

## The Effects of Fishing on Fish Habitat

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*Abstract.*—The 1996 Magnuson–Stevens Fishery Conservation and Management Act mandates that regional fishery management councils must designate essential fish habitat (EFH) for each managed species, assess the effects of fishing on EFH, and develop conservation measures for EFH where needed. This synthesis of fishing effects on habitat was produced to aid the fishery management councils in assessing the impacts of fishing activities. A wide range of studies was reviewed that reported effects of fishing on habitat (i.e., structural habitat components, community structure, and ecosystem processes) for a diversity of habitats and fishing gear types. Commonalities of all studies included immediate effects on species composition and diversity and a reduction in habitat complexity. Studies of acute effects were found to be a good predictor of chronic effects. Recovery after fishing was more variable depending on habitat type, life history strategy of component species, and the natural disturbance regime. The ultimate goal of gear impact studies should not be to retrospectively analyze environmental impacts but ultimately to develop the ability to predict outcomes of particular management regimes. Synthesizing the results of these studies into predictive numerical models is not currently possible. However, conceptual models can coalesce the patterns found over the range of observations and can be used to predict effects of gear impacts within the framework of current ecological theory. Initially, it is useful to consider fishes' use of habitats along a gradient of habitat complexity and environmental variability. Such considerations can be facilitated by a model of gear impacts on a range of seafloor types based on changes in structural habitat values. Disturbance theory provides the framework for predicting effects of habitat change based on spatial patterns of disturbance. Alternative community state models and type 1–type 2 disturbance patterns may be used to predict the general outcome of habitat management. Primary data are lacking on the spatial extent of fishing-induced disturbance, the effects of specific gear types along a gradient of fishing effort, and the linkages between habitat characteristics and the population dynamics of fishes. Adaptive and precautionary management practices will therefore be required until empirical data become available for validating model predictions.

*Habitat alteration by the fishing activities themselves is perhaps the least understood of the important environmental effects of fishing.*—National Research Council (1994)

Stationary fishing gear (e.g., traps, gill nets, and longlines) and small-scale mobile gear (i.e., beam trawls and shellfish dredges) towed from sailing vessels were used in the 19th century to harvest living marine resources. The widespread use of mobile fishing gear beyond nearshore regions and the use of larger vessels for all gear types became possible only after the development of motorized propulsion and the steam capstan and winch. This widespread and critical change in fishing technology began in England with the launch of the steam trawler *Berta* in the late 1800s. Fishing effort and the range of technologies that support the industry have increased greatly during the last century. For a large number of harvested species, catch per unit effort has greatly

decreased, and the populations of those species have also declined (FAO 1997). Many species are targeted throughout their geographic range, and the wide array of harvesting systems (e.g., traps, gill nets, longlines, trawls, scallop dredges, hydraulic clam dredges) allow fishing to occur over the widest range of habitat types.

A lack of understanding of the ecological consequences of removals of fish, and the direct effects of fishing and fishing gear on community and ecosystem functions, have produced questions about the sustainability of current levels of fishing. The number of reviews on this topic that have been produced during the past decade is perhaps the best indicator of this concern (ICES 1988, 1992, 1996; Hutchings 1990;

Messieh et al. 1991; Jones 1992; Langton 1994; National Research Council 1994, 1995; Dayton et al. 1995; Roberts 1995; Jennings and Kaiser 1998). In the United States, the need for information leading to predictive capabilities and precautionary approaches to this topic will only increase as a result of the legal requirement to manage essential fish habitat (Langton et al. 1996; Auster et al. 1997a).

The 1996 reauthorization of the Magnuson–Stevens Fishery Conservation and Management Act (the Magnuson–Stevens Act) requires the regional fishery management councils and the National Marine Fisheries Service (NMFS) to identify and designate essential fish habitat (EFH) for each managed species, identify adverse impacts to EFH (including those caused by fishing activities), and develop actions to conserve and enhance EFH. The Magnuson–Stevens Act defines EFH as “those waters and substrate necessary to fish for spawning, breeding, feeding, or growth to maturity.” For the purpose of interpreting the definition (and for defining the scope of this report), “waters” is interpreted by NMFS as “aquatic areas and their associated physical, chemical, and biological properties that are used by fish, and may include areas historically used by fish where appropriate,” and “substrate” is defined to include sediment, hard bottom, structures, and associated biological communities. These definitions provide substantial flexibility in defining EFH based on our knowledge of the different species and allow EFH to be interpreted within a broad ecosystem perspective. “Disturbance” has been defined as “any discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment” (Pickett and White 1985). Disturbance can be caused by many natural processes including currents, predation, and iceberg scour (Hall 1994). Human-caused disturbance can result from activities such as harbor dredging and fishing with fixed and mobile gear. Disturbance can be gauged by both intensity (as a measure of the force of disturbance) and severity (as a measure of impact on the biotic community). Table 1 summarizes the relative effects of the range of agents that produce disturbances in marine communities. From an ecological perspective, fishing is the most widespread form of direct disturbance in marine systems below depths that are affected by storms (Watling and Norse 1998).

One of the most difficult aspects of estimating the extent of fishing impacts on habitat is the lack of high-resolution data on the distribution of fishing effort. Fishers are often resistant to reporting effort based on locations of individual tows or sets (for the obvious reason of divulging productive locations to competitors and regulators). Effort data in many fisheries are therefore apportioned to particular statistical areas for monitoring purposes. Using this type of data it has been possible to obtain averages of effort, and subsequent extrapolations of area impacted, for larger regions. For eight of the most heavily fished areas in the southern North Sea, for example, Rijnsdorp et al. (1996) estimated that between 1993 and 1996 a mean of 51% of the area was trawled one to five times per year, 33% was trawled less than once per year, and 4% was trawled 10–50 times per year. Trawling effort in the Middle Atlantic Bight off the northeast United States was summarized by Churchill (1989). Trawled area estimates were extrapolated from fishing effort data in 30′ latitude × 30′ longitude blocks. The range of effort was quite variable but the percent area impacted in some blocks off southern New England in 1985 was more than 200% with one block reaching 413%. Estimating the spatial impact of fixed gears is even more problematic. For example, during 1996 there were 2,690,856 lobster traps fished in the state of Maine (Maine Department of Marine Resources, unpublished data). These traps were hauled on average every 4.5 d, or 81.4 times per year. Assuming a 1-m<sup>2</sup> footprint for each trap, the area impacted was 219 km<sup>2</sup>. If each trap was dragged across an area three times the footprint during set and recovery, the area impacted was 657 km<sup>2</sup>. A lack of data on the extent of the area actually disturbed makes analysis of the impacts of fishing on habitat in those fisheries difficult.

The overall impact of fishing on the North American continental shelf is unknown despite research efforts in the United States spanning nearly 80 years. Alexander et al. (1914) reported that the effect of trawling on the bottom was negligible and stated that “otter trawls do not seriously disturb the bottom over which they are fished nor materially denude it of organisms which directly or indirectly serve as food for commercial fishes.” Their conclusion was based on data from the catches, discounting the lack of data on organisms that passed through the trawl meshes. They also attributed shifts in species composition and abundance only to harvesting by the fishery with no connection to

TABLE 1.—Comparisons of intensity and severity of three types of sources of physical disturbance to the seafloor (based on Hall 1994; Watling and Norse 1998). Intensity is a measure of the force of physical disturbance, and severity is the impact on the benthic community.

Source	Intensity	Severity
<b>Abiotic</b>		
Waves	Low during long temporal periods but high during storm events (to 70–80 m depth)	Low over long temporal periods because taxa adapted to these events but high locally depending on storm behavior
Currents	Low because bed shear normally lower than critical velocities for large volume and rapid sediment movement	Low because benthic stages rarely lost due to currents
Iceberg scour	High locally because scouring results in significant sediment movement but low regionally	High locally due to high mortality of animals but low regionally
<b>Biotic</b>		
Bioturbation	Low because sediment movement rates are small	Low because infauna have time to repair tubes and burrows
Predation	Low on a regional scale but high locally due to patchy foraging	Low on a regional scale but high locally due to small spatial scales of high mortality
<b>Human</b>		
Dredging	Low on a regional scale but high locally due to large volumes of sediment removal	Low on a regional scale but high locally due to high mortality of animals
Land alteration (causing silt-laden runoff)	Low because sediment-laden runoff per se does not exert a strong physical force	Low on a regional scale but high locally where siltation over coarser sediments causes shifts in associated communities
Fishing	High due to regionwide fishing effort	High due to regionwide disturbance of most types of habitat

changes in habitat structure or the benthic community. This conclusion is not surprising given the state of ecological knowledge at the time (Auster 1988). Many more studies, using a wide range of gear types, have been conducted since that time at locations around the world.

