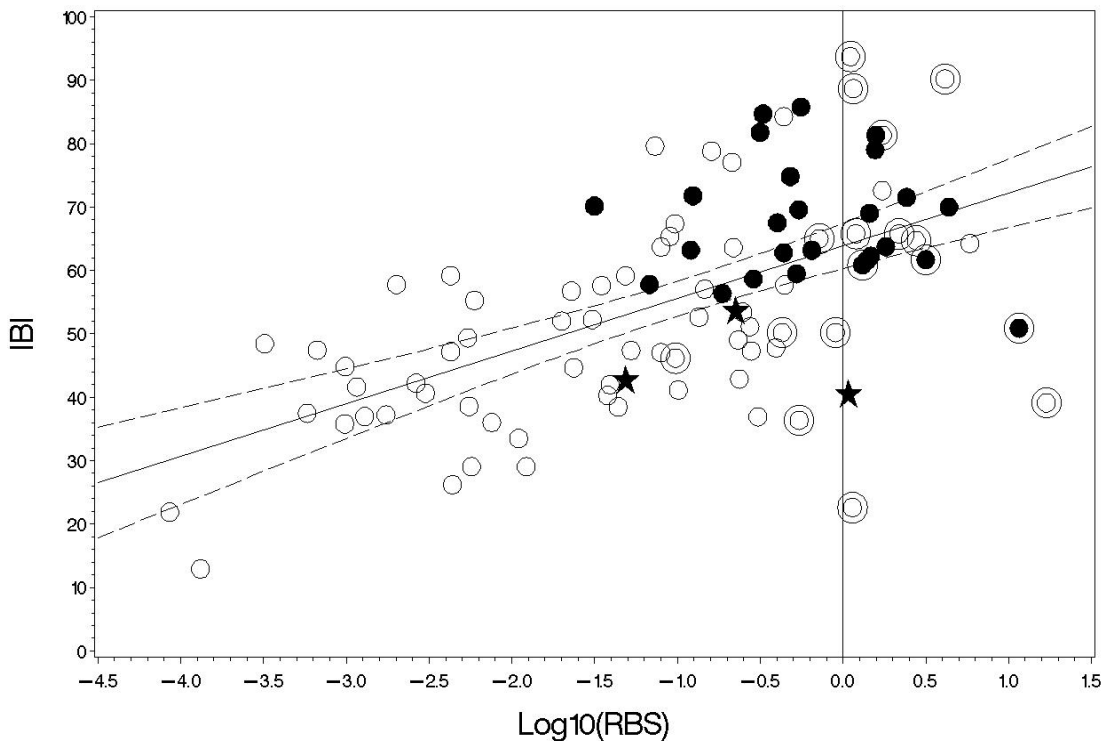


Figure 5. Stream reach IBI versus \log_{10} of relative bed stability at bank-full flows (RBS). Open circles denote sedimentary catchments; black dots and stars are volcanic catchments. Circled black dots and double circles denote reaches with bed surface greater than 25% bedrock and black stars are volcanic reaches with more than 5% excess silt (EX_FN). The vertical line originating at 0.0 is the value of RBS indicating $D_{gm} = D_{cbf}$. Regression lines and their 95% confidence limits about the mean were calculated for all sample reaches ($IBI = 63.85 + 8.28 \times \text{LogRBS}$), with $R^2 = 0.35$, $RMSE = 13.6$, and $p < 0.0001$. The regression without circled and starred points is $IBI = 67.39 + 9.95 \times \text{LogRBS}$, with $R^2 = 0.49$, $RMSE = 11.5$, and $p < 0.0001$.

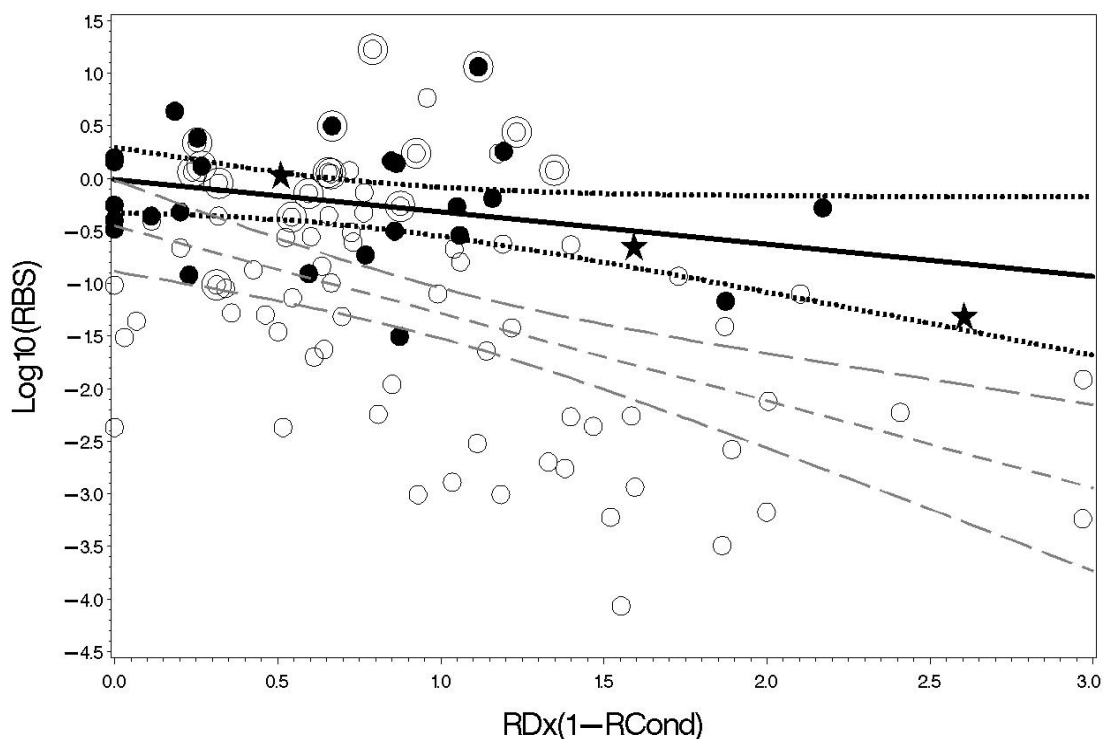


Figure 6. Log_{10} of stream reach relative bed stability (RBS) versus the interaction between watershed and riparian disturbances, represented by $\text{RDx}(1-\text{RCond})$. Open circles denote sedimentary catchments; black dots and stars are volcanic catchments. Circled black dots and double circles denote reaches with bed surface greater than 25% bedrock, and black stars are volcanic reaches with more than 5% excess silt (EX_FN). The regression line and its 95% confidence limits about the mean are shown separately for volcanic reaches ($\text{LRBS} = 0.015 - 0.305 \text{ RDx}(1-\text{RCond})$, with $R^2 = 0.13$, $\text{RMSE} = 0.57$, and $p < 0.0586$) and sedimentary reaches ($\text{LRBS} = -0.451 - 0.831 \text{ RDx}(1-\text{RCond})$, with $R^2 = 0.22$, $\text{RMSE} = 1.03$, and $p < 0.0001$).

and weathering). Streams with more than 25% bedrock were associated with moderate levels of basin-riparian disturbance. LRBS, in the formulation by Kaufmann et al. (1999), increases with bedrock exposure. Therefore, variation in the response of IBI to LRBS increases when bedrock is present, because the apparent response of IBI to bedrock can be positive or negative according to the geomorphic setting of a stream.

LQsp, the log transformed ratio of summer low flow discharge divided by drainage area, appeared as a moderate to minor predictor of IBI in many of the models in various strata, always as a positive term, and frequently along with positive elevation, negative temperature, or positive stream water electrical conductivity terms.

LQsp was not related to the date of sampling during the summer low flow period ($r = 0.09$, $p = 0.39$). We cautiously interpret it to be a measure of the groundwater contribution to base flow. However, its expected regional association with lower water temperatures ($r = -0.41$, $p < 0.0001$) was not evident within each lithology stratum, nor was it correlated with conductivity ($r = -0.11$, $p = 0.32$). It was generally higher in volcanic than in sedimentary lithology (Table 2) because of its fractured nature and greater permeability (Hicks 1989). Even though rainfall and runoff are probably higher in volcanic drainages because they tend to include higher elevations, LQsp was not correlated with elevation overall ($r = 0.014$, $p = 0.18$) or within separate lithologies. Interestingly,

LQsp was negatively correlated with riparian disturbances ($r = -0.40$, $p < 0.0001$), particularly in volcanic lithology ($r = -0.60$, $p = 0.0006$). This association might be explained by anthropogenic augmentation of winter runoff. Higher runoff per unit precipitation would reduce groundwater recharge, and therefore reduce summer base flow, when precipitation is sparse. This possible anthropogenic connection is highly conjectural at this time, but merits further investigation.

The final general pattern evident in the MLR models was the contrasting role of bedrock between the two lithologies. Bedrock influenced IBI positively in streams draining sedimentary lithology but negatively in volcanic streams. In sedimentary streams, bedrock was commonly observed as a major component together with high percentages of sand and silt in low gradient streams where boulders, cobbles, and coarse gravel were relatively uncommon. This pattern is consistent with relatively rapid weathering of sandstone and siltstone to loose sand and silt. In many fine bedded streams, bedrock may be a positive influence on structural complexity, as it can form deep pools, particularly where large woody debris is sparse or too small to be stable or hydraulically influential (Kaufmann 1987). In volcanic streams, large proportions of bedrock were found in the steepest and coarsest-bedded streams, and its presence may be an indicator of past catastrophic scouring by debris torrents (Swanson and Dyrness 1975; Kaufmann 1987), naturally occurring phenomena with spatial and temporal frequency augmented by human activities.

DISCUSSION

Few studies in the Pacific Northwest have been designed to address specific relationships between changes in habitat attributes and structure of fish assemblages (Bisson et al. 1992; Spence et al. 1996); even fewer (e.g., Herger et al. 2003; Hughes et al. 2004) have addressed such questions on a regional scale. Although not spe-

cifically designed to investigate the influence of habitat on aquatic vertebrate assemblages, the statistical survey data we analyzed allowed a regionally representative description of these assemblages in the population of 23,700 km of wadeable first- through third-order Coast Range streams. Further, because of the ancillary physical, chemical, and landscape data collected at the same locations, we were able to examine the strength and character of associations between biotic assemblages and potential causes and influences. Though such data do not demonstrate cause, they provide weight-of-evidence concerning the dominance of processes and influences in the region.

Although the strongest single predictors of IBI were raw measures of percent fine streambed particles, we did not include these in the variables available to MLR because a substantial proportion of their regional variance was associated with channel slope and stream size. The strongest predictor variables in MLR models built from in channel physical-chemical data and natural landscape controls for the whole region and all substrata were indicators of anthropogenic sedimentation, calculated by scaling substrate size by bed shear stress (which incorporates slope and stream size). In the whole region and in both stream size classes draining sedimentary lithology, the scaled substrate size measure was LRBS (which we interpret here as an inverse indicator of anthropogenic sedimentation). In volcanic lithology, LRBS was not a good predictor of IBI. Instead, the scaled substrate size measure EX_FN was the best in-channel predictor, with percent bedrock as an additional negative term. Because bedrock and silt influence LRBS in opposite directions, the utility of LRBS as a predictor of IBI was "neutralized" in volcanic streams. These results also suggest that, in the naturally coarser-bedded volcanic streams, general fining of streambeds was less deleterious than accumulation of small amounts of silt that do not substantially affect the mean substrate diameter (as we usually measure it). Weathering of basalt in this region generally proceeds from boulders to

gravel, then to silt, without generating much sand. This pattern is in contrast to the weathering of sandstones, which degrade quickly from bedrock and boulders to abundant silt, sand and fine gravel with less in the gravel and cobble size fraction.

When human disturbances and natural landscape controls were presented to MLR, road density alone, riparian condition (RCond), or the interaction of road density with riparian disturbance, $\{RD \times (1 - RCond)\}$ were the major predictors of IBI in the whole region or in any single stratum. When in-channel variables were presented at the same time as human disturbances and landscape controls, road density or its riparian interactions either replaced or were replaced by an indicator of anthropogenic sedimentation (LRBS as inverse indicator in sedimentary lithology and EX_FN in volcanics). This pattern was due to the covariance among IBI, sedimentation indices, and human disturbances.

Reporting on results of the same survey data we examined in this chapter, Herger et al. (2003) found weak correlations between aquatic vertebrate composition and human disturbances at the landscape and local scales, reporting that assemblages were primarily structured by natural physical and biogeographical gradients. They suggested scaling assemblage metrics and combining them further into an IBI to more clearly reveal the impacts of human activities on streams in the region. Hughes et al. (2004) developed an IBI for the Coast Range ecoregion that confirmed those expectations. For the region as a whole, they found that the IBI, which includes a set of eight aquatic vertebrate assemblage characteristics, was negatively related to riparian disturbances and basin road density. Within the channel, they found a relatively strong positive association of IBI with LRBS, an inverse measure of excess fine sediments that we found to be negatively associated with the anthropogenic disturbances (Figure 6). Hughes et al. (2004) reported that the IBI was significantly (negatively) correlated with a number of different estimates of anthropogenic disturbance, with IBI scores

significantly higher in minimally disturbed reference sites than in randomly-selected sites. Increases in the percentages of coolwater fish and amphibian species, nonnative species, and tolerant individuals were also associated with human disturbances. Conversely, declines in the proportions of coldwater fish and amphibian species, the number of size- (age-) classes, and the species richness and numeric abundance of native coldwater species were also associated with human disturbance.

Hughes et al. (2004) did not examine the relationships of their IBI to possible controls within the different stream sizes or lithologies that we address in this chapter. However, our results for the region as a whole, examining habitat and landscape associations with the same IBI, are very similar to their reported positive correlations of IBI with local reach-scale bed stability, instream cover, and the cover and structural complexity of riparian vegetation. We also agree with their findings that IBI was negatively correlated with local reach-scale fine sediment and riparian human disturbances, and with catchment road density. Their findings and ours are consistent with those of Reeves et al. (1993), who showed reduced diversity in juvenile anadromous salmonid assemblages in selected Oregon Coast Range basins with high levels of timber harvest and road construction.

Some studies in the Pacific Northwest have shown higher salmonid and salamander density and biomass in streams subject to clear-cutting than in old-growth reaches and attributed these differences to higher primary productivity (Murphy et al. 1981; Hawkins et al. 1983). Although these studies also reported increases in macroinvertebrate diversity, they did not report findings on age structure or diversity of the entire aquatic vertebrate assemblage. Other studies (Bisson and Sedell 1984; Bisson et al. 1992) report similar increases in salmonid biomass and abundance with logging disturbances, but also reported that streams subjected to logging and channel cleaning lacked age-class diversity, consistent with our results and those of Reeves et al. (1993).

Our analysis of factors controlling IBI scores extended beyond that of Hughes et al. (2004) by strengthening the weight-of-evidence supporting anthropogenic effects (particularly from sediment) and by examining differences in potential controls as a function of stream basin size and lithology. Streambed particle size and channel morphology are influenced strongly by catchment geology (Hack 1973). Volcanic rock (generally basalt), relatively hard and resistant to weathering, underlies the steeper terrain of this region (Pater et al. 1998). Though the underlying rock is resistant to erosion, and delivery of sediment to streams by surface erosion is minor, this steep terrain is subject to infrequent, but catastrophic mass-failures (shallow, rapid landslides) that can deliver large amounts of sediment and wood to streams (Swanson and Dyrness 1975; Dietrich and Dunne 1978). These events sometimes trigger debris torrents that can scour parts of the stream network to bedrock, while depositing large amounts of debris downstream. By contrast, much of the less steep terrain in the region is underlain with softer, more erodible sedimentary rock, which generates more fine sediment (sand, silt, clay), than does volcanic rock. The modes of delivery are similar in sedimentary catchments (Benda et al. 1998, 2003), though slower-moving, deep-seated earth flows and rotational failures sustain large inputs of fine sediments over longer periods of time (Swanston 1991). The stream margins and valley bottoms in sedimentary terrain are large sediment reservoirs held intact by the roots of streamside vegetation. As a result, and in contrast with streams in volcanic terrain in this region, activities that damage riparian vegetation in sedimentary basins result in larger chronic inputs of fine sediment.

Kaufmann and Larsen (unpublished) reported that streams draining soft sedimentary lithology showed greater apparent sedimentation response to disturbance than did those draining basins underlain by hard basalt (volcanic). Furthermore, they showed that RBS was likely to be lower in smaller and lower gradient streams than in larger or higher gradient streams subject to

apparently equal levels of anthropogenic stress. Kaufmann and Larsen (unpublished) reported stronger negative correlations between land disturbance and the numerator (substrate mean diameter) of the RBS ratio than with its denominator (critical diameter). They argued that this pattern strongly suggested that land use has augmented sediment supplies and increased streambed fine sediments in Coast Range wadeable streams.

Generally, we found higher IBI scores in volcanic than in sedimentary terrain, but this resulted from greater landscape disturbance and greater sedimentation response to that disturbance in streams draining sedimentary lithology. We observed high IBI values in minimally disturbed streams in both lithologies, making it unlikely that there is an inherent difference in biotic integrity as measured by the highest IBI scores. The generally lower IBI values in streams of sedimentary lithology likely resulted because there are more disturbed basins and streams in the more productive sedimentary lithology. We found that IBI in streams draining steep catchments of volcanic lithology were more negatively associated with catchment disturbances than with riparian disturbances (Table 4). However, the negative association of IBI with riparian disturbance (W1_Hall) in volcanic catchments was stronger in smaller streams than in larger ones (Table 4). In sedimentary basins, by contrast, the negative association of IBI was stronger with catchment disturbance in small streams than large streams, but its negative association with riparian disturbance was stronger in large streams.

Kaufmann and Larsen (unpublished) and Scott (2002) reported, respectively, higher correlation of RBS and percent substrate less than 2 mm with riparian disturbance in streams of sedimentary lithology, but higher correlation with catchment disturbances (road density) in streams of volcanic lithology. These are the same patterns that we observed between IBI and disturbance in the two lithologies. The authors attributed this pattern to the likelihood that

sediment supply entering streams by mass failures in the typically steep, constrained, V-shaped valleys of volcanic watersheds would show greater response to road disturbances in steep areas remote from the channel. Their findings are supported by Reid et al. (1981) and Furniss et al. (1991), who concluded that mass-wasting from forest roads was the largest contributor of sediment to streams in forest lands of this region. In milder sloping sedimentary terrain where valleys are wider and streams are less constrained, Scott (2002) and Kaufmann and Larsen (unpublished) expected that most sediment supplies originated from banks and riparian zones. Delivery processes in these streams might be more similar to those in a lowland Wisconsin drainage described by Trimble (1999), where riparian vegetation removal and disturbances increased sediment delivery from channel movement, bank cutting, and incision. Our finding that IBI was negatively associated with excess silt or positively associated with relative bed stability in these lithologies may explain why IBI associations with basin and riparian disturbances also differ depending on catchment lithology.

Beyond the major negative association of IBI with disturbance-related sedimentation that was present in both lithologies and generally across the range of stream sizes, we found differing habitat-biota associations in the two lithologies. In small sedimentary streams, bedrock provides stable substrate in streambeds dominated by silt and sand, and may also form pools. The negative association between IBI and the percent of the stream bed composed of bedrock in volcanic streams may reflect a response to the overabundance of stable substrate in channels severely scoured due to natural or anthropogenic debris torrents (Swanson and Dyrness 1975; Kaufmann 1987). However, Kaufmann (1987) and Reeves et al. (1993) reported that bedrock exposure was also typical of streams draining volcanic basins with old growth forest. In both cases, these conditions indicate a low sediment supply rate relative to transport capacity, or a

stream adjustment to prolonged increases in stream power sufficient to mobilize finer substrates (i.e., past bed instability, or low past RBS). Kaufmann and Larsen (unpublished) reported that low RBS in Coast Range volcanic streams was associated both with an increase in fine sediments, as well as an increase in streambed shear stress, and that both are associated with catchment roads and riparian disturbances. Elevated shear stress (from hydrologic alteration or channel simplification) without an increase in sediment supply is likely to lead, eventually, to bedrock exposure. Other in-channel factors associated with IBI in volcanic streams (higher conductivity, lower temperature, shading, abundant instream large wood) are consistent with channel conditions that foster high salmonid densities in the region (Spence et al. 1996). The lack of a strong relationship of IBI with pool depth in volcanic streams is perplexing. FEMAT (1993), for example, cited studies that documented substantial decreases in the number of large deep pools in river systems west of the Cascade Mountains. However, these decreases could be attributed to the loss of large wood and boulders as pool-forming structures (Lisle 1982), filling of pools with sediment (Lisle and Hilton 1992), and loss of sinuosity in stream channels, all of which are consistent with augmented sediment supplies and lowering of RBS, which is a strong predictor of IBI.

Index of biotic integrity was negatively associated with indicators of anthropogenic disturbance (roads and degraded riparian vegetation), their effects on sediment supply (excess fine sediments, bed and bank instability, turbidity), and other effects related to these factors (lack of deep residual pools, higher temperatures, higher nutrients, bedrock exposure). These findings agree with the scientific understanding concerning salmonid habitat requirements and limiting factors, as well as their relationship to human disturbances in streams that are the focus of coho salmon research and management in the region (Reiser and Bjornn 1979; Spence et al. 1996)

Key Findings

We demonstrated four key aspects about Coast Range streams. First, scaling abundance and richness IBI metrics by stream size aided interpretation of human effects by removing systematic natural variability (Hughes et al. 2004). Second, scaling substrate size by bank-full shear stress, as employed by Kaufmann et al. (1999) and USEPA (2000) to assess anthropogenic stream-bed fining, removed natural variability in substrate data and facilitated our detecting the effects of anthropogenic sedimentation on aquatic vertebrates. Third, lower IBI values, reflecting low richness and abundance of salmonids, tailed frogs and other coldwater and sediment-intolerant taxa, were associated with higher catchment road density and riparian disturbances, and in turn with lower RBS, higher excess fine sediment, reduced frequency of deep residual pools, higher water temperature and dissolved nutrient concentrations, and reductions in cover complexity. Fourth, anthropogenic effects were more pronounced in streams draining erodible sedimentary bedrock than in those draining more resistant volcanic terrain. We advise ecologists seeking to understand the effects of anthropogenic disturbance on stream systems to first evaluate the influences of natural gradients or differences in stream size, stream power, geology, and other natural drivers on their candidate disturbance indicators. The indicators can then be calibrated to remove consistent natural variation, improve predictions, and reduce the data scatter common in ecological dose–response relationships.

Management Implications

Natural disturbances are a major influence on habitat and biota in Coast Range streams (Reeves et al. 1995). Episodic landslides, fire, and other natural disturbances contribute a wide range of sediment sizes to stream channels. When large wood is delivered along with sediment, it stabilizes stream bed gravels and fine sediments, aid-

ing the development of spatially and hydraulically complex habitat for stream biota. In this region, human activities have augmented natural rates of sediment supply to streams. Conversely, human influences have reduced the present and potential future supplies of large wood to these streams. Consequently, streams currently exhibit highly mobile beds with excess fine sediments and simplified morphology. This trend is likely to lead to more bedrock channels where slopes are high and increased fine sediments in lower gradient channels downstream. The beneficial effects of natural disturbances will lessen over time if rates of sediment and large wood transport (or decay) exceed their rates of replacement from upland and riparian areas within stream catchments.

If attaining or approaching the biotic integrity of fish and amphibian assemblages in wadeable streams throughout the Coast Range ecoregion are desired outcomes, our findings suggest the following habitat management and restoration goals. First, reduce watershed activities that exacerbate erosion and mass-wasting (e.g., landslides and other hillslope failures). Second, protect and rehabilitate riparian zone vegetation, fostering the development of multilayered structure and large, old trees. Third, manage landscapes so that large wood is delivered along with coarse and fine sediments in both natural and anthropogenic mass-wasting events. These three measures would likely increase relative bed stability and decrease excess fines by decreasing sediment inputs and increasing energy-dissipating roughness from in-channel large wood and deep residual pools. Reducing sediment supply and transport to sustainable rates should also ensure adequate future supplies of sediment. In addition, these measures would provide more shade, bankside cover, pool volume, colder water, and more complex habitat structure.

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A Spatially Explicit Approach for Evaluating Relationships among Coastal Cutthroat Trout, Habitat, and Disturbance in Small Oregon Streams

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Abstract.—Small stream systems are complex networks that form a physicochemical template governing the persistence of aquatic species such as coastal cutthroat trout *Oncorhynchus clarkii clarkii*. To gain new insight into these interactions, we initiated an integrated program of landscape-scale sampling that is focused on fine- and broad-scale relationships among upslope landscape characteristics, physical stream habitat, and the spatial patterns of cutthroat trout abundance. Our sample of 40 catchments (500–1,000 ha) represented approximately 15% of the 269 barrier-isolated catchments in western Oregon that support populations of cutthroat trout. Because data were collected in a spatially contiguous manner throughout each catchment, it was possible to collect biological and geographic information necessary to assess the spatial structure of cutthroat trout abundance. Results underscore the influence of the physical habitat template at a variety of spatial scales. For example, cutthroat trout move throughout the accessible portions of small streams. Some cutthroat trout congregate in areas of suitable habitat and form local populations that may exhibit unique genetic attributes. At times, some cutthroat trout move into larger downstream portions of the network where they may contribute to the genetic character of anadromous or local potamodromous assemblages. Results underscore the advantages of viewing habitats that are critical to the fitness and persistence of cutthroat trout populations as matrices of physical sites that are linked by movement. It is apparent that human activities that impede movement among suitable habitat patches can have unanticipated consequences for metapopulations of cutthroat trout and may ultimately affect their persistence.

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INTRODUCTION

Two basic questions in aquatic ecology relate to how aquatic systems are organized in space and how they change in time. In a more general sense, interest in the relationship between organisms and their habitats undoubtedly dates to the earliest hunter/gathers. Although the questions are simple (e.g., what influences the distribution and abundance of animals), the answers are extremely complex because they represent the integration of environmental heterogeneity and the adaptation of organisms to that habitat template (Southwood 1977; Healey and Prince 1995).

The spatial and temporal dynamics of landscapes increase habitat complexity (Frissell et al. 1986; Pickett and Cadenasso 1995) and complicate the study and interpretation of habitat–fish relationships at multiple scales (Turner et al. 1989; Frissell et al. 1997). Interactions among physical, chemical, and biological characteristics of terrestrial, riparian, and aquatic systems further obfuscate understanding of habitat–fish relationships, especially at broad spatial scales. Frissell et al. (1986) developed a hierarchical method for classifying stream systems in the context of the catchments of which they are a part, and this type of integrated multiscale approach is widely accepted as a means of understanding the influence of disturbance and land management in catchments (Imhof et al. 1996).

Habitat studies for aquatic ecosystems most often have been conducted at the local scale (Imhof et al. 1996), which seems inappropriate for organisms, such as salmonids, that require a variety of habitats depending on season or life stage (Northcote 1997). Furthermore, research has often focused on the relationship between physical habitat and anadromous salmonids (Nickelson et al. 1992; Reeves et al. 1995), but strong inferences are difficult to develop because anadromous fish spend much of their lives in the ocean where they are affected by an array of environmental variables that are not accounted for, including commercial harvest (Hicks et al.

1991) and fluctuating ocean conditions (Pearcy 1992). In contrast, potamodromous coastal cutthroat trout *Oncorhynchus clarkii clarkii* live in freshwater their entire lives. Thus, they are likely to be more tightly linked to changes in terrestrial habitats than anadromous fishes, but much less effort has been expended to describe these linkages.

Interactions between terrestrial and aquatic systems are especially relevant in small streams that often are inhabited by cutthroat trout. These stream channels can represent more than 70% of the cumulative channel length in mountainous catchments of the Pacific Northwest (Benda et al. 1992). In addition, small streams are often directly affected by natural and anthropogenic disturbance (Gomi et al. 2002; May and Gresswell 2004). Fortunately, in small stream systems it may be possible to quantify the spatial and temporal extent of these processes and their influence on the spatial patterns of cutthroat trout abundance.

We describe a research approach developed for small western Oregon streams. Our goals were to investigate (1) patterns of cutthroat trout abundance in small streams, (2) habitat quality and quantity in these systems and how it influences patterns of cutthroat trout abundance, and (3) how relationships between habitat and cutthroat trout abundance change through space and time in response to natural and anthropogenic disturbance (Figure 1). These goals were integrated into a program of landscape-scale catchment sampling to investigate the fine- and broad-scale relationships among upslope landscape characteristics, stream physical habitat, and the abundance of cutthroat trout. We present a general overview of our research with associated strengths and weaknesses and a summary of results to date.

METHODS

Geographical and Ecological Context

The historic range of coastal cutthroat trout extended from Humboldt Bay, California to Prince William Sound, Alaska. The subspecies exhibits

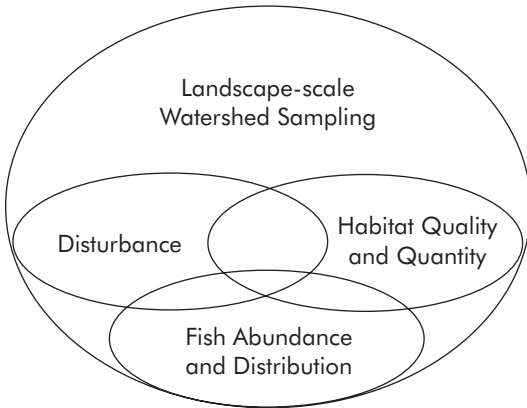


Figure 1. Conceptual framework for assessing inter-relationships among habitat quality and quantity, coastal cutthroat abundance and distribution, and natural and anthropogenic disturbance. Relationships among fish, habitat, and disturbance are captured by landscape-scale catchment sampling.

a diverse array of life histories, including anadromous, amphidromous, potamodromous, and nonmigratory forms (Trotter 1989). Recent range-wide declines in abundance and distribution have raised concerns about the persistence of the subspecies, especially the anadromous form (Nehlsen et al. 1991; Hall et al. 1997), and petitions have been submitted to list coastal cutthroat trout under the Endangered Species Act.

Potamodromous and nonmigratory forms are relatively abundant in small stream systems, but little is known about factors influencing the spatial patterns of abundance of the subspecies in these areas. We focused on catchments above barriers inhibiting upstream migration, where there are no confounding effects from the presence of anadromous salmonids. We hypothesized that it would be easier to identify and interpret the interactions among terrestrial and aquatic components of isolated catchments because coastal cutthroat trout in these systems are directly linked to the freshwater habitat and the surrounding drainage throughout their lives. In addition, coastal cutthroat trout may be much more vulnerable to disturbance in small isolated streams, and information concerning the effects of land management activities (e.g., timber harvest, ag-

gregate mining, and associated road construction and maintenance) is scarce for these systems.

Sampling Design

Two spatial scales were particularly important for this study. The first concerns the large-scale variation across western Oregon using catchments as analytical units and the influence of geologic, geomorphic, and climatic factors on natural and anthropogenic disturbance regimes. The second spatial scale of interest focused on channel units, geomorphic reaches, and stream segments as analytical units to investigate variation within catchments. Although there is a substantial amount of information at the channel unit (10–100 m), and in some cases the stream-segment level (100–1,000 m), the effects of natural disturbance and land-management activities at the catchment scale are poorly understood. Because consequences of anthropogenic and natural disturbance vary substantially within a catchment, managing catchments as systems may be critical for the persistence of many aquatic organisms.

In order to make inferences about coastal cutthroat trout across western Oregon, we defined the sample unit as an entire catchment. To capture the spatial context of the population of catchments, the sample was extended across all of the known barrier-isolated Oregon catchments west of the Cascade Range divide where coastal cutthroat trout was the only salmonid ($N = 269$; Gresswell et al. 2004). We used standard sampling procedures to subsequently select study catchments from the group of known populations (Scheaffer et al. 1990). Because physiographic province and geology were expected to influence cutthroat trout-habitat relationships across western Oregon, the above-barrier catchments were grouped by ecoregion: (Coast Range, Klamath Mountains, and Cascades; Pater et al. 1998) and erosion-potential class (resistant or weak rock types; Gresswell et al. 2004). A sample of 40 catchments was selected in proportion to the number of isolated catchments with coastal

cutthroat populations occurring in each of the six strata (Figure 2). A sample size of 40 catchments represents approximately 15% of the population of barrier-isolated catchments with cutthroat trout in western Oregon, and we as-

sumed that it would be feasible to complete the sample within a period of 3 years.

We sampled during low-discharge periods from June through September. To sample 40 catchments in 3 years, it was necessary to limit

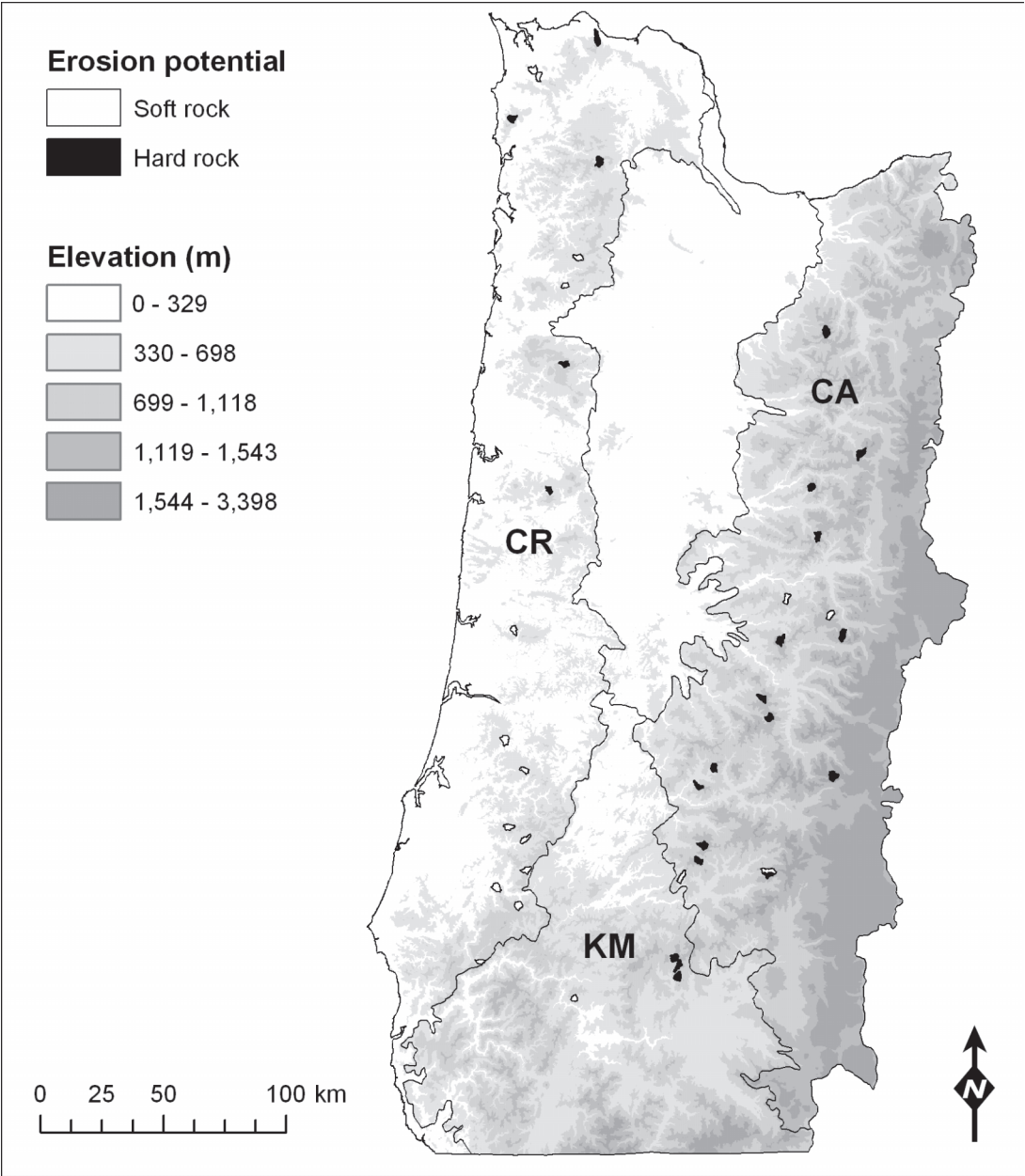


Figure 2. Locations of 40 catchments selected from 269 barrier-isolated coastal cutthroat populations in western Oregon. Catchments were grouped by ecoregion (Coast Range [CR], Klamath Mountains [KM], and Cascades [CA]) and erosion potential (resistant rock types and weak rock types); sample catchments were subsequently selected from each of the six strata.

the amount of time to 3 d for sampling an individual catchment. Pilot studies suggested that to meet time constraints for the field portion of the project, it would be necessary to limit the maximum drainage area of sample catchments to approximately 1,000 ha. In cases where a barrier-isolated catchment exceeded 1,000 ha, the area above each tributary junction (moving progressively farther upstream) was estimated until at least one subcatchment less than 1,000 ha was identified and that upstream subcatchment was sampled. If two or more subcatchments (500–1,000 ha) occurred above a tributary junction, one was randomly selected for sampling.

Because each catchment was surveyed only once, we selected an additional catchment to serve as an interannual temporal reference. Camp Creek (Umpqua River drainage) was sampled annually 1998–2004. Camp Creek also was used as the study site for within-catchment assessments of cutthroat trout movement and genetic structure.

Field Surveys of Physical Habitat and Cutthroat Trout

Prior to initial surveys, the channel network of each catchment was divided into stream segments (Frissell et al. 1986; Moore et al. 1997) using existing databases, topographic and geologic maps, aerial photographs, and field reconnaissance to identify tributary junctions (tributaries contributing $\geq 15\%$ of mainstem flow) and geologic barriers to fish movement (waterfalls > 2 m). In the field, each segment was divided into geomorphic reach types (beaver complex, cascade, step-pool, plane-bed, pool-riffle, dune-ripple, colluvial, or bedrock channel) based on substrate, gradient, bed morphology, and pool spacing (Montgomery and Buffington 1997); minimum reach length was 10 active channel widths. Subsequently, channel-unit types (pool, riffle-rapid, cascade, and vertical step) were classified in each reach according to criteria developed by Bisson et al. (1982). Physical variables including channel-unit size (e.g., length, maximum depth, and width), substrate

size-class (bedrock, boulder, cobble, gravel, sand, and silt; Moore et al. 1997), valley segment type (broad and narrow; Moore et al. 1997), channel type (constrained and unconstrained; Moore et al. 1997), and woody debris accumulations (i.e., ≥ 5 pieces, ≥ 15 cm in diameter and 3 m in length; classified in 10-piece aggregations; Moore et al. 1997) were recorded for all channel units.

Following physical habitat assessment, we estimated relative abundance of cutthroat trout ≥ 70 mm in all pools and cascades using single-pass electrofishing (Bateman et al. 2005). To identify the upstream extent of cutthroat trout distribution, the main-stem segment and tributaries were electrofished for 50–300 m (approximately 10–40 individual pool sample units) beyond the point at which no more cutthroat trout were detected. All captured cutthroat trout were anesthetized with clove oil to reduce handling stress (Taylor and Roberts 1999), measured (fork length; ± 1 mm), and weighed (± 0.1 g). Scale samples (23–254 per catchment) were collected from up to 10 cutthroat trout in each 10-mm length category for age determination.

Repeated sampling of Camp Creek provided the means to examine both within- and among-year changes in physical habitat and cutthroat trout abundance patterns (Hendricks 2002). In Camp Creek, tagged and marked individuals (753 tagged with a passive integrated transponder [PIT] and 5,322 fin-clipped) were monitored bimonthly from June 1999 to August 2000. To increase the probability of relocating individual cutthroat trout, each survey included all channel-units from the waterfall at the downstream terminus of the study area to the end of fish distribution in the main stem and tributaries. To further increase temporal resolution, locations of 35 radio-tagged cutthroat trout were recorded 3–5 d each week, January–June 2000. Emigration out of the catchment was estimated with a rotating fish trap.

Genetic Diversity

Caudal-fin tissue was collected from up to 100 cutthroat trout from each catchment to assess

genetic diversity. Tissue collections were distributed spatially within a catchment by sampling up to 10 fish in 10-mm size-classes from each stream segment until 100 samples were obtained or the end of fish distribution was reached. If end of fish distribution was reached before 100 samples were obtained, we assumed that a large percentage of the population was sampled (Bateman et al. 2005), and therefore, the range of genetic variation in the population was represented. Fin tissue was preserved in a buffer solution (100 mM trisHCl pH8, 100 mM EDTA pH8, 10 mM NaCl, 0.5% (w/v) SDS) or a desiccant (anhydrous sulfide crystals) prior to genetic analysis (Guy 2004). Seven microsatellite loci in three multiplexed sets were chosen after screening for reliable PCR amplification, ease of scoring, and polymorphism (Guy 2004).

Additional tissue samples were collected in Camp Creek to assess cutthroat trout population structure within a small stream network and to evaluate the effects of fish passage barriers on coastal cutthroat trout genetic variation (Wofford et al. 2005). Genetic sampling occurred at 10 sites in the Camp Creek watershed. Prior to sampling, the catchment was surveyed to identify barriers to cutthroat trout passage. Genetic sampling sections were bounded by tributary junctions or fish-passage barriers, except in the upper portion of the main stem where two additional sections were added because no tributaries or passage barriers occurred in a relatively extensive section of stream. Sample collection proceeded as noted above except that tissue was collected from all cutthroat trout captured in six sections where abundance was low. Sample processing was conducted in the manner described above (Wofford et al. 2005).

Analysis of Spatial Structure

The spatial patterns of cutthroat trout abundance in channel networks were evaluated with geostatistical techniques. Variograms were used to indicate the degree of spatial autocorrelation among samples. For 22 catchments where a

spherical variogram model was applicable, the range (i.e., the distance over which observations were autocorrelated) was used to determine the dominant scale of variation (i.e., patch size) in the spatially referenced data (Rossi et al. 1992). Initial variogram analysis was limited to the main-stem channels of four streams. To rigorously quantify spatial structure in cutthroat trout abundance throughout the channel network of a catchment, it was necessary to (1) develop an automated method of determining the network distance (distance along the stream channel) between all sampled points (Torgersen et al. 2004), and (2) create a software routine to perform network variogram analyses in a commercially available statistical application (Ganio et al. 2005).

RESULTS AND INTERPRETATION

Spatial Patterns of Abundance

Because all pools and cascades were sampled in each catchment, it was possible to develop a spatially explicit representation of cutthroat trout abundance in the channel network (Figure 3). Visual examination revealed that cutthroat trout abundance was not uniform within individual catchments, and some stream sections had greater numbers than others. In fact, in many catchments, abundance patterns were highly structured, and the number of cutthroat trout in individual channel units was more similar to neighboring units than those farther away. Conversely, patterns of abundance varied substantially among catchments.

By incorporating supporting data layers, it was possible to build hypotheses concerning the physical processes and structures that may influence patterns of cutthroat trout abundance. Drainage patterns of the fish-bearing portion of the channel network also varied, but dendritic (one or more tributaries) and simple (no tributaries) patterns were the two most common groups. Although a myriad of physical factors and processes can influence the patterns of cutthroat trout abundance in channel networks,

bedrock lithology was the dominant factor among those we examined. For example, a greater proportion of complex, dendritic patterns were found in the Coast Range ecoregion (87%) where sedimentary bedrock was common, but simple patterns were more common in the Cascades ecoregion (13%), where the bedrock lithology was predominantly basalt (Guy 004). Kaufmann and Hughes (2006, this volume) found that anthropogenic disturbances were higher and fish assemblage condition was lower in stream sections with sedimentary bedrock when compared to equivalent sections with volcanic geology.

Initial variogram analysis conducted along the main-stem channels of four streams showed spatial autocorrelation in cutthroat trout abundance; however, visual examination of cutthroat trout abundance patterns suggested that spatial structuring was occurring throughout the channel network (Figure 3). Results of network variogram analyses revealed a number of different spatial structures and scales of variation as indicated by the shapes of the variograms. Patterns of cutthroat trout abundance in the 40 sampled catchments ranged from completely random to highly structured (gradients, patches, and nested patches; Ettema and Wardle 2002; C. E. Torgersen and R. E. Gresswell, unpublished data). The dominant scale of variation (i.e., patch size) in cutthroat trout abundance was assessed for 22 catchments that fit the spherical model, and 75% of the variation in patch size was explained by rock stability (Figure 4). Resistant rock types (basalt, granite, and hard sedimentary) subject to narrow, shallow debris flows were associated with shorter spatial scales of variation in cutthroat trout distribution than weaker rock types. Weak rock types (pyroclastics, tuff, schists, and soft sedimentary) had gentle slopes formed by wide, deep earthflows and were associated with longer spatial scales of variation in cutthroat trout distribution. Other physical catchment characteristics, including the average distance between tributary junctions and the maximum pathway distance (maximum distance separat-

ing any two points in the distribution of cutthroat trout) in the network, were also positively associated with the dominant scale of variation in cutthroat trout abundance, but not correlated with each other ($r = 0.41$, $P > 0.05$) (Torgersen and Gresswell, unpublished data).

Physical factors influencing the spatial extent of stream occupied by cutthroat trout (number of kilometers occupied by cutthroat trout upstream of the starting point) are of particular interest to fisheries managers. Previous research on coastal cutthroat trout distribution in small streams has not had the advantage of spatially contiguous data, so the task of developing predictive models has been challenging (Latterell et al. 2003). Data from 40 catchments in western Oregon enabled analyses to relate patterns of cutthroat trout relative abundance to three landscape variables derived from remote sensing imagery and geographical information system (GIS) data layers. We used information derived from field surveys of cutthroat trout distribution in the channel network to develop statistical models that predicted the spatial extent of cutthroat trout distribution as a proportion of catchment size. The spatial extent of cutthroat trout distribution was negatively correlated with mean stream slope ($r = -0.65$, $P < 0.01$) and positively correlated with mean annual precipitation (Daymet 2004) ($r = 0.50$, $P < 0.01$) and forest vegetation type ($r = 0.51$, $P < 0.01$) (Cohen et al. 2002; Torgersen and Gresswell, unpublished data). The total abundance of cutthroat trout in the study catchments as a proportion of watershed area was much more difficult to predict than spatial extent and was not significantly associated ($r = 0.10$, $P = 0.52$) with forest vegetation type.

Temporal Patterns and Movement

Cutthroat trout moved frequently in Camp Creek, but distances were short. Habitat-unit-scale (2–95 m) movement was common throughout the year, and reach-scale (66–734 m) and segment-scale (229–3,479 m) movements were more common during the late winter and

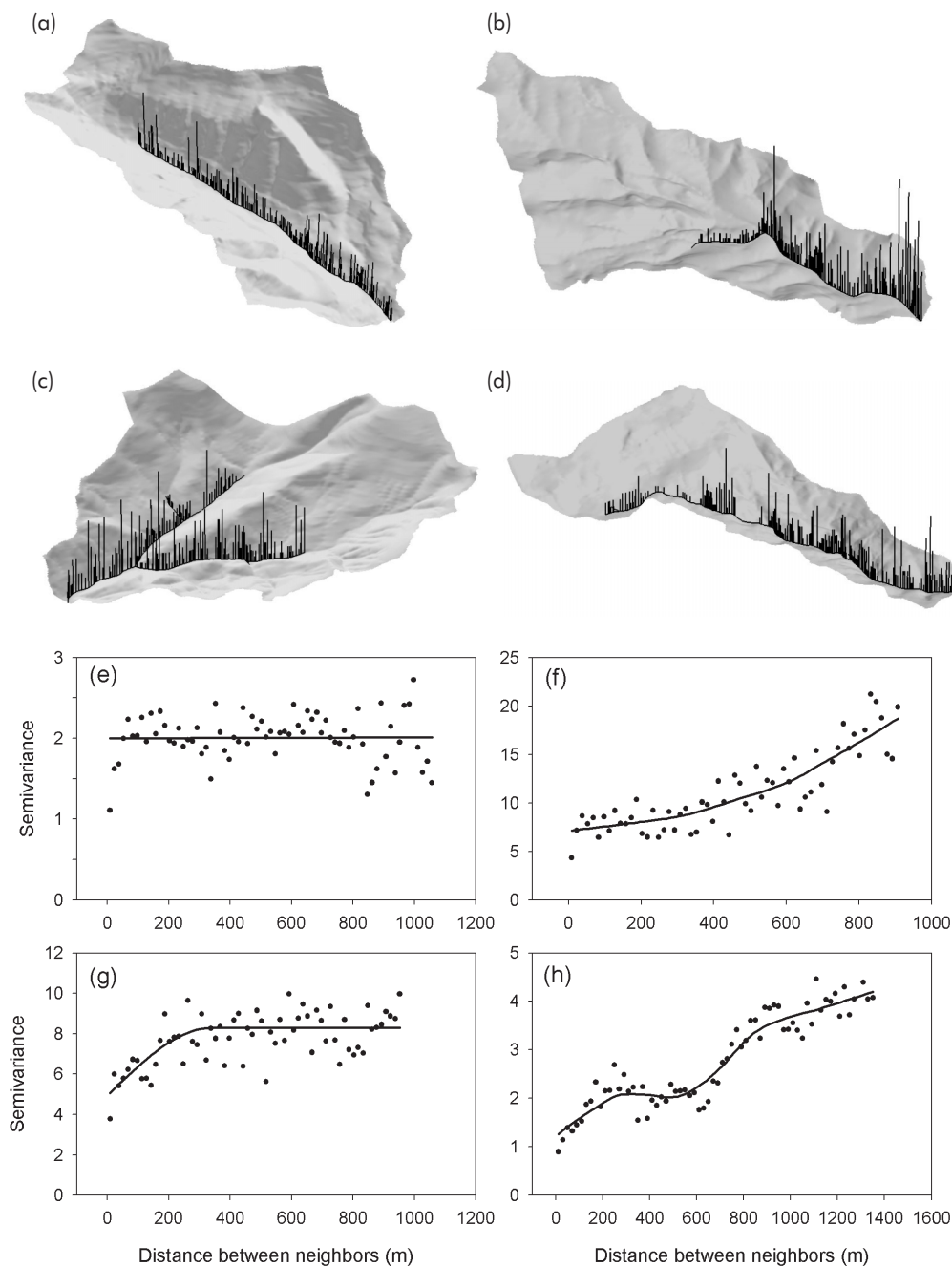


Figure 3. Spatial variation in the distribution and relative abundance of coastal cutthroat trout (length ≥ 70 mm) in four small streams in western Oregon. Vertical bars in three-dimensional representations of Hardy Creek (a), East Fork Laying Creek (b), Rock Creek (c), and Miller Creek (d) indicate the relative abundance of cutthroat trout sampled in pool and cascade habitats with single-pass electrofishing. Paired three-dimensional representations and semivariograms of cutthroat trout counts illustrate different patterns of spatial autocorrelation: (a, e) no spatial structure, (b, f) large-scale heterogeneity with a pronounced trend or gradient, (c, g) small-scale heterogeneity with distinct patches, and (d, h) nested heterogeneity at two different scales (Ettema and Wardle 2002).

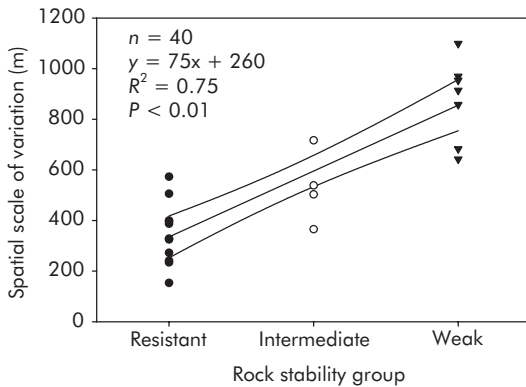


Figure 4. Relationship between the dominant spatial scale of variation in coastal cutthroat trout counts and rock stability in headwater basins of western Oregon.

spring (Hendricks 2002). Movements over greater distances were associated with annual spring spawning events; the least movement occurred when discharge was at a minimum in October. About 80% of PIT-tagged cutthroat trout occupied pool habitats from June through October, but from December through March, when discharge was high and water temperatures were low, pools were used almost exclusively. Only 63 cutthroat trout (<1% of those tagged and marked) were captured in the downstream trap between February and June (Hendricks 2002).

Using a kernel density estimator (Silverman 1986) to quantify spatial variation in fish counts, we identified several interannual patterns of cutthroat trout relative abundance in Camp Creek (Figure 5). Although it is apparent that abundance varies substantially among years, some areas in Camp Creek consistently exhibit high relative abundance of cutthroat trout (Figure 5). Concomitantly, some areas exhibited consistently low numbers of cutthroat trout. Similar interannual patterns of abundance have been noted in another small stream in the Umpqua River drainage that has been monitored annually since 2001 (Gresswell, unpublished data). Efforts to identify habitat characteristics related to areas of consistently high and low relative abundance are ongoing.

Genetic Structure

Genetic differentiation among 27 isolated populations of cutthroat trout in this study was high (mean $F_{st} = 0.33$), but intrapopulation genetic diversity determined by microsatellite analysis (mean number of alleles per locus = 5, mean $H_e = 0.60$) was only moderate (Guy 2004). When all populations were combined, there was evidence of genetic isolation by geographic distance, but isolation by distance was not observed if populations were compared by ecoregion. Differences in genetic diversity between the Coast Range ecoregion (mean alleles = 47) and the Cascade Mountains ecoregion (mean alleles = 30) were statistically significant ($P = 0.02$), and Guy (2004) suggested that this pattern was related to the interactions of drift, gene flow, and the physical environments of the two ecoregions. Topological stream channel complexity (ratio of summed tributary lengths to the main stem length) and connectivity (number of vertical steps > 1 m divided by the mean step height) were greater in the Coast Range (0.54 and 27.7, respectively) than the Cascade Mountains (0.1 and 18.7, respectively), and differences were statistically significant ($P = 0.00$ and $P = 0.02$ for complexity and connectivity, respectively). Results suggested that genetic patterns in the Coast Range were more strongly influenced by gene flow than in the Cascade Mountains, where drift appeared to be the dominant factor influencing genetic diversity (Guy 2004).

At the catchment spatial scale, Wofford et al. (2005) found that dispersal barriers strongly influenced coastal cutthroat trout genetic structure among sample locations in Camp Creek, and barriers were associated with reduced genetic diversity and increased genetic differentiation. In Camp Creek, cutthroat trout exhibit many small, partially independent populations that are directly influenced by genetic drift. For example, mean gene diversity was 0.50 within populations, and mean allelic richness was 3.96. Gene diversity and allelic richness decreased with increasing distance upstream and above barriers to

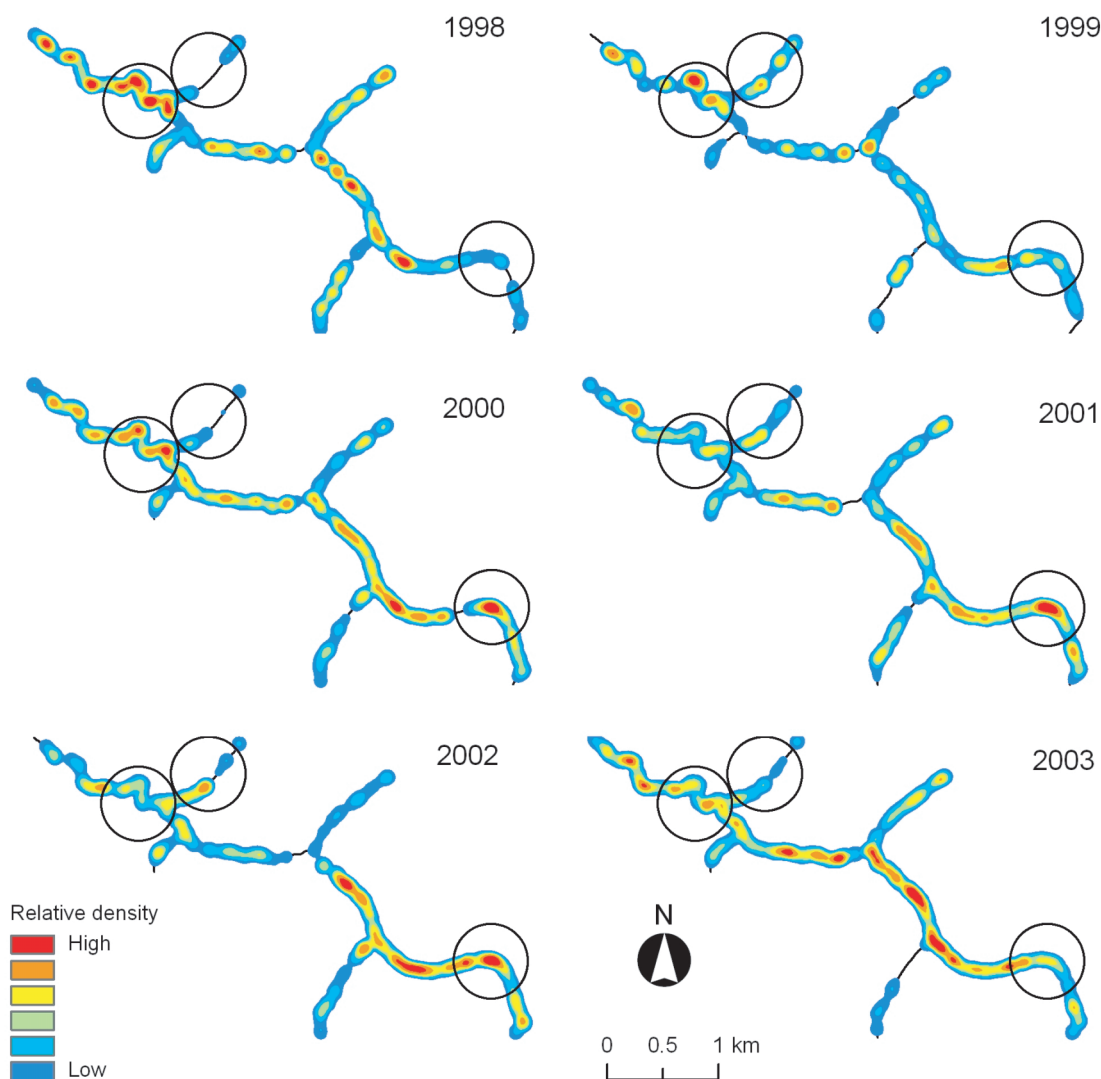


Figure 5. Interannual variation in the summer distribution of coastal cutthroat trout in Camp Creek (1998–2003). The relative density (fish/m²) of trout was estimated using a kernel density function. Circles provide a spatial reference for comparing patterns among years.

movement. Tributaries that were connected with the main stem usually had relatively high levels of allelic richness and gene diversity, but samples obtained upstream of barriers to gene flow exhibited low values for both measures of diversity. Wofford et al. (2005) hypothesized that increased habitat fragmentation in small streams may result in genetic and demographic isolation that leads to reduced genetic diversity of cutthroat trout populations and compromises long-

term population persistence.

DISCUSSION

Although thorough examination of the data collected in this research program has only begun, it is evident that the approach has several strengths that differentiate it from previous attempts to quantify relationships between physical habitat and the pattern of cutthroat trout

abundance. First, using a probability-based process to sample catchments provided a known scope of inference (Stevens and Olsen 1999), and we are not aware of any other study that has combined this spatial extent with the intensity of sampling within each of the sample catchments. The use of probability-based sampling in itself is not unique, and there are examples of both broad landscape scale and fine instream scale studies (Johnson and Gage 1997; Paulsen et al. 1998; Larsen et al. 2004); however, using the catchment as the sample unit and measuring variables at each level of the spatial hierarchy within each catchment is unparalleled. Our sample of 40 catchments represents approximately 15% of the 269 barrier-isolated catchments that support populations of coastal cutthroat trout in western Oregon. Furthermore, because the samples were selected in proportion to their occurrence in six strata based on geographic location and erosion potential, it is possible to investigate the influence of these broad-scale factors on the observed catchment-scale relationships.

A second major contribution of this research is related to the collection of spatially contiguous data throughout each of the catchments (Fausch et al. 2002). This approach provided the biological and geographic information to examine the spatial structure of cutthroat trout abundance in all 40 study catchments. Several recent studies have employed spatially contiguous sampling in stream systems (Labbe and Fausch 2000; Fausch et al. 2002; Torgersen et al. 2006, this volume), but none of these studies has combined the spatial extent and fine-scale detail to examine spatial structure of cutthroat trout abundance with geostatistical techniques in stream networks (Torgersen et al. 2004; Ganio et al. 2005). Our results underscore the influence of the physical habitat template on the spatial pattern of cutthroat trout abundance at a variety of spatial scales. Moreover, through repeated sampling within individual catchments, it is possible to evaluate how the pattern of relative abundance changes through time, and thereby identify those areas, and characteristics of those areas, that

more frequently support higher numbers of cutthroat trout and those that consistently support lower numbers of cutthroat trout.

By examining a wide variety of biological traits it was possible to develop what may be the most thorough and spatially explicit picture of life history organization of any fish taxon to date. Data collected in this survey of catchments across western Oregon have already yielded new insights into patterns of relative abundance, movement, and genetic structure of cutthroat trout populations that are isolated above migration barriers. Ongoing studies are further evaluating the effects of physical landscape and catchment-scale features on patterns of cutthroat trout abundance and relationships with age structure and growth of isolated populations of the subspecies. Related studies have examined intra-annual variation of food availability and diet in relation to riparian vegetation (Romero et al. 2005), and the influence of wood and sediment distribution on the geomorphology of small streams in the Oregon Coast Range (May and Gresswell 2003a, 2003b, 2004).

Finally, variation in cutthroat trout abundance patterns among catchments reflects diverse environments and selective factors, such as geology, geomorphology, climate, and land-management history. These results underscore the advantages of viewing physical habitat as a matrix of physical sites critical to the fitness and persistence of cutthroat trout populations that are linked by movement (Kocik and Ferreri 1998). Consequently, human activities that impede movement among habitat patches can have lasting consequences for local cutthroat trout populations and assemblages and may ultimately affect persistence (Labbe and Fausch 2000; Kruse et al. 2001; Harig and Fausch 2002).

Although we are not advocating use of the methodological approach discussed in this paper for all research on cutthroat trout-habitat relationships, it does have distinct advantages. The relationships we identified with this methodology provide information needed to develop hypotheses that can be evaluated further using

alternate statistical and experimental designs. Our methods also present the means to “scale up” from the local scale (individual channel units) to regional scale (ecoregions). The approach does have disadvantages, however. For example the effort, time, and expense required to collect these data are not trivial, and in many cases may be cost prohibitive. Furthermore, contiguous sampling may not be practical for long-term monitoring applications over large regions (Pacific Northwest). Numerous sampling protocols have been developed to meet this objective (Hankin and Reeves 1988; Hughes et al. 2000; Larsen et al. 2004). Such monitoring methods can be used to attain accurate and precise estimates of central tendency and expanded approximations for a variety of biotic and physical variables, but it is less certain that these data are appropriate for investigating the underlying ecological relationships that determine distribution and abundance of biota in a catchment. Without thorough understanding of these critical relationships, however, we suggest that it is difficult to identify the linkages between natural and anthropogenic disturbance on physical habitat and the resulting consequences for cutthroat trout and other aquatic biota. The sampling strategies described in this paper provide an alternative approach for assessing relationships between salmonid distribution and physical habitat that opens the door for continued methods development and innovation in the near future.

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Landscape Influences on Longitudinal Patterns of River Fishes: Spatially Continuous Analysis of Fish–Habitat Relationships

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Abstract.—Longitudinal analysis of the distribution and abundance of river fishes provides a context-specific characterization of species responses to riverscape heterogeneity. We examined spatially continuous longitudinal profiles (35–70 km) of fish distribution and aquatic habitat (channel gradient, depth, temperature, and water velocity) for three northeastern Oregon rivers. We evaluated spatial patterns of river fishes and habitat using multivariate analysis to compare gradients in fish assemblage structure among rivers and at multiple spatial scales. Spatial structuring of fish assemblages exhibited a generalized pattern of cold- and coolwater fish assemblage zones but was variable within thermal zones, particularly in the warmest river. Landscape context (geographic setting and thermal condition) influenced the observed relationship between species distribution and channel gradient. To evaluate the effect of spatial extent and geographical context on observed assemblage patterns and fish–habitat relationships, we performed multiple ordinations on subsets of our data from varying lengths of each river and compared gradients in assemblage structure within and among rivers. The relative associations of water temperature increased and channel morphology decreased as the spatial scale of analysis increased. The crossover point where both variables explained equal amounts of variation was useful for identifying transitions between cool- and coldwater fish assemblages. Spatially continuous analysis of river fishes and their habitats revealed unexpected ecological patterns and provided a unique perspective on fish distribution that emphasized the importance of habitat heterogeneity and spatial variability in fish–habitat relationships.

INTRODUCTION

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Studies of river fish assemblages often focus on describing and understanding patterns in species composition that occur along the length of river systems. In general, fish assemblage structure is thought to change predictably from headwaters

to downstream reaches, with biotic zones (e.g., cold- and warmwater assemblages) occurring in which species are added or replaced in response to continuous gradients in temperature, channel morphology, and water velocity (Huet 1959; Sheldon 1968; Horwitz 1978; Hughes and Gammon 1987; Li et al. 1987; Rahel and Hubert 1991; Paller 1994; Belliard et al. 1997). Biotic zonation and species addition are dominant, coarse-scale patterns that have been described by numerous studies during the last century (Matthews 1998). Beyond these patterns, however, there is little understanding of spatial heterogeneity in fish distribution and habitat relationships within biotic zones or the effects of spatial scale and context on observed fish assemblage patterns in rivers (Collares-Pereira et al. 1995; Duncan and Kubecka 1996; Poizat and Pont 1996; Bult et al. 1998; Fausch et al. 2002). Consequently, there are likely many more patterns and spatial relationships that have yet to be described, and these may be essential to understanding river fish assemblages.

Discovery of new patterns and spatial relationships may be constrained by repeated use of traditional study approaches. Relatively short sampling reaches (<500 m) spaced at wide intervals (>10 km) along the longitudinal profile or throughout a channel network may provide the information necessary to detect coarse gradients in fish assemblage structure associated with factors such as temperature and stream order (Vannote et al. 1980). However, such site-based studies lack the spatial resolution necessary for detecting patterns in fish–habitat relationships across a range of spatial scales. Consequently, the perception that river fish assemblages change gradually with respect to longitudinal habitat gradients may be driven largely by the resolution and extent of data collection and analysis (Naiman et al. 1988; Wiens 1989; Poole 2002). As a consequence of the discontinuous and spatially limited manner in which river fishes are traditionally sampled, fundamental questions about the nature and extent

of spatial variability in river fish–habitat relationships remain unanswered: How finely tuned are longitudinal patterns in fish assemblages to key habitat factors such as thermal heterogeneity, channel morphology, and velocity? Can the effects of temperature on fish assemblages be isolated from the effects of other factors? How are assemblage patterns at one scale mediated by context at larger spatial scales? Does perception of habitat relationships change with the spatial extent of a study? We propose that these questions can be addressed only by adapting and changing the manner in which fish assemblage and habitat data are collected and analyzed.

Here we illustrate a new approach to collecting and analyzing fish assemblage and habitat data that provides a more spatially continuous view of fishes and the riverine landscapes, or “riverscapes,” they inhabit (Fausch et al. 2002). Our objectives were to (1) collect spatially continuous data on fish assemblage structure and habitat along the length of three rivers with contrasting physical environments, (2) characterize and compare longitudinal patterns and habitat relationships (water depth, velocity, channel gradient, and water temperature) among and within these riverscapes, and (3) evaluate the effect of spatial extent and geographical context of survey data on observed fish–habitat relationships.

METHODS

Study Area

We studied fish assemblages in three small rivers in the Blue Mountains of northeastern Oregon: the Middle Fork John Day (MFJD; upper 49 km), the North Fork John Day (NFJD; upper 70 km), and the Wenaha River (WEN; lower 35 km; Figure 1). Study section elevations ranged from 500 m in the lower WEN to 1,700 m in the upper NFJD and shared a similar geology of Columbia River basalt at lower elevations and folded metamorphosed rocks partially overlain by volcanic tuff in headwater reaches (Orr et al.

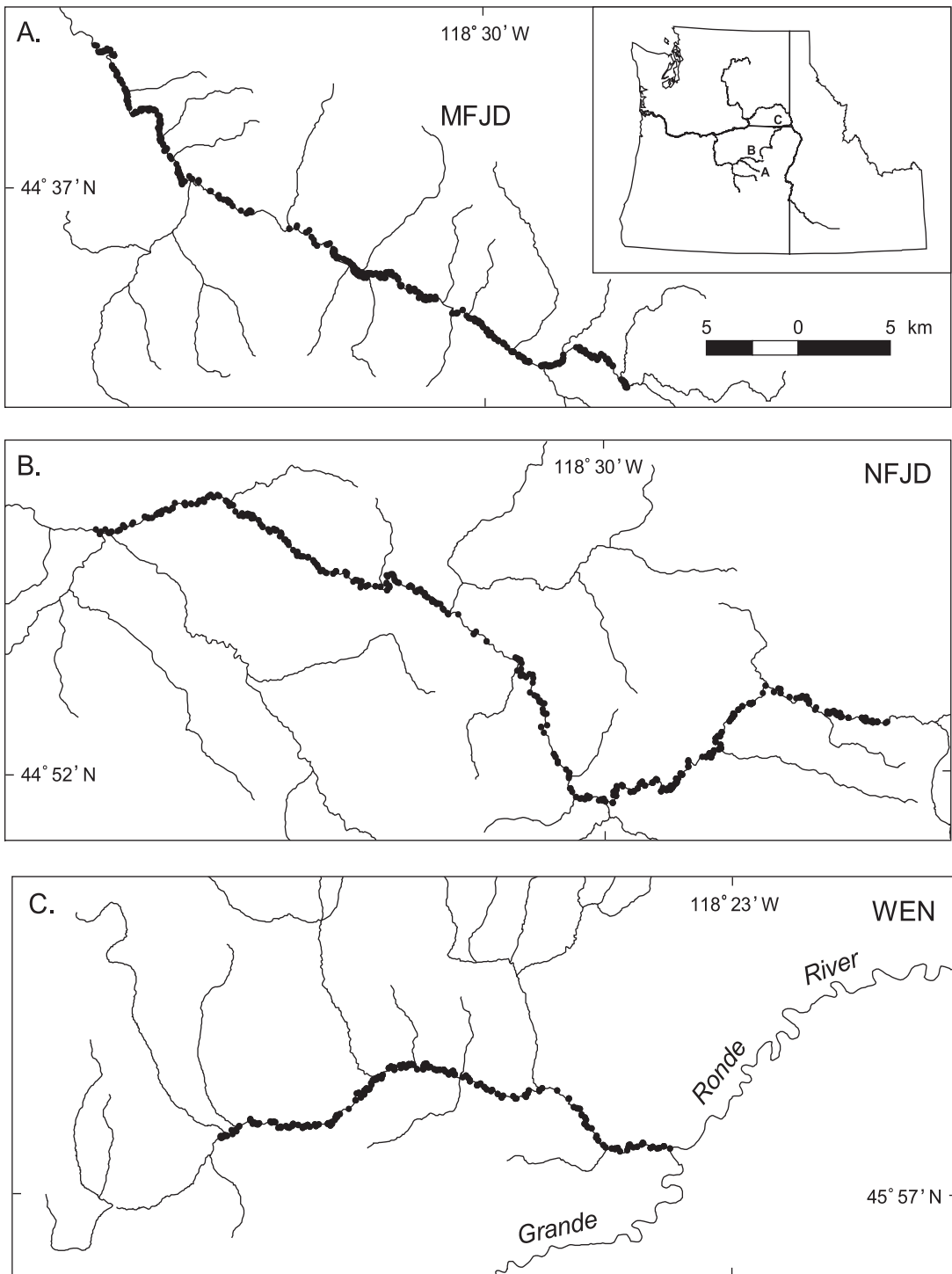


Figure 1. Study area and river sections surveyed for fish assemblages in northeastern Oregon. Study rivers included (A) the Middle Fork John Day (MFJD), (B) the North Fork John Day (NFJD), and (C) the Wenaha River (WEN). Black dots indicate the spatial extent and continuity of underwater visual surveys.

1992). Although the NFJD study section had the largest drainage area and the highest elevations, the WEN received more annual precipitation and had higher summer base flow (Table 1). Longitudinal gradients in elevation and annual precipitation were steepest in the WEN, followed by the NFJD and the MFJD. Maximum summer water temperature patterns reflected differences in streamflow among basins and represented a range of cool and cold thermal environments (Table 1).

Seasonal weather patterns throughout the study area are typical of high desert climates with hot, dry summers and cold, relatively wet winters (−15–38°C; Loy et al. 2001). The Blue Mountains ecoregion is characterized by contrasts in temperature, precipitation, and vegetation corresponding with steep elevation gradients (Clarke and Bryce 1997). Canyons and alluvial valleys in the Wenaha and John Day River basins are vegetated with mixed conifer forest (ponderosa pine *Pinus ponderosa*, grand fir *Abies grandis*, Douglas-fir *Pseudotsuga menziesii*, western larch *Larix occidentalis*, and lodgepole pine *Pinus contorta*) on the upslopes and broadleaf assemblages of black cottonwood *Populus trichocarpa*, willow *Salix* spp., and red alder *Alnus rubra* in the valley bottoms. The upper NFJD and the WEN are designated wild and scenic rivers situated within public wilderness areas, whereas the MFJD flows mainly through private cattle

ranches. Land-use impacts are minimal in the relatively pristine WEN compared to the NFJD and the MFJD, which have experienced extensive mining, grazing, and logging during the last century.

Fish Assemblages

Native fish species common in the study rivers included four salmonids, three catostomids, four cyprinids, and two cottids. Two nonnative fishes (brook trout *Salvelinus fontinalis* and smallmouth bass *Micropterus dolomieu*) were extremely rare and therefore not included in our analysis. We selected a subset of species for assemblage analysis based on their relative abundance and ease of identification underwater (Figure 2). We noted sculpins *Cottus* spp., longnose dace *Rhinichthys cataractae*, and mountain sucker *Catostomus platyrhynchus* during surveys but did not include them in analysis because they were difficult to detect and identify underwater, as determined by comparisons of snorkeling and electrofishing in selected sections of the MFJD (H. W. Li, unpublished data).

