16 Predator–Prey Interactions

David A. Beauchamp, David H. Wahl, and Brett M. Johnson

16.1 INTRODUCTION

This chapter focuses on the analysis and interpretation of predator–prey interactions among vertebrates and invertebrates in freshwater systems associated with fisheries. All aquatic species are subject to predation during some phase of life (Mittlebach and Persson 1998). Predator–prey interactions play a major role in determining the structure and function of aquatic communities (Brooks and Dodson 1965; Carpenter et al. 1985; Kerfoot and Sih 1987; Northcote 1988) by influencing parameters such as survival, size structure, growth, behavior, and distribution, as well as biodiversity and water quality of these systems. These interactions are mediated by the physical–chemical environment (Kitchell 1979; Crowder et al. 1981; Coutant 1985; Gregory 1994) and habitat characteristics (Cooper and Crowder 1979; Wiley et al. 1984; Walters and Juanes 1993; Sogard 1994), which, in turn, are affected by human-induced alterations to the environment (Coutant et al. 1979; Jenkins 1979; Sandheinrich and Atchison 1990; Mesa 1994; Mesa et al. 1994).

Predation can regulate the dynamics of prey populations directly by reducing recruitment and survival (Miller et al. 1988; Luecke et al. 1990a; Tonn et al. 1992) or indirectly by altering prey behavior (Eggers 1978; Stein 1979; Clark and Levy 1988; Lima and Dill 1990), distribution, habitat choice, foraging, or growth (Dill and Fraser 1984; Werner and Gilliam 1984; Wurtsbaugh and Li 1985; Clark and Levy 1988; Jakobsen et al. 1988; Ibrahim and Huntingford 1989; Fraser and Gilliam 1992; Milinski 1993; Sogard 1994) or by altering competition and predator–prey interactions (e.g., Paine 1980; Werner et al. 1983; Mittlebach 1986, 1988; Persson 1991; Persson et al. 2000). Humans are very efficient aquatic predators: fishing can have large direct and indirect effects by selectively removing piscine predators, thereby altering food web structure and ecosystem function (He and Kitchell 1990; Schindler et al. 1998; Gislason and Sinclair 2000; Link and Garrison 2002). Prey can also influence predators as prey quantity and quality affect feeding rates, growth, and reproductive success of predators. Temporal and spatial changes in prey availability and vulnerability may influence movement and distribution patterns of predators.

Understanding the role of predation is important for successfully managing both self-sustaining and artificially enhanced fisheries, protecting water quality, conserving sensitive species, and maintaining the ecological integrity of aquatic communities. Because larval and juvenile fishes serve as both predators and prey, recruitment success is often related to the size-dependent ability to forage on available prey (Mittlebach 1981), temporal and spatial patterns in food supply, and interactions with predators and competitors (Dettmers et al. 1996; Mittlebach and Persson 1998; Persson et al. 2000). Introductions of nonnative predators and prey have resulted in extirpations, reduced biodiversity, and significant changes in community structure (Brooks and Dodson 1965; Zaret and Paine 1973; Nesler and Bergersen 1991; Schindler et al. 1998). Managers should consider whether host waters can absorb the additional consumption demand by stocked fishes or if predation losses will undermine the goals of a stocking program. Overfishing predators or enhancing prey populations can disrupt predation rates and result in depensatory declines in predatory fish populations (Johnson and Goettl 1999; Walters and Kitchell 2001; Post et al. 2002). Trophic interactions can also affect water quality. When linkages among multiple trophic levels are strong, changes in abundance at one level can result in a trophic cascade through some or all trophic levels from apex predators to primary producers, thus affecting water transparency (Carpenter et al. 1985; Carpenter and Kitchell 1988; Luecke et al. 1990b; Brett and Goldman 1996). However, the magnitude and effects of predation vary under different environmental and ecological conditions (Abbey and MacKay 1991; Persson et al. 1991; Beauchamp et al. 1999).

In this chapter, we outline methods for analyzing predator–prey interactions at multiple levels: from mechanistic to holistic studies and from examining behavior of individual predators or prey to quantifying predator–prey interactions and determining their effects on the structure and function of freshwater populations, communities, and ecosystems (Table 16.1). Topics are organized into sections on field, experimental, and modeling approaches with regard to spatial, temporal, and size relationships, which commonly underlie predator–prey interactions and are important for minimizing interpolation–extrapolation error in the analysis. Other authors provide descriptive, empirical, and theoretical reviews of predator–prey interactions and the effects of predation on inland aquatic systems (Stroud and Clepper 1979; Zaret 1980; Kerfoot and Sih 1987; Carpenter 1988; Carpenter and Kitchell 1993).

16.2 PREDATOR–PREY QUESTIONS: OBJECTIVES AND APPROACHES

The complexity of predator–prey interactions often requires a complementary, multi-pronged approach that uses some combination of field observation and measurement, experimentation or management manipulation (e.g., stocking, introductions, harvest, or removal), and modeling. The design and analysis of a predator–prey study should be guided by specific information needs, and the study objectives and approaches should follow logically from these questions. Common questions in freshwater fisheries vary in scale and complexity from the behavior

Table 16.1 A spectrum of perspectives for studying fish predation varying from the mechanistic, organismal level (top of table) to the more holistic, ecosystem level (bottom of table). Selecting the appropriate approaches and analytical tools will depend on the research question and the ecological phenomena of interest. Note that uncertainty in measurements may be lower at the mechanistic level but transferability to dynamics in nature may be questionable. Studying more holistic phenomena may rely on integrating results from a variety of measurements and approaches, with a concomitant increase in uncertainty as errors may be compounded. Abbreviations are as follows: analysis of variance (ANOVA); multivariate analysis of variance (MANOVA); available prey to predator ratios (AP/P); forage species biomass to consumer biomass ratio (F/C); and proportional stock density (PSD)

Research question	Approaches	Analytical tools	Examples
Predator and prey behavior	Laboratory trials	ANOVA, MANOVA, multiple regression, path analysis, and ethograms	Wahl and Stein 1988; Hambright 1991; Christensen 1996; Einfalt and Wahl 1997
Predator preferences (e.g., species or size)	Laboratory trials	Electivity indices Diet composition	Hambright 1991; Einfalt and Wahl 1997
	Field measurements	Electivity indices Stable isotope analysis Optimal foraging	Pyke 1984; Mittlebach and Osenberg 1994; Vander Zanden et al. 2000
Predation rate versus prey abundance or availability	Laboratory trials	Functional responses—linear, nonlinear, and multivariate regression	Koski and Johnson 2002
"Balance" between prey and predator populations	Field measurements	Indices: AP/P, F/C, and PSD	Swingle 1950; Anderson and Weithman 1978; Ploskey and Jenkins 1982
Consumption in terms of prey biomass, nutrients, dollars, or contaminant fluxes	Field-based estimates	Fullness-gastric evacuation methods	Elliott and Persson 1978; Ney 1990
	Simulation modeling	Production-based models	Ney 1990
		Bioenergetics models	Kitchell et al. 1977; Ney 1993
	Stable isotopes or tracers	Mass-balance models	Trudel et al. 2000
In situ foraging behavior	Field observations and simulation modeling	Spatially explicit models	Brandt et al. 1992; Stockwell and Johnson 1997; Luo et al. 2001
		Bioenergetics models	Stewart et al. 1981; Baldwin et al. 2000; Burke and Rice 2002
		Visual foraging models	Wright and O'Brien 1984; Beauchamp et al. 1999
Ecosystem structure and function: for example, the role of fishing, trophic cascades, key stones, and cultivation effects	Natural and planned ecosystem "experiments" and simulation modeling	Bioenergetics models	Kitchell 1992; Schindler et al. 1998
		Multispecies virtual population analysis	Pope 1991
		Ecopath/Ecosim	Walters and Kitchell 2001; Walters et al. 1997

and interactions of individual predators or prey to community or ecosystem level dynamics (Table 16.1). Does predation occur? How much predation occurs? Can predation regulate specific prey populations? What factors contribute to the timing, duration, and magnitude of predation? Can the effects of predation be minimized or maximized? More specific questions may follow from the primary questions above. Which predators (species and size) eat which prey (again, by species and size); when is predation occurring (timing and duration of predation), and where is it occurring (is it basinwide or in specific or isolated habitats)? What are the appropriate spatial, temporal, and body size scales that relate to specific predator–prey interactions? What characteristics of predators, prey, or their habitat foster or inhibit predation? Do predators feed selectively on specific prey or feed opportunistically on a variety of prey in proportion to their abundance? Can prey supply support a desirable size structure and abundance of predators?

The nature of each question and desired level of resolution determine the types of studies (e.g., field sampling, experiments, and modeling) and corresponding analyses that should be employed. Effective studies require tight integration of sampling and experimental design tailored to the study objectives with explicit definition of independent and response variables, sampling or experimental units, and appropriate measurement units (e.g., numbers, biomass, nutrients, dollars, or contaminant loading). The desired level of resolution should be specified: presence versus absence of predation; a quantified estimate of predation (in biomass or numbers of prey consumed); predation translated into a mortality rate for prey; predator–prey "balance"; or the strength of different factors contributing to predator–prey interactions. Here, we briefly discuss common questions related to predator–prey interactions and introduce some alternative approaches to address them.

Is there evidence of predation (presence versus absence)? This question can be addressed by laboratory experiments (e.g., will a predator eat this prey under experimental conditions?), an approach that is particularly useful in situations with novel predators or prey, such as invasions (e.g., Nesler and Bergersen 1991; Moyle and Light 1996a, b). Presence of predation may also be addressed by sampling stomach contents of potential predators at times and locations where predation most likely occurs (will the predator eat this prey under natural conditions?); however, stomach contents provide a short-term snapshot of feeding by some individuals and may not be representative of feeding by the predator population over longer periods. Alternatively, stable isotopes (Peterson and Fry 1987) and growth provide broader-scale integration of the feeding history of a consumer but with less temporal resolution. A predation signal may be inferred from stable isotope analysis (e.g., $\delta^{15}N$), especially in relatively simple aquatic communities where the prey of interest could produce a unique isotopic signature (Vander Zanden et al. 2000; Johnson et al. 2002).

Under what conditions will predation occur? Experiments can examine specific factors that influence predation such as predator–prey size relationships (Juanes 1994), prey density (Peterman and Gatto 1978; Koski and Johnson 2002), habitat elements (Savino and Stein 1982), alternative prey, and environmental conditions; however, spatial scale, oversimplification, or experimental artifacts may constrain the generality of these results (Huston 1999). Field data on diet and distribution can identify potentially important influences on predation if stratified by size-class of predators, at appropriate temporal and spatial scales, and accompanied by data on ambient environmental conditions. Such comprehensive studies, however, are logistically challenging. Inferences may suffer from small sample sizes in many temporal–spatial–size cells. Experimental and field data can be combined to construct foraging models (e.g., functional response models [Peterman and Gatto 1978; Eby et al. 1995], encounter rate models [Gerritsen and Strickler 1977; Beauchamp et al. 1999]; spatially explicit growth models (Brandt et al. 1992); or optimal foraging models [Mittlebach and Osenberg 1994]).

How much predation occurs? Estimates of per capita consumption rates in the wild can be computed from diel gut fullness and evacuation rates (Eggers 1977; Elliott and Persson 1978) or by using mass-balance and energy budget models (Forseth et al. 1992; Hanson et al. 1997; Trudel et al. 2000; Chapter 12). These estimates require considerable investment in the collection of data on temporal and size-specific diet composition, the thermal experience of the consumers, and for bioenergetics models, incremental growth by the consumer. Estimates of the size structure and relative or absolute abundance of predators are required to expand estimates of individual consumption to population level predation rates.

What fraction of the prey population is lost to predation (predatory impact)? This analysis compares quantitative estimates of predation losses to estimates of prey abundance. When dealing with size-structured populations over extended periods, these comparisons would be stratified by time interval and by size-classes of predators and prey. Spatial stratification might also be required if predator–prey interactions differ significantly among locations. If the predation period is long in comparison to the growth rate or reproductive cycle of prey, then predation rates should be compared with the production rate of prey rather than just to prey biomass.

Can prey populations support the desired growth and production of predators? If predator–prey relationships can be quantified, are appropriately sized prey abundant enough, at times and locations where predators can encounter and successfully consume them, to satisfy target or observed growth rates for a given density of predators? This requires the ability to translate prey biomass, size structure, abundance, and distribution into the fraction of the prey population that can be consumed through functional response curves (Holling 1966; Peterman and Gatto 1978), encounter rate models (Gerritsen and Strickler 1977), and capture success models. Alternatively, simple empirical relationships such as proportional stock densities (PSD) of predators and prey (Gabelhouse 1984), available prey to predator ratios (AP:P; Jenkins and Morias 1978), mass-balance models (production: biomass; Ney 1990), and production-conversion efficiency relationships (Eck and Brown 1985) provide holistic estimates of the prey supply or balance required to support predator populations. Ecopath and Ecosim models (Christensen and Pauly 1993, 1994, 2001) provide estimates of biomass transferred among species or functional groups at each trophic level in an ecosystem. Most of these approaches estimate trophic rates on an annual time step for whole populations or feeding guilds but require considerably less data than interactions that can be modeled at finer temporal, spatial, taxonomic, or ontogenetic scales with bioenergetics models or field-based estimates.

16.3 CONCEPTUAL FRAMEWORK FOR ADDRESSING PREDATOR–PREY INTERACTIONS

Predator–prey interactions occur only under conditions that allow detection and successful capture of prey. It is important to recognize and define the segments of predator and prey populations included in a particular type of analysis. The predation sequence (search, encounter–detection, attack, and capture) provides a useful framework for organizing questions about predator–prey interactions and identifying the most appropriate or feasible methods (laboratory or field experiments, field measurements, or modeling) for addressing these questions (Holling 1966; Box 16.1).

Whether dealing with individuals or larger segments of predator and prey populations, the predation sequence is related to the abundance, availability, and vulnerability of prey (Box 16.2). A prey population exists at some abundance in an aquatic system, but only a fraction of that abundance may be available to predators due to incomplete temporal and spatial overlap between prey and predators. Where, when, and how predators search will determine what fraction of the prey population is available for encounter. Encounters depend on how prevailing environmental and habitat conditions affect detection of prey that overlap with predators in time and space (e.g., Beauchamp et al. 1999). Of the available fraction, a smaller proportion of prey may be vulnerable to consumption due to predator avoidance behavior (e.g., refuging), size constraints, and evasion capabilities that reduce capture success once prey are encountered. Given an encounter, prey vulnerability to capture depends on morphological and behavioral characteristics of both the prey and predator, and the probability of an attack is influenced by how inclusion of that prey in the diet would affect the rate of net energy gain to the predator.

Diet composition patterns and prey electivities from field samples subsume the combined effects of the prey abundance–availability–vulnerability hierarchy. In contrast, laboratory experiments can explore how individual factors contribute to variability in predator–prey interactions under different conditions. Models provide a conceptual framework for incorporating field data, experimental results, and theory into a mechanistic simulation of predator–prey responses to different conditions.

Predator–prey investigations vary from studies on the behavior of individual predators or prey to community and ecosystem level responses, patterns, and dynamics, which may require one or a combination of field, experimental, or modeling approaches (Table 16.1). As analyses progress from individual to systemwide responses, the potential for propagation of error increases tremendously. Therefore, identification of key factors that contribute to the variability in predator–prey responses and appropriate incorporation of these factors into experimental

Box 16.1 Elements of the Predation Sequence

Behavioral elements of the predation sequence (Holling 1966) are described below (see figure), followed by a listing of common or feasible approaches (lab or field experiments, field measurements, or modeling) for studying these topics.

Prey Search

Search. Aquatic predator–prey interactions occur in three-dimensional space and can be complex due to highly mobile predators and prey utilizing different habitats or locations over a variety of spatial and temporal scales. Predators employ either active or stationary (sit-and-wait) foraging modes (Norberg 1977; Bell 1990; O'Brien et al. 1990). The temporal distribution and movement patterns of predators and their prey reflect these foraging strategies.

Temporal and spatial overlap of predators and prey can be inferred from distribution patterns in catch per unit effort (*C/f*) data when sampling each with comparable methods and by assuming similar catchability among sizes, species, times, or locations (see Chapters 3, 7, and 8). Overlap may be determined more directly with biotelemetry (Chapter 14), hydroacoustics, and active net sampling in pelagic environments (Brandt 1996). At the microhabitat scale, experimental (e.g., Eklov and Hamrin 1989; Eklov and Diehl 1994; Christensen 1996), video, or acoustic surveillance methods (e.g., Boisclair 1992; Collins et al. 1991; Collins and Hinch 1993) can be effective for determining search patterns in natural habitats or experimental arenas.

The search strategy (i.e., periodicity, location, search mode, or search image) may be specialized for a specific habitat, prey type, or combination and based on the mobility of predator or prey, patch dynamics, antipredator responses, such as schooling or shoaling, diel migration, or sheltering patterns.

Approaches for studying this element are lab and field experiments, modeling, and field measurements.

Encounter. Predator–prey encounters are a function of the sensory mechanisms used to detect food or threats (e.g., visual [Wright and O'Brien 1984; Henderson and Northcote 1985; Hughes and Dill 1990; Breck 1993; Beauchamp et al. 1999], chemical [Atema 1980], or pressure and tactile [Gerritsen and Strickler 1977; Janssen 1997] detection fields). Therefore the number of encounters, at least in open-water environments, depends on the temporal distribution patterns of prey and predators and the area or volume searched times the density of prey contained within or passing through that search volume.

Approaches for studying this element are field measurements with modeling and lab experiments.

Predator Response to Encountered Prey

Optimal foraging rules (Pyke 1984; Stephens and Krebs 1986) for maximizing net energy gain per unit time provide a useful framework for predicting the predator's response after encountering a specific prey organism. Prey selectivity indices provide empirically derived measures of the proportional contributions of various prey to the diet in relation to the proportions of these prey that were available in natural or experimental environments; however, field estimates of the overall abundance or density of prey has generally been used as a crude substitute for the amount of prey actually available to, or encountered by, the predators.

(Box continues)

Box 16.1 *(continued)*

Orient or reject. Upon encounter, predators either orient toward prey and continue the predation sequence or reject the prey and resume searching or other activity.

The approach for studying this element is lab experiments.

Follow. The predator maneuvers toward prey to maintain close proximity and seek opportunity to attack. The follow segment can range from being quite prolonged to an abrupt transition from orienting to pursuing and striking prey.

The approach for studying this element is lab experiments.

Pursue. Predator accelerates toward prey to close distance in preparation for striking.

The approach for studying this element is lab experiments.

Strike. Predator attempts to grasp, injure, or stun prey. A strike can result in a hit (capture) or miss. If missed, search resumes for another prey.

The approach for studying this element is lab experiments.

Capture. Once captured, a predator could either ingest the prey or expel it and resume searching.

The approach for studying this element is lab experiments.

Ingest. The probability of successfully capturing and consuming prey given an attack is dependent on morphological and behavioral traits of both prey and predator. The net energy gained by ingesting each prey depends on its mass, energy density (J/g), and the time and energy required to capture and handle that prey item.

The approach for studying this element is lab experiments.

Digest. Digestion rate will determine the maximum volume of food that can be consumed per unit time and can depend on temperature and prey size and type.

Approaches for studying this element are lab experiments and models.

designs, stratification schemes in field sampling, and architecture and scaling of models is critically important for minimizing estimation error.

16.4 STUDY DESIGN AND ANALYSIS OF FIELD DATA

Field observations might provide the first evidence of predation. Common objectives of a field data collection program include recording the timing, duration, and spatial extent of predator–prey interactions to bound interactions in space and time; describing the size structure of the predator and prey populations (Chapter 9) and size relationships of predator–prey interactions; estimating the abundance of predators and prey (Chapters 7 and 8); and collecting data on food habits (Chapter 11) of potential predators to determine the existence or relative magnitude of predation.

Resume search. During the last step in the predation sequence, predators either continue searching for prey or initiate other activity such as vigilance, refuge-seeking, territorial defense, thermoregulation, migration, courtship, or spawning.

Approaches for studying this element are lab experiments and field measurements (telemetry).

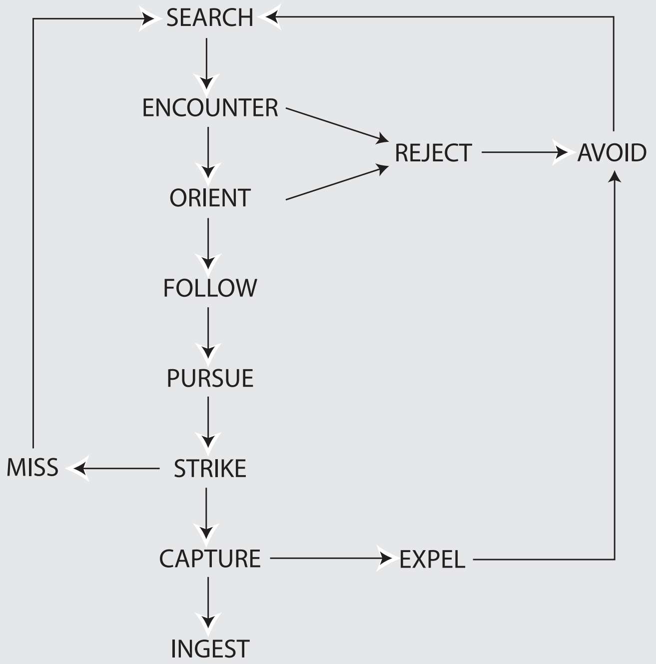

Figure Behavioral pathways from search through ingestion for a fish predator foraging on prey.

Because predation generally varies over time, with increasing body size (especially piscivory), and across some spatial dimension, these factors should be integrated explicitly into the sampling design. A stratified sampling design (Chapter 3) could be used to determine the temporal, spatial, and size-related dimensions of the predator–prey interactions. For instance, to evaluate predation on forage fishes in a lake or reservoir, the objectives of the sampling design would include (1) determining the seasonal distribution of predators (e.g., from catch per unit effort [*C/f*] data) among habitats and regions of the water body (e.g., benthic, pelagic, and littoral) and in relation to their prey; (2) determining the size structure of the predator and prey populations over the size range of interest; (3) determining the proportional weight contribution of forage fishes and other prey to the diet of different sizes of predators during each season; (4) and perhaps determining the abundance of predators and the abundance or availability of

Box 16.2 Hierarchical Measures of Prey Accessibility to Predators

Abundance
Interactions may not involve all members of the predator and prey populations. Consequently, abundance may not be the most ecologically relevant metric in predator–prey interactions. Population estimates or indices of relative abundance can be generated using standard methods, including mark–recapture, area or volume swept, depletion estimates, virtual population analysis (see Ricker 1975; Van Den Avyle 1993; Chapters 7–9), and hydroacoustics (Brandt 1996).

Availability
Temporal and spatial overlap allows some probability of encounter between predators and prey. Segregation may result from stage-specific distribution patterns related to environmental requirements or behavioral modification (e.g., foraging mode or predator avoidance). Ambient environmental conditions or habitat characteristics can mediate predator–prey encounters and the nature of their interactions. Data on seasonal or diel movement and distribution patterns, the effects of environmental conditions on physiology, detection capabilities of predators and prey, behavioral plasticity of predators and prey, and habitat complexity, gained through methods of capture, observation, hydroacoustics, and telemetry, give insight on availability.