Herein we summarize and interpret the current scientific literature on fishing impacts as they relate to fish habitat. We discuss these studies within three broad subject areas: effects on structural components of habitat, effects on benthic community structure, and effects on ecosystem-level processes. The interpretation is based on commonalities and differences between studies. Fishing gear types are discussed as general categories (e.g., trawls, dredges, fixed gear). The necessity for these generalizations is based on two overriding issues: (1) many studies do not specify the exact type and configuration of fishing gear used, and (2) each study reports on a limited range of habitat types. We recognize that individual units of fishing effort with different gears will produce a gradient of results (e.g., a scallop dredge or beam trawl will produce a greater force on the seafloor than a small whiting trawl, tickler chains will produce a different

effect than rock-hopper or “street-sweeper” gear on the groundline of a trawl, king crab *Paralithodes camtschaticus* pots are larger and heavier than pots used for American lobster *Homarus americanus*). However, our interpretation of the wide range of studies is based on the type and direction of impacts, not absolute levels of impacts. We do not address the issues of bycatch (Alverson et al. 1994), mortality of gear escapees (Chopin and Arimoto 1995), or ghost-fishing gear (Jennings and Kaiser 1998) as these issues do not directly relate to fish habitat and because recent reviews have been published that address these subjects.

### **Effects on Structural Components of Habitat**

#### *Interpretation of Results*

The environmental characteristics that define species distributions can be found at a variety of spatial and temporal scales (e.g., Langton et al. 1995). At regional scales, the seasonal variations in

TABLE 2.—Studies of the impacts of mobile fishing gear on the structural components of fish habitat.

Habitat	Gear type	Location	Results	Reference(s)
Eelgrass	Scallop dredge	North Carolina	Comparison of reference quadrats with treatments of 15 and 30 dredgings in hard sand and soft mud substrates within eelgrass meadows. Eelgrass biomass was significantly greater in hard sand than soft mud sites. Increased dredging resulted in significant reductions in eelgrass biomass and number of shoots.	Fonseca et al. (1984)
Eelgrass and shoalgrass	Clam rake and “clam kicking”	North Carolina	Comparison of effect of two fishing methods. In raking and “light” clam-kicking treatments, biomass of seagrass was reduced approximately 25% below reference sites but recovered within 1 year. In “intense” clam-kicking treatments, biomass of seagrass declined approximately 65% below reference sites. Recovery did not begin until more than 2 years after impact, and biomass was still 35% below the level predicted from controls to show no effect.	Peterson et al. (1987)
Eelgrass and shoalgrass	Clam rakes (pea digger and bull rake)	North Carolina	Compared impacts of two clam rake types on removal of seagrass biomass. The bull rake removed 89% of shoots and 83% of roots and rhizomes in a completely raked 1 m <sup>2</sup> area. The pea digger removed 55% of shoots and 37% of roots and rhizomes.	Peterson et al. (1983)
Sea grass	Trawl	Western Mediterranean	Noted loss of <i>Posidonia</i> meadows due to trawling (45% of study area). Monitored recovery of the meadows after installing artificial reefs to stop trawling. After three years plant density has increased by a factor of six.	Guillen et al. (1994)
Sponge–coral hard-bottom	Roller-rigged trawl	Off Georgia coast	Assessed effect of single tow. Damage to all species of sponge and coral observed; 31.7% of sponges, 30.4% of stony corals, and 3.9% of octocorals. Only density of barrel sponges ( <i>Cliona</i> spp.) significantly reduced. Percent of stony coral damage high because of low abundance. Damage to other sponges, octocorals, and hard corals varied but changes in density not significantly different. No significant differences between trawled and reference sites after 12 months.	Van Dolah et al. (1987)
Sponge–coral hard-bottom	Roller-frame shrimp trawl	Biscayne Bay, Florida	Damage to approximately 50% of sponges, 80% of stony corals, and 38% of soft corals.	Tilmant (1979) (cited in Van Dolah et al. 1987)
Various tropical emergent benthos	Trawl	Northwest shelf, Australia	Catch rates of all fish and large and small benthos show that in closed areas, fish and small benthos abundance increased over 5 years while large benthos (>25 cm) stayed the same or increased slightly. In trawled areas all groups of animals declined. Found that settlement rate and growth to 25 cm was on the order of 15 years for the benthos.	Sainsbury et al. (1997)

TABLE 2.—(Continued.)

Habitat	Gear type	Location	Results	Reference(s)
Gravel pavement	Scallop dredge	Georges Bank	Assessed cumulative impact of fishing. Undredged sites had significantly higher percent cover of the tube-dwelling polychaete <i>Filograna implexa</i> and other emergent epifauna than dredged sites. Undredged sites had higher numbers of organisms, biomass, species richness, and species diversity than dredged sites. Undredged sites were characterized by bushy epifauna (bryozoans, hydroids, worm tubes), while dredged sites were dominated by hard-shelled molluscs, crabs, and echinoderms.	Collie et al. (1996, 1997)
Gravel–boulder	Assumed roller-rigged trawl	Gulf of Maine	Comparison of site surveyed in 1987 and revisited in 1993. Initially, mud-draped boulders and high-density patches of diverse sponge fauna. In 1993, evidence of moved boulders, reduced densities of epifauna, and extreme truncation of high-density patches.	Auster et al. (1996)
Cobble–shell	Assumed trawl and scallop dredge	Gulf of Maine	Comparison of fished site and adjacent closed area. Statistically significant reduction in cover provided by emergent epifauna (e.g., hydroids, bryozoans, sponges, serpulid worms) and sea cucumbers.	Auster et al. (1996)
Gravel	Beam trawl	Irish Sea	An experimental area was towed 10 times. Density of epifauna (e.g., hydroids, soft corals, <i>Alcyonium digitatum</i> ) was decreased approximately 50%.	Kaiser and Spencer (1996a)
Boulder–gravel	Roller-rigged trawl	Gulf of Alaska	Comparisons of single-tow trawled lane with adjacent reference lane. Significant reductions in density of structural components of habitat (two types of large sponges and anthozoans). No significant differences in densities of small sponge and mobile invertebrate fauna. However, 20.1% of boulders moved or dragged, and 25% of ophiuroids ( <i>Amphiphiura ponderosa</i> ) in trawled lanes were crushed or damaged compared to 2% in reference lanes.	Freese et al. (in press)
Gravel over sand	Scallop dredge	Gulf of St. Lawrence	Assessed effects of single tows. Suspended fine sediments and buried gravel below the sediment–water interface. Overturned boulders.	Caddy (1973)
Bryozoan beds (on sand and cobble)	Otter trawl and roller-rigged trawl	New Zealand	Qualitative comparison of closed and open areas. Two bryozoans produce “coral-like” forms and provide shelter for fishes and their prey. Comparisons of fished site with reference sites and prior observations from fishers show reduced density and size of bryozoan colonies.	Bradstock and Gordon (1983)
Mussel bed	Otter trawl	Strangford Lough, Northern Ireland	Comparison of characteristics of trawled and untrawled <i>Modiolus modiolus</i> beds as pre- and post-impacts of a trawl. Trawled areas, confirmed with sidescan sonar, showed mussel beds disconnected with reductions in attached epibenthos.	Magorrian (1995)

TABLE 2.—(Continued.)

Habitat	Gear type	Location	Results	Reference(s)
			The most impacted sites were characterized by few or no intact clumps, mostly shell debris, and sparse epifauna. Trawling resulted in a gradient of complexity with flattened regions at the extreme. Immigration of <i>Nephtys</i> into areas previously dominated by <i>Modiolus</i> may result in burial of new recruits due to burrowing activities, precluding a return to a functional mussel bed habitat.	
Sand–mud	Trawl and scallop dredge	Hauraki Gulf, New Zealand	Comparisons of 18 sites along a gradient of fishing effort (i.e., heavily fished sites through unfished reference sites). A gradient of increasing large epifaunal cover correlated with decreasing fishing effort.	Thrush et al. (in press)
Soft sediment	Scallop dredge	Port Phillip Bay, Australia	Compared reference and experimentally towed sites. Bedforms consisted of cone-shaped callianasid mounds and depressions prior to impact. Depressions often contained detached sea grasses and macroalgae. Only dredged plot changed after dredging. Eight days after dredging the area was flattened; mounds were removed and depressions filled. Most callianasids survived, and density did not change in three months following dredging. One month post impact, seafloor remained flat and dredge tracks distinguishable. Six months post impact mounds and depressions were present, but only at 11 months did the impacted plot return to control plot conditions.	Currie and Parry (1996)
Sand	Beam trawl	North Sea	Observations of effects of gear. As pertains to habitat, trawl removed high numbers of the hydroid <i>Tubularia</i> .	de Groot (1984)
Gravel–sand–mud	Trawl	Monterey Bay	Comparison of heavily trawled (HT) and lightly (LT) sites. The seafloor in the HT area had significantly higher densities of trawl tracks while the LT area had significantly greater densities of rocks >5 cm and mounds. The HT area had shell debris on the surface while the LT area had a cover of flocculent material. Emergent epifauna density was significantly higher for all taxa (anemones, sea pens, sea whips) in the LT area.	Engel and Kvitek (1998)
Sand	Otter trawl	North Sea	Observations of direct effects of gear. Well-buried boulders removed and displaced from sediment. Trawl doors smoothed sand waves. Penetrated seabed 0–40 mm (sand and mud).	Bridger (1970, 1972)
Sand–shell	Assumed trawl and scallop dredge	Gulf of Maine	Comparison of fished site and adjacent closed area. Statically significant reduction of habitat complexity based on reduced cover provided by biogenic depressions and sea cucumbers. Observations at another site showed multiple scallop dredge paths resulting in smoothed bedforms. Scallop dredge paths removed cover provided by hydrozoans, which reduced local densities of associated shrimp species. Evidence of shell aggregates dispersed by scallop dredge.	Auster et al. (1996)

TABLE 2.—(Continued.)