Fish assemblage zones overlapped in each of the study rivers and provided an excellent opportunity to evaluate patterns in assemblage structure in relation to water temperature and channel morphometry. Cold- and coolwater temperature classifications were based on species

Table 1. Physical characteristics of study sections in the Middle Fork John Day (MFJD), the North Fork John Day (NFJD), and the Wenaha (WEN) rivers.

River	River kilometer (rkm) ^a	Drainage area (km ²) ^b	Elevation (m)	Stream order ^c	Precipitation (cm/year)	Summer base flow (m ³ /s) ^d	Water temperature (°C) ^e
MFJD	62–117	1,000	1,000–1,300	4th–5th	35–60	1.4	21.1–25.2
NFJD	95–165	1,600	800–1,700	4th–5th	50–90	2.8	19.1–25.0
WEN	0–35	750	500–1,100	4th–5th	50–150	5.7	15.1–21.3

^a Distance upstream from mouth.

^b Drainage area at lower boundary of study section.

^c Range in stream order between upper and lower boundaries of study section (determined from 1:100,000-scale U.S. Geological Survey topographic maps).

^d Streamflow estimates are approximations of summer low-flow conditions based on field measurements in late August and September 1997–1999.

^e Range in mean maximum water temperature on 1–7 August 1998 at the upstream and downstream boundaries of the study sections.

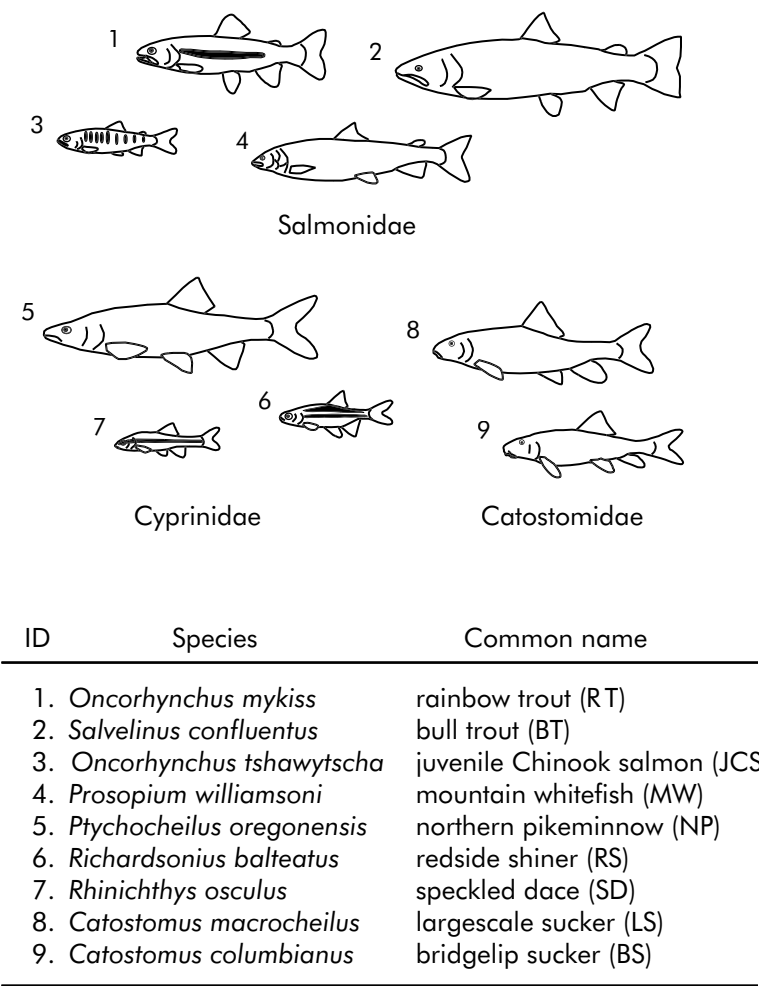


Figure 2. River fish assemblage surveyed in northeastern Oregon. Benthic fish species, including longnose dace *Rhinichthys cataractae*, mountain sucker *Catostomus platyrhynchus*, torrent sculpin *Cottus rhotheus*, and Paiute sculpin *C. beldingii*, were noted during surveys but not included in analyses. The species code used in subsequent figures is listed after the common name.

ranges, spawning seasons, spawning temperatures, and physiological optima (Zaroban et al. 1999). Coldwater species included only the salmonids, whereas coolwater species comprised both catostomids and cyprinids.

Longitudinal Surveys of Fish Distribution
and Aquatic Habitat

We conducted extensive snorkel surveys to quantify longitudinal patterns in river fish assemblages during summer low-flow conditions in July–

August 1996 (MFJD), 1997 (NFJD), and 1998 (WEN). Underwater snorkel surveys provide accurate assessments of fish abundance in flowing waters and offer an alternative to electrofishing when it is restricted by management agencies or when rivers are too large to sample effectively with a backpack electrofisher and too small to sample by boat (Cunjak et al. 1988; Zubik and Fraley 1988; Thurow and Schill 1996; Mullner et al. 1998; Joyce and Hubert 2003). We evaluated the distribution and abundance of river fishes using a modified version of point

abundance sampling (Persat and Copp 1990). The objective of modified point abundance sampling was to collect large numbers of closely spaced samples (<100 m separation), providing a relatively continuous assessment of fish distribution (Figure 1). Although the size of the study rivers prevented us from estimating the efficiency of our sampling procedure (e.g., via comparison with estimates from multiple-pass electrofishing), other work conducted in rivers of similar size has shown that visual estimates provide an accurate (though perhaps imprecise) assessment of fish distribution (H. W. Li and P. B. Bayley, Oregon State University, unpublished data). Three short gaps (2–3 km) in the extensive surveys of the MFJD and the NFJD occurred where access was denied to private lands or where steep canyons and rapids made sampling too dangerous. We divided survey sections into reaches of equal length and sampled fishes and habitat with two-person crews consisting of a diver and a data recorder walking along the shore. Divers counted fish in two or more passes near shore and mid-channel in an upstream or downstream direction depending upon water depth and velocity. Using this approach, a diver-recorder crew was capable of surveying an average of 2–4 km per day.

Divers recorded fish abundances in categories indicating whether a species was dominant (>50%), common (10–50%), or rare (<10%) in relation to the total number of fish observed in a sample unit. Relative abundance provided information on the composition but not the absolute abundance of fish species in a given channel unit. Relative abundances were representative of the proportion of all fish of all species estimated to be in a sampled channel unit. This measure of abundance is particularly useful for determining the ecological relationships among fish species (Rahel 1990; Rahel and Hubert 1991; Reynolds et al. 2003). In all cases, the divers were highly experienced in fish identification and evaluated their estimates of fish abundance regularly through repeat dives of the same channel unit by different divers. In addition to collecting

data on fish assemblages, field crews collected information on channel morphology (e.g., side channel/main channel, depth, width, velocity) and water temperature and recorded geographic coordinates (± 100 m) of individual sample units with a handheld global positioning system (GPS). Field crews placed slow- and fast-water habitats in four categories corresponding to water velocity: (1) pools, (2) slow-moving glides, (3) fast-moving glides, and (4) riffles (Bisson et al. 1982). Categorical estimates of current velocity explained 68% of the variation in current velocity measured with a flowmeter ($n = 33$, $P < 0.001$, $y = 0.39 + 0.26x + 0.08x^2$).

Geographical Analysis and Remote Sensing

A geographical information system (GIS) was essential for mapping, displaying, and analyzing the large number of sample points required to assess spatial patterns in aquatic habitat and fish distribution (Figure 1). We mapped sampled channel units as individual points linked to a database containing information on fish abundance and habitat characteristics. Longitudinal analysis was accomplished using route and dynamic segmentation procedures in ARC/INFO GIS (ESRI 1996; Radko 1997). We derived digital hydrography layers from 1:5,000-scale aerial photographs (MFJD) and 1:100,000-scale topographic maps (NFJD and WEN). Route-measure coordinates, defined as the distance upstream from the mouth (i.e., river kilometer, rkm), served as a common axis with which to compare longitudinal profiles of fish distribution and aquatic habitat. We generated a channel gradient profile from a 10-m digital elevation model (DEM) by sampling elevation every 100 m along the river channel and then calculating gradient using a 500-m moving window. Overlays of evenly spaced sample points on the spatially continuous channel gradient profile provided a coarse estimate of gradient that was consistent among channel units. Those units varied in length and generally decreased in size in an upstream direction.

We assessed spatially and temporally continuous patterns in water temperature with airborne thermal infrared (TIR) remote sensing and automated instream thermographs (Torgersen et al. 2001). Aerial surveys occurred on cloudless days 4–9 August 1998 at 1300–1400 hours. Thermographs served as ground-truth points for TIR remote sensing and provided temporal data necessary for comparing relative difference in mean and maximum water temperatures within and among basins.

Data Analysis

To evaluate spatial patterns and associations in fish distribution, channel morphology, water velocity, and temperature, we compared peaks and troughs in fish abundance to longitudinal profiles of habitat. We scaled the relative abundance estimates for fish (dominant, common, and rare) and categorical estimates of water velocity to 1.0, and then plotted fish and habitat variables versus distance upstream from the river mouth. To identify spatial trends in longitudinal profiles, we used locally weighted scatterplot smoothing (LOWESS), a robust, nonparametric regression technique used to identify trends in heterogeneous ecological data (Trexler and Travis 1993). Locally weighted regression calculations used a second-degree polynomial smoothing function in SigmaPlot statistical software (SPSS 2001). The objective of graphical analysis with LOWESS was to explore spatially continuous patterns and evaluate the extent to which longitudinal changes in species distribution and habitat were gradual or abrupt in contrasting riverine environments.

Multivariate analysis was necessary to distinguish patterns in fish assemblage structure both within and among rivers. Standard parametric multivariate methods (e.g., principal components analysis, detrended correspondence analysis, and canonical correspondence analysis) are commonly applied in studies of river fishes because they reduce complex species matrices into two or more dimensions, or axes, representing

gradients in assemblage structure (Hughes and Gammon 1987; Rahel and Hubert 1991; Paller 1994; Taylor et al. 1996). However, these methods are not appropriate for analyzing nonnormally distributed data sets, such as the spatially continuous fish assemblage and habitat data collected in this study (McCune 1997). Therefore, we computed multivariate ordinations with nonmetric multidimensional scaling (NMS) in PC-ORD, a software package specifically designed for multivariate analysis of ecological data (McCune and Mefford 1999). Nonmetric multidimensional scaling is a nonparametric procedure that calculates axis scores based on ranked distances and therefore alleviates the problems of zero truncation caused by heterogeneous ecological data sets (Clarke 1993; Tabachnick and Fidell 2001).

We calculated two-dimensional solutions in NMS using the Sørensen distance measure and 15 runs of real data with up to 200 iterations to evaluate stability. Because of the extremely large sample size, only 30 Monte Carlo runs were sufficient to evaluate the probability ($\alpha = 0.05$) that ordination axes explained more variation than would be expected by chance. To identify environmental gradients associated with ordination axes, we constructed joint plots and biplots (Jongman et al. 1995) of samples and species in ordination space and examined Pearson correlations between variables in a habitat matrix (mean depth, maximum depth, water velocity, channel gradient, and water temperature) and ordination axis scores. The statistical significance of Pearson correlations provided a relative means to compare correlation strength among habitat variables and ordination axes rather than to test specific hypotheses (McCune and Grace 2002). To facilitate interpretation of the ordinations, we rotated the point cluster around the centroid to align habitat variable vectors in the joint plots with the primary and secondary ordination axes. We produced ordinations with fish species and samples plotted in ordination space by calculating species scores with weighted averaging. We then labeled the primary and secondary gradients

in fish assemblage structure (ordination axes 1 and 2, respectively) according to the two habitat variables with which they were most highly correlated.

To evaluate the effect of spatial extent and geographical context on observed assemblage patterns and fish–habitat relationships, we performed multiple ordinations on subsets of our data from varying lengths of each river and compared gradients in assemblage structure within and among rivers. We divided each river section into 10 reaches of varying lengths (e.g., rkm 0–70, rkm 0–65, rkm 0–60, etc.) and performed a separate ordination for each reach. This process is essentially a scaling analysis that quantifies the effects of spatial extent and geographic context on assemblage composition. Specifically, by comparing Pearson correlations of environmental variables with ordination axis scores along the longitudinal profile, we were able to examine the combined effects of spatial extent (i.e., reach length) and geographic context on the observed relative influences of habitat on fish assemblage structure.

RESULTS

Longitudinal Patterns of Individual Fish Species

Longitudinal patterns in fish distribution were gradual for some species and abrupt for others, and differed markedly among rivers. In the MFJD, patterns were driven by differences in the distribution of juvenile Chinook salmon *Oncorhynchus tshawytscha* and rainbow trout *O. mykiss* versus mountain whitefish *Prosopium williamsoni*, catostomids, and cyprinids (Figure 3A). Juvenile Chinook salmon and rainbow trout were both relatively abundant in the middle section of the river (rkm 85–100). Rainbow trout increased in relative abundance upstream of rkm 105, whereas juvenile Chinook salmon were most common in a single reach downstream of rkm 100. Mountain whitefish were relatively abundant downstream of the reaches with high relative abundances of Chinook salmon and rainbow

trout (rkm 83–88). Catostomids (bridgelip sucker *Catostomus columbianus* and largescale sucker *C. macrocheilus*) had different patterns of relative abundance depending on the species. Peaks in the relative abundance of bridgelip sucker occurred downstream of rkm 65, at rkm 85, and upstream of rkm 110, and largescale sucker were relatively abundant at rkm 72 and rkm 97. Speckled dace *Rhinichthys osculus* and reddsideshiner *Richardsonius balteatus* were common throughout the MFJD but exhibited local peaks in relative abundance at rkm 83 (both species) and peaks and troughs, respectively, at rkm 101. Northern pikeminnow *Ptychocheilus oregonensis* were relatively rare in the MFJD except in reaches downstream of rkm 65 and at rkm 107–112.

Fish distribution in the NFJD exhibited distinct peaks and troughs in the relative abundance of juvenile Chinook salmon and mountain whitefish but was more gradual for rainbow trout, bull trout *Salvelinus confluentus*, largescale sucker, bridgelip sucker, speckled dace, reddsideshiner, and northern pikeminnow (Figure 3B). Rainbow trout increased in abundance gradually in an upstream direction but were rare in the uppermost reaches of the NFJD. Bull trout increased in abundance gradually in an upstream direction from the lowermost occurrence at rkm 150. Bull trout and coolwater species (catostomids and cyprinids) did not overlap spatially.

Salmonids dominated the fish assemblage in the WEN (Figure 3C). Juvenile Chinook salmon were relatively abundant throughout the study section but were most abundant in the middle reaches of the WEN (rkm 13–25). Rainbow trout were common throughout the study section but increased in relative abundance in downstream reaches (rkm 0–8) and in the uppermost reach of the study section (rkm 33–35). Relative abundances of bull trout and juvenile Chinook salmon increased gradually in an upstream direction and reached a peak at rkm 20–23. Mountain whitefish were relatively abundant throughout the lower 23 km of the WEN but decreased dramatically in relative abundance upstream of rkm 23. Largescale

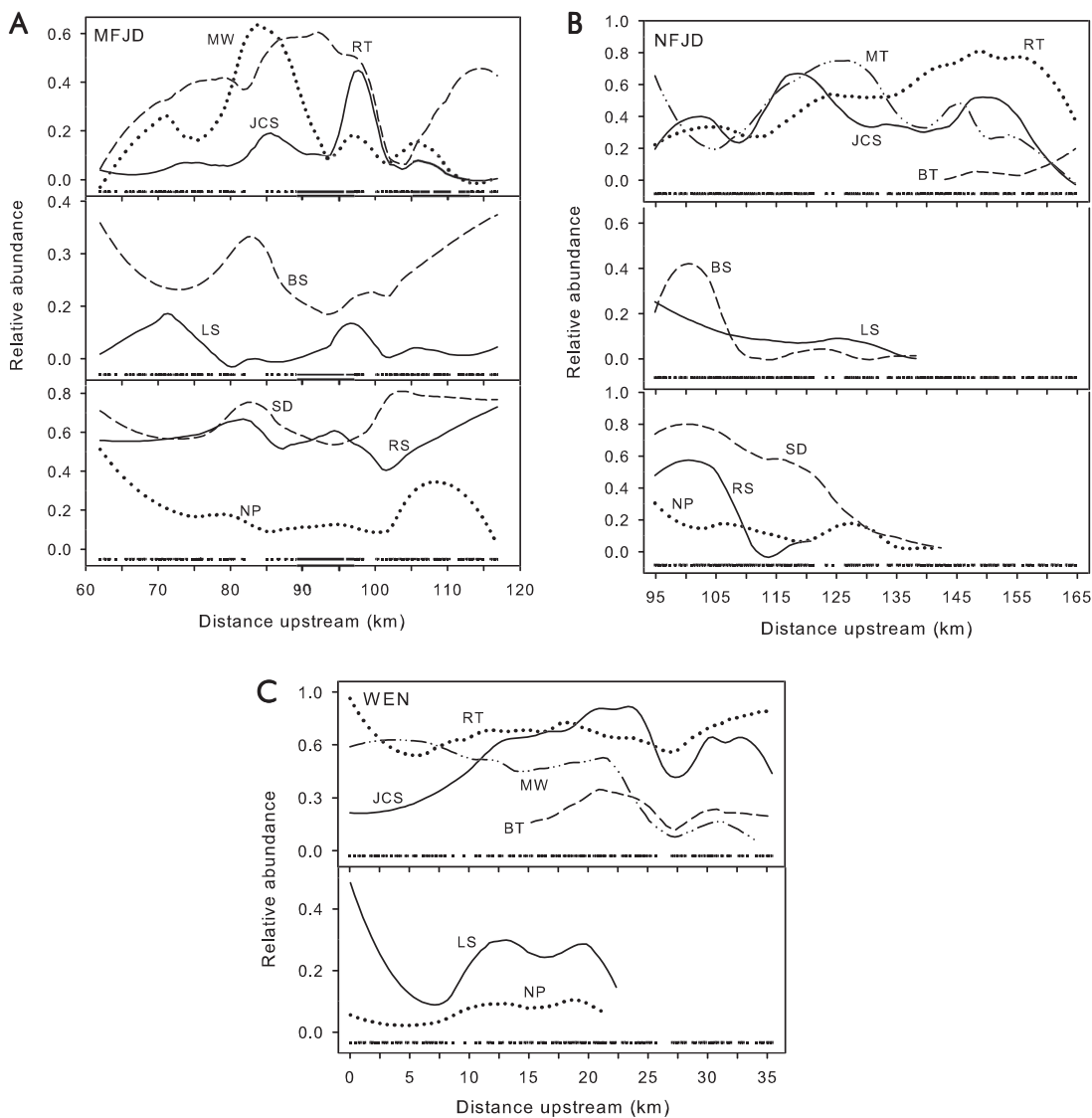


Figure 3. Longitudinal patterns of fish distribution in (A) the Middle Fork John Day (MFJD), (B) the North Fork John Day (NFJD), and (C) the Wenaha River (WEN). Trend lines are smoothed values from locally weighted scatterplot smoothing (LOWESS) of near-continuous fish survey data. Dashed horizontal bars below each trend line depict the spatial continuity of fish surveys and provide a relative indicator of the number of data points used to calculate LOWESS regressions. Relative abundance represents a continuum of rare to dominant on a scale of 0 to 1; panels are separated and scaled differently to clarify individual species-abundance patterns. See Figure 2 for definitions of species codes.

sucker and northern pikeminnow occurred throughout the lower 23 km of the WEN but represented a relatively small part of the fish assemblage, except in the lower reaches (rkm 0–3) where largescale sucker were nearly as common as mountain whitefish and rainbow trout.

Associations between Fish Species and Longitudinal Patterns of Aquatic Habitat

Longitudinal patterns of fish distribution corresponded with patterns in aquatic habitat, but these associations were nonlinear and complex

(Figures 3 and 4). In the MFJD, peaks in the relative abundance of juvenile Chinook salmon were associated with peaks in channel gradient and troughs in water temperature (Figures 3A and

4A). Peaks in the relative abundance of mountain whitefish, bridgelip sucker, speckled dace, and reddsides shiner corresponded with the highest peak in maximum depth at rkm 83 (Figures

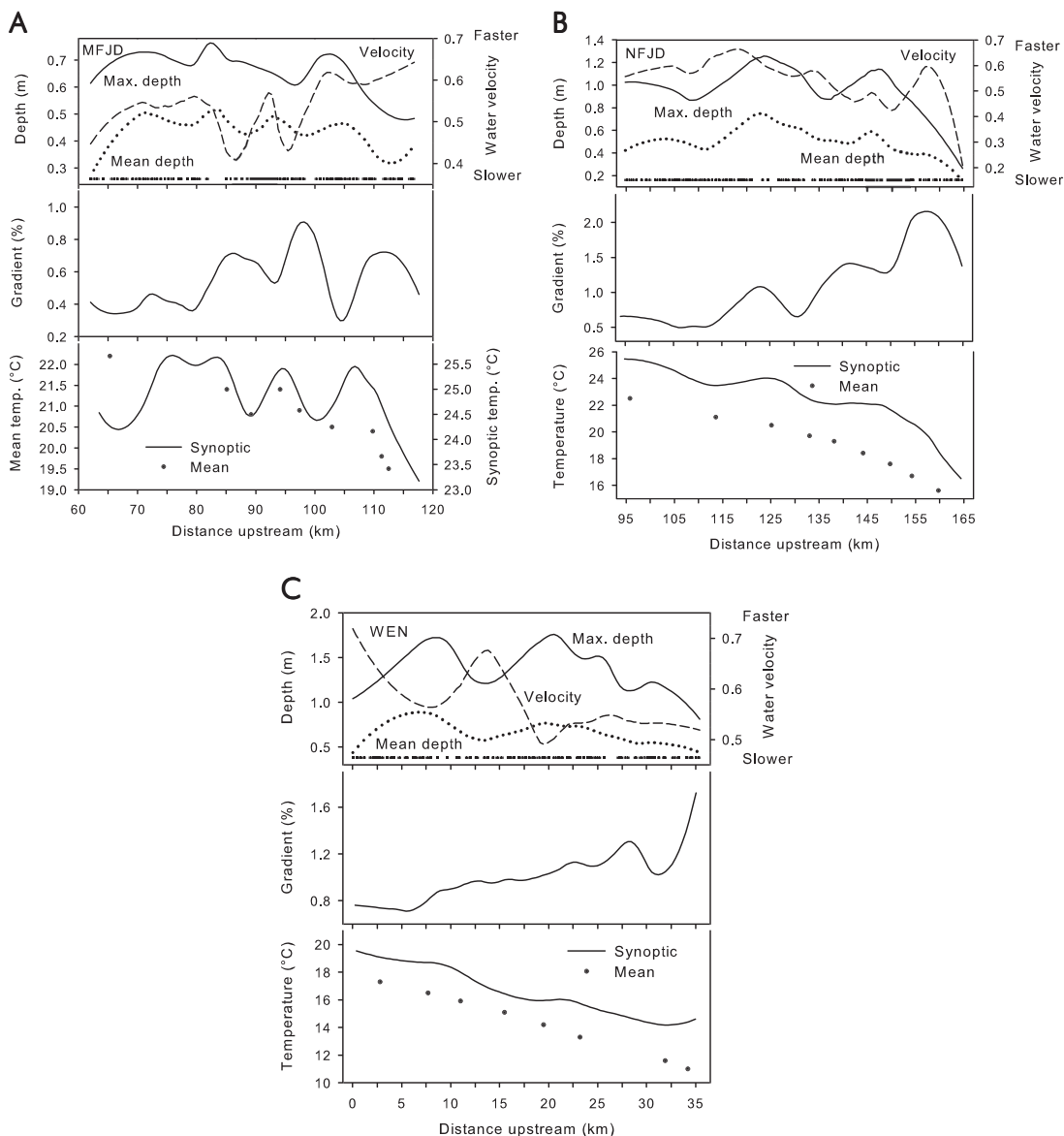


Figure 4. Longitudinal patterns of aquatic habitat in (A) the Middle Fork John Day (MFJD), (B) the North Fork John Day (NFJD), and (C) the Wenaha River (WEN). Trend lines are smoothed values from locally weighted scatterplot smoothing (LOWESS) of spatially continuous (channel gradient and temperature) and near-continuous survey data (depth and water velocity). Dashed horizontal bars below each trend line depict the spatial continuity of habitat surveys and provide a relative indicator of the number of data points used to calculate LOWESS regressions. Water velocity is scaled to 1.0 and represents a continuum of slow- to fast-water aquatic habitats. Mean daily water temperatures were recorded on the day of synoptic surveys with thermal infrared remote sensing.

3A and 4A). In the NFJD, spatial associations between fish distribution and channel morphology and water temperature were not as pronounced as they were in the MFJD (Figures 3A, 3B, 4A, and 4B). The two highest peaks in the relative abundance of juvenile Chinook salmon corresponded with the highest peak (rkm 120) and the lowest trough in water velocity (rkm 150). Peaks in the relative abundance of mountain whitefish corresponded with peaks in maximum depth. In the WEN, peaks in the relative abundance of rainbow trout were associated with high-velocity downstream reaches (rkm 0–8) and high-gradient reaches upstream (rkm 33–35) (Figures 3C and 4C). Peaks in the relative abundance of bull trout and juvenile Chinook salmon coincided with a peak in maximum water depth and a trough in water velocity.

Multivariate Gradients in Fish Assemblage Structure and Aquatic Habitat

Fishes exhibited distinct differences in assemblage structure with respect to habitat variables in the three rivers. Variation in fish assemblage composition in the MFJD corresponded with habitat gradients in depth, water velocity, channel gradient, and, to a lesser degree, water temperature (Figure 5A and Table 2). The primary ordination axis (depth and water velocity) explained 73% of the variation in fish assemblage structure, and the secondary axis (channel gradient and water temperature) explained 19% of the variation ($P < 0.05$). Fishes were strongly segregated among shallow riffles (rainbow trout, juvenile Chinook salmon, mountain whitefish, and speckled dace) and deep pools (reidside shiner, bridgelip sucker, northern pikeminnow, and largescale sucker). Fish species most strongly correlated with the primary axis (depth and water velocity) included bridgelip sucker, northern pikeminnow, largescale sucker, reidside shiner, and rainbow trout. Species strongly associated with the second axis (channel gradient and temperature) included juvenile Chinook salmon, rainbow trout, and northern pikeminnow (Table

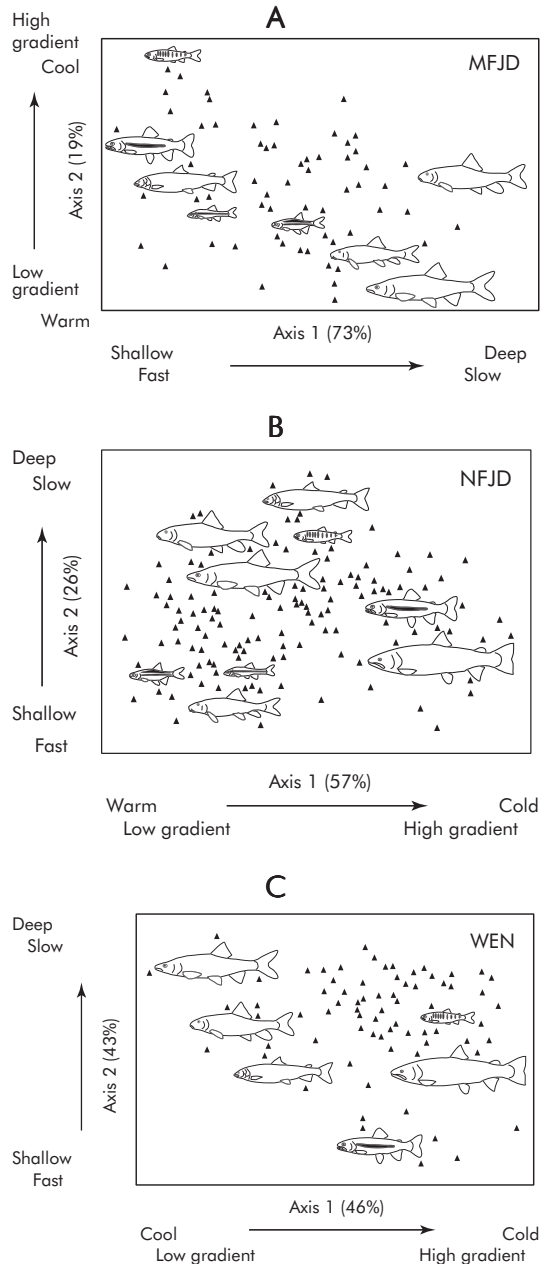


Figure 5. Ordination of nonmetric multidimensional scaling (NMS) analysis of fish assemblage structure in (A) the Middle Fork John Day (MFJD), (B) the North Fork John Day (NFJD), and (C) the Wenaha River (WEN). Fish species are plotted in ordination space, in which each fish outline indicates the position of the species' centroid with respect to the ordination axes. Solid triangles are sample units in species space. The amount of variation explained by each ordination axis is shown in parentheses. See Figure 3 for a key to the fishes.

Table 2. Pearson correlation coefficients of species and habitat variables versus axis scores from ordinations of fish assemblage structure in entire survey reaches. The surveyed lengths in the Middle Fork John Day, the North Fork John Day, and the Wenaha rivers are 49, 70, and 35 km, respectively. Ordinations were calculated from relative abundance data using nonmetric multidimensional scaling (NMS). The statistical significance of correlations between axis scores and habitat variables, indicated with one or two asterisk symbols ($P < 0.05$ or $P < 0.001$, respectively), provides a relative means to compare correlation strength among variables and ordination axes.

Variable	Middle Fork John Day River (n = 261)		North Fork John Day River (n = 244)		Wenaha River (n = 179)	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
<i>Species</i>						
Bull trout	–	–	0.30	–0.11	0.22	0.31
Juvenile Chinook salmon	–0.12	0.87	–0.24	0.29	0.50	0.76
Rainbow trout	–0.69	0.79	0.79	–0.18	0.24	–0.46
Mountain whitefish	–0.15	0.11	–0.29	0.71	–0.86	0.40
Northern pikeminnow	0.92	–0.50	–0.42	0.06	–0.29	0.31
Largescale sucker	0.76	0.05	–0.44	0.09	–0.50	0.19
Bridgelip sucker	0.95	–0.39	–0.40	–0.30	–	–
Redside shiner	0.74	–0.37	–0.54	–0.23	–	–
Speckled dace	–0.51	–0.40	–0.78	–0.42	–	–
<i>Habitat</i>						
Temperature	0.28**	–0.13*	–0.76**	0.00	–0.65**	–0.04
Channel gradient	–0.16*	0.32**	0.57**	–0.02	0.35**	–0.07
Maximum depth	0.40**	–0.12*	–0.22**	0.30**	–0.18*	0.35**
Mean depth	0.32**	–0.05	–0.18**	0.28**	–0.23**	0.29**
Water velocity ^a	–0.38**	0.04	0.14	–0.22**	0.11	–0.28**

^a Water velocity is a categorical variable that represents a continuum of slow- to fast-water aquatic habitats.

2). Mountain whitefish and speckled dace occupied intermediate positions.

Fish assemblages in the NFJD were structured along gradients of water temperature, channel gradient, and depth (Figure 5B). Temperature and channel gradient were strongly correlated with the primary axis, which explained 57% of the variation in fish assemblage structure ($P < 0.05$) (Figure 5B and Table 2). The distribution of fish species with respect to the primary ordination axis (temperature and channel gradient) indicated a separation between coolwater fishes (redside shiner, largescale sucker, bridgelip sucker, northern pikeminnow, and speckled dace) and rainbow trout and bull trout. Juvenile Chinook salmon and mountain whitefish were positioned at an intermediate location with respect to the primary ordination axis (temperature and channel gradient). Fish species most strongly correlated with the primary axis in-

cluded rainbow trout, speckled dace, and redside shiner (Table 2). The secondary axis explained 26% of the variation in fish assemblage structure ($P < 0.05$) and was associated primarily with mean and maximum water depth (Table 2). With the exception of bull trout and rainbow trout, fishes in the NFJD were generally grouped into deep-water (mountain whitefish, largescale sucker, juvenile Chinook salmon, and northern pikeminnow) and shallow-water (bridgelip sucker, speckled dace, and redside shiner) assemblages.

Fishes in the WEN responded to gradients in temperature, channel gradient, depth, and water velocity (Figure 5C, Table 2). Coldwater fishes (juvenile Chinook salmon, bull trout, and rainbow trout) were most abundant in colder, upstream reaches, while coolwater fishes (northern pikeminnow and largescale sucker) were most common downstream. Mountain whitefish, largescale sucker, and juvenile Chinook salmon

were strongly correlated with ordination scores on the primary axis, which explained 46% of the variation in the ordination ($P < 0.05$) (Figure 5C and Table 2). On the secondary ordination axis, depth and water velocity explained 43% of the variation in fish assemblage structure ($P < 0.05$). Fish species most strongly associated with the secondary axis included juvenile Chinook salmon, rainbow trout, and mountain whitefish (Table 2). Of the three coldwater fishes in the WEN, juvenile Chinook salmon exhibited the strongest positive association with the secondary ordination axis (water depth and slow-water habitats) (Table 2).

Effects of Spatial Extent and Geographical Context on Observed Fish–Habitat Relationships

The observed relationships between fish assemblage structure and aquatic habitat changed depending on the spatial extent and geographical context of analysis (Figure 6). In the MFJD and the NFJD, the relative influences of temperature and channel morphology increased and decreased, respectively, when the spatial extent of the data set was increased. Crossover points in the trends of correlations indicated where temperature and channel morphology explained approximately equal amounts of variation in fish assemblage structure (Figure 6). In the MFJD, the warmest of the rivers, the crossover point occurred in the upper portion of the study section (rkm 48), whereas in the NFJD, this transition occurred in the lower 20 km of the study section (rkm 115). In the WEN, the coldest and also the shortest river, the relative influence of channel morphology on fish assemblage structure increased as the spatial extent of the data set was increased. In the WEN, there was no consistent spatial trend in the relative influence of temperature on fish assemblage structure, and there was no crossover point at which water temperature and channel morphology explained equal amounts of variation in fish assemblage structure.

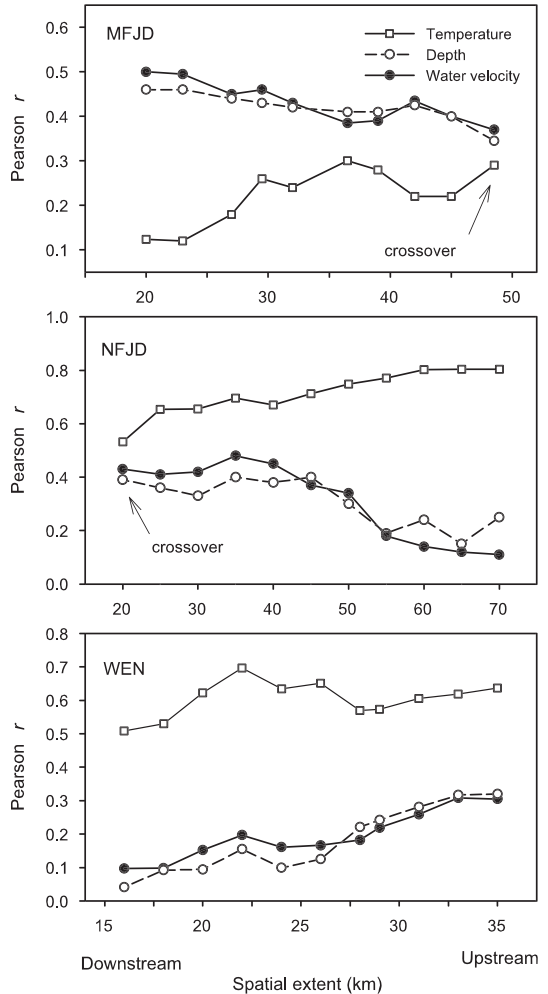


Figure 6. Scale-dependent effects of temperature and channel morphology on river fish assemblage structure in the Middle Fork John Day (MFJD), the North Fork John Day (NFJD), and the Wenaha River (WEN). Pearson correlation coefficients (r) indicate the relative influence of temperature and channel morphology on river fish assemblage structure over a range of spatial extents. Crossover points indicate the spatial extent and location where temperature and channel morphology explained approximately equal amounts of variation in river fish assemblage structure.

DISCUSSION

Longitudinal patterns of river fish in the MFJD, NFJD, and WEN ranged from gradual to abrupt and differed substantially among species and among rivers. At the scale of entire river sections

(30–70 km), longitudinal patterns of water temperature and channel gradient corresponded to zonation from a coldwater assemblage (Salmonidae) to a coolwater minnow–sucker assemblage (Cyprinidae–Catostomidae) as predicted by the river continuum concept and current models of river fish distribution (Vannote et al. 1980; Li et al. 1987; Rahel and Hubert 1991). However, embedded within the broad-scale template of cool- and coldwater fish assemblage zones, the distribution of fishes was highly variable and reflected reach-scale variation in channel morphology (i.e., depth and water velocity) and water temperature. Fish assemblage structure was particularly variable along the length of the MFJD where the longitudinal thermal gradient was not so pronounced as in the NFJD and the WEN. Although other studies have suggested a high degree of spatial heterogeneity in river fish distribution at spatial extents of 30–70 km (Stewart et al. 1992; Roper and Scarnecchia 1994), few studies have described such patterns with spatially continuous data (Baxter 2002; Torgersen 2002). This study provides an example of how spatially continuous data can be collected and analyzed to evaluate landscape influences on longitudinal patterns of cool- and coldwater fish assemblages in three Pacific Northwest rivers.

Effects of Landscape Context on Fish–Habitat Relationships

Longitudinal patterns of species and assemblages.—Detailed studies of the spatial distribution of fishes within entire river sections (10–100 km) are useful for evaluating how fish–habitat relationships change across scales and in different spatial contexts (Fausch et al. 1994). River fish responses to channel gradient provide a case in point. Within a given river basin, rainbow trout/steelhead (anadromous rainbow trout) are generally associated with relatively steeper, swifter habitats than juvenile Chinook salmon (McMichael and Pearsons 1998; Montgomery et al. 1999). Similarly, salmonids are usually associated with higher channel gradient than

warmwater fishes in North America (Rahel and Hubert 1991), but this relationship is difficult to interpret because elevation, channel gradient, and coldwater temperatures are often closely correlated (Isaak and Hubert 2000; Isaak and Hubert 2001). However, we were able to isolate the influence of channel gradient on species distribution from that of stream temperature. Our observations of fish distribution in the MFJD and NFJD provided a unique opportunity to evaluate the response of a coldwater fish (juvenile Chinook salmon) to relatively high-gradient reaches over a range of water temperatures. For example, we found that the relative abundance patterns of juvenile Chinook salmon in the warmer MFJD and lower NFJD were positively associated with relatively high-gradient reaches. In contrast, in the upper, colder section of the NFJD, a peak in the relative abundance of juvenile Chinook salmon corresponded with a local trough in channel gradient. Thus, landscape context (i.e., geographic and thermal conditions) reversed the observed relationship between this species and channel gradient. This effect of landscape context was also observed in patterns of fish assemblage structure. Comparisons between assemblage structure in the MFJD and the WEN indicated that juvenile Chinook salmon were associated with the shallow, fast-water fish assemblage at warm temperatures (MFJD) but were more associated with the deep, slow-water fish assemblage at cold temperatures (WEN).

Potential ecological mechanisms.—The potential ecological mechanisms underlying this changing habitat relationship require further investigation. The apparent reversal in habitat selection by juvenile Chinook salmon may be related to species interactions and bioenergetics. For example, coolwater fish species, such as redbelly shiner and northern pikeminnow, have a physiological advantage over coldwater fishes in the relatively warmer sections of the MFJD and lower NFJD. Coolwater fishes were the most abundant species in deep, slow-water habitats in the MFJD and the lower NFJD and may exclude

juvenile Chinook salmon through competition with reddsideshiner (Reeves et al. 1987) or through predation by northern pikeminnow (Isaak and Bjornn 1996). Increased riffle use by salmonids has also been shown to occur in response to higher metabolic demands at warmer water temperatures (Smith and Li 1983) because faster current velocities provide higher invertebrate drift rates and may actually balance out the increased metabolic costs of maintaining a position in faster current.

The heterogeneous distribution of river fishes we observed in these watersheds may also be influenced by historical constraints on distribution (geomorphology and biogeographic history), land-use history, and the spawning distribution of adults (Harding et al. 1998; Williams et al. 2003). All three factors likely play roles in the assemblage patterns of the study rivers, particularly in the MFJD and NFJD, which have complex histories of land use and have undergone considerable channel restructuring (Torgersen et al. 1999).

Spatial Scale of Observation and Gradients in Fish Assemblage Structure

The spatial scale of analysis influenced the observed gradients in fish assemblage structure. A number of studies have evaluated changing habitat relationships of individual fish species across multiple spatial scales (Fausch et al. 1994; Poizat and Pont 1996; Torgersen et al. 1999; Baxter and Hauer 2000; Thompson et al. 2001; Torgersen and Close 2004). However, investigations of the effects of scale on observed patterns of species diversity and assemblage structure are less common (Wilson et al. 1999). This is largely due to the expense of collecting data that are of sufficient resolution and extent to conduct sequential analyses while varying the spatial dimensions of the data set. The relative roles of temperature and channel morphology in structuring river fish assemblages are known to change as the spatial extent and location in the drainage are altered (Matthews 1998). However, the specific quantitative relationship between spatial scale and the observed effects of

these two variables has not been previously described. The quantitative approach that we employed in this study may be useful in river fish ecology and management both for understanding fish–habitat relationships and for identifying transitions in fish assemblage structure.

Transition zones between cool- and coldwater fish assemblages were difficult to identify in this study because the assemblages overlapped considerably in all three study rivers. However, crossover points in the relative influences of temperature and channel morphology on fish assemblage structure were useful for identifying potential habitat-specific transitions between cool- and coldwater fish assemblages. Differences in the structure of deepwater assemblages in the MFJD, NFJD, and WEN indicated that deep pool environments may be occupied by either cold- or coolwater fishes, depending on water temperature. Others have observed similar transitions at deep pools when continuously electrofishing large Pacific Northwest rivers (R. M. Hughes, Oregon State University, Corvallis, unpublished data). Without data of such high spatial resolution and extent, we would not have detected such crossover points in the habitat relationships of fish assemblages.

The crossover point in the relative influence of channel morphology (i.e., depth and velocity) versus water temperature on fish assemblage structure may provide a useful index for assessing and monitoring biological potential for cool- and coldwater fishes in rivers. In the MFJD and the NFJD, crossover points in assemblage structure occurred at 20–22°C (mean daily temperature during the hottest week of the year). This temperature range corresponds with the highest mean weekly temperatures recommended for coldwater fish species cited by Armour (1991) and the thermal transition zone recorded by Taniguchi et al. (1998) for trout and nontrout assemblages in the Rocky Mountains. Because this is the first description of such crossover points in fish assemblage structure, more examples are needed from a range of rivers over a broader geographic area to test the application and further develop the

utility of this approach for examining transitions in fish assemblage structure.

Spatially Continuous Analysis of Fish–Habitat Relationships

The response of riverine fishes to habitat heterogeneity at intermediate scales is poorly understood (Fausch et al. 1994, 2002). In part, this is due to the relative ease of either assessing broad-scale patterns in fish distribution with respect to geographic variation in elevation and air temperature (Rahel and Nibbelink 1999) or observing fine-scale patterns in fish behavior in individual pool–riffle sequences and in the laboratory (Reeves et al. 1987; Taniguchi et al. 1998). In both site-based and laboratory approaches, the number of samples used to evaluate statistical relationships is relatively small. To collect the large number of samples necessary for evaluating spatially continuous patterns in fish distribution, we used snorkeling and relative abundance estimates. In many instances, relative abundance categories (abundant, common, rare) and presence–absence data are sufficient for identifying important trends in river fish assemblages (Rahel 1990); however, estimates of relative abundance and presence–absence may be unreliable if they are uncorrected for sampling efficiency (Bayley and Dowling 1993). Nevertheless, many mountain rivers are too large to sample with a backpack electrofishing unit and too small to sample with boat electrofishing gear (Hughes et al. 2002; Mebane et al. 2003). These logistical challenges make it difficult to validate visual estimates of fish abundance. To compensate for the lack of precision in snorkeling surveys, we used a modified version of point abundance sampling (Persat and Copp 1990) and found that large numbers of visual estimates of fish abundance were quite effective for quantifying spatial patterns in river fish assemblages. Other studies have successfully employed snorkeling and less rigorous electrofishing methods (single-pass) to evaluate patterns of fish distribution in small streams (Hankin and Reeves 1988; Thurow and

Schill 1996; Mullner et al. 1998; Bateman et al. 2005). New sampling methods and statistical approaches, such as hydroacoustics, point abundance sampling, and replicate sampling (Barker and Sauer 1995; Duncan and Kubecka 1996; Cao et al. 2001), are all applicable to surveys of river fishes and represent an area needing more research in order to better describe and understand the spatial distribution of river fishes.

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Relative Influence of Environmental Variables at Multiple Spatial Scales on Fishes in Wisconsin's Warmwater Nonwadeable Rivers

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Abstract.—We analyzed data from 38 sites on 31 large rivers in Wisconsin to characterize the influence of environmental variables at the basin, reach, and site scales on fish assemblages. Electrofishing and site habitat data were collected for a distance of 1.6 km per site. Environmental variables included conductivity, substrate, and fish cover at the site scale; distance to impoundments, dams, and length of riverine habitat at the reach scale; and land cover, climate, and geology at the basin scale. Of the 77 fish species found, 39 occurred in more than 10% of the sites and were retained for analyses of fish abundance and biomass. Redundancy analysis (RDA) was used to relate species abundance, biomass, and 16 assemblage metrics to environmental variables at the three spatial scales. The site and basin scales defined fishes along a gradient from high conductivity, fine substrate, and agricultural land cover to low conductivity, rocky substrate, and forested land cover. For abundance and biomass, the strongest assemblage pattern contrasted northern hog sucker *Hypentelium nigricans*, blackside darter *Percina maculata*, and logperch *P. caprodes* with common carp *Cyprinus carpio*, channel catfish *Ictalurus punctatus*, and sauger *Sander canadensis*. The *H. nigricans* group, along with high values of index of biotic integrity and some assemblage metrics (percent lithophilic spawners, percent round-bodied suckers), corresponded with the forested end of the ecological gradient, whereas the *C. carpio* group and percent anomalies corresponded with the agricultural end. Natural environmental conditions, including bedrock geology type, bedrock depth, surficial geology texture, basin area, and precipitation, also influenced the fish assemblage. Partial RDA procedures partitioned the explained variation among spatial scales and their interactions. We found that widespread land cover alterations at the basin scale were most strongly related to fish assemblages across our study area. Understanding the influence of environmental variables among multiple spatial scales on fish assemblages can improve our ability to assess the ecological condition of large river systems and subsequently target the appropriate scale for management or restoration efforts.

INTRODUCTION

Environmental variables at multiple spatial scales drive the physicochemical and biological processes in streams and rivers (Hynes 1970). The

River Continuum Concept accounts for many physical and biotic interactions along the length of relatively homogenous rivers that are primarily confined to their channels (Vannote et al. 1980; Sedell et al. 1989). The Flood Pulse Concept discusses the lateral dimension that incorporates riverine–floodplain interactions to

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describe the ecology of dynamic rivers with intact floodplains (Junk et al. 1989). Ward and Stanford (1989) add that rivers are open systems with interactive pathways along longitudinal, lateral, vertical, and temporal dimensions. Many aspects of river ecology are illuminated by these concepts, especially if considering that lotic systems are largely organized as a nested hierarchy both spatially and temporally (Johnson et al. 1995).

Basin-scale disturbance, land cover alterations, geomorphology, and impoundments have strong links with fish assemblages (Lyons et al. 2001; Mebane et al. 2003; Gresswell et al. 2006; Kaufmann and Hughes 2006; both this volume). Such features at broad spatial scales can affect rivers directly or indirectly by constraining other environmental features at small spatial scales (Frissell et al. 1986; Poff 1997). Knowing which variables among multiple spatial scales integratively affect river fish assemblages increases our ability to detect anthropogenic influences, link biological response signatures with human-induced stress, and target management at the appropriate scale to ultimately improve river health (Karr and Chu 1999; Norris and Thoms 1999).

Biological monitoring of fish assemblages is valuable for determining natural and anthropogenic influences on river resources (Ohio EPA 1987; Simon and Lyons 1995). Indices of biotic integrity (IBIs) use combinations of assemblage attributes, or metrics, that encompass the structure, composition, and function of the biological assemblage to represent resource condition (Karr et al. 1986; Hughes and Oberdorff 1999; Lyons et al. 2001). The absolute abundance or biomass of fish species can represent how successful a species is in a system, revealing patterns of environmental influences on rivers. In this paper, we link environmental variables with river fishes.

Collectively, it has been shown that site and basin variables influence stream biota, but the most important spatial scale differs among studies. Several researchers found that local physicochemical variables that help determine the biotic

assemblages, such as nutrients, substrate, channel shape, and temperature, are largely dependent upon variables like climate, geology, and land cover at the basin scale (e.g., Hunsaker and Levine 1995; Richards et al. 1996; Johnson et al. 1997). Other studies show that the most influential spatial scale depends upon the inherent conditions and stressors among the study sites, the predictor variables, and the response variables used in the analyses (Allan et al. 1997; Weigel 2003; Weigel et al. 2003). Furthermore, the site scale may be very influential in basins having little agriculture or urbanization, but the basin scale becomes increasingly important in more modified basins where there are broad-scale differences among the sampling sites (Wang et al. 2003 and 2006, this volume). However, these studies are limited to wadeable streams, and there is incomplete understanding of the role of different spatial scales in nonwadeable river ecosystems.

Our first objective was to determine if environmental variables at the site, reach, and basin scales affect fish abundance, biomass, and assemblage metrics within riverine reaches of nonwadeable river ecosystems. Our second objective was to evaluate the importance of the environmental variables detected for objective one by measuring the degree of influence they had on each fish data set. Our third objective was to determine the influence of each spatial scale on the fishes. We discuss relations among the environmental variables at different spatial scales, patterns among the fishes, and relations between the environmental variables and the fishes.

METHODS

Wisconsin has at least 40 nonwadeable rivers with a combined length of more than 2,500 km as river and 1,500 km as impounded (Lyons et al. 2001; authors' unpublished data). We considered a river reach nonwadeable if it had at least 3 km of continuous channel too deep to sample effectively by wading during summer base flow. Each site was sampled once during the summers of 1996–2003. All of our sites were in warmwater

reaches, where summer water temperatures excluded resident salmonids. We sampled riverine and slightly impounded reaches. Our most impounded sites still had considerable flow, and we did not include lake-like reservoirs. For this study, we used data from 38 sites on 31 nonwadeable rivers spanning four ecoregions (Figure 1) to characterize the variety of Wisconsin's river types and

the kinds and intensities of human influences upon each river type. Some sites had minimal human influence, whereas others had moderate influences from nonpoint-source pollution or dams that caused fragmentation and hydrologic modifications. A few sites had multiple stressors, including cumulative effects of nonpoint-source and historic point-source pollution.

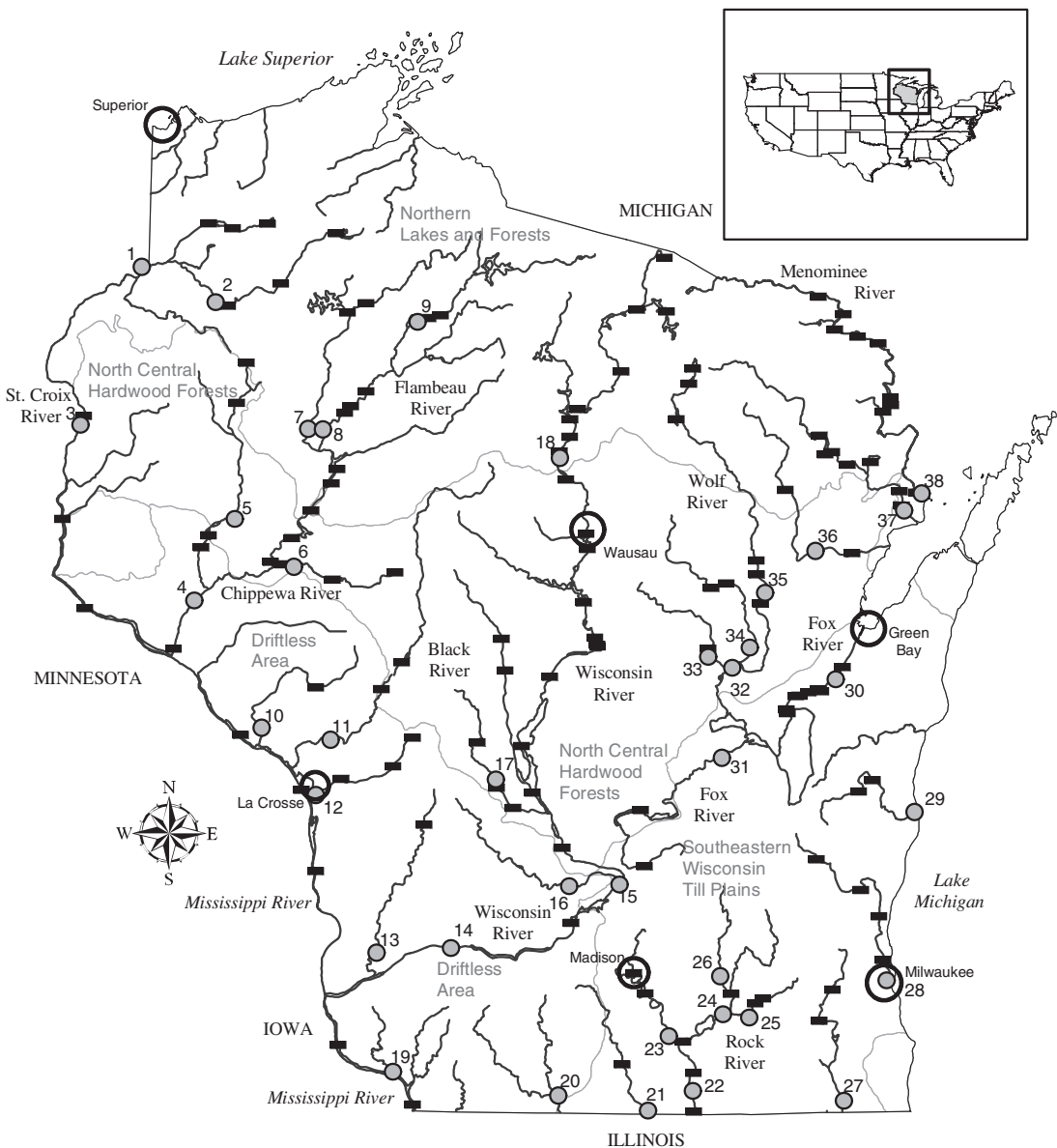


Figure 1. Sampling sites (dots), dams (bars), major cities, and ecoregions in Wisconsin. Site numbers correspond with Table 4.

Fish Data

We used standard methods for collecting fishes from Wisconsin's nonwadeable rivers to calculate IBI scores and assemblage metrics (Lyons et al. 2001). Sampling occurred once during daylight between June and September from 1996 to 2003. We boat electrofished downstream along one randomly chosen shore for 1.6 km, a distance at which estimates of species richness were asymptotic and insensitive to variation in sampling effort (Lyons et al. 2001). One person used a 17-mm (stretch mesh) dip net and tried to capture all fish seen. All captured fish were identified, counted, weighed in aggregate by species, and then released, except for a few voucher specimens.

Catch data were summarized by site as species abundance, biomass, and 16 assemblage measures, including IBI score (Table 1). The IBI

range is from 0 to 100 with qualitative categories at 20-point increments (e.g., 80–100 = excellent). Only species that were found in at least 10% of the sites were considered common and thus included in the abundance and biomass data sets (Table 2). We omitted rare taxa because they tend to skew multivariate analyses if the emphasis is on assemblage composition and environmental relations (Gauch 1982; McCune and Grace 2002).

Environmental Data

We collected environmental data at site, reach, and basin scales (Table 3). The site-scale corresponded with the 1.6 km of river sampled for fish. Conductivity was measured at the downstream end of the site, whereas broad categories of rock substrate, fish cover, and bank condition

Table 1. Fish metric definitions and summary statistics. Metrics with the abbreviation “n” were calculated from the total number of fish captured; metrics with “wt” were calculated from the total weight. See Lyons et al. (2001) for classification of species origin, tolerance, feeding, habitat, and spawning.

Metric	Definition	Min	Mean	Max
IBI	Index of biotic integrity tailored to Wisconsin's warmwater, nonwadeable rivers; scale 0–100 (Lyons et al. 2001)	5	64	100
CPUE	Catch per unit effort (1,600 m), excluding species tolerant to environmental degradation (e.g., hydropower peaking, organic pollution, sedimentation).	9	106	372
WPUE ^a	Weight per unit effort (kg/1,600 m), excluding tolerant species	3.9	29.2	151.4
% DELT ^a	Percent of total fish captured that had deformities, eroded fins, lesions, or tumors	0.0	0.5	6.7
Native ^a	Number of species, excluding alien species	4	13	27
Sucker ^a	Number of species in the sucker family (Catostomidae)	1	4	8
Intolerant ^a	Number of species considered intolerant of degradation	0	3	7
Riverine ^a	Number of species that were obligate river dwellers (i.e., typically not found in lentic habitats)	0	5	13
% riverine (n) ^a	Percent of total fish captured that were obligate river dwellers	0.0	26.0	79.0
% riverine (wt)	Percent of total biomass accounted for by obligate river dwellers	0.0	24.6	87.0
% invertivores (n)	Percent of total fish captured that were invertivores	1.3	63.0	94.0
% invertivores (wt) ^a	Percent of total biomass accounted for by invertivores	0.9	46.6	97.8
% round suckers (n)	Percent of total fish captured in the genera <i>Cycleptus</i> (blue sucker), <i>Hypentelium</i> (hog sucker), <i>Minytremia</i> (spotted sucker), and <i>Moxostoma</i> (redhorses)	0.5	26.8	87.1
% round suckers (wt) ^a	Percent of total biomass accounted for by round bodied suckers	0.6	38.9	97.4
% lithophil (n) ^a	Percent of total fish captured that were simple lithophilic spawners (i.e., spawn on clean rocky surfaces without preparing a nest or guarding their eggs)	1.5	51.5	93.5
% lithophil (wt)	Percent of total biomass accounted for by simple lithophilic spawners	0.7	42.6	99.3

^a Metric included in IBI (Lyons et al. 2001).

Table 2. Fish species occurring in at least 4 of 38 river sites (~10%). Percentiles were derived from the sites at which the species was present. P25 = 25th percentile, P50 = 50th percentile, and P75 = 75th percentile.

Common name	Scientific name	Number of sites	Abundance			Biomass (g)		
			P25	P50	P75	P25	P50	P75
Mooneyes Hiodontidae								
Mooneye	<i>Hiodon tergisus</i>	5	2	2	4	290	665	1,020
Herrings Clupeidae								
Gizzard shad	<i>Dorosoma cepedianum</i>	7	2	3	4	24	390	767
Minnnows Cyprinidae								
Common carp	<i>Cyprinus carpio</i>	25	5	10	19	13,520	20,300	34,400
Spotfin shiner	<i>Cyprinella spiloptera</i>	27	3	6	16	9	19	52
Common shiner	<i>Luxilus cornutus</i>	8	1	4	6	5	24	41
Hornyhead chub	<i>Nocomis biguttatus</i>	6	1	3	14	14	22	145
Emerald shiner	<i>Notropis atherinoides</i>	19	3	18	28	15	45	75
Sand shiner	<i>N. stramineus</i>	6	1	2	4	2	3	5
Bluntnose minnow	<i>Pimephales notatus</i>	8	2	4	7	6	11	25
Suckers Catostomidae								
Quillback	<i>Carpiodes cyprinus</i>	10	1	2	2	963	2,150	2,348
White sucker	<i>Catostomus commersonii</i>	14	2	3	6	636	1,294	1,857
Northern hog sucker	<i>Hypentelium nigricans</i>	15	4	5	16	894	1,450	5,001
Bigmouth buffalo	<i>Ictiobus cyprinellus</i>	5	1	3	4	5,300	7,800	7,900
Black buffalo	<i>I. niger</i>	4	1	1	1	2,713	3,425	4,150
Spotted sucker	<i>Minytrema melanops</i>	4	2	2	3	150	1,123	2,138
Silver redhorse	<i>Moxostoma anisurum</i>	20	1	4	10	1,985	2,970	9,538
River redhorse	<i>M. carinatum</i>	6	2	3	5	5,113	7,025	9,950
Golden redhorse	<i>M. erythrum</i>	21	2	5	8	1,056	2,448	4,200
Shorthead redhorse	<i>M. macrolepidotum</i>	37	4	11	19	1,550	4,519	10,662
Greater redhorse	<i>M. valenciennesi</i>	4	1	1	1	1,625	1,740	1,870
Bullhead catfishes Ictaluridae								
Channel catfish	<i>Ictalurus punctatus</i>	14	1	2	3	1,035	2,273	3,198
Pikes Esocidae								
Northern pike	<i>Esox lucius</i>	13	1	2	2	260	650	930
Codfishes Gadidae								
Burbot	<i>Lota lota</i>	4	1	1	1	8	16	102
Temperate basses Moronidae								
White bass	<i>Morone chrysops</i>	5	1	2	2	295	430	770
Sunfishes Centrarchidae								
Rock bass	<i>Ambloplites rupestris</i>	13	1	2	3	90	169	250
Pumpkinseed	<i>Lepomis gibbosus</i>	4	1	1	3	17	21	41
Bluegill	<i>L. macrochirus</i>	12	1	2	3	28	62	158
Smallmouth bass	<i>Micropterus dolomieu</i>	29	2	6	17	410	1,180	2,452
Largemouth bass	<i>M. salmoides</i>	7	2	3	4	38	67	409
Black crappie	<i>Pomoxis nigromaculatus</i>	11	2	2	4	166	202	360
Perches Percidae								
Banded darter	<i>Etheostoma zonale</i>	7	2	2	4	166	202	360
Yellow perch	<i>Perca flavescens</i>	11	1	2	5	20	35	198
Logperch	<i>Percina caprodes</i>	15	1	9	29	5	92	240
Gilt darter	<i>P. evides</i>	4	4	7	15	12	19	53
Blackside darter	<i>P. maculata</i>	14	1	4	9	3	12	35
Walleye	<i>Sander vitreus</i>	25	1	2	4	372	780	1170
Sauger	<i>S. canadensis</i>	9	1	4	5	425	623	1035
Drums Sciaenidae								
Freshwater drum	<i>Aplodinotus grunniens</i>	16	2	3	9	830	2,415	4,879

Table 3. Definitions and summary statistics of the environmental variables at the site, reach, and basin scales. Significant ($p = 0.05$) variables found using forward selection procedures were included in redundancy analysis (RDA) of fish abundance (A), biomass (B), and assemblage metric (M) models.

Variable	Definition	Min	Mean	Max	Model
Site scale					
Cond	Specific conductivity ($\mu\text{S} \cdot \text{cm}^{-1}$)	84	353	869	A,B,M
Rock	Visual estimate of riverbed covered with rock substrate > 2 mm from 0 (0%), 1 (1–24%), 2 (25–50%), to 3 (>50%).	0	1.2	3	A,B,M
Cover	Relative density of fish cover (e.g., large woody debris, boulders) from 0 (none) to 3 (high)	1	1.8	3	A
Bank	% of bank rip-rapped or altered from 0 (natural) to 3 (100% modified)	0	0.4	3	
Reach scale					
Impound	Length of river downstream to the nearest impoundment (km)	0.0	20.0	103.0	M
Dam	Length of river upstream to the nearest dam or source lake (km)	0.7	22.5	92.0	
Riverine	Total length upstream and downstream of the site not influenced by dams (km)	1.0	42.4	195.0	
Basin scale					
Lat	Latitude at downstream end of sampling site; measured by GPS	42.6	44.1	45.9	
Area	Basin area upstream of the site (km^2); measured with GIS using digital 1:24,000 maps	660	5,305	26,936	B
Grndwtr	Potential groundwater velocity ($\text{m} \cdot \text{d}^{-1}$) estimated with Darcy's law for entire basin	–3,321	–1,780	–21	
GDD	Growing degree days; reported from nearest weather station	1,484	2,038	2,635	
Precip	Annual mean precipitation for the basin (mm); reported from nearest weather station.	775	815	860	M
Ag	Uplands cultivated for agriculture	0.9	31.3	75.0	B
Forest	Uplands with forest crown closure > 67%	4.9	37.4	72.6	A,M
Grass	Uplands with idle and prairie grasses; pasture; timothy or rye	2.6	10.2	18.3	A,B
Water	Lake or river area without vegetation present	0.0	3.1	11.3	M
Wetland	Persistently wet meadow, lowland shrub or lowland forest with < 10% canopy closure	0.0	15.4	35.0	
Urban	Impervious surface of man-made origin (e.g., pavement, rooftops); golf courses	0.0	1.5	10.5	
Crbnt	Carbonate bedrock	0.0	17.9	100.0	A,B
Mtmrphc	Metamorphic bedrock	0.0	20.4	94.2	
Sndstn	Sandstone bedrock	0.0	36.4	98.8	
Vlcnc	Volcanic bedrock	0.0	17.0	99.5	
BD0-15	Percent of zone 0–15 m below the surface that is composed of bedrock	8.0	45.0	100.0	
BD15-30	Percent of zone 15–30 m below the surface that is composed of bedrock	0.0	24.3	47.6	B
BD30-60	Percent of zone 30–60 m below the surface that is composed of bedrock	0.0	25.1	61.4	
BD60-120	Percent of zone 60–120 m below the surface that is composed of bedrock	0.0	5.0	25.4	
BD120-180	Percent of zone 120–180 m below the surface that is composed of bedrock	0.0	0.1	1.7	
Fine	Fine texture	0.0	7.7	53.6	B,M
Med	Medium texture	0.0	6.2	32.1	
Coarse	Coarse texture	0.0	65.0	99.2	A
Peatmuck	Peat and muck texture	0.0	2.5	20.7	B

were visually estimated throughout the site. The reach-scale variables were measures of river fragmentation, including distances from the fish site to the nearest impoundment downstream, dam upstream, and total length of riverine habitat in both directions from the site. Dams are ubiquitous on Wisconsin's waterways, and they fragment or at least influence every system to some extent. Basin-scale measurements were taken throughout the basin upstream of the fish site. We delineated basins with ARC/INFO software (ESRI 1999) using digital elevation models and U.S. Geological Survey 7.5-min quadrangle maps. Natural basin conditions were characterized by latitude, mean precipitation, growing degree-days, groundwater delivery potential, bedrock geology, bedrock depth, surficial-geology texture, and basin area. Modeling of Darcy's law estimated the groundwater delivery potential as a function of hydraulic conductivity and hydraulic slope (Wiley et al. 1997). We used land cover proportions within the basin, measured from the WISCLAND digital land cover map (WDNR 1998), to characterize anthropogenic influences.

Data Analyses

We used direct gradient analysis techniques to relate multivariate environmental data directly to multivariate species abundance and composition data. Redundancy analysis (RDA) and canonical correspondence analysis (CCA) are examples of such methods that are appropriate for data sets having short gradients and linear responses by species (RDA), or long gradients and unimodal responses by species (CCA; Legendre and Legendre 1998). We ran detrended correspondence analysis separately on fish abundance, biomass, and assemblage metric data sets to identify gradient lengths and decide which ordination technique best fit our data (Hill and Gauch 1980). We used a site-by-species matrix for abundance and biomass data and a site-by-metrics matrix for the assemblage metrics data. The analyses indicated that RDA was the appropriate ordination

technique (gradient lengths < 2.4 ; ter Braak and Prentice 1988). Redundancy analysis explains variation in a set of response variables (e.g., species abundance) as a function of multiple axes that are combinations of explanatory (environmental) variables. Here, we only report the results of the first two axes because they explain the most variation and to simplify the results for clarity. The correlation of an environmental variable with each axis indicates the strength of its relationship with the fish characteristics.

Our statistical analyses were similar to those of Wang et al. (2003) and Weigel et al. (2003), and had three main components. First, we identified key environmental variables within the site, reach, and basin scales that influenced fish abundance, biomass, and assemblage metrics. Note that we had three environmental data sets (i.e., site, reach, and basin) and three fish data sets (i.e., abundance, biomass, metrics), requiring analyses on each of the nine scale and fish data-set pairs. To address our first objective, we ran RDA with forward selection procedures using CANOCO software to identify environmental variables that explained significant amounts of variation within each fish data set and scale combination ($p \leq 0.05$; ter Braak and Smilauer 2002). Abundance and biomass data were log transformed to better approximate normal distributions for each RDA performed, and 100 Monte Carlo simulations indicated the statistical significance of the environmental and fish relation (ter Braak and Prentice 1988).

For each fish data set, we combined the key environmental variables from the site, reach, and basin scales selected in the first RDAs to address our second objective. We ran one more RDA for each fish data set, but this time, we only used those key environmental variables detected by forward-selection procedures used in the first series of RDAs. Results from the second series of RDAs quantified the influence that each key environmental variable had on the corresponding fish data set.

Third, we determined the influence of each spatial scale on each fish data set. For this next

series of analyses, again we used the key environmental variables across spatial scales for each fish data set. Partial RDA procedures partitioned the explained variation among the multiple spatial scales for each data pair (Borcard et al. 1992; Okland and Eilertsen 1994; Legendre and Legendre 1998). Partial RDA is a multiple-step procedure in which all possible combinations of scales are sequentially used as covariates to determine the variation explained for each scale and combination of scales (interactions). Partitioning the variation indicated how much variation was explained for the overall model, each scale, each two-way interaction among scale pairs, and the three-way interaction of all scales. The number of variables were unbalanced among spatial scales, but Okland and Eilertsen (1994) found that as long as forward selection of variables is used prior to ordination, the number of variables included in a set does not bias the importance of that set.

RESULTS

At the 38 sites, we collected a total of 76 species, with 39 in at least 4 sites (Table 2). We caught a total of 4,769 individuals and 1,928 kg of fish. The species most frequently encountered were shorthead redhorse *Moxostoma macrolepidotum* (97% of sites) and smallmouth bass *Micropterus dolomieu* (76%), the most numerous individuals were shorthead redhorse (608 individuals) and logperch *Percina caprodes* (383), and the greatest biomasses occurred in common carp *Cyprinus carpio* (715 kg) and shorthead redhorse (346 kg; Table 4). Individual samples yielded from 5 to 29 species, from 11 to 432 individuals, and from 9 to 151 kg of biomass. At the site with the highest biomass, silver redhorse *M. anisurum* and shorthead redhorse comprised 81% of the biomass. The highest dominance by one species at a site occurred where 340 gizzard shad *Dorosoma cepedianum* comprised 88% of the catch.

Summary statistics at the site scale indicated that our sites represented a range of environmental conditions (Tables 3 and 4). Conductivity was

less than 200 $\mu\text{S}/\text{cm}$ at 13 sites (minimum = 84 $\mu\text{S}/\text{cm}$) and greater than 400 $\mu\text{S}/\text{cm}$ at 13 other sites (maximum = 869 $\mu\text{S}/\text{cm}$). No rock substrate was found at nine sites, whereas it was dominant at five sites, and present at intermediate levels in the other sites. Fish cover was present everywhere, and seven sites had a high density. Bank habitat was unmodified at 27 sites, 100% modified at 1 site, and somewhat modified elsewhere.

A range of conditions among sites existed at the reach scale as well (Tables 3 and 4). Ten sites were 0–5 km upstream from an impounded river reach, whereas eight sites were 40–166 km upstream. Nine sites were 1–5 km downstream from the nearest dam, and 13 sites were 40–148 km downstream. Nine sites had 0.3–25 km of riverine habitat, whereas 13 sites had 80–313 km of riverine habitat.

The study rivers had a wide variety of natural (e.g., size, climate, geology) and land cover conditions at the basin scale (Tables 3 and 4). The smallest basin area (660 km^2) strongly contrasted with the largest (26,936 km^2), and 20 sites had basin areas less than 2,500 km^2 , whereas five sites had areas greater than 15,000 km^2 . All basins had negative groundwater velocity values, meaning that more water flowed from the river to the groundwater than vice versa, and the values ranged from -21 m/d to $-3,321$ m/d. Growing degree-days varied from 1,484–2,635. In contrast, precipitation had a small range from 775 to 860 mm. Agriculture dominated in eight basins and covered less than 10% of the area in eight other basins. Forest dominated in 10 basins and covered less than 10% of the area in only four basins. Grass (range: 2–18%) and open water (range: 0–11%) varied relatively little among basins. The highest urban percentages ranged between 6% and 11% in three basins. Carbonate bedrock geology was present in only 14 basins, but was the dominant type in 8 of the basins. Sandstone bedrock dominated in 12 basins, metamorphic in 6 basins, and igneous in 5 basins. Bedrock-depth measurements were highly correlated (e.g., $r = 0.725$ – 0.945), but no surficial geology types were significantly correlated.

Table 4. Environmental and biological conditions per site. Site numbers correspond with Figure 1. Abbreviations as in Table 3. IBI = index of biotic integrity (Lyons et al. 2001).