Vulnerability
Only a fraction of the available prey is actually vulnerable to predators. Many factors reduce the probability of prey capture given an encounter, such as size–gape relationships, behavioral avoidance, evasion, vigilance, effects of habitat characteristics, temperature, turbidity, light, prey density, and predation rates or handling times as functions of predator–prey size relationships. Statistical analyses primarily involve analysis of variance (ANOVA), multivariate analysis of variance (MANOVA), and linear and nonlinear regressions.

prey. Generally, samples should be collected in a spatially representative manner; whether this requires formal stratification by region, habitat type, or depth will depend on characteristics of the water body, the species involved, and the specific study question. Fish should be captured with methods adapted to collect a representative sample of the population's size structure within each season and habitat type. The sampling design should allocate all data and specimen collection methods among representative spatial units, and this procedure should be repeated seasonally or at the temporal scale that is relevant to the study question. Species residing primarily in littoral or lotic habitats can be collected with active-capture methods (e.g., beach seining, electrofishing, pop nets, angling, or toxicants) or passive-capture methods (gill nets, trap nets, traps, or set lines) appropriate for the habitat characteristics and behavior and size range of the target species. Pelagic species can also be collected via active capture (surface, midwater, or bottom trawling; purse seining; or trolling) or passive capture (gill netting, set lines, or traps). This core sampling effort supplies the data for analyzing spatial–temporal distribution patterns and population size structure and provides some or all of the specimens needed for diet analysis or for determining age and growth. Additional collections might be required to satisfy sample size requirements for size-specific, seasonal diet analysis, but data from these supplementary samples would not necessarily be included in the analysis of size structure or spatial–temporal distribution patterns unless the additional sampling effort associated with these samples could be accounted for in calculations of *C/f* in an unbiased manner.

16.4.1 Distribution, Size Structure, and Abundance of Predator and Prey Populations

The distribution, size structure, and abundance of populations define boundaries on predator–prey interactions. Similar data collection methods are often employed for all three types of analyses. Distribution patterns dictate whether overlap in time and space provides the opportunity for predators and prey to interact and thus defines the availability of prey to predators. The size structure of the prey population determines the fraction of prey that is vulnerable to size-selective predators. The abundance and size structure of predators determine the magnitude of predation losses imposed on prey populations and how predation losses may be distributed among age- or size-classes of prey. If prey abundance is known, then population level predation rates can be converted into predation-specific mortality rates, and the relative importance of predation to the overall mortality of prey can be evaluated (e.g., Jones et al. 1993; Cartwright et al. 1998; Baldwin et al. 2000). Abundance estimates of predators or prey commonly represent the largest source of uncertainty in most analyses of population-level consumption.

Temporal distribution patterns vary considerably among life stages and species. These patterns must be identified and incorporated into the design of any population or community assessment program. Abundance estimates should explicitly define the target sizes or ages of the population and any restrictions imposed on the estimation procedure by sampling limitations. Different capture methods impose biases due to size or species selectivity and differential effectiveness among habitats (Chapters 3 and 9). Sampling with complementary methods can relieve some of these biases (Figure 16.1), and correction factors can be used in the analysis phase (e.g., size selectivity in gill nets: Rudstam et al. 1984; Van Den Avyle 1993). Although catch rates will not be directly comparable among sampling methods, the spatial–temporal patterns of maximum densities of each species could be inferred from the location and timing of peak *C/f* within each sampling method. It is important to acknowledge possible sampling biases and evaluate their potential effects on analyses either verbally or more formally through sensitivity analysis.

Population assessment techniques must be tailored for specific taxa and habitats. Population estimates from combined hydroacoustic–midwater trawl surveys have become routine for pelagic freshwater species like juvenile sockeye salmon and kokanee (Burczynski and Johnson 1986; Parkinson et al. 1994; Beauchamp et al. 1997), trouts (Stables and Thomas 1992; Yule 2000), ciscoes and whitefishes (Brandt et al. 1991; Luecke and Wurtsbaugh 1993), smelts (Burczynski et al. 1987; Appenzeller and Leggett 1995), and shads (Schael et al. 1995). Population estimates require intensive effort for littoral species (cove-rotenone treatments, depletion estimates, mark–recapture estimates, and relative abundance expansions) and river and stream fishes (e.g., depletion or mark–recapture estimators). Population

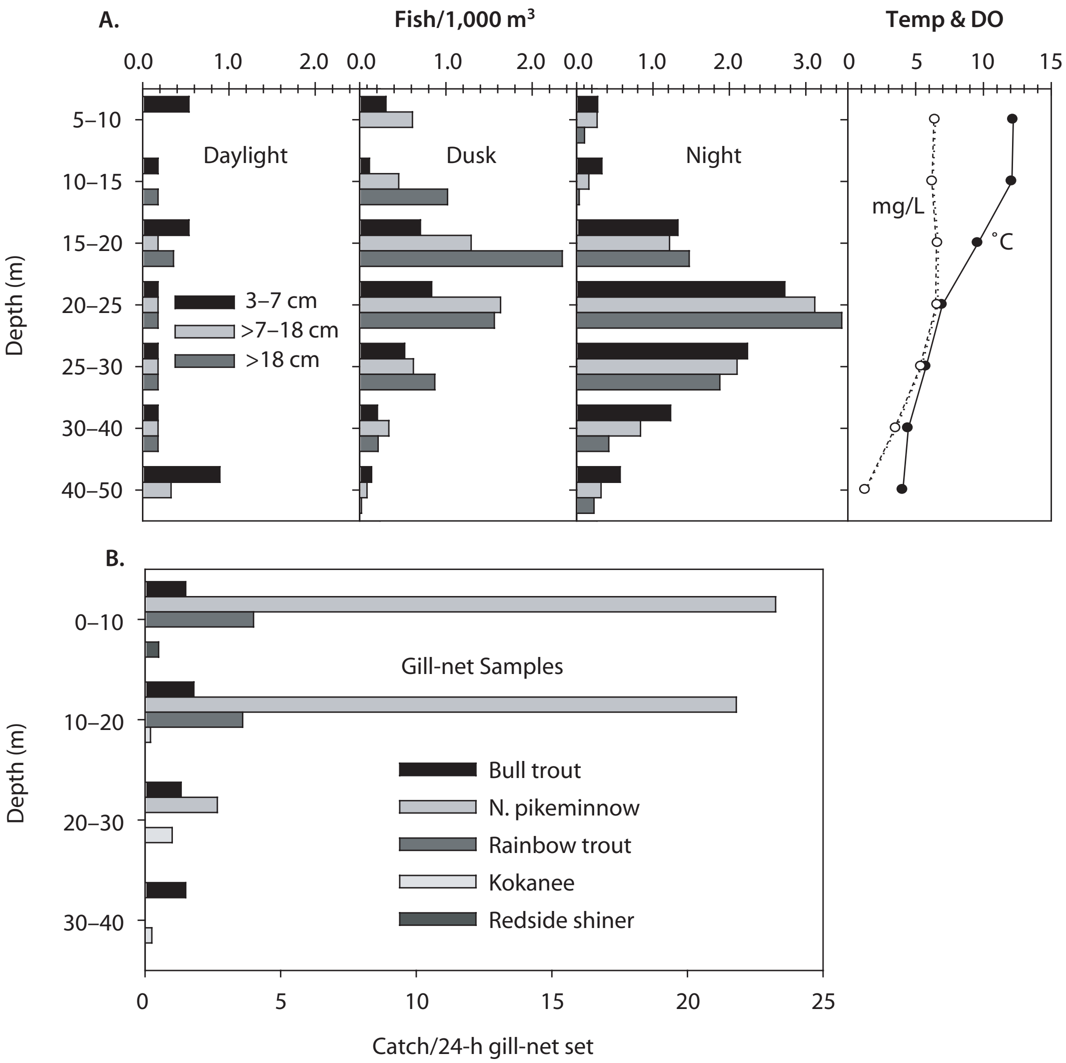

Figure 16.1 Depth distribution and relative abundance of potential predators and prey in Alturas Lake, Idaho (Beauchamp et al. 1997). Data were obtained with complementary sampling methods. (A) Hydroacoustics data provided volumetric densities for three size-classes of fish by depth and diel period. In right-most panel are temperature (temp, °C) and dissolved oxygen (DO, mg/L). Fish occupying the bottom and perimeter slope zones of the lake during daylight could not be detected until they dispersed into limnetic regions during dusk and night. Midwater trawling indicated that the pelagic targets at all depths were predominantly kokanee. Older age-classes of kokanee (in and below the thermocline) and redside shiners (above the thermocline) were vulnerable to sinking gill nets but not to trawls. (B) Depth-specific catches obtained with sinking gill nets indicated that high densities of potentially piscivorous northern pikeminnow (N. pikeminnow) and rainbow trout were primarily distributed in the upper 20 m along the slope zone, whereas predatory bull trout used all depths of the slope zone but at lower densities. Better information on movement and distribution patterns of the piscivores would require ultrasonic telemetry or more intensive hydroacoustic sampling and analysis.

assessments for deepwater demersal species or pelagic piscivore populations in freshwater systems may require a wide range of methods to estimate relative or absolute abundance of various species (e.g., hydroacoustics, volume- or area-swept approaches, distance sampling techniques, cove-rotenone treatments, depletion estimates, mark–recapture estimate, virtual population analysis, relative abundance from *C/f*, and others; Van Den Avyle 1993; Chapter 8).

16.4.2 Food Habits of Predators

A comprehensive treatment of food habits analysis is provided in Chapter 11, so only those aspects particularly relevant to analysis of predator–prey interactions are presented here. Predator–prey studies generally focus on particular prey species and perhaps some important alternative prey (e.g., a species that might buffer the effects of predation on the focal prey species). Beyond these species, additional prey items may be treated collectively as just "other food" for simplicity. Consequently, many analyses can focus on just the prey species of interest when examining the effects of different factors (independent variables) on the response variable (e.g., prey size or proportion of the focal prey in the diet). Some notable exceptions to this simplification scheme include electivity indices and optimal foraging models (Mittlebach and Osenberg 1994) because the full suite of prey species or groups is required for computations using these methods.

16.4.2.1 Explanatory Variables for Diet Analysis

Changes in feeding behavior and diet composition of predators can often be explained by factors such as body size, time (diel period, season, or year), and space (habitats, depths, regions, or geographic areas) and may vary in response to changes in availability or vulnerability of prey. At a minimum, predators should be sampled to detect seasonal changes in the proportion of the focal prey in the diet for each size-class of consumer. Spatial factors may influence diet composition of predators, with differences found between pools and riffles or nearshore and offshore zones (Beauchamp 1990; Beauchamp et al. 1992; Schindler and Scheuerell 2002), among depths (Beauchamp 1994; Stockwell and Johnson 1997), between macrophytes and open water areas (Savino and Stein 1982; Mittlebach 1984, 1988; Werner and Hall 1988; Persson and Eklov 1994), and, during prey migrations, in areas near tributaries or dams versus other zones (Poe et al. 1991; Rieman et al. 1991; Winemiller and Jepsen 1998). Conversely, the combined effects of predator movement and prey dispersal can homogenize diets from different vertical or horizontal regions of the basin (Cartwright et al. 1998; Baldwin et al. 2000, 2002).

16.4.2.2 Categorization of Continuous Data

Although diet data should always be initially examined in raw form (e.g., body length or sampling date), response variables often show similar patterns across a range of values for the explanatory variables. In these circumstances, different ranges of the explanatory variable could be grouped into categories to facilitate further analysis. Common examples include grouping continuous explanatory variables, like predator body lengths, into discrete size categories or pooling sample collection dates into broader, ecologically relevant periods. However, pooling continuous variables into categories might not always be appropriate. The challenge is to minimize the number of categories without pooling important sources of variability. Post hoc exploration of the data might be necessary to determine the appropriate number of categories and their boundaries. For instance, size categories of predators could be determined by inspecting scattergrams of predator lengths (continuous data) and the percentages of key prey in the diet by weight to identify the size-classes corresponding with no predation, increasing predation, and one or more plateaus of high(er) predation that indicate seasonal or ontogenetic shifts in diet composition (Figure 16.2).

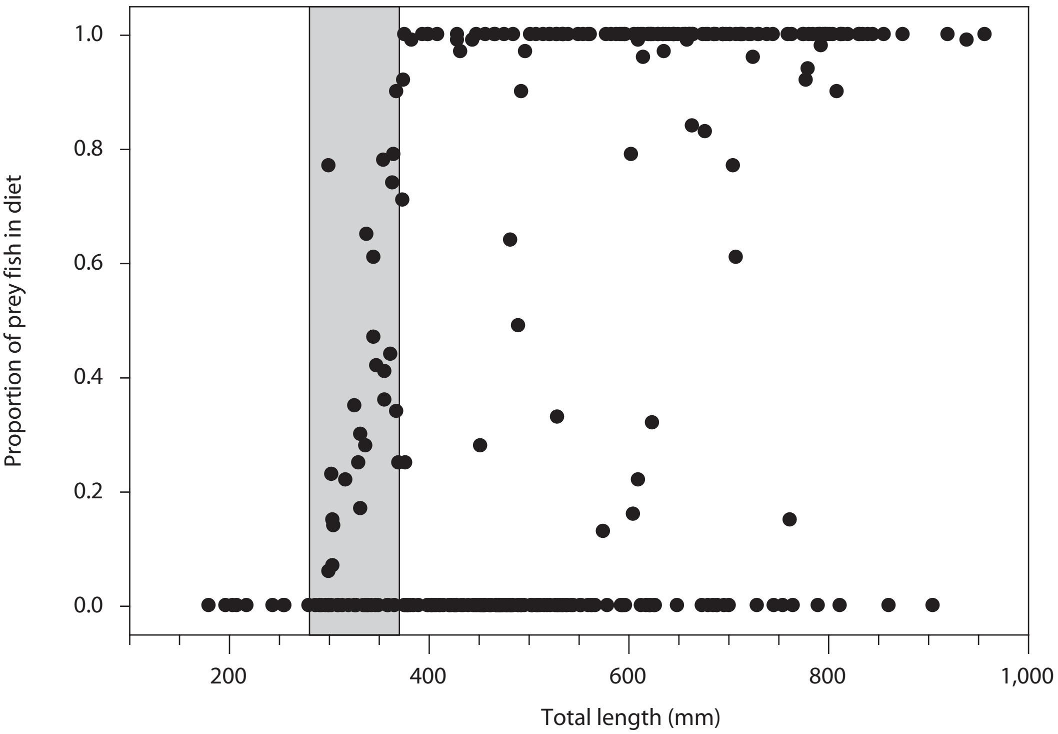

Figure 16.2 A scattergram of the proportion (by weight) of fish prey in stomachs versus predator length. The scattergram of 327 nonempty stomachs of lake trout, sampled across all seasons in Flathead Lake, Montana (D. Beauchamp, unpublished data), was used to stratify length data into size categories that minimized diet variation within size-classes by isolating most of the variability in a transition size-class (300–375 mm in total length, shaded area). Lake trout greater than 375 mm were considered fully piscivorous, with fish prey contributing up to 100% of the stomach contents. Note that fish prey were absent in some stomachs from all sizes of predators.

16.4.2.3 *Determination of Diet Composition*

The stomach contents of aquatic predators may contain prey that vary over one to three orders of magnitude in length and six orders of magnitude in mass (e.g., zooplankton to prey fishes); therefore, the variables chosen to characterize a predator–prey interaction will depend upon study objectives. Mean weight proportions (termed MW_i in Chapter 11; see Table 11.1 for descriptions of common diet indices) of prey in the diet are often the most useful response variable in predator–prey interaction studies. Weight proportion reflects the relative importance of each prey species to the energy budget of the consumer and can be used to estimate the loss of prey (in biomass or numbers) from predation by using bioenergetics models or other estimators of consumption (Ney 1990; Bowen 1996; Chapter 11). Counts or numerical percentages of prey in the diet are useful when evaluating prey encounter or consumption rates, as in optimal foraging models (e.g., Mittlebach and Osenberg 1994), and contribute to calculations of prey electivity. Frequency of occurrence O_i (the percentage of predators in the sample that contain a specific prey species) provides useful supplementary information about the fraction of predators in a sample that contain specific prey but should rarely be used as the primary response variable when analyzing predator–prey interactions.

When estimating the weight contribution of various prey to the diet, data should be recorded as dry weight, blotted-dry wet weight, or volumetric proportions for individual stomach samples. Samples should be collected within a sampling design that provides spatially representative samples of each size-class of consumer for each ecologically relevant period of the study. Each nonempty stomach is considered an individual sampling unit wherein the observed prey proportions are associated with the size of the consumer, the location and time of capture, and concurrent physical, chemical, and biotic conditions. For each prey category, the weight proportion, W_i, from each stomach is averaged with all other nonempty stomachs in the sample (MW_i) within each size-class of predator during each period of interest (Box 16.3). This analytical approach gives equal weight to the dietary proportions from each nonempty stomach, regardless of the level of stomach fullness. This minimizes the influence of rare stomachs that contain large quantities of a particular prey because each stomach can represent only 100% of one stomach out of N samples and attempts to reflect the average diet composition of all consumers within the same size × time cell. As with other methods, this approach has some limitations but produces less volatile estimates of diet composition.

Important underlying assumptions can be evaluated directly through pilot or supplemental studies. For instance, one can account for the assumption of similar digestion rates for all major prey taxa and test directly for diel differences in prey composition. Differential digestion among prey taxa becomes a greater concern if temperatures enter the warmer portion of a consumer's thermal range and if the prey of interest are small, soft-bodied organisms (e.g., larval fishes), which digest rapidly. This concern can be minimized by preliminary diel sampling to identify the timing of peak stomach fullness (e.g., dawn, midday, before dusk,

Box 16.3 Analysis of Diet Composition of Lake Trout by Season and Size-Class

The objective of this diet study was to estimate the proportional weight contribution of each prey type in the diet of lake trout by season and size-class in Flathead Lake (D. Beauchamp, unpublished data). To simplify the example, prey categories are reduced to just fish and invertebrates. Spatially representative samples of each size-class of lake trout were collected during winter, spring, summer, and fall from overnight sets of sinking experimental variable-mesh gill nets. Each season, two sampling locations were selected randomly in each of five regions and four depth intervals of the lake. Each lake trout stomach was considered a sampling unit, and its diet was associated with the total body length, weight, location, depth, date, and season of capture recorded on the same row. Lengths were categorized into length-classes based in part on visual inspection of the scattergram of length versus fish proportions in Figure 16.2. This abbreviated data set illustrates a useful format for analyzing diet composition data in spreadsheets or statistical packages. Other columns can be added for additional information (e.g., habitat, gear type, and diel period). Diet data are recorded first as the mass (g) of each prey category measured directly from the stomach contents (in columns Fish and Invert). Each prey category is then converted to a proportion of the total prey found in each stomach (in columns FishP and InvertP), computed as the weight of each prey category divided by the total weight of all prey from that stomach. Most analyses are conducted on prey proportions (e.g., diet composition by length-class and season). Note that prey mass and proportions are left blank for empty stomachs, as in fish 14.

Table Abbreviated data set of diet composition (fish versus invertebrate) of lake trout. The blotted wet mass of each prey category is measured for individual fish stomachs (fish number) and each prey category is then converted to a proportion of the total prey found in each stomach (in columns FishP and InvertP). Season abbreviations throughout this chapter are spring (spr), summer (sum), autumn (aut), and winter (win).

Fish number	Date	Season	Total length (mm)	Length-class (mm)	Fish weight (g)	Prey weight (g)			Diet proportions	
						Fish	Invert	Total	FishP	IInvertP
1	6/8/98	Spr	374	301–375	400	1.08	0.45	1.53	0.71	0.29
2	6/8/98	Spr	453	376–500	730	0.00	1.67	1.67	0.00	1.00
3	6/9/98	Spr	301	301–375	180	0.10	0.03	0.13	0.77	0.23
4	6/9/98	Spr	403	376–500	440	0.00	0.16	0.16	0.00	1.00
5	6/9/98	Spr	622	501–625	1,990	0.00	0.10	0.10	0.00	1.00
6	6/9/98	Spr	813	626–1,000	4,830	6.67	0.00	6.67	1.00	0.00
7	6/9/98	Spr	479	376–500	830	0.00	12.59	12.59	0.00	1.00
8	6/9/98	Spr	615	501–625	1,910	0.91	0.04	0.95	0.96	0.04
9	6/9/98	Spr	675	626–1,000	3,020	0.08	0.00	0.08	1.00	0.00
10	6/9/98	Spr	664	626–1,000	2,310	0.67	0.13	0.80	0.84	0.16
11	6/9/98	Spr	705	626–1,000	3,090	9.38	2.81	12.19	0.77	0.23
12	6/9/98	Spr	745	626–1,000	3,245	5.74	0.00	5.74	1.00	0.00
13	6/9/98	Spr	575	501–625	1,400	0.86	5.78	6.64	0.13	0.87
14	6/9/98	Spr	330	301–375	285					
15	6/15/98	Spr	293	100–300	210	0.00	0.10	0.10	0.00	1.00
16	6/15/98	Spr	287	100–300	195	0.00	0.28	0.28	0.00	1.00
17	6/15/98	Spr	332	301–375	280	0.14	0.33	0.47	0.30	0.70
18	6/15/98	Spr	379	376–500	445	0.00	0.33	0.33	0.00	1.00
19	6/15/98	Spr	539	501–625	995	0.00	0.44	0.44	0.00	1.00
20	6/15/98	Spr	845	626–1,000	4,540	7.15	0.00	7.15	1.00	0.00
. . .										
609	8/24/01	Sum	435	376–500		0.00	0.50	0.50	0.00	1.00

The data above represent a segment of a larger data set for predators during winter and spring. The sample sizes, mean proportions by weight (termed MW_i in Table 11.1), and 2SE for fish and invertebrates consumed by each length-class × season combination were summarized below in a Microsoft Excel spreadsheet by means of the "pivot table" analysis tool; the same summarization could also be produced using analogous tools in other spreadsheet software, PROC MEANS in SAS, or "multi-dimensional pivot tables" in SPSS.

Table Summary of lake trout diet composition data. The mean proportion by weight (*N* = number of nonempty stomachs) and 2SE for both food categories are given by length-class × season.

		Diet proportions			
Length-class (mm) and season	*N*	Fish	2SE	Inverts	2SE
100–300					
Winter	0				
Spring	8	0.00	0.00	1.00	0.00
Summer	15	0.01	0.06	0.99	0.06
Fall	12	0.00	0.00	1.00	0.00
301–375					
Winter	5	0.00	0.00	1.00	0.00
Spring	23	0.37	0.21	0.63	0.21
Summer	10	0.11	0.21	0.89	0.21
Fall	28	0.15	0.14	0.85	0.14
376–500					
Winter	25	0.21	0.17	0.79	0.17
Spring	67	0.20	0.10	0.80	0.10
Summer	20	0.10	0.14	0.90	0.14
Fall	27	0.30	0.18	0.70	0.18
501–625					
Winter	34	0.47	0.17	0.53	0.17
Spring	42	0.37	0.15	0.63	0.15
Summer	19	0.17	0.18	0.83	0.18
Fall	26	0.35	0.19	0.65	0.19
626–1,000					
Winter	26	0.83	0.15	0.17	0.15
Spring	77	0.79	0.09	0.21	0.09
Summer	13	0.74	0.25	0.26	0.25
Fall	20	0.90	0.14	0.10	0.14

after dusk, or night) and the variability in diet composition among diel periods (Figure 16.3). Net retrieval or active sampling should then be scheduled to maximize the number of samples captured during or slightly after the period of peak stomach fullness. If diet composition varies dramatically between the period with peak fullness and other periods, then stomach samples may be needed from two to three times per day to portray diet composition (or to determine feeding chronology and estimate daily consumption, see section 16.4.2.5); alternatively, prey reconstruction methods (Swenson and Smith 1973; Diana 1979) might be required to obtain good diet composition estimates.