Habitat	Gear type	Location	Results	Reference(s)
Sand-silt to mud	Otter trawl with chain sweep and roller gear	Long Island Sound	Diver observations showed doors produced continuous furrows. Chain gear in wing areas disrupted amphipod tube mats and bounced on bottom around mouth of net, leaving small scoured depressions. In areas with drifting macroalgae, the algae draped over net groundgear during tows and buffered effects on the seafloor. Roller gear also created scoured depressions. Spacers between discs lessened impacts.	Smith et al. (1985)

seawater temperature can explain annual variations in the distribution of fishes (e.g., Murawski 1993). Within regions, temporally stable associations of species have been found and tend to follow isotherms and isobaths (Gabriel and Tyler 1980; Colvocoresses and Musick 1984; Overholtz and Tyler 1985; Phoel 1986; Gabriel 1992). Species groups are sometimes seasonal and may split or show changes in composition that correlate with temperature patterns. Nested within regional scale patterns are small-scale variations in abundance and distribution of demersal fishes that can be partially attributed to variation in topographic structure. In contrast, habitat associations for coral reef fishes, kelp bed fishes, sea grass fishes, and rock reef fishes are relatively clear (e.g., Heck and Orth 1980; Ebeling and Hixon 1991; Sale 1991). The entire demersal stage of the life history of many species associated with these unique habitats have obligate habitat requirements or demonstrate recruitment bottlenecks. Without the specific structural components of habitat, the populations of fishes with these habitat requirements would not persist. However, a gradient of habitat dependence can be found in the range of demersal fish species globally. For example, early benthic phase Atlantic cod *Gadus morhua* require cobble or similar complex bottom for survival but have a refuge in size, and habitat associations are more facultative as size increases (Lough et al. 1989; Gotceitas and Brown 1993; Tupper and Boutilier 1995). Other species, however, have facultative habitat associations throughout their life (e.g., Auster et al. 1991, 1995, 1997b; Sogard and Able 1991; Able et al. 1995; Langton et al. 1995; Szedlmayer and Howe 1997). These associations may increase survivorship of individuals and may contribute to wide variations in recruitment, but they are not obligate for the survival of populations (e.g., Lindholm et al. 1998).

“Habitat” has been defined as “the structural component of the environment that attracts organisms and serves as a center of biological activity” (Peters and Cross 1992). Habitat in this case includes the range of sediment types (i.e., mud through boulders), bed forms (e.g., sand waves and ripples, flat mud) as well as the co-occurring biological structures (e.g., shell, burrows, sponges, sea grass, macroalgae, coral). A review of 22 studies (Table 2) all show measurable impacts of mobile gear on the structural components of habitat (e.g., sand waves, emergent epifauna, sponges, coral) when defining habitat at this spatial scale. Results of each of the studies show similar classes of impacts despite the wide geographic range of the studies (i.e., tropical to boreal). In summary, mobile fishing gear reduced habitat complexity by: (1) directly removing epifauna or damaging epifauna leading to mortality, (2) smoothing sedimentary bedforms and reducing bottom roughness, and (3) removing taxa that produce structure (i.e., taxa that produce burrows and pits). Studies that have addressed both acute and chronic impacts have shown the same types of effects (Figure 1).

Little has been written about the recovery of seafloor habitat from fishing gear effects. Recovery of storm-caused sedimentary features depends primarily on grain sizes of sediment and depth to which storm-generated surge and currents occur. Some features can be reformed after seasonal or annual storm events, while others will depend on larger meteorological events that occur on decadal time scales or longer. Recovery of biogenic features will depend on recruitment or immigration, depending on the spatial extent of impacts. Recovery will also depend on whether impacts are short term or chronic. For example, on coral-sponge hard bottom off the coast of Georgia, Van Dolah et al. (1987) found no long-

term effects of trawling on the benthic community. After one year the sponges and octocorals that were experimentally trawled recovered with densities reaching or exceeding pretrawling levels at the study site. However, it is important to note that this study did not address chronic effects but rather a single tow of a roller-rigged trawl.

Few accounts of the impacts of fixed gears on habitat have been published. Eno et al. (1996) studied the effects of crustacean traps in British and Irish waters. One experiment assessed the effects of setting and hauling pots on emergent epifaunal species (sea pens) on soft bottom. Both impacts from dragging pots across the bottom and pots resting for extended periods on sea pens showed that the group was able to mostly recover from such disturbances. Limited qualitative observations of fish traps, longlines, and gill nets dragged across the seafloor during set and recovery showed results similar to mobile gear such that some types of epibenthos were dislodged, especially emergent species such as erect sponges and corals (SAFMC 1991; W. L. High, Alaska Fisheries Science Center, unpublished data). Although the area impacted per unit of effort is smaller for fixed gear than for mobile fishing gear, the types of damage to emergent benthos appear to be similar (but not necessarily equivalent per unit effort). Quantitative studies of fixed-gear effects, based on acute and chronic impacts, have not been conducted.

The issue of defining pelagic habitats and elucidating effects of fishing is difficult because these habitats are poorly described at the scales that allow for measurements of change based on gear use. Although pelagic habitat can be defined based on temperature, light intensity, turbidity, oxygen concentration, currents, frontal boundaries, and a host of other oceanographic parameters and patterns, there are few published data that attempt to measure change in any of these types of parameters or conditions concurrently with fishing activity and associations of fishes. Kroger and Guthrie (1972) showed that menhaden (*Brevortia patronus* and *B. tyrannus*) were subjected to greater predation pressure, at least from visual predators, in clear versus turbid water, suggesting that turbid habitats were a greater refuge from predation. This same type of pattern was found for menhaden in both naturally turbid waters and in the turbid plumes generated by oyster shell dredging activities (Harper and Hopkins 1976). However, no work has been published that addresses the effects of variation in time and space of the plumes or the effects of turbid water refugia

on feeding and growth. There are also examples of small-scale aggregations of fishes with biological structures in the water column and at the surface. Aggregations of fishes may have two effects on predation patterns by: (1) reducing the probability of predation on individuals within the aggregation, and (2) providing a focal point for the activities of predators (a cue that fishermen use to set gear). For example, small fishes aggregate under mats of *Sargassum* (e.g., Moser et al. 1998), and high-density vessel traffic may disaggregate mats. Also, fishes have been observed to co-occur with aggregations of gelatinous zooplankton and pelagic crustaceans (Auster et al. 1992; Brodeur, in press). Gelatinous zooplankton are greatly impacted as they pass through the mesh of either mobile or stationary gear (P. J. Auster, unpublished observations), which may reduce the size and number of zooplankton aggregations and disperse associated fishes. These changes could reduce the value of aggregating, resulting in increased mortality or reduced feeding efficiency.

#### *Implications for Management*

Commonalities in gear impact studies on habitat structure allow for the production of a conceptual model to visualize the patterns in gear impacts across a gradient of habitat types. Auster et al. (1998) developed a hierarchical, categorical approach for classifying habitats on the cold temperate and boreal continental shelf of the northwest Atlantic. This type of classification scheme has proven very useful in habitat management for freshwater fisheries. The range of habitat types was condensed into eight habitat categories increasing from simple to complex (Table 3). For example, currents form sand wave fields that provide shelter for fish from high current speeds. This shelter reduces the energy needed to maintain position on the bottom and permits ambush predation of drifting demersal zooplankton. Storm currents sort loose sediments and deposit shells and cobbles in the troughs of sand waves. These small crevices provide an ephemeral habitat for small fishes and crustaceans. Cobble bottoms provide interstices for shelter sites but also provide a hard surface for epibenthic organisms such as sponges and bryozoans to attach. These emergent epifauna provide additional cover value. Scattered boulders also provide shelter from currents, and boulder piles provide deep crevices for shelter required by some species such as redfish *Sebastes* spp.