Site no.	River name	Area (km ²)	Cond (µS/cm)	Rock	Impound (km)	Ag (%)	Forest (%)	IBI	Impact category	Dominant species by abundance	Dominant species by biomass (kg)
1	St. Croix	4,079	143	2	66	1	72	95	minimal	52 Shorthead redhorse 37 Common shiner	4.9 Shorthead redhorse 2.0 Silver redhorse
2	Namekagon	1,264	181	3	66	2	67	90	dam	43 Shorthead redhorse 32 Northern hog sucker 35 Emerald shiner	29.3 Shorthead redhorse 11.9 Golden redhorse 34.4 Common carp
3	St. Croix	16,162	155	1	24	12	52	75	dam	19 Common carp 49 Emerald shiner	11.0 River redhorse 10.7 Shorthead redhorse
4	Chippewa	23,336	128	1	20	18	49	100	minimal	23 Spottfin shiner 60 Northern hog sucker 50 Common shiner	10.6 River redhorse 13.1 Northern hog sucker 10.4 Golden redhorse
5	Red Cedar	2,720	185	3	5	29	45	100	minimal	72 Yellow perch 56 Shorthead redhorse 19 Logperch	46.5 Shorthead redhorse 11.9 Walleye 7.0 Shorthead redhorse
6	Eau Claire	2,062	105	1	0	32	41	75	dam	15 Shorthead redhorse 185 Logperch	4.4 Golden redhorse 8.2 Shorthead redhorse
7	Chippewa	4,403	89	1	14	4	62	90	minimal	22 Smallmouth bass 26 Silver redhorse 15 Golden redhorse	3.6 Northern hog sucker 22.0 Silver redhorse 10.0 Golden redhorse
8	Flambeau	4,817	93	2	9	3	57	85	dam	27 Emerald shiner 11 Shorthead redhorse 28 Emerald shiner	13.7 Common carp 3.7 Freshwater drum 20.3 Common carp
9	NF Flambeau	2,370	103	1	31	2	57	95	minimal	17 Spottfin shiner 48 Shorthead redhorse 17 Smallmouth bass	8.7 Silver redhorse 31.0 Shorthead redhorse 14.7 Silver redhorse
10	Trempealeau	1,668	282	0	9	32	44	35	nonpoint	6 Shorthead redhorse 36 Shorthead redhorse 24 Spottfin shiner	3.0 Common carp 2.0 Shorthead redhorse 22.7 Shorthead redhorse
11	Black	5,177	114	1	23	25	45	90	minimal	37 Spottfin shiner 22 Emerald shiner 18 Emerald shiner	10.1 Common carp 16.4 Common carp 11.9 Shorthead redhorse
12	LaCrosse	1,212	340	0	5	34	45	60	nonpoint	14 Common carp 14 Shorthead redhorse 11 Shorthead redhorse	5.8 Freshwater drum 28.1 Common carp 12.8 Shorthead redhorse
13	Kickapoo	1,787	460	1	40	43	42	55	nonpoint	8 Yellow perch 83 Shorthead redhorse 36 Silver redhorse	61.7 Silver redhorse 61.1 Shorthead redhorse 25.2 Common carp
14	Wisconsin	26,936	220	0	45	25	42	100	minimal	10 Common carp 5 Sauger	3.3 Black buffalo
15	Wisconsin	21,160	153	1	5	32	33	65	nonpoint		
16	Baraboo	1,492	321	0	22	48	31	55	nonpoint		
17	Lemonweir	1,132	137	0	2	17	33	35	nonpoint		
18	Wisconsin	5,905	84	3	2	1	59	80	minimal		
19	Grant	818	668	1	0	75	16	50	multiple		

(Table continues)

Table 4 (continued)

Site no.	River name	Area (km ²)	Cond (µS/cm)	Rock	Impound (km)	Ag (%)	Forest (%)	IBI	Impact category	Dominant species by abundance	Dominant species by biomass (kg)
20	Pecatonica	2,461	667	1	103	65	20	50	nonpoint	15 Shorthead redhorse	28.2 Common carp
21	Sugar	1,730	576	0	22	63	17	70	nonpoint	14 Common carp	7.8 Bigmouth buffalo
22	Rock	8,858	661	1	1	60	7	5	nonpoint	13 Shorthead redhorse	18.3 Common carp
23	Yahara	1,339	669	2	20	55	7	70	nonpoint	11 Silver redhorse	11.5 Bigmouth buffalo
24	Rock	4,900	675	0	6	61	7	15	nonpoint	19 Common carp	45.2 Common carp
25	Bark	660	659	0	17	44	17	30	nonpoint	6 Sauger	4.0 White sucker
26	Crawfish	2,020	590	2	13	68	5	50	nonpoint	58 Northern hog sucker	20.8 Northern hog sucker
27	Fox (IL)	2,202	869	1	0	41	15	75	nonpoint	18 Spottin shiner	9.3 Channel catfish
28	Milwaukee	1,813	570	1	0	45	13	35	multiple	26 Common carp	59.9 Common carp
29	Sheboygan	1,083	633	2	2	61	10	30	multiple	5 Emerald shiner	7.9 Bigmouth buffalo
30	Fox	15,670	370	2	0	36	28	10	multiple	29 Common carp	72.7 Common carp
31	Fox	3,626	339	2	7	35	24	70	minimal	14 Spottin shiner	4.1 Golden redhorse
32	Wolf	5,853	330	0	30	28	42	70	minimal	44 Freshwater drum	29.2 Common carp
33	Little Wolf	1,313	464	3	9	32	30	85	minimal	28 Shorthead redhorse	18.1 Shorthead redhorse
34	Embarrass	1,764	364	1	30	28	31	95	minimal	40 Emerald shiner	18.1 Quillback
35	Wolf	2,953	283	1	91	5	73	80	minimal	20 Quillback	17.2 Common carp
36	Oconto	1,831	264	1	0	11	63	44	dam	5 Gizzard shad	6.0 Common carp
37	Peshigo	2,823	231	2	7	15	54	50	multiple	2 Common carp	2.1 Greater redhorse
38	Menominee	10,179	254	3	13	3	67	80	minimal	2 Greater redhorse	50.4 Common carp
										2 Gizzard shad	26.6 Gizzard shad
										23 Smallmouth bass	13.5 Common carp
										10 Common carp	1.7 Freshwater drum
										4 Emerald shiner	
										4 Smallmouth bass	
										27 White bass	19.9 Common carp
										18 Freshwater drum	9.2 Silver redhorse
										21 Emerald shiner	2.0 Freshwater drum
										8 Bluegill	1.5 Greater redhorse
										33 Logperch	15.6 Shorthead redhorse
										25 Shorthead redhorse	5.9 Northern hog sucker
										31 Emerald shiner	11.1 Common carp
										15 Shorthead redhorse	6.1 Channel catfish
										155 White sucker	82.9 Common carp
										64 Silver redhorse	3.4 Silver redhorse
										32 Smallmouth bass	12.8 Smallmouth bass
										4 Northern hog sucker	1.0 Northern hog sucker
										40 Smallmouth bass	79.7 Common carp
										20 Common carp	1.5 Freshwater drum
										24 Logperch	2.0 Silver redhorse
										17 Smallmouth bass	1.7 White sucker

Coarse-textured surficial geology dominated 31 basins. Medium and fine textures were present at less than 10% in 27 basins and between 10% and 30% in 11 basins. Peat and muck textures were present at less than 20% in 15 basins.

Fish Abundance Model

Environmental variable selection.—For fish abundance, RDA retained conductivity, rock, and fish cover at the site scale; no reach-scale variables; and forest and grass land covers, carbonate bedrock geology, and coarse-textured surficial geology at the basin scale (Table 3).

Relations between fish abundance and combined spatial scale variables.—For the fish abundance data set, RDA on the seven environmental variables retained from the site and basin scales explained 36% of the variation using multiple axes ($F = 2.45$; $P = 0.005$). The first two RDA axes accounted for 68% of the total variation that was explained by the full model (i.e., with multiple axes). On the first RDA axis, abundance of northern hog sucker *Hypentelium nigricans*, blackside darter *Percina maculata*, logperch, and smallmouth bass were positively related to percent forested land cover, rock substrate, and coarse-textured surficial geology (Figure 2a; Table 5). Abundance of channel catfish *Ictalurus punctatus*, emerald shiner *Notropis atherinoides*, sauger *Sander canadensis*, and common carp were positively related to grassland cover, conductivity, and carbonate bedrock geology. The second RDA axis accounted for 16.2% of the total variation explained. Gizzard shad was positively related to carbonate bedrock geology and conductivity, whereas spotfin shiner *Cyprinella spiloptera*, emerald shiner, shorthead redhorse, and river redhorse *Moxostoma carinatum* were positively related to grass and forested land covers.

Fish Biomass Model

Environmental variable selection.—For biomass, RDA retained conductivity and rock at the site scale; no reach-scale variable; and basin area,

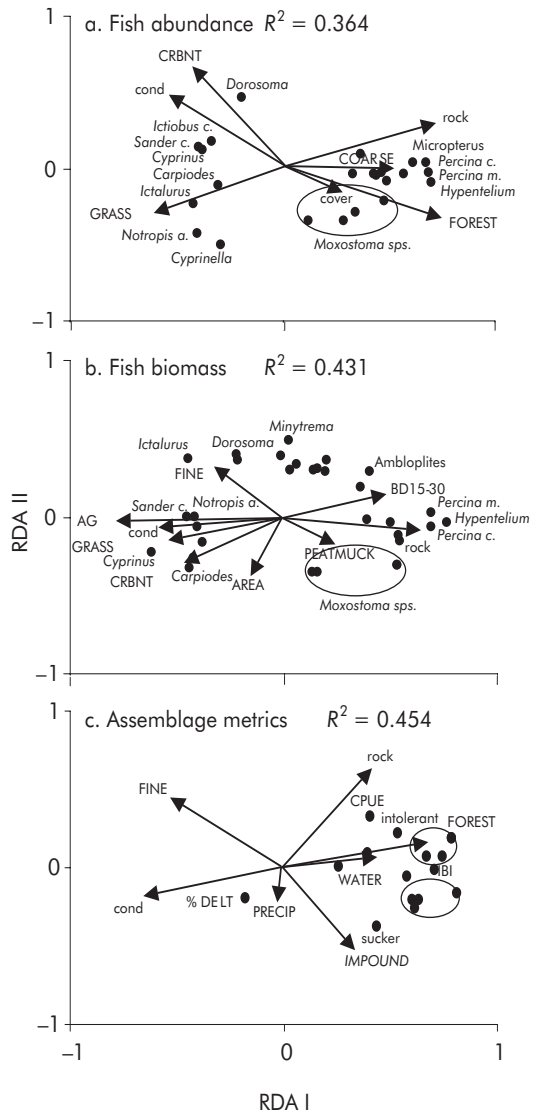


Figure 2. Redundancy analysis plots of the significant environmental variables on fish (a) abundance, (b) biomass, and (c) assemblage metrics. Arrow length corresponds with the importance of the environmental variable, and its direction indicates its correlation with the axes. Only species with high correspondence to an axis (score ≥ 0.3) were displayed to reduce clutter. Table 3 defines environmental variables. Basin scale variables are in uppercase, reach-scale variables are in uppercase italics, and site-scale variables are in lowercase. Taxonomic labels are by genus with the first letter of a species name included if necessary for clarification. The metrics %lithophil, %invertivores, %riverine, and %round suckers clustered by biomass (higher ellipse in panel "c") and abundance (lower ellipse in panel "c").

Table 5. Summary statistics on the second series of RDAs used to quantify the importance of key environmental variables on fishes. Axis R^2 indicates how much of the total explained variation (model R^2) was attributable to the individual axis. Axis loadings indicate how strongly the variable is related to the axis. Abbreviations as in Table 3.

Model Variable	model R^2	F	P	Axis 1 R^2 Axis 1 loading	Axis 2 R^2 Axis 2 loading
Abundance	0.364	2.45	0.005	0.52	0.16
Grass				−0.6362	−0.3219
Conduct				−0.5644	0.4886
Crbnt				−0.4528	0.6898
Cover				0.2878	−0.1904
Coarse				0.5302	−0.0154
Rock				0.7327	0.2954
Forest				0.7643	−0.3606
Biomass	0.431	2.35	0.005	0.39	0.15
Ag				−0.8020	−0.0256
Conduct				−0.6016	−0.0677
Grass				−0.5492	−0.1519
Crbnt				−0.4725	−0.3043
Fine				−0.3270	0.3561
Area				−0.1496	−0.4038
Peatmuck				0.2607	−0.1788
BD15-30				0.5100	0.1633
Rock				0.6796	−0.0925
IBI metric	0.454	3.56	0.002	0.79	0.08
Conduct				−0.6877	−0.1978
Fine				−0.5490	0.4374
Precip				−0.0198	−0.2244
Impound				0.3607	−0.5388
Rock				0.4469	0.6381
Water				0.4725	0.0542
Forest				0.7293	0.1430

agriculture and grass land covers, carbonate bedrock geology, BD15–30, and peatmuck-textured surficial geology at the basin scale (Table 3).

Relations between fish biomass and combined spatial scale variables.—For the fish biomass data set, RDA on the nine environmental variables retained from the site and basin scales explained 43% of the variation ($F = 2.35$; $P = 0.005$). The first two RDA axes accounted for 54% of the variation explained by the full model. On the first RDA axis, biomass of northern hog sucker, logperch, blackside darter, and common shiner *Luxilus cornutus* were positively related to rock substrate and BD15–30 (Figure 2b, Table 5). Biomass of common carp, sauger, channel catfish, and quillback *Carpoides cyprinus* were positively

related to conductivity, and agricultural and grass land covers. The second RDA axis accounted for 15% of the total variation explained. Spotted sucker *Minytrema melanops* and freshwater drum *Aplodinotus grunniens* were positively related to fine-textured surficial geology, whereas river redhorse, shorthead redhorse, quillback, and golden redhorse *Moxostoma erythrurum* were positively related to basin area and carbonate bedrock geology.

Assemblage Metrics Model

Environmental variable selection.—At the assemblage level, RDA retained conductivity and rock at the site scale; impoundment at the reach

scale; and forest and water land covers, precipitation, and fine-textured surficial geology at the basin scale (Table 3).

Relations between fish assemblage metrics and combined spatial scale variables.—For the assemblage metric data set, RDA on the seven retained environmental variables from the site, reach, and basin scales explained 45% of the variation ($F = 3.56$; $P = 0.002$). The first two RDA axes accounted for 87% of the variation explained by the full model, with the first axis explaining 79% of the variation. On the first RDA axis, the metrics %lithophil (n, wt), %round-bodied suckers (wt), %invertivores (wt), and IBI were positively related to forested and open-water land covers (Figure 2c, Table 5). Low scores for those metrics were positively related to conductivity and fine-texture surficial geology. Along the second RDA axis, CPUE was positively related to rock substrate and fine-textured surficial geology, whereas the number of sucker species was positively related to impoundment.

Relative Importance of Spatial Scale on Fish Abundance, Biomass, and Assemblage Metrics

The RDA variation-partitioning procedures on the fish abundance data set with the three site variables and the four basin variables attributed most of the explained variation to the basin scale (38%; Figure 3). The site scale and site-basin interaction accounted for equal amounts of variation (31%). Partial RDA on the fish biomass data set with the two site and seven basin variables again attributed most of the explained variation to the basin scale (62%). The site scale accounted for 15%, whereas the site-basin interaction accounted for 23%. Partial RDA on the assemblage metrics with the two site variables, one reach variable, and four basin variables indicated that 35% of explained variation was attributable to the basin scale, 17% to the site scale, 6% to the reach scale, and 32% to the site-basin interaction.

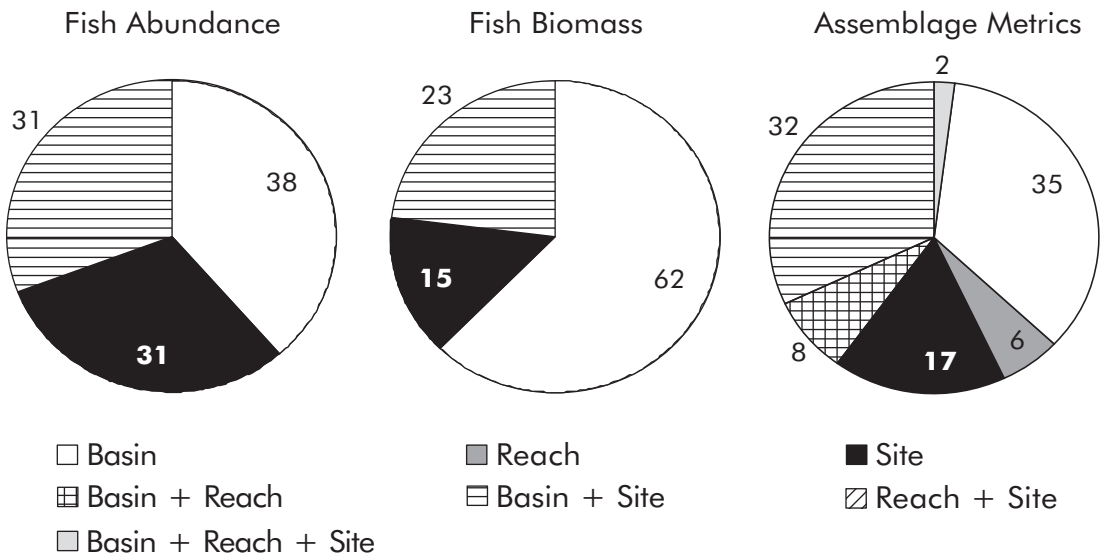


Figure 3. Partial RDA of environmental variables among multiple spatial scales on fish abundance, biomass, and assemblage metrics. The proportion of explained variation was attributed to environmental variables at different scales and interactions among the scales. Total variation explained was 36.4% for abundance, 43.1% for biomass, and 45.4% for assemblage metric data.

DISCUSSION

Relations among the Environmental Variables

The analyses identified a key set of environmental variables from multiple spatial scales that explained patterns in the fish data, and these key variables were related to one another. At the site scale, conductivity and rock substrate showed a strong and inverse correspondence along the first RDA axis in each analysis, suggesting that rocky rivers with low conductivity have particular fish assemblage characteristics. Similar analyses among small streams in a relatively undisturbed ecoregion found that no land cover, conductivity, or substrate composition measures were associated with patterns in fishes (Wang et al. 2003), but they were associated with patterns in macroinvertebrates (Weigel et al. 2003). Emery et al. (2003) used principal components analysis to relate fish assemblage characteristics with abiotic conditions and, in contrast to this study, found that coarse substrate and high conductivity were in the same direction along one axis. It is likely that substrate composition and covariates of conductivity affected the fish assemblage, not conductivity itself.

We assumed that reach-scale variables would be related strongly with all three fish data sets, but only "impound" was selected in one model. In the assemblage metric model, "impound" had little influence along the first RDA axis, but it strongly contrasted rock substrate along the second RDA axis. The rivers having greater length downstream to the nearest impoundment in this study tended to be on the lower reaches of sandy rivers. Other recent studies link dams and variables at the site-scale, which in turn, strongly influence fish (Dieterman and Galat 2004; Quist et al. 2004; Tiemann et al. 2004). However, our study underestimates these links because we only sampled riverine habitat.

At the basin scale, a land cover variable was significant in all three models. If agriculture or forest land cover was selected using forward selection

procedures, the other variable was not selected because adding it explained little additional variation among the fishes. Our analyses do not imply that forest, which was selected in two out of three models, was a better measure of human influence than agriculture. Rather, we infer that agriculture and forest indicate about the same thing because of their strong, inverse relation. Furthermore, urban land cover was omitted from the model because other basin-scale variables selected using forward-selection procedures of RDA explained a similar pattern among the fishes, so therefore, one should not conclude that urbanization is unrelated to fishes. Agriculture, forest, and urban land cover have consistently been helpful in understanding fish assemblages in Wadeable streams (e.g., Allan et al. 1997; Wang et al. 1997) and unwadeable rivers (Mebane et al. 2003), but the land cover and fish relations have been less documented for large rivers. Our results showed that differences in land cover were more influential than climate or geology, but these variables are inherently linked because, for example, precipitation, growing degree-days, and soil type partly determine where forest or agriculture appears on the landscape.

Collectively across the three fish models, we observed an environmental gradient from rivers with high agricultural land cover and conductivity to rivers with high forestland cover and rock substrate. Conductivity and agriculture had similar direction and magnitude along the first axis in each RDA model, in direct contrast to rock and forest, meaning that these variables at different spatial scales explained similar patterns. The analyses suggest that a single conductivity sample and substrate estimate explained about the same pattern as intensive land cover quantification for our three fish data sets. From a management or monitoring standpoint, the results reaffirm the usefulness of supplementing biomonitoring data with basic physical and chemical information.

Relations among Fish

Similar patterns in fish assemblages emerged from RDA on abundance and biomass data sets.

Along the first RDA axis, common carp, channel catfish, sauger, emerald shiner, quillback, bigmouth buffalo *Ictiobus cyprinellus*, and black buffalo *Ictiobus niger* contrasted with species in the opposite direction, including northern hog sucker, blackside darter, logperch, common shiner, golden redhorse, smallmouth bass, and rock bass *Ambloplites rupestris*. Fish patterns along the second RDA axes were less clear, but river redhorse and shorthead redhorse were consistently located towards one end of the gradient. The northern hog sucker group tended to correspond with the axes more closely than the common carp group, which is represented by how far the species are plotted from the origin in Figure 2. Species in the common carp group tolerate environmental degradation, warmer water, higher turbidity, or are more ubiquitous river species (Becker 1983; Lyons et al. 2001). Black buffalo seems to be an exception to the group in that it is an intolerant fish that inhabits relatively strong currents, but it does dwell in turbid water over a variety of bottom types. In contrast, five of the seven species in the northern hog sucker group are considered intolerant of environmental degradation, and all prefer clearer water over rocky substrate (Becker 1983; Lyons et al. 2001). As expected, both groups of fish were predominantly river or large river specialists.

Redundancy analysis of the assemblage metrics indicates strong relations between IBI, IBI metrics, and species or species groups from the abundance and biomass analyses. For example, %lithophilic spawners was the strongest metric in the positive direction along the first RDA axis, which corresponded with the northern hog sucker group. Five of the seven members of that group are lithophilic spawners (two nest guarders), whereas in the contrasting group with common carp, only two of the seven are lithophilic spawners. The feeding guilds showed a similar pattern, with five of the seven in the northern hog sucker group being invertivores, whereas omnivores dominated the common carp group. Index of biotic integrity scores corre-

sponded with the northern hog sucker group. Lyons et al. (2001) also found that %invertivore, %riverine, %lithophil, and %round-bodied sucker metrics had similar patterns regardless of whether they were calculated by abundance or biomass.

Relations between Scale and Fish

Fragmentation and modified flow regimes caused by dams affect fish assemblages, particularly riverine and benthic specialists (Karr et al. 1985; Kinsolving and Bain 1993; Lyons et al. 2001). This study did not investigate impounded river reaches that are obviously altered by dams, but we focused on riverine reaches and assumed that dams would influence the fishes in the riverine sections upstream or downstream of the impoundments. Dams influenced sucker species but had weak relations with the individual species in our data sets regarding abundance and biomass. The assemblage metric data set was inherently less variable than the abundance or biomass data sets because it already summarized some information about the assemblage. Even our minimally influenced sites suffered cumulative effects of multiple dams that impeded fish migration, in turn, likely reducing the number of large river specialists or intolerant species like blue sucker *Cycleptus elongatus*, crystal darter *Crystallaria asprella*, paddlefish *Polydon spathula*, and shovelnose sturgeon *Scaphirhynchus platyrhynchus* (Lyons et al. 2000). We did not include these species in our analyses because rare species skew RDA of species and environmental data (Gauch 1982; McCune and Grace 2002), but their extirpation or reduction clearly indicates environmental problems.

Our surrogate measure of river size, basin area, influenced the biomass of some riverine species, but basin area was not significant in the abundance or assemblage metric models. The only metric Lyons et al. (2001) found that correlated with basin area was the percent weight of large river inhabitants, which was omitted from the final IBI. Here, we found that the biomass of

river redhorse, shorthead redhorse, quillback, and golden redhorse corresponded to basin area; all four species are riverine, with the river redhorse being a large river obligate. Our results reaffirm that the assemblage metrics and IBI can be compared among rivers of different sizes, but caution should be used when assessing species biomasses. Emery et al. (2003) found that river size, as determined by river kilometer, corresponded to several metrics along the Ohio River. Our results differed from theirs partly because we looked at size among rivers, whereas Emery et al. (2003) examined size along one river, which could have been confounded with river fragmentation by dams. In addition, fishes in the Ohio River may be reflecting a longitudinal gradient in which the river grades from a deep, clear river with rocky substrates and a narrow valley to a muddy, shallow river with a wide flood plain.

The basin scale was the most influential spatial scale in determining fish characteristics, but considerable differences existed depending upon the response variables of interest (Figure 3). We recognize that influential environmental variables may have been omitted from this study, but the amount of variation explained in each model and statistical significance indicates that we incorporated many key variables. The basin scale's lowest contribution towards variation explained was for the fish abundance model. In contrast, the basin scale accounted for 62% of the total explained variation in the biomass model, which also had more total variation explained (43%). These results suggested that abundance is inherently more variable than biomass or assemblage metrics. High numbers of small-bodied fishes can vary markedly in time and space, and can strongly influence abundance yet affect biomass little. The 185 logperch found at one site, for example, had large implications for abundance (66% of the catch) but had far less effect on biomass (5%).

The site scale variables explained substantial amounts of variation after accounting for variation at the basin scale. We found that environmental variables at multiple spatial scales had similar influence on fishes and, thus, are likely

related across spatial scales. Considering rivers in a hierarchical scale context (e.g., Frissell et al. 1986; Poff 1997) helps us understand why substantial amounts of variation were attributed to interactions among spatial scales in the abundance (31%), biomass (23%), and assemblage metric (42%) models. Large-scale features may select against biota directly and indirectly by influencing reach and site-scale features.

Few studies have explored how environmental variables among multiple spatial scales influence fish assemblages in riverine habitat of multiple large rivers. Dams obviously change fish assemblages in impounded areas, and we found evidence at the reach scale to indicate that dams influence fish assemblages in riverine sections upstream or downstream from dams as well. We conclude that basin scale conditions have a stronger direct relation with river fish assemblages than do site conditions in regions with widespread land cover alterations. Site scale conditions do strongly correspond with riverine fishes, but their influence appears to be a function of processes at a higher scale. These insights into how hierarchical structures affect ecological processes are useful because they suggest basin-scale management, restoration, and policy decisions.

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Modeling Brook Trout Presence and Absence from Landscape Variables Using Four Different Analytical Methods

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Abstract.—As a part of the Great Lakes Regional Aquatic Gap Analysis Project, we evaluated methodologies for modeling associations between fish species and habitat characteristics at a landscape scale. To do this, we created brook trout *Salvelinus fontinalis* presence and absence models based on four different techniques: multiple linear regression, logistic regression, neural networks, and classification trees. The models were tested in two ways: by application to an independent validation database and cross-validation using the training data, and by visual comparison of statewide distribution maps with historically recorded occurrences from the Michigan Fish Atlas. Although differences in the accuracy of our models were slight, the logistic regression model predicted with the least error, followed by multiple regression, then classification trees, then the neural networks. These models will provide natural resource managers a way to identify habitats requiring protection for the conservation of fish species.

INTRODUCTION

Knowledge of the habitats required to maintain the growth, survival, and reproduction of freshwater fish species and populations is necessary for conservation planning and decision making. In practical application, however, habitat requirements are often incompletely known. Therefore, biologists commonly use data on a fish's habitat selection, based on field observations of species occurrence or densities (Rosenfeld 2003). Given data on habitat characteristics and observed fish distributions, correlative habitat associations can be used to predict the occurrence or densities of

fish in locations where samples have not been collected. These predictions are useful for identifying habitat units important to target species but vulnerable to alteration and degradation by humans, and lacking protective status. Such habitats represent “gaps” in conservation strategy.

The goal of the U.S. Geological Survey, Gap Analysis Program (GAP) is to *keep common species common* by identifying those species not adequately represented in existing conservation areas (Scott et al. 1993). In the past decade, gap analyses have been performed in terrestrial systems across the United States and in the mid-1990s an aquatic gap pilot began in Missouri. In 2001, GAP funded the first regional aquatic gap analysis in the eight Great Lakes states: Minnesota,

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Wisconsin, Illinois, Indiana, Michigan, Ohio, Pennsylvania, and New York. The goals of this project, called the Great Lakes Regional Aquatic Gap Analysis, are (1) to evaluate biological diversity of Great Lakes aquatic habitats and identify gaps in the distribution and protection of these species and their habitats, and (2) to use an integrated approach in which common methods and protocols are established and results are comparable across the Great Lakes landscape (Myers et al. 2002; Morrison et al. 2003).

Prediction of patterns of species occurrence from regional habitat data are a critical step in achieving the aquatic gap project goals. Earlier aquatic gap projects used several different methods to model empirical associations of fish species presence and absence with habitat characteristics: (1) classification and regression trees (CART) analysis (Sowa 1999), (2) multiple linear regression (Sowa and Rabeni 1995; Sowa 1999), (3) and genetic algorithms (Alex Covert, U.S. Geological Survey, personal communication). In this study, we build on the earlier aquatic gap projects by assessing several methods (multiple linear regression, logistic regression, neural networks, and classification trees) and comparing their predictive abilities.

Predicting fish distributions from habitat variables using regression analysis has a long history in ecological applications and is well understood by researchers (Fausch et al. 1988). Neural networks and classification trees, however, are fairly new methods to the ecological field. This study uses these techniques but does not go into detail in describing how they work; this has been done well in other papers both for neural networks (Rumelhart et al. 1986; Mastorillo et al. 1997; Boddy and Morris 1999; Lek and Guegan 1999; Olden and Jackson 2001) and for classification trees (Breiman et al. 1984; Bell 1999; De'ath and Fabricius 2000; De'ath 2002).

Studies directly comparing these newer techniques with more traditional approaches are relatively rare, but where they exist have typically found that the new techniques are able to predict more accurately than simple linear modeling (Lek

et al. 1996; Franklin 1998; Vayssieres et al. 2000). However, careful comparisons of performance of these approaches for modeling fish distributions at the large geographic extent contemplated in the Great Lakes Aquatic Gap Program have not been previously reported (but see Mastorillo et al. 1997; Olden and Jackson 2001, 2002 for smaller scale analyses). Likewise, comparison of neural net and classification tree approaches for fishes have not been previously reported.

The main goal of this study was to evaluate the methodology for four different presence/absence modeling techniques (multiple regression, logistic regression, neural networks, classification trees) using data from fish sampling and enduring landscape habitat variables for rivers across the state of Michigan. This model comparison will aid us in selecting the approach, or approaches, to be used to produce fish distribution maps for the Great Lakes Regional Aquatic Gap Analysis. For this study, we analyzed the streams of Michigan for the presence and absence of brook trout *Salvelinus fontinalis*, a popular sport fish whose basic habitat requirements are well known (Smith 1985).

METHODS

Developing the Database

The Great Lakes Regional Aquatic Gap Analysis, in collaboration with the Michigan Department of Natural Resources (MDNR), has established a high-resolution, GIS-linked database with characteristics of Michigan's rivers. This database provided the environmental variables that served as the independent predictors for the models. The database is referenced to a group of ArcGIS line coverages (ESRI 2002), in which each river is broken down to confluence-to-confluence reaches, and each reach contains information for a wide variety of landscape-scale environmental variables, such as air temperature, soil permeability, land cover, and geology (S. Aichele, U.S. Geological Survey, personal communication) (Table 1; Figure 1). The line coverages are based on the U.S.

Table 1. Environmental variables included in the models. Variable order refers to the order in which the variables were entered into the regressions. Variables transformed for the regression models are marked.

Order	Variable name	Unit	Code	Transformation
<i>Air temperature variable</i>				
1	Watershed July mean air temperature	°C	W_JULY_MN	None
<i>Channel geometry/position</i>				
2	Shreve stream order	None	CHAN_LINK	Log
3	Lake immediately downstream	binary	DLAKE	None
4	Distance downstream to Great Lake	meters	DOWNLENGTH	None
<i>Flow/hydrologic variables</i>				
5	Channel slope	%	CHAN_GRAD	Log
6	Channel sinuosity	None	CHAN_SINU	None
7	Riparian mean Darcy value ^a	None	R_DARCY	None
8	Riparian mean slope	%	R_SLOPE	Square Root
9	Riparian mean soil permeability	cm/h	R_PERM	Square Root
10	Network mean Darcy value	None	RT_DARCY	None
11	Network mean slope	%	RT_SLOPE	Square Root
12	Network mean soil permeability	cm/h	RT_PERM	Square Root
13	Subwatershed mean Darcy value	None	W_DARCY	None
14	Subwatershed mean slope	%	W_SLOPE	Square Root
15	Subwatershed mean soil permeability	cm/h	W_PERM	Square Root
16	Watershed mean Darcy value	None	WT_DARCY	None
17	Watershed mean slope	%	WT_SLOPE	Square Root
18	Watershed mean soil permeability	None	WT_PERM	Square Root
19	Mean precipitation in watershed	mm	WT_PRECIP	None
<i>Surficial geology in watershed</i>				
20	Coarse soil texture	%	COARSE	None
21	Fine soil texture	%	FINE	None
22	Medium soil texture	%	MEDIUM	None
<i>Percent land cover</i>				
23	Riparian urban	%	R_URB	Log
24	Riparian agriculture	%	R_AGR	ArcSine
25	Riparian wetland	%	R_WET	ArcSine
26	Riparian forest	%	R_FOR	ArcSine
27	Riparian open/fields	%	R_OPEN	Log
28	Riparian open water	%	R_WAT	Log
29	Network urban	%	RT_URB	Log
30	Network agriculture	%	RT_AGR	ArcSine
31	Network wetland	%	RT_WET	ArcSine
32	Network forest	%	RT_FOR	ArcSine
33	Network open/fields	%	RT_OPEN	Log
34	Network open water	%	RT_WAT	Log
35	Subwatershed urban	%	W_URB	Log
36	Subwatershed agriculture	%	W_AGR	ArcSine
37	Subwatershed wetland	%	W_WET	ArcSine
38	Subwatershed forest	%	W_FOR	ArcSine
39	Subwatershed open/fields	%	W_OPEN	Log
40	Subwatershed open water	%	W_WAT	Log
41	Watershed urban	%	WT_URB	Log
42	Watershed agriculture	%	WT_AGR	ArcSine
43	Watershed wetland	%	WT_WET	ArcSine
44	Watershed forest	%	WT_FOR	ArcSine
45	Watershed open/fields	%	WT_OPEN	Log
46	Watershed open water	%	WT_WAT	Log

^a The Darcy value is a measure of groundwater potential (Baker et al. 2003).

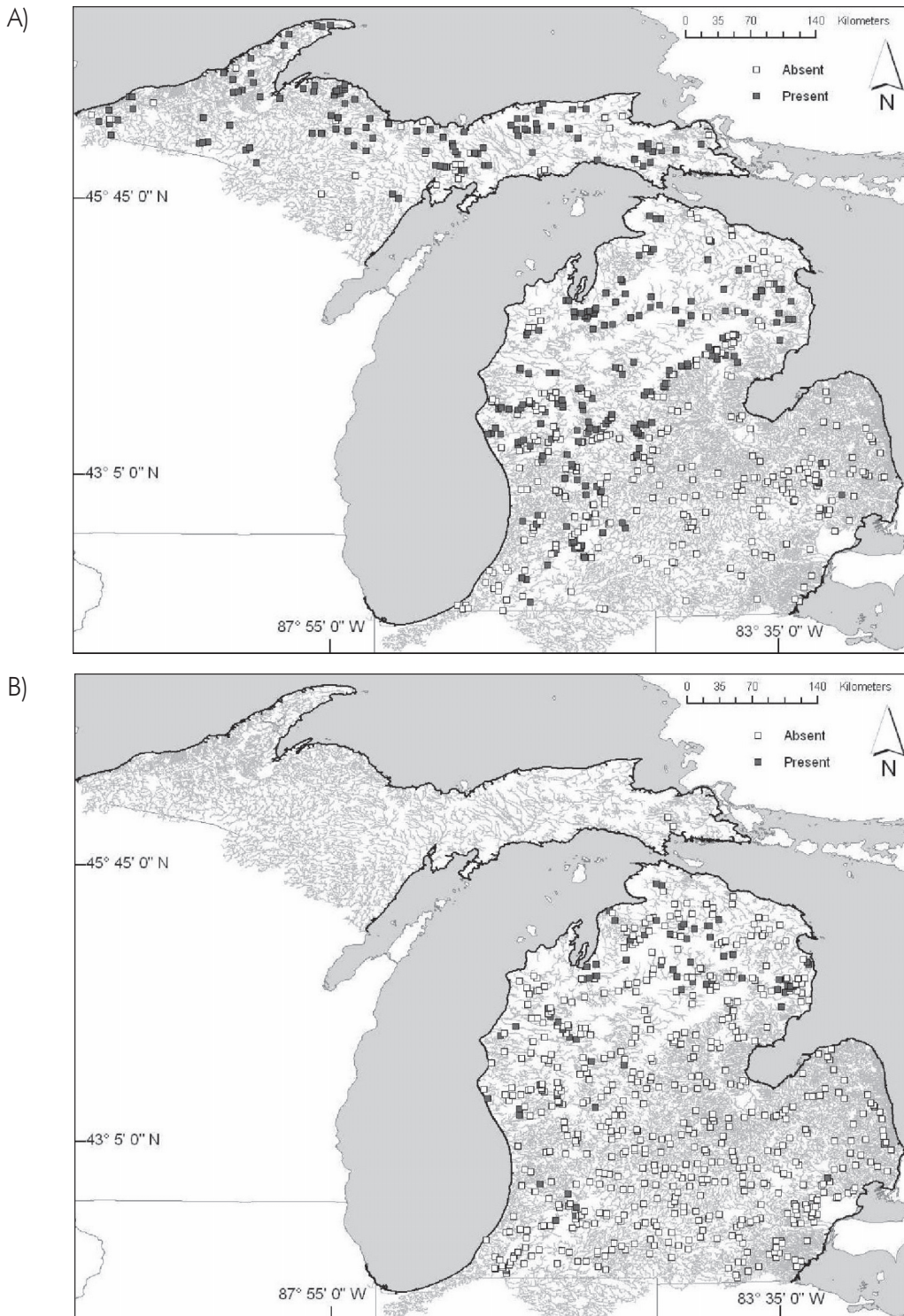


Figure 1. Michigan stream reaches containing habitat variables overlaid by (A) MDNR sampling points for brook trout presence and absence (training data), and (B) MRI sampling points for brook trout presence and absence (testing data).

Geological Survey National Hydrography Dataset at the 1:100,000 scale (<http://nhd.usgs.gov/>).

Many variables are measured at four different scales (Figure 2). Riparian variables refer to the land 60 m on each side of the stream reach of interest. Network variables refer to the 60-m riparian buffer, plus the 60-m riparian buffer of every stream reach upstream from the reach of interest. Subwatershed variables refer to that portion of the catchment immediately lateral to the stream reach, and watershed variables include the entire catchment.

We obtained spatially referenced fish assemblage samples from the Fisheries Division of the MDNR and extracted data for brook trout occurrences from this “training” dataset. Fish were collected by tow-barge, backpack, and boat electrofishing; rotenone; seines; trap nets; and fyke nets (Merna 1988). While the amount of data available from the MDNR was extensive, we limited our analysis to samples collected in 1980–2002, and we strived for even spatial coverage across the state (Figure 1A). To test our models, we used an independent data set from the Michigan Rivers Inventory (MRI) project (Seelbach and Wiley 1997), where fish were collected primarily by tow-barge and backpack electrofishing and rotenone in 1980–2002 (Figure 1B).

Sampling points were associated to the stream reaches in a single table in which rows represented stream reaches and columns contained values for the habitat variables and a record of brook trout presence (E. Bissell, U.S. Geological Survey, Water Resource Division, Lansing, Michigan, personal communication).

We deleted replicate samples so that every reach was represented by only one observation. When different samples for the same reach disagreed on brook trout presence, we kept the observation where the fish was present. After eliminating replicates, we had 901 observations for the MDNR data and 635 for the MRI data. Hereafter, observations marked as “present” are called “presence reaches” and observations marked as “absent” are called “absence reaches.”

As with many presence and absence databases, the number of absence reaches was much greater than the number of presence reaches (Zorn 2003). To prevent the models from weighting more towards absence prediction than presence, we randomly selected a subset of absence reaches equal to the number of presence reaches. To do this, we first divided the 682 absence reaches of the MDNR data into three groups by Shreve order. Next, we randomly selected 104 or 105 absence reaches from each size-group so that the total number of absence reaches (314) equaled the total number of presence reaches. These 628 MDNR observations were used as the training data for formulating the models. The absence segments that were not selected were discarded, but we kept all 635 reaches of the MRI data to validate the models formulated by the MDNR data.

Stratification by Shreve stream order was necessary to ensure that the whole range of stream sizes available were included in the modeling. Had we merely used simple random sampling to select the 314 absence reaches, the sampling would have been biased towards smaller rivers

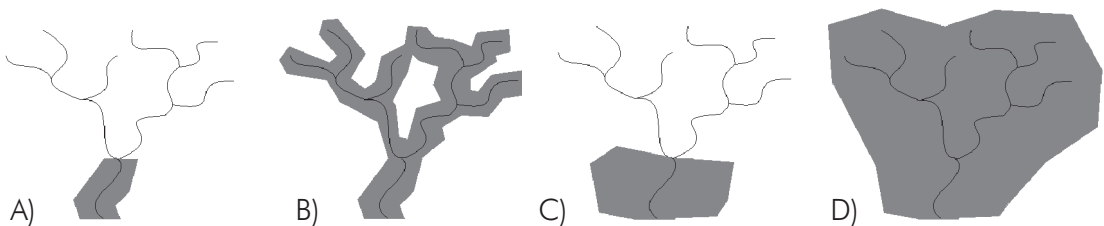


Figure 2. Variables are measured on four scales for each individual stream reach: (A) Riparian, (B) Network, (C) Subwatershed, and (D) Watershed. See text for details.

due to the high ratio of small to large streams in the database. The end result would have been models only applicable to small streams.

Multiple Regression and Logistic Regression Modeling

For the multiple regression model, when necessary we transformed each variable with one of three transformations (logarithmic, square root, or arcsine) in order to meet the assumption of a linear relationship between the independent and dependent variable (Zar 1999) (Table 1). Upon creation of the final multiple regression model, partial regression plots were created for each of the model's predictors to test the assumption of linearity. These plots show the effect of a predictor on the response variable with the effect of all of the other predictors removed (Faraway 2005). For both the multiple regression and logistic regression, each variable was standardized (mean 0, standard deviation 1) to allow for easier comparison of the relative importance of the regression coefficients (Faraway 2005).

Using a stepwise selection technique similar to that of Zorn (2003), we ran multiple linear regression and logistic regression models in SPSS 12.0 for Windows (SPSS, Inc. 2003). For both regression models, we manually entered a habitat variable into the equation. If the variable was significant ($p < 0.10$), we left it in the equation and added another variable. If the new variable was not significant ($p \geq 0.10$), we removed it from the model. If the new variable was significant and caused the original variable to become insignificant, we removed the original variable if its removal caused the model's adjusted R^2 to increase. We repeated this procedure until every environmental variable had been given a chance to enter the model. While SPSS can carry out this procedure automatically, we performed it manually in order to dictate the order that variables entered the model (Table 1). We placed variables assumed to have a more direct effect on fish presence and absence higher in the list,

and variables with indirect or unknown effects lower in the list. This procedure gives variables assumed to be more important to fish a greater chance of being included in the model (Zorn 2003).

As the next step, we examined the β -value (regression coefficient) and the 90% confidence interval of the β -value for each variable included in the model. If the β -value had a confidence interval large enough that we were not confident in its predictive abilities, we would remove the variable from the model. If we believed a variable to be important, but it was not included in the model, we would add this variable and recalculate the model. If the variable was significant ($p < 0.10$) we allowed the variable to stay in the model. By adding these steps to the end of the regression modeling process, we added subjective decision making based on our ecological knowledge of the fish to an otherwise objective routine.

To check if the constant variance and independence assumptions of the error terms of the multiple regression model held true, we created a diagnostic plot of the residuals versus fitted values. Patterns in this plot indicate assumption violations (Faraway 2005). A Q-Q plot of the residuals was created to check error normality; a straight line in this plot indicates normality (Faraway 2005).

After creating the final regression models, we applied the model to the MRI test data and also performed n -fold (leave-one-out) cross validation on the training data as a secondary test of the model's performance. Reaches with a predicted value ≥ 0.5 were considered to have trout present; those with values less than 0.5 were considered as lacking trout.

Neural Network Modeling

In using a neural network, it is possible to include all of the data available to us in the network and get a solution that effectively predicts the dependent variable (Lek et al. 1996). However, many of

our environmental variables are probably not related to brook trout presence, and including them in the model will increase computation times and cloud our ability to understand the relationship between the fish and more important variables (Olden and Jackson 2002). Therefore, in order to build a model that can both predict and provide some explanatory value, we needed to reduce the initial 46 habitat variables into a more manageable number.

Olden and Jackson (2002) have developed a randomization approach for both pruning variables and understanding how variables contribute to a neural network. To use this approach with our data, we first developed several neural networks in a feed-forward, back propagation procedure using the training data and the computer software program Neuralyst 1.4 (Rumelhart et al. 1986; Shih 1995; Boddy and Morris 1999). The networks were constructed with three layers of 46 neurons, 46 neurons, and 1 neuron, respectively, and were trained for 1,000 epochs (Shih 1995). However, each of these networks had different random initial weights and so performed differently in how well they predicted the test data.

From these networks, we selected the network that had the greatest percentage of correct predictions for the test data (our “optimized” network) and calculated the sum of the input layer-hidden layer weights and the hidden layer-output layer weights for each input variable (Figure 3). Essentially, the contribution of each variable to the network depends on the magnitude and direction of the sum of these weights. The greater this sum (either negatively or positively), the more impact that variable has on the final solution produced by the network (Olden and Jackson 2002).

The sum of the weights alone does not fully inform us of how important a variable is because at this point, we do not know if the sum is significantly different than random. To determine significance, we randomly rearranged the brook trout presence and absence values among the different observations and then constructed a new neural network with the same parameters and initial weights that were used in our optimized network. This network was allowed to train for 1,000 epochs, and then as we did earlier, we computed the sum of the input layer-hidden layer weights and the hidden layer-output layer

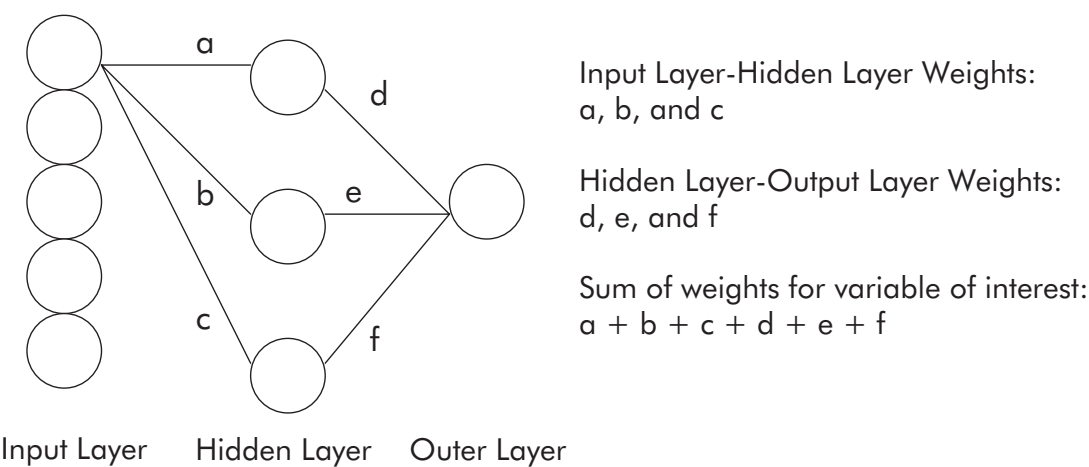


Figure 3. In order to prune the neural network, the sum of the input layer-hidden layer weights and the hidden layer-output layer weights is calculated for each input variable. In this example, we calculate this sum for one variable in a neural network with three hidden neurons in the hidden layer.

weights for each habitat variable. Since we rearranged the presence/absence values among the observations, if a variable is important to brook trout, the new network will not produce a sum of weights that is of greater magnitude than the sum of weights from the original network.

However, there is a slight chance that by rearranging the values, we actually made a variable more important to brook trout presence. Therefore, we created a new network many times (in this case, 1,000 times), each time randomly rearranging the presence/absence values and each time calculating the sum of the weights for each variable. The statistical significance of each habitat variable was the proportion of the values (including the original sum) that were more extreme than the observed sum (Olden and Jackson 2002). For example, if only 9 of the 1,000 sums are greater than our observed sum, then the probability of a type I error and statistical significance of the variable was $(9 + 1)/1,000 = 0.01$. When a variable had a low *P*-value, we inferred that it played an important role in the formation of the neural network. This significance test is similar to the significance test of a regression coefficient: we are testing the null hypothesis that a variable does not have an effect, and at low probabilities, the null hypothesis is rejected and we conclude that the variable does have an effect.

After the 1,000 iterations, seven variables had a significance level less than 0.1. These variables were considered to be the most important of the original 46 habitat variables and were used to construct a new neural network. This neural network was created with the training data in a manner similar to our original network. We applied this new network to the MRI test data to determine its predictive abilities and applied the network to the training data through an *n*-fold cross-validation procedure as a secondary test of the model's performance. Reaches with a predicted value ≥ 0.5 or greater were considered to have trout present; trout were presumed absent at values less than 0.5.

Classification Tree Modeling

We used CART 5.0 to train the training data in a classification tree (Steinberg and Colla 1997). Since the program selects the variables that result in the best training of the data, we did not have to enter variables individually or prune variables as we did for the regression and neural network techniques. CART produced a series of trees in which different predictor variables were used as binary splits. As CART created the trees, it also tested the training data in an *n*-fold cross-validation procedure. The tree that we selected to use as our predictive model was the one that resulted in the highest agreement between the predicted presence and absence classification and the known presence and absence classification for the cross-validation. After selecting the optimal tree, we ran the MRI test data through the tree as a measure of the model's validity. Unlike the other modeling methods, the classification tree did not predict a value for each reach; rather, the model directly classified a reach as either "present" or "absent."

Model Application

The models were used to predict brook trout presence and absence for all the stream reaches in Michigan. We used these predictions to create statewide distribution maps in ArcMap 8.3 (ESRI 2002). The predictions were entered into a spreadsheet and then joined to the stream layer by a number unique to each reach. The background layers for these maps came from the Michigan Geographic Data Library (<http://www.michigan.gov/cgi/>) and the stream layer was developed by the Great Lakes GAP Project and the MDNR, as mentioned above.

After building the predictive maps, we visually compared these with the Michigan Fish Atlas 2003, v.1.1, 2nd edition (<http://www.michigan.gov/cgi/>). The Michigan Fish Atlas is a point shapefile that contains 2468 georeferenced brook trout samples collected from 1847 to the present.

As these samples came from locations where brook trout are known to live, a successful predictive map will have similar distribution patterns to the Michigan Fish Atlas.

RESULTS

Multiple Regression

Eight variables were included in the multiple regression model (Adjusted $R^2 = 0.436$, Table 2). Of these, the most influential was the July mean air temperature (W_JULY_MN, $\beta = -0.184$). Other important variables included stream size (CHAN_LINK, $\beta = -0.133$), and the percentage of forest land cover in the watershed (W_FOR, $\beta = 0.091$).

The model was applied to the MRI test data and predicted 86% of the presence reaches correctly and 76% of the absence reaches correctly (Table 3). When the training data were used in a cross-validation test, 81% of the presence reaches were predicted correctly and 80% of the absence reaches were predicted correctly.

Logistic Regression

Nine variables were included in the logistic regression model (Cox and Snell $R^2 = 0.480$, Table

Table 3. Percentage of correct predictions for the MRI test data and the training data upon cross-validation. "Performance" is the sum of the correct predictions for a model and gives a measure of the model's relative predictive ability. (MLR- multiple linear regression; LR – logistic regression; CART – classification tree; NN(46) – neural network with 46 habitat variables; NN(7) – pruned neural network with 7 habitat variables).

	MRI		X-validation		Performance
	Presence	Absence	Presence	Absence	
MLR	85.7	75.7	80.6	79.6	321.6
LR	87.1	75.9	79.9	81.2	324.1
CART	84.3	77.7	75.2	78.3	315.5
NN (46)	85.7	71.8	75.4	77.7	310.6
NN (7)	81.3	77.4	68.8	84.4	311.9

4). Most of the same variables that were significant in the multiple regression were also significant in the logistic regression. The most influential variable in both models was July mean air temperature (W_JULY_MN, $\beta = -1.3614$). Stream size (CHAN_LINK, $\beta = -1.2475$) and percentage of forest land cover in the watershed (W_FOR, $\beta = 0.4737$) were again important.

The logistic regression model was applied to the MRI test data and predicted 87% of the presence reaches correctly and 75% of the absence reaches correctly (Table 3). In cross-validation tests, 80% of the presence reaches were

Table 2. Variables significant in the multiple linear regression, their β values (regression coefficients), standard error of the β , and significance. Variables were entered into the model in a stepwise procedure and were included in the final model if found significant ($p < 0.10$).

Variable	β	Standard error	Significance
(Intercept)	0.500		
W_JULY_MEAN	-0.184	0.023	<0.001
CHAN_LINK	-0.133	0.016	<0.001
W_FOR	0.091	0.022	<0.001
R_PERM	0.061	0.017	<0.001
WT_WET	-0.058	0.018	0.001
R_DARCY	0.055	0.016	<0.001
RT_WAT	-0.042	0.016	0.01
WT_OPEN	0.036	0.017	0.03

Table 4. Variables significant in the logistic regression, their beta values, standard error of the β values, and significance. Variables were entered into the model in a stepwise procedure and were included in the final model if found significant ($p < 0.10$).

Variable	β	Standard error	Significance
(Intercept)	-0.0726		
W_JULY_MEAN	-1.3614	0.186	<0.001
CHAN_LINK	-1.2475	0.153	<0.001
W_FOR	0.4737	0.179	0.008
WT_WET	-0.4224	0.14	0.002
R_PERM	0.4139	0.127	0.001
W_SLOPE	0.3823	0.153	0.013
R_DARCY	0.3615	0.133	0.007
DOWNLENGTH	0.3486	0.131	0.008
WT_OPEN	0.2317	0.133	0.082

predicted correctly and 81% of the absence reaches were predicted correctly.

Neural Network

We tested two different sizes of neural networks: a full model, which used all 46 variables, and a pruned model, which used the seven most important variables from the full model. The full model predicted the MRI validation data set well: 85.7% of the presence reaches were predicted correctly and 71.8% of the absence reaches were predicted correctly (Table 3). The cross-validation of the full model predicted the presence and absence reaches correctly 75.4% and 77.7%, respectively.

By using the randomization procedure, we identified the seven most important variables from this model (Table 5). These included the July mean air temperature, which had a negative relationship with brook trout presence, and the Darcy value of the riparian zone, which had a positive relationship with brook trout presence. Also important were channel gradient, and wetland and open/field land covers.

The simplified model, which contained these seven predictors, was also applied to the MRI test data and the training data were cross-validated (Table 3). The pruned model predicted absence reaches better than the full neural network, but presence reaches were predicted worse. For the MRI data, 81.3% of the presence reaches were

predicted correctly and 77.4% of the absence reaches were predicted correctly (Table 3). The cross-validation of the pruned model predicted the presence and absence reaches correctly 68.8% and 84.4%, respectively.

Classification Tree

The CART program produced several trees of differing sizes, and the tree selected as the final model was the one that best predicted the cross-validation data (Figure 4). The first split in the tree was made by July mean air temperature (W_JULY_MN), and similar to the regression models, other important variables included stream size (CHAN_LINK) and percent of forest land cover in the watershed (W_FOR). One unique property of classification trees is that the model can use the same variable more than once; at the bottom of the tree, the model uses the W_JULY_MN variable again to make another split.

We applied the MRI test data to the tree to validate the model. The tree predicted 84.3% of the presence reaches and 77.7% of the absence reaches correctly. (Table 3). Cross-validation of the training data predicted 75.2% of the presence reaches and 78.3% of the absence reaches correctly.

Predicted Distribution Maps and Model Comparisons

The Michigan Fish Atlas shows that brook trout has historically been found throughout Michigan's Upper Peninsula and northern Lower Peninsula (Figure 5A). While the populations are not as dense as in the north, brook trout is also found in southwest Michigan, as well. This species generally does not live in southeast Michigan, although the Michigan Fish Atlas does record a few scattered populations there.

The distribution maps produced from our four models were able to repeat this general pattern (Figure 5B–F). Each map predicted brook trout to be widespread in the Upper Peninsula, with

Table 5. Variables determined to be significant after a neural network randomization procedure, their relationship to brook trout presence, and associated *p*-values. These variables were then used to construct a pruned neural network.

Variable	Relationship	P-value
WT_OPEN	+	0.016
W_JULY_MN	–	0.017
CHAN_GRAD	+	0.021
RT_WET	+	0.044
R_DARCY	+	0.053
W_OPEN	–	0.057
WT_WET	–	0.087

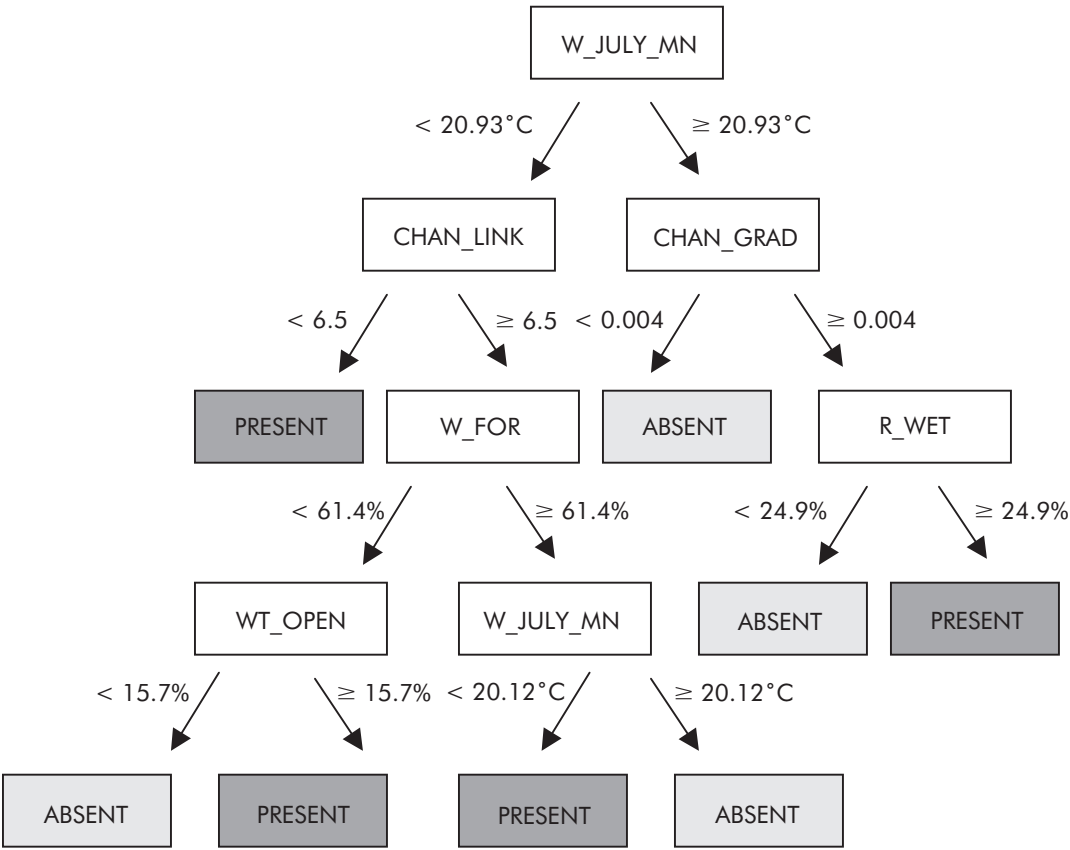


Figure 4. Classification tree created by CART that had highest correct percentage of predictions for the test data. An observation is tested one at a time, starting with the top of the tree and working down, following the splitting rules until it is classified as present or absent.

an occasional stream marked as absent. In the Lower Peninsula, the models predicted brook trout throughout the north and along the west coast, and generally predicted absence in south-east Michigan. The map created by the logistic regression model appeared to be most accurate when compared to the Michigan Fish Atlas; all of the maps are examined more closely below.

DISCUSSION

Ecological Significance

An advantage of performing this modeling exercise on brook trout is that habitat requirements of this fish are well known, so it is relatively easy

to determine if our models are consistent with ecological knowledge of the fish. In general, we would expect brook trout to prosper in small to medium size streams with plenty of groundwater flow, which provides cold water and a stable environment (Smith 1985; Zorn et al. 2002). Wehrly et al. (2003) reported that brook trout in lower Michigan are restricted to streams with mean July water temperatures less than 21°C. Since streams typically grow warmer as they grow larger (Wehrly et al. 1997), we should expect to find brook trout more consistently in smaller, headwater streams rather than in larger rivers (Smith 1985; Zorn et al. 2002). In terms of land cover, we expect that streams favorable to brook trout would have minimal thermal



Figure 5. (A) Brook trout samples in the Michigan Fish Atlas, and (B–F) predicted brook trout distributions in Michigan using (B) multiple linear regression, (C) logistic regression, (D) neural network with all variables, (E) neural network with seven variables, and (F) classification tree. A black stream indicates predicted presence, and a light gray stream indicates predicted absence.

pollution. Therefore, we expect that streams with riparian zones and catchments high in forests, and low in urban and agricultural land uses, would be more likely to provide suitable habitat for the fish.

Regression Models

In the multiple regression model, six of the variables have β value signs that are consistent with our knowledge of brook trout ecology (Table 2), and in the logistic regression model, eight variables have consistent signs (Table 4). For example, the lower the July mean air temperature (W_JULY_MN) and the smaller the stream (CHAN_LINK), the more likely that brook trout is predicted present. If the stream has a high slope in the catchment (W_SLOPE) and high soil permeability in the riparian zone (RT_PERM), two variables that increase groundwater flow, we would also expect a greater chance of brook trout presence. All of these variables are more likely found in headwater streams, so it is reasonable that the further away the reach is from the Great Lakes (DOWNLENGTH), the more likely it is to contain brook trout.

Prior to examining the regression coefficients, we were unsure of how two of the significant variables would affect brook trout presence: percent of land cover containing wetlands and percent of land cover containing open water. The models predicted that wetlands and open water would negatively influence presence. This seems reasonable as these land covers could result in surface water warming, which contributes to poor brook trout habitat (Wehrly et al. 2003).

Hindering our interpretation of the significant regression variables is the problem of multicollinearity. Due to existing correlations between the variables, we can only interpret the effect of a predictor on the response when we also consider the effect of every other variable on the response at the same time (Faraway 2005). Understandably, with close to 10 predictors in our models, this is a very difficult task. The result is that we can really only generalize about

an individual predictor; we can say a predictor seems to have a certain effect but cannot say the exact magnitude of that effect. However, multicollinearity does not affect the accuracy of our predictions; it only affects the explanatory value of the model.

The multiple regression and logistic regression models fit the MRI test data well, especially in regards to predicting presence, which both models correctly predicted more than 85% of the time (Table 3). The cross-validation of each model was also quite successful, predicting the reaches correctly about 80% of the time. In order to determine which model predicted better overall, we added the percent correct prediction for the MRI test data and cross-validation to produce a value that we called "Performance" (Table 3). Using this value, we can see that logistic regression predicted the data slightly better than the multiple regression ($324.1 > 321.6$).

The statewide mapped predictions seem generally reasonable for both models, both predicting brook trout occurrences not only in the north, but also scattered in the southern interlobate and glacial outwash regions of western Michigan where in fact isolated populations do occur (Figure 5B–C). However, the logistic regression map followed the Michigan Fish Atlas patterns more closely. In the Michigan Fish Atlas, brook trout is uniformly distributed in the Upper Peninsula, except for a few areas (i.e., the Manistique, the Cedar, and the Escanaba watersheds) in which there are "holes." The map produced by logistic regression properly models both the Manistique hole and the Cedar-Escanaba hole. In the Lower Peninsula, the Michigan Fish Atlas shows that brook trout are not found in the streams of the Pigeon and Birch watersheds, which are located in the area of land protruding into southern Lake Huron (this area is called the "tip of the thumb" due to the generally accepted idea that the Lower Peninsula looks like a mitten). The logistic regression model accurately predicts absence in this area; the multiple regression largely predicts absence but does predict presence in several streams.

In addition, the logistic regression model predicted a band of brook trout presence in southeast Michigan that runs in a southwest–northeast direction. Part of this band can be seen in the Michigan Fish Atlas (Figure 5A). This band lies on a glacial interlobate formation and has higher slopes, higher soil permeability, and faster groundwater flow than the flat lake plain geology of the rest of southeast Michigan (Bent 1971). It is reasonable to expect that the streams of this area have the proper habitat to support brook trout.

Multiple Regression Assumptions

In general, multiple regression works best when the response variable is continuous, not dichotomous or categorical (Zar 1999). The multiple regression model predicted quite well, but the question must be asked if it is acceptable to use this model with presence–absence data.

We checked the assumptions of the models with diagnostic plots. The partial regression plots demonstrated that transformations of the variables helped improve the linear relationship between the predictors and the response, but did not achieve perfect linearity, resulting in a model that has less fit than a perfect linear model. In addition, diagnostics on the residuals showed that while the error terms met the assumption of linearity, they violated the assumption of constant variance and independence. As a result, probability based assessments of the model parameterization and goodness of fit are in question. While this model was interesting as an intellectual exercise, the result of these problems is that we would hesitate to use a model of this type for critical management decisions. Logistic regression, which was developed for dichotomous responses and which has much less stringent assumptions, is certainly the presence/absence regression model of choice.

Neural Network Models

Both the full neural network and the pruned neural network did a good job in predicting the

test data and accurately cross-validating the training data. The variables identified as significant in the full model were, in general, consistent with our ecological knowledge of brook trout. Air temperature had a negative relationship with brook trout presence; the regression models predicted the same relationship (Table 5). In addition, the Darcy variable and channel gradient had a positive relationship with brook trout presence, which is also similar to the regression models. The effect of the land cover variables on brook trout was not clear. Both open/field land-cover and wetland land-cover variables were significant in the model, but each of these variables were included in two different scales that had opposite relationships to brook trout. For example, WT_OPEN had a positive relationship to presence, but W_OPEN had a negative relationship to presence (Table 5). As these two variables are positively correlated ($r = 0.66$), we would expect them to have a similar effect, but our analysis showed that they did not.

Interestingly, the pruned network predicted the test data and the cross-validation of the training data just as well as the full network (performance value: 311.9–310.6), demonstrating the validity of the randomization approach for network pruning (Table 3). However, examination of the predictive maps produced by the models showed that the full network map was more realistic than the pruned network map (Figure 5D–E). The pruned network captures well the Manistique hole and the Cedar-Escanaba hole in the Upper Peninsula and the glacial interlobate band in the southeast Lower Peninsula, but it predicts presence in the thumb and draws an unexpected straight line of predicted presences running west to east across the Lower Peninsula. After some investigation into this line, it appeared that the line marks a change in the stream reaches' air temperature values. A similar problem with the air temperature variable was seen in the classification tree model and is discussed more in the next section.

The predictive abilities of the pruned network seemed reliable until they were applied to the

whole state and viewed geographically. For this particular study, we decided it would be best to run the randomization procedure to determine variable significance, but use the full model in making the predictions. Other fish may be able to be modeled reasonably through the pruned network; each case should be evaluated individually.

Classification Tree Model

The classification tree model included several variables that were also in the regression models (i.e., W_JULY_MN, CHAN_LINK, W_FOR). The tree splits the data with these variables in a way that is consistent with our ecological knowledge of brook trout, and this model predicted the test data and cross-validation of the training data almost as well as the regression models. The performance value of this model (315.5) is lower than the regression models and higher than the neural network models, but all of these differences are actually quite small (Table 3).

The statewide predictive map is generally reasonable for the classification tree model; it follows the general pattern shown in the Michigan Fish Atlas and in the regression models (Figure 5F). The model does not correctly capture the Manistique hole and the Cedar-Escanaba hole, as did the logistic regression model. In addition, several streams at the tip of the thumb are predicted present, but the Michigan Fish Atlas does not record brook trout being found in this area. This problem is most likely the result of the importance placed on the July mean air temperature variable; the tip of the thumb is far enough north to have a lower air temperature than the rest of the thumb, and lower air temperatures cause the fish to be predicted present. This problem actually represents an important problem with all of the models using air temperature.

Studies have shown that water temperature, not air temperature, is the most important habitat variable for fish (Wehrly et al. 2003; Zorn 2003). In this study, water temperature data were not available, so we used air temperature only. It is a curious coincidence that the air temperature

the classification model chose as a maximum cutoff for brook trout is the same mean water temperature (21°C) reported by Wehrly et al. (2003) as the upper limit for Michigan brook trout. Water temperatures and air temperatures are in fact not predictably related in Michigan due to the spatially variable contribution of groundwater to stream channels (Wiley et al. 1997; Baker et al. 2003; Wehrly et al. 2003;). However, in general, northern Michigan has lower air temperatures than southern Michigan, and due to Michigan's glacial history, northern Michigan tends to have higher soil permeability, greater groundwater flows, and thus colder water temperatures than southern Michigan (Bent 1971). This coincidence results in all of the models being able to capture the north-south distribution gradient when using air temperature, even though the driving factor is water temperature. In the southern part of the state, the models seem to struggle with presence predictions since the air temperature and water temperature are not as closely related as they are in the northern half of Michigan. As mentioned above, this problem becomes especially evident in the predictive map of the pruned neural network.

In order to more thoroughly check this north-south distribution problem, we examined the residuals of the MRI data. We divided the data into two parts by presence and absence and constructed linear regressions of the residuals of the MRI test data on the latitude of the observations (Figure 6). Regressions for all of the models showed that presence reaches in the northern Lower Peninsula tend to have lower residuals than presence stream reaches in the southern Lower Peninsula. This indicates that the models were able to more accurately predict presence reaches in the north than in the south. Absence reaches followed the opposite pattern: residuals in the southern Lower Peninsula tend to be smaller than residuals in the northern Lower Peninsula, which indicates the models can more accurately predict absences in the southern Lower Peninsula than the north. In future studies, this problem will be addressed as water temperature

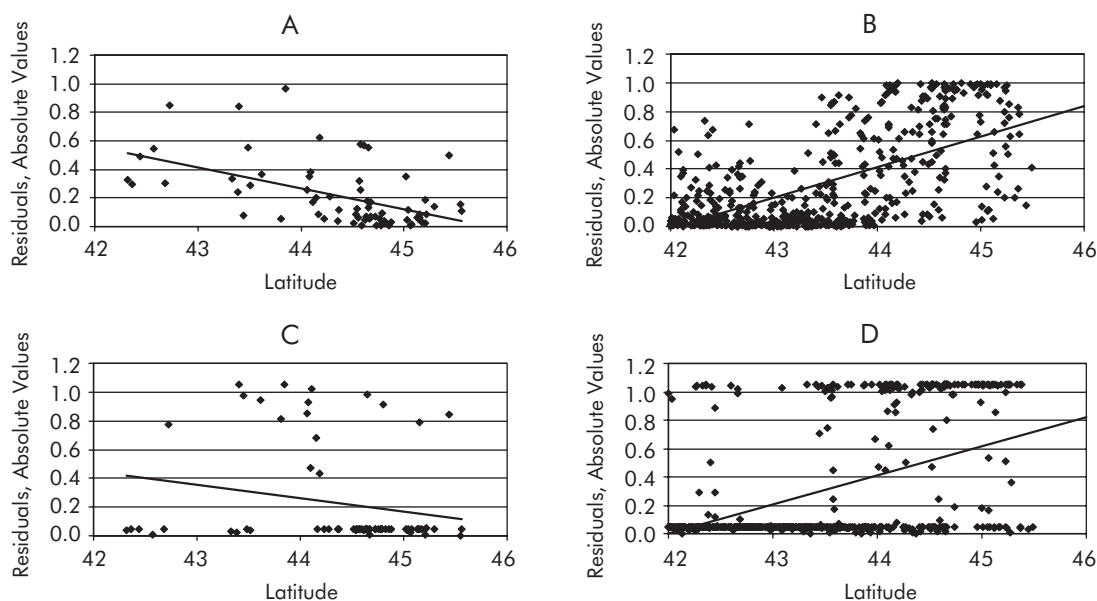


Figure 6. Scatterplots of absolute values of residuals for the MRI test data regressed against the latitude of the sampling point for the (A) presence samples in the logistic regression model ($R^2 = 0.27$, $F = 25.4$, P -value < 0.000); (B) absence samples in the logistic regression model ($R^2 = 0.41$, $F = 402.4$, P -value < 0.000); (C) presence samples in the full neural network model ($R^2 = 0.04$, $F = 3.1$, P -value = 0.084); and (D) absence samples in the full neural network model ($R^2 = 0.25$, $F = 187.4$, P -value < 0.000). Graphs for the other models are not shown; all of the models displayed the same patterns demonstrated by the graphs shown here.

data are obtained and built into the models. We expect that the inclusion of water temperature will remove this inconsistency in the models between the north and the south, as the water temperature value does not rely fully on latitude.

Error in Databases

The fish samples used in this study were obtained by several methods. Different sampling methods have different catch efficiencies depending on the fish species and stream in question, and at some sampling points, the method may not have been optimal for sampling brook trout. Consequently brook trout may be found at sites where we marked them as absent. It is difficult to say that a fish does not reside in a particular location; it may be that we simply have not found them. However, this issue may be of greater consequence for a different fish; trout are susceptible to all the sampling methods and so were

probably collected with little error. Patton et al. (2000) and Cao et al. (2005) found that electrofishing and seining yielded 97% comparability in species captured from Wyoming streams.

In addition, the data were collected over a period of 22 years. Over this time, sampling sites where fish were present may now be absent, and vice versa, due to normal fish movement and changing habitat conditions. Land-cover data and stream line segment locations are likewise dated. Land cover was based on air photos taken in 1978. However, we believe these data are generally representative of conditions in the past 25 years, which is what we examined. In using data of this type, we can avoid the naturally occurring year-to-year variation.

Another less obvious source of error in our evaluation is the unintended bias in our training data itself. Since it represents a random sample of the larger database, the models are

likely to favor methods that are best at predicting sites near the average (center of the distribution) and be biased against methods that provide a better fit to the tails of the distribution relative to the center. This may be the reason why the classification tree was able to slightly out-perform the neural network.

Model Comparison

In this study, all four models did well at predicting the distribution of brook trout throughout the state of Michigan. When applied to test data and when cross-validated with the training data, the order for accuracy was as follows: logistic regression, multiple regression, classification tree, and neural network. The predictive map produced by the logistic regression model also was the closest to the Michigan Fish Atlas patterns. However, the relative differences in the model predictions were quite small. Therefore, if we were to select the model that we deemed to be most useful, the choice might need to be based on criteria other than this predictive success.

As discussed above, multiple linear regression is not ideal for predicting dichotomous response variables (Zar 1999). Statistical assumptions about the error terms are never met with dichotomous data. However, logistic regression was developed for modeling with presence/absence data and has much less stringent assumptions than multiple regression. Logistic regression is also quite familiar to most ecologists, is widely used in the literature, and is included in most statistical packages.