16.4.2.4 *Statistical Analysis of Diet Composition*

Descriptive statistics for dietary responses by predators can be summarized effectively in spreadsheets (e.g., pivot tables in Microsoft Excel or analogous data summary tables in other spreadsheet programs, such as PROC MEANS in SAS [SAS

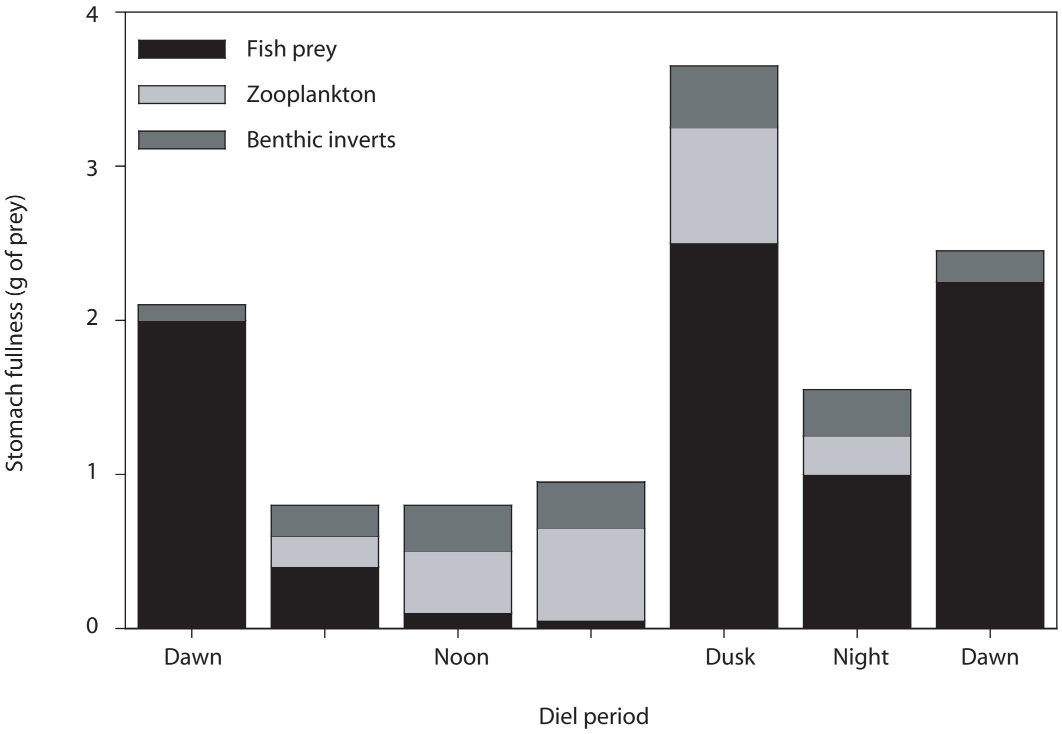

Figure 16.3 Diet composition and stomach fullness can change dramatically over a 24-h period. In this example (D. Beauchamp, unpublished data from Flathead Lake), the dusk samples captured peak stomach fullness for all three prey categories and provided the most representative diet samples for the predator. Fish prey would have been severely underrepresented if stomach contents were sampled only during mid-day, whereas zooplankton would have been seriously underrepresented in dawn samples. This potential diel variability should be considered when designing a sampling program and analyzing diet samples of predators with regard to the limitations of sampling methods and study design.

Institute 1990] or multidimensional pivot tables in SPSS [SPSS 1999]) to produce a table of averages, standard deviations, maximum, minimum, or median values, and sample sizes for response variables for any combination of independent variables or factors (e.g., Box 16.3). Careful design and formatting of the data set and careful selection of response and predictor variables can greatly facilitate these analyses.

Because proportions of key prey species in diet composition generally vary in response to more than one predictor variable, statistical methods should be capable of simultaneously examining the effects of several factors on the average proportion of key prey species in the diet of predators. Changes in proportions of key prey with size of the predator can be examined by regression, whereas the effects of seasons, size-classes of predators, and habitat groups can be analyzed effectively using various analysis of variance (ANOVA) techniques (see Chapter 11). The ANOVA techniques are relatively robust to moderate deviations from normality when sample sizes are adequate because of the central tendencies of the data. For instance, in diets of lake trout from several western lakes, mean proportions of the major prey types tended to stabilize at sample sizes of 7–15 nonempty stomachs per season × size-class cell (D. Beauchamp, unpublished data). The diet proportions of focal prey can also be transformed (e.g., by square root or arcsine transformations for weight proportions) to achieve or approach normality in the distribution of means (or slope coefficients for regressions). Alternatively, various ANOVA techniques can be applied to rank-transformed weight proportions for each prey species of interest. The single-factor version of this nonparametric method is the Kruskal–Wallis test, but this test becomes awkward and ineffective when more than one factor is involved. Multifactor ANOVAs on rank-transformed data offer less statistical power than do parametric ANOVAs of similar design but can be helpful for determining the relative importance of the main effects of different predictor variables, such as size-class, time, habitat type, or region, on the proportion of focal prey in the diet of predators. Although rank-transformed ANOVAs identify significant main effects, and levels of these effects can be compared with multiple- range tests (Conover and Iman 1981), a major disadvantage of rank-transformed ANOVAs is that significant interaction terms cannot be interpreted as in a parametric ANOVA (Hora and Conover 1984; Thompson 1991). If significant interactions exist, the relative importance of prey in response to different levels of a factor must be examined separately within each level of the other factor involved in the interaction. Despite these limitations, rank-transformed ANOVAs provide a useful framework for organizing and prioritizing how results are reported.

16.4.2.5 *Field-Based Estimates of Consumption*

A daily consumption rate for the average predator can be estimated from field data by using methods appropriate to the feeding chronology of the consumer, such as stomach fullness–gut evacuation rate methods and prey reconstruction (see and Ney 1990 for reviews). The most common approach involves serial sampling of stomach contents over a 24-h period. A temperature-dependent stomach evacuation rate, R, is applied to the mean mass of food in the stomach, S, over the 24-h period to obtain a daily consumption estimate, C_d, for the average predator.

$$C_d = 24 \cdot S \cdot R\,, \tag{16.1}$$

where the stomach evacuation rate, R (h^{-1}), is the proportion of food digested per hour. It is obtained as the slope of the proportion of food (W_t/W_0) remaining t hours after feeding and is generally expressed as a decaying exponential function of time t (Eggers 1977; Elliott and Persson 1978):

$$W_t/W_0 = a \cdot e^{-Rt}. \tag{16.2}$$

The intercept, a, should theoretically equal 1.0, and the slope R(h^{-1}) represents the evacuation rate. The evacuation rate generally increases with increasing temperature and can also vary considerably among prey types or sizes (He and Wurtsbaugh 1993). Daily ration size should be calculated separately for different size-classes of predators or if diet composition varies considerably among size-classes. Daily consumption can be partitioned among prey types based on the proportional contribution by weight of each prey category to the diet. Multiplying daily consumption estimates of the focal prey by the number of predators in each appropriate size-class and the duration of the interaction in days generates the biomass of prey consumed by each size-class of predator over a given period.

For top predators, adequate sample sizes may be difficult to achieve for each size × time cell. Field-generated estimates of daily consumption reflect the ambient environmental conditions immediately preceding and during the period of sample collection, and estimates can vary considerably from day to day (Smagula and Adelman 1982) and seasonally (Cochran and Adelman 1982). Consequently, a field-generated estimate of consumption may have limited generality to broader periods of interest longer than 1 d.

16.4.2.6 *Special Considerations for Analyzing Short-Term Acute Predation*

The temporal scale of predator–prey interactions can be extremely important when attempting to quantify consumption in response to large pulses of prey (e.g., recruitment pulses, stocking, or migration of prey). Sampling should be scheduled to measure the magnitude and duration of the predatory response accurately. In systems where we have examined predation on stocked juvenile walleye, pikes, and trouts and salmons, the response has been immediate, severe, and of relatively short duration (e.g., 2 d to 2 months: Wahl et al. 1995; Cartwright et al. 1998; Baldwin et al. 2000).

Samples collected prior to stocking provide baseline data on the diet composition of predators. Stomach samples should be collected for at least three consecutive days during and after stocking, then once every 2–3 d, followed by a progressively lower frequency of sampling (Figure 16.4). The reduction in sampling frequency can be adjusted by evaluating how quickly the proportional

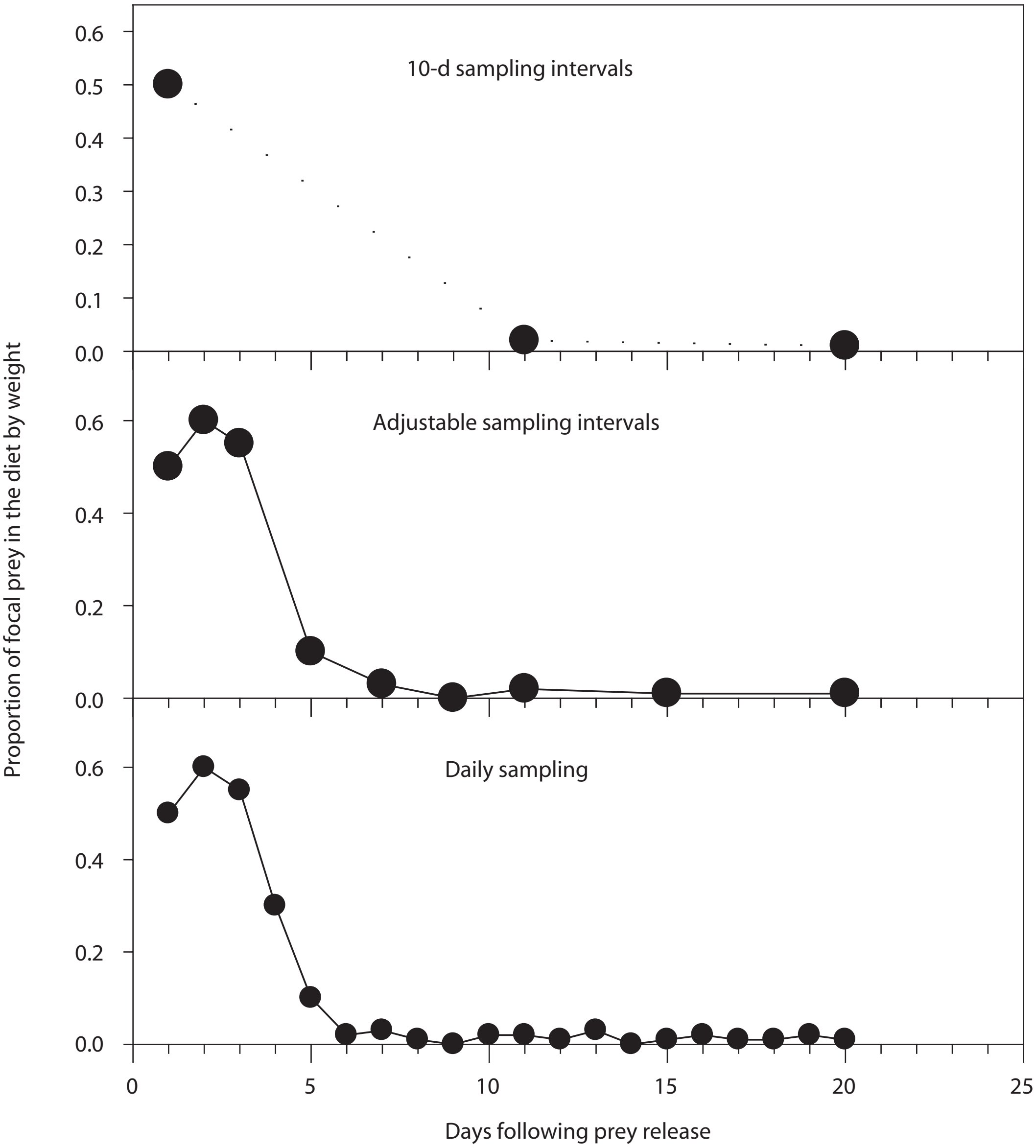

Figure 16.4 Sampling frequency can affect the amount of interpolation error in estimates of predation when acute periods of interaction are potentially short lived. In this example, a 10-d sampling interval (upper panel) missed the rapid decline of focal prey in the diet and results in an overestimate of the duration and magnitude of the predation response. The adjustable sampling frequency scheme (middle panel) captured the initial decline by sampling on three consecutive days before sampling effort was progressively reduced as the proportion of prey in the diet stabilized through time. The adjustable sampling frequency design minimized interpolation error and required less than half the effort as that of a daily sampling regimen (lower panel).

contribution of the focal prey, by weight or volume of the stomach contents, changes in the diet between sampling dates. If the prey disappears quickly from the diet (e.g., within a couple days), then sampling can be reduced to measure monthly or seasonal changes as appropriate. If the diet composition changes measurably, but at a more moderate rate, then a relatively frequent sampling schedule should be maintained (e.g., sample once every 3–7 d) until the prey of interest disappears or stabilizes at a relatively constant percentage of the diet through time. The rate of change of focal prey in the diet can be calculated by regressing its weight percentage in the diet against the number of days after the pulse of prey appeared.

The spatial extent of predator–prey interactions during acute predation periods is important as well because we need to know what fraction of the predator population is involved in order to estimate the total magnitude of predation losses. If prey are concentrated in a localized area (e.g., stocking locations or location where larval or juvenile fishes are migrating into lakes or reservoirs from streams or spawning areas), predators may concentrate in response to an influx of prey. Alternatively, predation may involve only those predators that happen to occupy that region. Studies should be designed to detect whether the relative density of predators (e.g., measured by C/f) or their dietary response (measured by the proportional weight contribution of focal prey in the diet) changes between areas of high prey concentrations and other regions. Sampling along a distance gradient from the point of prey entry as well as before and after prey entry (a BACI design, that is, before–after-control-impact design) addresses this issue.

16.5 ANALYSIS OF DATA FROM BEHAVIORAL EXPERIMENTS AND RELATED MODEL DEVELOPMENT

Several aspects of predator–prey interactions of fishes can be assessed under controlled experimental conditions to help understand foraging ecology in natural systems and answer fisheries management questions. A number of systems have been used for these types of experiments, varying from aquaria to large pools and tanks; these should be scaled to the size of the fish of interest. Experimental results can be used to construct models that simulate processes that underlie predator–prey interactions. Several techniques can be used to record behavior, including direct observation in real time (with entry directly to a portable computer) and videography.

16.5.1 Predation Sequence

The generalized predation sequence described in section 16.3 can be documented with several nonoverlapping categories (Wahl and Stein 1988; Box 16.1): inactive (resting and motionless), search (moving, not orienting to prey), observe (motionless but oriented to an individual prey), follow (moving and orienting to prey), pursue (following at burst speed), attack (striking at prey), and capture (grasping prey). Because these behaviors may be correlated, multivariate analysis of variance

(MANOVA) is the preferred analysis approach for these data (Box 16.4). Behavioral probabilities can be calculated at each step in the sequence (e.g., orient–follow–pursue or strike–capture). Handling time can be defined as the time from prey capture until search is resumed (in the vein of Werner and Hall 1974; Mayer and Wahl 1997) or as the time required to ingest prey (Holling 1966).

Important differences exist among fish functional groups in components of the predation sequence. Because planktivores ingest many small prey with relatively low mobilities, they have higher capture success (usually >80%; Confer and Blades 1975; Mayer and Wahl 1997) than do piscivores (usually <70%; Wahl and Stein 1988; Einfalt and Wahl 1997). Similarly, planktivorous prey are small and relatively defenseless, so prey are pursued, captured, and ingested within a second or less (Mittelbach 1981; Koski and Johnson 2002) whereas handling times for individual prey by piscivores are considerably higher (3–6 min for pikes, Wahl and Stein 1988; 2–10 min for walleye, Einfalt and Wahl 1997). An interesting exception is found for bluegill foraging on an exotic cladoceran *(Daphnia lumholtzi)*. Because of the large helmet and tail of this cladoceran, bluegill face foraging constraints more similar to piscivores (Kolar and Wahl 1998). In general, because of the high capture success and short handling times of planktivores, search time is of much greater importance to a particulate feeder than is capture success (Juanes 1994) or handling time. For benthivores, or drift-feeders (e.g., trouts and salmons in streams), feeding territories are common in many species, suggesting that prey are patchily distributed and search costs are high; thus consumers might shift costs from search to territory defense.

16.5.2 Optimal Foraging

Animals forage by selecting prey that maximize the rate of energy intake while minimizing costs associated with searching and handling prey (Stephens and Krebs 1986). Optimal foraging models are often employed to predict diet selection for given characteristics of the predator and prey and can successfully predict resource use (Mittelbach 1981; Mittelbach and Osenberg 1994). To increase fitness, predators choose prey that minimize energy spent on search, capture, and handling while maximizing energy intake. Energy return (J/min) can be calculated as

$$\frac{E_n}{T} = \frac{\sum_{i=1}^{n} \lambda_i E_i - C_s}{1 + \sum_{i=1}^{n} \lambda_i T_{hi} P_i}, \tag{16.3}$$

for each prey type i out of n available prey types. The parameter λ_i is the number of encounters with prey i during a feeding trial (sensu Charnov 1976); E_i is the expected energy gain (J) per individual prey item; P_i is the probability of a capture occurring after an encounter; C_s is the energy cost of searching; and T_{hi} is the handling time for each prey type i. Prey types are added sequentially until E/T is maximized (Pyke 1984). In this and many formulations of optimal foraging

Box 16.4 Multivariate Analysis of Variance for Predator–Prey Behavioral Data

The multivariate analysis of variance (MANOVA) is appropriate for cases in which several dependent variables have been measured in a single experiment. This technique is more appropriate than performing multiple univariate tests, which can increase the probability of a type I error (Scheiner 1993). As a result, this test is generally appropriate for analysis of multiple behaviors in the predation sequence (Box 16.1). Below we use a SAS program to perform a MANOVA in an example concerning the effects of predator size and prey density on behaviors in the predation sequence.

In our hypothetical example, we examine the effect of walleye length, prey density, and their interaction on individual walleye feeding behaviors in aquaria experiments (similar to T. Galarowicz, Central Michigan University, and D. Wahl, unpublished data). Foraging was examined for three different sizes of walleye (20, 50, and 100 mm) feeding at three different densities (1, 10, and 25 bluegill per m^3) of optimal-sized bluegill prey. Five replications at each size and density combination were performed with five individual walleye. The total number of searches, orientations, follows, pursuits, strikes, and captures in the predation sequence (Box 16.1) were recorded for each trial.

We first perform a MANOVA. If significant multivariate effects are found (known as a protected ANOVA), we then examine the univariate responses (ANOVAs) for significant effects. The ANOVAs that are not significant are deleted, and the remaining ANOVAs are run again. In the MANOVA, a test for significant differences among groups is based on eigenvectors (linear combinations of all dependent variables) and eigenvalues of the matrix (the amount of variation explained by eigenvectors). Pillai's trace is the measure most robust to violations of assumptions and is the most commonly used statistic.

One consideration when using MANOVA is that power decreases as the number of response variables increases, which can lead to type II error. It is also possible to use a univariate approach and a Bonferroni adjustment to alpha. In addition, MANOVA can be used only when all subjects have been measured for all response variables; it is assumed that multivariate error effects are normal and covariances equal among groups (Scheiner 1993). Other assumptions are the same as for ANOVA.

Below, we examine the effect of three distinct classes of walleye length (20, 50, and 100 mm) and prey density (1, 10, 25 per m^3), and the interaction of predator length and prey density on the total number of searches, orientations, follows, pursuits, strikes, and captures in the predation sequence. Each combination of predator size and prey density was replicated five times using different walleye. The total number of searches, orientations, follows, pursuits, strikes, and captures were recorded for each trial.

Program

```
   data fishprey;
   input length density search orient follow pursue strike capture;
   cards;
   (input data);
   proc glm;
   class length density;
   model search orient follow pursue strike capture=length density
length*density;
   manova h=length density length*density /printe printh;
   run;
```

Output and Interpretation

Table Results of MANOVA examining the total number of searches, orientations, follows, pursuits, strikes, and captures in the predation sequence for three different size-classes of walleye (20, 50, and 100 mm) feeding at three different densities (1, 10, and 25 bluegill per m^3) of optimal-sized bluegill prey.

Source	Pillai's trace	*F* (df)	*P*
Length	1.01	5.42 (12, 64)	<0.0001
Density	1.07	6.26 (12, 64)	0.0001
Interaction	0.67	1.15 (24, 136)	0.31

The MANOVA test shows that foraging behaviors of walleye were significantly affected by both walleye length and bluegill density but not by their interaction. Because the interaction was not significant, the analysis should be run again without the interaction term.

Table Individual ANOVAs for predation sequence behaviors with walleye length and bluegill density as independent variables. The *F*-statistic has 2, 36 df.

	ANOVA			
	Walleye length		Bluegill density	
Behavior	*F*	*P*	*F*	*P*
Searches	13.67	0.0001	65.47	0.0001
Orientations	12.41	0.001	57.73	0.0001
Follows	5.32	0.009	61.95	0.0001
Pursuits	17.87	0.0001	93.80	0.0001
Strikes	1.99	0.15	27.51	0.0001
Captures	2.29	0.11	28.43	0.0001

Individual ANOVAs show walleye length affected the number of each behavior in the predation sequence from search through pursuit but did not affect the number of strikes and captures. Larger walleye initiated more searches, orientations, follows, and pursuits than did smaller walleye but attacked a lower proportion of the prey. As a result, the number of captures was similar across size-classes of walleye. Density of bluegill prey significantly affected all components of the predation sequence. At higher prey densities, walleye increased the number of all individual behaviors.

models, the true costs associated with components of the predation sequence, from orientation through capture, are often not accounted for explicitly in the models. These costs are extremely difficult to determine in laboratory experiments but could be important if predation costs differ significantly among prey. Other constraints on fitness (predation, reproduction, and habitat) may result in a fish not foraging optimally, and several assumptions of these models may not be met (e.g., prey encountered sequentially rather than simultaneously). Nevertheless, these models have been usefully applied to understanding several aspects of predator–prey interactions, particularly under experimental conditions.