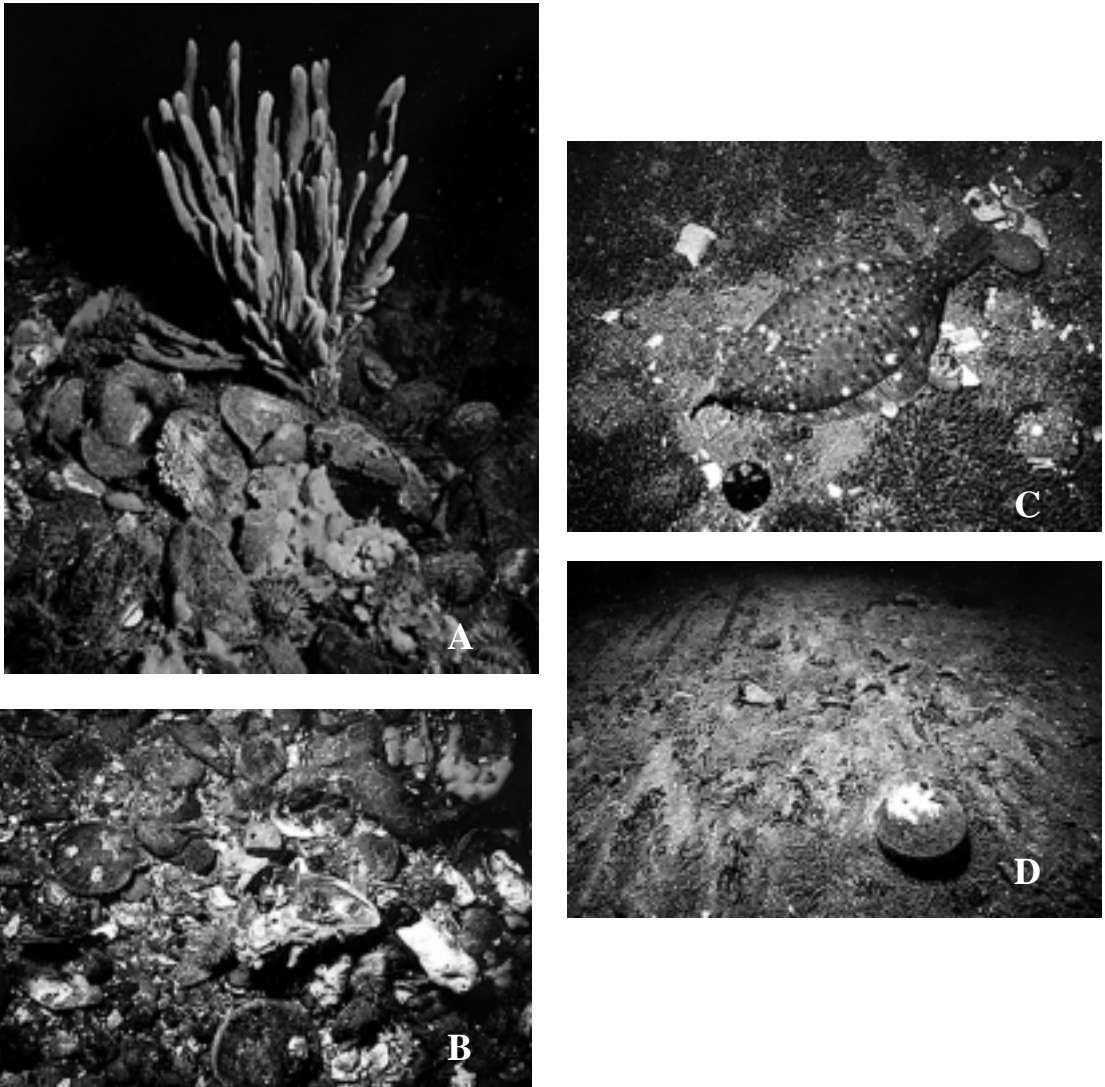


FIGURE 1.—Photographs A–G compare impacts at sites with acute and chronic disturbance by fishing gear. Acute disturbance by a single pass of a scallop dredge at a coastal site in the Gulf of Maine (ca. 20 m depth). Photographs were taken within hours after the pass of the scallop dredge. Photographs A and B represent before-and-after images from a cobble–shell habitat. Note that the sponge colonies that stabilize the shell aggregates are removed in the impacted state. Photographs C and D represent before-and-after images from a sand–shell habitat. Note that the worm tube mats are severely disrupted in the impacted state (Auster, in press). Photographs E–G show chronic disturbance due to continued fishing on the northeast peak of Georges Bank. All photographs taken in July 1997. Photograph E shows an undisturbed area on the Canadian side of the bank which has been closed to fishing (84 m depth). Photograph F shows a site closed to fishing since December 1994. Photograph G shows a site still impacted by fishing gear. (Georges Bank images courtesy of Page Valentine, U.S. Geological Survey).

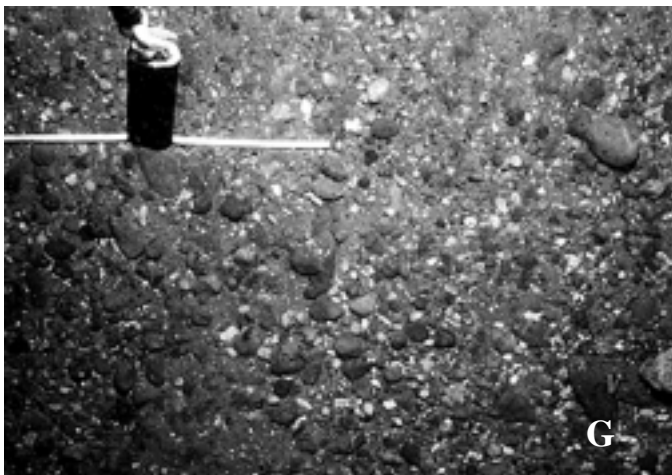
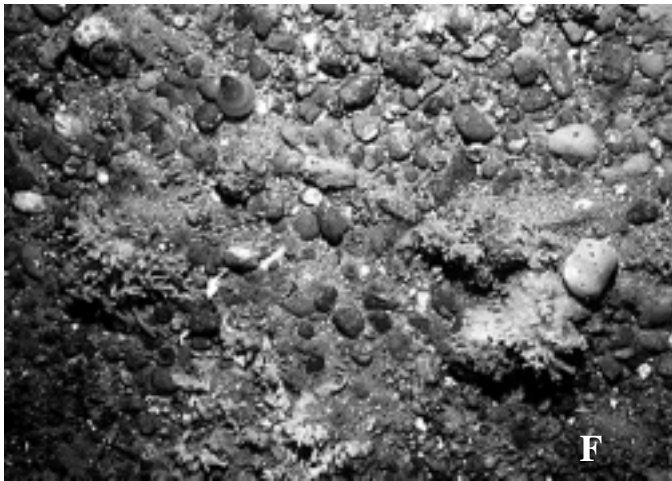
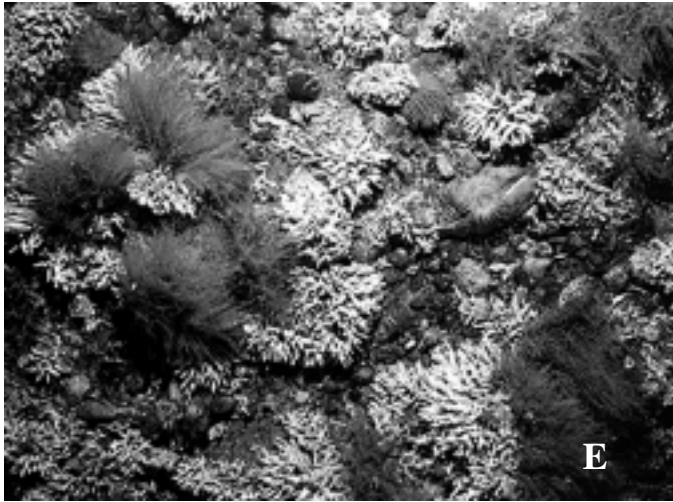


TABLE 3.—Hierarchical classification of fish habitat types (from Auster 1998; Auster et al. 1998) on the outer continental shelf of the cold temperate and boreal northwest Atlantic. (Categories are based on Auster et al. 1995; Langton et al. 1995; Auster et al. 1996; and unpublished observations).