Classification trees and neural networks, on the other hand, are distribution-free, nonlinear modeling procedures and therefore especially of interest to ecologists, who often encounter messy data and nonlinear responses. However, these methods are fairly new and unfamiliar to many researchers, and while the software is available, it will need to be purchased separately from a standard statistical package and may be expensive. Given that a researcher has software for both of these modeling types on hand, classification

trees will probably be preferred due to their easy setup and clear explanatory value. It is very logical and easy to follow classification trees and understand how and why the trees make the classification decisions. In contrast, a neural network can be quite confusing to the beginner and requires many more steps and more time to get any type of explanatory value. For these reasons, we prefer classification trees to neural networks in habitat analysis.

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A Broadscale Fish–Habitat Model Development Process: Genesee Basin, New York

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Abstract.—We describe a methodology for developing species–habitat models using available fish and stream habitat data from New York State, focusing on the Genesee basin. Electrofishing data from the New York Department of Environmental Conservation were standardized and used for model development and testing. Four types of predictive models (multiple linear regression, stepwise multiple linear regression, linear discriminant analysis, and neural network) were developed and compared for 11 fish species. Predictive models used as many as 25 habitat variables and explained 35–91% of observed species abundance variability. Omission rates were generally low, but commission rates varied widely. Neural network models performed best for all species, except for rainbow trout *Oncorhynchus mykiss*, gizzard shad *Dorosoma cepedianum*, and brown trout *Salmo trutta*. Linear discriminant functions generally performed poorly. The species–environment models we constructed performed well and have potential applications to management issues.

INTRODUCTION

Knowledge of species' distributions and habitat needs is vital information for fisheries and wildlife managers. Gap analysis is a national program developed by the U.S. Geological Survey to map gaps between the spatial distributions of species and protected areas. Gap analysis consists of a set of methodologies that organize and display the best available estimates of species' distributions on regional to local scales and characterize associated habitat conditions, based on georeferenced landscape data (Scott et al. 1993; Jennings 2000). Aquatic gap analysis focuses on aquatic habitats and uses models of the associations among observed species occurrences and

the broad-scale, enduring features of habitat conditions (e.g., underlying geology, physiography, climate, etc. that change slowly over ecological or geological time scales) to estimate species occurrences for an ecosystem (Sowa et al. 2004; Wall et al. 2004). Use of enduring environmental features helps to filter out the short-term, often anthropogenically induced, variation in species occurrence and abundance, providing a view of underlying zoogeographic distribution and more naturally determined occurrences. The resulting model provides a data-based, species-specific mapping tool that aids examination of species distributions at regional (100s–1,000s km) to metahabitat (~1–2 km) scales.

Construction of species–habitat models is critical to a successful aquatic gap analysis (Wall et al. 2004). Accurate correspondence of species

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occurrences and diversity to areas protected or unprotected for conservation depends on the quality of predictions from those models. We describe a development methodology for aquatic species–habitat models built from available data and compare model effectiveness. Although gap analysis is typically focused on presence or absence of species, information about abundances of species is more useful, providing more accurate estimates of centers of populations and the distributions of marginal habitats. As part of aquatic gap analysis, we tested the hypothesis that enduring environmental variables are sufficient to model both the presence and relative abundance of lotic fish. We focus on fish and habitat data from the Genesee River system (Figure 1), which is one of New York’s largest rivers and contains many of the lotic habitat types of the Great Lakes basin.

METHODS

Fish Samples

The general modeling process entails (1) filtering and standardizing spatially oriented fish abundance and habitat data, (2) detection of significant structure among fish assemblages, (3) direct gradient analysis to identify major habitat variables influencing fish abundances, (4) developing alternative models linking fish abundances with habitat conditions, and (5) predicting fish species abundances from those models.

Data are often available from statewide fisheries surveys and research projects. Such data often incorporate several shortcomings: (1) they result from different gear types applied several ways; (2) they may focus only on target species, rather than entire fish assemblages; (3) efficiencies and effort are rarely recorded; and (4) collection locations are often not georeferenced. The New York State Department of Environmental Conservation (NYS DEC) has an extensive georeferenced fish database that documents fish sampling over the last 100 years. Samples recorded in that database generally involved col-

lection of all species from each sample site, though efforts targeting only game fish were also included.

Standardization of fishing effort and area sampled are important for accurate estimation of relative abundance, but were not directly available for most samples. Data were filtered to include only electrofishing collections. Since many factors influence electrofishing effectiveness (Reynolds 1983) and several types of electrofishing gear were used in the NYS DEC sampling, data were standardized using a crude estimate of electrofishing effectiveness (i.e., 10 m² fished per minute of effort; McKenna and Johnson 2005). The abundance index was then computed as

$$\text{CPUE} = [\text{catch}/(q * f)] * 100,$$

where CPUE is fish/100 m², q is 10 m²/min of electrofishing, and f is minutes of effort.

Our model development process used survey data (release no. 14) for 1987–2002, which included 585 Genesee basin samples and 76 fish species. Species richness in fish samples from the Genesee system ranged from 0 to 20, and CPUE was as high as 493. The most commonly occurring species (>200 occurrences) were brown trout *Salmo trutta*, white sucker *Catostomus commersonii*, eastern blacknose dace *Rhinichthys atratulus*, and creek chub *Semotilus atromaculatus*. Thirty-eight species occurred more than 10 times and 30 species occurred fewer than 5 times.

Observed fish catches were examined for accurate spatial locations on streams depicted by the national hydrography data set (NHD) at the 1:100,000 scale, using descriptive location records. Only those samples located on a stream segment or that could be confidently placed on the stream based on written description of the sample site were used.

Habitat Data

Habitat variables were applied to segments of the NHD by collecting available spatial data layers

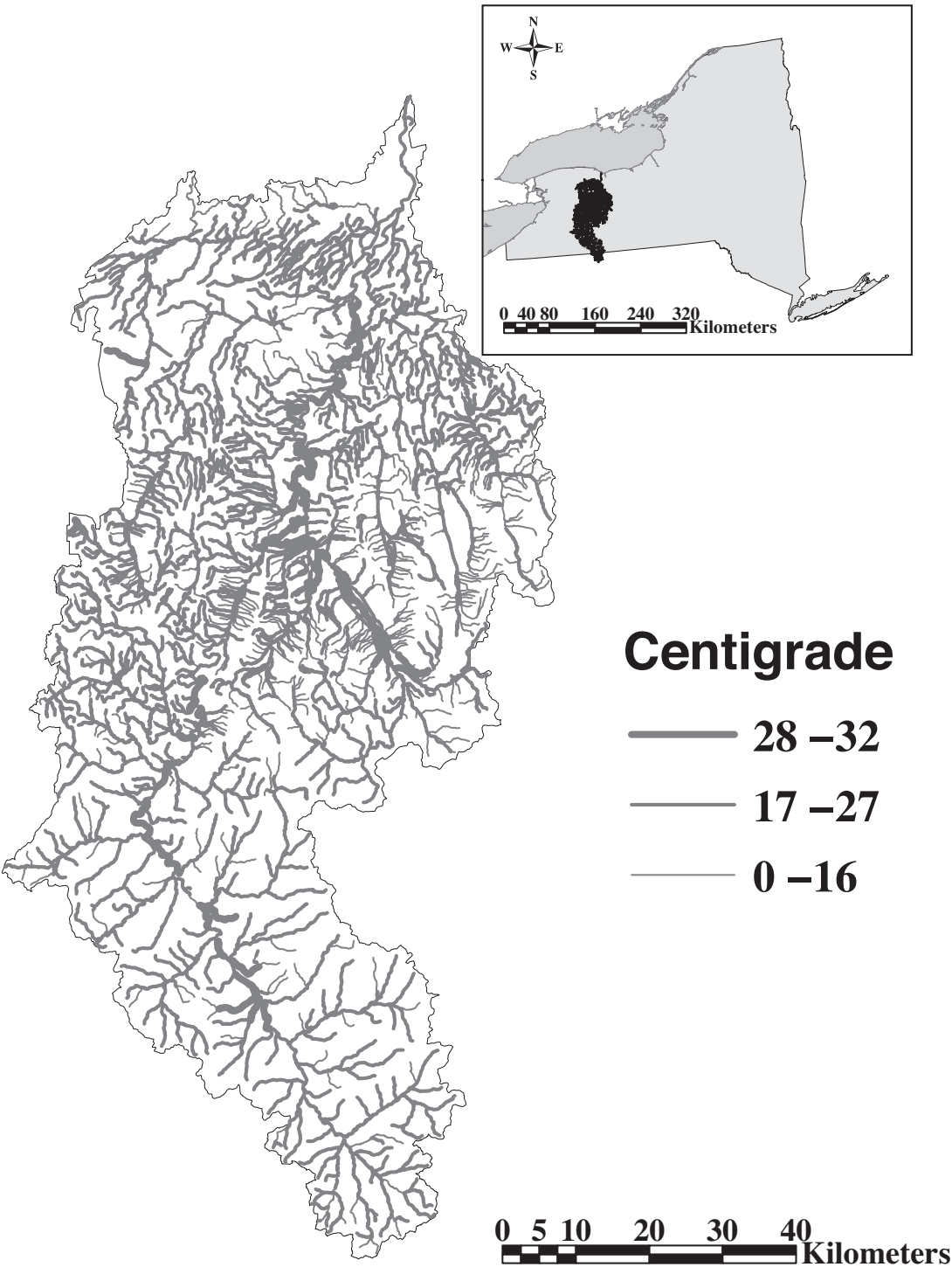


Figure 1. Predicted summer daytime water temperatures for each stream in the Genesee River drainage system. The five temperature classes are displayed in three categories to show general pattern.

($\geq 1:250,000$ scale) compatible with the ArcGIS software (ESRI 2002) and adjusting map projection and map datum information to achieve correct spatial alignment. National hydrography data set processing and attribution consisted of numerous steps. Habitat layers consisted of GIS coverages of ecoregions, bedrock geology, climatic information (e.g., July mean, minimum, and maximum air temperature; mean annual air temperature; mean July precipitation; and mean July growing degree-days), elevation, land use, soil permeability, surficial geology (both material type and depth to bedrock), watershed basin, and subbasins.

We prepared coverages in three steps. First, the NHD base layer (1:100,000 scale) was manually edited to correct all loops, braids, disconnected lines, and erroneous flow directions, producing a single continuous line arc network. Multiple 8-digit hydrologic unit codes (HUCs) within each major drainage were joined before cleaning. In the second step, habitat layers were conditioned and converted to a raster (point grid) format using a modified version of the Albers Equal Area projection and shifting the latitude of projection origin to the approximate center of the Great Lakes to preserve both area and distance. The rasterized NHD stream network and the habitat layers were reprojected to this standard projection and datum information. Finally, a series of Arc Macro Language (AML) programs (ESRI 2002) were run that produced coverages and tables of information about the streams and habitat features. The value of each area-based habitat attribute for each stream segment was determined from the proportion of all 30-m pixels that lined up on the stream and had positive values. The Genesee drainage was represented by 2,375 map line arcs in the modified NHD. Abiotic variables (including temperature) were assigned to each arc as attributes of those lines. Habitat conditions were then associated with fish sampling points located on or close to the arcs.

Complete spatial landscape coverage of stream temperature was not available for this

project. Therefore, we used spot temperature measurements recorded during fish sampling events from June through September. Spot measurements are much more variable than means of continuous measurements and poorly represent conditions experienced by aquatic organisms (Wehrly et al. 2003). Water temperatures were placed into five 10-degree (Fahrenheit) classes, identified by mid-points of 45°F (7.2°C)–85°F (29°C) to accommodate the imprecise measurements. The temperature class for each stream segment was estimated using a linear discriminant function developed with a suite of habitat variables as independent predictors (Venables and Ripley 2002). Linear discriminant analysis (LDA) seeks linear combinations of variables that best separate groups (Pielou 1977; James and McCulloch 1990). The linear discriminant function for Genesee stream temperatures consisted of five multivariate equations (one for each temperature class). The predicted temperature class for each stream segment was determined by the equation with the maximum value. Although normality is not strictly required for LDA, it works best when data are normal and covariances are the same for each group (James and McCulloch 1990). The distribution of temperature values was close to normal (skewness = 0.23, kurtosis = -0.25) and covariances were similar. The LDA function was based on month, Shreve link, downstream order, gradient, proportion as deciduous forest (LU41), proportion as open water (LU50), proportion of bedrock as carbonate (BR3), proportion of surficial geology as coarse alluvium (QG19), and proportion of depth to bedrock in the range 100–200 ft (BRD3). The resulting temperature classes were used as a predictor variable for species abundance models (Figure 1).

Fish Species Modeling Techniques

Cluster analysis (CLUS), canonical correspondence analysis (CCA), multiple linear regression (MLR), stepwise MLR (STEP), linear discriminant analysis (LDA), and neural networks (NN)

were applied, in a specific sequence, to develop and compare models for predicting species abundances. Only observations where a species was present were used to develop linear regression models, which predicted continuous values of CPUE. This avoids determining the strength of the model (r^2) based on the influence of many observations where that species was not collected. All observations were used in developing LDA and NN models, which predicted CPUE categories.

Cluster analysis provides much information about species assemblage structure (McKenna 2003), but was applied here simply to determine whether spatial structure existed among the fish abundance data. It is unlikely that substantial environmental influence on species abundances would be found in the absence of spatial species assemblage structure. The CANOCO program (version 4.5 for Windows) provided a direct gradient analysis via canonical correspondence analysis (CCA), which identifies gradients within species data that are best explained by abiotic variables, assuming a unimodal response (ter Braak and Smilauer 2002). Unimodal responses to environmental conditions are common in nature, often more realistic than a linear response, and indicate that species have optimal habitat conditions (Whittaker 1956; Hill 1977; ter Braak 1987, 1995; ter Braak and Looman 1995). The abiotic variables were standardized to a mean of zero and a standard deviation of one to remove differences in ranges and measurement units. Canonical correspondence analysis forward selection with permutation tests was used to identify significant ($P \leq 0.05$) variables for subsequent model development.

Although CPUE index data were used in the cluster and CCA analyses, the error in constructing that index hinders precise prediction. Our objectives were better met by providing a less precise abundance indicator. Therefore, CPUE values were transformed into log-scale abundance categories (0, 1, 2–10, 11–100, 101–1,000, or >1,000 individuals) before predictive model development.

Multiple regression models are typically used to relate diversity or fish abundance to environmental conditions (e.g., Matuszek and Beggs 1988; Beamish and Lowartz 1996; Beechie and Sibley 1997; Dunham and Vinyard 1997; Leftwich et al. 1997). Predicted values are continuous and the model assumes linearity. The stepwise procedure helps streamline MLR models. Full MLR models used all CCA-identified variables if sample size was sufficient. If a singularity matrix error occurred, the predictor variable list was trimmed by removing the least influential variables (based on CCA scores). The stepwise procedure selected a subset of these variables via a backward elimination procedure (Insightful 2001).

Linear discriminant analysis constructs linear functions that predict class membership based on a suite of predictor variables. The function is developed by preclassifying a species' observed abundance into defined classes. The discriminant analysis constructs the function that best predicts the abundance class based on the associated environmental variables. The full set of CCA-identified variables was used and the most basic LDA model (assuming homogeneity of variance and the classical model family) was constructed. Cross validation by leaving one observation out and repeating the analysis was used to test model results, provide predicted classifications, and measure misclassification rate. Correlation coefficients and coefficients of determination for LDA results were calculated by simple linear regression of the predicted CPUE categories on the observed abundance categories.

Linear regression and linear discriminant analysis assume linear models, but nonlinear relationships are common in ecology. Neural networks directly model nonlinear relationships between response variables and the factors upon which they depend (Lek et al. 1996; Guegan et al. 1998). Neural networks can be more effective than, and do not suffer from many of the shortcomings of, regression models (Hertz et al. 1991; Kosko 1992). They are complex systems that

iteratively learn how to best predict a value or class membership of a value. The neural network development process (e.g., Rumelhart et al. 1988; Olden and Jackson 2001, 2002; McKenna 2005) entails iteratively reweighting habitat variable values to learn the model structure that best predicts values in the training or other dataset, or both. The simplest three-layer backpropagation model was used. The default number of neurons per hidden layer was determined by the following:

$$N_H = \frac{1}{2} (N_I + N_O) + \sqrt{D_T},$$

where N_H = the number of neurons per hidden layer, N_I = the number of input neurons, N_O = the number of output neurons, and D_T = the number of observations in the training data set (Ward Systems 2000). A logistic activation function was applied. All CCA-identified variables were used.

All four model types were developed for each of 11 species, which represented a range of abundances and optimum locations along the first three ordination axes (Table 1). Species occurring ≤ 20 times were not used. Models with $r \geq 0.60$ were considered successful. The S+ statistics software (Insightful 2001) was used for developing and testing multiple regression and linear discriminant functions (LDA). Neural

networks were developed with the NeuroShell 2 software (Ward Systems 2000).

We examined model performance in three ways: (1) visual inspection of distribution maps showing predicted and observed abundances, (2) rates of omission and commission errors, and (3) coefficients of determination and correlation between observed and predicted values.

RESULTS

Eighty-four percent of Genesee River fish samples included a water temperature measurement. The misclassification rate for the temperature function was quite high for some temperature classes (Table 2). However, most misclassifications occurred in adjacent temperature classes. Only 3% of samples were misclassified two or more temperature classes away from the correct class.

Cluster analysis indicated the presence of spatial structure among the Genesee basin fish and identified 21 distinct assemblages. Further analysis of those assemblages is beyond the scope of this work. The first three CCA axes explained 59% of the species–environment relationship and species–environment correlations were high (>0.70). The forward selection procedure of the CCA identified 25 abiotic variables that had a significant influence on the distribution of fish

Table 1. Names, codes, frequency of occurrence, and maximum sample abundances (catch/ha) for species selected for modeling.

Species code	Common name	Scientific name	Frequency of occurrence	Maximum CPUE
BNDC	Eastern blacknose dace	<i>Rhinichthys atratulus</i>	237	20,000
BROK	Brook trout	<i>Salvelinus fontinalis</i>	133	4,125
BTRT	Brown trout	<i>Salmo trutta</i>	335	13,508
CHUB	Creek chub	<i>Semotilus atromaculatus</i>	207	12,500
FANT	Fantail darter	<i>Etheostoma flabellare</i>	144	6,667
GIZZ	Gizzard shad	<i>Dorosoma cepedianum</i>	20	353
MOTT	Mottled sculpin	<i>Cottus bairdii</i>	117	10,000
RAIN	Rainbow trout	<i>Oncorhynchus mykiss</i>	38	5,760
ROCK	Rock bass	<i>Ambloplites rupestris</i>	53	1,511
SFSH	Spotfin shiner	<i>Cyprinella spiloptera</i>	24	4,889
WSUK	White sucker	<i>Catostomus commersonii</i>	239	7,083

Temperature class observed	Predicted				
	7°	13°	18°	24°	29°
7°	0	2	5	0	0
13°	1	49	69	0	1
18°	1	22	238	14	5
24°	0	1	84	31	16
29°	0	0	5	0	6

Most predictive models were significantly different from no relationship, but ranged widely in the amount of variation explained (Table 4; Appendix A). The four models differed in their accuracies of predicting abundance and distribution. For example, brook trout was predicted, in general, to be found in greatest abundances in low-order and high-elevation stream reaches, particularly in the upper half of the watershed (Figure 3). The MLR model predicted brook trout abundance in the 11–100 category for the large majority of stream reaches with only a few reaches in the lowest part of the watershed having abundance values of 0–1 (Figure 3A). It was expected to be absent from most of the main stem and a few other isolated stream reaches. In

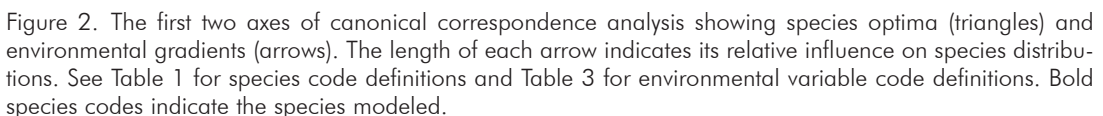


Table 3. Abiotic variables identified by CCA as having significant influence on fish assemblages.

Variable code	Description
AVG_ELEV	Mean elevation of stream reach
BR1	Bedrock as sandstone
BR3	Bedrock as carbonate
BRD_2	Depth to bedrock: 50–100 ft
BRD_3	Depth to bedrock: 100–200 ft
BRD_4	Depth to bedrock: 200–400 ft
DLINK	Number of stream segments downstream of a given reach
DOWNORDER	Stream order immediately downstream of a given reach
ECOCODE	Omernik’s level III ecoregion code
GRADIENT	Slope of stream reach
LU11	Land use: urban/commercial/industrial
LU22	Land use: row crop agriculture
LU41	Land use: deciduous forest
LU42	Land use: evergreen forest
LU50	Land use: open water
LU62	Land use: nonwooded wetland
QG1	Surficial geology: coarse outwash
QG10	Surficial geology: coarse lacustrine
QG19	Surficial geology: coarse alluvium/fluvial
QG7	Surficial geology: medium ground-moraine
QG9	Surficial geology: fine lacustrine
SHREVE	Shreve designation of stream order
SINUOUS	Sinuosity: measure of stream course curvature
STRAHLER	Strahler designation of stream order
TEMPERATURE	Estimated water temperature classified into 10°F classes

contrast, LDA provided the most restricted view of brook trout distribution, predicting absence from most of the watershed, including nearly all of the lower third of the drainage (Figure 3C). Highest abundances (2–10) were predicted for high gradient streams in the middle reaches of the drainage and some small streams in the uppermost part of the watershed. Stepwise MLR (Figure 3B) and NN (Figure 3D) model predictions were intermediate and similar for brook trout. Both predicted about half the stream reaches to contain 2–10 brook trout and many of the remainder to contain at least 1. The STEP model predicted somewhat higher abundance in the middle section of the watershed than did the NN model.

Model omission rates in this study were quite low for multiple regression and NN models (<8%, except for creek chub), but high for LDA (11–73%) (Table 5). Commission rates showed a large range (0–81%). Neural network models generally displayed lower omission and commission rates than those of the linear models.

All but five regression models were significant (Table 4), but correlation coefficients ranged from 0.28 to 0.95; rainbow trout regressions were clearly the strongest of the linear models. The STEP procedure produced simpler models that explained the same amount of variability as full MLR models or only slightly less. However, only 9 of the 22 MLR and STEP models met the success criterion of $r \geq 60\%$ (Table 4). Correlations

Table 4. Coefficients of determination (r^2) and (correlation coefficients) associated with results of various predictive models. * indicates regression/network $P < 0.05$, **bold** indicates $r \geq 0.60$.

Species modeled	Linear		Stepwise linear		Discriminant analysis		Neural network
Blacknose dace	0.28	(0.53)*	0.28	(0.53)*	0.08	(0.28)*	0.56 (0.75)*
Brook trout	0.27	(0.52)*	0.24	(0.49)*	0.41 (0.64)*		0.77 (0.87)*
Brown trout	0.37 (0.61)*		0.38 (0.62)*		0.14	(0.37)*	0.35 (0.60)*
Creek chub	0.08	(0.28)*	0.08	(0.28)*	0.04	(0.20)*	0.45 (0.67)*
Fantail darter	0.47 (0.68)*		0.46 (0.68)*		0.07	(0.26)*	0.64 (0.80)*
Gizzard shad	0.42 (0.65)*		0.28	(0.53)	0.89 (0.94)*		0.57 (0.75)*
Mottled sculpin	0.34	(0.58)*	0.32	(0.57)*	0.09	(0.30)*	0.72 (0.84)*
Rainbow trout	0.91 (0.95)*		0.91 (0.95)*		–		0.48 (0.69)*
Rock bass	0.52 (0.72)*		0.43 (0.66)*		0.12	(0.35)*	0.67 (0.82)*
Spotfin shiner	0.23	(0.48)	0.21	(0.46)	0.17	(0.41)*	0.36 (0.60)*
White sucker	0.29	(0.53)*	0.27	(0.52)*	0.19	(0.44)*	0.56 (0.75)*

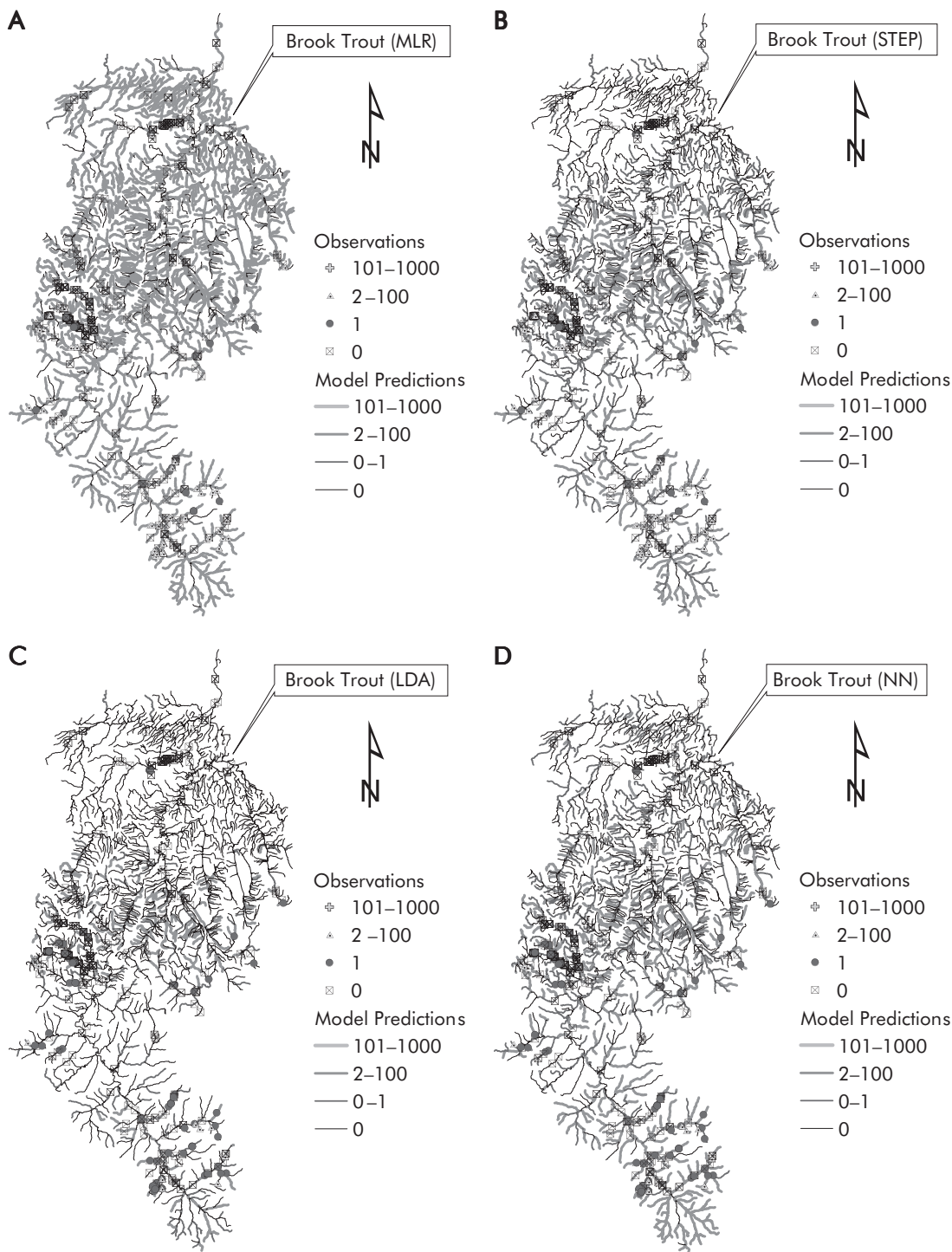


Figure 3. The Genesee River drainage system comparing brook trout abundances predicted for each stream arc by each model type developed and observed sample abundances. The 2–100 category combines the 2–10 and 10–100 abundance categories for ease of presentation. See text for correct abundances. The neural network (NN) model is the preferred choice for this species.

Table 5. Omission and (commission) error rates associated with results of various predictive models.

Species modeled	Linear	Stepwise linear	Discriminant analysis	Neural network
Blacknose dace	2% (42%)	2% (40%)	60% (16%)	1% (23%)
Brook trout	1% (44%)	0% (20%)	39% (6%)	0% (0%)
Brown trout	4% (24%)	4% (26%)	17% (26%)	0% (3%)
Creek chub	2% (39%)	23% (16%)	73% (13%)	3% (9%)
Fantail darter	7% (45%)	6% (53%)	64% (12%)	0% (2%)
Gizzard shad	0% (86%)	0% (78%)	11% (0.4%)	0% (0%)
Mottled sculpin	0% (76%)	1% (62%)	62% (7%)	0% (3%)
Rainbow trout	0% (64%)	0% (62%)	—	0% (0%)
Rock bass	1% (56%)	1% (52%)	72% (44%)	0% (0%)
Spotfin shiner	0% (17%)	0% (81%)	26% (3%)	0% (1%)
White sucker	3% (51%)	3% (51%)	42% (22%)	0% (12%)

between observed and predicted results from LDA also displayed a wide range (0.20–0.94) and generally performed poorly (Table 4). LDA models could not be developed for rainbow trout due to insufficient rank errors. Neural network models performed considerably better than the linear models, often explaining more than twice as much variability (Table 4). Only the rainbow trout NN model performed markedly worse than the linear models (Table 4). All NN models met the $r \geq 60\%$ criterion.

Visual inspection of species distribution maps showed that model predictions were quite good. Gizzard shad was observed in only low abundances (one individual) and in only the lower main stem (Figure 4A). However, the models (except for the LDA model) predicted it to be much more widespread. Brook trout was found in abundances of at least 2–10 in the upper two-thirds of the drainage, especially in the smallest streams; it was less common or absent from the lower two-thirds of the drainage where it was predicted to be less abundant (Figure 3). Brown trout reached abundances of 0–100 in a number of areas, including the lower drainage as predicted (Figure 4B); it was absent from the high gradient streams in the middle of the drainage (Figure 4B). Rainbow trout was predicted to be abundant nearly everywhere, except in the main stem in the lower half of the watershed and many streams in the narrowest section of the drainage (Figure 4C). However, it was observed in only a

few places within the watershed. Predicted minnow abundances tended to be slightly higher than those observed, but in general, there were no substantial deviations of the pattern of predicted abundances from observed values, except where noted below. Blacknose dace was abundant (11–100) in the upper two-thirds of the drainage as predicted and common (2–10) throughout most of the rest of the watershed; but despite predictions, it was absent from assorted streams, especially in the lower half of the watershed (Figure 5A). Creek chub occurred in abundances of 2–100 in the upper watershed as predicted; it was less abundant than predicted in the lower basin (Figure 5B). Spotfin shiner was predicted to be found throughout the watershed in low abundance, but more widespread in the lower half of the drainage; observed abundances were restricted to main stem locations in the lower half of the watershed (Figure 5C). White sucker was predicted to occur in moderate abundances (2–10) throughout the watershed; observed abundances reflected its predicted abundances (Figure 6A). Mottled sculpin was found in small streams and was more abundant in the upper portion of the watershed and high-elevation streams than elsewhere. It was absent from the large streams of the lower half of the watershed and from the western section of the drainage where it was predicted to be abundant (Figure 6B). Rock bass was found in low abundances in large streams in the uppermost and

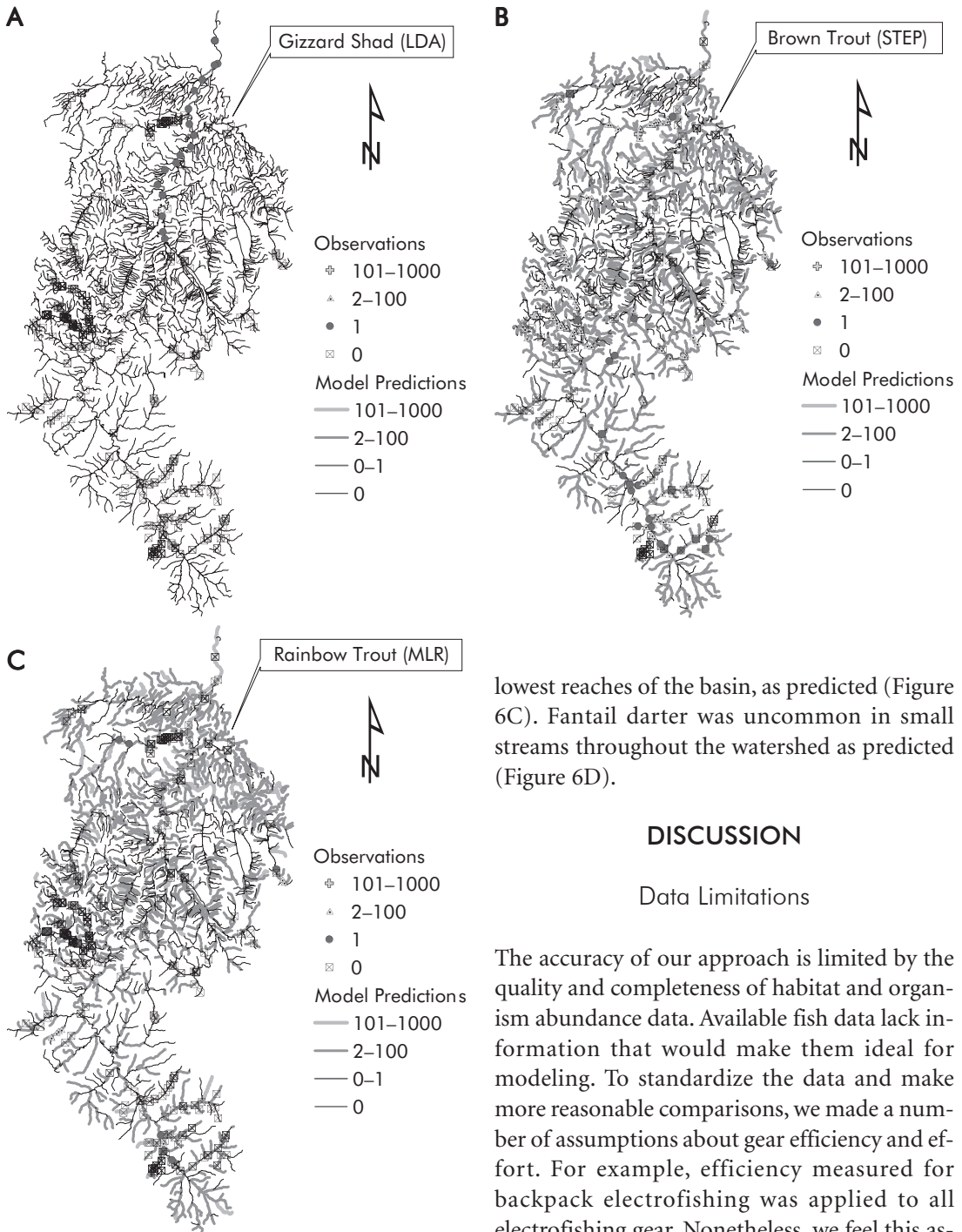


Figure 4. The Genesee River drainage system showing the best model predictions of (A) gizzard shad (LDA), (B) brown trout (STEP), and (C) rainbow trout (MLR) abundances for each stream arc. The 2–100 category combines the 2–10 and 10–100 abundance categories for ease of presentation. See text for correct abundances.

lowest reaches of the basin, as predicted (Figure 6C). Fantail darter was uncommon in small streams throughout the watershed as predicted (Figure 6D).

DISCUSSION

Data Limitations

The accuracy of our approach is limited by the quality and completeness of habitat and organism abundance data. Available fish data lack information that would make them ideal for modeling. To standardize the data and make more reasonable comparisons, we made a number of assumptions about gear efficiency and effort. For example, efficiency measured for backpack electrofishing was applied to all electrofishing gear. Nonetheless, we feel this assumption provided adequate accuracy for successful modeling.

The scale of habitat variables also limited model success. We only used stream buffer attributes associated with each reach. However, fish

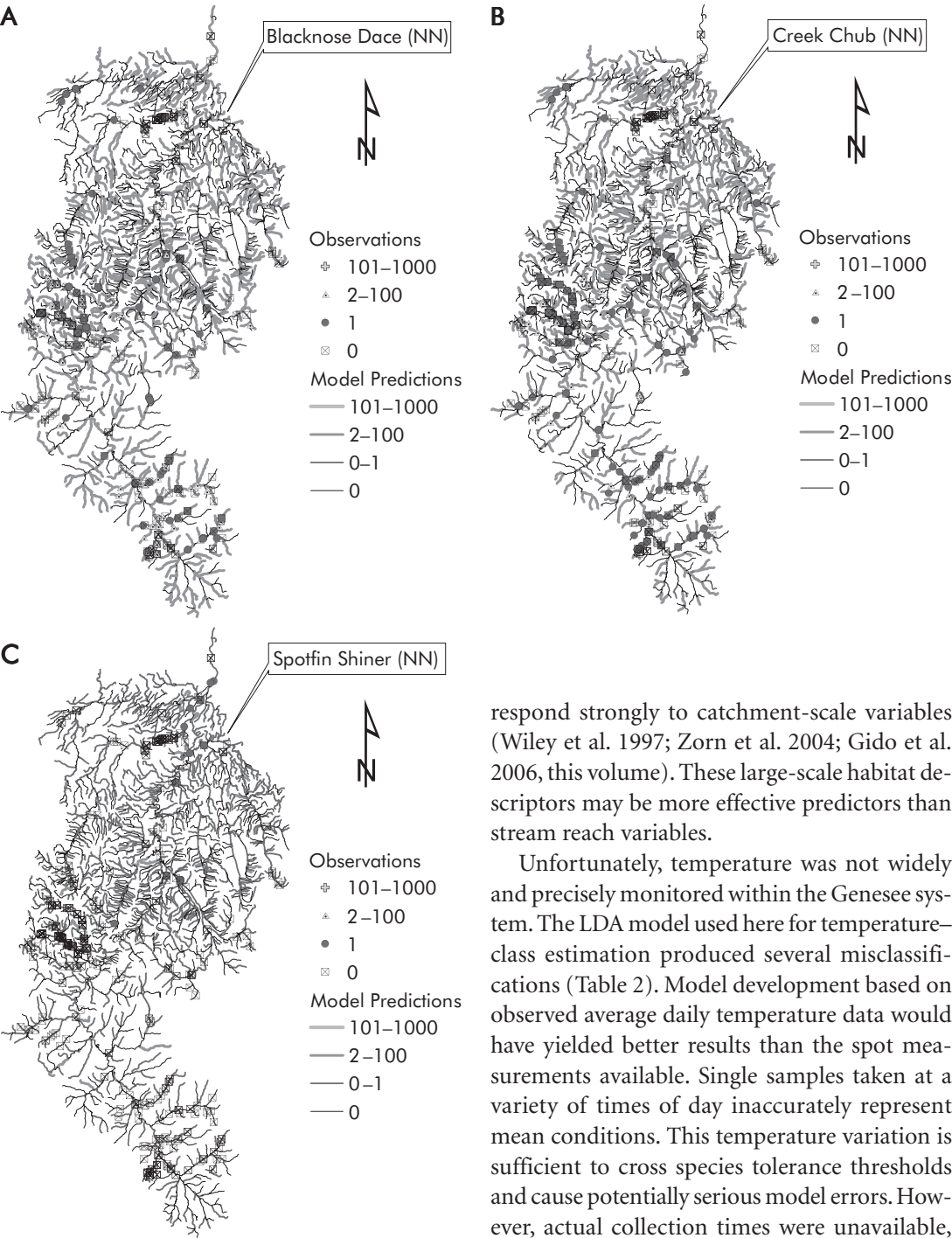


Figure 5. The Genesee River drainage system showing the best model predictions of (A) blacknose dace (NN), (B) creek chub (NN), and (C) spotfin shiner (NN) abundances for each stream arc. The 2–100 category combines the 2–10 and 10–100 abundance categories for ease of presentation. See text for correct abundances.

respond strongly to catchment-scale variables (Wiley et al. 1997; Zorn et al. 2004; Gido et al. 2006, this volume). These large-scale habitat descriptors may be more effective predictors than stream reach variables.

Unfortunately, temperature was not widely and precisely monitored within the Genesee system. The LDA model used here for temperature-class estimation produced several misclassifications (Table 2). Model development based on observed average daily temperature data would have yielded better results than the spot measurements available. Single samples taken at a variety of times of day inaccurately represent mean conditions. This temperature variation is sufficient to cross species tolerance thresholds and cause potentially serious model errors. However, actual collection times were unavailable, precluding time of day adjustments. Despite these shortcomings, the temperature model predicted a spatial pattern generally consistent with thermal conditions in natural watersheds of this region. The need for continuous temperature

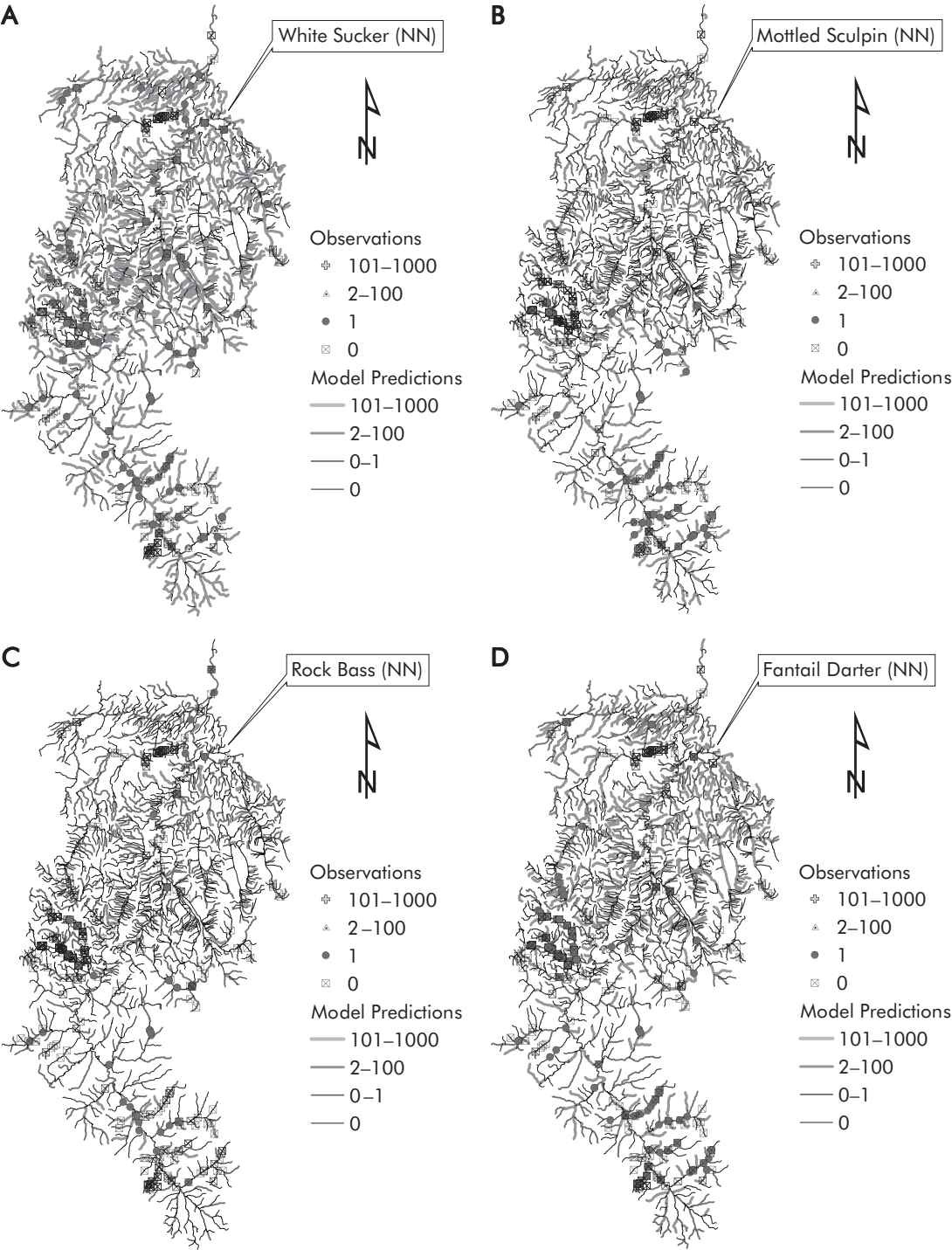


Figure 6. The Genesee River drainage system showing the best model predictions of (A) white sucker (NN), (B) mottled sculpin (NN), (C) rock bass (NN), and (D) fantail darter (NN) abundances for each stream arc. The 2–100 category combines the 2–10 and 10–100 abundance categories for ease of presentation. See text for correct abundances.

measurements is clear (Wiley et al. 1997; Fausch et al. 2002).

Predictive Models

The variables identified by CCA provided an effective suite of predictors. Each predictive model produced plausible species distributions, but maps produced by the full MLR models appeared exaggerated, based on what is known about species life history requirements and present-day distributions (Figure 3) (Smith 1985). Distributions and abundances based on LDA predictions were the most conservative; many stream segments were not expected to support any of the fish species examined. Neural network and STEP model predictions were intermediate between the other two model types. The correspondence of model predictions to observed fish abundances revealed many mismatches (Figures 3–6). Most of the observed high abundances (2–100) for species like brown trout and blacknose dace were grouped in the same areas or stream reaches as samples in the 1–100 categories. This tends to produce a picture of the average of those abundances during model development. Our models often predicted those average conditions, particularly the NN models. Also, misclassified abundances often occurred adjacent to stream segments in which they would have been correct. Therefore, strict examination of the misclassifications of abundances may provide an inaccurate assessment of model performance.

Most of the predictive models were significant (Table 4), but many explained relatively small amounts of the observed species abundance distributions. This indicates that important variables were not considered. Choice of correlations $\geq 60\%$ as a criterion for success was arbitrary and more models would have been considered successful if 50% was used. However, 50–60% of variation in stream biota may be explained by spatial influences (Wiley et al. 1997; Van Sickle and Hughes 2000; Herlihy et al. 2006,

this volume). Some of the remainder may be associated with temporal variation. The best model predictions for each species we evaluated accounted for at least 60% of the variation in the observed data.

Prediction of presence and absence is less demanding of predictive models than abundance, but still useful in zoogeographic investigations. Prediction error rates indicate model inaccuracies and environmental changes. Omission rates measure error in terms of what is known (i.e., observed presence of a species) and generally carry more weight as measures of model validity than do commission rates; commission measures error in terms of what is not known (i.e., observed absences). Omissions may indicate model error, but may also indicate changes in stream habitat allowing a species to colonize where it would not be expected. Omission rates less than 10% are generally good; all NN and regression models but one achieved lower rates (Table 5). In contrast, omission rates for the LDA models were greater than 10%. Commission rates were generally higher than omission rates, though NN model commissions were much better than those for other models. Like omission, commission error may indicate model inaccuracy. However, it is likely that many of these errors are due to inadequate sampling. For example, a fish may have been absent from a sample simply because it was missed by the gear or was ignored during sampling targeted for a different species. Commission errors may also be useful in identifying important habitat changes that have resulted in exclusion or extirpation of a species. If this is the result of degradation, it can indicate areas where managers may wish to consider mitigation or research.

Predicted distributions within the watershed were consistent with what is known of the life histories of the species examined. For example, brook trout is a coldwater species typical of small streams (Scott and Crossman 1973; Smith 1985). Brown trout has similar habitat requirements, but is more tolerant of warm temperatures and

often inhabits larger streams than does brook trout (Scott and Crossman 1973; Smith 1985). Creek chub is a widely distributed species that is generally tolerant of a wide range of stream conditions (Scott and Crossman 1973; Halliwell et al. 1998). White sucker is common and generally tolerant of a wide range of stream condition and is typically found in nearly every stream of New York State (Smith 1985). Fantail darter and mottled sculpin are typical of cool to cold, small streams with rocky or sand substrata, but often do not share the same habitat (Scott and Crossman 1973; Smith 1985).

Model Effectiveness

All our models provide correlative results that explain a portion of observed variability. The sources of the remaining variability are unknown. Linear discriminant analysis and MLR models explained the least amounts of species' variabilities and had high error rates. As such, they cannot be recommended for species model development. The additional effort to develop LDA models is not warranted. Stepwise MLR produced models that often explained as much variability as that of full MLR models, and were more frequently significant. Neural network models often accounted for twice as much variability as the linear models. Abundance errors were often off by only a single abundance class, and spatial errors would often have been correct in an adjacent arc. Neural network models require more effort to develop than linear regression models and are difficult to describe because model specifics are so extensive. However, the increase in explanatory ability and low error rates make the effort worthwhile.

Other modeling methods not examined here may prove to be as effective as or better than those described above. Gaussian regression is essentially the same as linear regression, but fits a unimodal rather than a linear model (ter Braak and Looman 1995). Results from the CCA and NN models suggest that Gaussian regression

might be an effective modeling tool. Decision trees usually classify observations based on a series of rule-based binary decisions (Venables and Ripley 2002; Herlihy et al. 2006). This may also be an effective tool if modeling goals are limited to prediction of fish abundance classes (Sowa et al. 2004).

Development of effective species–habitat models is a critical step in providing a useful tool for examining biodiversity and conservation needs. Reliable model predictions of abundances and distributions for each species allow estimates of diversity, richness, and other ecological descriptors for each habitat unit (Scott et al. 1993 and Kilgour and Stanfield 2006; Stanfield and Kilgour 2006; Stanfield et al. 2006, Steen et al. 2006; all this volume). This aids description of the habitat types, based on distribution and diversity of fish assemblages, and ultimately assessment of the conservation and protection status for each part of the Great Lakes drainage. Such information can be used to redirect survey effort to where information is critically needed, identify potential fishery areas, help allocate funding for conservation and protection effort, enhance restoration efforts, or aid in research planning and design.

Our models produced good predictions, based on comparison with the data used to develop them. However, field verification of the hypotheses established by these models remains the ultimate test of their accuracy and reliability.

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Appendix A. Parameter values for each linear model function (MLR, STEP, and LDA) for each of the 11 example species from the Genesee River system. Any negative predictions were forced to zero. Each neural network model is specified by more than 1,100 lines of Microsoft Visual Basic 6.0 code, which is not reproduced here but is available upon request. See Table 3 for abbreviation definitions.

Model type	Species	constant	Temp- erature	STRAHLER	SHREVE	DOWN ORDER	SINUOUS	AVG_ELEV	GRADIENT	Eco_code	LU11	LU22	LU41	LU42
MLR	BNDC	21.0026	-0.3441	-10.0052	0.0351	2.436	23.7402	0.0189	-155.637	-0.1356	-99.1462	11.0501	7.3671	29.6081
	BROK	-7.9835	-0.1027	0.4659	-0.0832	-1.372	24.7665	0.0135	60.7122	-1.0121	-60.6666	-15.697	-6.3897	-
	BTRT	-61.8364	0.8007	1.0929	0.1978	-1.4345	9.2573	0.0514	-199.537	0.4745	-144.91	-23.244	-30.841	-
	CHUB	18.5326	0.1144	-3.7329	0.0061	0.036	-7.0097	0.0157	-206.164	-0.7164	12.0562	-7.9297	0.6349	71.3114
	FANT	-40.4658	0.3068	-0.549	0.065	3.7569	14.4681	0.0317	184.0734	-1.8765	32.2024	-21.808	4.6392	-
	GIZZ	-77.5588	-0.0539	4.5866	0.0034	-0.8747	-	0.3726	-425.832	-	-	-	-	-
	MOIT	3.4632	-0.2844	2.1554	-0.1498	4.1704	-	-0.0689	801.7482	2.3089	-	-	-	-
	RAIN	157.192	-1.1603	-23.1332	0.6744	-27.2536	69.1879	0.1145	-2671.42	-3.9046	-	-	-	-
	ROCK	74.153	-1.2352	0.693	-0.026	5.4354	-2.6124	-0.0118	192.7999	-0.347	9.0664	50.8784	3.3458	633.6978
	SFSH	-7.4801	0.1719	-0.0434	-0.0006	-	-	-0.0155	171.7281	-	-	-	-	-
STEP	WSUK	17.6469	-0.2034	0.787	0.0108	-2.1585	4.4612	0.0215	-273.034	0.0761	-52.4752	-20.783	-7.2174	35.7001
	BNDC	53.3364	-0.5251	-6.6244	-0.2615	-	13.9752	-	-	-	-114.661	-	-	-
	BROK	2.0235	-0.0428	-	0.0008	-	-	0.0016	38.3086	-	-	-	-	-
	BTRT	-55.5193	0.5892	-	0.2518	-	9.2136	0.0684	-	-	-118.31	-	-28.885	-
	CHUB	9.8303	0.1933	-3.4622	0.0041	-	-4.0242	0.0146	-181.177	-0.7358	-	-	-	-
	FANT	-16.8923	-0.0212	0.5775	-0.0164	2.7646	15.4717	0.0304	185.5858	-1.9746	-	-24.154	4.7784	-
	GIZZ	-54.0852	-0.0548	3.4832	0.0013	-	-	0.2396	-	-	-	-	-	-
	MOIT	8.4125	-0.2855	-	-0.0361	3.5115	-	-0.0424	708.7855	1.6697	-	-	-	-
	RAIN	-108.804	2.494	-	-0.1039	-17.6659	43.686	0.0719	-630.445	-6.0231	-	-	-	-
	ROCK	48.4431	-0.8755	-	-0.0223	4.8907	-	-0.0161	-	-	-	40.7813	4.5264	306.7497
LDA	SFSH	-10.5453	0.1799	-	-0.0027	-	-	-	-	-	-	-	-	-
	WSUK	24.3973	-0.2446	-	0.0065	-1.8862	-	0.0253	-298.888	-	-53.9126	-	-5.3053	-
	BNDC 0	-255.823	5.506	17.577	-0.071	-14.9	79.13	0.076	1187.611	-0.49	5.155	65.363	32.458	-1376.26
	BNDC 1	-252.949	5.523	17.379	-0.077	-14.445	75.921	0.08	1148.996	-0.678	17.837	59.335	30.226	-1327.17
	BNDC 10	-255.758	5.533	16.747	-0.071	-14.766	78.448	0.08	1165.857	-0.578	14.463	59.198	30.78	-1363.99
	BNDC 100	-252.275	5.445	14.829	-0.068	-14.829	80.812	0.089	1008.819	-1.14	-9.995	58.795	29.839	-1333.03
	BROK 0	-253.713	5.558	17.065	-0.076	-14.63	76.52	0.082	1155.895	-0.675	14.792	59.513	30.938	-1313.85
	BROK 1	-261.697	5.606	17.082	-0.074	-15.29	76.023	0.088	1252.72	-0.641	14.783	61.317	32.487	-1283.2
	BROK 10	-260.547	5.458	17.002	-0.07	-15.036	78.567	0.096	1309.358	-0.9	10.823	64.238	30.826	-1393.75
	BROK 100	-	-	-	-	-	-	-	-	-	-	-	-	-

(Appendix continues)

Appendix A (continued)

Model type	Species	LU50	LU62	BR1	BR3	QG1	QG7	QG9	QG10	QG19	BRD_2	BRD_3	BRD_4
MLR	BNDC	54.7426	138.379	0.0152	-1.072	0.002	-0.042	0.2873	-0.066	-0.137	-0.395	-	-
	BROK	70.4619	30.2486	0.0213	-0.049	-	-	-	-	-0.057	-	-	-
	BTRT	-104.869	11.3764	-0.034	0.2416	-	-	-	-	-0.189	-	-	-
	CHUB	-5.625	-5.2131	-0.0005	0.004	-0.004	-0.014	0.0005	0.0086	0.0223	-0.068	0.0064	0.0053
	FANT	289.5242	15.7168	0.009	-0.861	-	-	-0.033	-	-0.068	-	-0.1093	-
	GIZZ	-1.4241	-	0.3455	-	-	-	-	-	-	-	-	-
	MOTT	39.0075	39.9928	0.0131	-	-	0.0086	-	-	-	-	-	-
	RAIN	-830.173	-24.835	0.2828	-	-	-0.119	-	-	-	-	-	-
	ROCK	13.6017	-18.108	0.0276	0.0156	-0.001	-0.048	-0.007	-0.023	0.0393	-0.011	-0.0893	0.0489
	SFSH	-5.2594	-	-0.007	-	-	-	-	-	-	-	-	-
	WSUK	-11.402	89.9786	0.0211	0.0004	0.0085	-0.023	0.0705	-0.023	0.022	-0.067	-0.0265	-0.061
	BNDC	-	144.587	-	-	-	-0.027	0.2276	-	-	-	-	-
STEP	BROK	-	-	0.0056	-	-	-	-	-	0.0036	-	-	-
	BTRT	-116.877	-	-0.042	0.2341	-	-	-	-	-0.188	-	-	-
	CHUB	-	-	-	-	-	-0.012	-	-	-	-0.066	-	-
	FANT	-	-	-	-	-	-	-0.039	-	-	-	-0.0729	-
	GIZZ	-	-	0.1883	-	-	-	-	-	-	-	-	-
	MOTT	-	-	-	-	-	-	-	-	-	-	-	-
	RAIN	-244.88	-	0.1858	-	-	-0.034	-	-	-	-	-	-
	ROCK	20.0087	-	-	-	-	-0.018	-	-0.024	-	-	-0.0398	0.0758
	SFSH	-	-	-	-	-	-	-	-	-	-	-	-
	WSUK	-	109.826	-	-	-	-0.013	0.0786	-	-	-	-	-
	BNDC 0	31.33	4.06	-0.109	-0.034	0.013	0.122	0.089	-0.187	-0.399	0.186	-0.127	-0.265
	BNDC 1	35.083	-1.276	-0.109	-0.036	0.025	0.123	0.086	-0.178	-0.391	0.169	-0.143	-0.291
LDA	BNDC 10	30.226	11.421	-0.106	-0.037	0.021	0.12	0.089	-0.182	-0.395	0.163	-0.132	-0.28
	BNDC 100	19.375	11.278	-0.089	-0.051	0.039	0.107	0.116	-0.19	-0.396	0.084	-0.128	-0.263
	BROK 0	33.271	0.366	-0.106	-0.033	0.024	0.122	0.087	-0.181	-0.392	0.163	-0.145	-0.295
	BROK 1	33.249	-2.984	-0.102	-0.018	0.018	0.125	0.079	-0.185	-0.386	0.178	-0.161	-0.315
	BROK 10	29.132	1.845	-0.086	-0.027	0.018	0.123	0.084	-0.19	-0.383	0.179	-0.155	-0.29
	BROK 100	-	-	-	-	-	-	-	-	-	-	-	-
	BROK 100	-	-	-	-	-	-	-	-	-	-	-	-

(Appendix continues)

Comparison of Coarse versus Fine Scale Sampling on Statistical Modeling of Landscape Effects and Assessment of Fish Assemblages of the Muskegon River, Michigan

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Abstract.—We used data sets of differing geographic extents and sampling intensities to examine how data structure affects the outcome of biological assessment. An intensive sampling ($n = 97$) of the Muskegon River basin provided our example of fine scale data, while two regional and statewide data sets ($n = 276, 310$) represented data sets of coarser geographic scales. We constructed significant multiple linear regression models (R^2 from 21% to 79%) to predict expected fish assemblage metrics (total fish, game fish, intolerant fish, and benthic fish species richness) and to regionally normalize Muskegon basin samples. We then examined the sensitivity of assessments based on each of five data sets with differing geographic extents to landscape stressors (urban and agricultural land use, dam density, and point source discharges). Assessment scores generated from the different data extents were significantly correlated and suggested that the Muskegon basin was generally in good condition. However, using coarser scale data extents to determine reference conditions resulted in greater sensitivity to land-use stressors (urban and agricultural land use). This was due in part to significant covariance between land use and drainage area in the fine scale data set. Our results show that the scale of data used to determine reference condition can significantly influence the results of a biological assessment. The training data sets with broader spatial range appeared to produce the most sensitive and accurate catchment assessment. A covariance structure analysis using a data set with broad spatial range suggested that impounded channels and point source discharges have the strongest negative effects on intolerant fish richness in the Muskegon River basin, which provides a focus for conservation, mitigation, and rehabilitation opportunities.

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INTRODUCTION

The ability to predict quantitatively the biological assemblage expected at a specific site is useful for both planning and inventory (Barbour et al. 1999; Seelbach et al. 2002). In the case of conservation planning, predictions can be used to identify management gaps and to prioritize conservation activities (Davis and Henderson 1978; Klijn 1994; Rabeni and Sowa 1996; Higgins et al. 1999; Steen et al. 2006, this volume). In the case of ecological assessment, predicted reference conditions can be used in the absence of historical data (Gallant et al. 1989; Claessen et al. 1994; Seelbach et al. 2002; Wiley et al. 2002). In either case, the modeling approaches used to predict fish assemblages are highly varied and range from simple physical classification, through standard statistical modeling, to more complex nonlinear modeling techniques involving, for example, neural nets (Mastorillo et al. 1997; Olden and Jackson 2001), regression and classification trees (De'ath 2002), and other emerging computational approaches (see Steen et al. 2006).

Regardless of the program context or specific modeling approach, a fundamental methodological issue arises in all regional assessment studies related to the scale of data used to construct (parameterize) the predictive models. Is it better to allocate available sampling resources intensively (i.e., at a fine scale) to maximize the capture of patterns of variation within a focal region, or is it a better strategy to allocate effort more extensively (i.e., coarse scale) to capture the larger regional context and maximize the overall variation in the data set used to train the predictive model? For example, in an assessment of a specific catchment, should the search for reference conditions (whether modeled or based on classified subsets) be restricted to sites within that catchment? If not, and sites are included in the training data set from the larger regional context, what is the appropriate scale: adjacent catchments, the ecoregion, or similar ecotopes in neighboring ecoregions? Answers to these questions have practical and theoretical impli-

cations both for model development and for the general design of regional assessment studies.

We hypothesized that a combination of both spatially intensive and extensive training data would maximize our ability to discriminate effects of human landscape alteration on fish assemblages in the Muskegon River basin. We explored these issues by comparing the sensitivity of statistical assessment models (Wiley et al. 2002; Wang et al. 2003) developed from data sets of different geographic extents. We describe the effects of data set scale on model parameterization, and on performance in terms of correlations between normalized fish assemblage metrics and multiple stressors, including urban land cover, agriculture, point source impacts, and river fragmentation by impoundment. Based on this analysis we produce an optimized assessment of the Muskegon basin based on fish assemblage attributes and a structural model relating multiple landscape-scale stressors to observed indicator values.

METHODS

Study Area

We obtained data for this study from three data sets with different geographic extents across Michigan to test the effects of spatial extent and sampling intensity on sensitivity of modeled biological assessments (Figure 1; Table 1). We used sites from a 2-year sampling effort for the Muskegon River Watershed Ecological Assessment Project (MRWEAP; <http://www.mwrp.net>) to represent fine-scale, intensive spatial sampling across a focal catchment ($n = 97$). Located in western mid-Michigan, the Muskegon River is a cool and cold water tributary of Lake Michigan that drains a high outwash plain and then flows through glacial till and drowned river mouth wetlands (O'Neal 1997). Much of the 6,500 km² catchment is undeveloped (23%), and urban and agricultural development is concentrated in several subcatchments. To expand the geographic extent we used a regional data set compiled as

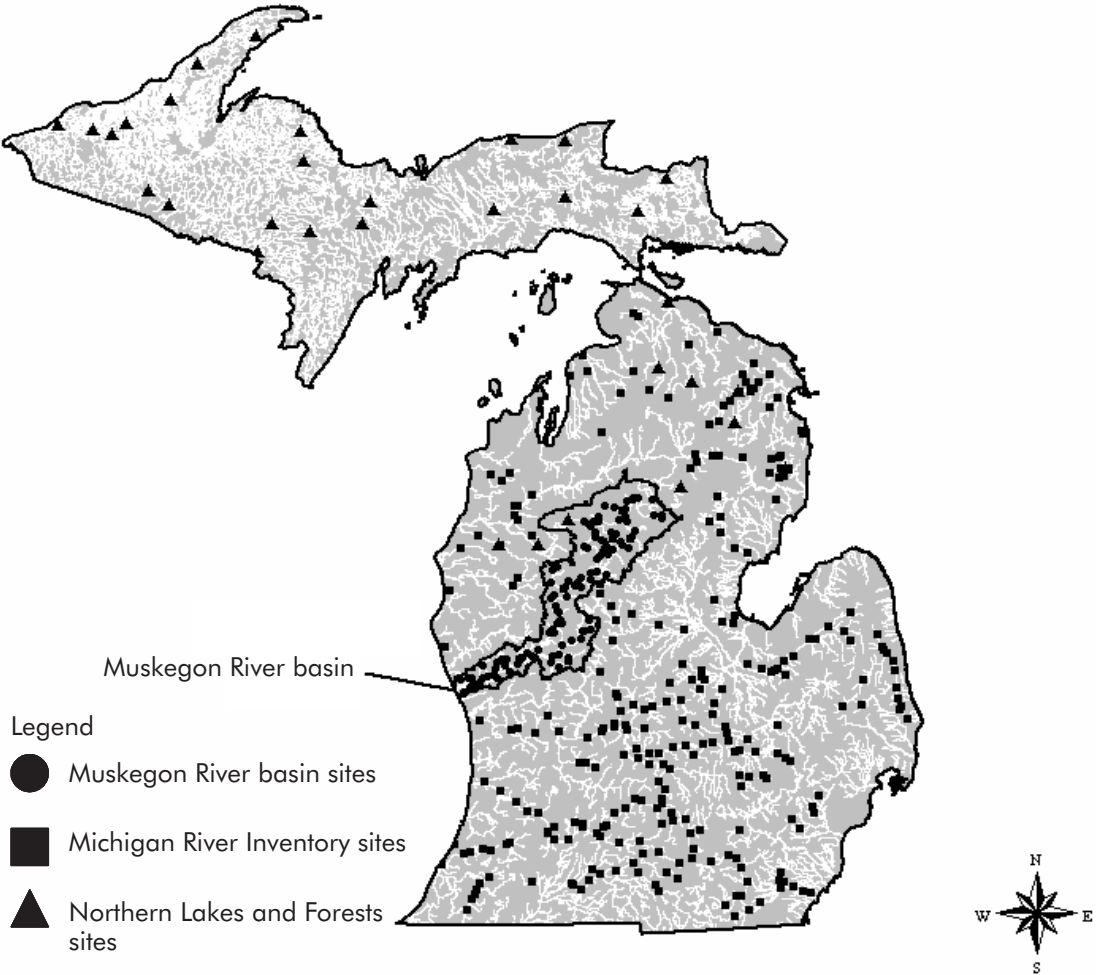


Figure 1. Sample site locations for the three different training data sets; data were obtained from three studies: (1) the Muskegon River Watershed Ecological Assessment Project, (2) the Michigan Rivers Inventory database, and (3) the Northern Lakes and Forest study.

Table 1. Data set combinations for five data extents used in this analysis identifying number of sites, spatial extent, and geographic area. Data sets include Muskegon River Watershed Ecological Assessment Project (MRWEAP), Michigan Rivers Inventory (MRI), and Northern Lakes and Forests (NLF).

Data extent	Data set combination	<i>n</i>	Spatial extent	Geographic area
Extent 1	MRWEAP	97	Intensive	Muskegon River watershed
Extent 2	MRI	276	Extensive	Michigan's Lower Peninsula
Extent 3	MRI and NLF	310	Extensive	Michigan's Upper and Lower Peninsulas
Extent 4	MRWEAP and MRI	373	Intensive and extensive	Muskegon River watershed and Michigan's Lower Peninsula
Extent 5	MRWEAP and MRI and NLF	476	Intensive and extensive	Muskegon River watershed and Michigan's Upper and Lower Peninsulas

part of the Michigan Rivers Inventory (MRI) to include streams across the lower peninsula of Michigan (Seelbach and Wiley 1997). The MRI sites ($n = 276$) include glacial till, outwash sand and gravel, and glacial lakebed geology. Land use and drainage area are highly variable resulting in a large range of combinations of land use, geology and drainage area. Agricultural and urban development is concentrated in the southern half of the Lower Peninsula and the northern half has a higher proportion of forests and wetlands. To expand the geographic context of the analysis further we included more sites ($n = 34$) from Regional Ecological Mapping and Assessment (REMAP) sampling of streams in the Northern Lakes and Forests (NLF) ecoregion (Baker et al. 2005). The REMAP sampling of the NLF ecoregion encompassed both the northern Lower Peninsula and the Upper Peninsula of Michigan. Surficial geology includes glacial deposits but also areas of bedrock not common in the Lower Peninsula. The dominant land use is forest, forested wetland, and marshes with relatively fewer developed areas though forested areas have likely experienced timber harvesting.

We used five combinations of these three data sets to incorporate varying spatial extents into modeled reference conditions for biological assemblages and test our hypotheses (Table 1). We used the MRWEAP data set alone for the spatially intensive data (Extent 1). The MRI data set and the combined MRI and NLF data sets represented two spatially extensive data sets (Extents 2 and 3, respectively). We combined the MRI and the MRWEAP data sets to represent a combination of spatially extensive and intensive data (Extent 4). And finally, we combined all three data sets to provide both intensive spatial sampling in the focal region (the Muskegon River basin) and the most extensive geographic coverage in the regional context (Extent 5).

Environmental Data

For each fish sampling site, we summarized landscape-scale variables by site (local impoundment,

gradient, substrate, temperature indicator, and stream width and depth), catchment (latitude, land use, impervious surfaces, and drainage area), or linear distance from the site (dams and point-source discharges) using ArcView 3.3 GIS (ESRI, Redlands, California). Landscape-scale variables expected to influence natural stream fish assemblages included latitude, drainage area, a temperature indicator, forested and non-forested wetland, and open water surface area. Landscape-scale stressors expected to influence fish assemblages included percent of urban and agricultural land use in the catchment, percent impervious area (Brabec et al. 2002), dams or impounded water and point source discharges. To capture only the stressor effects of developed land, we also created threshold land-use variables that set values below 10% urban land (Brabec et al. 2002) and below 30% agricultural land to zero. Catchment boundaries of each site were delineated by the Michigan Department of Natural Resources (MDNR) from U.S. Geological Service 1:24,000 scale topographic maps and modified for each site using 1:250,000 scale resolution (Baker et al. 2005). Major land-use categories (urban, agriculture, forest, forested wetland, nonforested wetland and water) were summarized by catchment using 1978 Michigan Resource Inventory System (MIRIS) land-cover maps. We used established coefficients for each land-use type to calculate a percentage of impervious area in the catchment (Brabec et al. 2002). The number of major dams with storage capacity greater than 0 within 0.16, 1.6, 3.2, 6.4, and 12.8 km of each site was summarized for each site based on the MDNR dam database. In addition, sites located within impounded river reaches (based on field observations or personal communications) were identified as "impounded." We obtained compiled Michigan Department of Environmental Quality data identifying the permitted discharges to waterways throughout the state and used GIS to locate the number of permits issued within 0.16, 1.6, 3.2, 6.4, and 12.8 km of each site. July temperature was not available for all the databases so we developed a coldwater

index based on the percentage of coldwater species (brook trout *Salvelinus fontinalis*, brown trout *Salmo trutta*, mottled sculpin *Cottus bairdii*, and slimy sculpin *C. cognatus*) as an indicator of stream temperature.

Fish Data

Fish assemblage composition data were from three studies with different objectives and sampling methodologies from surveys conducted from 1975 to the present (65% of data from after 1990). Fish sampling methods are summarized in Table 2 and detailed descriptions occur elsewhere (Seelbach and Wiley 1997; Zorn et al. 2002; Baker et al. 2005). The MRWEAP used a bioassessment protocol that included one-pass, blocked tow-barge, and back-pack electrofishing in wadeable streams and a combination of boat and tow-barge electrofishing in nonwadeable rivers to sample mid-channel and edge habitats. The MRWEAP used stratified random site selection but included extremes of catchment size and land-use alteration. The NLF project used back-pack electrofishers and no block nets to sample randomly selected wadeable streams. Both the MRWEAP and NLF databases include a representative species list and estimates of proportionate abundance. The MRI database includes population estimates from tow-barge electro-

fishing or rotenone sampling at randomly selected sites.

Electrofishing was the most common sampling method (60%): of these samples, 36% were three-pass and 24% one-pass; 10% used a back-pack, 3% a boat, and 47% a tow-barge; and 52% used block nets. The remaining 40% of the samples were collected via rotenone sampling. Electrofishing site length was generally proportionate to the stream width, typically about 40 × stream width for wadeable streams and 20 × stream width for nonwadeable streams. Rotenone sampling site length was longer than that of electrofishing sites.

Fish species were classified into four categories: total number of species, number of intolerant species (Lyons 1992; Lyons et al. 1996; Roth 1994), number of game species and number of sculpin and darter species. We chose these metrics to describe representative measures of richness, composition, tolerance, and habitat requirements for a variety of fish assemblages (Wiley et al. 2002).

Data Analysis

We employed a regional ecological normalization approach (Wiley et al. 2002; Baker et al. 2005) to assess the condition of the Muskegon basin based on fish assemblage samples (Figure 2). Multiple

Table 2. Site selection and fish sampling methods used in the three data sets: Muskegon River Watershed Ecological Assessment Project (MRWEAP), Michigan Rivers Inventory (MRI), and Northern Lakes and Forests (NLF).

Data set	<i>n</i>	Year	Site selection method	Sampling method	Gear
MRWEAP	97	2001–2002	Stratified random reach with basin extremes added	1-pass, blocked	Backpack, tow-barge and boat electrofish
MRI	276	1975–1997	Stratified random survey ^a	1–3 pass, blocked; rotenone	Backpack, tow-barge electrofish and rotenone
NLF	34	2000–2001	EMAP random sampling ^b	1-pass, rapid bioassessment, not blocked	Backpack electrofish

^a Seelbach and Wiley 1997.