16.5.3 Size and Species Selection

Size-specific attributes of the predator, prey density, and characteristics of the prey can all influence predator–prey interactions. Changes in prey type may be associated with an increase in predator size. Prey size can constrain selection for a variety of prey types, including zooplankton (Bremigan and Stein 1994; Mayer and Wahl 1997) and fish (Hambright 1991; Juanes 1994; Christensen 1996; Lundvall et al. 1999). Prey encounter rates increase with size-related changes in swimming speeds (Gerritsen and Strickler 1977) and size-dependent reactive distances to invertebrates (Breck and Gitter 1983) and larval fishes. In contrast, the effect of prey size on the reaction distance of piscivorous fishes to larger (postlarval) fish prey appears to differ among taxa: sunfishes exhibited increasing reaction distance with prey size (Howick and O'Brien 1983), whereas lake trout showed no effect of reaction distance to prey size (Vogel and Beauchamp 1999). Many fish undergo ontogenetic diet shifts and change their diet as they grow. These shifts are associated with changes in ability to capture more energetically beneficial prey types successfully and are often correlated with discrete periods of growth that may occur at critical periods in the life history of fishes (Buijse and Houthuijzen 1992; Stahl and Stein 1994). Several electivity indices are available that can be used to assess changes in prey preferences by predators (see Chapter 11).

It is often assumed that fish predators actively choose the sizes and species of their prey. This concept is central to optimal foraging models, which have been used to account for the influence of prey species and sizes on diet composition of predators (Werner 1974; O'Brien et al. 1976; Werner and Mittelbach 1981). However, a review of laboratory studies with controlled prey densities showed a variety of piscivorous fish chose the smallest prey available, and many of the prey consumed were smaller than optimal (Juanes 1994), suggesting that prey capture was a passive process (Sih and Moore 1990) rather than predators actively choosing prey. Under this scenario, predators attack all sizes of prey as encountered, but differential vulnerabilities lead to smaller, more vulnerable prey being consumed in higher proportions (Juanes 1994). Although prey handling times and associated optimal foraging models have been used to explain planktivore foraging successfully, these models have been criticized as unrealistic for piscivores foraging on mobile prey. These prey require measurable energy demands involved with stalking and capturing that can vary considerably with size of prey (Sih and Moore 1990). Foraging behavior of piscivores, such as pikes (Wahl and Stein 1988), largemouth bass (Savino and Stein 1982; Hambright 1991), and walleye (Einfalt and Wahl 1997) have been examined extensively. Differences in cost–benefit relationships (handling time/prey dry mass) have successfully predicted selection for different prey species, but piscivores sometimes select larger prey (see Figure 16.5, an example for walleye) than predicted by an optimal foraging model, at least in confined experimental arenas. For piscivores, prey encounter rates may be more important than handling times in determining prey size selection, and different decision rules may be necessary to evaluate foraging decisions (Breck 1993).

Several studies have focused on prey morphology and behavior as factors determining species selection (e.g., Wahl and Stein 1988; Einfalt and Wahl 1997). Fusiform or soft-rayed prey are generally preferred over sunfishes, and several mechanisms have been proposed to account for these preferences. Prey differ behaviorally in response thresholds (Webb 1986) and escape tactics (Savino and Stein 1982; Wahl and Stein 1988; Einfalt and Wahl 1997). These prey-specific behaviors can also interact with habitat complexity to determine foraging success of predators (Savino and Stein 1982; Savino et al. 1992). In addition, body morphology can influence capture success and handling time (Webb 1986; Wahl and Stein 1988; Hambright 1991) with predators choosing larger sizes of fusiform minnows than deep-bodied sunfishes.

16.5.4 Functional Response Curves

Prey density is an important factor determining foraging success and can influence search time and behavior of predators (see Box 16.4 for analysis of prey density and predator lengths on feeding behaviors). Functional response curves are used to describe the relationship between prey abundance and the number of prey eaten per predator (Holling 1959; Figure 16.6) and can be a useful, experimentally based approach for modeling the link between ambient prey availability and feeding rates. The type I functional response curve describes a linear increase in the number of prey consumed with prey density but is often unrealistic as the predator eventually becomes satiated. The type II curve is often more realistic and can be defined as

$$N_{\text{eaten}} = a \cdot T_i N/(1 + a \cdot T_h \cdot N), \tag{16.4}$$

where a is the attack coefficient (attacks/s), T_{i} is the total time available for foraging (seconds), T_h is the handling time per prey, and N is the prey density. Nonlinear least-squares regression (SAS procedure NLIN) can be used to estimate parameters for these equations (Juliano 1993; Box 16.5). The type III equation may be appropriate when the predator switches the prey of interest as that type becomes more common or the predator learns to hunt more effectively for that prey.

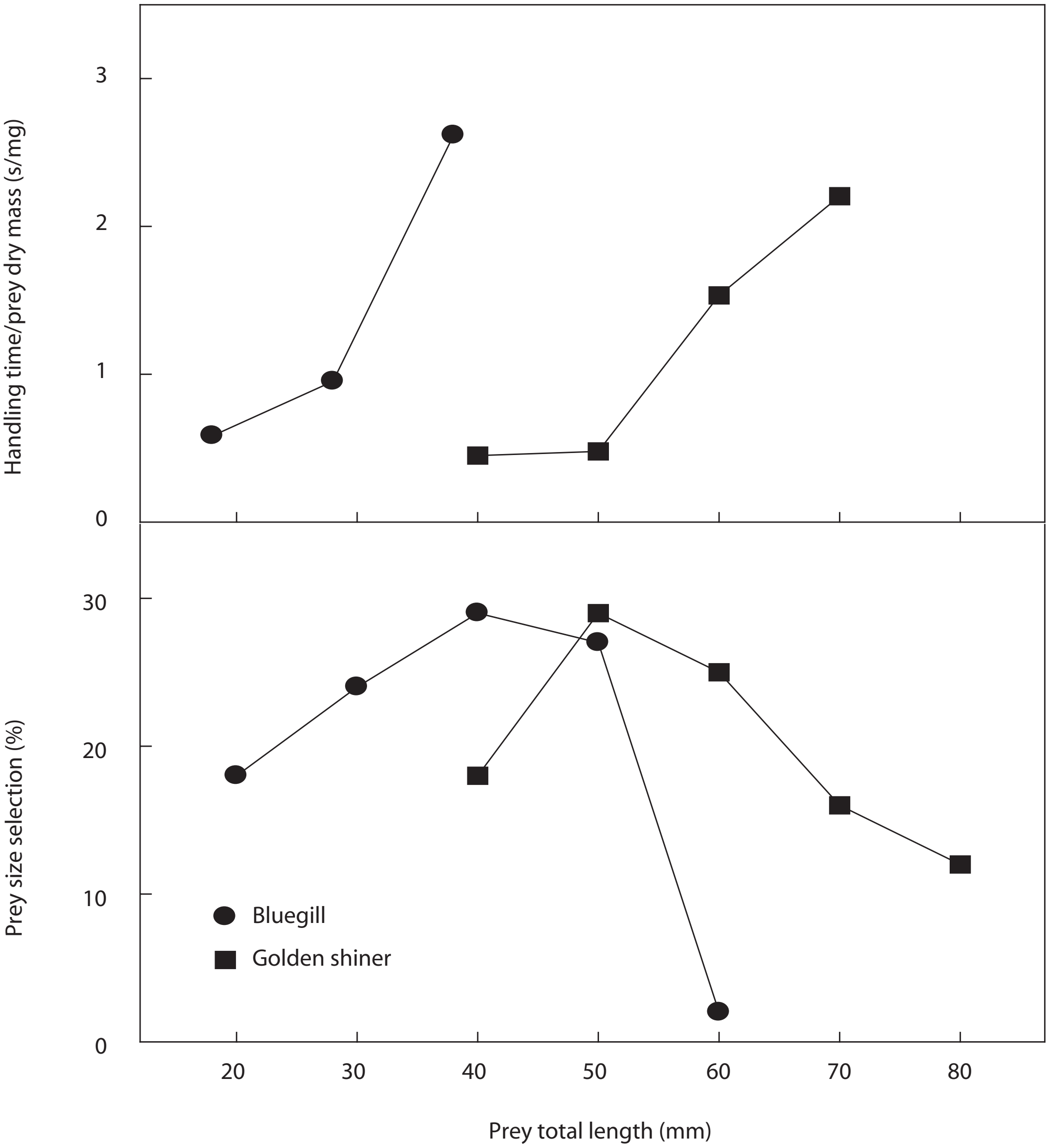

Figure 16.5 Example of cost–benefit relationships (handling time/prey dry mass) used to predict prey size and species selection for 150-mm age-0 walleye feeding on different sizes of bluegill and golden shiner prey (from Einfalt and Wahl 1997). Handling times were recorded for individual walleye in aquaria (*N* = 10) fed individual prey that varied in 4-mm size increments. To determine size preference, predators were fed five prey, one from each size-class. Minimum handling time/dry mass values indicate optimal values and suggest differences between prey species (13–20% of predator length for bluegill and 27–33% for golden shiner). Walleye have a more difficult time handling deep-bodied prey with spines such as bluegill compared with fusiform soft-rayed prey such as golden shiner. An optimal foraging construct successfully predicted differences in prey size selection with walleye choosing smaller bluegill than golden shiner; however, prey preference was for larger individuals of both species than predicted.

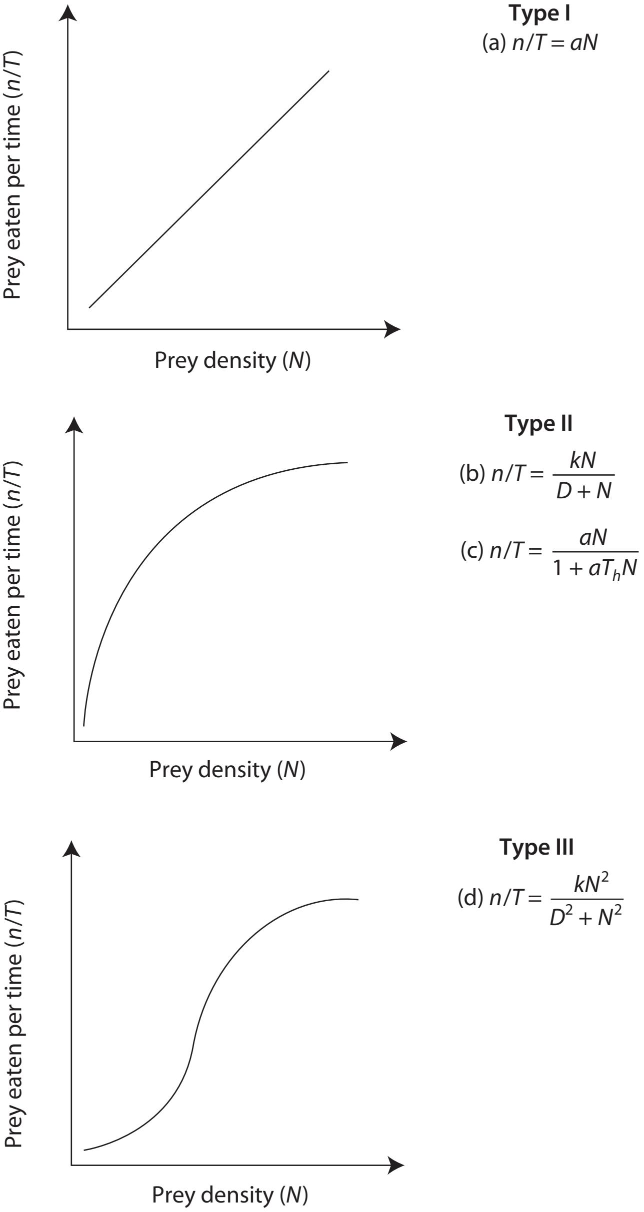

Figure 16.6 Functional response curves describing the relationship between prey abundance and the number of prey eaten per predator per unit of time. The terms of the type I equation (a) are n = number of prey, T = duration of foraging period, a = the predator's capture efficiency, and N = prey density. Some of these same terms apply to type II and type III equations. Two formulations of the type II response are shown; equation (b) gives the relationship in the form of Michaelis-Menten kinetics, where k is the asymptote (maximum feeding rate) and D is the half-saturation coefficient (prey density at which feeding rate is half of maximum). The same coefficients are used in the type III functional response (equation [d]). Equation (c) is a type II response specified in terms of foraging parameters where T_h = handling time.

Box 16.5 Functional Response Curves

Functional response curves quantify predator feeding rates as a function of prey density. The following example demonstrates how a functional response curve was determined for kokanee feeding on zooplankton.

The functional response, or the relationship between predator feeding rate and the density of its prey, is a fundamental framework for studying predator–prey interactions (Begon et al. 1996; Gotelli 1998). Three basic curves are commonly found, depending on the mechanics of the predation process (Figure 16.6). Functional responses are useful for predicting how changes in prey populations may affect fish feeding rates. They are also essential components of models that seek to predict fish foraging behavior and growth rates in the wild (e.g., Stockwell and Johnson 1997; Stockwell et al. 1999).

Laboratory experiments to estimate the parameters of a functional response involve trials in which predator consumption rate is measured under a range of prey densities. Pilot experiments can be used to estimate the variance in consumption rate among trials. That variance can then be used in a power analysis to estimate the number of trials needed to estimate the parameters of the functional response to within the desired level of precision (Chapter 3). Prey density in trials should cover the range of densities that are expected in the wild, and investigators should evaluate whether the experimental setup adequately mimics predator–prey conditions in the wild. The manner in which trials are conducted may affect fish behavior. For example, for some species intraspecific aggression in the confines of a laboratory arena may require the investigator to conduct trials with individual fish. If the same individual fish is to be used in multiple trials then the investigator should evaluate bias from possible carryover effects such as learning during previous trials.

Table Zooplankton (*Daphnia*) density, number of *Daphnia* consumed, trial duration, and kokanee consumption rate from a subset of laboratory trials by Koski and Johnson (2002).

Zooplankton density (*Daphnia*/L)	*Daphnia* consumed	Trial duration (min)	Consumption rate (*Daphnia*/min)
3.0	176	9.41	18.7
4.0	234	9.57	24.5
5.0	267	9.57	27.9
7.5	259	8.30	31.2
8.3	324	9.57	33.9
9.9	364	9.82	37.1
10.9	370	9.61	38.5
12.5	345	9.44	36.5
13.1	356	9.57	37.2
15.6	368	9.44	38.9
17.0	406	9.97	40.8
23.4	416	9.32	44.7
26.0	392	9.90	39.6

The following SAS program was used to fit a nonlinear regression by least squares and obtain the parameters of a type-2 functional response. The model's intercept was forced through the origin on theoretical grounds. Note that nonlinear regression models are more difficult to fit than are linear ones. They also require the user to input starting parameter values; reasonable starting values are essential to insure rapid and accurate fitting of parameters. Starting values can be determined from a visual inspection of plots showing feeding rate as a function of prey density. The parameter *k* (maximum consumption rate) can be estimated from a plot if the data cover a sufficiently broad range of prey densities such that an asymptote is apparent. Given an estimate of *k* one can then estimate *D* (prey density at half of maximum consumption rate, *k*/2).

Program

```
   data typeIIfr;
   input N C;
   /* k = maximum consumption rate
   D = density at which consumption rate is 1/2 max
   N = prey density
   C = consumption rate (n/T)*/
   proc nlin;
   model C=(k*N)/(b1+N);
   parameters k = 50, D = 5; /* Input starting values for estimates of k and D*/
   output out=b p=yhat u95m=u95m l95m=l95m;    /* Prints observed, predicted, and
95% confidence intervals around the mean*/
   proc print;
   run;
   proc gplot data=b;
   plot C*N yhat*N /overlay; /* Plots predicted and observed values to examine lack
of fit*/
   symbol1 value=plus;
   symbol2 interpol=join;
   run;
```

Output

Table Results of SAS program used to fit a nonlinear regression by least squares to obtain the parameters of a type-2 functional response for kokanee feeding on *Daphnia*. Parameters are *k* (maximum consumption rate) and *D* (prey density at half of maximum consumption rate, *k*/2).

		Regression			
Source	*df*	Sum of squares	Mean square	*F*-value	Approximate $P > F$
Regression	2	16121.7	8060.4	2564.13	<0.0001
Residual	11	34.5785	3.1435		
Uncorrected total	13	16155.3			
Corrected total	112	627.5			

Parameter Estimates

Parameter	Estimate	Approximate SE	Approximate 95% confidence limits	
b_0 (*k*)	50.0521	1.8421	45.9977	54.1065
b_1 (*D*)	4.1969	0.5419	3.0041	5.3897

(Box continues)

Box 16.5 *(continued)*

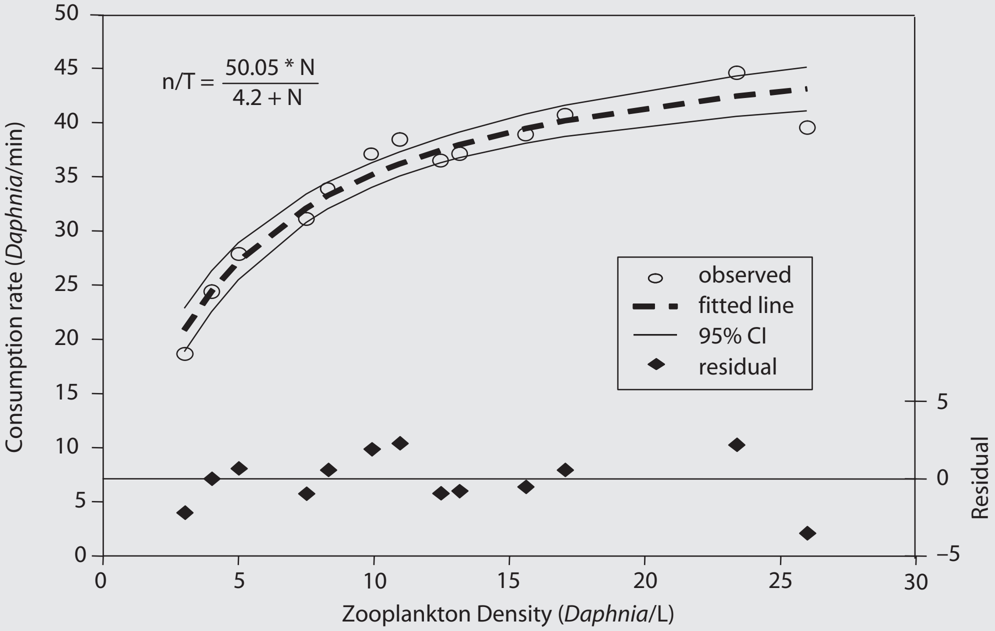

Figure Observed (circles) and predicted (dashed line) consumption rate (*n/T, Daphnia* per minute) as a function of zooplankton density (*N, Daphnia* per liter), and the upper and lower 95% confidence limits (CI, solid lines) on the regression line fit by nonlinear regression. Residuals from the regression (diamonds) are also plotted against zooplankton density.

Interpretation

Kokanee feeding rate increased rapidly as zooplankton density was increased, but the increase in their feeding rate began to slow at higher zooplankton densities, suggesting that handling time was beginning to limit consumption rate. However, feeding trials at zooplankton densities greater than the 26 *Daphnia*/L shown here (which undoubtedly occur in the wild) would be necessary to describe fully the functional response for this planktivore. Goodness-of-fit indicators suggest a good fit of the type-II model to the data: the regression explained a large fraction of the total variation in the data, there was no pattern in the residual plot (see figure), and the 95% confidence limits on the regression fit were not large. Akaike's Information Criterion (AIC; Burnham and Anderson 2002) could also be used to evaluate the appropriateness of the type-II model versus alternative models (e.g., a type I or a type III).

16.5.5 Application of Experimental Results to Management

Experimental studies of predator–prey interactions can be useful in helping guide a variety of fisheries management decisions. As an example, survival and growth can be highly variable for stocked sport fishes, and stocking strategies can be guided by information from predator–prey experiments. Losses to predation have been quantified for several species of stocked sport fishes, including pike (Stein et al.

1981; Wahl and Stein 1989), walleye (Santucci and Wahl 1993), channel catfish (Santucci et al. 1994), and Pacific salmons and trouts (*Oncorhynchus* spp.; Cartwright et al. 1998; Baldwin et al. 2000). Information on the effects of prey availability and predation on growth and survival of stocked fishes can be used to make decisions about when, where, and at what size to stock fishes (Box 16.6). Similarly, understanding of predator–prey interactions under experimental conditions have been usefully applied to predicting effects of exotic species (i.e., zebra mussels and round gobies) and have helped to guide and develop management options. These are just a few of the many ways in which these types of studies can be useful in management situations.

16.6 MODELS OF PREDATION RATES IN NATURAL SYSTEMS

Modeling approaches span a continuum of empirically through mechanistically based constructs. The experimental data section above (section 16.5) introduced models that were developed directly from controlled experiments on prey selection, optimal foraging, and functional response models, whereas this section will focus on models used to quantify predation in natural systems. Estimating the amount of prey consumed by predators is a common but challenging goal in predator–prey investigations. Predation rates can be calculated directly from field-based consumption estimates (e.g., Eggers 1977; Elliott and Persson 1978) or indirectly using empirical relationships (e.g., production:biomass ratios and predator–prey biomass ratios) or simulation models that are often supported by field measurements or laboratory experiments. Each method has strengths and weaknesses and differs considerably with regard to data requirements, validity of assumptions, and the degree of resolution along various dimensions of interest (Ney 1990). The most suitable approach will depend on the level of resolution required (e.g., annual averages versus finer temporal scales; whole population or trophic level averages versus size- or age-structured processes or individual predators; or whole-basin averages versus finer spatial scales) and on the type and quality of data or sampling resources available. Three mass- or energy-balance approaches (production-based estimates, bioenergetics models, and EcoPath with EcoSim model) and an encounter rate model are presented below. These methods should be viewed as complementary or sequential approaches, based on the primary question of interest, existing information, and available resources.

16.6.1 Production-Based Estimates of Consumption

Simple approaches such as production-based models provide first-order approximations of annual predation rates and can be computed quickly if common population dynamics data are available (Ney 1990). These estimates require knowledge of annual production by cohorts of predators (i.e., abundance and biomass at the beginning and end of a year) and food conversion efficiency. In these models,

$$P_t = G_t \cdot B_t , \qquad (16.5)$$

Box 16.6 Case Study of Predation and Stocking of a Sport Fish

Stocking or introductions of sport and forage fishes are common management actions. Sport fish species are stocked to maintain fisheries in waters where habitat degradation and overexploitation have reduced existing populations or to establish new populations in waters such as ponds and reservoirs. Fish may be stocked at catchable size for immediate harvest or as juveniles in a put-grow-and-take stocking strategy. In Midwestern reservoirs, smaller northern pike are more vulnerable to predation by largemouth bass than are larger individuals (Wahl and Stein 1989), so size at stocking influences predatory mortality (see flow diagram below). Predation mortality on stocked northern pike declined from 30% for 145-mm fish to about 2% for 205-mm fish (panel **[A]**, left side flow diagram), as indicated by increased *C/f* (panel **[B]**).