Category	Habitat type	Description and rationale	Complexity score
1	Flat sand and mud	Areas such as depressions, ripples, or epifauna that provide no vertical structure.	1
2	Sand waves	Troughs that provide shelter from currents. Previous observations indicate that species such as silver hake <i>Merluccius bilinearis</i> keep on the down-current sides of sand waves and ambush drifting demersal zooplankton and shrimp.	2
3	Biogenic structures	Features such as burrows, depressions, cerianthid anenomes, and hydroid patches that are created and used by mobile fauna for shelter.	3
4	Shell aggregates	Areas that provide complex interstitial spaces for shelter. As an aside, shell aggregates also provide a complex high-contrast background that may confuse visual predators.	4
5	Pebble-cobble	Areas that provide small interstitial spaces and may be equivalent in shelter value to shell aggregate. However, shell is a more ephemeral habitat.	5
6	Pebble-cobble with sponge cover	Attached fauna such as sponges provide additional spatial complexity for a wider range of size classes of mobile organisms.	10
7	Partially buried or dispersed boulders	Although not providing small interstitial spaces or deep crevices, partially buried boulders do exhibit high vertical relief, and dispersed boulders on cobble pavement provide simple crevices. The shelter value of this type of habitat may be less or greater than previous types based on the size class and behavior of associated species.	12
8	Piled boulders	Areas that provide deep interstitial spaces of variable sizes.	15

Habitat value for each habitat type does not increase linearly. Each category was assigned a numerical score based on its level of physical complexity (note that this model does not include effects of fishing on biodiversity per se). Categories 1 through 5 increase linearly. Starting at category 6, the score of 10 is based on a score of 5 (i.e., the score for cobble) from the previous category plus a score of 5 for dense emergent epifauna that is assumed to double the cover value of small interstices alone. Category 7 is scored for cobble and emergent epifauna (i.e., 10) plus 2 more points for shallow boulder crevices and refuges from current. Finally, category 8 is scored as 15 because of the presence of shallow crevices and current refuges (previously scored as 12), plus deep crevices scored as 3. These scores are therefore the starting points representing unimpacted habitats.

A pictorial representation of the model, shown in Figure 2, indicates the response of the range of seafloor habitat types to increases in fishing effort (Auster, in press). The range of fishing effort in-

creases from left to right along the  $x$ -axis with 0 indicating no gear impacts and 4 indicating the maximum effort required to produce the greatest possible change in habitat complexity. The numbers at present are dimensionless because better data are needed on the effects of various gear types at various levels of effort over specific habitats. The  $y$ -axis is a comparative index of habitat complexity. Each habitat type starts near the  $y$ -axis at the value of the habitat in an unimpacted condition. The habitat categories are representative of the common types of habitat found across the northeast U.S. continental shelf and are likely to be found on most other continental shelf areas of the world. The responses to different types of bottom-contact fishing gear are assumed to be similar.

This model shows a range of changes in habitat complexity based on gear impacts. It predicts reductions in the complexity provided by bedforms from direct smoothing by gear. Biogenic structures are reduced by a number of mechanisms such as direct gear impacts as well as removal of organisms

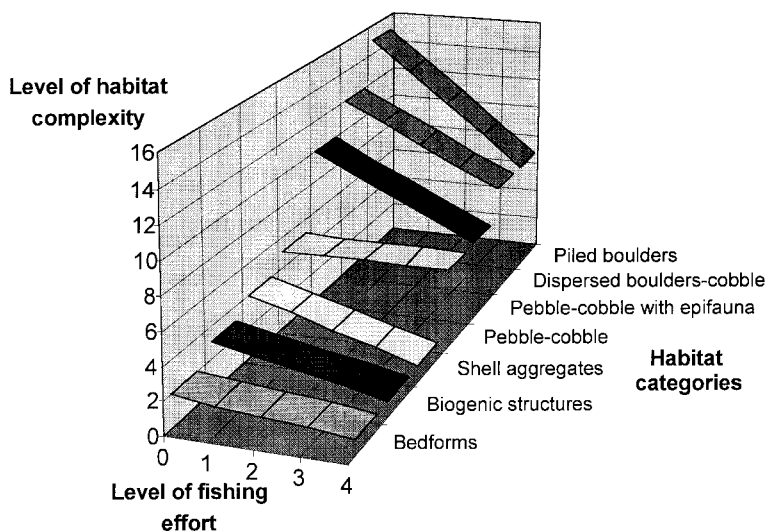


FIGURE 2.—Conceptual fishing gear impact model. The range of fishing effort increases from left to right along the x-axis with 0 as a pristine condition and 4 as a maximally impacted state. The y and z axes are based on information in Table 3. The y-axis is a comparative index of habitat complexity. The z axis shows the range of habitat categories from simple (bedforms) to complex (piled boulders).

that produce structures (e.g., crabs that produce burrows). There are some habitats where the model shows no significant reductions, such as gravel areas with very little epifaunal settlement. Although mobile gear would overturn pebbles and cobbles, the actual structural integrity of the habitat would not be reduced (although organisms on the undersides of cobbles are exposed to predation). However, the value of cobble pavements are greatly reduced when epifauna are removed, as biogenic structures provide additional cover. Gear can move boulders and still provide some measure of hydraulic complexity to the bottom by providing shelter from currents. On the other hand, piles of boulders can be dispersed by large trawls, and this reduces the cover value for crevice dwellers. The model should be widely applicable as the habitat types are widely distributed worldwide and the impacts are consistent with those described in the literature.

This conceptual model serves two purposes. First, it provides a holistic summary of the range of gear impacts across a range of habitat types. The end points in the model are based on empirical data and observations and should be useful for considering management actions for the conservation of fish habitat. The second purpose for developing the model is to provide a basis for future research. Although it is possible to ascribe the endpoints of habitat complexity at both unimpacted and fully impacted states, the slope of the line remains unknown, and the level of fishing effort

required to produce specific rates of change is also unknown for all gear types. Responses may be linear or nonlinear (e.g., logarithmic). Perhaps there are thresholds of disturbance beyond which some habitat types exhibit a response. Regardless, responses will most likely be habitat specific.

The impact model does not have an explicit time component. Here we add such a conceptual framework to the discussion. Cushing's match-mismatch hypothesis (Cushing 1975) has served as one of several hypotheses that explain annual variation in larval recruitment dynamics and has been the focus of large amounts of research effort for several decades. Here we propose a similar type of match-mismatch paradigm for linking variation in the survivorship of early benthic-phase fishes with the abundance of epibenthic organisms, particularly those with annual life histories, that may serve as habitat. Figure 3 shows the pattern in percent cover for an idealized benthic species that produces emergent structure (e.g., hydroid stalk, amphipod tube, mussel). This type of species has widespread settlement and occurs at high densities. At the time of settlement, large areas of the seafloor are occupied by this species. Over the course of time, predation and senescence reduce the cover provided by such taxa. The timing of settlement of early benthic-phase fish will greatly effect the cover value provided by the benthic taxa. In addition to natural processes, fishing gear impacts further reduce the cover value over time and can

## Decline in Cover (Epifaunal Density) Over Time: Natural Versus Impacted

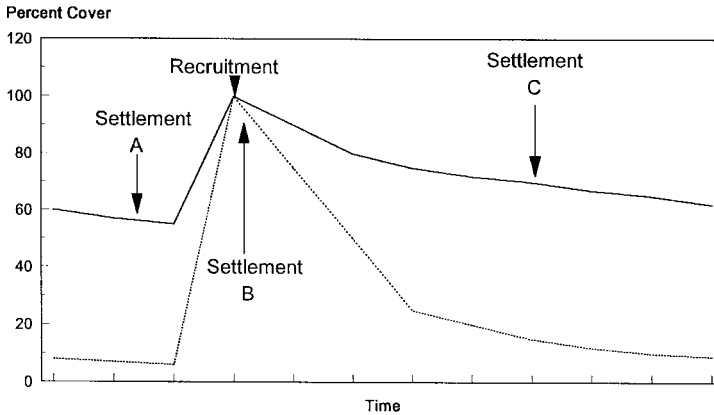


FIGURE 3.—Habitat match–mismatch paradigm that links variation in the survivorship of early benthic-phase fishes with abundance of epibenthic organisms. The illustration shows a temporal pattern in percent cover for an “idealized” benthic species with emergent structure (e.g., hydroid, amphipod tubes) under conditions of natural variation (solid line) and when impacted by fishing activities (dotted line). The habitat value of such areas is dependent on the timing of recruitment of fishes in relation to settlement and subsequent mortality of epibenthos from natural and human-caused sources. For example, at the time period marked A, settlement into unimpacted benthos provides greater cover for fishes than an area impacted by fishing. However, at the settlement period marked B, recruitment of epibenthos has recently occurred and the cover provided under either state is nearly identical. The settlement period marked C is similar to A and reflects the dichotomy of natural versus fishing-enhanced changes in a dynamic habitat.

narrow the window in which particular patches of epibenthos serve as effective cover for newly settled fishes. The time scale ( $x$ -axis) and patterns in the figure were developed to show an annual pattern representative of many taxa with such life history strategies, but this pattern can also be extended in time for longer-lived organisms. Like the conceptual impact model above, the timing and changes in slope of these lines are critical for understanding the dynamics of this interaction.