^b Baker et al. 2005

linear regression (MLR) models were developed to predict fish assemblage metrics from catchment-scale variables using each of the five training data extents discussed above. Each MLR model included both nonstressor variables (drainage area, temperature indicator, forested wetland, water, and gradient) and stressors related to human impacts (urban and agricultural land uses, dams, and point source discharges). Data were log-transformed or squared when necessary to meet assumptions of normality and only significantly correlated independent variables ($p < 0.05$) were included in regression analyses. Where raw variables included zero values, a small number (0.001) or the integer 1 was added to the variable prior to log transforma-

tion. The different fish sampling methods could bias estimates of fish assemblage composition due to differences in sampling efficiency, so we included sampling method as an indicator variable in our analysis to account for differences due to sampling method versus environmental conditions. We included a temperature indicator in our models so the model differentially specified the expectations for coldwater (streams where $> 90\%$ of species were coldwater taxa) and warmwater streams. We constructed different models for total number of fish species, number of intolerant species, number of benthic species, and number of game fish species (see Table 3). We built two different sets of regression models for each of the four fish metrics. The first, referred

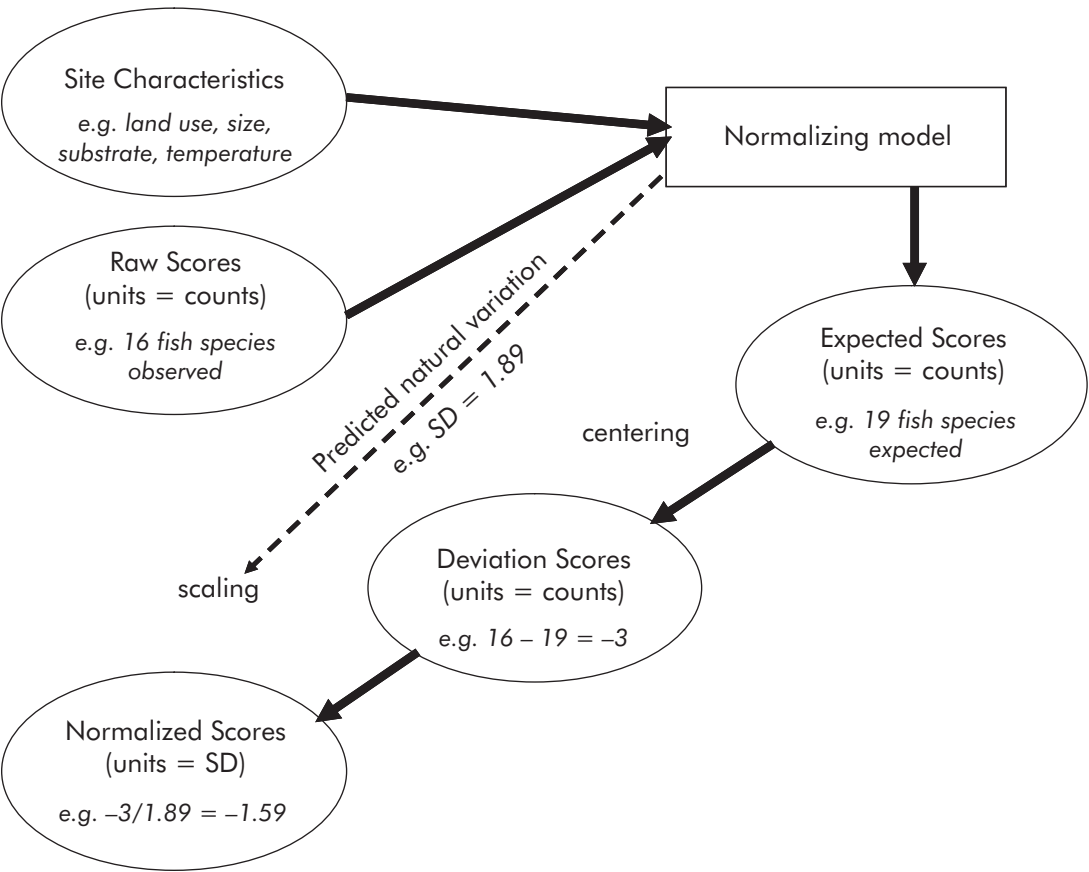


Figure 2. The regional normalization process.

Table 3. Mean fish assemblage statistics for each geographic extent. Bold indicates significant difference from Extent 1 (Muskegon River data set) at $p \leq 0.05$.

Variable	Geographic extent							
	Extent 1 Muskegon River sites $n = 97$				Extent 2 Lower Peninsula sites $n = 276$			
	Mean	SD	Min	Max	Mean	SD	Min	Max
# fish species	13.7	7.03	0	32	17.6	9.52	1	40
# native species	13.2	6.71	0	31	16.6	9.28	0	38
# intolerant fish species	3.3	3.15	0	14	4.1	2.78	0	13
# mod-tolerant fish species	5.5	3.29	0	15	7.6	5.09	0	22
# tolerant fish species	4.9	1.91	0	10	5.8	2.96	0	11
# game fish species	5.2	4.19	0	18	8.4	5.02	0	22
# benthic fish species	1.9	1.34	0	5	2.1	1.41	0	5
# sculpin species	0.6	0.49	0	1	0.3	0.51	0	2
# darter species	1.3	1.17	0	4	1.8	1.39	0	5
# coldwater fish species	1.1	0.99	0	3	0.7	0.98	0	4
Brown trout present	0.2	0.41	0	1	0.2	0.40	0	1
Brook trout present	0.3	0.46	0	1	0.1	0.35	0	1

Variable	Extent 3 Lower and Upper Peninsula sites $n = 310$				Extent 4 Lower Peninsula and Muskegon River sites $n = 373$			
	Mean	SD	Min	Max	Mean	SD	Min	Max
	Mean	SD	Min	Max	Mean	SD	Min	Max
# fish species	16.9	9.41	1	40	16.6	9.06	0	40
# native species	15.9	9.13	0	38	15.7	8.81	0	38
# intolerant fish species	4.0	2.71	0	13	3.9	2.90	0	14
# mod-tolerant fish species	7.3	4.97	0	22	7.1	4.78	0	22
# tolerant fish species	5.6	2.98	0	11	5.6	2.76	0	11
# game fish species	7.8	5.07	0	22	7.7	4.95	0	22
# benthic fish species	2.0	1.40	0	5	2.0	1.38	0	5
# sculpin species	0.4	0.55	0	2	0.4	0.52	0	2
# darter species	1.7	1.39	0	5	1.6	1.35	0	5
# coldwater fish species	0.8	1.01	0	4	0.8	1.00	0	4
Brown trout present	0.2	0.40	0	1	0.2	0.39	0	1
Brook trout present	0.2	0.40	0	1	0.2	0.40	0	1

Variable	Extent 5 All sites $n = 476$			
	Mean	SD	Min	Max
	Mean	SD	Min	Max
# fish species	16.1	9.00	1	40
# native species	15.3	8.68	0	38
# intolerant fish species	3.9	2.83	0	14
# mod-tolerant fish species	6.8	4.68	0	22
# tolerant fish species	5.4	2.78	0	11
# game fish species	7.2	4.99	0	22
# benthic fish species	2.0	1.38	0	5
# sculpin species	0.4	0.55	0	2
# darter species	1.6	1.35	0	5
# coldwater fish species	0.9	1.02	0	4
Brown trout present	0.2	0.40	0	1
Brook trout present	0.2	0.41	0	1

to as the *best-fit* models, represented the best fitting regression we could build for each fish metric and each training data Extent (1–5). Best-fit models for different data sets had different independent variables and thus included variables unique to streams in a specific geographic extent. Fits were evaluated in terms of R^2 , standard error of the estimate, F -statistic, and significance of the regression coefficients. The second set, referred to as *standard-form* models, were based on a single good fitting model developed for each fish metric from the Extent 5 data set, and then was reparameterized using each of the other four data extents. These standard-form models allowed evaluation of the effects of different training data sets on identically structured regression models, in contrast to the best-fit series in which there were minor differences in model structures for each data extent. The best-fit approach would be typical of that used in an applied assessment. The standard-form approach provided more experimental control for addressing our question about the effects of training data extent.

We constructed normalizing models for each fish metric from the MLR models by setting stressor variables to zero (or to the increment added to log-transformed variables with zero values) and predicted the expected metric value for each site under least-disturbed (reference) conditions (Figure 2). Deviation scores were calculated as the observed minus the expected values for each metric. We then scaled the deviation scores by dividing the deviation by the standard deviation of the modeled expectation across that data extent. The result gave us a normalized assessment score for each site in terms of model standardized deviations from the predicted expectation. Negative or positive scores represented sites that had observed scores below or above what would be expected based on the predictive model. The value of the score indicates how much it deviated from reference condition. We established assessment classifications based on standard deviation units (SDU) from the expected score, zero; scores that were ± 0.5 SDUs

of 0 were considered no different than the expected score thus “acceptable,” scores above $+0.5$ SDUs were considered above expectations (or “good”), scores less than -0.5 and greater than -1 were considered “threatened” and scores less than -1 were considered “poor.” In our stressor sensitivity analyses, we sometimes truncated positive normalized scores to the value of zero. We will refer to these as truncated scores throughout; they, in some cases, provided a more linear response to stressors of interest and were therefore useful in sensitivity analysis.

Pearson correlation analysis was used to determine which data extent provided the most sensitivity to multiple stressors of interest (percent urban land use $> 10\%$, percent agricultural land use $> 30\%$, reach impoundment, dam density within 8 mi, and point source density within 4 mi). Correlations between the stressors and both normalized and truncated normalized scores were summarized and ranked based on data extent. The breadth of stressor response was calculated from the range of the response distribution (Levin 1968). Simple correlation, multiple linear regression, and mean, minimum, maximum, and standard deviation statistics were performed in Datadesk (Velleman and Velleman 1988).

Covariance Structural Analysis

After selecting a final model and training data extent based on overall sensitivity to landscape stressors, we examined the relative effects of specific stressors on fish assemblages in the Muskegon River basin using covariance structure analysis (CSA). The CSA model is a network of hypothesized causal interactions that can be statistically compared to the structure of the data (Riseng et al. 2004). Covariance structure analysis tests the correspondence between explicit causal assumptions and patterns of correlation and variance in the data set (Bollen 1989). In CSA, partial correlation coefficients between variables are decomposed into direct, indirect, and spurious effects based on a theoretical model structure. A path diagram (Figure 3) is an

explicit illustration of the hypothesized set of causal relationships to be tested in CSA. In the path diagram direct effects between two variables are noted by single headed arrows, indirect effects are the effects between two variables mediated by an intervening variable and double headed arrows represent spurious or noncausal correlations between variables. Exogenous variables in the model were the multiple stressors: urban land use, moderate to high levels of agricultural land use (>30%), impounded river-

ine conditions due to major dams and point source discharges to waterways. The endogenous variable was the normalized score for intolerant fish richness calculated by the best-fit model for geographic Extent 4.

Amos 4.0 (Arbuckle and Wothke 1999) software was used to fit the data to the hypothesized model using the maximum likelihood function for model fitting because it is reasonably robust against departures from multivariate normality. Squared multiple correlations were used to

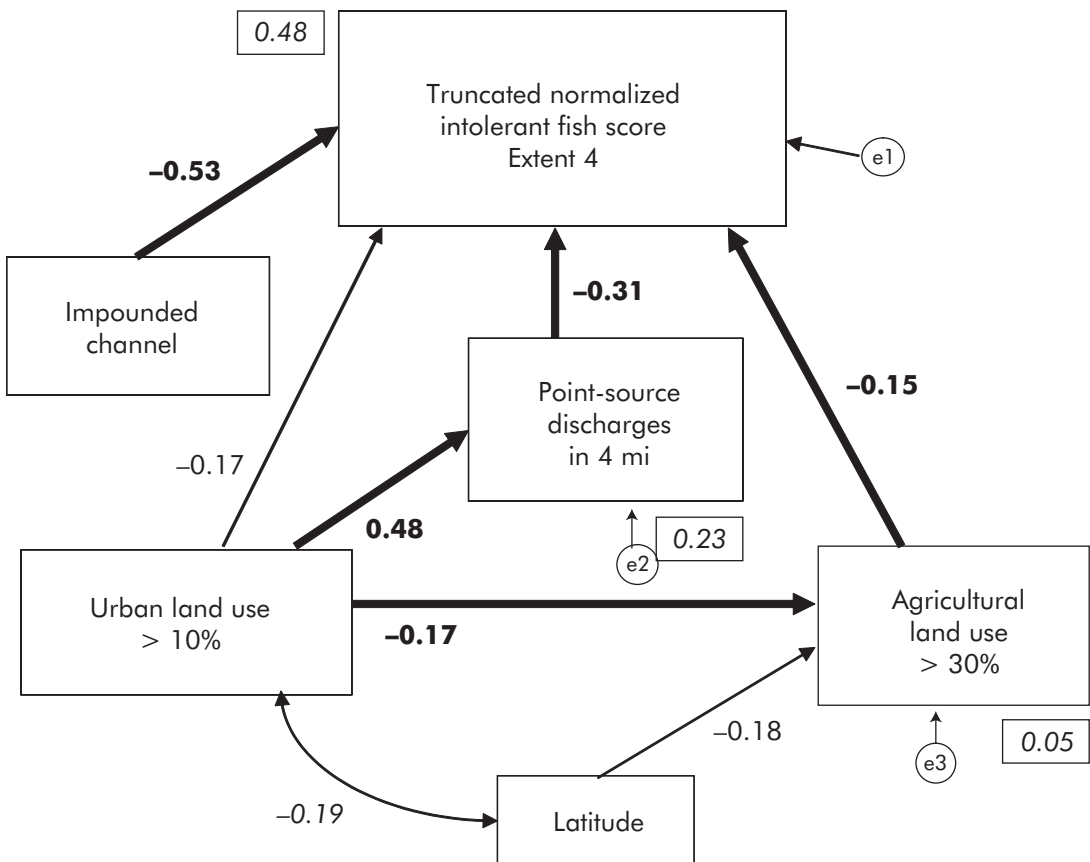


Figure 3. Results of covariance structure analysis (CSA) of the effects of human stressors on truncated normalized intolerant fish species scores in the Muskegon River watershed. Rectangles are measured variables, small circles are residual errors, and small rectangles are squared multiple correlations for endogenous variables. Arrows indicate direct effects and adjacent numbers are the magnitude of standardized direct effects. Double headed arrows indicate spurious correlations. Direct effects are equivalent to standardized regression coefficients (effect of one variable on another with all other variables held constant), and indirect effects are the effects mediated by intervening variables. Bold numbers and thick arrows indicate significant effects at $p \leq 0.05$; italics indicate significant effects at $p < 0.09$. $n = 97$.

determine how well the model explained variation in the endogenous variables. Direct, indirect, and total (sum of direct and indirect) effects were analyzed for statistical significance (t distribution, $p \leq 0.05$) using Monte Carlo bootstrapped standard errors and for compatibility with theoretical expectation for effects of one variable on another. Standard assumptions of linear modeling such as multivariate normality, independence, linear response, and additivity were reasonably met. The ratio of sample size to estimated paths was 8.8, which is considered large enough to ensure stable parameter estimates (Petraitis et al. 1996).

RESULTS

Differences between Data Sets

In general, there were small compositional differences between each of the five training data sets, but the intensively sampled Muskegon River basin set (Extent 1) was the most distinctive of the five. The total number of fish species, native fish species, moderately tolerant, intolerant, and game fish species were all lower in the Muskegon River basin than in the larger geographic extents (Table 3). On the other hand, brook trout were present more frequently in Extent 1 than in larger Extents 2 and 3. Agriculture was proportionately less, and forest was more represented in the Muskegon basin relative to the Lower Peninsula and state as a whole (Table 4). Impoundments, dams, and permitted point source discharges (PSDs) were significantly underrepresented in the Muskegon sampling relative to the larger regional data; however, three large hydroelectric dams are located along the main stem of the Muskegon River.

Regression Modeling of Reference Conditions

Regression models for the metrics were all statistically significant and explained between 21% and 80% of the variance in fish variables (Table

5). In general, the best-fit regression models explained slightly more variation in each case than their standard-form counterparts. For both types of models, using Extent 1 training data gave the highest R^2 values and lowest SE of the regression (Table 5). Generally the models for total number of fish species and number of game fish species explained more variance in the dependent variable, while the benthic species model explained the least. All models included significant relationships between fish assemblage metrics and landscape scale stressors (urban and agricultural land use, dams, and point source discharges).

Effects of Data Extent on Assessment

Normalized assessment scores generated from the different data extents and different model types were significantly correlated (Tables 6a and 6b) and provided generally similar assessments of the condition of the Muskegon basin (Figure 4). The scores based on the total number of fish species, an overall summary score (average of assessment scores of four fish metrics), and the number of intolerant fish species were (in that rank order) most highly correlated with stressor variables (Table 7). Irrespective of the training data set extent or model, the majority of the Muskegon sites fell within ± 0.5 standard deviation units of zero indicating that most sites in the catchment were not significantly different than expected (Figure 4).

There were, however, interesting differences between the assessments, particularly with respect to detectable impacts associated with land-use change and impoundment stressors. In this sensitivity analysis, stronger negative correlations between normalized scores and stressors imply greater sensitivity. Correlation analyses (Table 8) indicated that for both best-fit and standard-form models, Extent 2 data set generated assessments most sensitive to urban and agricultural land use. In contrast, assessments based on the Extent 1 data set appeared most sensitive to PSD and proximity of the site to an impoundment, but were not sensitive to land-use alteration. The

Table 4. Mean landscape and channel shape variables for stream sites in each of five geographic extents. Bold indicates significant difference from Extent 1 (Muskegon River data set).

Variable	Geographic extent							
	Extent 1 Muskegon River sites n = 97				Extent 2 Lower Peninsula sites n = 276			
	Mean	SD	Min	Max	Mean	SD	Min	Max
Latitude	43.8	0.38	43.21	44.41	43.2	1.01	41.7862	45.56
% urban land use	7.6	11.38	0	77.39	6.2	8.14	0	78.40
% urban land use > 10%	3.8	12.31	0	77.39	3.0	8.68	0	78.40
% agriculture land use	23.4	20.50	0	71.50	46.8	25.16	0	90.45
% agriculture land use > 30%	16.5	23.96	0	71.50	42.2	29.99	0	90.45
% forested land cover	40.8	20.58	6.62	85.18	22.4	24.18	1.42	100
% forested wetland cover	9.7	5.65	0	28.02	9.6	6.96	0	51.92
% nonforested wetland cover	5.7	4.84	0	40.61	3.9	2.95	0	13.75
% water land cover	2.4	4.46	0	28.03	1.4	1.70	0	11.16
# dams within 1.6 km of site	0.03	0.17	0	1	0.12	0.36	0	3
# PSDs within 6.4 km of site	1.4	2.63	0	13	2.2	3.66	0	25
Site within dam impoundment	0.02	0.14	0	1	0.06	0.23	0	1
Gradient (m/m)	0.0026	0.0021	0.0000	0.0092	0.0017	0.0054	0.0000	0.0512
Drainage area (km ²)	780.0	1850.97	1.12	6850.00	1026.7	2030.58	1.32	14181.90
Stream width (m)	7.3	7.44	1.62	43.98	20.7	18.94	1.22	106.68
Mean stream depth (m)	0.3	0.18	0.04	0.73	0.5	0.26	0.05	1.47
Width/depth ratio	28.9	15.79	6.84	84.91	35.7	32.58	3.64	357.14
Variable	Extent 3 Lower and Upper Peninsula sites n = 310				Extent 4 Lower Peninsula and Muskegon River sites n = 373			
	Mean	SD	Min	Max	Mean	SD	Min	Max
	Mean	SD	Min	Max	Mean	SD	Min	Max
Latitude	43.5	1.30	41.79	47.17	43.4	0.92	41.79	45.56
% urban land use	5.5	7.89	0	78.40	6.5	9.12	0	78.40
% urban land use > 10%	2.7	8.24	0	78.40	3.2	9.74	0	78.40
% agriculture land use	42.7	27.18	0	90.45	40.6	26.13	0	90.45
% agriculture land use > 30%	38.4	31.05	0	90.45	35.5	30.67	0	90.45
% forested land cover	22.4	24.18	1.42	100	27.3	24.63	1.42	100
% forested wetland cover	10.2	9.04	0	72.39	9.6	6.63	0	51.92
% nonforested wetland cover	3.7	3.24	0	21.89	4.4	3.63	0	40.61
% water land cover	1.4	2.03	0	21.43	1.7	2.75	0	28.03
# dams within 1.6 km of site	0.1	0.35	0	3	0.1	0.33	0	3
# PSDs within 6.4 km of site	2.0	3.53	0	25	2.0	3.44	0	25
Site within dam impoundment	0.05	0.22	0	1	0.01	0.07	0	1
Gradient (m/m)	0.0016	0.0051	0.0000	0.0512	0.0020	0.0048	0	0.0092
Drainage area (km ²)	925.2	1937.01	0.92	14181.90	962.2	1985.70	1.12	14181.90
Stream width (m)	19.0	18.44	1.22	106.68	17.1	17.67	1.22	106.68
Mean stream depth (m)	0.5	0.26	0.05	1.47	0.4	0.25	0.04	1.47
Width/depth ratio	35.7	32.58	3.64	357.14	33.5	28.32	3.64	357.14
Variable	Extent 5 All sites n = 407							
	Mean	SD	Min	Max				
	Mean	SD	Min	Max				
Latitude	43.6	1.15	41.79	47.17				
% urban land use	6.0	8.89	0	78.40				
% urban land use > 10%	2.9	9.37	0	78.40				
% agriculture land use	38.0	27.00	0	90.45				
% agriculture land use > 30%	33.1	30.93	0	90.45				
% forested land cover	27.3	24.63	1.42	100				
% forested wetland cover	10.1	8.34	0	72.39				
% nonforested wetland cover	4.2	3.78	0	40.61				
% water land cover	1.7	2.85	0	28.03				
# dams within 1.6 km of site	0.09	0.32	0	3				
# PSDs within 6.4 km of site	1.8	3.34	0	25				
Site within dam impoundment	0.05	0.21	0	1				
Gradient (m/m)	0.0019	0.0046	0.0000	0.0512				
Drainage area (km ²)	890.4	1915.49	0.92	14181.90				
Stream width (m)	16.2	17.19	1.22	106.68				
Mean stream depth (m)	0.4	0.25	0.04	1.47				
Width/depth ratio	33.5	28.32	3.64	357.14				

Table 5. Standard-form and best-fit normalization regression model statistics for each geographic extent (Ag = Agriculture, and PSD = point-source discharges). Plus indicates a positive effect and minus indicates a negative effect and bold indicates significance at $p \leq 0.05$.

Geographic extent	Dependent variable	R ²	SE	Intercept	Catch- ment area	Lati- tude	Cold index	Urban index > 10%	Ag > 30%	Non- forested wetland	Forested land	Samp- ling method	Independent variables			
													PSD in 6.4 km	PSD in 12.8 km	Dams in 0.16 km	Dams w/in 1.6–12.8 km
Standard models Extent 1 (n = 97) Muskegon River sites	# fish species	73.7%	0.26	+	+	+	-	-	-	-	-	+	-	-	-	-
	# intolerant species	74.0%	0.35	+	+	-	+	-	-	-	-	+	-	-	-	-
	# game species	71.5%	0.38	+	+	-	-	-	-	-	-	+	-	-	-	-
	# benthic species	45.6%	0.38	-	+	+	+	-	-	-	-	+	-	-	-	-
	# fish species	63.3%	0.39	+	+	-	-	-	-	-	-	+	-	-	-	-
Extent 2 (n = 276) Lower Peninsula sites	# intolerant species	49.6%	0.42	+	+	-	+	-	-	-	-	+	-	-	-	-
	# game species	64.0%	0.39	+	+	-	+	-	-	-	-	+	-	-	-	-
	# benthic species	23.6%	0.50	+	+	-	+	-	-	-	-	+	-	-	-	-
	# fish species	65.4%	0.39	+	+	-	+	-	-	-	-	+	-	-	-	-
	# intolerant species	48.3%	0.42	+	+	-	+	-	-	-	-	+	-	-	-	-
Extent 3 (n = 310) Lower and Upper Peninsular sites	# game species	67.8%	0.39	+	+	-	-	-	-	-	-	+	-	-	-	-
	# benthic species	20.6%	0.51	+	+	-	+	-	-	-	-	+	-	-	-	-
	# fish species	65.9%	0.37	+	+	-	+	-	-	-	-	+	-	-	-	-
	# intolerant species	57.5%	0.41	+	+	-	+	-	-	-	-	+	-	-	-	-
	# game species	67.4%	0.39	+	+	-	+	-	-	-	-	+	-	-	-	-
Extent 4 (n = 373) Muskegon River and Lower Peninsula sites	# benthic species	23.1%	0.49	+	+	-	+	-	-	-	-	+	-	-	-	-
	# fish species	65.1%	0.37	+	+	-	+	-	-	-	-	+	-	-	-	-
	# intolerant species	55.9%	0.41	+	+	-	+	-	-	-	-	+	-	-	-	-
	# game species	68.4%	0.39	+	+	-	+	-	-	-	-	+	-	-	-	-
	# benthic species	21.2%	0.49	+	+	-	+	-	-	-	-	+	-	-	-	-
Best-fit models Extent 1 (n = 97) Muskegon River sites	# fish species	80.1%	0.23	+	+	+	-	-	-	-	-	+	-	-	-	-
	# intolerant species	77.2%	0.34	+	+	+	+	-	-	-	-	+	-	-	-	-
	# game species	70.4%	0.38	+	+	-	+	-	-	-	-	+	-	-	-	-
	# benthic species	47.6%	0.37	+	+	+	+	+	-	-	-	+	+	-	-	-
	# fish species	70.5%	0.36	+	+	-	+	-	-	-	-	+	-	-	-	-
Extent 2 (n = 276) Lower Peninsula sites	# intolerant species	46.9%	0.43	+	+	+	+	-	-	-	-	+	-	-	-	-
	# game species	66.9%	0.36	+	+	-	+	-	-	-	-	+	-	-	-	-
	# benthic species	26.7%	0.49	+	+	-	+	-	-	-	-	+	-	-	-	-
	# fish species	70.2%	0.36	+	+	-	+	-	-	-	-	+	-	-	-	-
	# intolerant species	50.1%	0.41	+	+	-	+	-	-	-	-	+	-	-	-	-
Extent 3 (n = 310) Lower and Upper Peninsular sites	# game species	69.6%	0.37	+	+	-	-	-	-	-	-	+	-	-	-	-
	# benthic species	25.7%	0.49	+	+	-	-	-	-	-	-	+	-	-	-	-
	# fish species	75.6%	0.31	+	+	-	-	-	-	-	-	+	-	-	-	-
	# intolerant species	60.7%	0.39	+	+	-	+	-	-	-	-	+	-	-	-	-
	# game species	71.1%	0.37	+	+	-	+	-	-	-	-	+	-	-	-	-
Extent 4 (n = 373) Muskegon River and Lower Peninsula sites	# benthic species	24.1%	0.49	+	+	-	-	-	-	-	-	+	-	-	-	-
	# fish species	66.0%	0.37	+	+	-	-	-	-	-	-	+	-	-	-	-
	# intolerant species	56.4%	0.41	+	+	-	+	-	-	-	-	+	-	-	-	-
	# game species	69.7%	0.38	+	+	-	+	-	-	-	-	+	-	-	-	-
	# benthic species	21.2%	0.49	+	+	-	+	-	-	-	-	+	-	-	-	-

Table 6. Correlation between normalized fish richness scores for the Muskegon River calculated for the five data extents for the best-fit and standard-form models (A), and between best-fit and standard form models for each data extent (B). Correlations > 0.19 are statistically significant at $p \leq 0.05$.

A						B					
Extent	1	2	3	4	5	Extent	Standard form models				
<i>Standard form models</i>						Extent	1	2	3	4	5
Extent 1	1					<i>Best fit models</i>					
Extent 2	0.670	1				Extent 1	0.849	0.801	0.779	0.881	0.861
Extent 3	0.671	0.996	1			Extent 2	0.681	0.998	0.996	0.975	0.978
Extent 4	0.808	0.973	0.966	1		Extent 3	0.724	0.991	0.996	0.980	0.989
Extent 5	0.809	0.974	0.975	0.996	1	Extent 4	0.890	0.832	0.817	0.929	0.912
<i>Best fit models</i>						Extent 5	0.810	0.973	0.974	0.995	1.000
Extent 1	1										
Extent 2	0.824	1									
Extent 3	0.815	0.992	1								
Extent 4	0.940	0.850	0.868	1							
Extent 5	0.866	0.977	0.990	0.922	1						

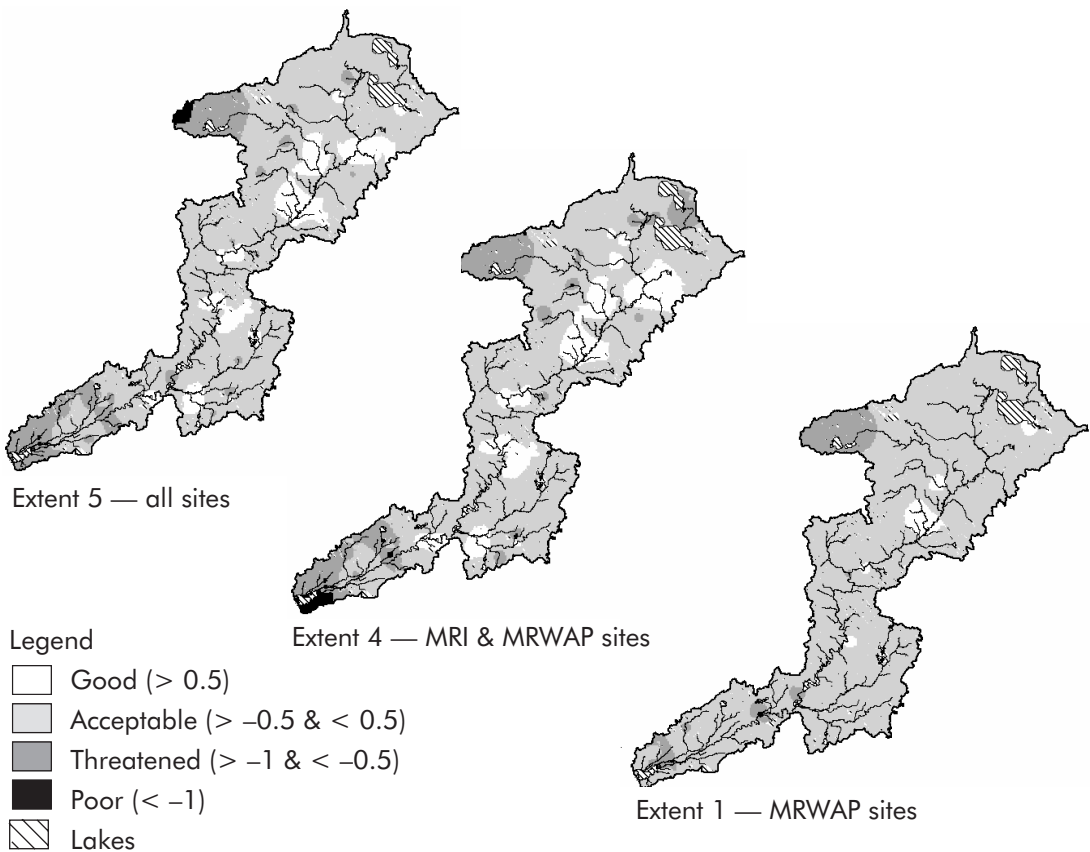


Figure 4. Current status of the Muskegon basin as modeled from three different model training data sets: Extents 5, 4, and 1. The assessment was based on spatially interpolated regionally normalized overall scores (average of total species, intolerant species, benthic species, and game species richness normalized scores), which were scaled as in Table 9.

Table 7. Correlation between normalized fish scores and multiple stressors (% urban land > 10 %, % agricultural land [Ag] > 30 %, reach impoundment, permitted point source discharge density [PSD], and dam density) calculated for five data extents and sum of significant correlations for the five normalized fish scores for Muskegon sites (n = 97). Bold indicates significant at $p \leq 0.05$.

Normalized scores	Urban > 10%	Ag > 30%	PSD density	Impounded reach	Dam density	# sig responses
<i>Extent 1</i>						
Fish richness	-0.386	-0.231	-0.392	-0.244	-0.076	4
Intolerant fish richness	-0.082	-0.114	-0.247	-0.421	-0.143	2
Game fish richness	-0.116	-0.220	-0.193	-0.228	0.030	2
Benthic fish richness	-0.096	-0.023	-0.268	-0.026	0.037	1
Overall score	-0.198	-0.140	-0.354	-0.200	-0.014	2
<i>Extent 2</i>						
Fish richness	-0.447	-0.282	-0.294	-0.118	-0.074	3
Intolerant fish richness	-0.209	-0.257	-0.143	-0.125	-0.114	2
Game fish richness	-0.180	-0.330	0.080	0.038	0.023	1
Benthic fish richness	-0.352	-0.135	-0.363	0.028	-0.019	2
Overall score	-0.357	-0.240	-0.284	-0.027	-0.049	3
<i>Extent 3</i>						
Fish richness	-0.417	-0.284	-0.235	-0.091	-0.079	3
Intolerant fish richness	-0.166	-0.235	-0.197	-0.242	-0.116	2
Game fish richness	-0.180	-0.343	0.075	0.046	0.030	1
Benthic fish richness	-0.361	-0.153	-0.340	0.049	-0.021	2
Overall score	-0.360	-0.266	-0.266	-0.039	-0.049	3
<i>Extent 4</i>						
Fish richness	-0.405	-0.199	-0.396	-0.281	-0.091	3
Intolerant fish richness	-0.178	-0.218	-0.270	-0.288	-0.112	3
Game fish richness	-0.219	-0.344	-0.072	-0.052	0.060	2
Benthic fish richness	-0.350	-0.119	-0.334	0.053	-0.065	2
Overall score	-0.371	-0.206	-0.357	-0.074	-0.074	3
<i>Extent 5</i>						
Fish richness	-0.408	-0.257	-0.273	-0.156	-0.087	3
Intolerant fish richness	-0.166	-0.235	-0.197	-0.242	-0.116	2
Game fish richness	-0.157	-0.311	-0.015	-0.094	0.040	1
Benthic fish richness	-0.222	-0.131	-0.409	-0.048	-0.040	2
Overall score	-0.289	-0.242	-0.351	-0.141	-0.069	3
<i>Summary</i>						sum # sig responses
Fish richness						16
Intolerant fish richness						11
Game fish richness						7
Benthic fish richness						9
Overall score						14

Extent 3 analysis (which included the Upper Peninsula) had the lowest mean sensitivity and low overall response although it was sensitive to both urban and agricultural land-use change.

Based on the mean correlation across all measured stressors (Table 8), the assessment based on Extent 4 data appeared to provide overall the

most sensitive analysis. The assessment based on Extent 5 data provided the broadest response to the stressor set. The Extent 4 data set also provided the best overall response, product of mean sensitivity and breadth of response, to stressors in our analysis. In both these cases, combining a wide regional sample with an intensive local

Table 8. Average correlation (sensitivity) of all normalized scores (truncated and nontruncated fish, intolerant fish, game fish, and benthic fish richness, and overall score) to multiple stressors (% urban land > 10 %, % agricultural land [Ag] > 30 %, reach impoundment, permitted point source discharge density [PSD], and dam density) calculated for five data extents. Summary indicators include the mean correlation (average of five stressor sensitivities), breadth of stressor response (calculated as Levin's [1968] niche breadth), overall response (product of mean correlation and breadth), and rank of overall response. Analysis is for Muskegon basin sites only ($n = 97$). Bold indicates significance at $p \leq 0.05$; bold and italic indicates significance at $p \leq 0.10$.

Geographic extent	Average correlations					Mean correlation	Breadth of response	Overall response	Rank of overall response	Significant stressor responses
	Urban >10%	Ag > 30%	Impounded reach	Dam density	PSD density					
Best fit models										
Extent 1	-0.164	-0.078	-0.262	-0.012	-0.318	-0.167	0.712	-0.114	3	2
Extent 2	-0.343	-0.210	-0.032	-0.011	-0.226	-0.165	0.597	-0.104	4	3
Extent 3	-0.317	-0.208	-0.062	-0.017	-0.220	-0.165	0.793	-0.114	3	3
Extent 4	-0.334	-0.176	-0.145	-0.036	-0.310	-0.200	0.645	-0.154	1	2-3
Extent 5	-0.261	-0.187	-0.157	-0.032	-0.275	-0.182	0.826	-0.148	2	2-3
Standard form models										
Extent 1	-0.133	-0.054	-0.316	-0.060	-0.331	-0.179	0.684	-0.122	3	
Extent 2	-0.350	-0.200	-0.065	0.004	-0.302	-0.182	0.646	-0.118	4	3
Extent 3	-0.322	-0.184	-0.065	-0.005	-0.271	-0.169	0.665	-0.113	5	2-3
Extent 4	-0.291	-0.162	-0.176	-0.013	-0.329	-0.194	0.754	-0.146	1	2-3
Extent 5	-0.274	-0.150	-0.169	-0.024	-0.296	-0.183	0.776	-0.142	2	2-3

sample seemed to provide a useful balance between responsiveness to land-use stressors and responsiveness to more localized stressors like discharges and impoundment effects.

As might be expected from the results above, site impairment levels varied depending on geographic extent of the data set (Table 9) used to

Table 9. Impairment classifications (% of total Muskegon basin sites) based on fish assemblage summary score (average of normalized scores for richness of fish species, intolerant species, game species, and benthic species) using different training data extents. Normalized scores were classified as good (>0.5), acceptable > -0.5 and <0.5), threatened (< -0.5 and > -1.0), and poor (< -1.0).

Geographic extent of data set	Site status			
	% Good	% Acceptable	% Threatened	% Poor
Extent 1	11	83	6	0
Extent 2	22	44	20	14
Extent 3	16	49	23	12
Extent 4	19	52	20	9
Extent 5	20	49	28	3

construct the reference model. For example, using the Muskegon survey data set (Extent 1), 0% of the Muskegon sites would be classified as poor (normalized score < -1.0). In contrast, using normalized scores based on a regional reference sample of the entire Lower Peninsula but no data from the Muskegon itself (Extent 2) indicated that 14% were poor. Expanding the modeling data sets to include the Upper Peninsula (Extent 3) resulted in an assessment similar to that based on geographic Extent 2. Adding the intensive Muskegon data set to either the Lower Peninsula sites (Extent 4) or to Upper and Lower Peninsula sites (Extent 5) resulted in 9% and 3% being classified as poor, respectively.

Relative Effects of Multiple Landscape Stressors

We examined the relative impacts of each stressor on the normalized intolerant fish score using covariance structure analysis (CSA), which allowed us to evaluate the strengths and implications of their interactions. We used the Extent

4 data set since it seemed to be the most sensitive to multiple stressors in our analysis. Our CSA model (Figure 3; Table 10) fitted the observed structure of the data well and explained 48% of the variance in the truncated normalized intolerant fish richness score (scores > 0 set to 0). In the model, intolerant fish richness was significantly influenced by the total effects of all four stressors in the model. Total effects are the sum of direct and indirect effects. Direct effects are equivalent to standardized regression coefficients and indicate the effect of one variable on another, whereas indirect effects are effects mediated by intervening variables (Riseng et al. 2004). Direct effects of point source discharges within 6.4 km and dam impoundment on intolerant fish richness were significant at $p < 0.05$ (-0.31 , -0.53 , respectively), whereas indirect effects of urban land use greater than 10% (-0.13) were significant at $p < 0.05$ (Table 11). The total effects of all stressors in the model were significant at $p < 0.05$, except for agricultural land use greater than 30% ($p = 0.08$). Total effect of reach impoundment was the strongest and total effect of agricultural land use greater than 30% was the weakest of the multiple stressors in the model. Multivariate kurtosis was 42.3, suggesting tolerable departures from multivariate normality due primarily to the reach impoundment binary indicator variable.

DISCUSSION

Our results indicate that the extent of a data set used to generate reference conditions in a bio-

logical assessment significantly influences the outcome of the assessment. This is obvious in cases when a small set of physical reference sites are selected for a local impact analysis. But when large regional samples are used to generate expectations, as is common in IBI scoring (Karr et al. 1986; Lyons et al. 1996; McCormick et al. 2001; Klemm et al. 2003; Mebane et al. 2003; Hughes et al. 2004), analyses based on classification and discriminant function models (Wright et al. 1989; Norris and Georges 1993; Turak et al. 1999; Hawkins et al. 2000), and regional normalization scoring (Wiley et al. 2002), the impacts of data set extent become less obvious. Like the choice of metrics themselves, structure of reference data sets shapes the biases and sensitivity of resulting analyses and should always be considered an important methodological caveat (Hughes et al. 2004; Whittier et al. 2006, this volume).

In our assessment of the Muskegon basin, using an intensive local sampling design to generate reference models provided a less sensitive assessment than modeling from a larger and less intensive regional data set with minimal representation of that particular basin (Extent 2). However, an even larger regional data set with a geographic extent that included both the Lower and Upper Peninsulas of Michigan (Extent 3) proved less sensitive to PSD effects, while the entire data set (Extent 5) was less sensitive to land alteration effects than Extents 2 and 3. The reasons for these results appear to be related to the specific structures of the data sets themselves.

Table 10. Several standard indices of approximate fit that quantify how well the covariance structure analysis model fit the observed data (Bollen 1989; Mitchell 1992; Shipley 2000). $N = 97$.

Model fit index	Test statistic	Rule for good fit	Definition
Chi-square (χ^2)	$(\chi^2) = 6.202, df = 6,$ $p = 0.401$	$p > 0.05$	Tests hypothesis that absolute difference between data and model is not significant
RMSEA	0.02	< 0.05	Tests hypothesis that difference between observed and model covariances are 0
Tucker Lewis Index (TLI)	0.995	> 0.95	Comparative evaluation index especially robust to sample size
Goodness of Fit Index (GFI)	0.980	> 0.95	Comparative evaluation index similar to TLI but scaled from 0 to 1.0

Table 11. Standardized direct, indirect, and total effects from the fitted model. Direct effects are interpreted like standardized regression coefficients (effect of one variable on another with all other variables held constant) and indirect effects are the effects between two variables mediated by an intervening variables. Bold indicates significance at $p \leq 0.05$; bold and italics indicate significant effects at $p < 0.09$. $n = 97$.

Stressors	CSA standardized effects of stressors on truncated normalized intolerant fish score - Extent 4 data		
	Direct	Indirect	Total
Urban land use > 10 %	-0.17	-0.13	-0.29
Agricultural land use > 30%	-0.15	0	-0.15
Point source discharges in 6.4-km radius	-0.31	0	-0.31
Dam impoundment	-0.53	0	-0.53

For example, in the intensive Muskegon data (Extent 1) high levels of urban land use only occurred in several small order streams, either in the vicinity of the city of Muskegon near the river outlet to Lake Michigan or in headwater tributaries near the cities of Cadillac and Houghton Lake. As a result, there was a significant negative correlation in this data set between urban land use and catchment size. The reference model constructed from this data set showed relatively weak urban land-use effects because it partitioned much of the variance likely caused by high urbanization into effects related to catchment size. In effect, the assessment model expectations could not discriminate between small drainage area and urban land use as predictors of low species numbers. In this case, the larger MRI data set (Extent 2) contained both small and large urbanized catchments so that catchment size and urban land use were not significantly correlated. As a result the model constructed from those data partitioned the effects of catchment size and urban land use such that the assessment scores for small nonurban streams were higher, and small urbanized streams correctly received lower normalized scores than they did when the assessment was

based on Extent 1 models. Expanding the modeling set to include NLF sites in the Upper Peninsula did not improve performance in this regard. The Upper Peninsula data contained very little urban data and what was present had a distribution similar to that of the Muskegon (only small basins were highly urbanized).

Responses to agricultural land use followed a similar pattern, in part for similar reasons. However, for agricultural land use none of the data extents completely removed the correlation between catchment size and agricultural land use. The sensitivity to agricultural land use was strongest in Extent 2 and weakest in Extent 1. In the Extent 1 data set the correlation between catchment size and agricultural land cover was significantly negative indicating that only small streams tended to be completely dominated by agriculture. In the larger extent data sets, the correlations were weaker and positive, driven by the inclusion of large catchments (e.g., the Grand and Kalamazoo River basins) in predominantly agricultural regions. For example, the size range of agriculture dominated catchments in Extent 2 was twice that of Extent 1. The reference models based on the geographically larger data sets yielded assessments that were markedly more sensitive to agricultural land use (Table 8).

For sensitivity to the dam-related stressors and to point source discharge permit density, the Extent 1 data set provided the most responsive assessment. For these stressors, the Muskegon data set had the widest variance in stressor values, and lower colinearities between the stressor intensity and catchment size.

Implications for the Design of Multistressor Assessments

The results of this investigation suggest that both covariances between stressors and other key variables, and the variability of stressors and covariates within the data set as a whole, can influence the sensitivity and therefore the results of biological assessment. Large sample size and large regional extent are important for modeling expected

conditions. In methods akin to RIVPACS (e.g., Turak et al. 1999; Hawkins et al. 2000; Oberdorff et al. 2002; Pont et al. 2006) where the model is built without explicit reference to stressors, the ideal data set would contain wide variations in the fish metrics, as well as wide variations in other natural driving variables such as stream size, slope, and geology. If the approach involves regional normalization, the training data set should include wide ranges of the stressor variables themselves. In practical terms this implies that the assessment of a specific catchment should include some provision for obtaining a larger regional training data set to provide a strong statistical context for determining reference conditions. We believe that this is likely to be true for any assessment approach, and it has significant logistic and design cost implications. In the case of our Muskegon assessment, the larger regional data sets were already available and could be applied to the assessment of the Muskegon basin after the fact. Where such data sets are not available, a local assessment would also presumably have to include sampling outside of the focal catchment to ensure a regional context for the expectation (Hughes 1994; Bailey et al. 2004). Failure to provide a robust data set for the modeling of reference condition would likely result in reduced sensitivity of the assessment, as we observed when we used data from the Muskegon basin alone.

Our results also have important social and political implications since assessment results can influence management and rehabilitation decisions. Development of rehabilitation plans typically requires a vision of the natural potential or reference condition of the river ecosystem (Jungwirth et al. 2002). Theoretical models that include explicit terms for a range of landscape and geomorphic settings as well as stressors that could influence river ecological function are widely used to assess ecological potential in aquatic ecosystems (Seelbach et al. 2002). Geographically extensive data that include a range of natural and impaired conditions to adequately

discriminate impaired conditions in rivers can provide managers with a theoretical context for decisions making and fund allocation.

Assessment of the Muskegon Basin

An assessment of the ecological condition of the Muskegon basin based on fish assemblage sampling was the motivation for the analyses reported here. Overall, all training data sets pointed to the same conclusion: the general condition of the Muskegon River basin appears good (Table 9; Figure 4). Based on the Extent 4 training data set, which includes a wide regional data set and the more intensive Muskegon data set, 71% of the sampled sites are ranked acceptable or good, 20% of the sites are ranked threatened, and only 9% of the sites are ranked poor. The latter tend to drain heavily urbanized or farmed small catchments.

The CSA of multiple stressor effects on normalized scores in the Muskegon River watershed for intolerant fish species richness suggests that each of the stressors has a potentially strong impact on the biological metric. Based on the magnitude of the standardized total path coefficients, reach impoundment appears to be the strongest of the stressors included in our analysis; agricultural land use greater than 30% appears the weakest. Since urban land use is expanding in this basin, while agriculture is contracting, urbanization with its positive effects on impervious surfaces and point-source discharges will be the stressors of most concern in the immediate future. The normalized intolerant fish scores were sensitive to impoundment stress. The negative impacts of impoundment primarily affected pool headwaters of main-stem impoundments, which are a controversial focal point of discussion among the catchment's stakeholders. The structure of the model suggests that opportunities for conservation and mitigation likely lie in reducing rates of urban sprawl and the impact of point source discharges.

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Effects of Percent Impervious Cover on Fish and Benthos Assemblages and Instream Habitats in Lake Ontario Tributaries

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Abstract.—We demonstrate the effects of percent impervious cover (PIC) on biophysical properties of Lake Ontario tributary streams. Biophysical data (fish assemblages, benthic invertebrate assemblages (benthos), instream physical habitat, and temperature) were collected from more than 575 wadeable stream sites. A geographic information system application was developed to characterize the landscape upstream of each site (i.e., drainage area, surficial geology, land use/land cover, slope, stream length, and climate). Total PIC of catchments was estimated from land use/land cover, and a base flow index was derived from the surficial geology. The relationship between PIC and biophysical responses was determined after statistically removing the effects of natural landscape features (i.e., catchment area, slope, base flow index) on those responses. Contrasts in PIC from natural conditions (<3% to 10%) were related to variations in fish and benthos assemblages. Both coldwater sensitive and warmwater tolerant fish and diverse benthos assemblages were found in catchments with low PIC. At more than 10 PIC (i.e., about 50% urban), both fish and benthos consisted of mainly warmwater or tolerant assemblages. For example, trout were absent and minnows were dominant. While some of the apparent PIC effect may have been confounded by land use/land cover and surficial geology, the consistency of the findings even after natural catchment conditions were considered suggests that the threshold response is valid. Percent impervious cover had a weaker effect on instream geomorphic variables than on biological variables. The models derived from this study can be used to predict stream biophysical conditions for catchments with varying levels of development.

INTRODUCTION

Human populations in the Greater Toronto Area (GTA) and central Ontario are predicted to increase by nearly 3 million over the next 24 years (Statistics Canada 2003), and urban development associated with those increases threatens ecosystems dependent on the Oak Ridges Moraine. Human land use has direct and indirect effects on physical, chemical, and biological char-

acteristics of streams and has been modeled using a variety of land-use/land-cover descriptors. Metrics such as catchment population density (Jones and Clark 1987), agriculture (Harding et al. 1999), width of riparian zones (Barton et al. 1985), and land use/land cover (Kilgour and Barton 1999) have been related to instream biological responses. In general, more intensive development degrades fish and benthos assemblages and instream habitats. A quantitative understanding of the relationships between development and ecological conditions enables

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planners to predict and mitigate impacts from future land conversions, particularly to ensure that thresholds are not exceeded that would lead to irreversible damages to the ecosystem.

Percent impervious cover (PIC) is a metric that integrates various types of human development activities in catchments. Impervious lands are those that have been covered by materials such as concrete, asphalt, and rooftops or result in severe compaction or draining of the soils, all of which restrict infiltration. Different land covers are variably permeable (impermeable). The PIC in a catchment is the weighted average imperviousness for the entire catchment. Percent impervious cover is typically low in natural landscapes, intermediate in agricultural landscapes, and high in urban landscapes. Leopold (1968) recognized that the transition from natural forest cover to agricultural and urban landscapes resulted in increased PIC of the land and led to reduced infiltration of precipitation into soils and increased overland flow. Streams in disturbed catchments tended to respond faster and more severely to storm events, had lower base flows during dry seasons, and were wider, shallower, more polluted, and warmer than streams in undisturbed catchments (Leopold 1968).

Percent impervious cover is recognized as a master variable for quantifying both physical and biological stressors in streams. Shaver and Maxted (1995) demonstrated in Delaware that percent Ephemeroptera-Plecoptera-Trichoptera taxa (mayflies, stoneflies, caddisflies) was significantly lower in streams with PIC greater than 10%. Klein (1979) demonstrated that fish species richness declined linearly with PIC such that catchments with 30–50% PIC either had severely impaired fish assemblages or fish were absent. Several authors have identified impairments to fish metrics at PIC levels greater than 10%. For example Steedman (1988) and Wang et al. (2000) both reported that the number of fish species and/or an index of biotic integrity (IBI) decreased in streams above this threshold. Limburg and Schmidt (1990) documented declines in

anadromous fish egg and fry densities above a PIC of 10%. Results for benthos are comparable, although evidence of threshold responses are less convincing. Jones and Clark (1987) identified a threshold response at 15% PIC, while Yoder et al. (1999), Shaver and Maxted (1995), and May et al. (1997) determined that benthos taxa diversity declined above 5–8% PIC. Klein (1979) however was unable to identify a threshold response and suggested that confounding factors such as the presence of riparian zones may buffer the overall effect of PIC on streams. Several studies have confirmed even lower threshold responses to geomorphic variables. Dunne and Leopold (1978) found dramatic change in channel dimensions at only 4% PIC. Booth and Jackson (1997) found that even at low levels of effective impervious cover, flow patterns were significantly altered and that by PIC levels of 6–10% PIC, there is a loss of aquatic system function that may be irreversible.

We believe there are three key factors that explain the differences in response to PIC in these studies: differences in resilience to PIC between ecoregions, differences in how instream features (e.g., fish, substrate, etc.) are measured between studies, and differences in how PIC has been estimated. Until comparisons can be made between ecoregions using similar measures of instream conditions and PIC, application of the relationship between PIC and stream condition must rely on locally derived models.

Our objective was to quantify the relationship between catchment PIC and biophysical characteristics of streams. We recognize that much of the variability in the biophysical makeup of streams is due to natural catchment characteristics and the location of the stream within the catchment. Therefore, we accounted for catchment characteristics that might influence stream hydrology and sediments. By including both the biotic and abiotic properties of streams, we attempt to demonstrate how biotic–abiotic relationships can assist managers in predicting changes from future development scenarios.

METHODS

Study Area

Fish, benthic invertebrates, and instream habitat conditions were characterized at wadeable sites along the north shore of Lake Ontario. The Oak Ridges Moraine and Niagara Escarpment dominate this landscape and ensure strong base flow to streams, which historically provided valued salmonid fisheries for the early settlers in the region (Figure 1). Data were collected 1995–2002 by several agencies using methods described in Stanfield et al. (1997). Sites were selected using multiple stratified random designs. Several studies covered the entire ecoregion. Most studies were stratified based on a measure of stream size. Sampling intensity and the types of data collected

(not all methods were applied at all sites) within each stratum were designed to meet the desired precision of each study. Once the study design was determined, sites were randomly selected within each stratum. Sites were a minimum of 40 m long, with boundaries at crossovers (i.e., the location where the thalweg is in the middle of the stream) (Stanfield et al. 1997). In streams in our study area, this site length provides a reliable measure of fish biomass (Jones and Stockwell 1995), species richness (L. W. Stanfield, unpublished data), and instream habitat (Stanfield and Jones 1998). This design enabled many more sites to be sampled in a day and provided an opportunity to develop a more robust estimate of fish assemblages within an entire stream than if a single long site (e.g., 40 bank-full widths; Lyons 1992) were sampled.

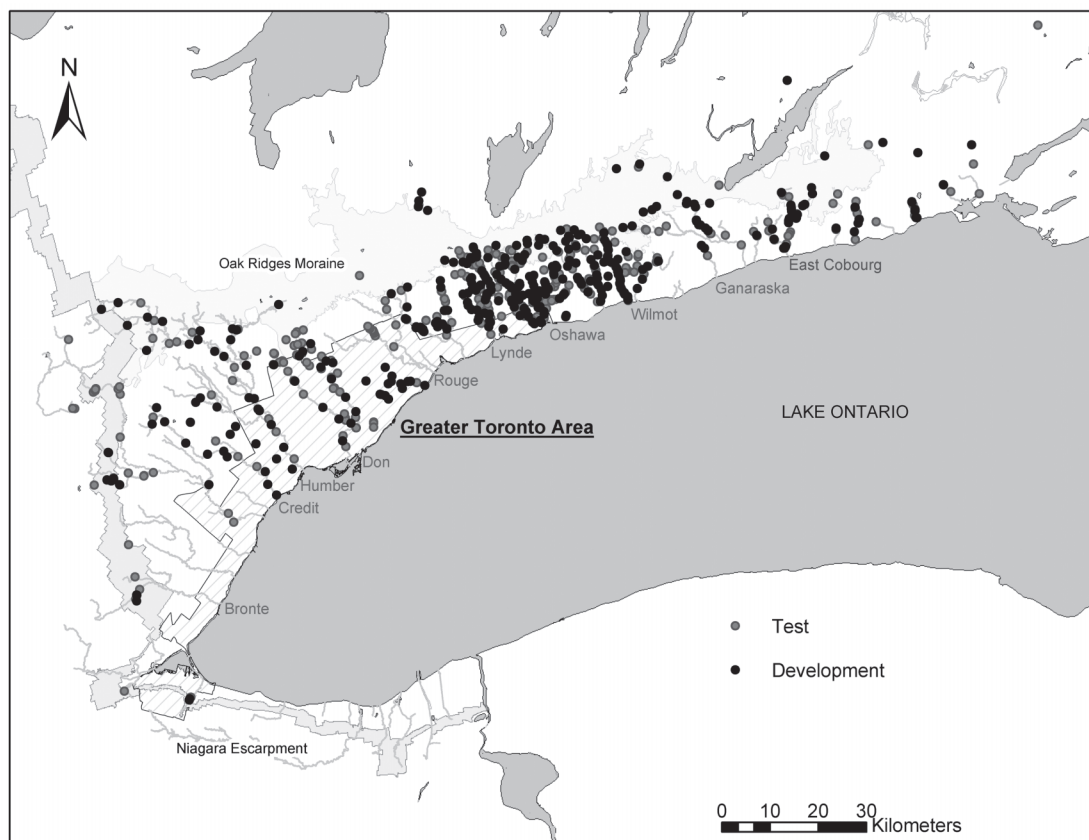


Figure 1. Major features of the study area and distribution of sample sites.

Fish Assemblage Data

Fish were collected by single-pass electrofishing at 721 sites, without bias, for size or species. Effort expended per site varied (4–15 s/m²), but was sufficient to provide comparable assemblage measures at each site (Stanfield, unpublished data). All fish were immediately weighed, identified to species, and released, except those kept for laboratory identification. Mottled sculpin *Cottus bairdii* and slimy sculpin *C. cognatus* and American brook lamprey *Lampetra appendix* and sea lamprey *Petromyzon marinus* were inconsistently identified and were therefore combined by genus for this analysis.

Benthos Assemblage Data

Benthos were sampled at 583 sites using a modified version of Plafkin et al. (1989). Two benthos samples were collected from within crossovers, using a 2-min stationary kick-and-sweep method, with 1-mm mesh, over approximately 1 m². Organisms were picked from sampling trays until at least 100 individuals were obtained for each replicate or the entire sample was processed. Benthos were identified to major taxonomic groups (see Table 1).

Instream Habitat Data

Instream habitat data were collected from 578 sites using a point-transect survey design. Depending on stream width, from 10 to 20 transects (>3 m width = 10) were established at regular

spacing within each site and then 2–6 observation points (>3 m width = 6) were identified on each transect. This design explained 90% of the variability in instream habitat from streams within this study area (Stanfield and Jones 1998). At each observation point (total of 40–60/site), depth, substrate, and hydraulic head were measured. Hydraulic head was used as a surrogate for stream velocity and represents the height water climbs a ruler held at right angles to flow. Cover and maximum particle size (largest present) were measured within a 30-cm ring that was centered on each observation point. Cover (converted to percent) was an object 10 cm wide on its median axis that intersected a 30-cm ring, centered on each observation point. Percent fines (particles ≤ 2 mm) and the D16, D50, and D85 were determined from substrate particle size measurements. Proportions of 16 categories of morphological features were determined based on the classes of depth (10, 60, 100 and >100 cm) and hydraulic head (<3, 4–7, 8–17, and >17 mm) at each observation point. A measure of channel homogeneity was determined by summing the proportion of a site within one category of the dominant morphologic feature at the site. The width-to-depth ratio was determined by averaging the sum of the wetted width to depth ratios of each transect.

Four metrics were calculated to provide measures of channel stability (Table 2). The vulnerability to erosion for streambanks was determined at each bank intercepted at a transect. Field measurements of bank angle, bank material, presence of undercuts, rooted vegetation

Table 1. Benthos taxa identified and adjusted ratings used to calculate the Hilsenhoff biotic index score. Ratings based on a review of the original ratings of families common to southern Ontario.

Taxa	Rating	Taxa	Rating	Taxa	Rating
Hydracarina	6	Amphipoda	6	Simuliidae	6
Oligochaeta	8	Isopoda	8	Other Diptera	5
Hirudinea	8	Chironomidae	7	Tipulidae	3
Hemiptera	5	Coleoptera	4	Megaloptera	4
Anisoptera	5	Zygoptera	7	Trichoptera	4
Gastropoda	8	Pelecypoda	8	Ephemeroptera	5
Decapoda	6	Plecoptera	1	Ostracoda	7

Table 2. Criteria used to score metrics used to create an overall rating of channel stability for each site. Results from field surveys derived summary statistics for each metric. Ratings were developed based on the relative importance of each metric as a measure of channel stability and thresholds for each metric were based on results of local geomorphic studies (John Parish, Parish Geomorphic, personal communication). Final score for channel stability was the cumulative ratings from the four metrics

Metric	Ratings			
	0	0.1	0.2	0.3
Width/depth	>60	>40 ≤ 60	>20 ≤ 40	<20
Bank stability	≤0.4	>0.4 ≤ 0.59	>0.6 ≤ 0.79	>0.8
Sediment sorting	≤70	> 70 ≤ 120	> 120	
Sediment transport	>36	> 12 ≤ 36	≤12	

and riparian vegetation type were interpreted with a dichotomous key. Bank height information and substrate size at four horizontal distances (0, 0.25, 0.75, and 1.5 m) from the stream edge were used to determine whether the bank angle exceeded 45° and consisted of erodible material. Undercuts more than 5 cm deep were recorded, and the percent of rooted vegetative cover in the first 1 m of bank was measured by counting the number of squares in a grid occupied by live vegetation. Finally, the dominant vegetative type in a 2-m² grid at the intersection of each transect was recorded. Bank ratings ranged from 0.2 (e.g., undercut present and no forest cover present) to 1.0 (e.g., no undercut present, bank angle less than 45% and greater than 70% of squares with root cover). The coefficient of variation for the maximum particles was used as a measure of sediment sorting at each site. Sediment transport potential was estimated by dividing the D50 for the point and maximum particle sizes. Channel stability for each site represented the cumulative ratings for the four metrics (Table 2).

Stream Temperature Data

Water temperatures were recorded at 622 sites, between 1600 hours and 1700 hours, during low-flow conditions (mid-July to mid-September), when the daily air temperature exceeded 24°C for three consecutive days. We standardized stream temperatures for each site as follows. The

observed water and air temperatures were used to classify each site as either cold, cool, or warm using the nomogram developed by Stoneman and Jones (1996). The appropriate regression line (Table 3) was used to predict the stream temperature at an air temperature of 30°C. Finally, the difference between the observed and predicted temperature was added to the predicted temperature at 30°C to obtain the standardized stream temperature at 30°C for each site. For example, if a stream temperature of 25°C was determined at an air temperature of 27°C, it would be classified as warm. This site is 1.2°C warmer than predicted from the algorithm for a warmwater stream (Table 3), and therefore, the standardized stream temperature would be 26.7°C:

$$\text{standardized temperature} = (30 \times 0.555 + 8.838) + (25 - 23.8). \quad [1]$$

Table 3. Regression parameters used to predict water temperatures from air temperatures for reference stream types. Sites were assigned a reference class based on the lowest deviation from the observed and the predicted water temperature for the air temperature on the day of collection.

Reference Class	Slope	Constant
Cold	0.251	7.513
Cool	0.583	3.497
Warm	0.555	8.838

Landscape Data

Landscape variables were generally derived for the total catchment, through use of a geographical information systems application, following Stanfield and Kuyvenhoven (2003). Measured attributes from a 1:10,000 DEM with 25-m resolution included drainage area, link number, elevation, stream length, and site slope (determined from elevations at 100 m up and downstream of each site). The Ontario Ministry of Natural Resources developed a land cover GIS layer at 1:10,000 that assigns 1 of 28 classes to each 25-m pixel. Land classifications were based on interpretation of Landsat imageries collected from 1995 and 1996. From this classification, we quantified the amount of forest, urban, pasture, intensive agriculture (row crops and orchard), and water (lake, river, and wetland) in each catchment.

The area covered by each class of quaternary surficial geology (1:250,000) (Ontario Geological Survey 1997) was determined for each catchment. A base flow index (BFI) for each site was derived from relationships demonstrated by Piggott et al. (2002) between this index and base flow (Table 4). The BFI was calculated by summing the ranked percentage of each quaternary surficial geology unit for each catchment:

Table 4. Baseflow index (BFI) ratings for quaternary geology classes from the Ontario geological survey (1997) (Source: Piggott et al. 2002).

Geology type	BFI rating
Bedrock (Paleozoic)	0.4
Tavistock Till (Huron - Georgian Bay lobe)	0.29
Port Stanley Till (Ontario - Erie lobe)	0.27
Newmarket Till (Simcoe lobe)	0.43
Wentworth Till (Ontario - Erie lobe)	0.68
Kettleby Till (Simcoe lobe)	0.38
Halton Till (Ontario - Erie lobe)	0.39
Clay till	0.28
Till	0.4
Glaciofluvial ice-contact deposits	0.67
Glaciofluvial outwash deposits	0.77
Glaciolacustrine deposits	0.14
Fluvial deposits	0.38
Organic deposits	0.35

$$\text{BFI per site} = \sum_{ij} (\% \text{geology type}_i \times \text{BFI rating}_i)_j \quad [2]$$

Impervious ratings for each land-use/land-cover category were selected based on an understanding of how closely the land-cover categories related to published ratings. Intensive agriculture and pasture lands are typically both rated low and similarly (i.e., 0.02, NCDE 2002, 2003; and 0.094, Prisloe et al. 2001). We chose to split these categories and rate intensive agriculture higher (0.10) than pasture lands (0.05) because in our study area, intensive agriculture often involves tile drainage and compaction from heavy machinery. Urban land ratings vary considerably depending on the detail available from the base data: 0.23–0.86 (NCDE 2002), 0.10–0.38 (NCDE 2003), 0.12–0.51 (Prisloe et al. 2001), and 0.20–0.95 (Arnold and Gibbons 1996). We chose a conservative rating of 0.20 for urban lands because of the coarseness of our land-use/land-cover data. Forested lands (0.01) and water/wetlands (0.0) were both given low ratings.

A rating for catchment percent impervious cover (PIC) was estimated as the sum of the products of percent cover by each land-use/land-cover class and the associated impervious rating of each class. An upstream catchment area with 25% water, 25% intensive agriculture, and 50% urban area, for example, would have a PIC of 12.5 (i.e., $0 \times 25\% + 0.1 \times 25\% + 0.2 \times 50\%$).

Data Analysis

The objective of the data analysis was to determine if attributes of fish and benthos assemblages and instream physical habitat characteristics were related to PIC, after accounting for natural landscape influences. Fish assemblage metrics included total biomass (g/m²) and species richness, while a modified Hilsenhoff biotic index (HBI; Hilsenhoff 1987) and taxa richness were calculated for the benthos assemblage. Both benthos metrics were based on higher level taxonomy, and as such, the HBI ratings were assigned based on a review of the original scores

for lower taxa developed by Hilsenhoff (1987; Table 1).

Correspondence analysis (CA) was used separately for fish and benthos assemblages to evaluate assemblage composition. Correspondence analysis ordination calculates a set of "synthetic" variables (axes) that best explain variations in taxa abundances across samples. Calculation of sample and taxa scores on the first ordination axis is done by iteratively estimating the weighted-average sample scores and the weighted average taxa scores. For the first iteration, axis scores are arbitrarily assigned to each taxon. For each sample, the procedure determines the weighted-average axis score, which is the average of the taxa scores weighted by the abundances of each taxon. The next iteration produces new weighted average axis scores for the taxa, calculated from the sample scores. The iterative procedure continues until there is little change in the sample and taxa scores. Estimation of second and third ordination axes follows a similar routine, except that the sample scores of additional axes are orthogonal (uncorrelated) with the first and subsequent axes. Sample scores in CA are usually scaled to a mean of zero and standard deviation of 1 (ter Braak 1992). The distribution of samples in a CA diagram indicates the relative similarities and differences in composition based on taxa abundances. Sites with similar scores have taxa in similar proportions. The scatter diagram for taxa portrays the dispersion of taxa along the theoretical variables (axes). Thus, a sample with an axis-1 score of 2 would be dominated by taxa that also had axis-1 scores close to 2. With CA, the configuration of ordination diagrams tends to be sensitive to rare taxa (Gauch 1982). Therefore, we retained for analysis only those taxa found in more than 5% of sites.

Canonical correspondence analysis (CCA; ter Braak 1992) was used to illustrate how fish and benthos assemblages varied with landscape attributes. Canonical correspondence analysis is an extension of CA, except that the ordination of the response (i.e., fish or benthos assemblage) is

constrained to a set of predictor variables (i.e., landscape features). As with CA, CCA was conducted separately for fish and for benthos. The method is commonly used in ecological studies of this nature and has been used to demonstrate fish-landscape relationships (Kilgour and Barton 1999; Wang et al. 2001, 2003). Bi-plots of taxa and environmental variable scores indicate general associations between taxa and environmental conditions.

We used backward stepwise multiple regression to construct empirical models that relate instream biophysical responses to landscape variables. Predictor landscape variables included catchment area, stream slope, and base flow index (BFI). Area was selected because it is a measure of stream size and provides a coarse estimate of the amount of water or space available to fish and benthos. Catchment areas varied considerably (seven orders of magnitude) and were \log_{10} transformed. Slope was selected because it is a major factor determining flow velocity and, together with area, provides a measure of stream power. The BFI was selected because it reflects the water permeability through surrounding soils (Piggott et al. 2002). In addition to these primary landscape variables, multiple regression models also included PIC. Predictors were retained in this backward stepwise regression when they accounted for significant amounts of variation in the response variable (at $P < 0.05$, typically much lower). The fish assemblage variables included biomass, species richness, and site scores for the first CA axes. The benthos assemblage variables included richness, HBI, and site scores from the first two benthos CA axes. Instream habitat variables included average stream width, width:depth, proportion stable banks, stability index, $D50_{\text{point}}$, $D50_{\text{max}}$, sorting index, sediment transport, homogeneity index, and standardized stream temperature.

Percent impervious cover and BFI scores covaried, with a correlation typically around 0.5, depending on the specific data set. Percent impervious cover was more strongly related to biotic responses than were BFI scores in some cases.

Three sets of models were, therefore, constructed to help us understand how much variation in biophysical responses was solely attributable to PIC. The first model included all possible predictors (including their squared terms to take into account possible curvilinear relationships). The second model included only the primary landscape variables (with their square terms) and excluded PIC. The second model, therefore, demonstrated the variation attributable to the primary landscape variables. The third model related the residual variation from model 2 to PIC (and the squared term). The variation accounted for in model 3 represented the variation attributable to PIC alone.

Model Validation

Prior to constructing these models, data were split into calibration and validation sets. Sites available from each data set (i.e., fish, benthos, and habitat) were randomly selected after first stratifying the data by quaternary catchment and stream order (see model outputs for number of sites used). We applied two approaches to validate the models. First empirical models were used to estimate expected biotic index values or instream habitat features for each validation site, and comparisons were made following the approach of Carr et al. (2003). Differences in precision between calibration and validation data

sets were tested using an *F*-ratio of residual mean squares. The slope of the relationship between observed and predicted index values was also determined, as was the probability that the slope was significantly different from one, indicating that the model did not fit the validation set. The minimum, maximum, median, and mean of the residuals for the validation data, as well as the probability that the residuals were different from zero were determined. A nonzero mean residual implies that the model from the calibration data were poor. Additionally, we were concerned that the power in our data sets, due to the large number of sites, could result in differences in slope due to this factor alone; therefore, we also plotted the data and explored whether patterns and trends were similar between the calibration and validation data sets.

RESULTS

There was considerable contrast in the distribution of sites and level of catchment development (Figure 1; Table 5). Catchments included those that were principally forested (usually smaller headwater sites) and others with high percent agriculture or urbanization. Forested catchments tended to occur in headwater areas, on morainal deposits, with high-porosity soils, while urban areas tended to co-occur with larger catchment areas and lower porosity soils (i.e., clay till plains).

Table 5. Minimum, maximum, and median values of landscape conditions in the data set.

Variable	Minimum	Maximum	Median
Catchment area (km ²)	0.018	873.3	17.8
Stream order	1	7	3
Site elevation (masl)	75	440	176
Precipitation (mm)	775	975	875
% high porosity soils	0	100	25
% moderate porosity soils	0	100	< 1
% low porosity soils	0	100	61
% slope (100 m up and downstream)	0	10	<1
% water and wetlands	0	41	<1
% forest	0	98	24
% pasture	0	68	12
% crop (intensive agriculture)	0	100	52
% urban	0	100	0

Fish Assemblages

We collected 64 fish species; 43 were present in less than 5% of the calibration sites. Of the remaining species, eastern blacknose dace *Rhinichthys atratulus* was found at 73% of all sites with a mean biomass of 67 g/100 m² (Table 6). Sculpins *Cottus* sp., creek chub *Semotilus atromaculatus*, brook trout *Salvelinus fontinalis*, brown trout *Salmo trutta*, rainbow trout *Oncorhynchus mykiss*, and white sucker *Catostomus commersonii* were commonly occurring and abundant. Total fish biomass was 1.0–7,000 g/100 m², and the number of fish species per site varied from 1 to 14.

The CCA illustrated four fish assemblage clusters (Figure 2). Axis 1 separated sites where salmonids were dominant from those with a more diverse mix of fishes where salmonids were a smaller component of the assemblage. Sites with abundant salmonids tended to have higher forest cover and BFI ratings and lower PIC, whereas sites lacking salmonids tended to have less forest cover, more urban area, lower BFI, and higher PIC. The second CCA axis separated sites with salmonid assemblages into those with brook trout from those with other salmonid species. Brook trout tended to occur in sites with smaller catchments and greater elevations and slopes, while brown trout and rainbow trout tended to

occur in sites with larger catchments and lower elevations and slopes. The second axis also separated sites with nonsalmonid taxa. Sites in smaller catchments supported species such as northern redbelly dace *Phoxinus eos*, fathead minnow *Pimephales notatus*, and brook stickleback *Culaea inconstans*, while darters *Etheostoma* spp. and rock bass *Ambloplites rupestris* were more common in sites with larger catchments.

Percent impervious cover was a significant predictor of each of the fish assemblage responses, regardless of whether we modeled raw fish metrics or their residuals after accounting for landscape features (Table 7). Relationships between PIC and fish assemblage metrics were less apparent with residuals than with the original variables (Table 7; Figure 3) because PIC and BFI were related (Figure 2). Biomass weakly decreased linearly with PIC (Figure 3). Species richness was highest at 5–10 PIC, regardless of whether the full or residual model was used (Figure 3). However, there was a weak bimodal pattern, where two sites with more than 15 PIC had species richness comparable to areas with less than 10 PIC. Scores of fish CA Axis 1 increased with PIC. The models for CA Axis 1 predict the presence of salmonids in streams with low PIC and an absence of salmonids in streams with high PIC (Figure 2; Table 8). Scatterplots of the raw

Table 6. Distribution and biomass of common species^a used in the model development.