Prey preference and prey demographics also influence both survival and growth of stocked piscivores. In laboratory experiments, northern pike captured herrings, carps, and minnows more successfully than they captured sunfishes (Wahl and Stein 1988; panel **[C]**), and they preferred gizzard shad over bluegill in the field. Morphology (body depth and spines) and antipredatory behavior unique to each prey species (bluegill are more evasive) contribute to differential vulnerability. As a result, northern pike grow more slowly with sunfish prey than with herrings (panel **[D]**). In addition to prey preference, availability of appropriately sized prey will also influence growth of stocked sport fishes (Madenjian et al. 1991; Santucci and Wahl 1993; Wahl and Stein 1993; Johnson et al. 1996). Access to the appropriate forage base is more important for smaller stocked fishes than for larger ones. As diet breadth increases (owing to increased gape sizes), predator dependence on specific sizes and types of prey declines (Stahl and Stein 1994). In addition to growth, prey characteristics influence survival of stocked sport fishes. Survival of northern pike is lower in sunfish communities than in those with herring or carp and minnow prey (Wahl and Stein 1988). Reduced survival may relate directly to reduced capture ability or indirectly to reduced growth and the resulting increased vulnerability to predation or disease.

Timing of stocking can influence predatory losses as well. Cool water temperatures in autumn reduce food consumption rates by largemouth bass, thus reducing the potential for predatory impact by warmwater predators. In contrast, as cooler fall temperatures reduce thermal stratification in coldwater lakes and reservoirs, spatial overlap can increase between coldwater predators like trouts and their prey (Baldwin et al. 2002), as most of the water column approaches optimal growth temperatures for the predators, and predation rates increase (Baldwin et al. 2000).

These and similar results for other stocked sport fish species suggest that stocking should be pursued within an ecological framework that integrates the relative importance of predator–prey interactions across all life stages (Wahl et al. 1995). This framework provides a guide for making management decisions concerning species, sizes, and timing of fish introductions into systems with specific characteristics. Similar approaches can assess potential negative consequences of stocking on community structure and function. In this way, the use of stocking as a management tool can be optimized.

where production P represents the amount of mass or energy accrued by a population or cohort per unit time (including growth of individuals that die during that interval), G_t is the instantaneous growth of the average individual during time t (e.g., $t = 1$ year), and B_t is the mean biomass of the population or cohort during the time interval. The instantaneous growth of the average individual, G_t, is given by

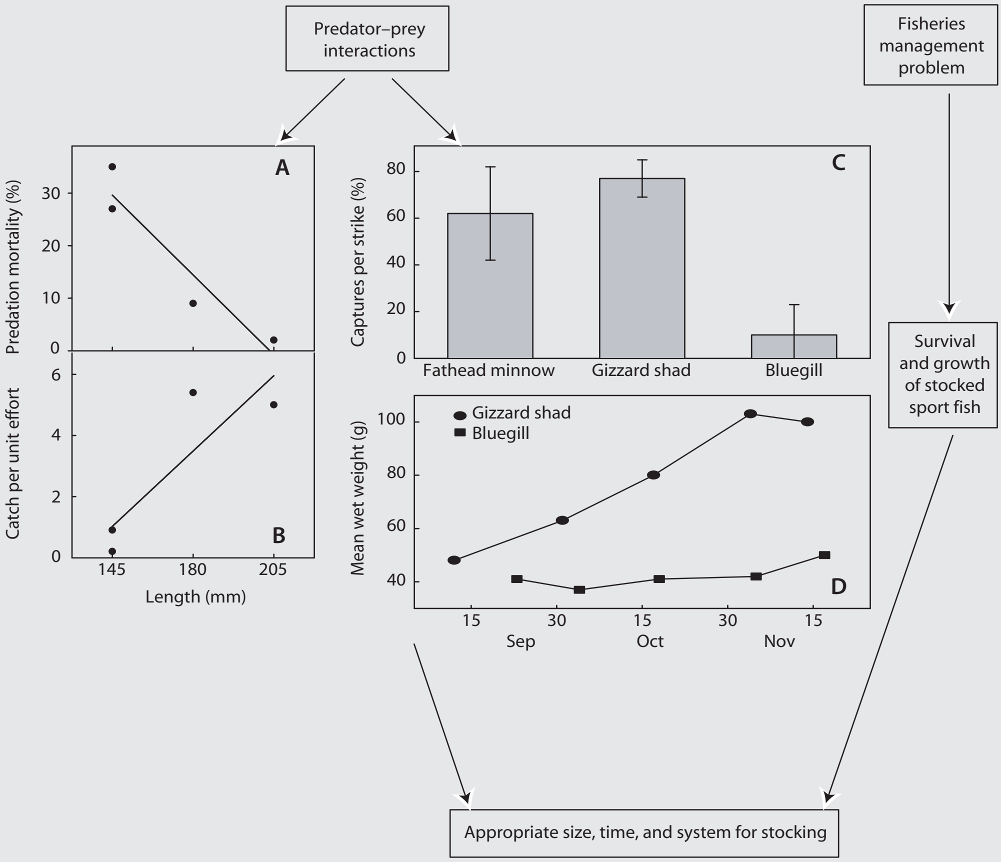

Figure Diagram of how experimental and field results can be used to address a management problem. Predation mortality for northern pike stocked into Midwestern reservoirs was higher for smaller than larger northern pike (**A**, lab experiments and field trials). This differential predation mortality was also reflected by higher catch per unit effort of the larger size-groups of northern pike stocked in reservoirs **(B)**. Juvenile northern pike exhibited higher capture success rates on soft-finned fathead minnow and gizzard shad compared with spiny-rayed bluegill in lab experiments **(C)**, and this was reflected in higher growth rates for northern pike in reservoirs where the predominant prey were gizzard shad rather than bluegill **(D).** When combined with information about the environmental conditions and community structure of the host waters, these type of results enable informed decisions about when, where, and at what size to stock sport fishes.

$$G_t = \log_e(W_t/W_0)/t, \qquad (16.6)$$

where W_0 and W_t are the mean weights of individuals at the beginning and end of the interval, respectively. Food conversion efficiency, CE, is the amount of growth ($W_t - W_0$) by an individual that resulted from consuming a known quantity of food, C' (e.g., from long-term controlled growth experiments using natural prey):

$$\mathrm{CE} = (W_t - W_0)/C'. \tag{16.7}$$

The estimated consumption C_t over time t would then be

$$C_t = P_t/\mathrm{CE}. \tag{16.8}$$

If conversion efficiency was assumed to remain at a constant 10% for all age-classes and years, then total annual consumption of all prey species by the predator could be easily calculated in a speadsheet based on the relationships above (Box 16.7).

In reality, estimates of food conversion efficiency are rare for fish feeding in natural environments, as such estimates depend on estimates of individual consumption and growth over specified time intervals. Moreover, conversion efficiencies can change dramatically with body size, temperature, and food quality, thus potentially causing major errors in consumption estimates. Knowledge of the population dynamics of predators in some freshwater systems may also be insufficient to estimate annual production. If the predation events of interest vary considerably among size-classes of predators, through time, or among habitats, then very serious interpolation or extrapolation errors may result if the sampling design and subsequent analysis do not account for these important sources of variability. Nonetheless, such estimates could provide valuable "first-cut" evaluations for questions such as, Can predation potentially account for enough mortality to regulate specific prey populations?

If such an analysis suggested that predation removed a very small fraction of prey (e.g., mortality < 1%), then the direct effects of predation could be dismissed as a major source of mortality, even though the production-based estimator of consumption potentially erred several-fold from actual mortality. In this case, the uncertainty around the predation estimate did not exceed a threshold value at which predation losses were considered a serious source of mortality. However, if the consumption estimates suggested that predation represented, say, greater than 30% of the prey population, and the associated uncertainty resulted in a three- to fivefold difference in the predation estimate, then fisheries scientists might conclude that (1) predation could be a significant source of mortality, and (2) additional study might be required to reduce the greatest sources of uncertainty.

Ney (1990) proposed a variation of the conventional production-based approach, where consumption, C_t, represented constant multipliers of predator production, P, and biomass B:

$$C_t = 2 \cdot P + 3 \cdot B. \tag{16.9}$$

This approach implies that annual maintenance costs require the equivalent of three times the predator's body mass in food per year, and that after these metabolic demands are met, 50% of the remaining energy can be converted into growth while the remaining 50% is lost as waste. Consumption estimates from this method

Box 16.7 Production-Based Estimate of Consumption

Presented here is an hypothetical example of a production-based estimate of consumption of a focal species, prey A, by each age-class of a predator population. Fisheries scientists wish to calculate a quick, first-order estimate of predation on prey A and want to know which age- or size-classes consume the most biomass of prey A.

Table Consumption of prey A by age-class of predator. The mean body weight, *W;* the instantaneous growth of the average individual, G_t; abundance, N_t; cohort biomass B_t; and annual average production, P_t, of prey A in the diet varies among ages (*t*). Annual production, P_t, is divided by conversion efficiency (CE = 10% in this example) to estimate annual consumption, C_t, per cohort.

Predator age (*t*)	*W*(g)	G_t	N_t	B_t	P_t	CE	Total consumption C_t (g)	Percent prey A	Consumption prey A
0	0.3	3.9120	1,000	300	9,389	0.1	93,890	0%	-
1	15	2.6856	300	4,500	68,079	0.1	680,790	5%	34,040
2	220	0.7156	210	46,200	40,200	0.1	402,000	25%	100,500
3	450	0.2187	147	66,150	13,534	0.1	135,340	40%	54,136
4	560	0.0690	103	57,624	3,479	0.1	34,790	75%	26,093
5	600		72	43,218		0.1			

In this example, overall annual consumption was greatest for age-1 predators (680,790 g/year); however, since the percentage of prey A in the diet increased with the age of the predator, age-2 predators consumed the greatest annual biomass of prey A (100,500 g/year) based on this production-based estimate of annual consumption.

Note that conversion efficiency for piscivores can vary widely (e.g., CE = 5% to 30%) depending on variation in thermal conditions and energetic value of the primary prey. A first-order approximation of CE for multi-cohort piscivore populations could be 20% (e.g., Lane et al. 1979) and is consistent with a generalized annual energy budget for carnivorous fish of 60% of the consumed energy going to metabolism, 20% to waste, and 20% to growth (Brett and Groves 1979).

The data above are hypothetical, so no variability for the estimators is available. Because P_t is a product ($P_t = G_t \cdot B_t$), and C_t and CE are ratio estimates ($C_t = P_t/\mathrm{CE}$; $\mathrm{CE} = G/C'$), error estimates for products and ratios would be needed to compute error around the estimates for consumption using this method. Note that C' used in calculating CE would be derived independently from a different data set (e.g., consumption in a controlled growth experiment or an average from other studies) than the consumption C_t we are trying to estimate here.

$$\mathrm{Var}(\hat{P}) = \bar{G}^2 \cdot \mathrm{var}(B) + \bar{B}^2 \cdot \mathrm{var}(G) - \mathrm{var}(B) \cdot \mathrm{var}(G).$$

$$\mathrm{Var}(\widehat{\mathrm{CE}}) = \mathrm{CE}^2 \left[\frac{\mathrm{var}(G)}{G^2} + \frac{\mathrm{var}(C')}{C'^2} - \frac{2\mathrm{cov}(G, C')}{P \cdot C'} \right].$$

$$\mathrm{Var}(\hat{C}) = C^2 \left[\frac{\mathrm{var}(P)}{P^2} + \frac{\mathrm{var}(\mathrm{CE})}{\mathrm{CE}^2} - \frac{2\mathrm{cov}(P, \mathrm{CE})}{P \cdot \mathrm{CE}} \right].$$

compared favorably to independent field-derived estimates or bioenergetics model simulations, but the production-based and bioenergetic estimates of consumption diverged for older cohorts of predators (Ney 1993).

16.6.2 Bioenergetics Modeling

Bioenergetics modeling, particularly the Wisconsin bioenergetics model (Hewett and Johnson 1987, 1992; Hanson et al. 1997), has become a frequently used tool for estimating consumption or predation rates (e.g., Stewart et al. 1981; Hartman and Margraf 1992; Jones et al. 1993; LaBar 1993; Beauchamp et al. 1995; Baldwin et al. 2000; Johnson and Martinez 2000) or growth potential (e.g., Brandt et al. 1992) for many of the major freshwater fishes and some predatory invertebrates like mysid shrimp. Bioenergetics models are based on an energy balance equation:

$$\begin{gathered}\text{Consumption} = \\ \text{Metabolism (standard and active plus specific dynamic action [SDA])} + \\ \text{Waste (excretion and egestion)} + \text{Growth},\end{gathered}$$

where maximum daily consumption and metabolism are modeled as species-specific functions of body mass and temperature (see Chapter 12 for more detail). The models are most commonly used to estimate the consumption required to satisfy growth observed or targeted over a specified time interval (Kitchell et al. 1977). These models are data intensive, requiring many species-specific parameters and extensive inputs from field data, but they offer the flexibility to address trophic responses at high temporal, spatial, and size-structured resolution if adequately supported by directed field sampling (Ney 1990, 1993; Brandt and Hartman 1993; Hansen et al. 1993).

Consumption estimates are constrained by growth increments observed for each age-class or growth cohort over specified time intervals, and seasonal consumption can be partitioned into predation rates on different prey categories by incorporating seasonal diet information from field sampling. An important advantage of the Wisconsin bioenergetics model is that it operates on a daily time step and can account for temporal changes in predator size, diet composition, temperature, and prey quality (energy density). Therefore, important short-term interactions like acute predation events can be simulated effectively. The input data requirements for this model can be demanding, but most data (size at age, size structure, diet, distribution, and temperature) are often recorded by fisheries scientists during routine population monitoring surveys. Data from routine assessments may not be collected at the frequency required to address specific predator–prey issues, but minor modifications to sampling and data recording protocols can satisfy the input requirements for these models. When compared with independent estimates of consumption, the Wisconsin bioenergetics model has performed well for a variety of salmons and trouts (Beauchamp et al. 1989; Brodeur et al. 1992; Ruggerone and Rogers 1992; Cartwright et al. 1998; Madenjian and O'Connor 1999) and largemouth bass (Rice and Cochran 1984) but differed significantly from field-based estimates for pike (Wahl and Stein 1991) and perches (Boisclair and Leggett 1989a, 1989b, 1989c, 1989 d; but see Hewett et al. 1991 and Boisclair and Leggett 1991). A more thorough description of the Wisconsin bioenergetics model's construction, testing, refinement, and comparisons with alternative approaches (e.g., field-based stomach fullness and gut evacuation rate methods) are presented elsewhere (Ney 1990, 1993; Hansen et al. 1993; Chapter 12). We will explain how bioenergetics models can be used to quantify predator–prey interactions at multiple trophic levels and emphasize considerations for study design and analysis that minimize interpolation or extrapolation error.

Trophic interactions can be quantified by estimating the biomass or numbers and sizes of prey consumed by different predators in a food web. Consumption rates by individuals from each species or life stage can be estimated using a bioenergetics model, given field estimates of (1) incremental growth for each age-class of consumer; (2) the temporal diet composition of each age-class over the period of interest; (3) the average daily temperatures experienced by consumers (termed "thermal experience"); and (4) the energy density of the consumer and prey. Predation rates by individuals from each age- or size-class can be expanded to population level consumption rates if the mortality rates, abundance, and size structure of the consumer's population is known. As with other methods, the major challenge of this modeling approach is to minimize interpolation or extrapolation errors caused by inappropriately pooling input data across size-classes or life stages, by lumping dynamic periods of feeding, distribution, or growth with static periods, or by careless expansions from individual predation rates to population level impacts on prey populations.

16.6.2.1 *Growth Inputs*

Annual growth.—The accuracy of the consumption estimates are dependent on accurate estimates of growth by the predator because the Wisconsin bioenergetics model calculates the amount of food required to achieve the changes in the body weight of predators over specified time intervals. Annual growth increments should be considered the longest acceptable growth period used for fitting consumption. However, when modeling acute predation over relatively short periods, fitting consumption to an annual growth increment could produce considerable error in the estimated predation rate (discussed in following section on seasonal growth). Routine monitoring data often provide estimates of annual growth, either by tracking the modal lengths of each age-class through time or by back-calculating length at age from otoliths, scales, or other appropriate bony parts (Summerfelt and Hall 1987; Ricker 1992; Chapter 5). These length-at-age estimates are converted to weight-at-age estimates using length–weight regressions and provide a first approximation of annual weight change by different age-classes in the consumer population. Body mass at a given length can vary tremendously, so direct measurements of weight at age, when available, are preferred over the back-calculation method. Unfortunately, weights are recorded less frequently than are lengths. The accuracy and precision of these estimates will depend entirely on inherent variability of the data and the adequacy of the sample sizes for each age-class.

Accuracy and precision of annual growth increments can be improved tremendously by generating size and growth estimates from a relatively short, consistent sampling period just after annulus formation.

For older, slow-growing age-classes of long-lived species (e.g., lake trout), most of the annual growth is elaborated as seasonal gain and loss of gonadal tissue rather than somatic growth and will not be adequately reflected by annual growth increments. Therefore, the change in gonadal weight may provide a reasonable minimum estimate of both seasonal and annual growth. The Wisconsin bioenergetics model allows the user to specify the date and amount of gonadal loss for mature fishes. The question then becomes whether adults spawn every year and whether the sex ratio of spawners is highly skewed toward one gender or the other. Accurate measurement of growth becomes progressively harder with the older age-classes of long-lived or slow-growing species. Therefore, consider whether these older cohorts still represent an ecologically significant component of the predator population, based on their relative abundance, diet composition, and consumption rate. If the older cohorts impose minimal predation compared with more abundant younger cohorts, then the older cohorts may not require the additional effort needed to address minor sources of uncertainty or error.

Tracking weight change from tagged individuals can provide direct estimates of growth over a variety of time intervals; however, recapture and accurate measurement of the tagged fish in sufficient numbers at strategic times may be too limited to provide reliable estimates of growth. Tagged fish might also grow slower than untagged fish, thus potentially underestimating growth. Nonetheless, mark–recapture studies are commonly employed for population abundance estimates, and these studies can serve as the primary source of growth estimation or as supplementary information to help interpret age and growth patterns inferred from other methods.

When consumption is fitted to annual growth increments in bioenergetics models, changes in daily consumption estimates will be driven primarily by the temperature regime used in the model and, secondarily, by any large seasonal changes in energy density for a large fraction of the diet. Consequently, if the true seasonal growth pattern differs significantly from the temperature-driven growth trajectory produced by the model, short-term consumption estimates (e.g., acute predation periods) will be biased in the same direction that the simulated growth deviates from the true seasonal growth trajectories.

Seasonal Growth. More accurate estimates of consumption are generated when bioenergetics models are fit to multiple growth intervals per year instead of annual growth increments (Rice and Cochran 1984; Beauchamp et al. 1989; Wahl and Stein 1991). Aquatic organisms rarely grow at a constant rate throughout the year because temporal changes in food supply, temperature, and other environmental conditions operate independently or in concert to produce seasonal growth patterns. Because the Wisconsin bioenergetics model estimates consumption to satisfy observed growth over specified time intervals, it is important to allocate growth rates as accurately as possible to the ecologically significant periods of the year. For example, predation may be concentrated over a short period (e.g., a week or month) when the predators' growth is either much higher or lower than the average annual growth rate. Consequently, errors in estimated predation would depend on how much the actual seasonal growth of the predators deviated from the average growth rate over the year (Figure 16.7).

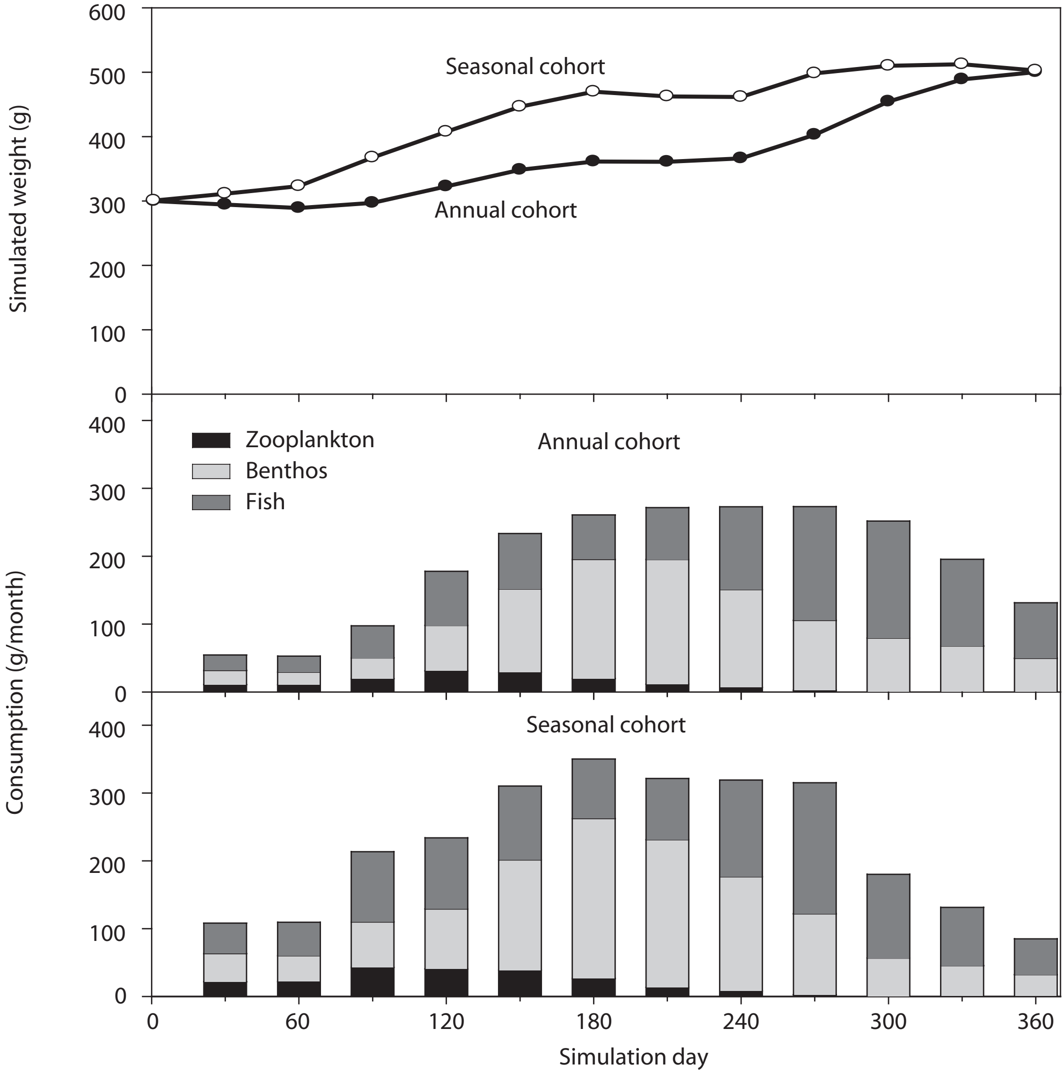

Figure 16.7 Comparison of monthly growth and consumption from bioenergetic simulations based on a single annual growth cohort versus four seasonal growth cohorts when both simulations grow from 300 g to 500 g in 365 d. Mean body weight was consistently higher each month in the seasonal-cohort simulation. The different growth trajectories resulted in different monthly consumption rates. Total consumption was estimated as 2,273 g/year for the annual-cohort and 2,677 g/year for the seasonal-cohort simulation; consumption of benthos was 20% higher per year from the seasonal-cohort estimate and fish consumption 11% higher in the seasonal-cohort simulation.