Ultimately, it will be necessary to develop models that include sensitivity indices for specific habitats, communities, and key taxa based on the effects of specific gear types, levels of effort, and life history patterns (of both fish and taxa that serve a habitat function). MacDonald et al. (1996) has developed such a sensitivity index to quantify the impact of fishing on particular epifaunal taxa in the North Sea region. The index is a function of recovery time after damage, fragility of the animal, and intensity of the impact.

Lack of information on the small-scale distribution and timing of fishing makes it difficult to ascribe the patterns of impacts observed in field studies to specific levels of fishing effort. Auster et al. (1996) estimated that between 1976 and 1991, Georges Bank was impacted by mobile gear (e.g., otter trawl,

roller-rigged trawl, scallop dredge) on average between 200 and 400% of its area on an annual basis, and the Gulf of Maine was impacted 100% annually. Fishing effort, however, was not homogeneous. Sea sampling data from NMFS observer coverage demonstrated that the distribution of tows was non-random (Figure 4). Although these data represent less than 5% of overall fishing effort, they illustrate that the distribution of fishing gear impacts is quite variable.

Recovery of habitat following trawling is difficult to predict as well. Timing, severity, and frequency of the impacts all interact to mediate processes that lead to recovery (Watling and Norse 1998). For example, sand waves may not be reformed until storm energy is sufficient to produce bedform transport of coarse sand grains (Valentine and Schmuck 1995), and storms may not be common until a particular time of year or may infrequently reach a particular depth, perhaps only on decadal time scales. Sponges are particularly sensitive to disturbance because they recruit aperiodically and are slow growing in deeper waters (Reiswig 1973; Witman and Sebens 1985; Witman et al. 1993). However, many species such as hydroids and ampelescid amphipods reproduce once or twice an-

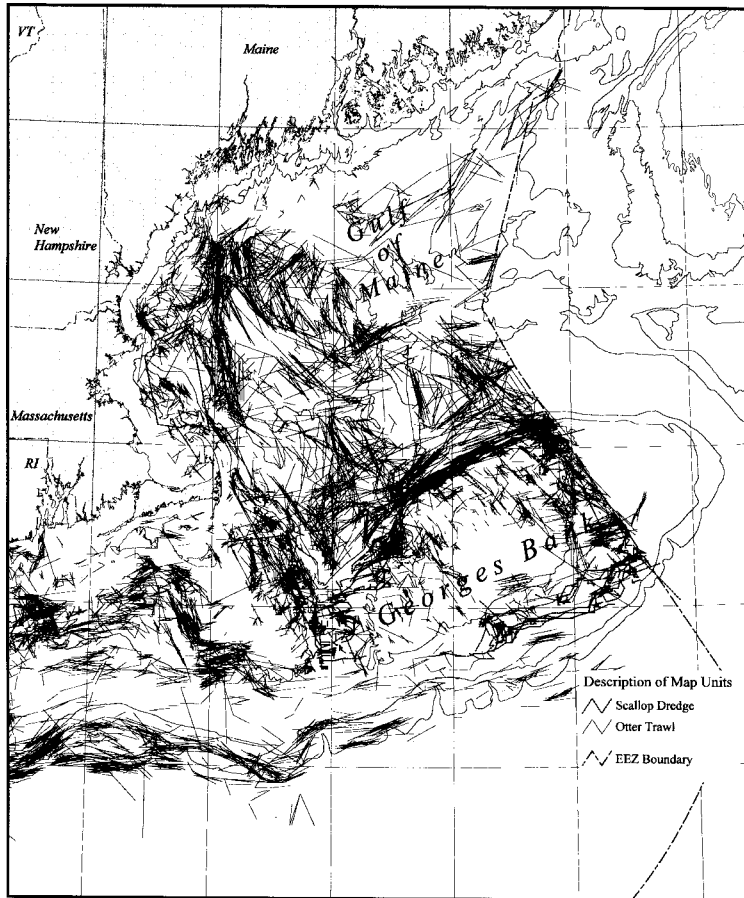


FIGURE 4.—Spatial distribution of trawl and scallop dredge tows from the National Marine Fisheries Service sea sampling database for 1989–1994 (April). This illustration represents a total of 14,908 tows. Note that the spatial distribution of effort is not homogeneous but aggregated in productive fishing areas.

nually, and their stalks and tubes provide cover for the early benthic phases of many fish species and their prey (e.g., Auster et al. 1996, 1997b). Where fishing effort is constrained within particular fishing grounds, and where data on fishing effort are available, studies that compare similar sites along a gradient of effort have produced the types of information on effort impact that will be required for effective habitat management (e.g., Collie et al. 1996, 1997; Thrush et al., in press).

The role these impacts on habitat have on harvested populations is unknown in most cases. However, a growing body of empirical observations and modeling demonstrates that effects can be seen in population responses at particular population levels. For example, Lindholm et al. (1998) have modeled the effects of habitat alteration on the survival of 0-year cohorts of Atlantic cod. The model results

indicate that a reduction in habitat complexity has measurable effects on population dynamics when the adult stock is at low levels (i.e., when spawning and larval survivorship does not produce sufficient recruits to saturate available habitats). At high adult population levels, when larval abundance may be high and settling juveniles would greatly exceed habitat availability, predation effects would not be mediated by habitat, and no effect in the response of the adult population to habitat change was found.

Empirical studies that most directly link changes due to gear impacts on habitat structure to population responses are being carried out in Australia. Sainsbury (1987, 1988, 1991) and Sainsbury et al. (1997) have shown a very tight coupling between a loss of emergent epifauna and fish productivity along the northwest continental shelf. In these studies there was a documented decline in the

bycatch of invertebrate epifauna in trawl catches, from 500 kg hr<sup>-1</sup> to only a few kg hr<sup>-1</sup>, and replacement of the most commercially desirable fish associated with the epifaunal communities by less valuable species associated with more open habitat. By restricting fishing the decline in the fish population was reversed. This corresponded to an observed recovery in the epifaunal community, although the recovery for the larger epifaunal invertebrates showed a considerable lag time after trawling ceased. This work is based on a management framework developed to test hypotheses regarding the habitat dependence of harvested species. The hypotheses, described in Sainsbury (1988, 1991), assessed whether population responses were the result of:

1. independent single-species (intraspecific) responses to fishing and natural variation;
2. interspecific interactions such that as specific populations are reduced by fishing, nonharvested populations experienced a competitive release;
3. interspecific interactions such that as nonharvested species increase from some external process, their population inhibits the population growth rate of the harvested species; and
4. habitat mediation of the carrying capacity for each species, such that gear-induced habitat changes alter the carrying capacity of the area.

This is a primary example of adaptive management in which regulations were developed to test hypotheses and were the basis for modifying subsequent management measures. This type of management process exemplifies management of fisheries based primarily on an understanding of ecological relationships.

### Effects on Community Structure

#### *Interpretation of Results*

Studies on the effects of fishing on benthic communities have often produced variable results regarding the impact on community structure. The reasons for these differences may include sampling strategies, use of different metrics, different methods of fishing, different functional groups of species that compose the community, and subtle differences in habitat type. Furthermore, studies have often been conducted in areas that have a history of fishing activity and therefore may not have truly undisturbed reference areas for comparison, despite the efforts of the investigator (see Hall

et al. 1993; M. J. Kaiser, University of Wales-Bangor, unpublished data). Changes in benthic community structure also have to be understood against a background of natural disturbance and variability (Thrush et al., in press). Bearing in mind these caveats, the literature on fishing gear impacts can be divided into short-term and long-term studies that reveal some common characteristics and patterns resulting from fishing on the seafloor.

An immediate reduction in the density of non-target species is often reported following impacts from mobile gear (Table 4). In assessing this effect it is common to compare numbers and densities for each species before and after fishing and with an undisturbed reference site. Kaiser and Spencer (1996a), for example, found a reduction in diversity and abundance of some taxa at one location in the Irish Sea where sediments were relatively stable. They reported a 58% decrease in mean abundance and 50% reduction in the mean number of species per sample. In contrast, at a location where the sediments were more mobile the impact of beam trawling was not as substantial. In other European studies, Bergman and Hup (1992) and Santbrink and Bergman (1994) have documented species- and size-specific differences in macrofaunal abundance and mortality, with densities decreasing for some species, and mortality increasing, after trawling. However, in other cases there were no observable effects. In a scallop-dredging study in New Zealand, two experimentally fished sites showed an immediate decrease in macrofaunal densities in comparison to corresponding reference sites (Thrush et al. 1995). In an 88-d study of scallop dredging in Australia, Currie and Parry (1994) found that the number of individuals at the dredged sites was always lower than at the reference sites despite an overall increase in animal numbers due to amphipod recruitment to both the experimental and reference areas.