% of sites with each taxa	Mean log biomass (g/100 m ²)				
	0–0.5	0.5–1.0	1.0–1.5	1.5–2.0	2.0–2.5
5–10	BST	CHS, FTD	COS, LAM, NRD	ROB	
10–20			RBD, PKS, BNM,	CSH	
20–30			FHM		BKT
30–40			JOD		BNT
40–50				LND	RBT
50–60				SCU	CRC, WS
60–70				BND	

^aBST = brook stickleback *Culaea inconstans*; CHS = Chinook salmon *Oncorhynchus tshawytscha*, FTD = fantail darter *Etheostoma flabellare*, COS = coho salmon *O. kisutch*, LAM = lamprey family Petromyzontidae, NRD = northern redbelly dace *Phoxinus eos*, ROB = rock bass *Ambloplites rupestris*, RBD = rainbow darter *E. caeruleum*, PKS = pumpkinseed *Lepomis gibbosus*, BNM = bluntnose minnow *Pimephales notatus*, CSH = common shiner *Luxilus cornutus*, FHM = fathead minnow *P. promelas*, BKT = brook trout *Salvelinus fontinalis*, JOD = Johnny darter *E. nigrum*, BNT = brown trout *Salmo trutta*, LND = longnose dace *Rhinichthys cataractae*, RBT = rainbow trout *O. mykiss*, SCU = sculpin family Cottidae; CRC = creek chub *Semotilus atromaculatus*, WS = white sucker *Catostomus commersonii*, BND = eastern blacknose dace *R. atratulus*.

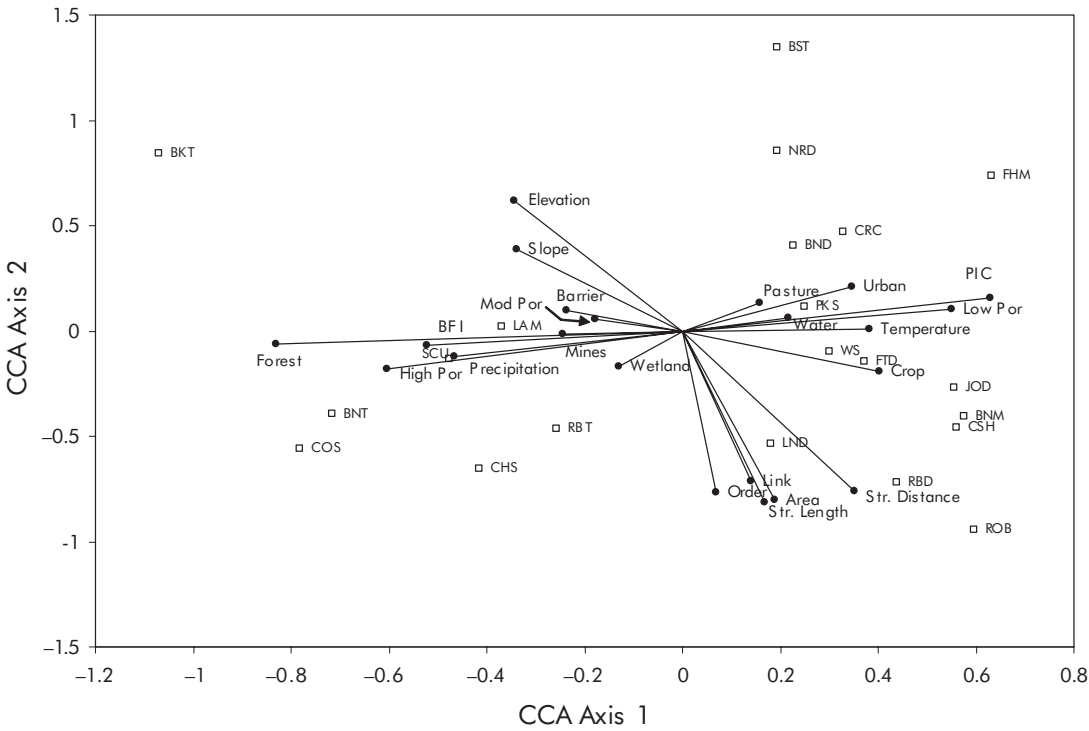


Figure 2. Relationship between landscape and fish assemblage composition as determined through canonical correspondence analysis (CCA). Species acronyms are defined in Table 6. Por = porosity of soils; str = stream; PIC = percent impervious cover; BFI = baseflow index.

Table 7. Regression models relating fish assemblage metrics to landscape and percent impervious cover (PIC) variables. There were three models for each response. Model 1 (the full model) relates the best landscape and PIC predictions to the response. Model 2 (reduced landscape model) relates the best landscape predictors (not including PIC) to the response. Model 3 relates the residuals from Model 2 to PIC.

Model parameters	Response variable								
	Log fish biomass			Fish taxa richness			Fish canonical axis 1		
	1	2	3	1	2	3	1	2	3
Constant	-3.841	-5.075	0.129	-6.582	-3.741	-1.801	-1.625	2.465	-1.243
Area	1.866	1.667							
Area ²	-0.125	0.113		0.189	0.184				
Slope		0.125			-0.298		-0.243	-0.499	
Slope ²		-0.017					0.027	0.052	
BFI		0.051					-0.016	-0.047	
BFI ²	<-0.001	<0.001							
PIC	-0.066			0.619		0.519	0.476		0.234
PIC ²			-0.002	-0.035		-0.031	-0.016		-0.008
N	361	361	361	361	361	361	361	361	361
MSE	0.215	0.242	0.218	5.895	6.380	5.835	0.804	0.949	0.870
R ²	0.185	0.085	0.087	0.372	0.319	0.085	0.394	0.280	0.081

Note: Each metric was squared to account for possible curvilinear relationships.

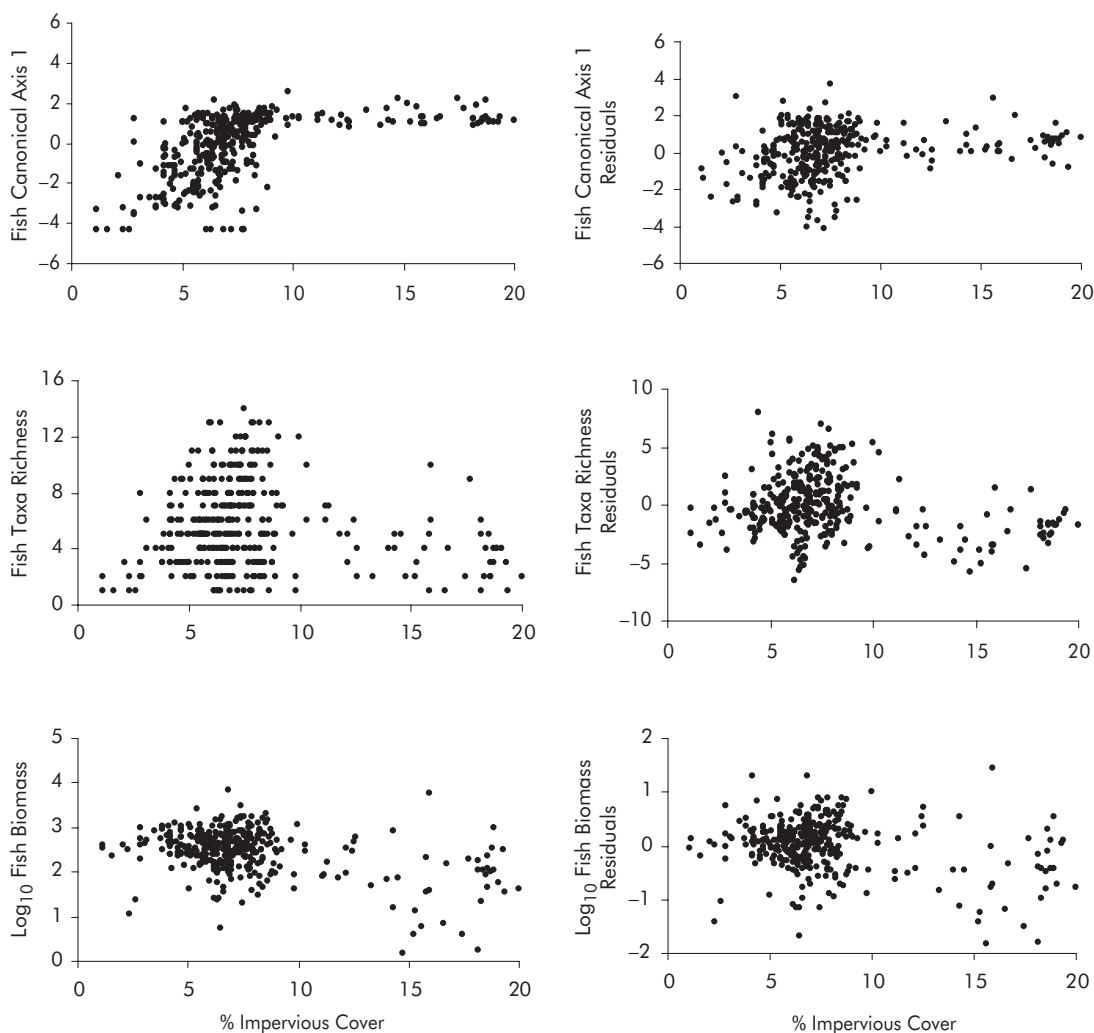


Figure 3. Relationship between percent impervious cover (PIC) and fish variables and their residuals after accounting for landscape variables.

and residual data indicate large changes in axis scores at less than 10 PIC, with smaller changes in axis scores at more than 10 PIC (Figure 3). There was, thus, a threshold at 10 PIC for CA Axis 1 scores.

Benthos Assemblages

There were 20 benthos taxa collected, including the typical sensitive groups Ephemeroptera, Plecoptera, and Trichoptera and the more toler-

ant groups Oligochaeta and Chironomidae. Turbellaria, Hirudinea, Isopoda, Amphipoda, Gastropoda, and Pelecypoda were also relatively common. Site taxa richness ranged from 1 to 17, and the modified HBI ranged from 3 to 8.

Tolerant taxa (chironomids, platyhelminths, oligochaetes, isopods, etc.) were generally found at sites with higher PIC and lower BFI scores. Sensitive taxa (Plecoptera, Ephemeroptera, Coleoptera) were generally found in streams with higher forest cover and BFI scores (Figure 4). A

Table 8. Regression models relating benthos assemblage metrics to landscape and percent impervious cover (PIC) variables. There were three models for each response. Model 1 (the full model) relates the best landscape and PIC to the response. Model 2 (reduced landscape model) relates the best landscape predictors (not including PIC) to the response. Model 3 relates the residuals from Model 2 to PIC.

Model parameters	Response variable											
	Hilsenhoff			Benthos taxa richness			Benthos canonical axis 1			Benthos canonical axis 2		
	1	2	3	1	2	3	1	2	3	1	2	3
Constant	8.685	10.961	-0.454	10.068	5.378		16.263	7.514		-0.279	2.783	-0.494
Area	-0.417	-0.360					-3.396	-0.671				
area ²						No sig-	0.191		No sig-			
slope	-0.171	-0.201				nificant	-0.199	-0.206	nificant		-0.094	
slope ²						predic-			tors			
BFI	-0.017	-0.088			0.159	ors	-0.077	-0.095		-0.011	-0.092	
BFI ²		0.001			-0.001		0.001	0.001			0.001	
PIC	0.092		0.061				0.042			0.102		0.066
PIC ²				-0.008								
n	332	332	332	332	332		332	332		332	332	332
MSE	0.653	0.714	0.664	4.842	5.143		0.760	0.779		0.827	0.896	0.839
R ²	0.306	0.242	0.061	0.080	0.026	N/A	0.255	0.232	N/A	0.180	0.114	0.058

Note: Each metric was squared to account for possible curvilinear relationships.

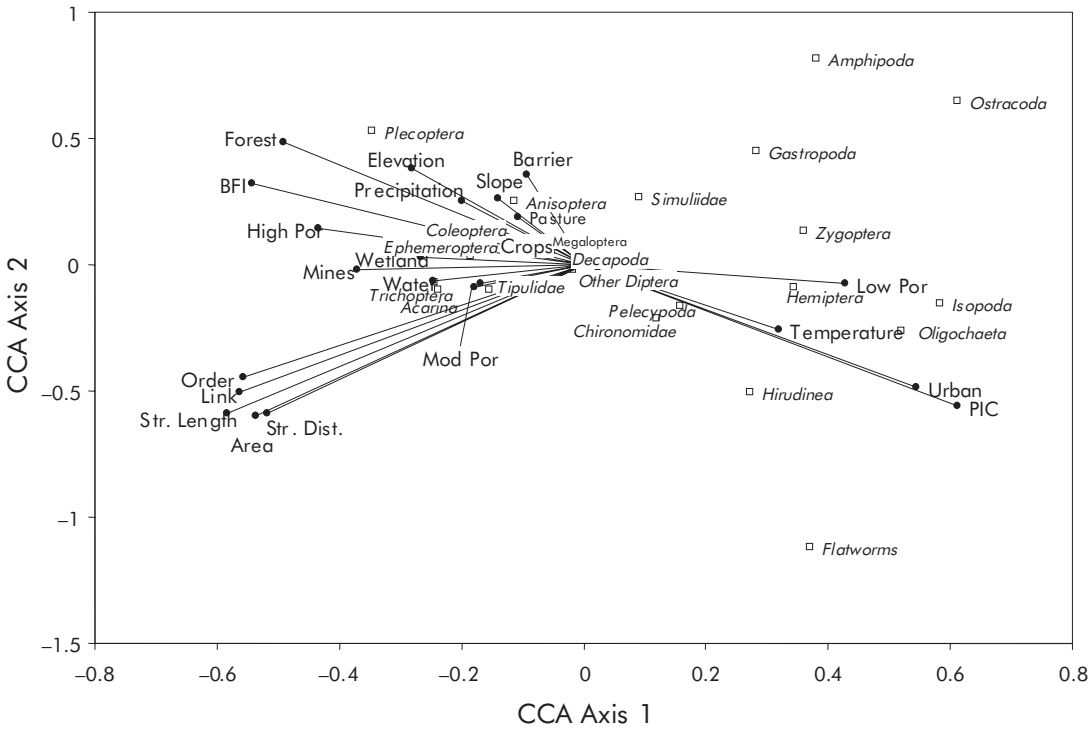


Figure 4. Relationship between landscape and benthos assemblage composition as determined through canonical correspondence analysis (CCA). Por = porosity of soils; str = stream; PIC = percent impervious cover; BFI = baseflow index.

secondary environmental gradient was apparent in the data, with amphipods, ostracods, and gastropods being more prevalent in smaller catchments.

As with fish assemblage metrics, indices of benthos assemblage composition were generally related to PIC, even after accounting for the underlying influences of natural landscape features (Table 8). The HBI predictably increased with PIC, indicating degraded conditions. Values were 4–5 for sites without development and averaged about 6 for sites with full urbanization (i.e., 20% PIC). The HBI exhibited a weak threshold response at a 10 PIC (Figure 5). The relationship between richness and PIC was statistically significant but not convincing. Benthos taxa rich-

ness was not significantly related to landscape features other than BFI (Table 8). The benthos CA Axis 1 scores increased weakly with PIC (Figure 5), but only for the full model (not the residuals), indicating that PIC may not be important for this metric. Correspondence analysis Axis 2 scores, however, did relate to PIC after removing the effects of natural landscape factors and exhibited a weak threshold response (Figure 5). Correspondence analysis axis 2 scores varied between -2 and 3.5 at PIC less than 10, and there were no values greater than 0 above PIC of 10. Sites with PIC greater than 10 contained higher proportions of mayflies, chironomids, isopods, and worms.

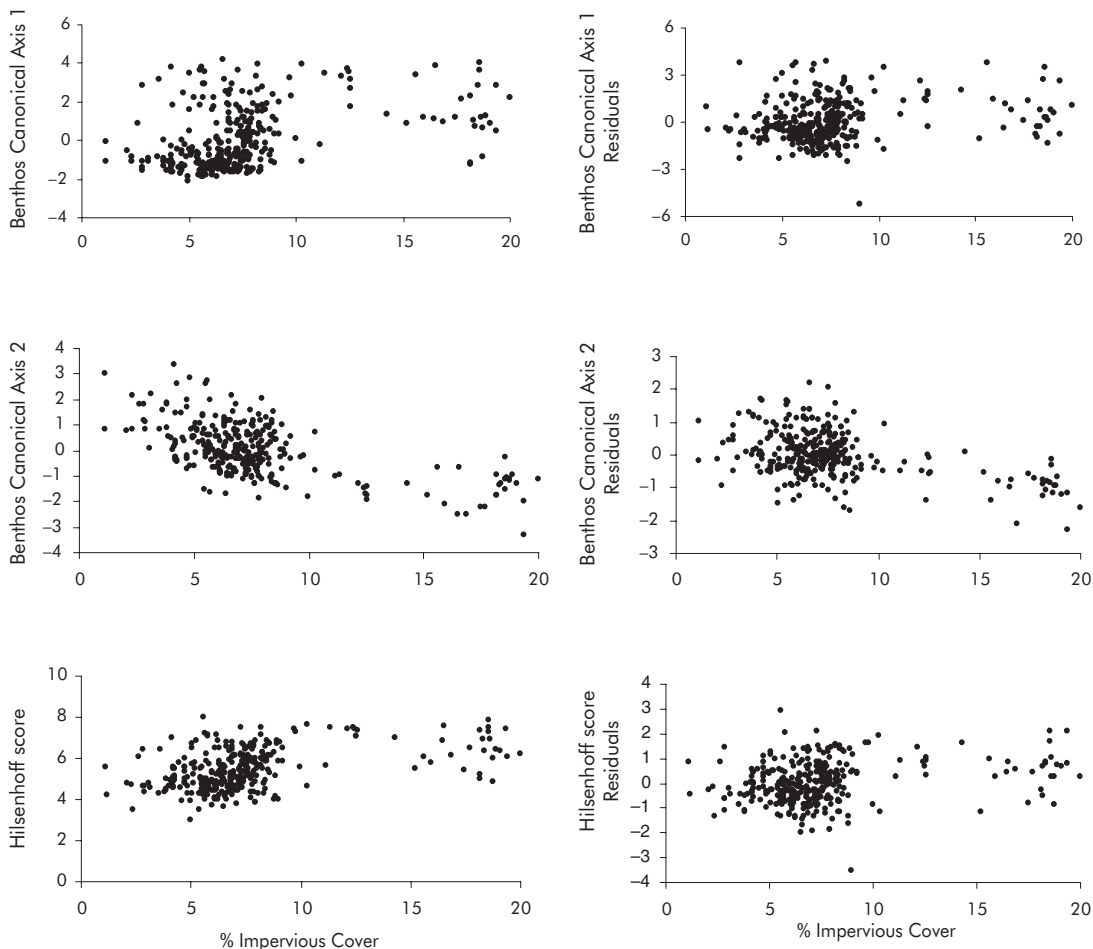


Figure 5. Relationship between percent impervious cover (PIC) and benthos variables and their residuals after accounting for landscape variables.

Instream Habitat

The standardized stream temperature, proportion of stable banks, and mean width were related to PIC, after the landscape conditions were taken into consideration (Table 9). The other physical habitat and channel stability metrics were not related to PIC.

Standardized stream temperature and mean width were the only habitat attributes to demonstrate threshold-type responses to PIC, for both the main and residual models, but these were weak relationships (Figure 6). There was a mix of cold- and warmwater sites at less than 8 PIC, and there were no coldwater sites above this threshold (Figure 6). Mean stream widths were 0.5–20 m in catchments with PIC less than 10, but narrow streams were absent in catchments with higher PIC (Figure 6).

Model Validation

Fish CA axis 1, the modified HBI, standardized temperature, and the log of the width:depth ratio had the highest model fits with landscape data (Figure 7; Table 10). The slope of the predicted values for the validation and calibration data sets differed from unity for the fish CA axis 1 (Figure 7). The validation data sets for all of the variables, however, tended to produce scatterplots that were similar to the calibration scatterplots, suggesting that the models produced were relatively robust and that the data used to construct the models were representative of the larger data sets. The lack of fit for the fish CA axis 1 is likely related to either the extreme power in our data or to other factors (not included in the model) also being important in explaining variation in fish assemblages.

DISCUSSION

There are three principal conclusions from this study. First, landscape measures accounted for significant variability in the responses of fish and benthos assemblages, instream temperature, and

some instream habitat metrics. Second, PIC was a significant modifier of the fish and benthos assemblage responses, as well as temperature, width:depth, and percent stable banks, even after removing or accounting for the influences of natural landscape conditions. Third, fish and benthos assemblages were clearly altered above 10 PIC, and there were no coldwater streams above that threshold. Below the threshold, the biophysical responses indicated that change in PIC would change fish, benthos, temperature, and the percent stable banks in an incremental way. The landscape models developed here can be used to predict fish and benthos assemblages and habitat conditions, under a variety of land-use/land-cover scenarios, including an undisturbed reference state. Each of these main points is discussed below.

Natural Landscape Influence Biophysical Responses

In this study, catchment area, slope, and the base flow index were strong predictors of variation in indices of fish and benthos assemblages and stream temperature. These results were consistent with previous studies (e.g., Shaver and Maxted 1996; Richards et al. 1996, 1997; Kilgour and Barton 1999; Wang et al. 2001; Zorn et al. 2002; Wang and Kanehl 2003). As has been observed previously (Horwitz 1978; Kilgour and Barton 1999; Zorn et al. 2002), we observed a strong gradient in the fish assemblages related to catchment size. Similar to Barton et al. (1985) for southwestern Ontario and Zorn et al. (2002) for lower Michigan, we found that brook trout was generally limited to smaller catchments, while other salmonids were found in larger catchments. Stoneman and Jones (2000) provide evidence that this pattern of salmonid abundance is partly due to competition. It is also likely that this relationship relates to the location of sites relative to barriers in the catchment. The CCA of the fish assemblage (Figure 2) indicated a weak tendency for brook trout to be more prevalent upstream of barriers.

Table 9. Regression models relating indices of habitat metrics to landscape and percent impervious cover (PIC) variables. There were three models for each response. Model 1 (the full model) relates the best landscape and PIC to the response. Model 2 (reduced landscape model) relates the best landscape predictors (not including PIC) to the response. Model 3 relates the residuals from Model 2 to PIC.

Model parameters	Response variable											
	Stream temperature			Mean width:depth			Proportion stable banks			Channel stability		
	1	2	3	1	2	3	1	2	3	1	2	3
constant	12.5	21.382	-2.683	0.727	0.962	-0.027	0.992	1.167	-0.052	2.229	-0.455	0.123
area	0.989						-0.003	-0.030		-0.571	-0.256	
area ²		0.073		0.018	0.017					0.046	0.030	
slope	-1.818	-2.104		0.082	0.027		-0.012	-0.038		0.034	-0.066	
slope ²	0.183	0.206		-0.009				0.004				
BFI				-0.019	-0.023						-0.028	-0.035
BFI ²	-0.001	-0.001		0.0002	0.0002			-0.0001			<0.001	<0.001
PIC	0.891		0.560				0.022		0.011			-0.036
PIC ²	-0.034		-0.022	0.0005		0.0004	-0.0008		-0.0004		0.001	0.002
n	385	385		370	370	370	353	353		353	373	373
MSE	10.3	10.611	10.313	0.039	0.040	0.039	0.008	0.008	0.008	0.044	0.491	0.051
R ²	0.278	0.263	0.023	0.357	0.332	0.022	0.082	0.077	0.010	0.069	0.607	0.590
											0.590	0.048

Model parameters	Response variable											
	D50 _{point}			D50 _{max}			Sorting index			Homogeneity		
	1	2	3	1	2	3	1	2	3	1	2	3
Constant	-1.313	-1.130		-2.493	-2.180		0.635			2.052		
Area												
Area ²	0.040	0.040		0.067	0.066					-0.023		
Slope	0.401	0.406		0.674	0.618					-0.128		
Slope ²	-0.029	-0.029		-0.056	-0.048							
BFI		-0.010						0.049				
BFI ²				-0.0001	-0.0002			-0.0006		0.0001		
PIC	-0.0001											
PIC ²				0.002								
N	369			363			363			363		
MSE	0.345	NA	NA	1.0254	1.037	NA	0.061	NA	NA	0.866	NA	NA
R ²	0.237			0.224	0.213		0.032			0.053		

Note: Each metric was squared to account for possible curvilinear relationships. NA indicates no significant model determined.

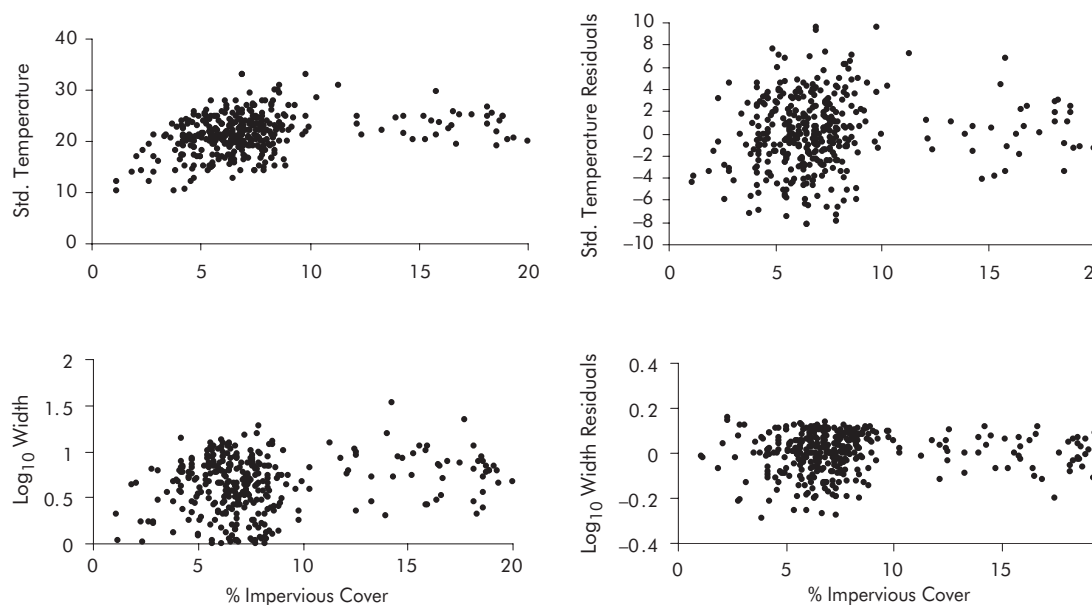


Figure 6. Relationship between percent impervious cover (PIC) and standardized temperature and mean width and their residuals after accounting for landscape variables.

In catchments with poorly drained soils, associations between catchment area and the fish fauna were not surprising. Brook stickleback, northern redbelly dace, and fathead minnow were more common in streams draining smaller catchments, while rock bass, rainbow darter *Etheostoma caeruleum*, and longnose dace *Rhinichthys cataractae* were more common in streams draining larger catchments. These associations were subtle, but have been reported before for southern Ontario (Kilgour and Barton 1999) and agree for the most part with findings from lower Michigan (Zorn et al. 2002). In lower Michigan, brook stickleback and northern redbelly dace were found in larger catchments than in our study and the difference in catchment size between where rock bass and rainbow darters were found was less distinct than what we observed. These differences are likely due to the much larger catchment size range in the Michigan study (i.e., maximum catchment sizes exceeded 10,000 km² compared to 873 km² in our study).

In this study, salmonids were generally found at sites with higher slopes. The influence of slope has been demonstrated in several other studies but notably by Wang and Kanehl (2003). Streams with greater slopes offer higher energy regimes (Rosgen 1996), higher groundwater contributions (Baker et al. 2003), and potential refuge for brook trout from migratory salmonid competitors. Catchments with higher gradients produce greater head for groundwater movement and streams with higher gradients tend to cut deeper into alluvial materials increasing the potential to intersect the water table.

The importance of surficial geology as a primary influence on fish and benthos assemblages was reconfirmed in this study. Many other studies have demonstrated the significance of surficial geology, notably Portt et al. (1989) for southern Ontario streams. In this study, we used an index of base flow to capture the surficial geology influence and found it highly predictive of fish and benthos assemblages. Though our index of base flow potential differed from others (e.g., Zorn et

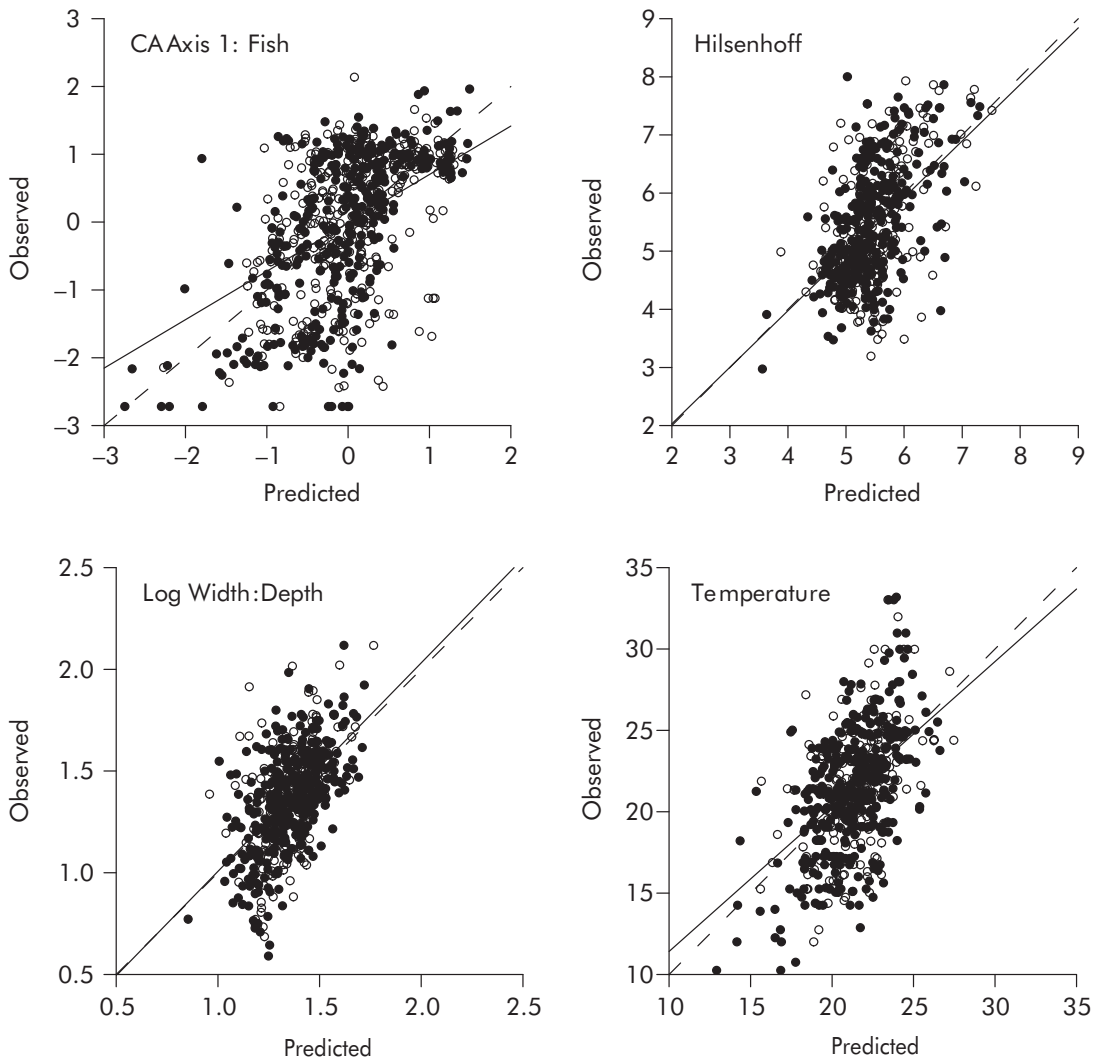


Figure 7. Relationship between observed and predicted biophysical indices illustrating the general fit of the best-fitting models. Filled circles are calibration data, open circles are validation data. The solid line is the 1:1 line of expectation (calibration data), while the dotted line is for the validation data.

al. 2002; Wang et al. 2003), the results were similar in that coldwater species were more frequently observed in streams with high base flow potential (i.e., were draining areas of high porosity glacial materials). Although our models explained relatively little variation in the response variables, the models were apparently robust and reflected what is intuitively known about the relationships between stream biophysical responses and landscape attributes. There should, therefore, be reasonable

confidence in using the derived models for understanding the relationships between stream biophysical responses and landscape and land-use/land-cover conditions.

PIC Effects

Even after considering the effects of natural landscape variables (i.e., size, surficial geology/base flow and slope), there were significant variations

Table 10. Validation of the best-fitting biophysical models. Differences in precision between calibration and validation data sets was tested using an *F*-ratio of residual mean squares. The slope of the relationship between observed and predicted index values was also determined, as was the probability that the slope was one, indicating that the model fit the validation set. The mean of the residuals for the validation data and the probability that the residuals were zero are also provided. A non-zero mean residual implies a bias in the validation data.

Model	Precision		Observed vs. predicted			Residual statistics	
	$F_{val/cal}$	$P_{val = cal}$	Slope (SE)		$P_{slope = 1}$	Mean	$P_{mean = 0}$
Fish canonical axis 1	1.032	0.384	0.714	(0.078)	0.0003	−0.009	0.852
Hilsenhoff biotic index	1.230	0.044	0.973	(0.112)	0.807	−0.064	0.284
Stream temperature	1.054	0.328	0.921	(0.115)	0.492	0.118	0.588
Log ₁₀ width:depth	1.301	0.017	1.199	(0.117)	0.090	0.017	0.282

in biophysical responses related to PIC. Metrics of fish assemblages and temperature varied with PIC between background conditions (~0–3) to highly urbanized (>10) (Figures 3 and 6). Below 10 PIC, there was considerable noise in the biological metrics, reflecting influences of other landscape variables (i.e., base flow, catchment size, slope) and local modifying factors such as riparian zones (Barton et al. 1985), adjacent land use, and instream habitat complexity. The observed relationships, however, indicate that increase in PIC will result in changes (i.e., degradation) in biological assemblages. These data also suggest that locally applied best-management practices and restoration activities are likely to be most effective when applied to streams with less than 10 PIC. Wang et al. (2006, this volume) reached a similar conclusion for Wisconsin and Michigan streams.

It was surprising that few geomorphic metrics were associated with PIC (Table 9). The measures used have been demonstrated to be precise (Stanfield and Jones 1998); therefore, the lack of association is unlikely related to measurement error. We also know that geomorphic attributes of streams respond to changes in PIC in the catchment (Leopold 1968) and that hydrologic factors are important in determining the kinds of fish and invertebrates found in streams (Zorn et al. 2002). The geomorphic variables that did vary in relation to landscape variables (includ-

ing PIC) included width:depth ratio, which is a classic indicator of an urbanized stream (i.e., wider and shallower in urban areas), and percent stable banks. The other geomorphic variables (stability, $D50_{point}$, $D50_{max}$, sorting index, and homogeneity) are essentially measures of substrate. That these factors did not relate well to landscape features indicates that they may be more controlled by local factors, such as sinuosity, gradient and riparian conditions (Rosgen 1996), and potentially local soil types.

An alternative hypothesis is that our data set included an insufficient number of sites exhibiting stable geomorphic conditions. Several studies suggest that channel stability is even more sensitive to PIC than biological variables (Dunne and Leopold 1978; Booth and Jackson 1997). Further, geomorphic processes require hundreds to thousands of years to reestablish equilibrium. The study area was deforested in the 1800s and sustained serious instream modifications until reforestation and soil protection began in the 1930s (Richardson 1944). Stream morphology and stability in this study area likely reflect the historic changes in the landscape and recent development patterns (i.e., urban sprawl). Our findings suggest that more effort is required to sort historic from current impacts on channel geomorphology and to assess the value of these geomorphic metrics as indicators of overall stream condition.

The PIC Threshold

There were no apparent relationships above a 10 PIC, probably because the biological assemblages at those levels were very tolerant (consisted of thermal and pollution tolerant species). Other studies examining PIC have arrived at similar conclusions; that is, critical effects tend to occur at 8–15% PIC. In our data set, the specific threshold (i.e., the critical percentage) depended on the assumed impervious ratings of each land-use/land-cover class. Urban lands were identified where infrastructure covered more than half of a 30-m pixel, ensuring that many smaller structures (including roads) would not be classed in this category, and we also assumed a 0.2 rating for urban PIC. Assuming a less conservative impervious cover rating of 0.5 for urban lands had little effect on the location of the threshold, but did increase the dispersion of points (Figure 8). Similarly, assuming an impervious cover rating of 0.05 (versus 0.1) for agriculture halves the

threshold to 5% (Figure 8). This supports our hypothesis that biological and physical conditions were influenced by the combined effects of agriculture and urbanization and that there is value in developing an overall metric of catchment disturbance such as PIC. In our study, a catchment with a PIC of 10 was 40–50% urban, 80–100% agriculture, or more frequently a combination of the two. These data then indicate that fish, benthos, and instream temperatures vary widely with incremental changes in urban area to about 40%, or 80% agriculture, above which there is little additional degradation in fish and benthos assemblages and instream temperatures.

The correlation between surficial geology (BFI), land use/land cover, and catchment size, as well as potential autocorrelation in our data set, should be considered when interpreting the PIC effect. The correlation (r) between BFI and PIC was about 0.55. Urban development tends to occur near Lake Ontario on clay till plains, while forested areas tend to occur in the smaller upstream tributaries on morainal deposits. Clearly, some of the variation in biological responses, temperatures, width:depth, and percent stable banks that are related to PIC are also related and thus confounded with geology. There are three factors that provide comfort that the PIC effect is real. First, while many of our sites are close together, the geographic coverage of our study area is extensive, and it is unlikely that neighboring site correlations affect our conclusions. Second, our various analyses were designed to determine how much of the residual variation in biophysical responses was related to PIC, after we accounted for the effects of the other landscape variables. That the observed patterns were consistent and that we had a large sample size of sites from catchments with high PIC provide confidence in our conclusions. Finally, many other studies have come to similar conclusions about PIC. None of the studies that we reviewed examined covariation of base flow (surficial geology) and PIC, but it is difficult to believe that all studies would be confounded, particularly

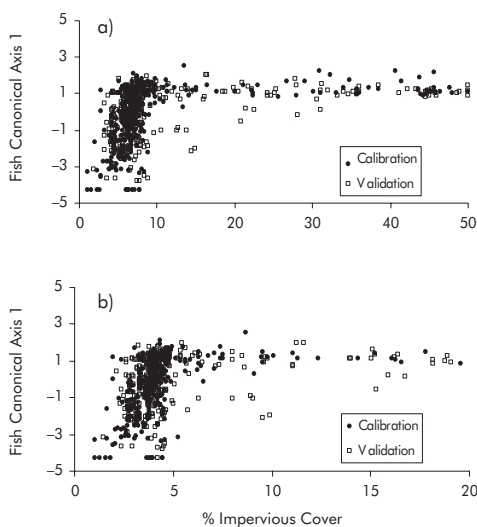


Figure 8. Relationship between fish CA axis 1 scores and two alternate scenarios for estimating imperviousness. In (a), urban lands are rated at 0.5 PIC (versus 0.2), while in (b), intensive agriculture is rated at 0.05 PIC (versus 0.1). Remaining ratings for land use/land class were unchanged from previous analysis.

those studies conducted in places like Delaware that have not experienced glaciations. Regardless, our understanding of the PIC effect in southern Ontario would benefit from additional data from sites on morainal deposits, with higher levels of PIC.

Use of Models for Hindcasting

Our models illustrate the magnitude and nature of relationships between biophysical responses and landscape features (natural and anthropogenic), and they can be used for two contrasting but interrelated purposes: hindcasting expected reference conditions and predicting future conditions assuming development scenarios. The ability to hindcast allows one to predict the biophysical makeup of a stream in the absence of development. The reference-condition approach (Hughes 1994; Bailey et al. 1998), in which regional reference sites are used to characterize acceptable biological conditions, requires least or minimally disturbed reference sites. In southern Ontario, there are no unaltered catchments. Defining reference condition, therefore, is biased toward disturbance and the definition might have to change with catchment size because there are no large catchments lacking development. Our models, however, have taken catchment size and other variables into consideration. They can therefore be used to estimate what conditions might have been in the absence of development. Current and future conditions can then be compared to the predicted historical condition, to estimate the magnitude and nature of change in condition. One limitation to the models is that they should not be used to hindcast to conditions that did not exist as part of the calibration data set. Thus, the hindcast reference condition for large catchments might not be 100% forest cover. Kilgour and Stanfield (2006, this volume) are using this approach to compare current conditions with hindcast historical conditions in the Lake Ontario study area as a means of characterizing the state of the ecosystem.

Other Considerations

We developed models for a few fish, benthos, and instream habitat metrics, which likely differ from those others might have chosen. The methods we selected provide both an overview of basic features of assemblages (i.e., biomass for fish and number of taxa for fish and benthos), as well as axis scores from correspondence analysis. As a result, we are confident that the models produced here are robust and that it would be unlikely that a different conclusion would be reached with a different set of variables. Given that the results obtained for fish and benthos in southern Ontario are similar to results obtained for other parts of North America, we are confident that the patterns identified in this data set are robust.

Finally, this study employed fairly coarse measures of land use/land cover and no analysis of proximity effects (i.e., the degree to which features closer to a site influenced its condition). Future efforts will be directed at refining the relationships shown here, using finer measures of land use/land cover and proximity effects and to identifying those additional variables that contribute to explained variability in fish assemblages. In addition, we intend to explore the degree to which riparian best management practices and instream habitat complexity buffer the effects of PIC.

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Using a Landscape Approach to Identify the Distribution and Density Patterns of Salmonids in Lake Ontario Tributaries

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Abstract.—Effective management of salmonid populations in the Great Lakes basin requires understanding how their distribution and density vary spatially. We used a hierarchical approach to evaluate the predictive capabilities of landscape conditions, local habitat features, and potential effects from coinhabiting salmonids on the distribution and densities of rainbow trout *Oncorhynchus mykiss*, brook trout *Salvelinus fontinalis*, brown trout *Salmo trutta*, and coho salmon *O. kisutch* within the majority of the Canadian tributaries of Lake Ontario. We collected fish assemblage, instream habitat, and water temperature data from 416 wadeable stream sites. Landscape characteristics were obtained for each site's catchment and summarized into six key attributes (drainage area, base flow index, percent impervious cover (PIC), reach slope, elevation, and location with respect to permanent fish barriers). Classification trees indicated that PIC in a catchment was a critical predictor of salmonid distribution, in that beyond a threshold of 6.6–9 PIC, all salmonids were predicted to be absent. Base flow index and barriers were also important predictors of the distribution of salmonids. Models generally provided higher classification success at predicting absence (86–98%) than predicting presence (63–87%). Landscape features were the best predictors of densities of rainbow and brook trout (adjusted $r^2 = 0.49$ and 0.30 respectively), although the local habitat features were almost as effective for predicting brook trout ($r^2 = 0.23$). Local habitat features (proportion of riffles and pools, substrate, cover, and stream temperature), and presence of other salmonids produced the best predictive model for brown trout. Coho salmon was only locally distributed in the basin, and the derived model was driven by spatial characteristics rather than ecological processes. Our models estimate 653,000 juvenile rainbow trout and 231,000 brook trout (all age-classes) in our study streams. Finally, we estimate that current brook trout distribution in our study area is only 21% of its historic range.

INTRODUCTION

Traditionally, efforts to relate fish densities to habitat involved measures of local habitat features that were intended to capture both local morphology and the influence of larger scale fea-

tures and biotic interactions (Binns and Eiserman 1979; Bowlby and Roff 1986; Stoneman and Jones 2000). A hierarchical perspective of stream systems, whereby properties at the site level are constrained by processes occurring in the catchment, provides a useful analytical framework (Vannote et al. 1980; Frissell et al. 1986; Tonn 1990; Imhof et al. 1996). For

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example, substrate composition, water temperature, and some aspects of channel structure have been shown to vary predictably with topography, geology, and land use (Rabeni 1992; Sowa and Rabeni 1995; Richards et al. 1996; Regetz 2003). As a result, the landscape scale has been suggested as the appropriate scale for managing Great Lakes fisheries (Lewis et al. 1996). We believe that landscape conditions constrain the fish assemblage and range of densities expected at a site, while instream habitat and biotic interactions influence the realized species and densities. Recent advances in geographic information systems (GIS) have led to a rapid increase in our capabilities to quantify the importance of various landscape features in influencing aquatic assemblages (Wiley et al. 1997). A number of studies have shown the importance of landscape features in affecting assemblage composition and species distribution, in portions of the Great Lakes basin (Steedman 1988; Richards et al. 1996; Wang et al. 1997, 2000, 2001; Zorn et al. 2002). More recently, studies have included a number of composite metrics intended to quantify the overall disturbance from land use on the landscape. For example, Thompson and Lee (2000) used road density, Van Sickle et al. (2004) used total urban and agricultural land use/land cover within the riparian zone, and Stanfield and Kilgour (2006, this volume) among others used percent impervious cover (PIC).

In addition, instream habitat and biotic interactions structure fish assemblages (Bowlby and Roff 1986; Stoneman and Jones 2000; Stanfield and Jones 2003). Mullett et al. (2003) demonstrated that using a combination of landscape features (i.e., drainage area and geographic location) and biotic conditions provided a good predictor of sea lamprey *Petromyzon marinus* abundances across the Great Lakes basin. Therefore, analyzing both landscape and site level features provides a more holistic approach to assessing salmonid populations. Some studies have partitioned variation across scales (e.g., Wang et al. 2001); however, few, if any, have attempted to partition the variance associated with

landscape and local features related to Great Lakes fish populations. This information may help guide managers in taking actions needed to improve fish production.

We sought to first determine the relationships between landscape variables and the distribution and density of stream resident salmonids (i.e., rainbow trout *Oncorhynchus mykiss*, brook trout *Salvelinus fontinalis*, brown trout *Salmo trutta*, and coho salmon *O. kisutch*). We then explored how much additional variation was explained by incorporating site level features into the landscape-density model. We combined the distribution and density models to identify the spatial distribution of salmonid populations. Finally, we used the outputs of landscape models to develop population estimates of salmonids in the study area and discuss management implications of these findings.

METHODS

Study Area

The Oak Ridges Moraine and the Niagara Escarpment provide source waters to the majority of the coldwater streams draining into the Canadian portion of Lake Ontario (Figure 1). These two physiographic features provide an abundance of groundwater discharge, ensuring that headwater segments are cold and that water temperatures gradually increase towards the mouth. The basin's landscape is dominated by agriculture in the east (e.g., row crop) and southwest (orchards), with an extensive band of urban area (GTA) in the west and central portion of the study area. Most forested areas are located on top of the moraine and escarpment. The tributaries draining the moraine consistently have coarse sands and gravels in the headwaters, while those draining the escarpment have fractured sedimentary rock with a shallow overburden of finer materials. Lower segments of all tributaries pass through finer grained glacio-lacustrine material (Chapman and Putnam 1984). This area is managed for six salmonid species: native brook trout

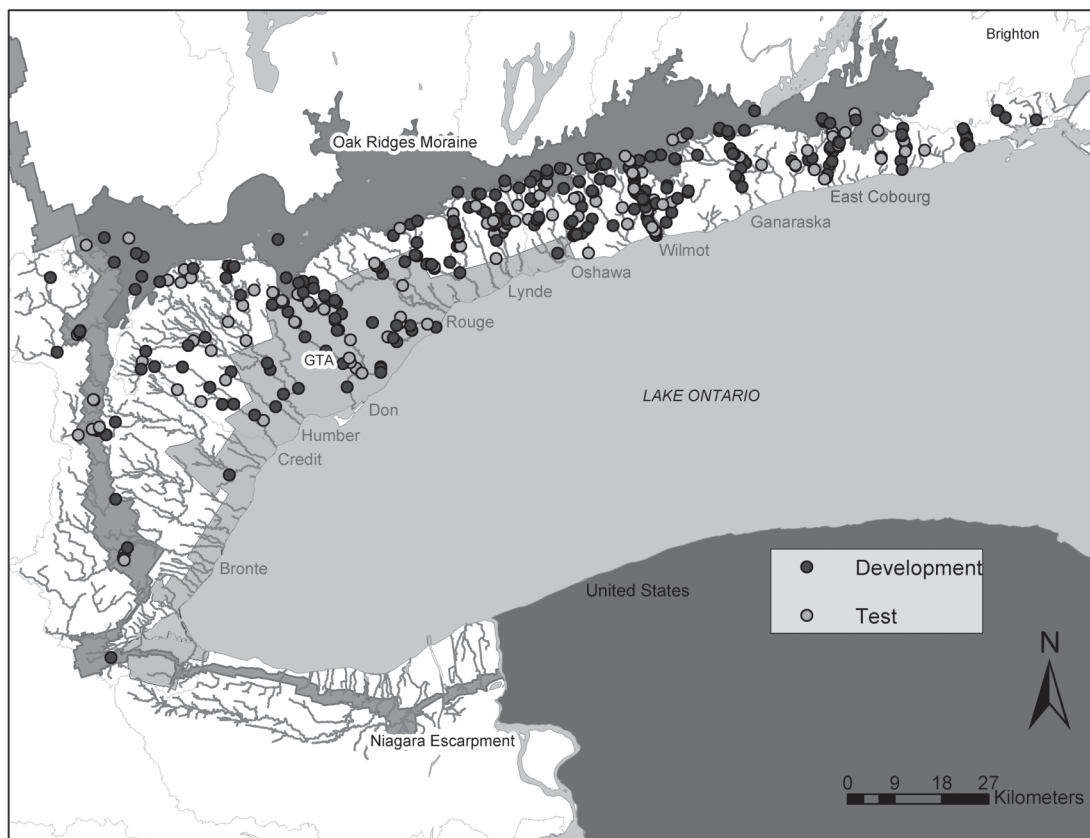


Figure 1. Major landform features and location of development and test sites used for development of the salmonid distribution models in this study.

and Atlantic salmon *Salmo salar* and naturalized nonnative rainbow trout, Chinook salmon *O. tshawytscha*, coho salmon, and brown trout.

Field data were collected by a variety of agencies and guidance on study design and site selection were provided by Stanfield et al. (1997). Each agency defined its own study area based on project objectives and whether stratification was necessary. Study areas were generally a subcatchment or landscape (i.e., the Oak Ridge Moraine study area), and most studies were stratified by stream size. Sampling intensity within each stratum was designed to meet the desired precision of each study. Sites were then randomly selected within each stratum. Sites began and ended at a cross-over (i.e., where the thalweg is in the middle of the channel) and were at least 40 m long.

Fish Assemblage Data

Fishes were collected at 416 sites on 61 streams along the north shore of Lake Ontario (Figure 2). Sites were sampled between 1995 and 2002, with methods described in Stanfield et al. (1997). Only sites where effort exceeded five electrofishing seconds per square meter and sampling date was after June 21 (the earliest capture of a young-of-year rainbow trout in the region) were used in this analysis. Fish assemblage data were collected using single-pass electrofishing, which provides acceptable estimates of salmonid abundance in Lake Ontario streams (Jones and Stockwell 1995). Salmonids were identified, enumerated, weighed, and then released.

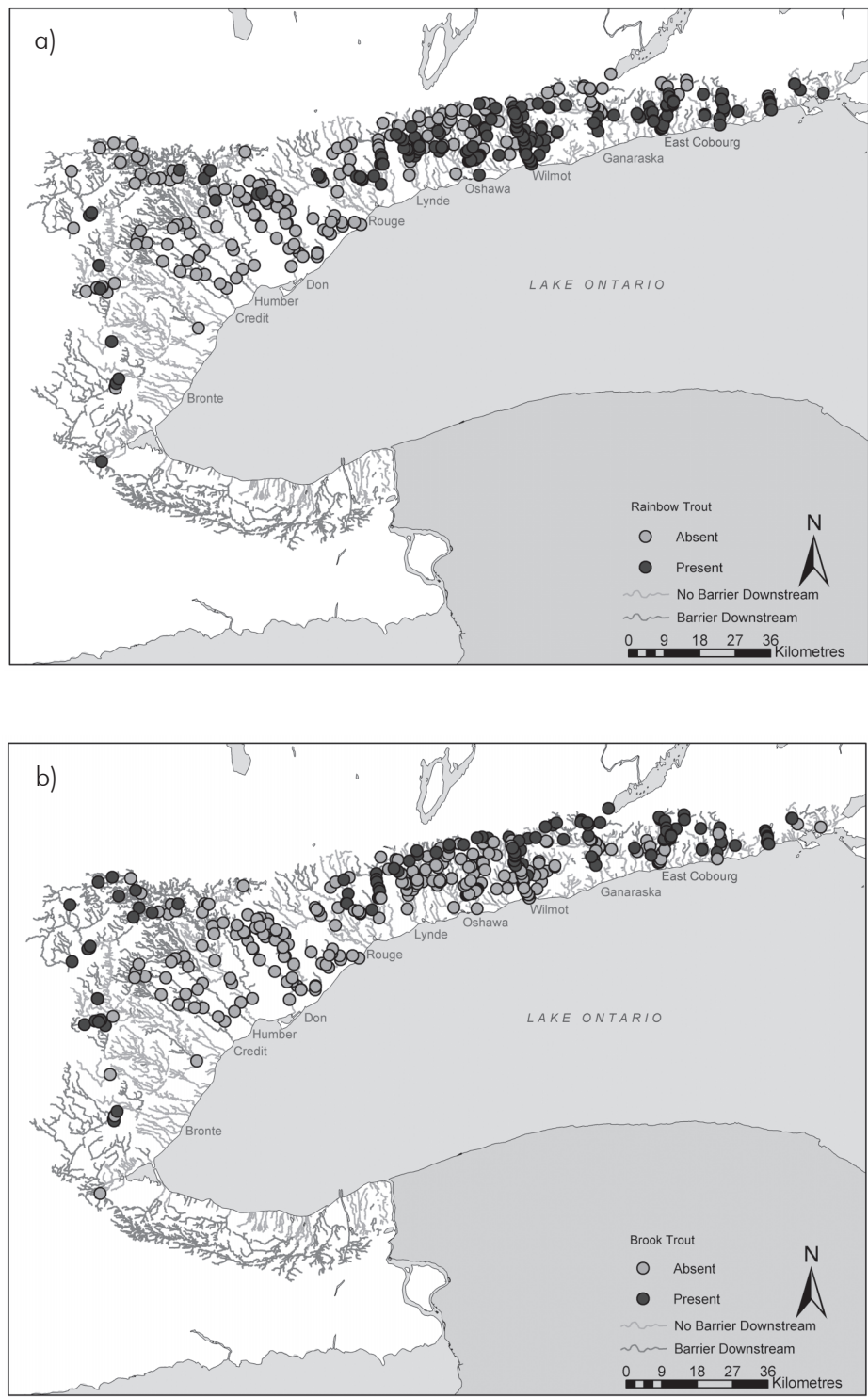


Figure 2. Distribution of rainbow trout (a), brook trout (b), brown trout (c) and coho salmon (d) at study sites where streams have been classified as being accessible (no barrier downstream) or inaccessible (barrier downstream) to rainbow trout from Lake Ontario.

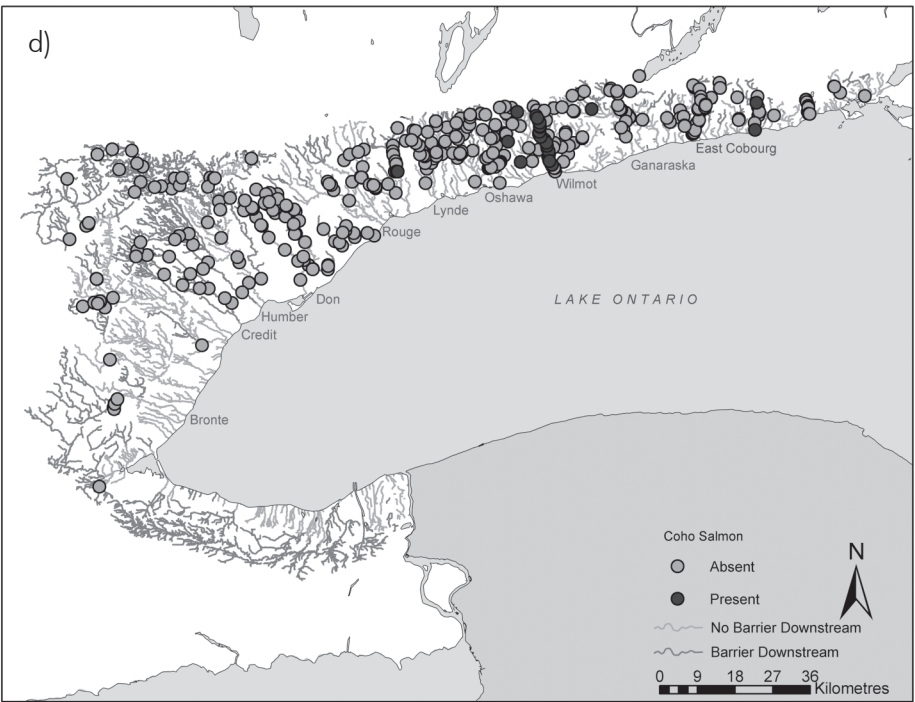
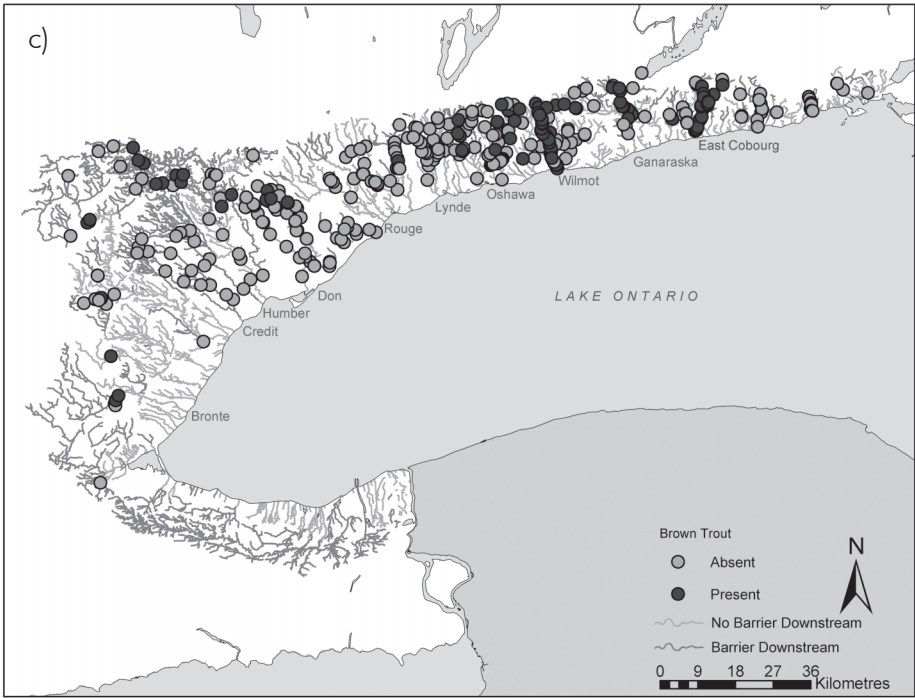


Figure 2 (continued)

Landscape Data

For each site, we delineated catchment boundaries using a flow accumulation model based on a 1:10,000 digital elevation model (DEM) with 25-m resolution. We used GIS to attribute each site's catchment area, stream length, land use/land cover, quaternary geology, elevation, and stream slope. Additionally we developed a GIS layer locating the first impassable barrier to salmonids upstream from the lake for all streams in the basin. Each site was classified as to whether it was accessible to rainbow trout or coho salmon. To capture the full contrast in land use/land cover and quaternary geology, data were converted to composite measures of PIC and a base flow index (BFI). PIC was calculated by summing the ranked percent of each catchment occupied by each land use/land cover, following the rankings of Stanfield and Kilgour (2006), (i.e., forest [0.01], pasture [0.05], agriculture [0.1], urban [0.2]). Therefore, PIC varied between 1 (completely forested) and 20 (100% urban). Following the methods of Piggott et al. (2002), we calculated BFI by summing the ranked proportion of each catchment covered by quaternary geology types (Ontario Geological Survey 1997), where the ranking reflected a measure of its contribution to base flow. Rankings for our study area varied from 12 for silt-clay till to 77 for gravel-sand outwash material. These variables or their correlates related to the main landscape factors limiting fish distributions and assemblages in northern temperate streams (Wang et al. 2001; Zorn et al. 2002; Stanfield and Kilgour 2006). Drainage area was log transformed to approximate normalized data. The six variables were all weakly correlated ($r < 0.46$) with one another and variance inflation factors for each were relatively low (1.2–1.6), (Neter et al. 1996; Graham 2003) indicating low multicollinearity among variables.

To aid in landscape modeling, streams were divided into segments based on changes in hydrography (i.e., confluence of tributaries with stream order less than three, or boundaries with

lakes and wetlands), access to Lake Ontario (i.e., barriers), and hydraulic conductivity (soil porosity), using an Arc GIS application. Landscape attributes, comparable to those collected for each site, were obtained for each segment's catchment. Stream segments of Strahler order less than three were combined.

Site-Level Data

Physical habitat features and stream temperature were collected at 243 of the 416 sites with fish data. Variables included water temperature, substrate size, microhabitat type, riparian woodland width, percent rock cover, and percent wood cover (Table 1). Water temperature was standardized by determining the predicted temperature at an air temperature of 30°C for each site. Observed air and stream temperature for each site were used to select the most appropriate thermal class and algorithm as described by Stoneman and Jones (1996). The deviation from predicted temperature was added to the predicted temperature at 30°C to obtain the standardized temperature.

Microhabitat, cover, and substrate data were collected using a point transect sampling design (Stanfield and Jones 1998). Transects were equally spaced and oriented at right angles to current with typically six equally spaced points on each transect. Number of points per transect were reduced and number of transects increased on smaller streams to provide from 40 to 60 point observations per site. Depth and velocity data were used to classify the proportion of a site occupied by four velocity categories representing pools, glides, and slow and fast riffles. These data were summarized as a continuous variable corresponding to a gradient from pools to fast riffles, as determined by site scores along the first axis of a correspondence analysis (CA). This axis represented 71.7% of the variation in the microhabitat data. Rock and wood cover were measured as the proportion of observations, which contained a cover type with a median axis greater than 10 cm falling within a 15-cm radius of the observation point.

Table 1. Instream habitat and competition variables used in the density models.

Variable	Definition
Water temperature	Taken at 1545 and 1645 hours during a heat wave and standardized to 30°C air temperature using algorithms for reference cold-, cool-, and warmwater stream types. Log transformed.
Riparian	Summation of width of natural vegetation from both banks at four categories bounded by 1, 10, 30, and 100 m determined from a point transect survey.
Microhabitat	Summary statistic of the first CA axis based on percent of each of 4 microhabitat types (i.e., <3, 4–7, 8–17, >17 mm hydraulic head) where hydraulic head represents the height of water on a ruler held in the water at each point on transects.
Rock & Wood	Percentage of point observations where substrate particles or pieces of wood with median axis greater than 10 cm occur within 15 cm of the observation point.
D50max	Fiftieth percentile size of the distribution of maximum particles sampled from within a 30-cm ring. Sampling followed a point transect survey. Log transformed.
Number of salmonid species	Number of salmonid taxa at site.
Density of other salmonids	Density of salmonid taxa other than the target species for the analysis.

Substrate was determined from measured particles at each observation point. The two biotic variables used in our analyses were the total number of salmonid species at a site and the total density of salmonids other than the target species at a site (\log_{10} transformed). These were included because other studies in the region have shown effects from competition among the different species of juvenile salmonids (Stoneman and Jones 2000; Stanfield and Jones 2003).

Distribution Analyses

Catches of rainbow trout, brown trout, brook trout, and coho salmon were converted to presence/absence (distributional) data. In cases where sites had been sampled on multiple visits (in different years or seasons), the median value of the distributional data were rounded to the nearest integer (0 or 1). Species presence–absence models were created using classification and regression trees (CART) (Breiman et al. 1984), as it provided a reliable methodology for predicting the distribution of each species on the landscape. Classification trees assume no specific statistical distribution, do not assume linear relationships between predictor and response vari-

ables, can accommodate large complex datasets, incorporate a variety of response types, and are not influenced by severe outliers (De’ath and Fabricius 2000; Vayssieres et al. 2000). As such, CART models have become prevalent in the ecological literature, particularly for predicting species distributions on the landscape (Magnuson et al. 1998; Emmons et al. 1999; Rathert et al. 1999; Rejwan et al. 1999; Stoneman and Jones 2000; Stanfield and Jones 2003; Herlihy et al. 2006, this volume).

To evaluate model performance we split the data sets of each species into two groups, randomly assigning two-thirds of the sites for model development and one-third for testing. Data sets were first stratified based upon quaternary watersheds, such that there were equal proportions of sites with and without a species for each subwatershed, similar to Manel et al.(1999). Models were evaluated for the overall correct classification rate, model “sensitivity” (correct classification of presences), and model “specificity” (correct classification of absences) (Fielding and Bell 1997). In addition, Cohen’s Kappa statistic *K* (Titus et al. 1984) was used to estimate how well the model performed compared to the expectations based simply on chance.

Density Analysis

Catches of rainbow trout, brown trout, brook trout, and coho salmon were converted to densities (# fish/100 m²) and then $\log_{10} + 1$ transformed. In cases where sites had been sampled on multiple visits (in different years or seasons), the median density was used. General linear models (GLM) (StatSoft, Inc. 1995) were used to develop relationships between landscape attributes and densities of the four species. This technique ensured that predictions for segments would be continuous, rather than categorical, and would therefore provide better contrast in suitability criteria between segments. To evaluate how much additional variance was explained by site-level habitat features and the presence of other salmonid species, we reanalyzed the landscape models on the sites that had landscape features, instream habitat, and biotic features. The residuals from this analysis represented any variation that could not be explained by the six landscape attributes. Thus, we used the residuals as the response variable and regressed these data against two sets of site variables: (1) six physical habitat metrics, and (2) two biotic metrics, representing effects from cooccurring salmonids at a site. The resulting adjusted r^2 values provide a measure of the amount of independent variation that these variables explain. We then took the residuals from each of these analyses and regressed these against the opposite set of predictors (i.e., the residuals from the physical habitat were regressed against the two biotic variables and vice versa) to evaluate how much of the variance was explained by these variables alone. It was hypothesized that by the time the second set of residuals were used, there would be very little remaining variation to explain.

Application of Models

We used models to predict the spatial distribution and densities of salmonids in sampled and unsampled segments across the basin. Predictions were confined to segments with drainage

areas less than 328 km². This ensured that predictions were made only on segments where landscape attributes were within the same range as those from which the models were developed.

We used model results for species whose densities were predicted by landscape features, to develop coarse population estimates for our study area. We applied the CART models to determine which sites were predicted to have each species absent. The density models were applied to each remaining segment to derive a predicted log density. Results were used to classify each segment into four additional categories based on the quartiles of the predicted log densities (i.e., low, medium, high, and very high). Estimated stream width was determined for each segment using the model developed by Stanfield and Kilgour (2006), and each segment was then assigned a width category based on the quartiles of the distributions. Observed mean density and width were calculated for all five categories for which field data were available and were applied to each segment to determine population estimates (e.g., segment population = observed mean category width*observed mean category density*segment length).

RESULTS

The 416 sites with fisheries data collectively covered most of the main salmonid waters on the Canadian side of Lake Ontario (Figure 1). Where salmonids occurred their densities varied considerably, regardless of whether they were isolated or in the presence of other salmonid species (Table 2). Brook trout tended to be more abundant in the absence of other salmonids although the four highest density sites were at locations where either brown trout (10 g/100 m²) or rainbow trout (11–43 g/100 m²) were also present, but not both. Brown trout and rainbow trout tended to be more abundant in the presence of other salmonids; however, interpretation of these results was confounded, as a much greater proportion of the sites had multiple species, compared with only a few having one species of

Table 2. Densities (#/100 m²) of four salmonid species when occurring by themselves and when cooccurring with other salmonid species.

	No other salmonids at site				Other salmonids at site			
	N	Min	Max	Median	N	Min	Max	Median
Rainbow trout	61	0.2	86.4	12.8	143	0.1	142.3	14.6
Brown trout	10	0.2	34.9	0.8	117	0.1	23.7	3.5
Brook trout	30	0.2	32.9	7.8	95	0.1	71.0	2.5
Coho salmon	0	–	–	–	34	0.1	16.1	1.2

salmonid present. Coho salmon densities were always low in our study area.

Rainbow trout was present at 49% of the sites and was widely distributed across the study area (Figure 2). Brook and brown trout were less common (30% of sites) and were generally captured in headwater areas. Coho salmon was caught at only 8% of sites and was restricted to Wilmot Creek and neighboring streams. All four salmonids were absent from 32% of the sites, most of which were located in the GTA.

Our data set included a wide range of catchment size, geology (BFI), slope, and land-use/land-cover conditions (Table 3). PIC ranged from 20 (100% urbanized catchments) to 1 (fully forested catchments), and 37% of sites had bar-

riers downstream, thus limiting access by migratory salmonids. While some confounding of the data exists (i.e., most forested catchments were in higher slope and higher porosity areas), there was sufficient contrast (Table 3) to test our hypotheses. There was also considerable contrast in instream habitat features in our data set (Table 3), such as proportions of pool versus riffle habitat (i.e., positive versus negative CA scores), substrate size, amount of both wood and rock cover, and water temperature.

Distribution Models

The presence-absence models for the four species produced more than 80% correct classification rates for the test data sets (Table 4), and the rainbow trout model had the highest presence ratings (87%). The brook and brown trout models were more effective at predicting absence of these taxa (87% and 91%, respectively) than presence (68% and 63%). All four models had K-values greater than 0.55 (Table 4), indicating that model performance was moderately to substantially greater than that expected by chance (Landis and Koch 1977). Although the coho salmon model displayed the highest overall classification and absence, the unequal proportions of presence and absence sites may produce spurious results (Forbes 1995) and should be interpreted with caution.

The presence of barriers downstream and PIC were the two most influential variables in the species distribution models (Figure 3). Base flow index (BFI) was also highly influential as it was included in all but the rainbow trout model and,

Table 3. Minimum, maximum and median values of the six landscape features characterizing the upstream catchments and the six instream habitat variables used in this study (*n* = 416 sites). Median density of other species is not presented as it varied among the four species. Na = not applicable.

	Min	Max	Median
<i>Landscape attributes</i>			
Drainage area (km ²)	0.1	328	22
Percent impervious cover (PIC)	1.1	20	7
Reach slope (%)	0	10	1
Elevation (masl)	75	403	156
Base flow index (BFI)	14	77	46
Dams downstream (binary)	0	1	0
<i>Instream habitat</i>			
d50max (mm)	0.01	340.0	80.0
Wood (%)	0	35	2
Rock (%)	0	100	38
Forested riparian width (m)	0	200	60
Microhabitat (CA1)	-1.24	0.85	-0.091
Water temperature (°C)	10.3	36.3	20.9

Table 4. Measures of classification success based on the classification tree models for each species. Classification success based on independent data set and expressed as a percentage of the total. Cohen’s Kappa expressed as a percent.

	Coho salmon	Rainbow trout	Brown trout	Brook trout
Number of sites with species	34	204	127	125
Overall correct classification rate	97.1	86.2	82.4	81.6
Specificity (correct absences)	98.4	85.9	90.6	87.4
Sensitivity (correct presences)	82.0	87.0	63.0	68.0
Cohen’s Kappa (K)	87.9	73.2	55.0	55.5

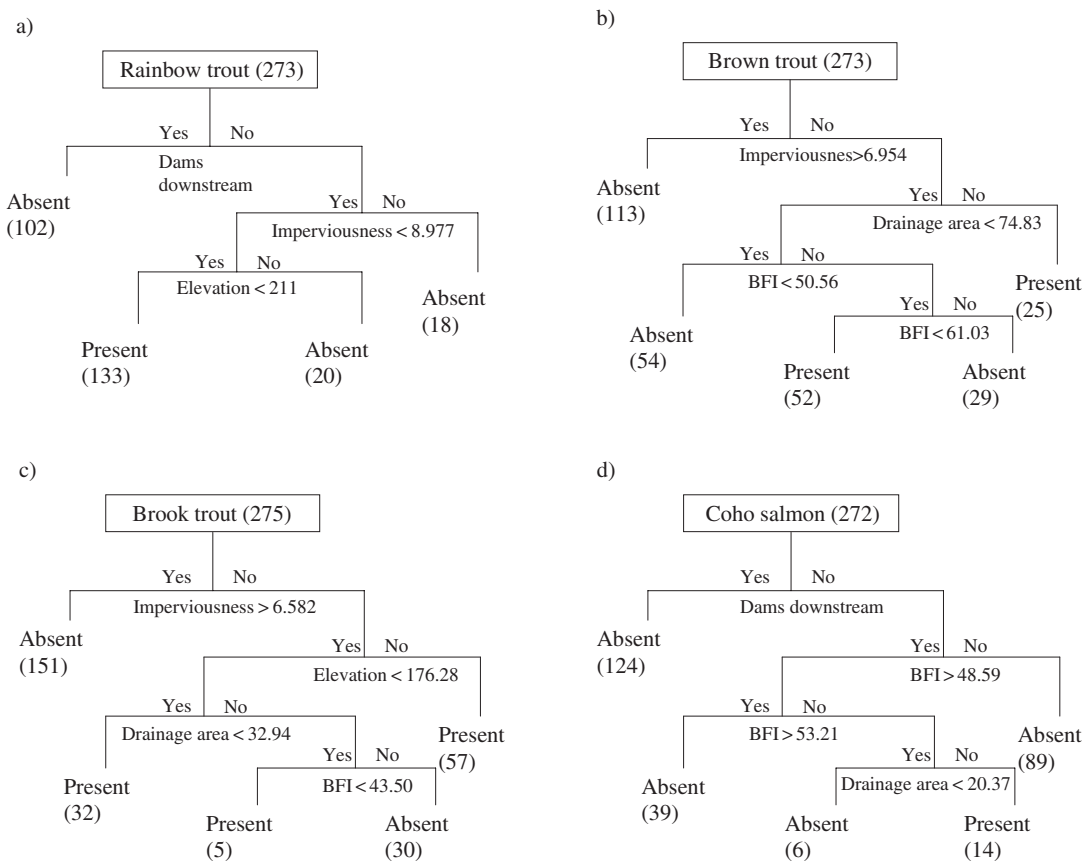


Figure 3. Classification trees for rainbow trout (a), brown trout (b), brook trout (c) and coho salmon (d). Numbers at the ends of each branch are the number of sites with the predicted response based on landscape conditions. Criteria for each split are given at each node.

in some cases (i.e., brown trout and coho salmon), was used as the split criteria twice in the model. Rainbow trout was predicted to be present at sites with no barriers downstream, in catchments with PIC less than 9, and in the lower

segments of streams (i.e., lower elevations). Brown trout were predicted in catchments with PIC less than 7 and moderate catchment size (i.e., <74.8 km²), or in smaller well-drained catchments. Brook trout was predicted in smaller

catchments, provided PIC did not exceed 6.6. Not surprisingly, coho salmon was predicted for a very restricted group of streams lacking barriers, BFI values between 49 and 53, and drainage area greater than 20 km².