Ideally, the mean body weight of each age-class would be sampled at the beginning and end of ecologically significant periods of the year by tracking changes in mean weight for each age-class or by tracking length–frequency modes and converting to body weights. Unless age-classes can be unambiguously separated into distinct size modes, age analysis will be needed to reconcile length modes into age-specific growth. Sample size requirements and logistical or political constraints often preclude the sampling intensity needed to measure growth directly over each of the periods of interest.

Alternative methods can be employed for allocating growth among periods of the year. Short-term growth can be back-calculated from circuli spacing in scales, otoliths, or other hard parts. Seasonal changes in relative weight or condition factor for groups of age-classes (e.g., ages grouped as juveniles, subadults, and adults) may improve temporal accuracy in growth with considerably less data than would be required to estimate seasonal growth of each age-class directly. Physiological measures of short-term growth may provide additional resolution in some instances (e.g., RNA:DNA ratios or insulin-like growth factors like IGF-1 [Beckman et al. 1998]), but these methods have shown mixed results among species or are still experimental. In general, consider whether seasonal growth will vary significantly for reasons other than temperature. If so, then it will be important to allocate weight changes for each age-class of the predator into multiple growth stanzas (termed "cohorts" in the Wisconsin bioenergetics model) within year-classes to estimate appropriate consumption rates during ecologically significant periods.

16.6.2.2 Diet Inputs

For many species, diet composition changes seasonally and with increasing body size, and this variability must be captured in order to model predation rates appropriately. Consumers should be segregated into different feeding guilds, based upon differences in diet composition and trophic position. Predators can be grouped into size categories based on the statistical and graphical approaches described in Chapter 11 and section 16.4.2. Diet information for any size-class of consumer is entered as an input file into the Wisconsin bioenergetics model as the proportional contribution of each prey category in the diet by wet weight (or volume) for different dates through the period of interest. A diet input file can be constructed to contain both periods of constant diet proportions and times of rapid dietary change. This is particularly useful for limiting certain diet patterns to discrete periods (e.g., heavy predation over 1–2 months) rather than allowing certain prey items to remain in the diet inappropriately over longer intervals. When diet compositions differ between sampling dates, the Wisconsin bioenergetics model will automatically interpolate the diet proportions for every day between the dates actually entered into the diet input file. To keep diet proportions constant through a time interval, enter the same diet proportions on the first and last day of that interval (Box 16.8).

Box 16.8 Diet Data for the Wisconsin Bioenergetics Model

An example of a diet input file used in the Wisconsin bioenergetics model is given here. Diet data were entered for every sampling date (or the median date of a sampling period can be used). When diet proportions change between sampling dates (among days 1, 91, 181, and between days 271 and 365), the model linearly interpolates a daily change in proportions of each prey type as indicated in the graph. The diet proportions remain constant over periods when the same proportions are entered at the start and end of that period, as between days 181 and 271. A combination of constant and interpolated diet proportions can be used to minimize error associated with applying diet proportions over too long a period in model simulations.

Table Hypothetical diet input file for Wisconsin Bioenergetic model.

Day	Zooplankton	Benthos	Fish
1	0.05	0.60	0.35
91	0.20	0.30	0.50
181	0.05	0.30	0.65
271	0.05	0.30	0.65
365	0.00	0.60	0.40

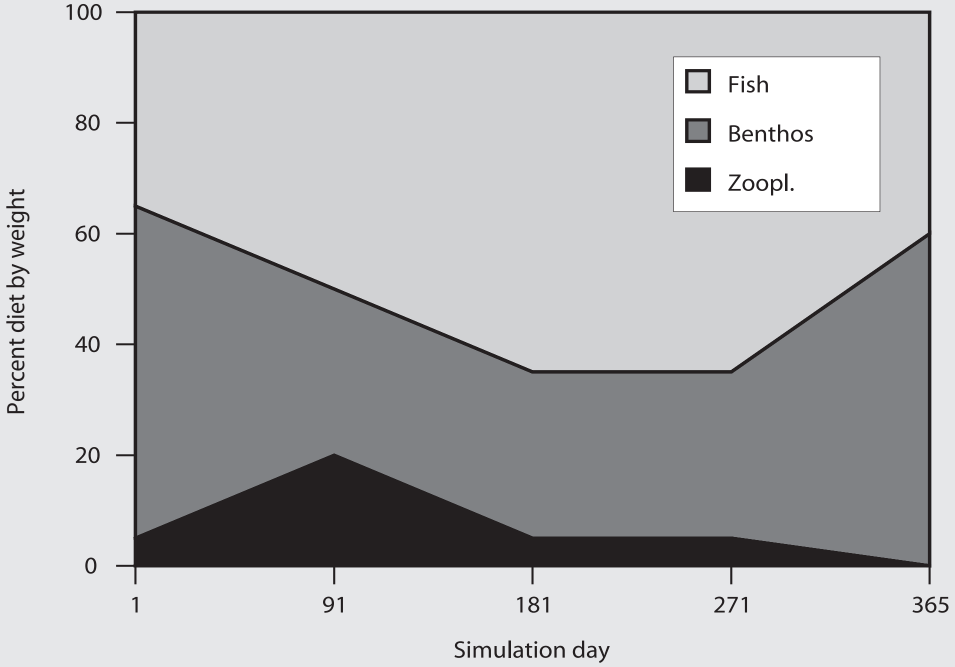

Figure Resulting model simulation of the daily change in diet from hypothetical data set (zoopl. represents zooplankton).

16.6.2.3 *Thermal Experience*

The thermal experience of consumers can be determined several ways based on field data or knowledge of their behavior and distribution patterns. In waters that do not thermally stratify, average daily temperature recordings from temperature loggers may be sufficient for estimating thermal experience unless organisms concentrate in thermal microhabitats (e.g., salmons and trouts congregating in groundwater intrusions). Warmwater species can often be assumed to occupy the warmest temperatures available during thermal stratification (e.g., littoral or epilimnetic regions of lakes during summer and the deepest water available during winter) and would be confined to the ambient temperature during isothermal conditions.

For pelagic and demersal species, or species with variable movement and distribution patterns, reconstructing thermal experience is more involved because the combination of vertical distribution and movement patterns with concurrent vertical temperature profiles determine the average daily thermal experience of these organisms. If vertical distribution information is available (e.g., diel hydroacoustic data for depth-specific densities of planktivores or depth-specific C/f data from gill nets), a weighted mean thermal experience for different species or size-classes can be computed for each sampling date by first multiplying the proportion of the total catch (for that species or size-class) in each depth interval by the mean temperature within that depth interval and then summing these products over all depth intervals. This sum represents the weighted average thermal exposure for the average individual of that species or size-class in the population (Box 16.9). When temporal depth distribution data or temperature profiles are unavailable, a common approach has been to assume “behavioral thermoregulation,” which means that fish will seek out temperatures closest to their physiological optimum temperature for growth. This may ignore other important behavioral or physiological constraints like foraging opportunities, predator avoidance, or tolerance for hypoxia or other suboptimal environmental conditions.

16.6.2.4 *Energy Density of Predators and Prey*

The energy density (in terms of calories or joules per gram body weight [cal/g or J/g]) of prey will determine how much prey biomass must be consumed for a predator to obtain any given amount of energy. For example, a fish would need to consume at least 1.5 times more biomass of invertebrates with energy densities of 3,000 J/g than of fish prey with 4,500 J/g to acquire the same amount of energy. Moreover, invertebrates generally contain a relatively large fraction of indigestible material in their exoskeleton (averaging 10–17% of their body weight across many taxa and 25% for crayfishes compared with an average of 3% indigestible material in fishes. Of the energy ingested, waste losses are subtracted and metabolic costs (standard and active metabolism plus SDA) are paid before any energy is allocated for growth. The remaining energy is divided by the energy density of the consumer to convert energy into new consumer biomass. So if a predator’s energy density was 6,000 J/g, and 4,000 J of energy remained after all waste and metabolic costs were accounted for and removed by the model, that remaining energy would be converted into 4,000 J/(6,000 J/g) = 0.67 g of new growth for the predator.

Box 16.9 Computation of Average Thermal Experience

Given here are two examples of computation of average thermal experience for cohorts, with and without vertical migration, occupying a range of depths under thermally stratified conditions.

Table Average thermal experience in the absence of diel vertical migration.

Depth (m)	Temperature (°C)	Fish density or *C/f*	Proportion of total fish	Proportion allocation × temperature
0	20	0	0.00	0.0
2	20	3	0.06	1.2
4	20	9	0.18	3.6
6	20	12	0.24	4.8
8	18	10	0.20	3.6
10	16	6	0.12	1.9
12	14	4	0.08	1.1
14	12	3	0.06	0.7
16	10	1	0.02	0.2
18	9	0	0.00	0.0
20	9	1	0.02	0.2
22	9	0	0.00	0.0
24	9	1	0.02	0.2
Total		50	1.00	17.5

The weighted average thermal experience on this sampling date in the absence of vertical migration was 17.5°C.

Table Average thermal experience when population undergoes diel vertical migration during periods of thermal stratification.

		Day (14 h)			Night (10 h)		
Depth (m)	Temperature (°C)	Fish density (*C/f*)	Proportion of total fish	Proportion allocation × temperature	Fish density (*C/f*)	Proportion of total fish	Proportion allocation × temperature
0	20	0	0.00	0.0	5	0.07	1.3
2	20	0	0.00	0.0	12	0.16	3.2
4	20	0	0.00	0.0	25	0.33	6.7
6	20	0	0.00	0.0	17	0.23	4.5
8	18	0	0.00	0.0	12	0.16	2.9
10	16	0	0.00	0.0	4	0.05	0.9
12	14	3	0.06	0.8	0	0.00	0.0
14	12	0	0.00	0.0	0	0.00	0.0
16	10	1	0.02	0.2	0	0.00	0.0
18	9	5	0.10	0.9	0	0.00	0.0
20	9	18	0.36	3.2	0	0.00	0.0
22	9	16	0.32	2.9	0	0.00	0.0
24	9	6	0.12	1.1	0	0.00	0.0
26	9	1	0.02	0.2	0	0.00	0.0
Totals		50	1.00	9.3	75	1.00	19.5

(Box continues)

Box 16.9 *(continued)*

To determine the weighted average thermal experience with vertical migration, the mean day thermal experience is multiplied by the hours of daylight and added to the mean night thermal experience multiplied by hours of night. The sum is devided by 24 h:

$$[(9.3°\text{C} \times 14\ \text{h}) + (19.5°\text{C} \times 10\ \text{h})]/24\ \text{h} = 13.5°\text{C}.$$

The same computations would be repeated for other sampling dates. These values would be entered into the temperature input file, and the model would interpolate daily temperatures between the dates when thermal experience data were entered.

Energy density varies considerably among organisms and can change seasonally or with increasing body size. In the Wisconsin bioenergetics model, energy densities are provided as default values in the parameter set for each of the 40 species or life stages provided in the existing model (Hanson et al. 1997). The consumer's energy is often held constant in the model for most species; however, for members of the Family Salmonidae, energy density increases linearly with increases in body mass up to a threshold weight, then remains relatively constant or increases more gradually thereafter. Although strongly recommended, energy densities of predators and prey have rarely been measured in conjunction with a bioenergetic analysis of trophic interactions (but see Luecke and Brandt 1993; Rand et al. 1994; Hartman and Brandt 1995; Bryan et al. 1996). Energy densities of prey are generally taken from the literature (e.g., Cummins and Wuycheck 1971; Hanson et al. 1997).

16.6.2.5 *Bioenergetic Simulations of Predation*

The Wisconsin bioenergetics model can estimate the biomass of each prey type consumed daily by individuals from each cohort of predators. The Wisconsin bioenergetics model reports individual or population level consumption as either a daily rate (g/d) or as cumulative consumption to date (g/period) from the start of the simulation period. Total consumption over a set period can be estimated by summing daily consumption rates within that time interval. Individual consumption from each age-class or size-class can be expanded to population level consumption over any ecologically relevant time steps of daily or greater time intervals by including the initial abundance and mortality of each cohort as inputs to the model (Figure 16.8). In an alternative approach, individual consumption rates are estimated from the model, then model output for individuals is transferred to a spreadsheet, and individual consumption is multiplied at each time step by the corresponding abundance of predator cohort(s). Predator abundance would occupy a column in the spreadsheet alongside columns for the individual consumption estimates at each time step. Each cell in the column would contain the standard formula for computing predator abundance at time t (N_t):

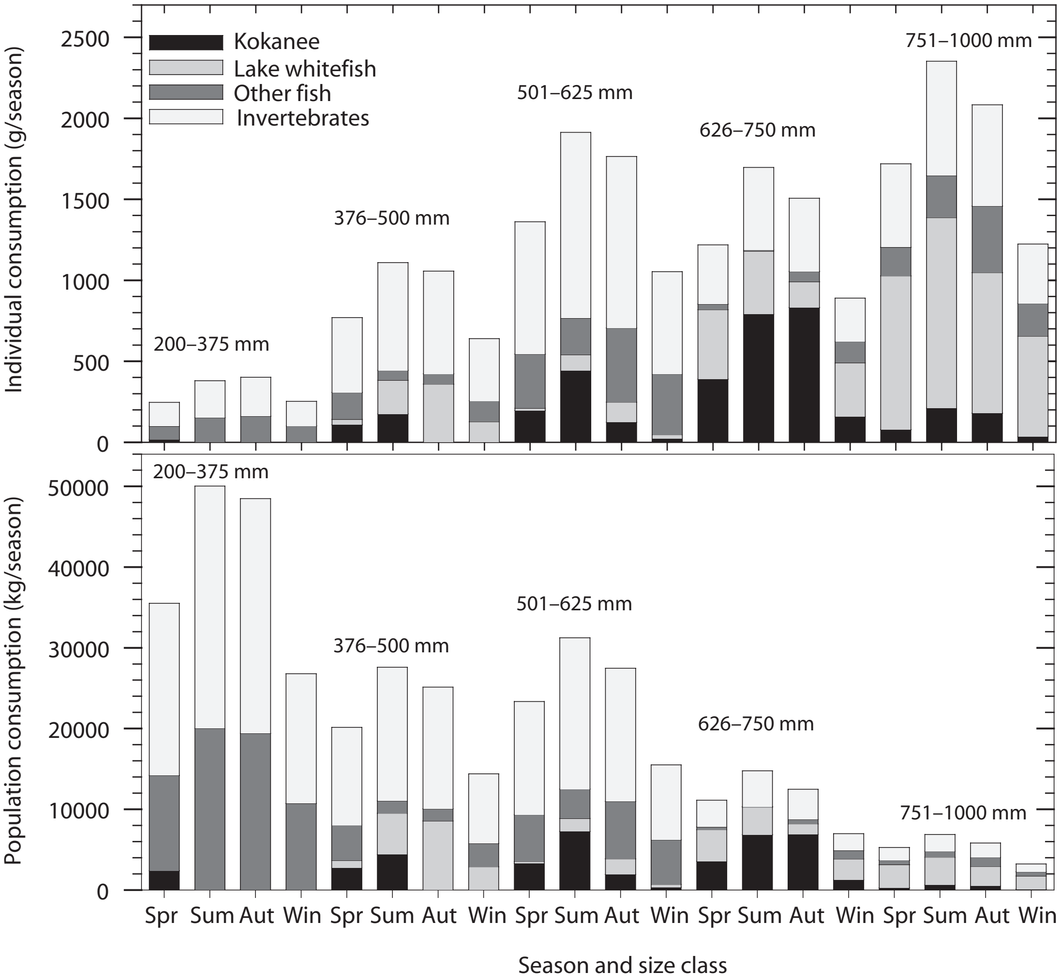

Figure 16.8 Seasonal consumption of major prey species by the average individual (upper panel) and population (lower panel) of each size-class of lake trout in Flathead Lake, Montana. Even though the largest lake trout eat more kokanee on an individual basis, the intermediate and smaller size-classes are much more important predators at the population level. Predation on kokanee varies considerably among seasons. Kokanee outgrew the smaller predators during spring or summer, but predation by the larger predators persisted through autumn and winter.

$$N_t = N_0 \cdot e^{-Zt}, \tag{16.10}$$

where t would relate to the different days in the simulation whereas the initial predator abundance, N_0, and instantaneous mortality, Z, would each refer to a fixed cell or cells where new values could be entered. Predator abundance and population level consumption would then change at every time step throughout the simulation period. The advantage of this approach is that we can rapidly explore the effects of different population dynamics scenarios for predators (e.g., changes in abundance or mortality rates) on predation rates of prey without rerunning the Wisconsin bioenergetics model for every scenario. Additional complexity could be added by incorporating stage-specific instantaneous mortality rates $Z = (M + F)$ to account for differences in natural mortality, M, or fishing mortality, F, among life stages. These additions would enable simulation of different management scenarios to evaluate the effects of various size and harvest limits (Luecke et al. 1994), stocking rates (Stewart et al. 1981; Jones et al. 1993), or interannual variability in survival and recruitment of predators.

The biomass of prey eaten can be converted to a numerical estimate of predation by dividing the biomass of each prey category consumed by the mean weight of an individual prey item. If prey size varies through time or varies among size-classes of predators, then the conversions from biomass to numbers of prey consumed should be computed separately for each combination of time and predator size-class. Large estimation errors can arise during conversions from prey biomass to numerical estimates of prey consumption, particularly if predation persists for more than a month when the prey (e.g., juvenile prey fishes) are growing rapidly, because the body mass of young fish can increase many-fold over relatively short periods (e.g., Cyterski et al. 2003). For example, lake trout in Flathead Lake, Montana, consumed kokanee averaging 145 mm in total length (TL) (25 g) in June and 215 mm in TL (93 g) in August, representing a 48% increase in prey length but a nearly fourfold increase in body mass over just a 2-month interval. Under these circumstances, numerical predation estimates could err considerably by careless averaging of consumption rates or prey sizes through time or across predator size-classes.

Although predation mortality is generally assumed to decline with increasing prey size, the magnitude of that decline has rarely been quantified in natural systems. Since per capita predation rates can be quantified for every size of predator, and predator–prey size relationships can be developed either experimentally (see Box 16.6, Figure 16.5) or empirically (Figure 16.9), the relationship between prey size and potential predation pressure can be formalized by including the abundance and size structure of both predators and prey. For instance, lake trout consume prey fish up to 50% of their own body length (Figure 16.9). Therefore, the number of lake trout, N_{pred}, capable of eating prey of any given length, L_{prey}, is the sum of all predators of length, L, equal to or greater than twice L_{prey} in the total population of predators, N:

$$N_{\text{pred}} = N \cdot \left(\sum_{L=2L_{\text{prey}}}^{K} n_L \Big/ \sum_{L=L_{\min}}^{K} n_L \right), \tag{16.11}$$

where n_L is the count of lake trout in length bin L of a length–frequency histogram from a representative sample of lake trout; K is the maximum length of lake trout in the population; and $L_{\min}$ is the length of the smallest lake trout included in the population estimate N (e.g., N = abundance of lake trout $\geq L_{\min}$, where $L_{\min}$ = 200 mm in TL). By quantifying how the maximum or optimum size of consumable prey increases with predator size, and using the abundance and size distribution of predators, we can examine how incremental changes in prey size affect

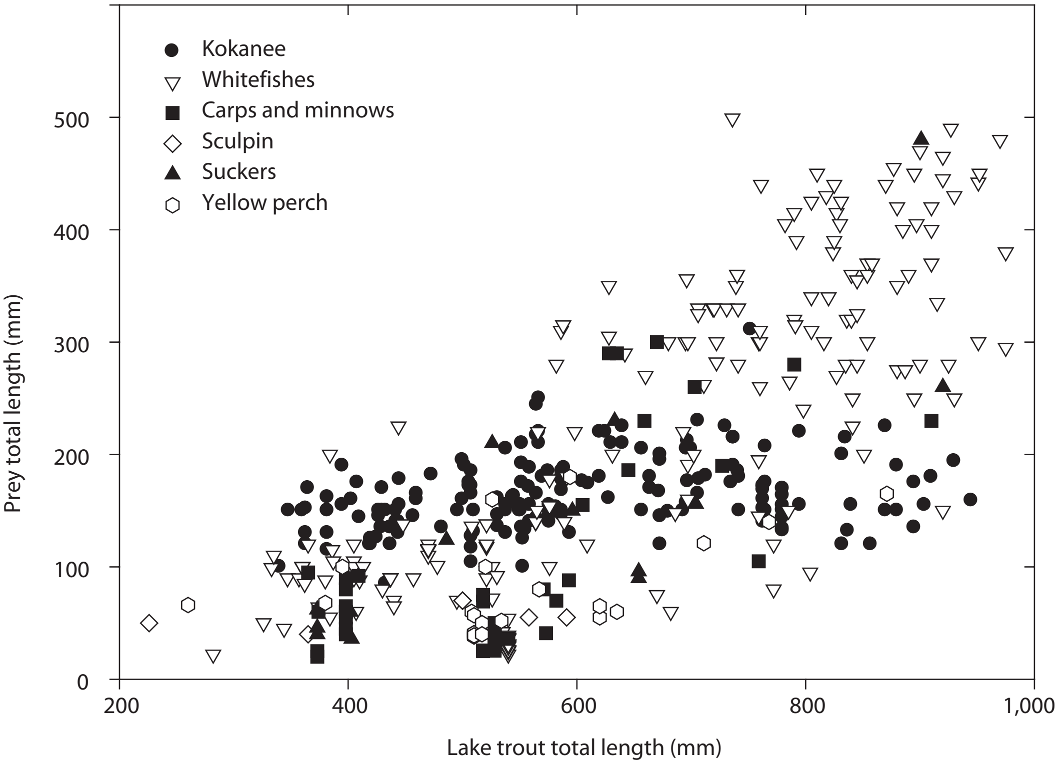

Figure 16.9 Relationship of lengths of piscivorous lake trout to the lengths of prey fishes by species in Flathead Lake, Montana. The predator–prey length relationship showed a classic wedge-shaped distribution for all fish prey collectively, but the pattern varied among prey species. Multiple age-classes of whitefishes were available year-round over a broad range of sizes, whereas most kokanee were available for only a few months after stocking and thus offered a relatively narrow size range to lake trout. This type of graph displays the size range and relative frequency of different fishes eaten by different sizes of predators. We can identify the size at which specific prey entered the diet, and size relationships can be quantified (e.g., mean, median, and lower and upper bounds; see Box 11.3).

predation potential in terms of (1) N_{pred}, the abundance of predators capable of eating a particular size of prey (Figure 16.10, upper panel); (2) the biomass and corresponding number of prey that could be consumed per unit time (e.g., kg/month or prey/month) by all predators greater than or equal to the smallest predator capable of eating a specified size of prey (Figure 16.10, lower panel); and (3) given the growth rate of prey , the period over which prey are vulnerable to predation (Figure 16.11). Larger predators can consume more biomass and larger-bodied prey, but predator abundance declines with increasing size and age due to the cumulative effects of natural and fishing mortality. These analyses can be used to evaluate trade-offs in stocking size versus changes in abundance, size