Time series data sets that allow for a direct long-term comparison of sites before and after fishing are essentially nonexistent, primarily because the extent to which the world's oceans are currently fished was not foreseen, or because time series data collection focused on the fish themselves rather than the impact of fishing on the environment. Nevertheless, there are several benthic data sets that allow for an examination of observational or correlative comparisons before and after fishing (Table 5). Perhaps the longest time series comparisons of long-term impact of fishing on benthic community structure are

TABLE 4.—Studies of short-term impacts of fishing on benthic communities.

Taxa	Gear; sediment type	Location	Results	Reference
Infauna	Beam trawl; megaripples and flat substrate	Irish Sea	Assessed the immediate effects of beam trawling and found a reduction in diversity and abundance of some taxa in the more stable sediments of the northeast sector of the experimental site but could not find similar effects in the more mobile sediments. Out of the top 20 species, 19 had lower abundance levels at the fished site, and 9 showed a statistically significant decrease. Coefficient of variation for numbers and abundance was higher in the fished area of the northwest sector, supporting the hypothesis that heterogeneity increases with physical disturbance. Measured a 58% decrease in mean abundance and a 50% reduction in the mean number of species per sample in the sector resulting from removal of the most common species. Less dramatic change in the sector where sediments are more mobile.	Kaiser and Spencer (1996a)
Starfish	Beam trawl; coarse sand, gravel and shell, muddy sand, mud	Irish Sea	Evaluated damage to starfish at three sites in the Irish Sea that experienced different degrees of trawling intensity. Used International Council for the Exploration of the Sea data to select sites and used side scan to confirm trawling intensity. Found a significant correlation between starfish damage (arm regeneration) and trawling intensity.	Kaiser (1996)
Horse mussels	Otter trawl; horse mussel beds	Strangford Lough; N. Ireland	Used video and remotely operated vehicle, side-scan sonar, and benthic grabs to characterize the effect of otter trawling and scallop dredging on the benthic community. There was special concern over the impact on <i>Modiolus</i> beds in the Lough. Plotted the known fishing areas and graded impacts based on a subjective six-point scale. Found significant trawl impacts. Side-scan sonar supported video observations and showed areas of greatest impact. Found that in otter trawl areas, the otter boards did the most damage. Side scan suggested that sediment characteristics had changed in heavily trawled areas.	Industrial Science Division (1990)
Benthic fauna	Beam trawl; mobile mega- ripple structure and stable uniform sediment	Irish Sea	Sampled trawled areas 24 hours after trawling and 6 months later. On stable sediment found significant difference immediately after trawling, specifically, a reduction in polychaetes but increase in hermit crabs. After six months there was no detectable impact. On megaripple substrate no significant differences were observed immediately after trawling or six months later.	Kaiser et al. (in press)



TABLE 4.—(Continued.)

Taxa	Gear; sediment type	Location	Results	Reference
Bivalves, sea scallop, surf clams, ocean quahog	Scallop dredge, hydraulic clam dredge; various substrate types	Mid-Atlantic Bight, USA	Submersible study of bivalve harvest operations. Scallops harvested on soft sediment (sand or mud) had low dredge-induced mortality rates for uncaught animals (<5%). Culling mortality (discarded bycatch) was low, approximately 10%. Over 90% of the quahogs that were discarded reburrowed and survived whereas 50% of the surf clams died. Predators, crabs, starfish, fish, and skates moved in on the quahogs and clams with predator density 10 times control-area levels within eight hours post dredging. Noted numerous "minute" predators feeding in trawl tracks. Non-harvested animals, sand dollars, crustaceans, and worms significantly disrupted, but sand dollars suffered little apparent mortality.	Murawski and Serchuk (1989)
Ocean quahog	Hydraulic clam dredge; sand-silt	Long Island, NY, USA	Evaluated clam dredge efficiency over a transect and changes up to 24 hours later. After dredge filled it created a "windrow of clams." Dredge penetrated up to 30 cm and pushed sediment into track shoulders. After 24 hours track looked like a shallow depression. Clams can be cut or crushed by dredge with mortality ranging from 7 to 92%, which is dependent on size and location along dredge path. Smaller clams survived better and were capable of reburrowing in a few minutes. Predators, crabs, starfish, and snails moved in rapidly and departed within 24 hours.	Meyer et al. (1981)
Macro- benthos	Scallop dredge; coarse sand	Mercury Bay, New Zealand	Benthic community composed of small short-lived animals at two experimental and adjacent control sites. Sampling before and after dredging and three months later. Dredging caused an immediate decrease in density of common macrofauna. Three months later some populations had not recovered. Immediately after trawling, snails, hermit crabs, and starfish were feeding on damaged and exposed animals.	Thrush et al. (1995)
Scallops and asso- ciated fauna	Scallop dredge; "soft sediment"	Port Phillip Bay, Australia	Sampled twice before dredging and three times afterwards, up to 88 days later. The mean difference in species number increased from 3 to 18 after trawling. The total number of individuals increased over the sampling time on both experimental and control sites primarily as a result of amphipod recruitment, but the number of individuals at the dredged sites was always lower than the control. Dissimilarity increased significantly as a result of dredging because of a decrease in species numbers and abundance.	Currie and Parry (1994)

TABLE 4.—(Continued.)

Taxa	Gear; sediment type	Location	Results	Reference
Sea scallops and associated fauna	Otter trawl and scallop dredge; gravel and sand	Gulf of St. Lawrence, Canada	Observed physical change to seafloor from otter doors and scallop dredge and lethal and nonlethal damage to the scallops. Noted an increase in the most active predators within the trawl tracks compared to outside, specifically, winter flounder, sculpins, and rock crabs. No increase in starfish or other sedentary forms within an hour of dredging.	Caddy (1973)
Macrofauna	Beam trawl; hard-sandy substrate	North Sea, coast of Holland	Sampling before and after beam trawling (*hours, 16 hours, and 2 weeks) showed species-specific changes in macrofaunal abundance. Decreasing density ranged from 10 to 65% for species of echinoderms (starfish and sea urchins but not brittle stars), tube-dwelling polychaetes, and molluscs at the two-week sampling period. Density of some animals did not change. Other animals' densities increased, but these increases were not significant after two weeks.	Bergman and Hup (1992)
Benthic fauna	Beam trawl and shrimp trawl; hard sandy bottom, shell debris, and sandy substrate-mud	North Sea, German coast	Preliminary report using video and photographs comparing trawled and untrawled areas. Presence and density of brittle stars, hermit crabs, other "large" crustaceans, and flatfish was higher in the controls than the beam trawl site. Difference in sand ripple formation in trawled areas was also noted. Formations looked disturbed, not round and well developed. Found a positive correlation with damage to benthic animals and individual animal size. Found less impact with the shrimp trawl; diver observations confirmed low level of impact although the net was "festooned" with worms. Noted large megafauna, mainly crabs, in trawl tracks.	Rumohr et al. (1994)
Soft bottom macrofauna	Beam trawl; very fine sand	North Sea, Dutch sector	Compared animal densities before and after trawling and looked at fish stomach contents. Found that total mortality due to trawling varied among species and size class of fish, ranging from 4 to 139% of pretrawling values. (Values >100% indicate animals moving into the trawled area.) Mortality for echinoderms was low (3 to 19%) and undetectable for some molluscs (especially solid shells or small animals), while larger molluscs had a 12 to 85% mortality. Burrowing crustaceans had low mortality, but epifaunal crustaceans approximated 30% mortality and ranged as high as 74% mortality. Annelids were generally unaffected except for <i>Pectinaria</i> , a tube-building animal.	Santbrink and Bergman (1994)

TABLE 4.—(Continued.)

Taxa	Gear; sediment type	Location	Results	Reference
			Generally, mortality increased with number of times the area was trawled (once or twice). Dab <i>Limanda limanda</i> were found to be the major scavenger, immigrating into the area and eating damaged animals.	
Hermit crabs	Beam trawl	Irish Sea	Compared the catch and diet of two species of hermit crab on trawled and control sites. Found significant increases in abundance on the trawl lines two to four days after trawling for both species but also no change for one species on one of two dates. Found a general size shift toward larger animals after trawling. Stomach-contents weight was higher post-trawling for one species. Diets of the crabs were similar, but proportions differed.	Ramsay et al. (1996)
Sand macro-fauna and infauna	Scallop dredge	Irish Sea	Compared experimental treatments based on frequency of tows (i.e., 2, 4, 12, 25). Bottom topography changes did not change grain size distribution, organic carbon content, or chlorophyll content. Bivalve molluscs and peracarid crustaceans did not show significant changes in abundance or biomass. Polychaetes and urchins showed significant declines. Large molluscs, crustaceans, and sand eels were also damaged. In general, there was selective elimination of fragile and sedentary components of the infauna as well as large epifaunal taxa.	Eleftheriou and Robertson (1992)

the studies of Reise (1982) and Riesen and Reise (1982) in the Wadden Sea. In reviewing change for 101 species in the benthic community over 100 years, Reise (1982) noted no long-term trends in abundance for 42 common species but found 11 of these species showed considerable variation. Sponges, coelenterates, and bivalves suffered the greatest losses while polychaetes showed the biggest gains. Subtidally there was a decrease in the most common species from 53 to 44 while intertidally the opposite was observed, an increase from 24 to 38. Riesen and Reise (1982) examined a 55-year data set and documented increases in mussel beds and the associated fauna. They noted a loss of oysters due to overexploitation and a loss of *Sabellaria* reefs because they were systematically targeted by trawlers, as well as the loss of sea grass from disease. In another European study, Pearson et al. (1985) compared changes in the Kattegatt (an arm of the

North Sea) following a 73-year hiatus in sampling. In this case, community composition had changed to the extent that there was only a 30% similarity between stations over time, with the primary shift being a decrease in sea urchins and an increase in brittle stars. They observed a general decline in deposit feeders and an increase in suspension feeders and carnivores as well as a decline in animal size. Holme (1983) also made some comparisons from data collected over an 85-year time span in the English Channel and noted changes in the benthic community that he speculated might relate to the queen scallop fishery. The results of these long-term studies are consistent with the patterns found in short-term studies of habitat and community structure.