Density Models

Correlation between the landscape predictors and densities of rainbow trout provided the strongest model ($r^2 = 0.491$; Table 5), with dams, PIC, and elevation having the greatest influence on the model (Table 6). The biotic variables alone were found to explain 35.8% of the variation in rainbow trout density (Table 5) and an additional 12.9% of the residual variation left over from the landscape models. Whether modeled individually (adjusted $r^2 = 0.156$) or in conjunction with landscape features, the instream habitat features did not relate well to rainbow trout density, explaining only an additional 2.8% of the residual variance.

Landscape models were able to explain 30% of the variation in brook trout densities (Table 5). PIC and the size of the drainage area were the dominant variables in the model (Table 6). Instream habitat variables explained a smaller amount of the variance in brook trout density (adjusted $r^2 = 0.23$), and water temperature was the most influential variable in this model. Biotic models were very poor predictors of brook trout density (adjusted $r^2 = 0.074$). However, there was similar explanatory power of brook trout density between the landscape model (adjusted $r^2 = 0.37$) and the combination of site features and cooccurring salmonids model

(adjusted $r^2 = 0.38$). All residual analyses on the brook trout models produced adjusted r^2 of less than 0.04, indicating that the addition of either cooccurring salmonids or site habitat features to landscape models did not substantially increase their predictive performance.

The landscape features were poor predictors of brown trout density (adjusted $r^2 = 0.115$) and BFI and PIC were the only variables contained in the model (Table 6). The instream habitat models explained more variance (adjusted $r^2 = 0.219$), however, the biotic models were found to be the best predictors (adjusted $r^2 = 0.413$). Instream habitat could increase landscape models by 11.9%, while biotic variables were shown to improve the landscape model predictive performance by 35.5%. Thus, landscape models may not be the best approach to predict brown trout densities in Lake Ontario tributaries.

Coho salmon models were quite poor when using landscape (adjusted $r^2 = 0.062$), instream habitat (adjusted $r^2 = 0.126$), and biotic (adjusted $r^2 = 0.192$) variables. Residual models were able to explain an additional 11.0–18.7% of the variation but were not enough to justify inclusion in a combined model. Evidently, factors other than the landscape variables included in this study are influencing coho salmon density in the study area.

Application of Models

Landscape models provided good predictive power (adjusted $r^2 > 0.3$) for rainbow trout and brook trout; thus, subsequent analyses focused

Table 5. Results of the density models for the four species. Numbers are adjusted r^2 values. Residuals were used as the response variable and regressed against the specified suite of variables in the last two models. Landscape indicates data derived from GIS. Site represents data collected in the field.

	Coho salmon	Rainbow trout	Brown trout	Brook trout
Landscape only ($n = 416$)	0.06	0.49	0.12	0.30
Landscape reduced ($n = 243$)	0.04	0.48	0.07	0.37
Site-level only (6 variables)	0.13	0.16	0.22	0.23
Cooccurring salmonids only (2 variables)	0.19	0.36	0.41	0.07
Site and Competition (8 variables)	0.26	0.58	0.44	0.38
Landscape residuals on site-level	0.11	0.03	0.12	0.03
Landscape residuals on cooccurring salmonids	0.19	0.13	0.36	0.02

Table 6. Model results for the four species density models based on the six landscape features, the six instream habitat features, and the two biotic features. The *B* coefficients represent the coefficients used in the predictive model, whereas the beta coefficients provide a measure of the relative contribution of each variable to the model. Bolded values are significant at $p < 0.05$.

		Coho beta	Coho <i>B</i>	Rainbow beta	Rainbow <i>B</i>	Brown beta	Brown <i>B</i>	Brook beta	Brook <i>B</i>
<i>Landscape models</i>									
<i>n</i> = 416	Constant		0.0098		1.7531		-0.0508		0.1245
	Percent impervious cover	-0.0731	-0.0026	-0.3570	-0.0585	-0.2036	-0.0185	-0.2579	-0.0263
	Slope	0.0124	0.0015	0.1106	0.0590	0.0173	0.0051	0.1066	0.0354
	Elevation	0.0882	0.0002	-0.2968	-0.0032	0.1005	0.0006	0.1851	0.0012
	Base flow index	0.0393	0.0005	-0.1232	-0.0070	0.1585	0.0050	0.1547	0.0055
	Drainage area ^a	0.0618	0.0159	0.1573	0.1831	0.0813	0.0525	-0.2651	-0.1920
	dams downstream	-0.2651	-0.0753	-0.3472	-0.4579	-0.0708	-0.0518	0.0858	0.0704
	df	6,404		6,404		6,404		6,404	
	adjusted <i>r</i> ²	0.0620		0.4910		0.1150		0.3010	
	<i>p</i> -value	0.0000		<0.00001		<0.00001		<0.00001	
<i>Site habitat features</i>									
<i>n</i> = 243	Constant		0.1251		1.3869		1.2206		2.2199
	Riparian	-0.1176	-0.0002	-0.1667	-0.0016	-0.0329	-0.0002	0.1768	0.0011
	Microhabitat	-0.1219	-0.0191	-0.3195	-0.3345	-0.2807	-0.1581	-0.0153	-0.0109
	Rock	-0.2506	-0.0780	-0.1110	-0.2304	-0.2039	-0.2275	0.0519	0.0731
	Wood	0.2557	0.3325	-0.0899	-0.7801	0.1047	0.4884	0.1364	0.8032
	D50max ^a	0.1619	0.0220	0.1360	0.1233	0.2074	0.1012	-0.0046	-0.0029
	Stream temperature ^a	-0.0893	-0.0878	-0.0983	-0.6447	-0.2464	-0.8694	-0.3659	-1.6290
	df	6,233		6,233		6,233		6,233	
	adjusted <i>r</i> ²	0.1660		0.1560		0.2190		0.2300	
	<i>p</i> -value	<0.00001		<0.00001		<0.00001		<0.00001	
<i>Biotic features</i>									
<i>n</i> = 243	Constant		-0.0149		0.1879		0.0166		0.1884
	Number of salmonid species	0.6544	0.0550	0.9281	0.4613	0.9273	0.2479	0.5388	0.1805
	Density of other salmonids	-0.2950	-0.0498	-0.5841	-0.6847	-0.4708	-0.2530	-0.4626	-0.3046
	df	2,240		2,240		2,240		2,240	
	<i>r</i> ²	0.2200		0.4410		0.4680		0.1240	
	<i>p</i> -value	<0.00001		<0.00001		<0.00001		<0.00001	

^aVariable was log₁₀ transformed.

on these species only. The predicted distributions of rainbow trout and brook trout demonstrate little overlap in species presence (Figure 4). The majority of the sampling has been conducted in stream segments classified as having low to medium densities of rainbow trout and brook trout (Table 7). Rainbow trout were predicted to be absent from a large portion of the study area (~80%), particularly in the western tributaries, where wadeable streams were, for the most part,

predicted to be unoccupied by this species. The central part of the basin contains the highest predicted densities of rainbow trout in the Lake Ontario basin. Analyses also identified several potentially productive segments where sampling has not occurred. Our models suggest that there are approximately 653,000 juvenile rainbow trout in the Ontario portion of the Lake Ontario basin. The majority of rainbow trout (39%) are produced in the eastern tributaries. This estimate

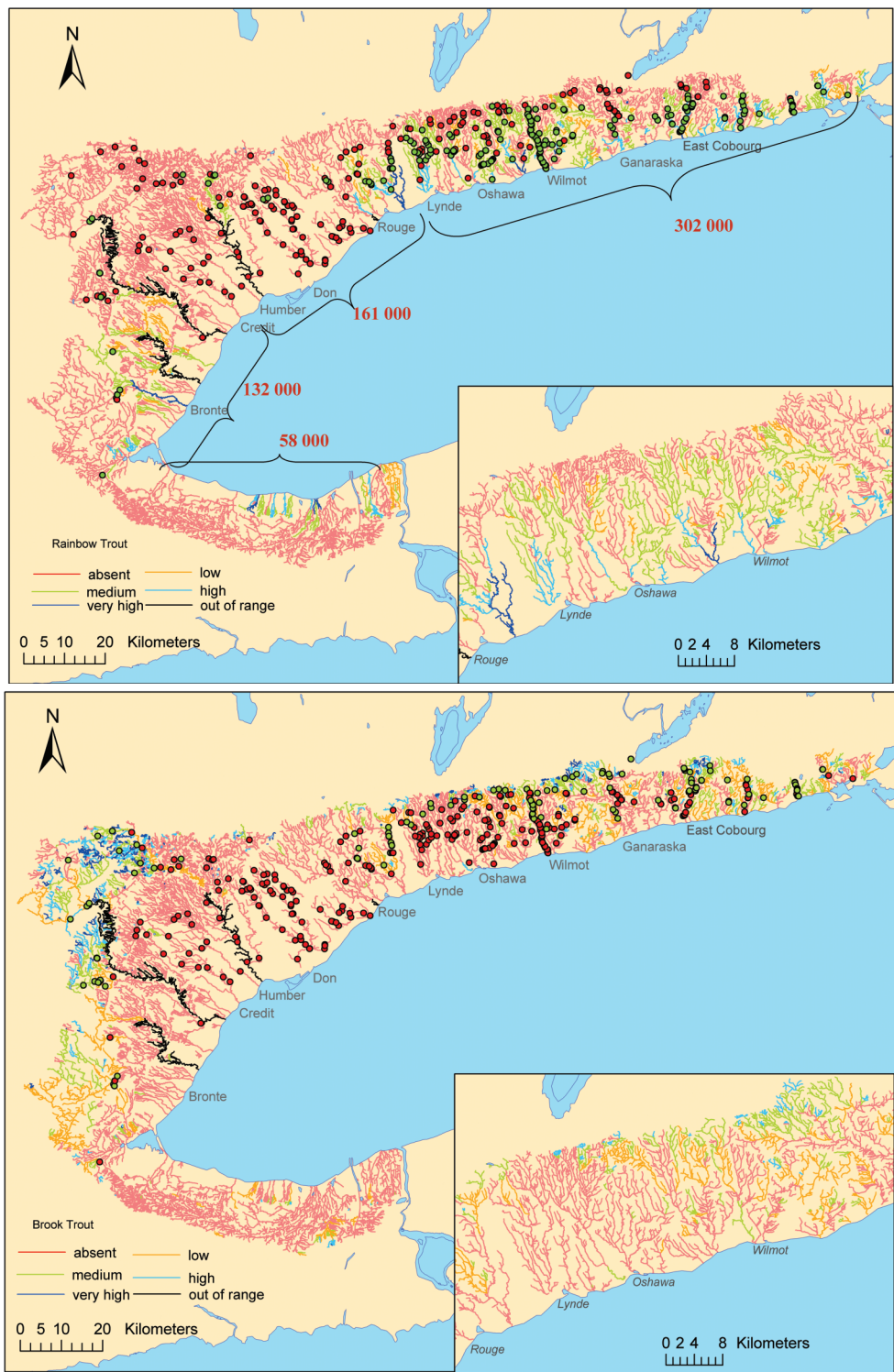


Figure 4. Predicted distribution and densities of rainbow trout and brook trout in stream segments of the Canadian waters of Lake Ontario and study sites classified by the presence or absence of this species. Drainage areas greater than 328.1 km² were outside the model range.

Table 7. Model thresholds for classifying stream segments and observed densities and standard deviations (in brackets) of rainbow trout and brook trout for Canadian tributaries to Lake Ontario.

Density categories	Model thresholds for rainbow trout	Densities of rainbow trout	Number of observations	Model Thresholds for brook trout	Densities of brook trout	Number of observations
Absent	0	0.12 (0.36)	65	0	0.04 (0.36)	66
Low	<4.11	1.97 (7.33)	161	<1.70	1.16 (4.59)	281
Medium	<6.52	13.15 (16.99)	63	<3.50	8.53 (13.22)	53
High	<9.44	20.05 (23.31)	68	<6.26	9.63 (9.89)	13
Very high	>9.44	23.58 (17.30)	59	>6.26	18.86 (16.98)	3

is conservative since it does not include segments from larger catchments (>328 km²) or for any waters in the eastern tip of the basin.

Brook trout are predicted to be present and abundant in the upstream segments of northwest (Bronte, Credit, and Humber rivers) and eastern (Cobourg and Shelter Valley) tributaries, and the overall population in the study area is estimated to be approximately 231,000 individuals (Figure 4).

DISCUSSION

The PIC, access from Lake Ontario, BFI, and drainage area were important predictors of the distribution and density of salmonids in our study area. In addition, salmonid species differed in their response to instream habitat and presence of other salmonids. Instream habitat conditions and densities of other salmonids added little explanatory power to landscape models for rainbow trout and brook trout, but were important for brown trout. The limited distribution of coho salmon in the basin diminished our ability to explore the role of landscape features for it. We have also demonstrated how the model results can be used to predict distribution and density in unsampled segments across the basin. We found that brook trout distribution is currently restricted to smaller catchments and areas with low levels of impervious cover (i.e., high forest cover). Finally, there is considerable natural reproduction of rainbow trout occurring in

streams across the basin. However, disproportionate numbers of these fish are produced from a small number of stream segments. These analyses may guide future fisheries management within and across tributaries of Lake Ontario.

Landscape Relationships

The primary landscape relationships we found were consistent with those of Zorn et al. (2002) and Wang et al. (2003), although the explanatory power and the relative importance of the individual attributes differed. For example, in our study, salmonid distribution and densities were more influenced by land use/land cover than catchment size, BFI, or slope. We found a clear signal indicating that development (PIC) in a catchment is a strong modifier of the salmonid distribution and densities in a catchment. Others have demonstrated that development has a modifying effect on the distribution of salmonids (Steedman 1988; Wang et al. 2003) and Van Sickle et al. (2004) demonstrated that the amount of agriculture in the riparian zone effects cutthroat trout *O. clarkii* densities, but to our knowledge, this is the first paper to demonstrate effects of catchment level development on salmonid densities. Zorn (2003) found that low flow yield was a more important predictor of fish abundances in lower Michigan streams than land use/land cover. Zorn et al. (2004) suggest that reasons for these results are related to their dataset having much larger gradients in river temperature and hydrologic conditions than in

land use/land cover. Few sites in their study area were from highly urbanized catchments.

Our measures of BFI and catchment area are comparable to the components that contributed to the low flow yield used in the Michigan study, further supporting the importance of these variables as predictors of salmonid assemblages. The importance of PIC as a predictor in this study reflects the high range of development in our study area (Wang et al. 2006, this volume). Van Sickle et al. (2004) also demonstrated that land use/land cover in the riparian network affected cutthroat trout only slightly better than catchment land use/land cover. We agree with Van Sickle et al. (2004) that confounding land use/land cover and geology is inevitable with this kind of study and makes interpretation challenging. In our study area, development pressure is greater on lands where soils support farming and urban areas and less on soils that have low productivity, high erodibility, or high water tables, such as those in the Oak Ridges Moraine and the Niagara Escarpment. This inherent bias is difficult to control in a landscape analysis and inevitably results in models having inflated r^2 values. The large sample size in our study and the observation that the patterns were consistent across the landscape give confidence that the data support our conclusions. Additionally, Stanfield and Kilgour (2006) demonstrated that the effect of PIC on the residuals of a variety of instream variables, including fish assemblages, was significant, even after accounting for primary landscape features.

Other studies have confirmed that barriers constrain fish distributions (Joy and De'ath 2001; Moyle et al. 2003); however, few studies within the Great Lakes basin have documented the influence of barriers on salmonid distributions. Our study confirmed that barriers are, for the most part, an effective means of segregating tributary systems into rainbow trout and brook trout waters. Our results suggest that our efforts to identify furthest upstream barriers will underestimate distribution of rainbow trout, likely due to either residual problems with our dam

data or as a result of anglers passing fish. Given our results, more emphasis should be placed on maintaining an accurate record of barriers across the basin. However factors influencing the distribution of these species are complicated. Catchment size, geology, location relative to barriers, and the amount of development in the basin interact to determine which species are likely to occur in a particular stream segment. Many of these factors primarily affect measures of hydrology/groundwater that others have reported as having a primary influence on the distribution or density of salmonids (Seelbach et al. 1997; Zorn et al. 2002; Wang et al. 2003).

We do not suggest that instream habitat conditions are not important to rainbow trout and brook trout. Rather, we suggest that landscape conditions define the range of densities for a species, likely through their influence on the overall hydrologic and geomorphic conditions, while site-level conditions define the actual densities at a site. Provided landscape conditions are suitable for a species, that is are below a minimum threshold, local habitat and biotic conditions determine whether a species will occur at high or low densities.

Constraints on Species Distributions and Densities

We believe that rainbow trout can reside in nearly any Lake Ontario tributary, provided no barriers are present to limit access, and PIC is less than 9. At this threshold, it is possible that the stream hydrology becomes unsuitable for rainbow trout. Our findings differ from those of Stoneman and Jones (2000), in that rainbow trout densities were higher in areas with higher numbers of other salmonids. This suggests that in Lake Ontario tributaries, high quality salmonid habitat is suitable for a variety of species. This may not be the case in other tributaries of the Great Lakes. In our study, instream habitat features were less important than reported by Stoneman and Jones (2000) or Wang et al. (2003). Although instream habitat features are important to these fish, the

landscape attributes and salmonid assemblage are better predictors of rainbow trout densities in the Lake Ontario basin.

It is clear that natural reproduction is contributing a substantial, but not equally distributed, number of rainbow trout to the basin. A disproportionate amount of production is occurring in the eastern portion of the study area. While we acknowledge that our results do not include tributaries east of Brighton or rivers wider than 15 m, we do not believe that production from these waters would greatly increase the overall population estimate for this species. Finally, geospatial analysis identified a number of segments where no data have been collected, but are predicted to contain high densities of rainbow trout and therefore should be considered in future monitoring programs.

Our results were similar to those of Wang et al. (2003) in that brook trout was generally found in sites with smaller catchments and low development. Stream temperature was the dominant variable in the site-level model, which is not surprising given that it is highly influenced by landscape features (Stanfield and Kilgour 2006). Therefore, the similarity in predictive capabilities between the landscape and site level models was expected. Our study confirmed that brook trout densities decreased with increasing densities of other salmonids; however, this variable added very little to the predictive capabilities produced by landscape models alone.

Larson and Moore (1985) observed that brook trout densities and distribution declined in the presence of rainbow trout in the southern Appalachian Mountains and speculated that eventually brook trout would be restricted to headwater areas or areas where rainbow trout lacked access. In most of our study area, brook trout is restricted to headwater areas or stream segments where other salmonids are absent or only one species is present. These observations give credibility to Larson and Moore's (1985) prediction, although the mechanisms are still uncertain. Brook trout distribution and densities were depleted by logging and farming prac-

tices, following European colonization. As such, it is difficult to separate historic effects from recent interactions with Pacific salmonids. Our findings also conform to those of Stoneman and Jones (2000), suggesting the overall importance of both stream temperature and the presence of cooccurring salmonids in providing suitable conditions for brook trout. However, our findings also suggest that rainbow trout now occupies many habitats in Lake Ontario tributaries that may be suitable for brook trout, and in the majority of the cases, brook trout is now absent. At this point, it is unknown if this is the result of competitive interactions or historic alterations to the landscapes.

We provide the first comprehensive assessment of the current distribution of brook trout in the study area, and the results are not encouraging. Ricker (1932) and Dymond (1965) suggested that brook trout was historically common in the study area and was found in all tributaries with cool clean water, including the main stem of streams where migratory salmonids currently reside. In estimating the preEuropean range of brook trout, we assumed that its range would include segments suitable for rainbow trout if forest cover was 100% and there were no barriers in the system. Our analysis indicated that historically, every segment in our data set would have been suitable for brook trout. With this assumption, the current distribution represents only 21% of its historic range. This reduction in distribution is an underestimate, given that our analyses assumed brook trout was absent in nonwadeable streams, despite its occasional capture in these waters recently.

We found that brown trout was only slightly less sensitive to the effects of PIC than brook trout. Below 6.9 PIC, its current distribution reflects historic stocking upstream of barriers and areas where streams could be populated by spawning fish from Lake Ontario. Our density models confirmed that instream habitat features and the densities and number of cooccurring salmonids are the best predictors for brown trout, corroborating the findings of Mortensen (1977)

and Stoneman and Jones (2000). We found that many of the features important to brown trout (i.e., abundant wood, deep pools, finer substrates, low amounts of rock cover, and cold/cool water) are not well correlated with landscape features. It is also likely that some of these features covary with biotic factors (i.e., number and densities of cooccurring salmonids). For example, rainbow trout tends to be more common in areas with abundant rock cover (Stanfield and Jones 2003).

Populations of coho salmon in the study area were low and were restricted to Wilmot Creek and its surrounding catchments. Coho salmon migrates great distances in the fall and winter in search of deep pools with wood and backwater habitats to overwinter (Bustard and Narver 1975). Wilmot Creek generally contains more wood than most other tributaries in the study area, has long stretches without barriers, and also has several backwater habitats/side channels that are used by this species (L. Stanfield, personal observation). These features are not easily captured with existing GIS information. Additional work is required to better understand the conditions influencing the distribution and abundance of this species in Lake Ontario.

Management Implications

Generally, our distributional models illustrate that brook trout and rainbow trout distributions do not overlap. Barriers, PIC, and coinhabiting salmonids play an important role in this segregation, however, the reasons for this segregation are still unclear. Migratory salmonids were present in the lower segments of streams, where productivity would generally be higher and impacts from historic land uses would be greater. Therefore, this confounding effect may have masked any negative effect of rainbow trout on brook trout. Clarifying the degree to which competition from other salmonids influence the distribution and densities of brook trout should precede stocking into waters where brook trout currently reside.

Both brook and rainbow trout were sensitive to fairly low PIC, with populations absent at greater than 6.6 and 8.9, respectively. These PIC values translate to approximately 33% urban or 65% agriculture. The thresholds identified here provide a lower PIC threshold than that described by Stanfield and Kilgour (2006) for a general fish assemblage index. It is clear that many tributaries in the greater Toronto area have lost the potential to produce salmonids because of excessive development in their catchments. This may in part explain why brook trout were only found in headwater segments, since in much of the study area, these are the only areas where PIC are below this threshold. The combination of the threshold response and the decline in densities that occur below the threshold for brook trout and rainbow trout provide a powerful management tool that can be used to set targets and predict changes associated with proposed development of a watershed.

Fisheries management in Canadian tributaries of Lake Ontario is complicated by the migratory pattern of salmonid populations. Management objectives are established to balance the provincial objective of maximizing the reliance on self-sustaining natural populations, while optimizing fishing opportunities for non-native naturalized fishes (OMNR 1992). In the tributaries, the objectives then recognize the need to protect native species such as brook trout, while optimizing production of naturalized non-natives such as rainbow trout, brown trout, or coho salmon (OMNR 1992; Stewart et al. 1999). Various strategies, including barrier management, instream habitat enhancement, stocking, and land stewardship are used to address the objectives in each management zone.

Our results provide tools for evaluating the benefits of various strategies for managing salmonid populations. For example, instream habitat restoration should be targeted in streams where brown trout are present, and PIC thresholds are useful for preserving constrained populations (i.e., brook trout). Catchments where land management plans ensure that PIC values

exceed the brook trout threshold and do not reach the rainbow trout threshold, may be candidates for increasing access for rainbow trout. Segments that still contain salmonids, even though the catchment is close to the PIC threshold, represent segments in need of immediate assistance to protect the remaining populations or to evaluate populations for genetic conservation.

This study expanded our understanding of the factors that influence the distribution and density of salmonids within the Great Lakes basin and can be used to strategically guide future management action. These results support the work of Seelbach et al. (1997) who suggested that landscape measures of slope, area, hydrography, and geology were critical factors determining fish assemblages in streams. Our findings suggest that in addition to these natural attributes, anthropogenic factors such as access to a Great Lake and the amount of impervious cover in the catchment should also be incorporated in classification strategies.

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Hindcasting Reference Conditions in Streams

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Abstract.—Assessments of stream fish or benthos assemblages normally involve a contrast of conditions at test sites to conditions represented by regional reference sites that are either minimally or least disturbed. Identification of reference sites is difficult and normally involves a variety of subjective criteria. The development of reference models for stream fish and benthos in the Canadian tributaries of Lake Ontario is particularly challenging because there are few undeveloped areas and there is no consensus on criteria for a least-disturbed condition. Rather than identify sites as representing a least-disturbed condition, we developed a series of models that relate the existing biophysical condition of streams (i.e., the fish, benthos, and instream habitat) to landscape (i.e., slope, geology, catchment area) and land use/land cover (percent impervious cover [PIC]). Relationships between indices of biophysical condition and PIC can be used to hindcast or estimate the expected biophysical condition at a variety of land cover scenarios. The models cannot be used to predict conditions outside the calibration data range, but this approach does allow us to make use of a disturbance gradient and make predictions with a minimal number of least-disturbed sites. The difference between the hindcast reference and present day conditions is an estimate of present-day impacts. Results from this exercise provided an estimate of the magnitude of impairment of streams in the Canadian portion of the Lake Ontario region.

INTRODUCTION

Ecological monitoring is required in order to understand if human-related stressors have undue influence on environmental resources. In aquatic systems, fish and benthic macroinvertebrate assemblages are often used as monitoring endpoints (Karr and Chu 1999). Data from reference sites are typically used to judge the degree of impairment of conditions in test sites that are physically or chemically disturbed as a result of human activity. Where there are large differences in biophysical conditions between reference and test sites, test sites are

deemed impaired (Environment Canada 1998; Bailey et al. 2003).

Impact assessments historically involved the comparison of conditions at one or a few reference sites, against conditions at the test site (Green 1979; Environment Canada 1998). No two locations are perfectly alike, and there can be large natural differences in biophysical conditions that are confounded with human disturbances and thus make an assessment of condition difficult. The reference condition approach (RCA) is a generalized sampling design (Hughes et al. 1986; Hughes 1994; Reynoldson et al. 1997; Bailey et al. 1998) in which multiple regional reference locations are sampled. Data from the reference sites serve two purposes. First, the data

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can be used to model an expected biophysical condition. Second, the data can be used to better characterize the background variability in biophysical conditions. When effects are shown to exceed the natural variation observed in regional reference locations, there is greater cause for concern than if effects exceed the variation at a single reference location. Reference-condition-approach models have been developed in Canada to conduct assessments of benthos assemblages in Great Lakes bays (Reynoldson and Day 1998), the Fraser River basin (Reynoldson et al. 1997; Reynoldson et al. 2001), and the Yukon (Bailey et al. 1998). However, the RCA can also be used to model the expected fish assemblage and physico-chemical attributes, so long as the variables used to predict the expected condition do not vary with anthropogenic disturbance (Oberdorff et al. 2002; Pont et al. 2005).

The RCA design relies on a relatively large number (10–100) of relevant reference locations. Reference sites are variously defined but are typically considered least- or minimally disturbed locations. Maude and Di Maio (1996) were able to develop an RCA model for benthos assemblages found in headwater tributaries of the Oak Ridges Moraine, Ontario. However, within the larger ecoregion that the moraine influences, there are 6–7 million people and the area has been developed for more than 200 years. Current land use is dominated by urbanization and agriculture. Reforested lands are limited and mainly restricted to headwater areas and riparian corridors. While many stream segments are in reasonably good condition, there are few streams that could truly be classified as unimpaired or minimally disturbed. There are very few minimally disturbed reference headwater and lower reaches. It is, therefore, difficult to use the conventional RCA design in the Ontario tributaries of Lake Ontario because there are too few sites of any one size or type to construct predictive models.

Variables used to predict expected conditions are termed primary or normative (Imhof et al. 1996) variables, which are not easily altered by humans, measured at the landscape scale, and

presumed to relate to fish, benthos, and physical features of streams. For example, underlying surficial geology is a reasonably good predictor of the kinds of fish found in a stream. Brook trout and other coldwater fishes are found in streams where well-drained soils or karst topographies predominate (Ricker 1932; Seelbach et al. 1997). The effects that surficial geology has on the receiving environment quality may, however, be altered by modifying land cover. Other obvious primary variables include stream size (Fausch et al. 1984) and slope (Hughes and Gammon 1987; Kilgour and Barton 1999).

Our objective is to describe an alternative approach to defining reference conditions for areas like the Lake Ontario region. The approach uses relationships between biophysical response variables and landscape features including indicators of human development, such as percent impervious cover (PIC). Relationships with PIC are then used to back-calculate or hindcast the condition that is expected to have occurred prior to development. Residual noise in the response variable, unaccounted for by the gradient in PIC or other natural features is considered to be a measure of the background variability. That residual variation is then used to standardize deviations from expected conditions, such that the degree of impairment is re-expressed in terms of standard deviations. Re-expressing effects as standard deviations puts all variables on a common scale, facilitating comparison among indices of biophysical condition (Kilgour et al. 1998). The general approach provides a means of quantifying the degree of impairment from pre- to postdevelopment for the Lake Ontario region. Others have used environmental gradients to develop tolerance indices for fishes and invertebrates (e.g., Hilsenhoff 1988; Fore et al. 1996; Whittier and Hughes 1998), but hindcasting to reference conditions is a new variation on that theme.

METHODS

Fish, benthos, temperature, and instream habitat conditions were characterized at stream sites

located on the north shore of Lake Ontario and draining parts of the Oak Ridges Moraine (Figure 1). Data were collected between 1995 and 2002 using methods described in the Ontario stream assessment protocol (Stanfield et al. 1997; Stanfield and Kilgour 2006, this volume). Randomly selected sites were a minimum of 40 m long, with boundaries at crossovers (i.e., where the thalweg is through the middle of the stream). About half of the total sites sampled during this period were used to develop the hindcasting models, while the remainder were used to validate them in a separate exercise (Stanfield and Kilgour 2006).

Fish assemblage data (721 sites) were collected by single-pass electrofishing and standardized as biomass (g/m^2) and richness (number of species). Benthic macroinvertebrates were sampled

from crossovers using a modified version of the U.S. Environmental Protection Agency rapid bioassessment protocol, involving a stationary kick from an area of about 1 m^2 , using a screen with $500\text{-}\mu\text{m}$ mesh to collect the animals. Benthic macroinvertebrates were live sorted and identified to major groups (families and orders; Plafkin et al. 1989). Benthos assemblage data (583 sites) were used to estimate the Hilsenhoff biotic index (HBI; Hilsenhoff 1988) with a modification as described in Stanfield and Kilgour (2006) and richness (number of major groups). Additional multivariate metrics of the fish and benthos assemblages were derived using correspondence analysis (CA; Rohlf 1993). Correspondence analysis is an ordination method that simultaneously orders sites and taxa in biplots. Sites close together in the biplots (i.e., similar site

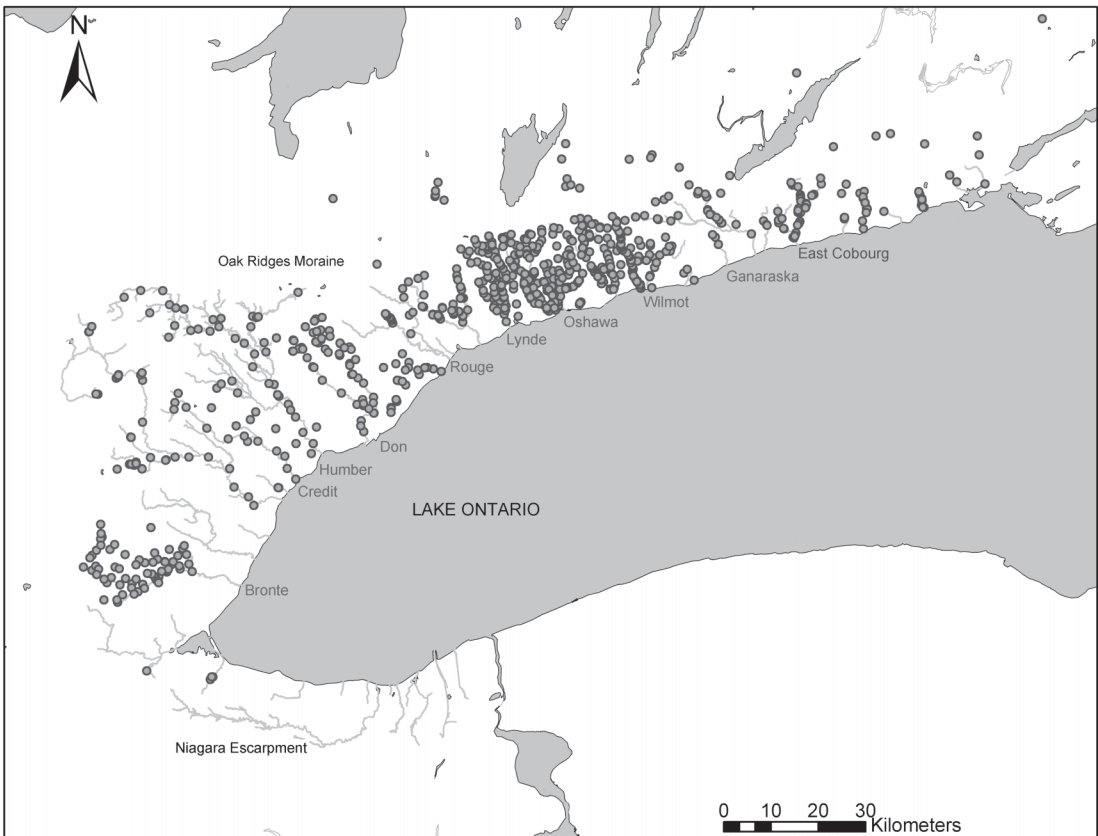


Figure 1. Study area and sampling sites.

scores) have similar assemblages, while taxa close together covary. Sites are assigned scores along each of two axes (in this case), and those scores were used as multivariate metrics of fish and macroinvertebrate assemblages.

Instream habitat data (578 sites) were collected using a point-transect survey design as described in Stanfield et al. (1997). Additional measures of stream width were obtained from sites where only one transect was surveyed as part of discharge measures (622 sites). Water temperatures were recorded between 1600 and 1700 hours, during low-flow conditions (mid-July to mid-September) when the daily air temperature exceeded 24°C for three consecutive days. Observed water temperatures were standardized to an air temperature of 30°C using known relationships between air and water temperatures (Stanfield and Kilgour 2006).

Digital mapping was used to estimate (1) the upstream catchment area (AREA), (2) the slope of a site (100 m upstream to 100 m downstream; SLOPE), and base flow index (BFI, Piggott et al. 2002; Stanfield and Kilgour 2006). A percent impervious cover (PIC) rating of the catchment was estimated based on the percent cover of a

catchment as water (0 PIC), natural/forest (1 PIC), pasture (5 PIC), intensive agriculture (10 PIC), and urban (20 PIC). These PIC ratings were based on a review of observed imperviousness values for different land classifications (see Stanfield and Kilgour 2006), and provide an approximation to the percentage of the surface cover that is impermeable to infiltration. The PIC rating of urban areas, for example, varies between 10 (low intensity housing) and 90 (high intensity industrial areas) (Stanfield and Kilgour 2006). Here, we have assumed that all urban areas have a PIC rating of 20, reflecting a predominance of lower intensity development. We acknowledge that a 20 PIC rating does not adequately reflect the true PIC of all urban areas in the study area.

Hindcast Modeling

Backward-stepwise multiple regression was used to construct multiple regression models that related attributes of fish and benthos assemblages and instream physical habitat characteristics to the landscape predictors (Table 1) (see Stanfield and Kilgour 2006 for details). Not all sites had

Table 1. Regression models relating indices of fish and benthos assemblages, and stream temperature and width, to percent impervious cover (PIC rating) and landscape variables. Values provided for predictors are model coefficients. The mean squared error (MSE) and percent of variance explained (R^2) are also provided. Predictors are defined in the text.

Predictor	Fish assemblage			Benthos assemblage			Physical		
	Log ₁₀ biomass	Rich	CA Axis 1	HBI	Rich	CA Axis 1	CA Axis 2	Temp	Width
Constant	-3.841	-6.582	-1.625	8.68	10.07	16.26	-0.28	43.84	-0.455
Area	1.866			-0.42		-3.40		-7.977	
Area ²	-0.125	0.189				0.19		0.635	0.030
Slope			-0.243	-0.17		-0.20		-1.813	-0.066
Slope ²			0.027					0.181	
BFI			-0.016	-0.017		-0.077	-0.011		-0.028
BFI ²	<-0.001					0.0007		-0.001	<0.001
PIC	-0.066	0.619	0.476	0.092		0.042	0.102	0.885	
PIC ²		-0.035	-0.016		-0.008			-0.003	0.001
MSE	0.215	5.895	0.804	0.653	4.842	0.760	0.827	10.177	0.491
R ²	0.185	0.372	0.394	0.306	0.08	0.255	0.180	0.299	0.607
n	361	361	361	332	332	332	332	385	373

Notes: BFI = base flow index, MSE = mean squared error, n = number of sites, Rich = richness or number of taxa, HBI = Hilsenhoff biotic index, Temp = temperature, CA = Correspondence Analysis, and PIC = percent impervious cover rating.

all biophysical data collected, so each model was constructed for a unique set of sites. Only those biological variables for which PIC was a significant predictor were used for hindcasting expected historical conditions (Figure 2). Models were developed for the \log_{10} of fish assemblage biomass, fish assemblage richness, site scores for the first axis from a CA of the fish assemblage data (fish CA Axis 1), Hilsenhoff biotic index, benthos assemblage richness, site scores for the first two axes from CA of the benthos assemblage (benthos CA Axes 1 and 2), water temperature, and average stream width. Predictors included catchment area, slope, base flow index and PIC. The squared term for each predictor was also included in the models in an attempt to explain curvilinear relationships. Predictors were retained in models if they explained a significant amount of variation in the response variables (at $p < 0.05$).

Model relationships (Table 1) were used to estimate the value of the various biophysical indices for expected reference conditions assuming an overall PIC of 1 (i.e., 100% forest cover; Table 2; Figure 2). As per Table 2, model coefficients for significant predictors were multiplied by the individual site conditions. The sum of the

products of model coefficients and site conditions provided the expected condition (i.e., 3.10 in Table 2). The difference between present day values of biophysical indices and the hindcast condition (0.76 in Table 2), was used to assess the level of disturbance. Deviations from expected can be expressed in terms of the original units of measurement (e.g., g/100 m² or number of taxa), but results between different indices can be difficult to compare. Alternatively, expressing deviations relative to background variability puts indices on a common scale (i.e., standard deviations, Kilgour et al. 1998; Figure 2). With each of the constructed models, unexplained residual variation (i.e., the mean squared error or MSE) included measurement error and unexplained noise or natural variation among sites that is unrelated to landscape features (Figure 2). The square root of the MSE term (0.215 in Table 2) is an estimate of the among-sites standard deviation. That is, after taking into account the primary features (area, slope, BFI) and PIC rating, the MSE provides an estimate of the among-sites variation. The MSE can, therefore, be used to re-express deviations in terms of the background variability (Figure 2) and facilitate comparison of deviations among different

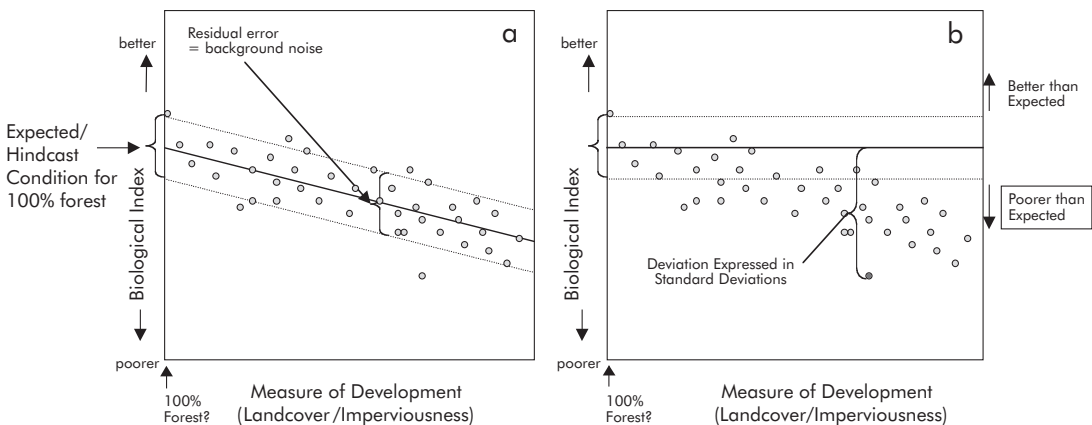


Figure 2. Conceptual illustration of (a) the hindcasting modeling approach, and (b) how the biophysical condition of sites is assessed relative to a hindcast or predicted historical condition. Based on the model in (a), the expected range of values is as shown in (a). Differences between what is predicted and what was observed is expressed relative to the unexplained variability (i.e., as standard deviations in (b)).

Table 2. Example calculations for hindcasting using the model for log₁₀ of fish biomass (g/100 m²) at a site in Wilmot Creek. BFI = base flow index; PIC = percent impervious cover rating.

Model parameters	Model coefficients	Site conditions	Result
Constant	-3.84	1	-3.84
Log ₁₀ area	1.87	7.41	13.86
Log ₁₀ area ²	-0.125	54.8	-6.85
Slope	0	0.49	0
Slope ²	0	0.24	0
BFI	-0.0001	51.8	-0.0052
BFI ²	0	2684	0
PIC	-0.066	1	-0.066
PIC ²	0	0	0
Hindcast (estimated) log ₁₀ fish biomass (a)		3.10	
Observed (present-day) log ₁₀ fish biomass (b)	2.34		
Difference (c)		(a) - (b)	0.76
MSE			0.215
Difference re-expressed in units of standardized deviation (SDs)		$\frac{(c)}{\sqrt{MSE}}$	1.64

biological indicators. In the example, the difference (0.76 g/100 m²) between present day (2.34 g/100 m²) and hindcast (3.10 g/100 m²) fish biomass, re-expressed relative to the unexplained variation (MSE = 0.215) was 1.64 standard deviations (Table 2). These reexpressed deviations are termed effect sizes (e.g., Kilgour et al. 1998).

Deviations from the expected hindcast reference condition were expressed relative to the estimated standard deviation for the nine variables for which PIC rating was a significant predictor (Table 1). Fish and benthos assemblages were classified as being (1) unimpaired when effects were within the expected range of hindcast conditions (i.e., within ± 2 SDs of the predicted mean value), (2) likely impaired when effects were between 2 and 3 SDs from the predicted mean and when the effect was in a “poorer” direction (e.g., reduction in richness or biomass), (3) impaired when effects exceeded 3 SDs and the effect was in a poorer direction, and (4) unimpaired when effects exceeded 2 SDs and were in a “better” direction (e.g., increase in richness or biomass). Sites were classified separately for each fish and benthos assemblage index, and measures of stream temperature and width.

RESULTS

The streams used in this study represented a broad assortment of typical wadeable streams in southern Ontario. Catchment areas varied from 2 to 90,000 ha (average of 4,500 ha), and in slope from 0% to 25% (average of 2%). Catchment land cover varied from 0 to 98% forest, from 0% to 100% urban, and from 0% to 100% agriculture. Fish and benthos assemblages included those representative of both high and low habitat quality.

Fish Assemblages

Present-day biomass of the fish assemblage varied from 1 to 7,000 g/100 m² (average of 540 g/100 m²), while the number of species varied between 1 and 15 (average of 6) per site. Correspondence Analysis (CA) Axis 1 separated coldwater salmonid assemblages (low Axis 1 scores) from warmwater cyprinid and centrarchid assemblages (high Axis 1 scores; Figure 3A). The hindcasting regression models (Table 1) were used to predict Axis 1 scores, biomass and richness of the fish assemblage assuming 100% forest cover. The expected fish

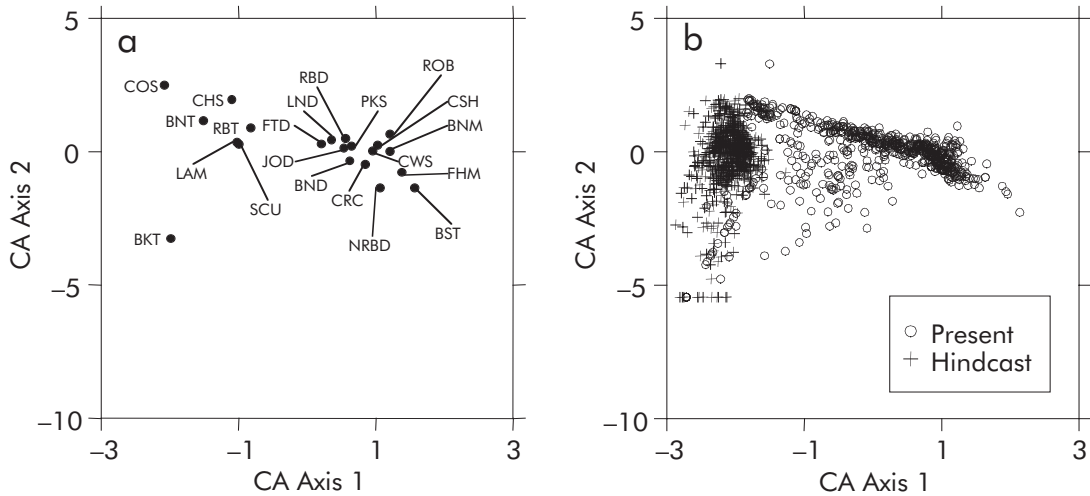


Figure 3. Correspondence analysis (CA) taxa scores (a) for the current fish assemblage, and site scores observed currently and hindcast (b). BST = brook stickleback *Culaea inconstans*; CHS = Chinook salmon *Oncorhynchus tshawytscha*; FTD = fantail darter *Etheostoma flabellare*; COS = coho salmon *O. kisutch*; LAM = lamprey family Petromyzontidae; NRBD = northern redbelly dace *Phoxinus eos*; ROB = rock bass *Ambloplites rupestris*; RBD = rainbow darter *Etheostoma caeruleum*; PKS = pumpkinseed *Lepomis gibbosus*; BNM = bluntnose minnow *Pimephales notatus*; CSH = common shiner *Luxilus cornutus*; FHM = fathead minnow *P. promelas*; BKT = brook trout *Salvelinus fontinalis*; JOD = Johnny darter *Etheostoma nigrum*; BNT = brown trout *Salmo trutta*; LND = longnose dace *Rhinichthys cataractae*; RBT = rainbow trout *O. mykiss*; SCU = sculpin family Cottidae; CRC = creek chub *Semotilus atromaculatus*; WS = white sucker *Catostomus commersonii*; BND = eastern blacknose dace *Rhinichthys atratulus*.

assemblage for most sites in the dataset was cold-/coolwater, consisting principally of salmonids and sculpins (Figure 3B). Hindcast biomass of fish assemblages varied between 6 and 1,000 g/100 m² (average of 600) that was generally higher

than was observed with the present-day data (Figure 4A). Hindcasting models predicted between 0 and 9 fish species (average of 4) per site, which was lower than the present-day condition of most sites (Figure 4B). Effects on the fish

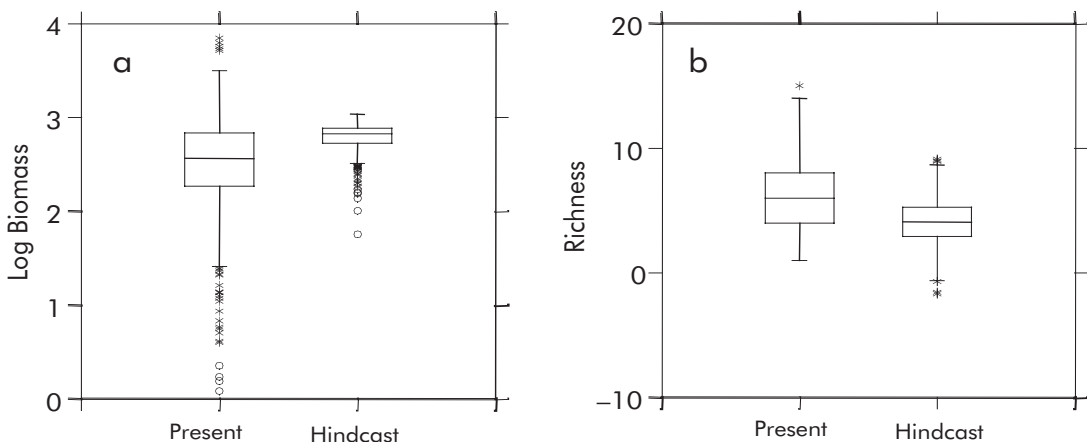


Figure 4. Present and hindcast conditions for the log of fish assemblage biomass (a) and number of taxa (b). In the box plots, the center horizontal line marks the median of observations; the box shows the range within which the central 50% of the values fall, while the whiskers illustrate the data range.

assemblage were most evident with the multi-variate descriptor (CA Axis 1), with effect sizes at most sites in the study area more than 2 SDs from the expected hindcast condition (Figure 5). Present day biomass and richness of the fish assemblages were generally within ± 2 SDs of the hindcast conditions (Figure 5). Fish assemblages within the immediate vicinity of Toronto (Humber, Don, Credit) and immediately east (Lynde, Oshawa) were mostly impaired, while those further to the east and south in the more agrarian catchments were generally in good condition (Figure 6C).

Benthos Assemblage

Benthos taxa richness varied between 1 and 17 (average of 10) per site, while the HBI varied between 3 and 8 (average 5.4). Low Axis 1 and 2 scores were coincident with benthos assemblages comprised of more sensitive groups such as mayflies (Ephemeroptera), caddisflies (Trichoptera), and stoneflies (Plecoptera), while higher Axis 1 and 2 scores were coincident with benthos assemblages more typically associated with

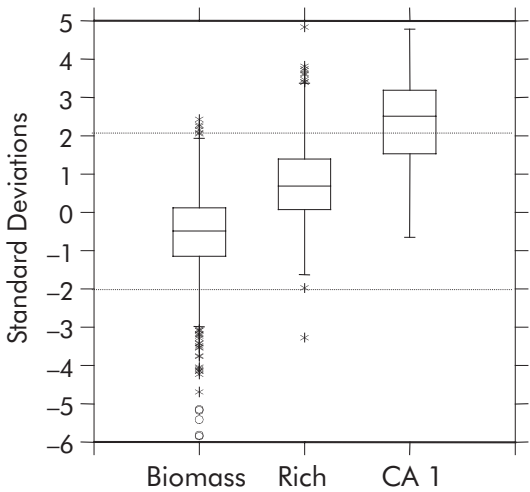


Figure 5. Standardized effect sizes for log of fish assemblage biomass, number of taxa, and CA Axis 1 scores. In the box plots, the center horizontal line marks the median of observations, the box shows the range within which the central 50% of the values fall, while the whiskers illustrate the data range.

degraded conditions (i.e., Oligochaeta, Chironomidae, Isopoda; Figure 7A). Based on the hindcasting models, benthos assemblages have changed from sensitive to tolerant assemblages (Figure 7B). Those changes were reflected in

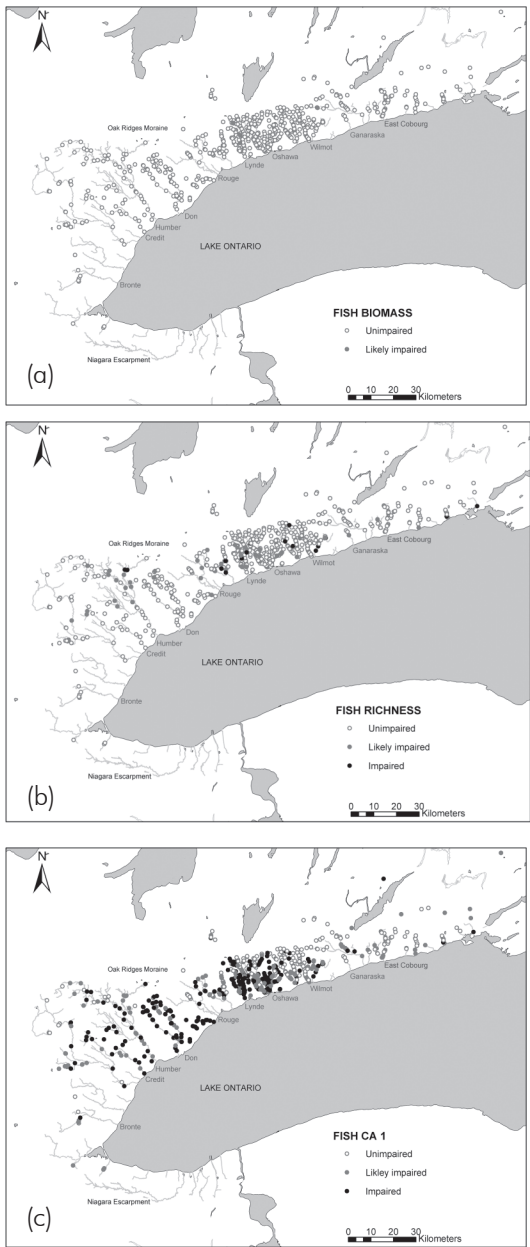


Figure 6. Spatial distribution of southern Ontario sampling sites and the estimated condition for log of fish biomass (a), number of fish species (b), and CA Axis 1 scores.

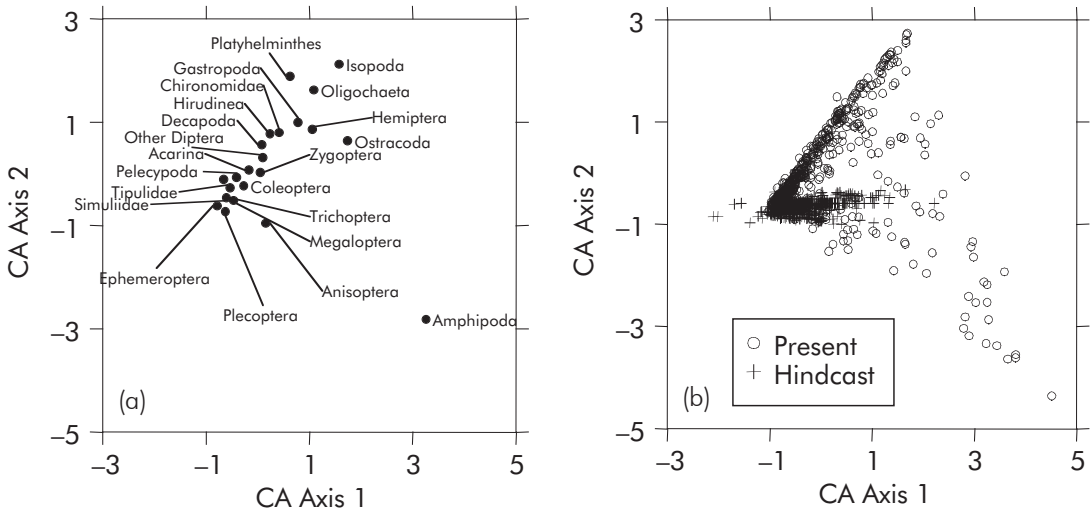


Figure 7. Correspondence analysis (CA) taxa scores (a) for the current benthos assemblage and site scores observed currently and hindcast (b).

significant shifts in the HBI and greater variation in richness of the benthos assemblage (Figure 8). The hindcast condition for the HBI was predicted to range between 3.2 and 5.9 with an average of 4.8, which is about half a unit lower than the present-day condition (Figure 8). Effects were also more evident with the multivari-

ate metrics of the benthos assemblage (i.e., CA Axes 1 and 2) and the HBI than they were with richness (Figure 9). Effects were not as evident with the benthos assemblage as they were with the fish assemblage, and streams in the Toronto area were not shown to be as degraded using benthos as they were with fish (Figure 10).

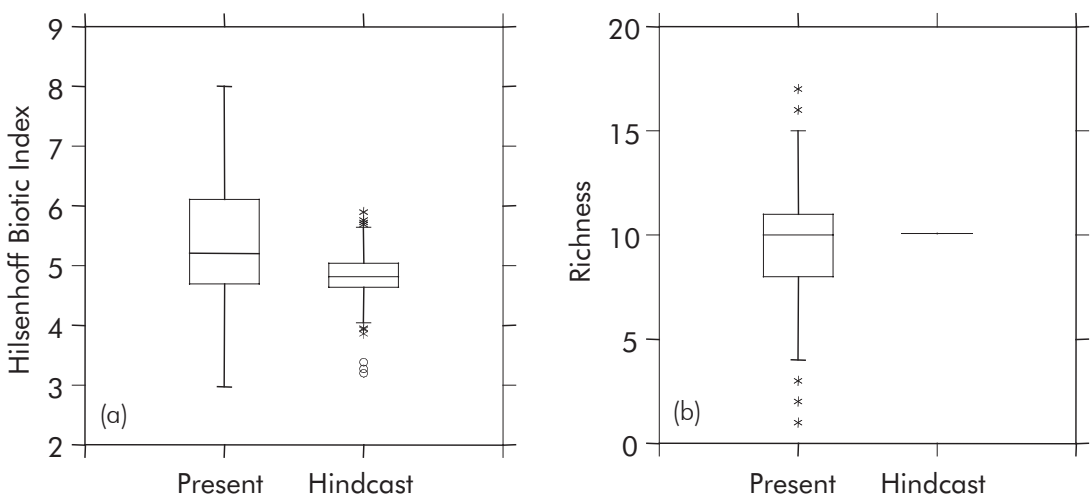


Figure 8. Present and hindcast conditions for the Hilsenhoff biotic index (a) and number of taxa (b). In the box plots, the center horizontal line marks the median of observations; the box shows the range within which the central 50% of the values fall, while the whiskers illustrate the data range.

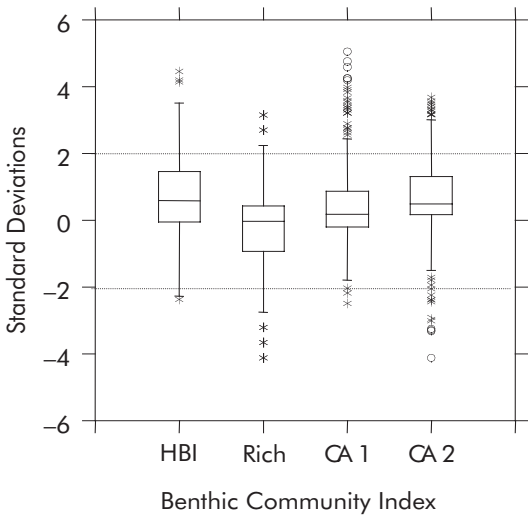


Figure 9. Standardized effect sizes for the Hilsenhoff biotic index, number of taxa, and CA Axis 1 and 2 scores. In the box plots, the center horizontal line marks the median of observations; the box shows the range within which the central 50% of the values fall, while the whiskers illustrate the data range.

Stream Temperature and Width

Present-day standardized stream temperature varied between 9°C and 33°C (average of 21°C), while historical temperatures were predicted to be lower and varied between 12°C and 25°C (average 17°C; Figure 11). Average stream widths varied between 0.4 and 11.5 m (average 4.3 m), while historically, streams were predicted to be narrower with widths varying between 0.1 and 9 m (average 1.1 m; Figure 11). The estimated changes in stream temperatures and widths were not large when expressed relative to the background noise in each of the two variables, with few effects exceeding 2 SDs from the hindcast condition (Figure 12). As with the benthos assemblage data, spatial trends in effects on width and temperature were not evident (Figure 13).

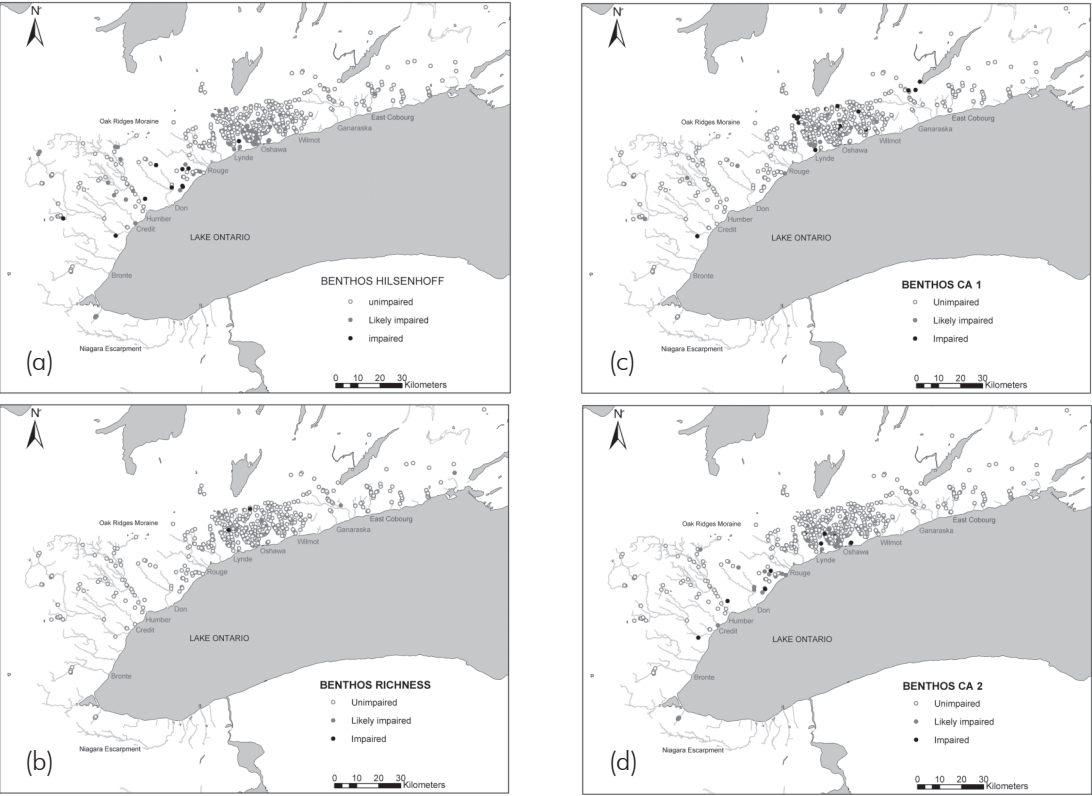


Figure 10. Spatial distribution of southern Ontario sampling sites and the estimated condition for the Hilsenhoff biotic index (a), number of taxa (b), and CA Axis 1 and 2 scores (c, d).

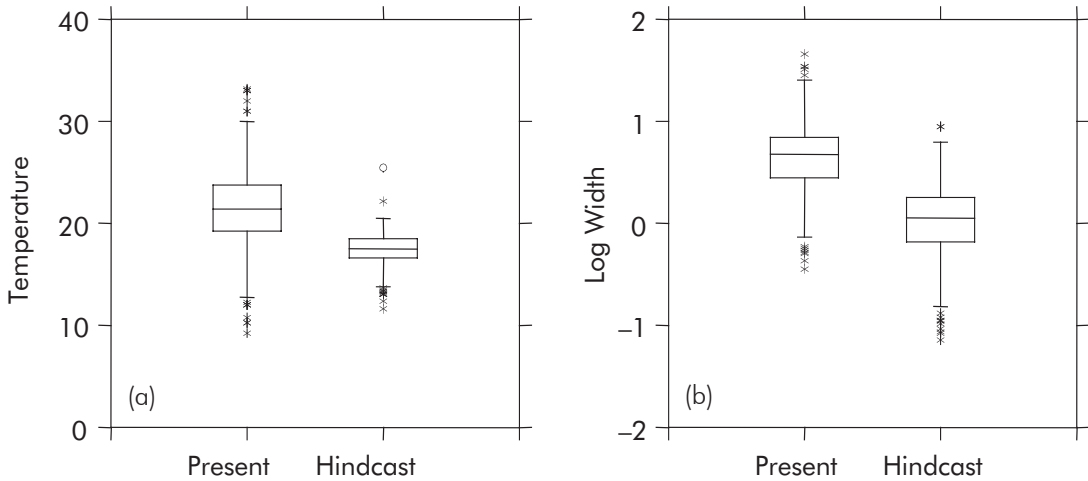


Figure 11. Present and hindcast conditions for maximum stream temperature standardized to an air temperature of 30°C (a) and average stream width (m) (b). In the box plots, the center horizontal line marks the median of observations; the box shows the range within which the central 50% of the values fall, while the whiskers illustrate the data range.

DISCUSSION

We have demonstrated how to hindcast historical expected conditions based on models that relate instream biophysical conditions to land

use/land cover with the PIC rating, and then how to assess present-day conditions. We demonstrated significant shifts in biophysical conditions in the study area, with fish and benthos assemblages shifting from sensitive coldwater taxa toward tolerant warmwater taxa. The assessments based on this hindcasting approach are conservative in potentially underestimating the true degree of impairment, and they reflect our understanding of how the streams in the study area have changed over time. Others (e.g., Martin 1984; Steedman 1988; Wichert 1994) have demonstrated impairment in fish assemblages in the greater Toronto area and have related indices of composition to measures of urbanization and agriculture. The hindcasting approach, however, provides an objective measure of the degree or magnitude of changes from presumed historical undeveloped periods. No previous studies have attempted to conduct a hindcast assessment of this study area, although Van Sickle et al. (2004) used hindcasting models to demonstrate fundamental historical changes in Willamette Valley, Oregon streams.

There are several caveats when using hindcast models in assessments. First, we assumed that the reference condition was represented or

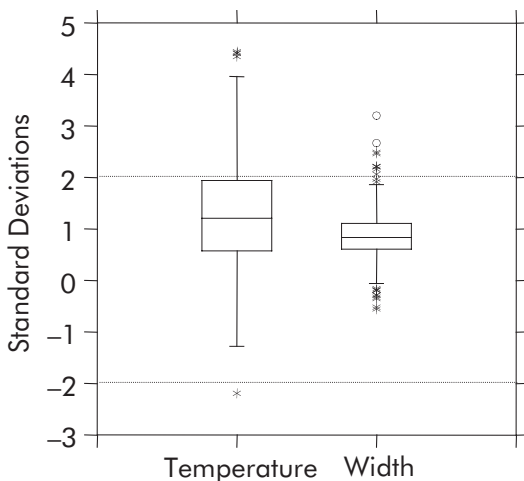


Figure 12. Standardized effect sizes for maximum stream temperature standardized to an air temperature of 30°C and average stream width. In the box plots, the center horizontal line marks the median of observations; the box shows the range within which the central 50% of the values fall, while the whiskers illustrate the data range.

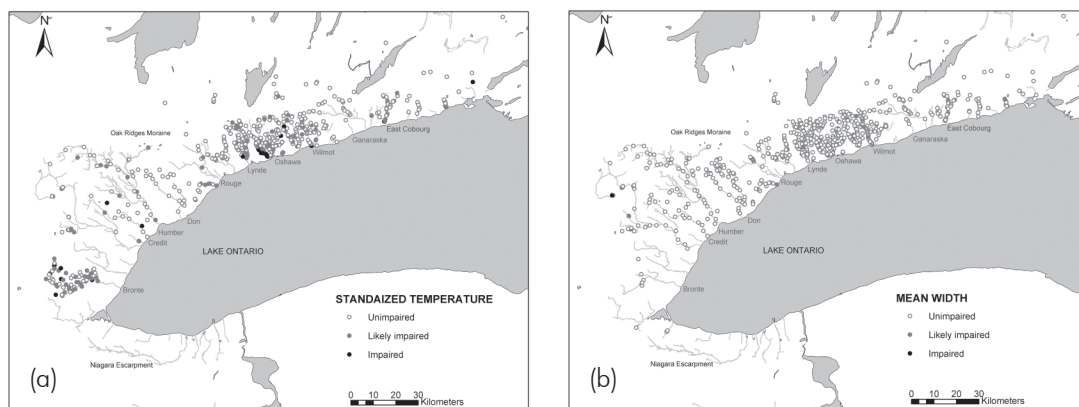


Figure 13. Spatial distribution of southern Ontario sampling sites and the estimated condition for maximum stream temperature standardized to an air temperature of 30°C (a) and average stream width (b).

characterized by 100% forest cover (1 PIC rating). Forest cover was set to 100% purposely to demonstrate the full extent of potential impairment that could have occurred at each of the sites in the dataset. Assessments based on other land cover targets are obviously possible.

Second, caution is necessary in hindcasting outside the calibration range. For example, if there are no minimally disturbed reference sites for larger reaches, then hindcasting to a pristine condition for large reaches is not recommended. In this study, there were at least a few sites in headwater catchments with 100% forest cover, which technically allowed us to hindcast to that level of forest cover. We did not observe 100% forest cover in larger streams near Lake Ontario, so hindcasting to 100% forest cover for larger reaches should only be done with caution.

Third, although we demonstrated that it is possible to hindcast an historical condition, we have not validated the predictions. It would be useful to demonstrate this approach using sites for which there are both present-day and historical reference data. That, however, is not possible for this study area for the following reasons. First there are no quantitative preEuropean settlement data. The entire landscape was clear-cut soon after European settlement in the area, and Atlantic salmon *Salmo salar* was locally extirpated

partially as a result. Loss of such a keystone species ensures that current fish assemblages are fundamentally different from historic ones (Gresh et al. 2000; Stanfield and Jones 2003).

Fourth, the chronological sequence of land use changes on the landscape was not unidirectional. That is, while much of the study area was clear-cut in the 1800s and early 1900s, some previously agricultural areas have recovered to a forested condition. Some of the unexplained variation in the models may be due to the differential rates and direction of land use changes, as well as ghost effects from past land uses (Harding et al. 1998). Incorporation of the chronology of events (if it can be determined) could improve the predictive power of relationships.

Fifth, hindcasting is only as good as the variables on which the hindcasting is based. In this demonstration it was assumed that PIC rating was the principle driving measure of effects in the study area. There is good reason to make that assumption considering the number of studies demonstrating effects related to PIC (Stanfield and Kilgour 2006). In the event that other variables override the effects of PIC (e.g., point source discharges, migration barriers), the hindcast models and associated predictions of historical conditions and present-day assessments will not apply. One concern with using

PIC rating in this study was the tendency for PIC to be naturally correlated with underlying surficial geology, and thus the base flow index. In this study area, urban development tended to occur on clay-till plains close to Lake Ontario, while agriculture and forest cover tended to be more prevalent on higher sand/gravel morainal deposits (Figure 1). Stanfield and Kilgour (2006) and Stanfield et al. (2006, this volume) demonstrated that PIC rating was able to account for significant amounts of variability in biophysical responses, through a process of partial regressions. The modeling conducted here has assumed that PIC rating effects overrode effects related to variations in surficial geology.

The strength of the relationship between the hindcasting and response variables is of little concern. Either the predictor variable explains significant amounts of variation in the response variable or not. When the predictor (PIC rating) explains a large amount of variation in the predictor, then the background range of natural variability will be a smaller range than when the predictors explain less variability in the response variable. Comparison of test sites to the normal range of variability follows the same process, whether the range is considered small or large. Through exploratory analyses, we found that the percent of variance explained in response variables was increased if models were developed for smaller portions of the overall study area, and therefore recommend the construction of models for smaller study areas when the data are available. The models constructed for the larger study area, however, provide information useful for screening assessments. That is, where indices of composition or habitat features exceed the normal range of hindcast conditions based on large-scale models, there is good certainty that effects are significant and deserve consideration. In contrast, not exceeding normal ranges based on large-scale models does not imply effects are not large or important. Also Riseng et al. (2006, this volume) found that large-scale data sets offered more sensitive models than smaller scale data sets

because the former included more minimally disturbed sites.

Finally, despite concerns over confounding, the observed effects developed by the hindcasting models were modest compared to what was anticipated. Streams in the Toronto area are considered highly degraded (Wichert 1994), and larger effects were anticipated. The models used here were derived from a large area and thus represented regional relationships. Subsequent modeling and analyses may demonstrate that subsets of models for smaller study areas further reduces unexplained variability in biophysical conditions and thus increases our ability to detect effects relative to unexplained variability. Riseng et al. (2006) found that smaller scale models were better able to incorporate local effects from dams and point source discharges. Our regional models provide a set of numeric biophysical criteria that can be used to assess the level of degradation. More subtle effects might be discernible with more local models, but effects documented using our regional models deserve management consideration. The noise associated with these regional models may partially explain why standardized effects on stream temperatures and widths were small, even though effects in terms of the original units of measurement were quite significant. Stream temperatures, for example, increased from an expected average of 17°C to a present-day average of 21°C. Differences of 4°C can substantially alter production of salmonids and invertebrate assemblages (Bisson and Davis 1976; Hughes and Davis 1986). When re-expressed in units of standard deviations, that difference (4°C) was just greater than 1, which is not a large statistical difference. Further stratification of the database to account for regional differences might make the assessment of effects on temperature, width, and other response variables more sensitive.

Benthos assemblage data and measures of stream temperature and width were relatively insensitive. Our method of sampling the benthos assemblage, however, was a fairly coarse tool,

principally recommended for use in rapid screenings of problem areas (Plafkin et al. 1989). Had the benthos assemblage been sampled more thoroughly and had more individuals been counted to lower taxonomic levels, greater effects would likely have been observed (Furse et al. 1984; Wright et al. 1995; Cao et al. 2002). The protocols for measuring stream width and temperature were fairly standard (and rigorous), so the lack of effects was probably a function of local factors such as groundwater inputs, shading, and adjacent land use being important. Gregory et al. (1991) emphasized that riparian trees are critical for shading small streams and for providing habitat structure.

In this analysis, we did not evaluate the statistical significance of differences from hindcast to present-day conditions. Rather, we visually examined the differences between expected hindcast and present-day conditions, expressed relative to the unexplained noise in the response variables. Effects expressed in terms of standard deviations are becoming a popular means of articulating the potential ecological significance of an effect (Lowell 1997; Kilgour et al. 1998). In the reference-condition approach, the comparison of one sample from one site to a set of reference samples from a number of sites can be analyzed as a typical two-sample contrast or *t*-test, though some (e.g., Kilgour et al. 1998) have argued it should be a one-sample contrast based on comparison to noncentral *t* or *F*-distributions. Sample sizes were very high in this study (500+) resulting in very high statistical power. Any site with an effect exceeding 2 SDs would very likely differ significantly from the hindcast reference condition. For the purpose of this manuscript, therefore, specific testing of statistical significance was not considered critical. Quantifying the magnitude of effects was, however, considered more informative.