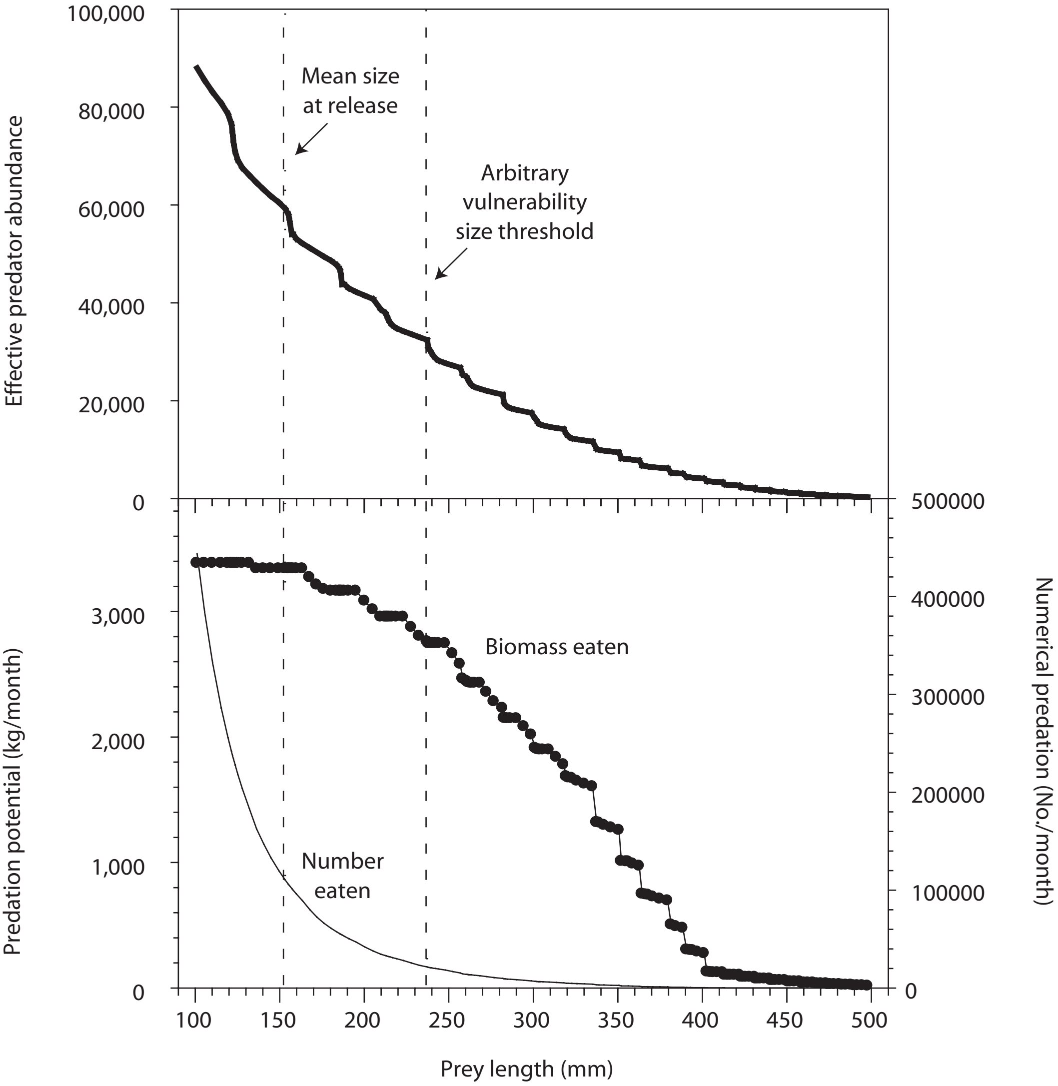

Figure 16.10 Relationships are graphed for lake trout in Flathead Lake, Montana, to demonstrate how predation declines as kokanee grow or as size at release increases. Predation rates declined as prey grew because fewer predators were large enough to capture them successfully. This reduces the total biomass of prey consumed. Also, as prey body mass increased, fewer prey were needed to satisfy the consumption demand of predators. In lower panel, the arbitrary size vulnerability threshold represents an 80% reduction in the number of kokanee lost to predation by lake trout.

structure, or survival of predators to regulate target prey populations (e.g., Box 16.10), or the feasibility of a population restoration program (Box 16.11).

16.6.2.6 *Size-Structured Relative Predation Rates*

When abundance estimates for the predator populations are lacking, a useful way to present model simulations is to report consumption demand in terms of

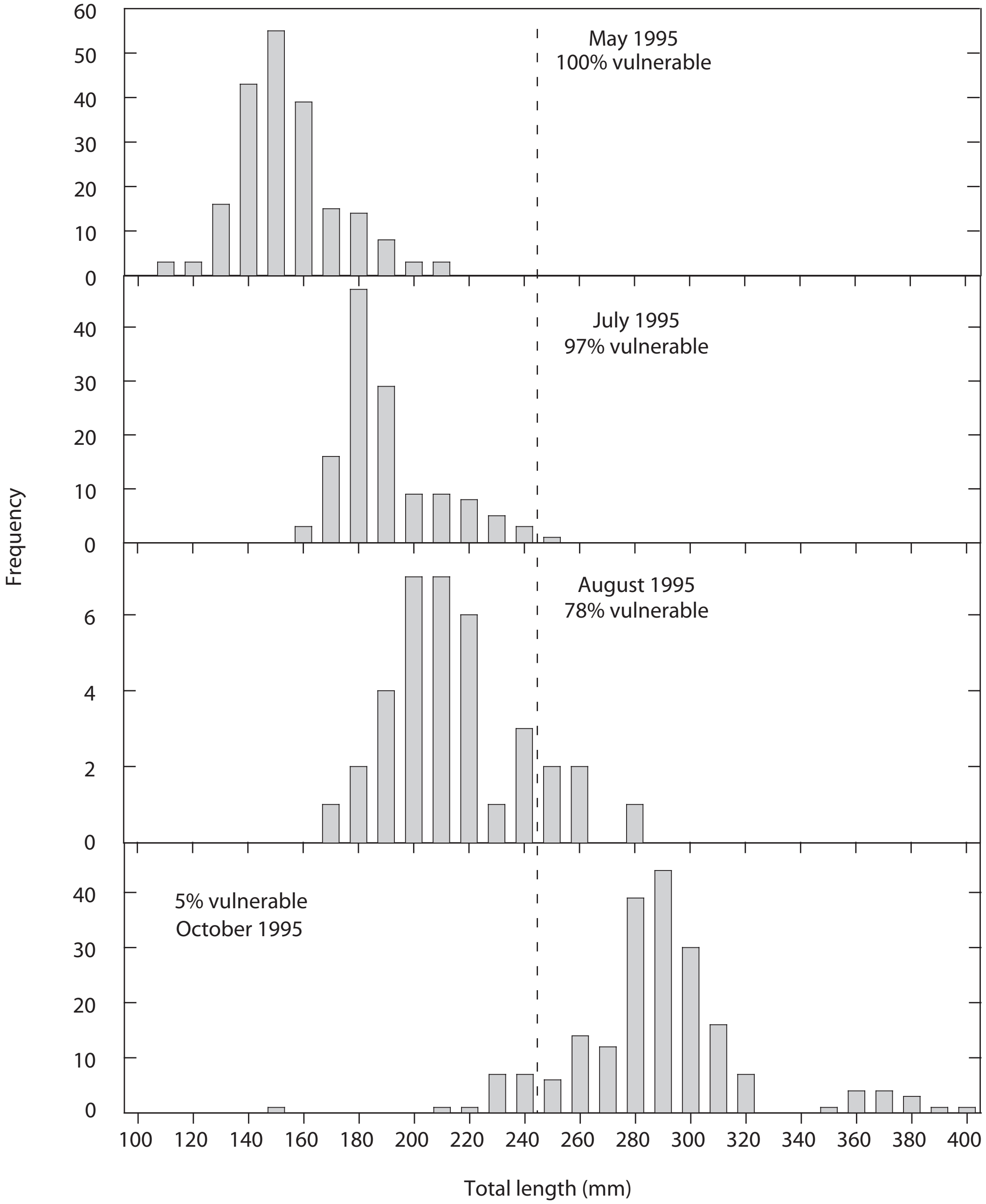

Figure 16.11 Temporal change in length frequency for kokanee stocked during May in Flathead Lake. The dashed vertical line is an arbitrary size vulnerability threshold that represented a 50% reduction in the number of lake trout still large enough to eat kokanee that size and a sixfold reduction in numerical losses due to predation. The size vulnerability threshold was based on a regression ($TL_{prey} = -100 + 0.65 \cdot TL_{lake\ trout}$, where TL is total length; $r^2 = 0.925$; $P < 0.0001$) of predator size versus maximum (95th percentile) of prey size in stomachs (see Chapter 11). All kokanee were vulnerable in May, but only 5% of the survivors remained below the vulnerability threshold by October.

Box 16.10 Case Study of Biomanipulation in Lake Mendota

Lake Mendota is a 4,000-ha eutrophic lake in south-central Wisconsin. The lake hosts a diverse assemblage of cool- and warmwater fishes. Expanding agricultural activities and urban development of the watershed increased external nutrient loading to the lake, contributing to nuisance algal blooms. Because nutrient inputs were mainly from nonpoint sources, and therefore difficult to control, limnologists and fishery scientists tried an innovative experiment to evaluate the potential for manipulating predation (biomanipulation) as a water quality management tool in a large, urban lake (Kitchell 1992). This "top down" experiment involved stocking nearly three million fingerling walleye and northern pike during 1987–1989 and protecting them with restrictive harvest regulations in an attempt to shift the balance among predators and their prey (mainly planktivorous fishes such as yellow perch and cisco). A major thrust of the study was predicting and quantifying the predatory impact by the stocked piscivores.

To forecast and then evaluate predator consumption rates, bioenergetics models (Chapter 12) were used to estimate the biomass of prey consumed by predator populations under various assumptions about predator stocking and mortality rates (Johnson et al. 1992a, 1992b). Applying the models to study predator–prey interactions required detailed field estimates made with a variety of analytical approaches covered in this book.

Analytical Methods

As can be seen below, estimating population-level effects of predators requires considerable field data and an involved set of numerical analyses (see figure below). However, these kinds of ecological questions are central to effective fisheries management, with implications that extend to the ecosystem scale (Kitchell et al. 1994).

1. Size-specific mark–recapture estimates (Chapter 8) of predator abundance were obtained using a suite of sampling gears aimed at minimizing sampling bias.
2. The abundance of size-classes of predators was converted to abundance by age using age–length keys (DeVries and Frie 1996) derived from scale sample analysis (Chapter 5). Scale samples also provided mean length at age of each predator, and these lengths were converted to weights at age using species- and sex-specific length–weight regressions (Chapter 10).
3. Fishing mortality rate (F) was computed from creel survey estimates of harvest by age and the mark–recapture abundance estimates (Johnson et al. 1992a; Chapter 6). Total mortality rate (Z) could not be estimated from a catch-curve analysis because of highly variable recruitment; thus the natural mortality rate (M) could not be estimated by difference ($M = Z - F$). Instead, natural mortality rates from the literature were used.
4. Diet (Chapter 11) was determined from a sampling program, stratified by predator size and season (Chapter 3). Energy density of predator and prey was also required for bioenergetics modeling (Chapter 12).
5. Spatial distribution and thermal history was determined from seasonally and depth- stratified gill-net surveys and radio telemetry (Chapter 14).

Each of the demographic, diet, and distribution inputs to a population-level analysis of consumption demand are associated with some degree of uncertainty. A formal treatment of this issue could involve a Monte Carlo simulation of key sources of error in input data. The parameters of the bioenergetics model itself are not known precisely either, but this uncertainty has been addressed (e.g., Bartell et al. 1986). In many cases uncertainty in field data probably exceeds that of the model.

Fisheries scientists should consider the degree of precision required for the questions at hand and allocate field sampling effort accordingly. For instance, fish abundance is likely to be much more

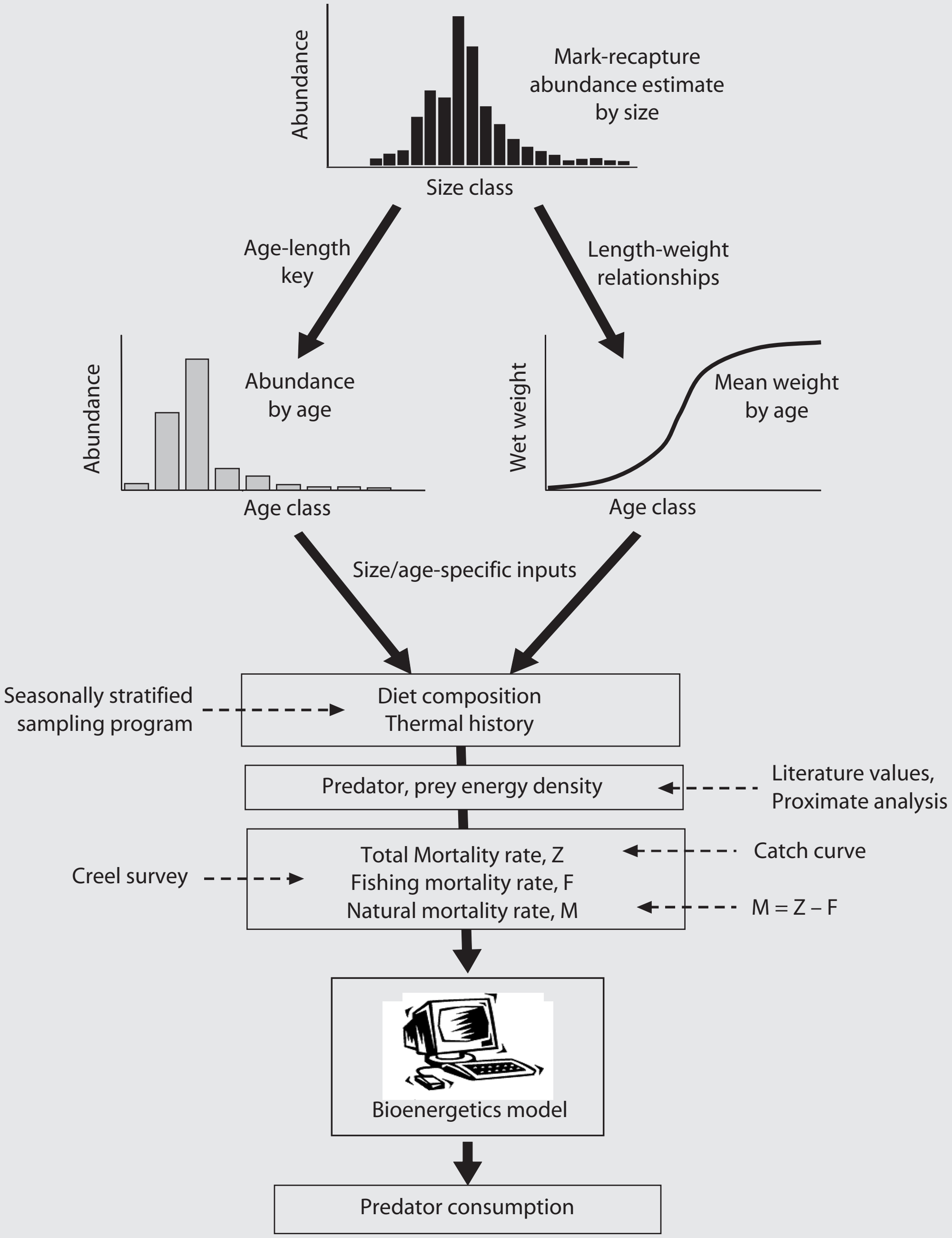

Figure Schematic of analytical methods used to generate data input to bioenergetics model, which, in turn, were used to estimate the biomass of prey consumed by predator populations under various assumptions about predator stocking and mortality rates.

(Box continues)

Box 16.10 *(continued)*

difficult to estimate precisely than is growth rate, especially in large systems. The level of effort devoted to estimating predator diet composition should also be suited to the question of interest. In some studies it may be sufficient to determine the fraction of fish versus invertebrates in the diet, which could be known with much less sampling effort than if species level diet composition were required.

Major Findings

The diets of piscivores varied seasonally and with the size of the predator. Age-0 sunfishes were the dominant prey for both piscivores in the fall (Johnson et al. 1992b). Yellow perch were important to the diet of northern pike and walleye greater than 304 mm in total length (TL), and the relative contribution of yellow perch to their diets depended on year-class strength of yellow perch. Ciscoes were not found in predator diets after the large summer kill in 1987 (Rudstam et al. 1993). However, given the extremely large size structure of the cisco population in the late 1980s, few ciscoes would have been within the gape limits of the piscivores, and distribution studies showed low spatial overlap among the pelagic cisco and the more littoral and benthic walleye and northern pike. Although stocked walleyes were relatively rare in walleye and northern pike guts, projections of total biomass of walleye consumed suggested that piscivory (Polis et al. 1989) was a significant source of mortality for walleye fingerlings. Simulations with an individual-based model of growth of age-0 walleye (Madenjian et al. 1991) predicted that if walleye fingerlings were stocked slightly earlier in the season or 20% larger (60 versus 50 mm TL) at the traditional time, then the proportion of fish in the walleye's diet, and their first year growth, would be enhanced greatly, with an expected increase in first-year survival of the cohort.

Biomass of both piscivore species increased rapidly from less than 1 kg/ha to 4–6 kg/ha throughout the 12-year evaluation period (Lathrop et al. 2002). Annual consumption by walleye and northern pike increased from about 5 kg/ha in 1987 to 10–29 kg/ha (mean 17 kg/ha) during 1989–1998. Premanipulation projections of piscivore biomass and consumption were higher; the shortfall was largely due to predation effects on both small and large piscivores. Low survival rates of stocked walleyes were attributed partly to the piscivory described above, with previously stocked piscivores preying on subsequent cohorts (Johnson et al. 1996). Dramatic increases in predation on larger piscivores by humans and the concomitant increases in fishing mortality during the experiment (Lathrop et al. 2002; Johnson and Carpenter 1994) also limited the effectiveness of the stocking program.

Total planktivore standing stock dropped from 140 kg/ha in 1986 to 50 kg/ha in 1987, primarily due to a large die-off of cisco. Planktivore biomass remained very low (20–40 kg/ha) during 1988–1998. Thus, piscivore consumption represented about half of the planktivore standing stock during the experiment, suggesting that piscivory may have suppressed planktivore populations. However, a large year-class of yellow perch was produced in 1997, indicating that under favorable conditions (abundant zooplankton food resources and weather conditions conducive to spawning) piscivores were not able to control planktivore recruitment.

Dramatically lower planktivory by fishes during the 1990s resulted in a trophic cascade (Carpenter et al. 1985) with higher densities of large cladoceran grazers (mainly *Daphnia pulicaria*), lower algal densities, and improved water clarity (Lathrop et al. 2002). Regardless of the efficacy of the biomanipulation effort to improve water quality, the Lake Mendota experiment stands as a clear example of the importance of a quantitative understanding of fish predator–prey interactions at multiple trophic levels.

Box 16.11 Case Study of Predation Losses Imposed by Lake Trout on Stocked Kokanee in Flathead Lake

Flathead Lake, Montana, historically supported one of the largest kokanee fisheries in North America. The kokanee population crashed in the mid-1980s, coincident with the establishment of high densities of the opossum shrimp, which had invaded from a lake higher in the watershed where they had previously been introduced (Beattie and Clancey 1991). Also coincident with the opossum shrimp increase was a marked increase in lake trout catch and reciprocal declines in native bull trout and westslope cutthroat trout. Federal, state, and tribal managers attempted to re-establish the kokanee population by stocking up to 1 million yearling kokanee each spring, but they needed to know whether any of the proposed stocking strategies would result in reasonable adult returns to the fishery and spawning traps. Of primary concern was whether predation by lake trout would prevent sufficient kokanee recruitment to satisfy a viable fishery and egg-taking operation.

The objective of this study (Beauchamp 1996) was to estimate the predation losses imposed by lake trout on 800,000 yearling kokanee stocked in June. The diet, distribution, size structure, and growth of lake trout and kokanee were obtained by sampling randomly selected locations in five regions of the lake and four depth intervals per location by means of overnight sets with sinking experimental variable-mesh gill nets. Sampling was conducted monthly during May–August, then once per season during fall, winter, and early spring. This provided diet and distribution patterns for lake trout before and after the kokanee release. The proportional weight contribution of each prey type in the diet of lake trout was estimated by season and size-class. The size structure of the lake trout population was corrected for size-selective bias for the array of mesh sizes used (Rudstam et al. 1984; Hansen et al. 1997). Length at age for lake trout was determined by measuring annual growth increments on otoliths, and lengths were converted to weights using a length–weight regression from this population. Abundance of lake trout was estimated in a separate study (Deleray et al. 1999) by use of several methods, including mark–recapture, hydroacoustics, and depletion estimators. Bioenergetics models were used to estimate monthly and seasonal consumption rates for individual lake trout from each age-class by fitting annual size and growth, using the monthly and seasonal change in proportional diet composition for each size-class (Boxes 16.3 and 16.8), and computing the thermal experience from seasonal vertical distribution patterns and temperature profiles (as in Box 16.9). Individual consumption was multiplied by the abundance of lake trout from each age-class (from abundance estimates and size structure data) to expand to seasonal population level predation estimates on kokanee and other key prey (Figure 16.8).

Bioenergetic model simulations suggested that lake trout predation imposed serious losses on the kokanee population in Flathead Lake, accounting for 87% of the total number stocked within the first year of their release. The heaviest predation in 1994 occurred during the first month after stocking 800,000 kokanee (120 mm in fork length [FL]) in June (351,000 kokanee eaten). Kokanee losses during this acute predation period exceeded total predation losses accrued during July–September (263,000 eaten). Lake trout in the 626–750 mm and 501–625 mm (TLs) size-classes were responsible for more than 64% of the estimated predation, and 376–500 mm lake trout consumed another 21% (Figure 16.8). Kokanee disappeared from the diets of progressively larger predators over time, suggesting that the kokanee could rapidly outgrow the smaller, more abundant predators (Figures 16.8, 16.9). The potential change in predation losses was computed as a function of increasing prey size, either through growth or by stocking kokanee at a larger size. The change in predation losse was based on the size-structured abundance of predatory lake trout N_{pred}, the size-specific bioenergetic consumption demand of lake trout, and the predator–prey size relationship,

(Box continues)

Box 16.11 *(continued)*

which indicated that lake trout could consume salmonid-shaped prey up to 50% their own body length (Figure 16.9). In Flathead Lake, the estimated predator population of nearly 900,000 lake trout of 200 mm or greater (TL) was capable of eating 100-mm (FL) kokanee, but the number of potential predators declined sharply as prey size increased (Figure 16.10, upper panel). Under the observed seasonal and size-specific diet composition and consumption rate patterns, lake trout could consume an estimated 3,500 kg or 450,000 100-mm kokanee per month (Figure 16.10, lower panel). As prey size increases, the number of kokanee that could potentially be lost to lake trout predation declines dramatically for two reasons: first, because of the sharp decline in N_{pred} (Figure 16.10, upper panel); second, because prey body mass increases rapidly with increasing length, thus fewer prey are required to satisfy predator demand (Figure 16.10, lower panel). In this case, when the mean size at release was increased from 120 mm (FL) in 1994 to 150 mm in 1995, the initial predation losses should have declined from 351,000 kokanee eaten per month to about 120,000 eaten per month for a nearly threefold reduction in predation rate (Figure 16.10, lower panel). Predation losses would then decline in subsequent months as kokanee grew. If fisheries scientists wished to limit the initial loss rate to only 20,000 kokanee per month, they would have to release kokanee at a length of nearly 240 mm (FL) (the arbitrary vulnerability size threshold in Figures 16.10, 16.11). The monthly change in length frequencies for stocked kokanee in 1995 indicated that all the kokanee stocked in May were below this vulnerability threshold; despite an apparent growth rate of 15 mm/month, 78% were still below the threshold in August, but only 5% were below the threshold in October (Figure 16.11).