Our analysis confirms that the biophysical condition of tributaries on the north shore of Lake Ontario varies with the amount of development in the region. Here, a measure of human development (percent impervious cover,

PIC rating) was used to hindcast to expected reference conditions. By expressing deviations from the expected hindcast condition relative to the unexplained residual variability (as in a standard deviation), deviations in all biophysical variables are expressed on a common scale and can thus be easily compared.

ACKNOWLEDGMENTS

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Associations among Catchment- and Site-Scale Disturbance Indicators and Biological Assemblages at Least- and Most-Disturbed Stream and River Sites in the Western United States

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Abstract.—At broad scales, the types and intensities of human disturbances to ecosystems vary along natural gradients. Biological assemblages also vary with natural and human disturbance gradients. We defined least-disturbed conditions for a set of water chemistry, catchment, and site-scale indicators of disturbance, for 835 Environmental Monitoring and Assessment Program sites in the Mountains, Xeric, and Plains regions of 12 conterminous western United States. For each disturbance indicator, the definition of least-disturbed was adjusted by the sites' locations on the primary natural gradients. For example, the least-disturbed condition for phosphorus in eastern Plains streams allowed up to 100 $\mu\text{g/L}$ total phosphorus, while in western Plains streams, less than 30 $\mu\text{g/L}$ total phosphorus was required. Sites were scored by the number of times they met the least-disturbed condition for all disturbance indicators. We also applied this process to score for most-disturbed condition. The importance of disturbance types varied regionally and along natural gradients. For example, catchment-scale disturbance measures did not distinguish between least- and most-disturbed sites for small streams at higher elevations, but were important for larger streams and at lower elevations. We examined regional-scale patterns in aquatic vertebrate species and assemblage metrics, and macrobenthos assemblage metrics at least- and most-disturbed sites. Most-disturbed sites in the Mountains and Xeric regions had higher proportions of nonnative and tolerant vertebrates and noninsect macrobenthos, and lower proportions of Ephemeroptera, Plecoptera, and Trichoptera individuals and taxa than did the least-disturbed sites. The Plains region has been extensively used by humans and showed less contrast between disturbance classes for most of these measures.

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INTRODUCTION

Traditionally, aquatic assessments based on biological indicators have estimated what the undisturbed ecological condition of assemblages and ecosystems would be and used that estimate to set expectations to evaluate the current condition (Karr et al. 1986; Hughes 1995; Reynoldson et al. 1997; Bailey et al. 2004). These expectations are based on the concept of biological integrity, defined in terms of the naturalness of the biota (structure, composition, function, diversity) that implies the absence of significant human disturbance or alteration (Steedman 1994; Hughes 1995; Jackson and Davis 1995). The biological characteristics in places where there is minimal or no human disturbance serve as the reference condition against which to judge the effects of human activity (Karr and Chu 1999). In practice, these concepts are implemented through a reference site approach, where the biological conditions at a set of existing sites, considered to be minimally affected by human activity, are quantified (Hughes 1995; Bailey et al. 2004). In some areas, such as high elevation mountains, where the natural features of the environment (e.g., soil, slope, climate) have placed limitations on human activity, it is fairly easy to find such reference sites.

However, in other areas, such as the Great Plains, the natural environment promotes extensive human use of the region (Dodds et al. 2004). In these regions, there are often no undisturbed locations, and the best available sites cannot be said to represent historical or minimally disturbed condition (Stoddard et al. in press). Stoddard et al. (in press) have suggested the use of the term “least-disturbed condition” (as opposed to reference condition) to describe what many assessments use to set regional expectations, recognizing that even the least-disturbed locations may show considerable human influence. Regional expectations based on generally undisturbed regions are often not appropriate for extensively disturbed regions because of the large natural differences in their landscape char-

acteristics. For example, we should not expect that 200 years ago, lower elevation, low-gradient streams in what are now agricultural valleys in the West had the same biological assemblages as neighboring high-gradient, high-elevation mountain streams (Vannote et al. 1980; Li et al. 1987). The covariance of the kind and intensity of human activities, and biological assemblages with natural gradients, complicates the process of determining reference condition in extensively disturbed regions.

In areas where all locations exhibit at least a moderate degree of human influence, we believe we can use the concept of least disturbed condition (and sites that represent that condition) to help infer what reference condition could be (Hughes 1995; Stoddard et al., in press). The contrast between conditions at least-disturbed and most-disturbed sites should be useful for developing biological criteria (Davis and Simon 1995) and for studying how human activity affects ecosystems. Least-disturbed needs to be defined in terms of the ecological context of the site (e.g., ecoregion, elevation, slope, stream size; Zorn et al. 1998; Seelbach et al. 2002; Baker et al. 2005). The difficulty has usually been in determining how much human disturbance constitutes the least amount for a particular setting. Recently, we developed a method to select least-disturbed sites across the full range of the natural gradients, from regional scale surveys of streams and rivers (T. R. Whittier and coworkers, unpublished data). In this chapter, we apply that method to select least-disturbed and most-disturbed sites from the U.S. EPA's Environmental Monitoring and Assessment Program (EMAP)—Western Pilot Survey (Hughes et al. 2000). We then examine regional-scale patterns in biological assemblages and physical, chemical, and catchment characteristics at those least- and most-disturbed sites.

METHODS

EMAP sampled 835 stream and river sites during late spring and summer 2000–2003, in 12

western states (Figure 1). Sample sites were selected using a probability-based design (Stevens 1997; Olsen et al. 1999) from the target population of all perennially flowing waters in the region, except the main stems of the Columbia, lower Colorado, and Missouri rivers. That is, sample sites ranged from the smallest headwater streams to all but the very largest rivers, at all elevations in the western United States (Table 1).

At each site, fish, periphyton, and macrobenthos assemblages were sampled, along with water quality, fish tissue contaminants, and instream and riparian physical habitat data following standard EMAP field protocols (Kaufmann et al. 1999; Peck et al. 2004a, 2004b). Catchments were delineated for each site, and characterized from a number of Geographic Information System (GIS) data layers. At 139 sites, fish were not

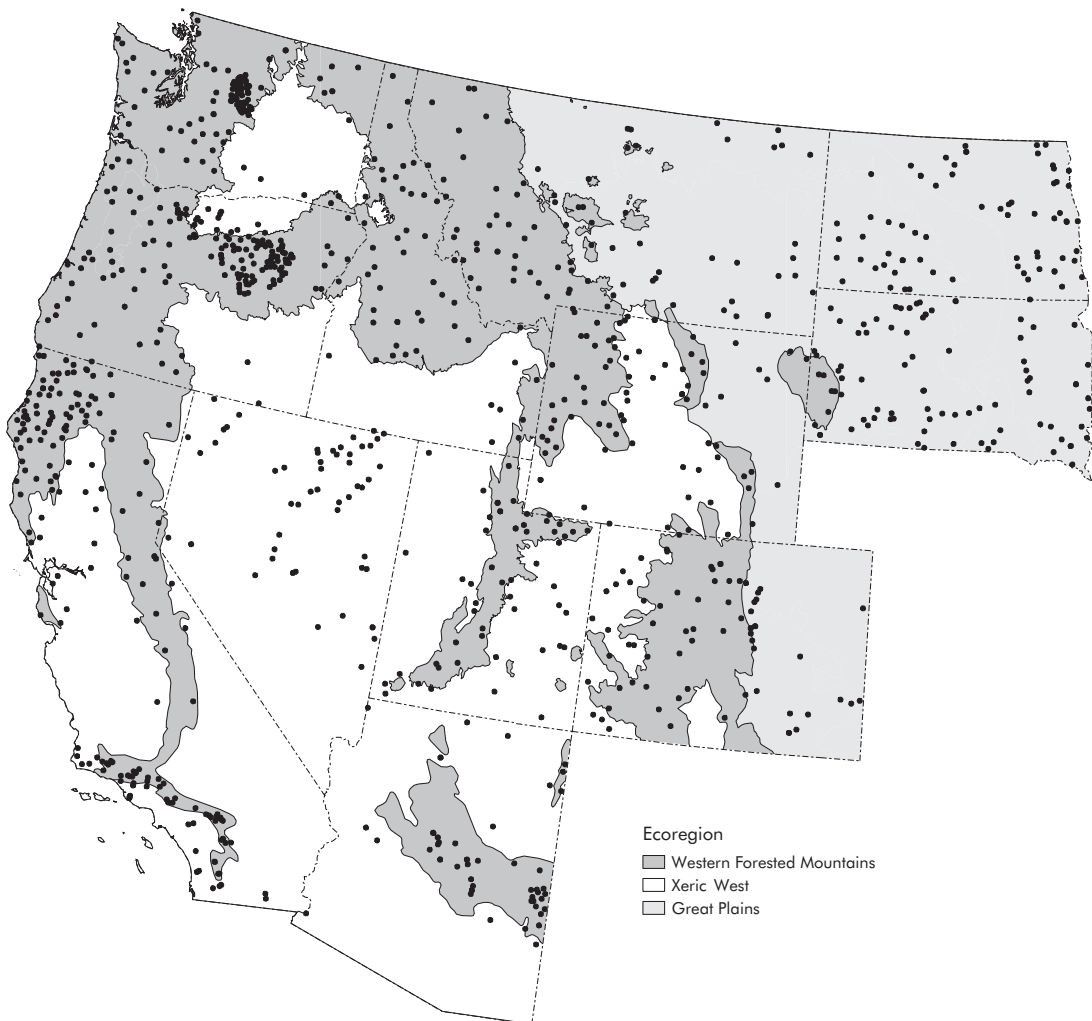


Figure 1. Locations of 835 stream and river sites sampled by the Environmental Monitoring and Assessment Program (EMAP)—Western Pilot during 2000–2002. Sites were selected using a probability design from the population of perennially flowing waters in these 12 states. Areas with a concentration of sites, such as northwestern California and the John Day River basin in Oregon, were given additional sites (i.e., an increased sampling density within the probability design) to support ongoing U.S. Environmental Protection Agency projects. The regions shown are aggregations of Omernik's (1987) Level III ecoregions.

Table 1. Selected characteristics of streams sampled by EMAP in 12 states of the western United States, by region. Data are presented as the range of values with the interquartile range in parentheses.

	Mountains	Xeric	Plains
Stream width (m)	0.09–148.0 (2.0–7.7)	0.20–185.0 (1.7–8.7)	0.06–170.0 (4.0–22.0)
Elevation (m)	0–3,659 (733–1,750)	5–2,632 (637–1,917)	238–2,146 (440–883)
Stream slope (%)	0–34.9 (1.5–5.6)	0–19.8 (0.7–3.1)	0–2.0 (0.2–1.0)

sampled, primarily due to permit restrictions. As a geographic framework for this study, we aggregated Omernik's Level III ecoregions (Omernik 1987; U.S. EPA 1996) into three regions, the Western Forested Mountains (490 sites), Xeric Lands (177 sites), and Great Plains (168 sites) (hereafter, Mountains, Xeric, and Plains, respectively; Figure 1).

Because of the random component of the probability-based site selection design, we assumed that sampled sites included examples of the full range of human disturbances. Whittier and coworkers (unpublished data) have developed a process to determine which of the sampled sites are least disturbed and which are most disturbed given their ecological context (Zorn et al. 1998; Seelbach et al. 2002; Baker et al. 2005), that is, given their ecoregion, elevation, size, slope, and so forth. The general procedure of the site classification is described below. The details of the process are freely available from the authors. Sites were classified separately for each aggregate region.

First, we determined the primary natural gradients for each region. We selected natural gradients that either appeared to have a large influence on ecosystem characteristics, including the types and intensity of human activities, or that correlated with the variation in conditions in the region. The stream continuum concept indicates that stream size, elevation, and slope determine lotic ecosystem characteristics (Vannote et al. 1980; Minshall et al. 1985). In the Mountains and Xeric regions, there are strong

natural gradients in elevation, slope, and stream size. Human use of the landscape in these regions also varies strongly with elevation and slope. In the Plains, there is very little variation in elevation (a majority of sites were between 400 and 900 m) or stream slope (nearly all sites had slope < 2%; most had slope \leq 1%). Instead, univariate analyses and ordinations indicated that many natural features (e.g., precipitation, long-term runoff, elevation) and indicators of human activity (e.g., % agricultural land, road density, nutrient concentrations) were correlated with longitude.

Second, we selected a set of 11 or 12 anthropogenic stressors appropriate for each region. Because human activities affect lotic ecosystems in a variety of ways, no single stressor or stressor type would be sufficient to indicate human disturbances fully. The set of disturbance indicators was similar among regions, with some substitutions to provide better resolution or account for natural regional conditions. For example, we used percent substrate composed of sand and finer particles as a sedimentation indicator in the Mountains and Xeric regions, while percent clay and finer particles was used in the Plains, where a sand substrate is considered a natural feature of many streams (Rahel and Hubert 1991; Quist et al. 2004). We used four water quality, three or four catchment-scale, and four site-scale instream and riparian physical habitat indicators of human disturbance to the ecosystem (Table 2).

Third, for each disturbance indicator, we determined the natural gradient with which it was most correlated. Using scatter plots of those data, we selected sites with least-disturbed values (e.g., a range of low total phosphorus concentrations for a given elevation) along the full length of the natural gradient to encompass 15–20% of the region's sites (Figure 2). We used the same procedure to select most-disturbed sites for each indicator.

Fourth, for each site we summed the number of times it was rated as least-disturbed for the indicators and did the same for number of most-

Table 2. Human disturbance indicators used to determine least-disturbed and most-disturbed classes. The disturbance indicators were used in all areas except where initials in parentheses denote regions (Mountains [M], Xeric [X], Plains [P]). Three of the physical habitat indicators are habitat quality measures (i.e., higher values indicate less disturbance).

Water quality ^a	Physical habitat (site-scale) ^{a, b}	Catchment
Turbidity	Substrate fines ^c	Road density ^d
Nitrogen (total)	Human impacts—instream and riparian ^e	Human population density ^f
Phosphorus (total) (M, P)	Natural fish cover	% human land use ^{g, h} (M, X)
Chloride (M, X)	Complex riparian vegetation—canopy, ground, and shrub layers (M, X)	% agricultural land use ^g (P)
Dissolved organic carbon (X, P)	Woody riparian shrub and ground cover (P)	% urban land use ^g (P)

^a Data collection methods in Peck et al. (2004 a, 2004b).

^b Disturbance indicator calculations in Kaufmann et al. (1999).

^c % silts, clays and finer in Xeric and Plains; % sands and finer in Mountains.

^d U.S. Geological Survey 1:100,000 digital line graph data set.

^e Average number of types of human disturbance visible at each of 11 stations.

^f U.S. Census Bureau 1990 cartographic boundary files.

^g U.S. Geological Survey national land cover data set (NLCD) 1992.

^h Total of agriculture, urban, and mining land uses.

disturbed cases. We plotted those least-disturbed and most-disturbed counts against the natural gradients used in that region. If the distribution of high scores along any gradient was skewed (e.g., few high scores at low elevations), we returned to the third step and adjusted the criteria to achieve a more balanced distribution of high scores along that gradient. We did this to assure adequate numbers of least disturbed sites across the full range of the natural gradients and to describe least-disturbed conditions for any given ecological context (e.g., small, low gradient, low elevation streams in the Xeric region). Finally, we set criteria for the least-disturbed and most-disturbed classes to each include about 15% of sites. Ideally, the least-disturbed sites should be in the top tier of least-disturbed total scores and should not be rated as most-disturbed for any indicator. However, in order to achieve the goal of about 15% of sites distributed across the full range of the natural gradients, we needed to accept some sites that were rated most-disturbed for one or two indicators.

We evaluated the site classification results in several ways. We mapped the locations of the least-disturbed and most disturbed sites. We examined boxplots of the natural gradients data

for the three classes of sites (least-disturbed, most-disturbed, and intermediate). Finally, we compared our site classes against an independently derived measure of disturbance, the rapid fine-screen (RFS) disturbance scores. The RFS rates the numbers, kinds, intensity, and proximity to the stream of human disturbances visible in digital (aerial) orthophotographs (1 m resolution) for each site's catchment (P. Lattin, Dynamac, Inc., unpublished data); scores ranged from 0 (no visible human disturbance) to 10 (extremely disturbed catchment).

In each region, we examined the degree of concordance and discordance between each disturbance indicator's least- and most-disturbed classifications and the sites' overall least- and most-disturbed classifications. We calculated concordance scores for each disturbance indicator at least-disturbed and at most-disturbed sites as the number of times the indicator class agreed with the overall class, divided by the number sites in the class (times 100 to give a percentage). Similarly, we calculated discordance scores based on the number of times the indicator and overall classes were in complete disagreement (i.e., one classed as least-disturbed with the other classed as most-disturbed; intermediate values were not

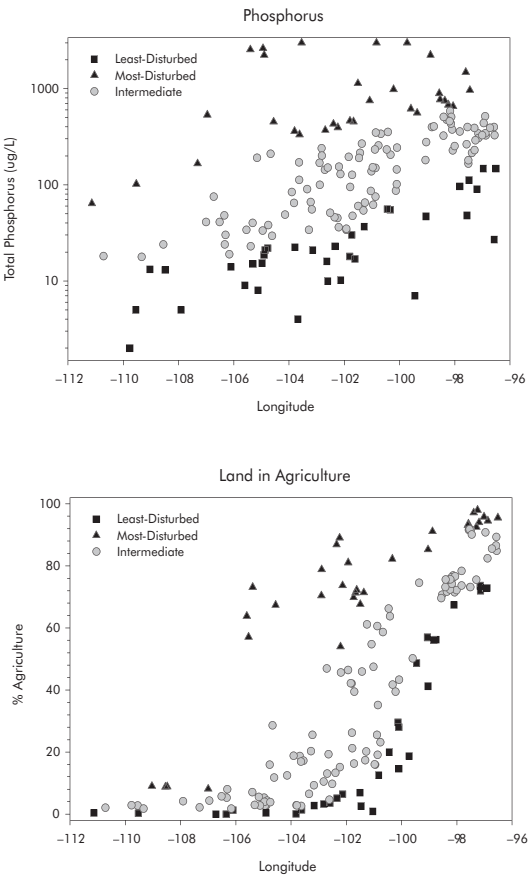


Figure 2. Example of the results of delineating least-disturbed (squares) and most-disturbed (triangles) condition for total phosphorus and percent agricultural land use at 167 sites in the Plains region. The sites are plotted by east–west geographic position (longitude; west to the left). Sites with least-disturbed and most-disturbed values were selected along the full length of the natural gradient to encompass 15–20% of sites for each disturbance class.

included). In the Mountains and Xeric regions, we calculated concordance and discordance separately for high, mid-, and low elevation sites (>2,000 m, 1,000–2,000 m, <1,000 m); in the Plains, we used eastern, middle, and western longitude classes.

Finally, we assessed biological assemblages at least- and most-disturbed sites. We classified vertebrate species tolerance of disturbances through use of weighted averaging (Dixit et al. 1999) and bubble plot (Whittier and Hughes 1998) meth-

ods. For each region, we characterized the differences in aquatic vertebrate assemblages between least- and most-disturbed sites (1) by comparing distributions of values of selected commonly used assemblage metrics (e.g., proportion of individuals of nonnative species, proportion of tolerant individuals), and (2) by comparing species presence at least- and most-disturbed sites. We also compared distributions of values of selected macrobenthos assemblage metrics at least- and most-disturbed sites in each region.

RESULTS

Site Distribution

Of the 490, 177, and 168 sites sampled in the Mountains, Xeric and Plains, respectively, we classified 71, 27, and 23 sites as least-disturbed and 85, 33, and 37 sites as most-disturbed (Table 3). The least- and most-disturbed sites were fairly well distributed geographically (Figure 3). The site classification procedure produced similar distributions of elevation, slope, stream size, and in the case of the Plains, longitude values for

Table 3. Comparison of the size of the regional vertebrate species pools for least-disturbed and most-disturbed sites in 12 states of the western United States, by region. Permit restrictions imposed by government agencies were the primary reasons sites were not sampled for vertebrates. Non-fish vertebrates were mostly amphibians.

Region	Sites	Not sampled for ver- tebrates	Fish species	Non- fish taxa
<i>Mountains</i>				
Least-disturbed	71	37%	22	8
Most-disturbed	85	14%	61	11
<i>Xeric</i>				
Least-disturbed	27	19%	27	6
Most-disturbed	33	24%	39	5
<i>Plains</i>				
Least-disturbed	23	4%	54	2
Most-disturbed	37	8%	61	5

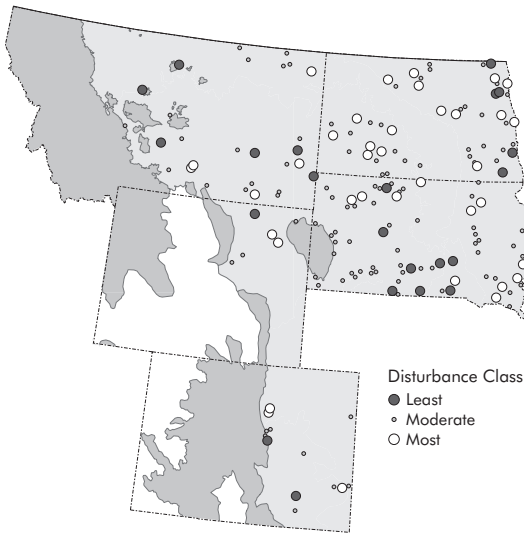


Figure 3. Locations of least-disturbed (dots), most-disturbed (large circles), and moderately disturbed (small circles) sites in the Plains region.

least-disturbed, intermediate, and most-disturbed sites (Figure 4). In each region, our least-disturbed and most-disturbed sites generally had low and high RFS disturbance scores, respectively (Figure 5).

Stressor Indicator and Overall Disturbance Concordance

We observed several patterns in the plots of disturbance indicator concordance and discordance with the site classifications (Figures 6–8). First, no disturbance indicator was completely concordant with the overall site classifications in any region. Second, some disturbance indicators were highly concordant with the overall least-disturbed classification, but showed some discordance with the most-disturbed classification. That is, a disturbance indicator can have least-disturbed values in nearly all least-disturbed sites, and in many of most-disturbed sites as well. An example is the disturbed land use indicator in the Mountains. Nearly all least-disturbed Mountain sites had no agriculture, urban, or mining land use in their catchments, but neither did a quarter and a third of the mid- and high-eleva-

tion most-disturbed sites (Figure 6). Third, for some disturbance indicators, concordance or discordance with site classification varied with ecological position in the landscape. For example, at least-disturbed sites in the Xeric region, the concordance of the disturbed land use indicator increased with elevation; at most-disturbed sites, discordance was also high at high elevation sites (Figure 7). In general, the water quality indicators showed somewhat higher concordance with the overall classifications, and the site-scale physical habitat indicators showed the least concordance, especially the natural fish cover indicator in the Mountains and Xeric regions. Overall, disturbance indicator concordance was lowest and discordance was highest in the Plains (Figure 8).

Vertebrate Assemblages and Species

The distribution of values of vertebrate assemblage metrics varied by region and by disturbance class within the regions (Figure 9). There was less contrast in vertebrate assemblage metrics between least- and most-disturbed sites in the Plains region and the greatest contrast in the Xeric. In general, most-disturbed sites had higher proportions of nonnative individuals, with the highest values in the Xeric. The four most widespread species (occurring in the greatest proportion of sites) in most-disturbed Xeric sites were nonnatives: common carp *Cyprinus carpio*, fathead minnow *Pimephales promelas*, western mosquitofish *Gambusia affinis*, and green sunfish *Lepomis cyanellus* (Tables 3, 4). In the most-disturbed Mountains sites, the most widespread nonnative species were brown trout *Salmo trutta* and rainbow trout *Oncorhynchus mykiss* (the latter being native to about one-half of the assessment area; Tables 3 and 5). In the Plains, the most widespread nonnative fish was the common carp, regardless of disturbance class (Tables 3, 6). The most widespread nonnatives in least-disturbed Mountains and Xeric sites were rainbow trout, brook trout *Salvelinus fontinalis*, and brown trout.

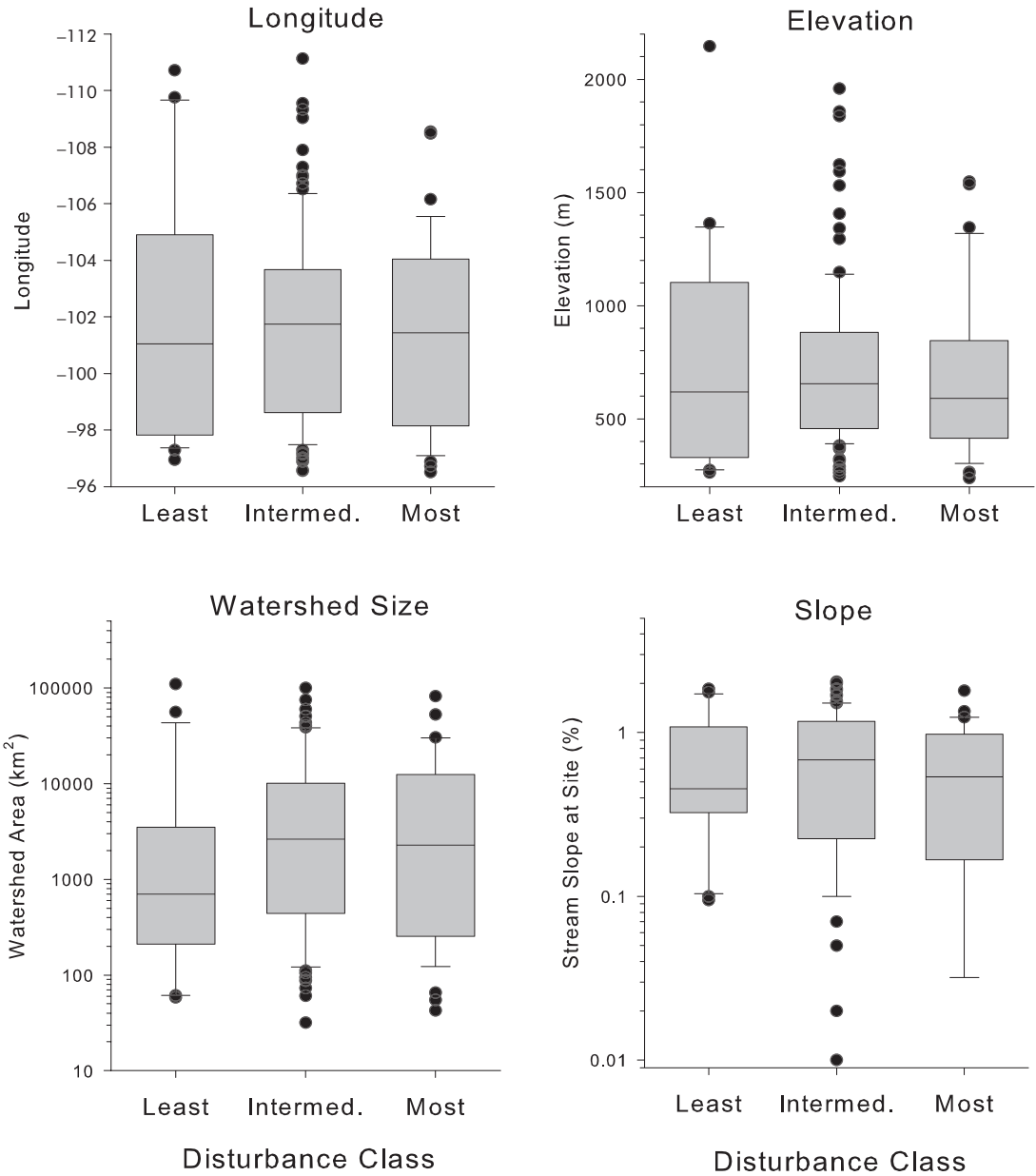


Figure 4. Boxplots of the distribution of least-disturbed, intermediate, and most-disturbed sites in the Plains along the longitude, elevation, stream size, and stream slope gradients. Boxes show medians and quartiles, whiskers indicate 10th and 90th percentiles, and circles indicate outliers.

Relative abundances of vertebrate species judged to be sensitive (intolerant) to human disturbance were much higher in least-disturbed sites than in most-disturbed sites in the Xeric and Mountains (Figure 9). The sensitive species in the

Xeric region were primarily rainbow trout, brook trout, and mountain whitefish *Prosopium williamsoni*; in the Mountains, they were rainbow trout, cutthroat trout *O. clarkii*, tailed frog *Ascaphus truei*, brook trout, and Pacific giant

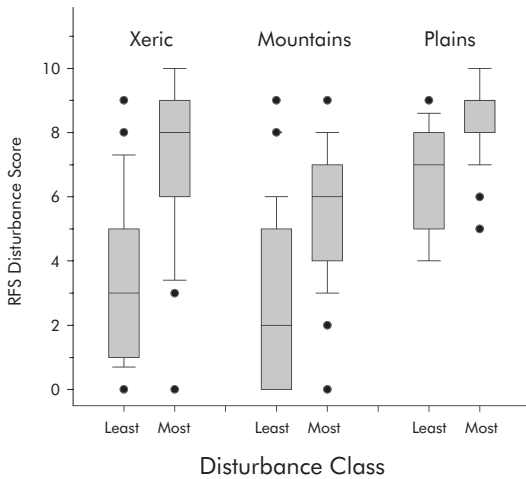


Figure 5. Boxplots of rapid fine-screen (RFS) disturbance scores for the least-disturbed and most-disturbed sites in the three regions. RFS scores were based on visual assessment of digital orthophotographs of the sites' catchments. Boxes show medians and quartiles, whiskers indicate 10th and 90th percentiles, and circles indicate outliers.

salamander *Dicamptodon tenebrosus*. Sensitive vertebrates were uncommon in the Plains, regardless of disturbance class. In contrast, species judged to be tolerant of human disturbance were not collected in least-disturbed sites in Xeric and Mountains regions, but occurred in most Plains sites, with somewhat higher relative abundances in the most-disturbed sites. Tolerant species were collected in 80% and 30% of assemblages at most-disturbed Xeric and Mountain sites.

In the Xeric and Mountains regions, 43% and 8% of assemblages at least-disturbed sites had more than 10% of omnivorous individuals, while assemblages in most-disturbed Xeric and Mountains sites had 75% and 35% omnivorous individuals. In the Plains, the distribution of percent omnivore values was nearly identical in least- and most-disturbed sites. Nontolerant (sensitive and intermediate tolerance) invertivores were more abundant in least-disturbed sites than in most-disturbed sites in all three regions.

Regional vertebrate species pools differed among the regions and between disturbance

classes within the regions in several ways (Tables 3–6). First, there were larger species pools in the most-disturbed sites compared to the least-disturbed sites in all three regions (Table 3). Many of the additional species in the most-disturbed sites in these regions were nonnative or tolerant species (especially in the Xeric) that tended to be characteristic of warmer, more productive waters. In the Mountains, the nonnative warmwater species individually tended to be found in relatively few sites (<10% of most-disturbed sites), whereas in the Xeric (Table 4), eight of these species occurred in more than 10% of the most-disturbed sites. In the Mountains, the only widespread nonnatives were trout (Table 5), with brook trout more common in least-disturbed sites and brown trout more common in most-disturbed sites. Rainbow trout was fairly evenly divided by disturbance class outside its native range.

A second pattern was the lack of contrast in the regional species pool between the Plains region least- and most-disturbed sites (Table 6). The numbers of species in the two disturbance classes were similar in the Plains, but differed much more in the other two regions (Table 3). Most species commonly collected at least-disturbed sites in the Xeric and Mountains were rarely or never collected at most-disturbed sites, and vice versa. In the Plains, however, only four species listed in Table 6 were exclusive to one of the disturbance classes.

Third, amphibians were a much larger component of the vertebrate assemblages in the Mountains than in the other two regions (Table 3), particularly in the least-disturbed sites (Table 5). Three most commonly collected species in the Mountains least-disturbed sites were amphibians. However, most of the Mountains' amphibians occur only in Washington, Oregon, California, and parts of Idaho. Many of the Mountains streams typically had fewer than three fish species. A subset of the least- and most-disturbed streams in the Mountains and Xeric apparently had no vertebrates.

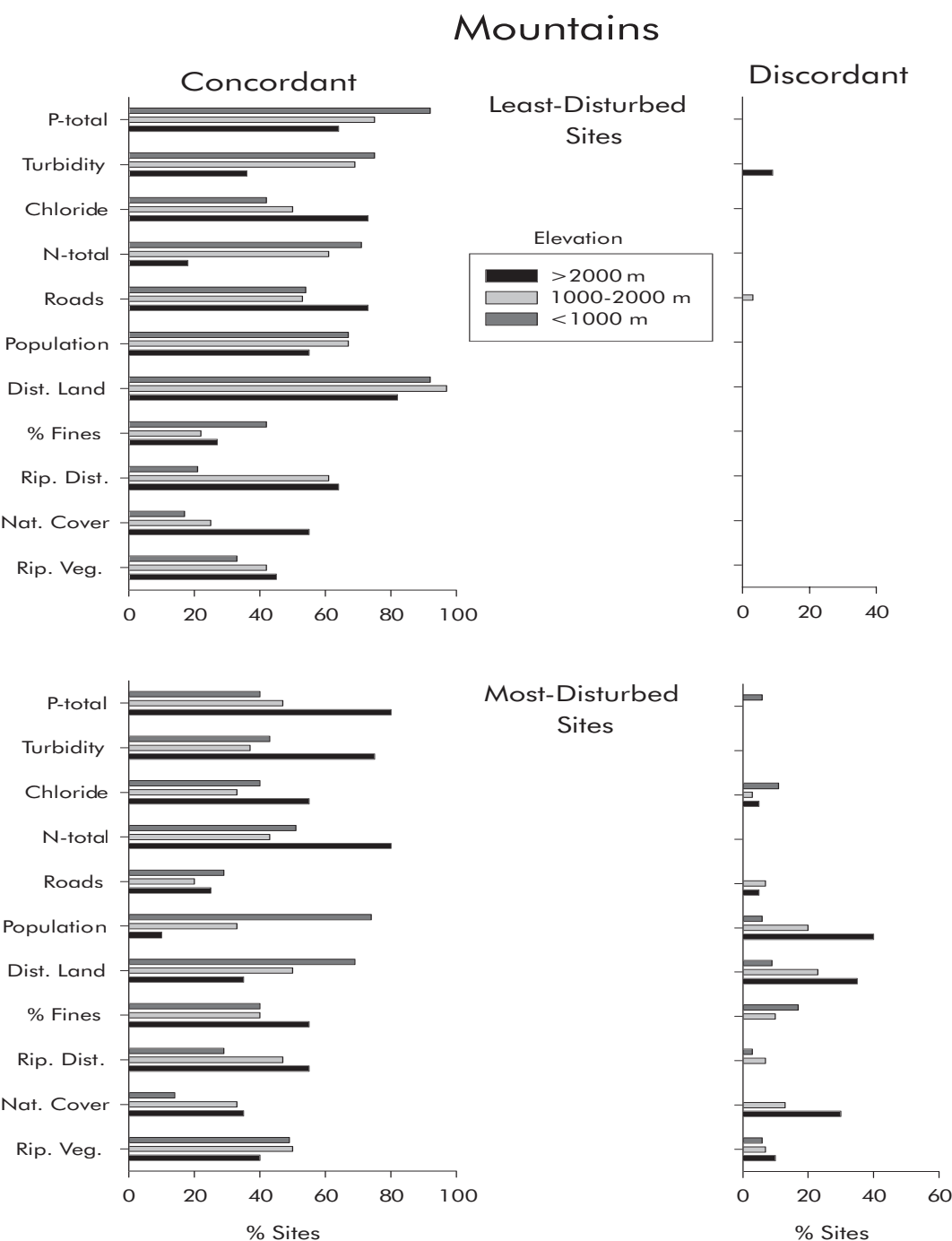


Figure 6. Concordance and discordance between disturbance indicators (Table 2) and the overall site classifications for least-disturbed and most-disturbed sites in the Mountains region, by elevation classes. Upper graphs are for least-disturbed sites and lower graphs are for most-disturbed sites. Concordances are on the left and discordances are on the right. Bar lengths are the percent of sites where the disturbance indicator agreed with the site classification (for concordance) or where the disturbance indicator was opposite the site classification (for discordance).

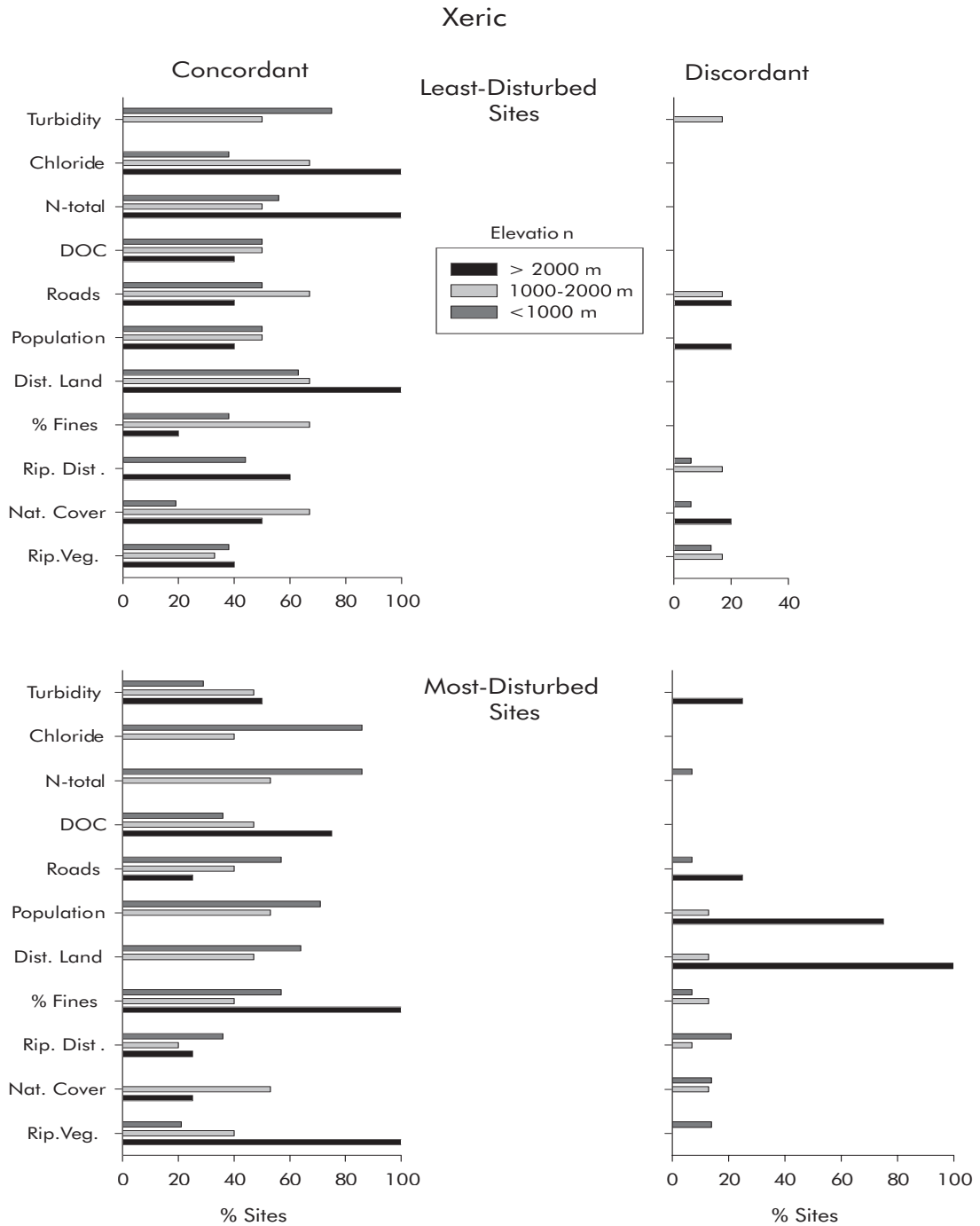


Figure 7. Concordance and discordance between disturbance indicators (Table 2) and the overall site classifications for least-disturbed and most-disturbed sites in the Xeric region, by elevation classes. Upper graphs are for least-disturbed sites and lower graphs are for most-disturbed sites. Concordances are on the left and discordances are on the right. Bar lengths are the percent of sites where the disturbance indicator agreed with the site classification (for concordance) or where the disturbance indicator was opposite the site classification (for discordance).

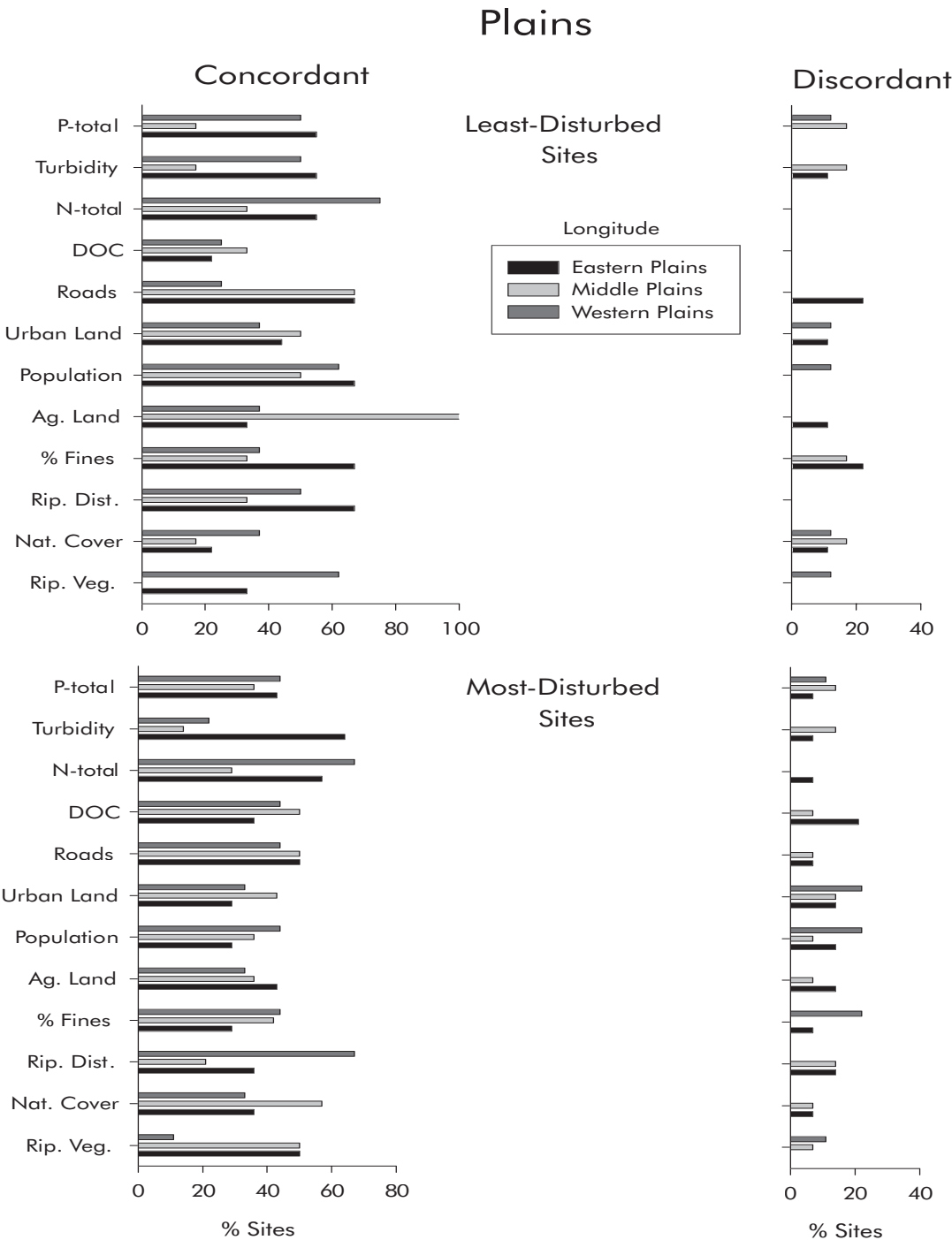


Figure 8. Concordance and discordance between disturbance indicators (Table 2) and the overall site classifications for least-disturbed and most-disturbed sites in the Plains region, by geographic location (east of 100°; between 100° and 104°; west of 104°). Upper graphs are for least-disturbed sites and lower graphs are for most-disturbed sites. Concordances are on the left and discordances are on the right. Bar lengths are the percent of sites where the disturbance indicator agreed with the site classification (for concordance) or where the disturbance indicator was opposite the site classification (for discordance).

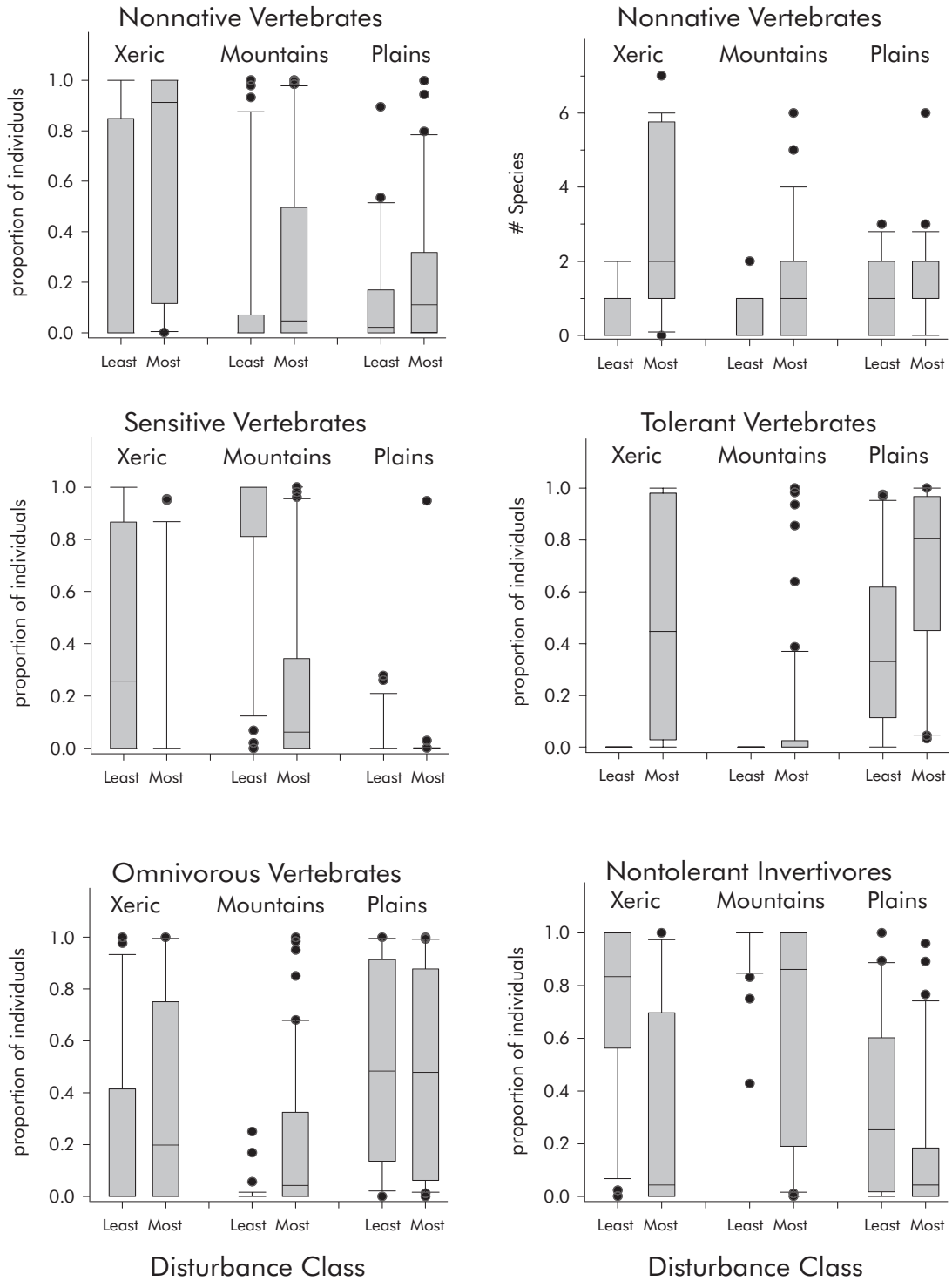


Figure 9. Boxplots of selected vertebrate assemblage metrics at least-disturbed and most-disturbed sites in the three regions. Boxes show medians and quartiles, whiskers indicate 10th and 90th percentiles, and circles indicate outliers.

Table 4. Vertebrate species commonly collected in the Xeric region. The percent of sites in the two disturbance classes is based on the total sites in each class sampled for vertebrates. No vertebrates were found at 9% of the least-disturbed sites and 16% of the most-disturbed sites. Parentheses around common names indicate nonnative species.

Common name	Scientific name	% least-disturbed	% most-disturbed
<i>More often at least-disturbed sites</i>			
rainbow trout	<i>Oncorhynchus mykiss</i>	68	8
speckled dace	<i>Rhinichthys osculus</i>	27	16
(brook trout)	<i>Salvelinus fontinalis</i>	23	4
sculpin ^a	<i>Cottus</i> spp.	23	8
longnose dace	<i>R. cataractae</i>	18	4
mountain whitefish	<i>Prosopium williamsoni</i>	14	4
other Salmonidae		18	4
sucker group A ^b	<i>Catostomus</i> spp.	23	4
<i>Similar between disturbance classes</i>			
(brown trout)	<i>Salmo trutta</i>	14	8
bluehead sucker	<i>Catostomus discobolus</i>	9	12
mountain sucker	<i>C. platyrhynchus</i>	8	9
<i>More often at most-disturbed sites</i>			
(common carp)	<i>Cyprinus carpio</i>	0	32
(fathead minnow)	<i>Pimephales promelas</i>	0	24
(western mosquitofish)	<i>Gambusia affinis</i>	0	24
sucker group B ^c	<i>Catostomus</i> spp.	0	24
(green sunfish)	<i>Lepomis cyanellus</i>	0	16
(bullfrog)	<i>Rana catesbeiana</i>	0	16
(yellow bullhead)	<i>Ameirus natalis</i>	0	16
(red shiner)	<i>Cyprinella lutrensis</i>	0	12
(channel catfish)	<i>Ictalurus punctatus</i>	0	12

^a Paiute sculpin *C. beldingii*, mottled sculpin *C. bairdii*, shorthead sculpin *C. confusus*, torrent sculpin *C. rhotheus* in least-disturbed sites; prickly sculpin *C. asper* in most-disturbed sites

^b Longnose sucker *C. catostomus*, largescale sucker *C. macrocheilus*, Sacramento sucker *C. occidentalis*, bridgelip sucker *C. columbianus*

^c Utah sucker *C. ardens*, white sucker *C. commersonii*, flannelmouth sucker *C. latipinnis*, Tahoe sucker *C. tahoensis*

Finally, some fairly widespread species that were characteristic of a particular disturbance class in one region may be indifferent or more characteristic of the other disturbance class in another region. For example, in the Xeric, rainbow trout was the most widespread species in least-disturbed sites (68% of sites) but uncommonly collected in most disturbed sites (8%). In the Mountains, it was also the most widespread species in least-disturbed sites (60%), but also in most-disturbed sites (42%). Likewise, speckled dace *Rhinichthys osculus* was found in nearly a quarter of the most-disturbed Mountains sites, and rarely collected at least-disturbed sites (4%). In the Xeric, this pattern was reversed. In the Plains, creek chub *Semotilus atromaculatus*, usually considered to be tolerant, was more commonly collected in least-disturbed sites.

Macrobenthos Assemblage Metrics

In all three regions, the macrobenthos assemblages in least-disturbed sites were dominated by insects, while assemblages in most-disturbed sites tended to have higher proportions of noninsects, such as oligochaetes (Figure 10). Proportions of individuals of Ephemeroptera, Plecoptera, and Trichoptera (EPT) taxa were higher in least-disturbed sites in all regions. Numbers of EPT taxa showed stronger differences between least- and most-disturbed sites in the Mountains and Xeric regions than did the proportion of EPT individuals. In the Plains, the median number of EPT taxa differed by two between least- and most-disturbed sites; the proportion of EPT individuals tended to be higher in least-disturbed sites. Overall, the EPT taxa

Table 5. Vertebrate species commonly collected in the Mountains region. The percent of sites in the two disturbance classes is based on the total sites in each class sampled for vertebrates. No vertebrates were found at 11% of the least-disturbed and most-disturbed sites. Parentheses around common names indicate nonnative species

Common name	Scientific name	% least-disturbed	% most-disturbed
<i>More often at least-disturbed sites</i>			
rainbow trout	<i>Oncorhynchus mykiss</i>	60	42
tailed frog	<i>Ascaphus truei</i>	26	0
Pacific giant salamander	<i>Dicamptodon tenebrosus</i>	24	3
(brook trout)	<i>Salvelinus fontinalis</i>	20	5
<i>Similar between disturbance classes</i>			
cutthroat trout	<i>Oncorhynchus clarkii</i>	18	12
mountain whitefish	<i>Prosopium willamsoni</i>	2	10
<i>More common at most-disturbed sites</i>			
sculpins ^a	<i>Cottus</i> spp.	22	33
(brown trout)	<i>Salmo trutta</i>	7	25
speckled dace	<i>Rhinichthys osculus</i>	4	22
longnose dace	<i>R. cataractae</i>	2	21
mountain sucker	<i>Catostomus platyrhynchus</i>	2	15
redside shiner	<i>Richardsonius balteatus</i>	0	12
white sucker	<i>C. commersonii</i>	0	10
largescale sucker	<i>C. macrocheilus</i>	0	10
threespine stickleback	<i>Gasterosteus aculeatus</i>	0	10

^a Seven *Cottus* species were collected at least-disturbed sites: torrent sculpin (7%), mottled sculpin (4%), Paiute sculpin (4%), reticulate sculpin *C. perplexus* (4%), shorthead sculpin (2%), ruffle sculpin *C. gulosus* (2%), and marbled sculpin *C. klamathensis* (2%); and nine species were collected at most-disturbed sites: reticulate sculpin (10%), prickly sculpin (8%), mottled sculpin (7%), ruffle sculpin (5%), torrent sculpin (5%), Paiute sculpin (4%), shorthead sculpin (2%), marbled sculpin (2%), and slimy sculpin *C. cognatus* (1%).

richness is low in the Plains (median = 4). In the Plains, the proportion of individuals of Chironomidae was higher in least disturbed sites, but there were no clear disturbance class differences for this metric in the Mountains and Xeric (Figure 10). The proportion of individuals in the five most abundant taxa was higher in most-disturbed Xeric and Mountains sites, but similarly high for both disturbance classes in the Plains.

DISCUSSION

Site Classification

Our site classification goal was to select sites from the EMAP survey that generally represent the least-disturbed and most-disturbed conditions for the range of ecological settings in each region. If successful, our procedure should produce similar distributions of natural gradient values

for least-disturbed, intermediate, and most-disturbed sites in a region, as shown in Figure 4 for the Plains. This assures inclusion of least-disturbed sites at the human-used ends of the natural gradients (e.g., low elevation, relatively flat land), and likewise, inclusion of most-disturbed sites at the less used ends of those gradients. We also expected that the least- and most-disturbed sites would be fairly well distributed geographically (Figure 3). If a majority of the sites in a disturbance class were located in a small part of their region or were absent from large areas, we would suspect that (1) the regional framework was too broad; (2) other natural gradients or stress indicators should have been assessed; or (3) there were serious differences in how the data were collected among geographic areas. A broad geographic distribution of least-disturbed sites partially achieves the goal of having regionally representative reference sites, as proposed by Hughes et al. (1986) and Hughes (1995).

Table 6. Vertebrate species commonly collected in the Plains region. The percent of sites in the two disturbance classes is based on the total sites in each class sampled for vertebrates. No vertebrates were found at 5% (1 site) of the least-disturbed sites. Parentheses around common names indicate nonnative species

Common name	Scientific name	% least-disturbed	% most-disturbed
<i>More often at least-disturbed sites</i>			
sand shiner	<i>Notropis stramineus</i>	44	29
creek chub	<i>Semotilus atromaculatus</i>	41	15
channel catfish	<i>Ictalurus punctatus</i>	32	18
shorthead redhorse	<i>Moxostoma macrolepidotum</i>	32	21
common shiner	<i>Luxilus cornutus</i>	27	9
longnose dace	<i>Rhinichthys cataractae</i>	27	12
blackside darter	<i>Percina maculata</i>	18	0
plains minnow	<i>Hybognathus placitus</i>	18	3
(brook trout)	<i>Salvelinus fontinalis</i>	14	0
tadpole madtom	<i>Noturus gyrinus</i>	14	0
<i>Similar between disturbance classes</i>			
fathead minnow	<i>Pimephales promelas</i>	50	59
(common carp)	<i>Cyprinus carpio</i>	36	44
red shiner	<i>Cyprinella lutrensis</i>	23	15
river carpsucker	<i>Carpionodes carpio</i>	18	15
goldeye	<i>Hiodon tergisus</i>	14	18
johnny darter	<i>Etheostoma nigrum</i>	18	12
longnose sucker	<i>Catostomus catostomus</i>	18	9
bigmouth shiner	<i>Notropis dorsalis</i>	18	9
stonecat	<i>Noturus flavus</i>	14	15
pumpkinseed	<i>Lepomis gibbosus</i>	9	15
emerald shiner	<i>Notropis atherinoides</i>	9	15
bluntnose minnow	<i>P. notatus</i>	14	9
flathead chub	<i>Platygio bio gracilis</i>	14	9
western silvery minnow	<i>Hybognathus argyritis</i>	14	6
sauger	<i>Sander canadensis</i>	14	6
<i>More often at most-disturbed sites</i>			
white sucker	<i>Catostomus commersonii</i>	55	68
black bullhead	<i>Ameiurus melas</i>	23	56
green sunfish	<i>Lepomis cyanellus</i>	18	35
northern pike	<i>Esox lucius</i>	14	32
walleye	<i>Sander vitreus</i>	5	18
brook stickleback	<i>Culaea inconstans</i>	0	12

The independently derived rapid fine-screen (RFS) disturbance scores were generally lower for our least-disturbed sites and higher for our most-disturbed sites (Figure 5). The RFS process assessed each site's catchment and did not incorporate site-scale chemical or physical habitat data (except as visible on digital orthophotographs), nor did it compensate for ecological position in the landscape (i.e., criteria were not relaxed in heavily used regions). We expected each method to detect certain disturbances not detected by the other. We also ex-

pected that some of our least-disturbed sites in lower elevation, lower gradient streams would have mid-range or higher RFS disturbance scores because often in those ecological settings, the least-disturbed conditions are at least moderately disturbed by human activity. Hughes et al. (1998) and Bryce et al. (1999a) also found no minimally disturbed sites at low elevations.

The patterns in Figure 5 conform to what would be expected for each region. In the Plains, the lowest RFS disturbance score was four. The median RFS score for our least-disturbed Plains

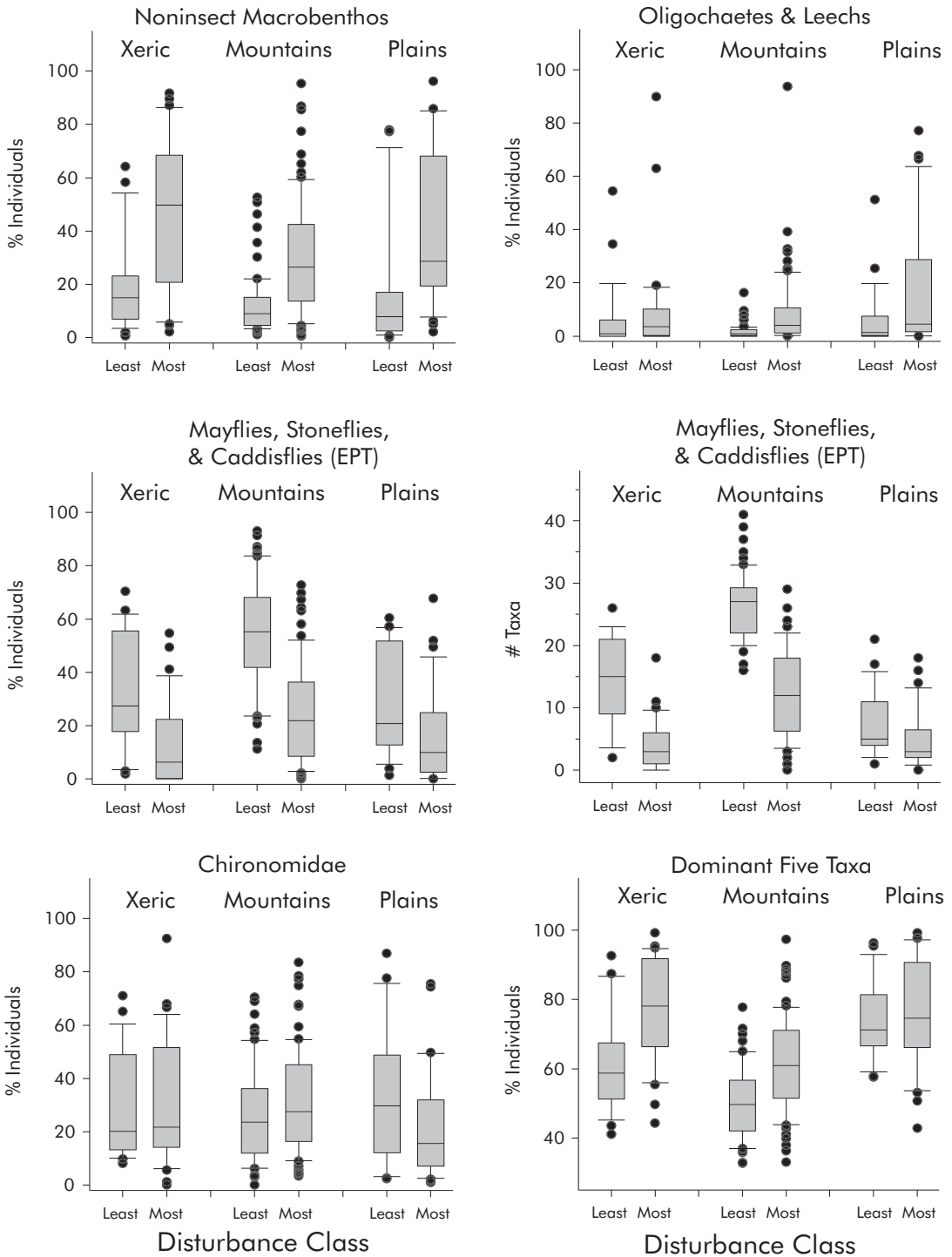


Figure 10. Boxplots of selected macrobenthos assemblage metrics at least-disturbed and most-disturbed sites in the three regions. Dominant five taxa is the percentage of individuals belonging to the five most abundant taxa at each site. Boxes show medians and quartiles, whiskers indicate 10th and 90th percentiles, and circles indicate outliers.

sites was seven, confirming that the least-disturbed locations in the Plains have moderate to moderately severe levels of human disturbance in the catchments. Thus, there is relatively little contrast between the least- and most-disturbed Plains sites. Conversely, in the Mountains, the median RFS score for most-disturbed sites was six, with the highest score being nine. On average, the least-disturbed catchments in the Plains are subject to more disturbance than the most-disturbed catchments in the Mountains. Similarly, Bramblett and Fausch (1991) found the lack of distinct disturbance differences in the Plains hindered index of biotic integrity (IBI) development. The greatest within-region contrast occurred in the Xeric, where most of the urban dominated catchments occurred. There are also large unpopulated areas in the Xeric, where grazing may be the only human influence.

Disturbance Indicator and Site Classification Concordance

The interactions and relationships among human disturbances may be nearly as complex as the interactions among natural ecosystems processes. In order to assess human impact on ecosystems, one would like to be able to rank stream sites along a continuum of human disturbance, from not disturbed through the various degrees of intermediate disturbance to severely disturbed. To our knowledge, there is no such quantitative human disturbance ranking for fluvial systems. This is partially due to the fact that different stressors act differently at different scales in different ecological settings (Wang et al. 2003) and at different disturbance levels (Wang et al. 2006, this volume). The patterns in the concordance and discordance between the disturbance indicators and the overall disturbance classes (Figures 6–8) provide some insights into these topics, beginning with the fact that no disturbance indicator was completely concordant with the overall site classifications in any region, and all were at least occasionally discordant. This confirms the idea that no single measure can be

relied upon to indicate all of the various anthropogenic disturbances in stream and river ecosystems (Bryce et al. 1999b).

The catchment-scale disturbance indicators (disturbed land uses, road density and population density) in the Mountains and Xeric regions illustrate that an individual indicator's concordance and discordance with overall disturbance classes can vary along the natural gradients and between disturbance classes. In the Mountains, a majority of sites had no agriculture, urban, or mining land uses, leading to the situation where the disturbed land use indicator and the site class were concordant at nearly all least-disturbed sites, but were discordant at about a third of the most-disturbed sites (Figure 6). This pattern was strongest at higher elevations ($>2,000$ m). Thus, at high elevations, one cannot assume that sites with no urban, agriculture, and mining in their catchments are in least-disturbed condition. However, one would not necessarily discard this disturbance indicator for Mountains sites because the disturbed land use signal, although uncommon, is likely to be important where it occurs. At lower elevations ($<1,000$ m), where we expect more human activity in general, this disturbance indicator becomes more concordant with most-disturbed condition.

The relatively low concordance of the site-scale habitat indicators with overall disturbance class illustrates that physical habitat at the site-scale does not necessarily represent the conditions of the catchment as a whole. Likewise physical habitat conditions at any given site should not be expected to greatly affect water quality; the site-scale effect should diminish with increasing stream size. Site-scale physical habitat disturbance indicators were significantly correlated with the catchment-scale indicators in less than half of the cases (significant correlations ranged from 0.12 to 0.34 in the Mountains, from 0.14 to 0.16 in the Xeric, and from 0.14 to 0.31 in the Plains [Pearson's r]). It is assumed that local physical habitat conditions are important for biological assemblage condition. However, the relative importance of local versus distal

disturbances has not yet been resolved. For example, Lammert and Allan (1999) found stronger associations between local site-scale habitat measures and biotic measures, while Roth et al. (1996), Angermeier and Winston (1998), and Gido et al. (2006, this volume) found stronger associations with catchment-scale measures. Pont et al. (2005) determined that 11 common European fish species responded differently to environmental scale, with half responding more strongly to catchment- and half to local-scale conditions. Wang et al. (2006) found that site-scale factors were less important when catchments were highly disturbed. An interesting future assessment would be to compare biotic condition at sites where site-scale, catchment-scale, and water quality indicators are concordant, with sites where they are discordant.

Biological Patterns in the Mountains and Xeric Regions

A primary motivation for developing our site classification process was as an aid for developing biological indicators of stream and river condition for all ecological settings in the western United States. The comparison of biological assemblage characteristics at least- and most-disturbed sites in comparable ecological settings will be useful for evaluating our assumptions and for stimulating new ideas.

We selected six commonly used vertebrate assemblage metrics (Figure 9) as a preliminary exploration of assemblage characteristics at least- and most-disturbed sites. The patterns in metric values tended to match our expectations in the Mountains and Xeric regions. In general, most-disturbed sites had more nonnative species and higher proportions of nonnative individuals. In higher elevation sites, the nonnatives were mostly rainbow trout, brook trout, and brown trout. Nonnative trout pose a paradox for ecological condition assessment; in addition to being prized as sport fish, they indicate good water quality and physical habitat conditions, but often are a biological disturbance (Moyle and

Light 1996; Dunham et al. 2004). At lower elevations in the Xeric region, many of the nonnatives were tolerant of disturbed conditions (Tables 3 and 4). Vertebrate assemblages in least-disturbed sites had more individuals of sensitive species, no tolerant species, and few omnivores and tended to be dominated by nontolerant invertivores. Sensitive species were uncommon at most-disturbed sites, while omnivores were fairly common.

A variety of human disturbances (particularly point-sources of pollution) are capable of eliminating fish from streams, and in many parts of the country, a fishless stream would be considered highly impaired. However, in the western United States, many small, high elevation streams are naturally fishless (as they are in the Appalachians; McCormick et al. 2001). In fact, the presence of fish may indicate human disturbance (e.g., stocked trout). Prior to classifying sites into disturbance classes, we were uncertain under which circumstances a lack of native fish might indicate poor biotic condition. In the Mountains, our data showed that for small streams (cross-section area $< 1 \text{ m}^2$), about the same number of least- and most-disturbed sites lacked fish. These results can help to define a range of ecological conditions in which fish should be considered an optional measure of ecological condition, that is, where it may not be appropriate to apply an IBI-type assessment based on fish.

The low fish species richness common in Mountains and Xeric coldwater streams challenges our ability to develop fish-based IBIs. Recently, Hughes et al. (2004) included amphibians in an IBI for western Oregon and Washington, based on work by Murphy and Hall (1981), Hawkins et al. (1983), and Moyle and Marchetti (1998) that showed amphibians can be the dominant vertebrates in small streams in the northwest. Our data indicate that this approach can be expanded to other areas in the Mountains and possibly the Xeric, where amphibians are likely to be found in streams.

As with vertebrate assemblages, distribution of the values of macrobenthos metrics in the

Mountains and Xeric regions (Figure 10) followed the patterns expected for least- and most-disturbed sites (Barbour et al. 1995; Klemm et al. 2003). That is, the patterns are in line with expectations about the characteristics of healthy macrobenthos assemblages and how those change with increased human disturbance. Insects dominated least-disturbed sites, while noninsects increased at most-disturbed sites. Among the insects, relatively high abundance of mayflies, stoneflies, and caddisflies (Ephemeroptera, Plecoptera, Trichoptera; EPT) is often considered an indication of a healthy assemblage. Both the proportion of EPT individuals and the number of EPT taxa were higher at least-disturbed sites in these regions. Dominance of macrobenthos assemblages by one or a few taxa, as occurred in many most-disturbed sites in these two regions, has been used as a metric indicating degraded conditions (Barbour et al. 1995; Klemm et al. 2003).

Biological Patterns in the Plains

There were either no differences or relatively minor differences between vertebrate metric values and disturbance classes in the Plains. The lack of pattern in vertebrate assemblage metrics may result from the higher level of human disturbance in this region where least disturbed is actually moderately disturbed. On the other hand, natural (undisturbed) Plains streams historically had highly variable flow regimes and tended to be more turbid, with finer substrates and less physical habitat complexity than undisturbed streams in other regions where these characteristics are usually the physical signs of disturbance (Bramblett and Fausch 1991; Dieterman and Galat 2004; Dodds et al. 2004). Undisturbed fish assemblages in the Plains should be expected to have many species tolerant of natural stress, which can mimic anthropogenic stress.

As with the vertebrate metrics, the differences in occurrence rates of individual species at least- and most-disturbed sites was not as strong as in the other two regions. Some of the species pat-

terns were not as we expected. For example, creek chub and common shiner *Luxilus cornutus* and, to a lesser extent, red shiner *Cyprinella lutrensis* were more commonly collected at least-disturbed sites (Table 6). However in most, if not all, IBIs for streams in the eastern United States (e.g., Ohio EPA 1987; McCormick et al. 2001), tolerant generalists such as creek chub are used in negative metrics. In the Xeric region, red shiner was collected only in most-disturbed sites. Clearly, developing a vertebrate assemblage IBI for the Plains will be a challenge, requiring consideration of the naturally stressful physical environment as well as the pervasive human use of the land.

A few of the macrobenthos metrics showed reasonably good separation for least- and most-disturbed sites, particularly the proportion of noninsect individuals (Figure 10). Somewhat surprising was the difference in proportion of EPT individuals between disturbance classes. However, the number of EPT taxa was low (median = 4; similar to most-disturbed Xeric sites) and not different between disturbance classes. EPT taxa are generally considered characteristic of well-oxygenated riffles in streams, an uncommon component of Plains streams. Thus, these low taxa numbers were not unexpected. The fairly high values for the Dominant 5 Taxa metric in both disturbance classes may reflect the characteristically simplified physical habitat in that region or the overall higher levels of human disturbance. We suspect it reflects both natural and human factors.

Another interesting outcome of our preliminary examination of potential macrobenthos metrics was the higher proportion of Chironomidae in least-disturbed Plains sites. Historically, dominance by Chironomidae and Oligochaetes indicated very degraded conditions, particularly from heavy nutrient loading (sewage and/or fertilizers) resulting in low oxygen conditions, or from sedimentation (industrial and municipal sludge or soil erosion) resulting in a simplified substrate (Kolkwitz and Marsson 1909; Bartsch and Ingram 1959). Wilton (2004)

used percent chironomids as a negative metric for Iowa wadeable streams. Conversely, Klemm et al. (2003) found that a Chironomidae metric was not useful in an EMAP survey in the mid-Atlantic Highlands, a result echoed in our data in the Mountains and Xeric lands (Figure 10). However, soft (sandy) substrates that favor chironomids are characteristic of the Plains. In that region, it appears that chironomids avoid more disturbed sites. Thus, our results suggest that in the Plains, proportions of chironomids should be used in positive, rather than negative, metrics.

In conclusion, our method for selecting least-disturbed and most-disturbed sites across the full ranges of a region's natural gradients provided a useful alternative to searching for reference sites in heavily used areas or extrapolating from reference sites in areas with significantly different natural conditions. In any ecological setting, the contrast between least-disturbed and most-disturbed is useful for developing and evaluating indicators of condition. For example, our results in the Plains demonstrate that some widely used biological assemblage metrics are not likely to be useful in that region, but that others, such as a Chironomidae metric, have potential for use. Likewise, in the western mountains, inclusion of amphibians has potential to strengthen vertebrate assemblage metrics and indices in streams with only a few fish species.

If we accept that humans are integral parts of most ecosystems, the contrast between least-disturbed and most-disturbed sites should also be useful for studying the trajectory ecosystems follow as the level and types of human disturbances change. The concordance and discordance of individual disturbance measures with overall human disturbance level, and how these vary with ecological setting has the potential to further our understanding of how human activities affect ecosystems at different scales. In heavily used regions, the differences in biological assemblages, and physical and chemical conditions, at least- and most-disturbed sites should help inform the process of defining a hypothetical undisturbed condition to serve as a restoration goal.

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