Different predation scenarios were modeled to examine the effects of different dietary responses by lake trout, different assumptions about the abundance and size structure of lake trout, and different stocking rates for kokanee. For example, a worst-case scenario could be constructed by assuming the predators fed exclusively on kokanee and achieved their physiological maximum consumption rate (i.e., *p*-value = 1.0 in the Wisconsin bioenergetics model; see Chapter 12) to determine an upper limit to predation losses. When modeling the effects of either an acute predation response (the diet of lake trout was composed of 100% kokanee) or a higher chronic predation response (i.e., the observed initial proportion of kokanee in the diet for each size-class of lake trout was sustained throughout the year), kokanee survival over the first year in the lake declined from 13.2% in the nominal run to 4.6% in the chronic predation scenario, whereas no kokanee survived past midsummer in the acute predation scenario. Lake trout abundance might have been underestimated in model simulations because size and abundance were based on a hydroacoustic survey in August 1995. Because standard hydroacoustic methods cannot detect fish 1 m or less from the bottom, some fraction (e.g., 10–50%) of the predator population might not have been detected. When simulations increased the lake trout population by 10%, survival for a release of 800,000 kokanee dropped from 13.2% to 4.2%; no survival was predicted if the lake trout population was 50% larger than the acoustic-based estimate. Model simulations suggested that the kokanee mitigation program could not meet its harvest or egg-taking goals under the current stocking regime of releasing 800,000–1,000,000 yearling kokanee in late spring.

Predation losses alone accounted for nearly all of the kokanee stocked (87%), but other sources of mortality (other predators or disease) could also reduce adult returns. The prohibitive cost and insufficient hatchery capacity prevented the production of more or larger kokanee to reduce predator demand enough to achieve acceptable and sustainable egg-taking and harvest goals. Based on this analysis, the kokanee mitigation program was terminated because of the unsustainably high predation losses.

consumption per standard unit of a size-structured predator population. For instance, we could create a standard population of 1,000 predators, varying from the youngest to the oldest age-classes that ate the prey species of interest. These 1,000 predators could be allocated into size-classes in proportion to the size structure observed in the population. Consumption by individuals in each age-class would be multiplied by the corresponding number of predators allocated to each age-class from the pool of 1,000 predators to estimate total predation by the size-structured population of 1,000 predators and the relative magnitude of predation exerted by each age- or size-class (Beauchamp et al. 1995; Beauchamp and Van Tassell 2001). Predation losses could then be reported in terms of numbers or biomass of prey consumed per 1,000 predators per year (or over other time scales). Although predator abundance estimates might be lacking, fisheries scientists often have some sense of their abundance, at least within an order of magnitude. Given this information, fisheries scientists can decide whether predation rates are severe enough to warrant further attention. If so, they will either have sufficient information to proceed with management actions or the rationale for justifying further examination into the abundance or dynamics of the predator population.

16.6.2.7 *Predation versus Prey Supply*

Population level predation rates can be compared with the abundance, biomass, or production of prey populations to determine whether predation represents a significant source of mortality for prey (Kitchell and Crowder 1986; Stewart and Ibarra 1991), the prey represent a sustainable source of food for the predator (Ney 1990; Cyterski et al. 2003), or potential bottlenecks in prey supply might develop during particular periods or locations (Johannsson et al 1994; Rand et al. 1995; Beauchamp et al. 2004). If growth or reproduction significantly alters the abundance or biomass of prey during the period of interest, then it may be more relevant to compare predation to prey production rather than to prey biomass (Figure 16.12). Comparing predation losses to the biomass of available and vulnerable prey represents a more severe estimate of predation mortality and thus provides a more conservative basis for managing the impacts of predation on sensitive prey species than if prey production were included in the analysis (Figure 16.12).

16.6.3 Prey Encounter Rate Models

These models combine the search volume of a predator with the densities of prey that overlap in time and space to estimate the encounter rate for the fraction of prey that are actually available (Box 16.2) during foraging periods (Gerritsen and Strickler 1977). Encounter rates can be calculated separately for different temporal–spatial cells to account for variability in factors that influence prey detection limits or localized differences in prey density. Encounter rate models are conceptually attractive because they link localized environmental conditions and prey densities to foraging success at temporal and spatial scales that are relevant to predators and consistent with primary sensory mechanisms involved in prey detection (e.g., visual, tactile, chemical, pressure, electrical, and sound).

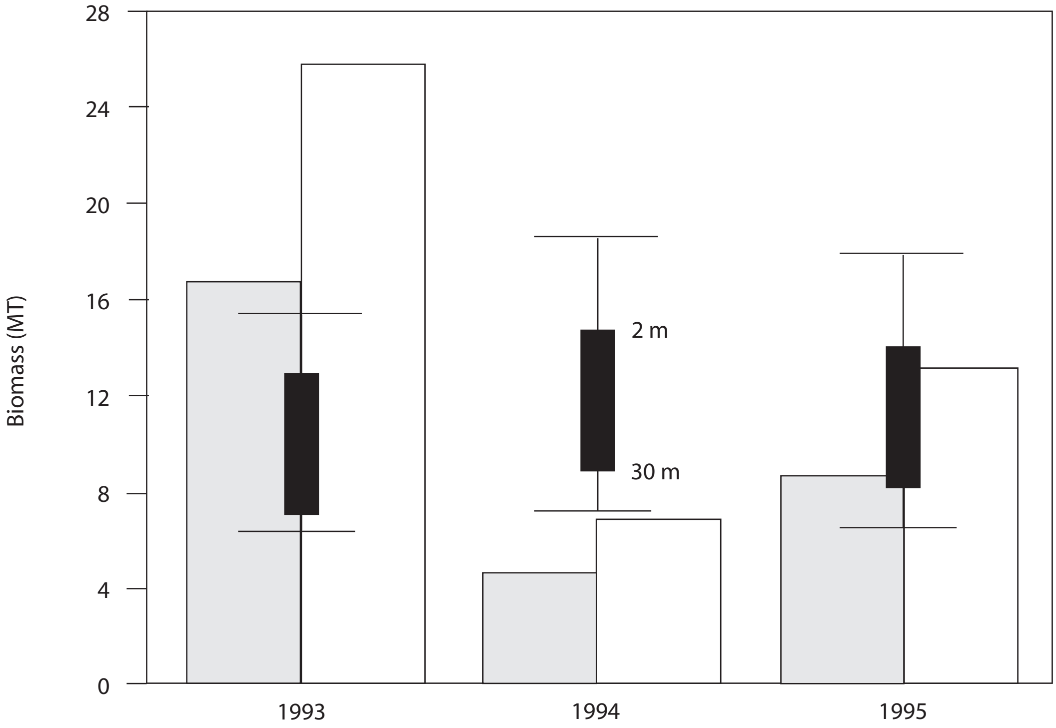

Figure 16.12 Standing stock (metric tons [MT], gray bars) and production (white bars) of rainbow smelt and walleye consumption (vertical lines) of rainbow smelt in Horsetooth Reservoir, Colorado. Uncertainty in walleye consumption is shown as heavy vertical lines representing the range of consumption under two hypothesized thermal regimes (temperatures measured at 2 m and 30 m) and thin vertical lines representing the 95% confidence interval around walleye abundance (adapted from Johnson and Goettl 1999).

Encounter rates can be equated to consumption in some cases; however, a probability of consumption would generally be applied to encounters. These probabilities could either be fixed proportions or functions of other factors that mediate capture success following detection. Encounter rates are essential elements of optimal foraging models and, though generally ignored, should also be incorporated into estimates of prey selectivity and functional responses (Koski and Johnson 2002) in environments where overlap between predators and prey vary through time and space. This approach is particularly valuable when applied to systems in which prey densities and detection capabilities vary through time or space. Encounter rate and bioenergetics models have been combined to estimate the profitability of various feeding positions in streams by drift-feeding fishes (Hughes and Dill 1990; Hill and Grossman 1993), growth potential of piscivores in lakes or estuaries (Brandt et al. 1992; Goyke and Brandt 1993), growth or survival in individual-based models (Breck 1993; DeAngelis et al. 1993), and variation in prey encounter rates by pelagic planktivores (Mason and Patrick 1993) or piscivores with time and depth in lakes and reservoirs (Beauchamp et al. 1999; Mazur and Beauchamp 2006; Box 16.12).

16.6.4 Community and Ecosystem Level Models

Because many fish species and humans are such potent predators, predation (or harvest) is a central process in the structure and function of aquatic ecosystems. Most fishes, and indeed all harvested species, are both predators and prey. Human interference with natural predator–prey systems may have sweeping and often unexpected effects on food webs and ecosystems. Overharvest of apical predators can allow less desirable competing species to expand (e.g., Fogarty and Murawski 1998) or in some cases may lead to a shift in community structure (Scheffer et al. 2001). Release of prey species from predation as top predators are overexploited can promote depensatory recruitment in the predator as expanding prey species compete with or prey upon juvenile predators (Walters and Kitchell 2001; Post et al. 2002). On the other hand, overprotection of predators in recreational fisheries may contribute to unsustainable management strategies when predation rates exceed prey populations' replacement rates (Johnson and Martinez 2000). And finally, overharvest of prey species may have unintended consequences for higher trophic levels (Cury et al. 2000).

Clearly a more inclusive and holistic view is needed to understand and manage fisheries better, but with holism can come greater complexity. Analytical and statistical tools developed for single species or simple predator–prey systems may not be adequate when expanding the fisheries scientist's purview to the ecosystem scale. A modeling package developed by University of British Columbia's Fishery Centre, Ecopath with Ecosim (Christensen 2001), is an exciting and widely used (Christensen and Pauly 1993) framework to cope with complexity of fished ecosystems. Basic analytical features of the package are shown in Box 16.13.

16.7 SUMMARY

Predator–prey interactions can be studied at the level of individual predators and prey up through ecosystem level effects. Investigations are often most effective when integrating field sampling, natural or laboratory experiments, and modeling in an interactive or complementary fashion. The question and temporal or spatial scale of interest will determine the most appropriate mix of these methods. Body size relationships, variability of processes at different temporal and spatial scales, and effects of habitat and environmental conditions consistently emerge as important factors affecting predator–prey interactions and should be considered as a conceptual framework for addressing any question of interest. Interpolation or extrapolation errors can be minimized by analyzing interactions at appropriate scales and by stratifying along important dimensions of variability for the process of interest.

Box 16.12 Visual Encounter Rate Model

Pelagic piscivores (e.g., salmons, trouts, walleye, and striped bass) feed visually in lakes and reservoirs where visual foraging conditions can be very dynamic. Visual search volumes change as photic conditions vary by depth and time of day. Prey densities also change dramatically by depth and time as prey fishes undergo diel vertical migrations. Under these conditions, visual encounter rates need to be calculated separately for different time and depth intervals.

Beauchamp et al. (1999) modeled prey encounter rates, $ER_{z,t}$ (prey/h), for each depth *z* and diel period *t* as the product of depth and temporally explicit search volumes, $SV_{z,t}$, and the vertical density distribution of prey fishes, $PD_{z,t}$, which was obtained for each 5-m depth interval from hydroacoustic surveys during each diel period *t* (daylight, dusk, and night).

$$ER_{z,t} = SV_{z,t} \cdot PD_{z,t}.$$

Within each depth and time cell, search volume was modeled as a cylinder with length equal to the average swimming speed, SS_t (m/·s), of predators (from telemetry and laboratory studies in the literature) during each diel period multiplied by the duration of each period:

$$SV_{z,t} = SS_t \cdot \pi \cdot RD_{z,t}^{\,2}.$$

The circular cross section of the cylinder has a radius equal to the reaction distance, $RD_{z,t}$ (m), to prey. Reaction distance changes as a function of light intensity, and light changes with depth and diel period; RD is further reduced by turbidity, which can change seasonally and among locations. For an ambient light intensity, $I_{z,t}$, of 17.8 lx or less,

$$RD = 0.120 \cdot I_{z,t}^{\,0.4747} \cdot NTU^{-0.624}.$$

For an $I_{z,t}$ greater than 17.8 lx,

$$RD = RD_{max} = 0.478 \cdot NTU^{-0.624}.$$

"Clear water" has a minimum turbidity of 0.3 nephelometric turbidity unit (NTU). Ambient light intensity declines exponentially with depth *z* and time *t*:

$$I_{z,t} = I_{0,t} \cdot e^{z \cdot -k},$$

where $I_{0,t}$ is surface light intensity (lux) at time *t,* and *k* is the light extinction coefficient (m^{-1}). Surface light intensity can be measured directly or approximated using a computer program by Janiczcek and deYoung (1987).

The visual encounter rate model described above was applied to the diel distribution patterns of prey in Alturas Lake, Idaho (Figure 16.1), using data inputs for the model summarized in the Table below. We assumed that turbidity (0.34 NTU) remained constant throughout the water column. The light extinction coefficient $k = -0.1535$ was applied to the average surface light intensity during daylight, mid-dusk, and night periods to estimate light intensity within each depth × time cell. Swimming speeds (m/h) for piscivores were computed for each diel period from telemetry and laboratory results reported in the literature (Henderson and Northcote 1985; Beauchamp et al. 1999; Baldwin et al. 2002).

Table Inputs for the visual encounter rate model applied to Alturas Lake, Idaho. Given are surface light intensity, I_0; light extinction coefficient, k; nephelometric turbidity unit, NTU; hours in each light period; and the swimming speed, SS, of piscivorous trouts.

Parameter	Daylight	Dusk	Night
I_0(lx)	35,842.29	11.326	0.014
k (m^{-1})	–0.1535	–0.1535	–0.1535
NTU	0.34	0.34	0.34
h/period	14	3	7
SS (m/h)	1,062	846	144

Based on the conditions summarized in the table above, light levels were computed for the midpoint of each 5-m depth interval. Reaction distances were computed for the light level at each depth interval with turbidity of 0.34 NTU. Search volumes (m^3/h) were applied to depth-specific densities of the smaller two size-classes of kokanee (3–18 cm TL; Figure 16.1) obtained by hydroacoustic and midwater trawl surveys (Beauchamp et al. 1997). For each diel period, prey encounter rates were estimated by multiplying search volume and the associated prey density for each depth cell. The results of these calculations are presented below in separate tables for each diel period.

Table Estimates of prey encounter rates for each diel period by 5-m depth intervals.

Depth interval (m)	Mid-interval depth (m)	Light (lx)	Reaction distance, RD (m)	Search volume, SV (m^3/h)	Prey density, PD (prey/1,000m^3)	Encounter rate, ER (prey/h)
			Daylight			
0–5	2.5	24,419.071	0.94	2,929.8	0.000	0.000
5–10	7.5	11,334.329	0.94	2,929.8	0.537	1.573
10–15	12.5	5,260.929	0.94	2,929.8	0.179	0.524
15–20	17.5	2,441.907	0.94	2,929.8	0.716	2.097
20–25	22.5	1133.433	0.94	2929.8	0.358	1.048
25–30	27.5	526.093	0.94	2929.8	0.358	1.048
30–35	32.5	244.191	0.94	2929.8	0.358	1.048
35–40	37.5	113.343	0.94	2929.8	0.358	1.048
40–45	42.5	52.609	0.94	2929.8	1.224	3.586
45–50	47.5	24.419	0.94	2929.8	1.224	3.586
50–60	55.0	7.722	0.62	1285.8	0.000	0.000
			Dusk			
0–5	2.5	7.716	0.62	1023.6	0.000	0.000
5–10	7.5	3.582	0.43	493.9	0.918	0.454
10–15	12.5	1.662	0.30	238.3	0.566	0.135
15–20	17.5	0.772	0.21	115.0	1.997	0.230
20–25	22.5	0.358	0.14	55.5	2.468	0.137
25–30	27.5	0.166	0.10	26.8	1.146	0.031
30–35	32.5	0.077	0.07	12.9	0.544	0.007
35–40	37.5	0.036	0.05	6.2	0.544	0.003

(Box continues)

Box 16.12 *(continued)*

Table (*continued*)

Depth interval (m)	Mid-interval depth (m)	Light (lx)	Reaction distance, RD (m)	Search volume, SV (m^3/h)	Prey density, PD (prey/1,000m^3)	Encounter rate, ER (prey/h)
			Dusk (*continued*)			
40–45	42.5	0.017	0.03	3.0	0.224	0.001
45–50	47.5	0.008	0.02	1.5	0.224	0.000
50–60	55.0	0.002	0.01	0.5	0.000	0.000
			Night			
0–5	2.5	0.010	0.03	0.3	0.000	0.000
5–10	7.5	0.005	0.02	0.1	0.544	0.000
10–15	12.5	0.002	0.01	0.1	0.492	0.000
15–20	17.5	0.001	0.01	0.0	2.542	0.000
20–25	22.5	0.000	0.01	0.0	5.843	0.000
25–30	27.5	0.000	0.00	0.0	4.339	0.000
30–35	32.5	0.000	0.00	0.0	2.069	0.000
35–40	37.5	0.000	0.00	0.0	2.069	0.000
40–45	42.5	0.000	0.00	0.0	0.892	0.000
45–50	47.5	0.000	0.00	0.0	0.892	0.000
50–60	55.0	0.000	0.00	0.0	0.000	0.000

Interpretation

High water transparency and associated low light extinction maintained maximum reaction distances (0.94 m) and search volumes (2,929.8 m^3/h) down to 50 m during daylight. Corresponding kokanee densities in the upper water column were low during daylight compared with dusk and night periods, and the highest daylight density occurred below 40 m (Figure 16.1, table above). Kokanee avoided the upper water column during daylight where predator densities were at least four times higher (particularly densities of rainbow trout and northern pikeminnow), and the visual search volumes of the piscivores were maximized. During daylight, the prey encounter rates for pelagic piscivores varied from 0.5 to 2.1 kokanee/h at depths above 40 m but increased to 3.6 kokanee/h below 40 m. Prey encounter rates during dusk and night periods were considerably lower (0.00–0.45 kokanee/h) than during daylight despite markedly higher prey fish densities in the water column. At dusk, the highest encounter rates occurred at 5-10 m, whereas the highest prey density was at 15–25 m. The model predicted no prey encounters at night at any depth.

These analyses demonstrated that kokanee reduced predation risk by undergoing diel vertical migrations. The fraction of prey fish actually available to piscivores was considerably lower than the abundance measured by standard assessment methods, and prey availability changed with time and depth. An important insight from this analysis was that prey encounters were relatively rare events. The visual encounter rate model enabled a quantitative evaluation of predation risk by prey fish and foraging opportunities by the piscivores. This approach can compare the potential impact of piscivores in waters of different transparency, productivity, and predator–prey assemblages (Beauchamp et al. 1999; Mazur and Beauchamp 2006). This could be a useful tool for evaluating the feasibility of introducing or enhancing predator or prey species in candidate waters. Further refinements of this approach could incorporate species-specific differences in reaction distance, swimming speed, and capture success after encounter, potentially as functions of light, turbidity, temperature, or other factors (Sweka and Hartman 2001; DeRobertis et al. 2003; Mazur and Beauchamp 2003, 2006).

Box 16.13 Framework of Ecopath with Ecosim Model for Fished Ecosystems

Ecopath Master Equation I

$B_i \cdot (P/B)_i \cdot EE_i = Y_i + \Sigma B_j \cdot (Q/B)_j \cdot DC_{ij}$,

where for each functional group *i*,
B_i = biomass of *i*;
B_j = biomass of *j* consumers of *i*;
$(P/B)_i$ = production to biomass ratio;
EE_i = fraction of production consumed or harvested (ecotrophic efficiency);
Y_i = biomass harvested (or otherwise lost from system);
$(Q/B)_j$ = food consumed per unit biomass of *j*; and
DCij = contribution of *i* to diet of *j*.

Ecosim

$$\frac{dB_i}{dt} = g_i \cdot \sum Q_{ij} - \sum Q_{ji} + I_i - (M_i + F_i + E_i) \cdot B_i,$$

where,
dB/*dt* = rate of change in biomass;
B_i = biomass of *i*;
g = growth efficiency;
F = fishing mortality rate;
M = natural mortality rate (excluding predation);
E = emigration rate;
I = immigration rate; and
Qij(*Qji*) = consumption rate of type *i* (or *j*) biomass by type *j* (or *i*) organisms.

Ecopath Master Equation II

$Q = P + U + R$,

where
Q = consumption;
P = production;
U = unassimilated food; and
R = respiration.

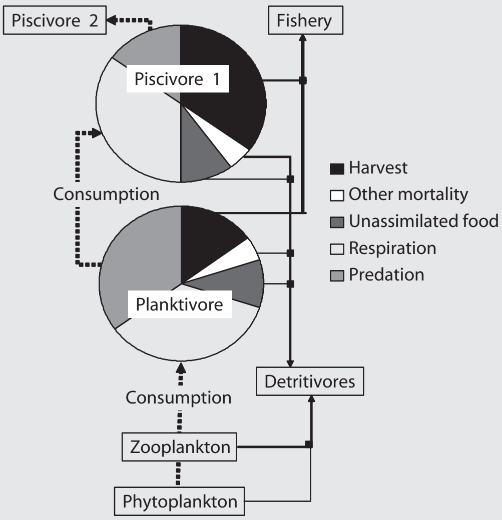

Figure Model of a trophic system. Pies represent biomasses of two fish species, one a piscivore and the other a planktivore, and arrows represent the flows of biomass in the system.

Ecopath (Polovina 1984; Christensen and Pauly 1992; Christensen 2001) organizes biomasses and flows into a static (i.e., baseline or historical average) picture of the ecosystem based on principles of mass-balance and thermodynamics as constraints. The model is solved as a system of simultaneous linear equations. A simple model of a trophic system is represented in the figure above; the pies represent biomasses of two fish species, one a piscivore and the other a planktivore, and arrows represent the flows of biomass in the system. The configuration of the food web and parameterization of flows can be facilitated by stable isotope analysis (e.g., Saito et al. 2001; see also Chapter 11). Both fish are harvested and both are prey for other species. Other components of the food web are simplified for clarity. By converting to differential equations and making the model dynamic, Ecosim (Walters et al. 1997; Pauly et al. 2000) allows the user to examine the trophic implications of a variety of fisheries policy options. Recent improvements to the model (Walters et al. 2000) incorporate compensatory responses in fish populations arising from changes in prey supply that may be direct or indirect effects of harvest. Ecosim can be a useful tool for fisheries scientists concerned about multi-species implications of a fishery management policy and for fisheries scientists who want to design adaptive management experiments at the ecosystem scale.

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