Data sets on the order of months to a few years are more typical of the longer-term studies on fishing impacts on benthic community structure. The impact of experimental trawling has been monitored

TABLE 5.— Studies of long-term impacts of fishing on benthic communities.

Habitat type; taxa	Time period	Location	Results	Reference
Sand; macro-benthos and meiofauna	2–7 months	Bay of Fundy	Experimental trawling in high-energy area. Otter trawl doors dug up to 5 cm deep, and marks were visible for 2 to 7 months. Initial significant effects on benthic diatoms and nematodes but no significant impact on macrofauna. No significant long-term effects.	Brylinsky et al. (1994)
Quartz sand; benthic infauna	5 months	South Carolina estuary	Compared benthic community in two areas, one open to trawling and one closed, before and after shrimp season. Found variation with time but no relationship between variations and trawling per se.	Van Dolah et al. (1991)
Sandy; ocean quahogs		Western Baltic	Observed otter board damage to bivalves, especially ocean quahogs, and found an inverse relation between shell thickness and damage and a positive correlation between shell length and damage.	Rumohr and Krost (1991)
Subtidal shallows and channel; macrobenthos	100 years	Wadden Sea	Reviewed changes in benthic community documented over 100 years. Considered 101 species. No long-term trends in changing abundance for 42 common species, with 11 showing considerable variation. Sponges, coelenterates, and bivalves suffered greatest losses while polychaetes showed the largest gains. Decrease subtidally for common species from 53 to 44 species and increase intertidally for common species from 24 to 38 species.	Reise (1982)
Intertidal sand; lug worms	4 years	Wadden Sea	Studied impact of lugworm harvesting versus control site. Machine dug 40-cm gullies. Immediate impact was a reduction in several benthic species and slow recovery for some of the larger long-lived species like soft-shelled clams. With one exception, a polychaete, the shorter-lived macrobenthic animals showed no decline. It took several years for the area to recover to pre-fishing conditions.	Beukema (1995)
Various habitat types; all species		North Sea	Review of fishing effects on the North Sea based primarily on International Council for the Exploration of the Sea North Sea Task Force reports. Starfish, sea urchins, and several polychaetes showed a 40 to 60% reduction in density after beam trawling, but some less-abundant animals showed no change, and one polychaete increased. At the scale of the North Sea, the effect of trawling on the benthos is unclear.	Gislason (1994)

TABLE 5.— (Continued.)

Habitat type; taxa	Time period	Location	Results	Reference
Sand; macrofauna	73 years	Kattegatt, coast of Sweden and Denmark	Compared benthic surveys from 1911 to 1912 with surveys from 1984. Community composition changed with only approximately 30% similarity between years at most stations. Primary change was a decrease in sea urchins and increase in brittle stars. Animals were also smaller in 1984. Deposit feeders decreased while suspension feeders and carnivores increased.	Pearson et al. (1985)
Subtidal shallows and channels; macrofauna	55 years	Wadden Sea	Documented increase in mussel beds and associated species such as polychaetes and barnacles when comparing benthic survey data. Noted loss of oyster banks, <i>Sabellaria</i> reefs, and subtidal sea grass beds. Oysters were overexploited and replaced by mussels; <i>Zostera</i> were lost to disease. Concluded that major habitat shifts were the result of human influence.	Riesen and Reise (1982)
Various habitats; ocean quahogs		Southern North Sea	Arctica valves were collected from 146 stations in 1991, and the scars on the valve surface were dated using internal growth bands, as an indicator of the frequency of beam trawl damage between 1959 and 1991. Numbers of scars varied regionally and temporally and correlated with fishing.	Witbaard and Klein (1994)
Various habitats; macrofauna	85 years	Western English Channel	Discussed change and causes of change observed in benthic community based on historic records and collections. Discussed role of fishing gear in dislodging hydroid and bryozoan colonies and speculated that gear effects reduce settlement sites for queen scallops.	Holme (1983)
Gravel and sand; macrofauna	3 years	Central California	Compared heavily trawled area with lightly trawled (closed) area using Smith MacIntyre grab samples and video transect data collected over three years. Trawl tracks and shell debris were more numerous in heavily trawled area, as were amphinomid polychaetes and oligochaetes in most years. Rocks, mounds, and flocculent material were more numerous at the lightly trawled station. Commercial fish were more common in the lightly trawled area as were epifaunal invertebrates. No significant differences were found between stations in terms of biomass of most other invertebrates.	Engel and Kvitek (1998)
Fine sand; razor clams		Barrinha, Southern Portugal	Evaluated disturbance lines in the shell matrix of the razor clam and found an increase in number of disturbance lines with length and age of the clams. Sand grains were often incorporated into the shell, suggestive of a major disturbance such as trawling damage and subsequent recovery and repair of the shell.	Gaspar et al. (1994)

TABLE 5.— (Continued.)

Habitat type; taxa	Time period	Location	Results	Reference
Fine to medium sand; ocean quahogs		Southern New Jersey	Compared areas unfished, recently fished, and currently fished for ocean quahogs using hydraulic dredges. Sampled invertebrates with a Smith MacIntyre grab. Few significant differences in numbers of individuals or species were noted, and no pattern suggesting any relationship to dredging was found.	MacKenzie (1982)
Gravel, shell debris, and fine mud; horse mussel community	8 years	Strangford Lough, Northern Ireland	Review paper of effects of queen scallop fishery on the horse mussel community. Compared benthic survey from the 1975–1980 period with work in 1988. Scallop fishery began in 1980. <i>Modiolus</i> community remained unchanged essentially from 1857 to 1980. The scallop fishery has a large benthic faunal bycatch, including horse mussels. Changes in the horse mussel community were directly related to the initiation of the scallop fishery, and there was concern about the extended period it would take for this community to recover.	Brown (1989)
Shallow muddy sand; scallops	6 months	Maine	Sampled site before, immediately after, and up to six months after trawling. Loss of surficial sediments and lowered food quality of sediments, measured as microbial populations, enzyme hydrolyzable amino acids, and chlorophyll <i>a</i> , were observed. Variable recovery by benthic community. Correlation with returning fauna and food quality of sediment.	L. Watling, R. H. Findlay, L. M. Mayer, and D. F. Schick (unpublished data)
Sand and sea grass; hard shelled clams and bay scallops	4 years	North Carolina	Evaluated effects of clam raking and mechanical harvesting on hard clams, bay scallops, macroinvertebrates, and sea grass biomass. In sand, harvesting adults showed no clear pattern of effect. With light harvesting, sea grass biomass dropped 25% immediately but recovered in a year. In heavy harvesting, sea grass biomass fell 65%, recovery did not start for >2 years, and sea grass had not recovered up to 4 years later. Clam harvesting showed no effect on macroinvertebrates. Scallop densities correlated with sea grass biomass.	Peterson et al. (1987)
Gravel pavement; benthic megafauna	Not known	Northern Georges Bank, USA	Used side-scan sonar, video, and naturalist dredge sampling to characterize disturbed and undisturbed sites based on fishing activity records. Documented a gradient of community structure from deep undisturbed to shallow disturbed sites. Undisturbed sites had more individual organisms, greater biomass, greater species richness, and greater diversity and were characterized by an abundant bushy epifauna. Disturbed sites were dominated by hard-shelled molluscs, crabs, and echinoderms.	Collie et al. (1997)

TABLE 5.— (Continued.)

Habitat type; taxa	Time period	Location	Results	Reference
Sand; epifauna	3 years	Grand Banks, Canada	Experimentally trawled site 12 times each year within 31 to 34 hours for 3 years. Total invertebrate bycatch biomass in trawls declined over the three-year study. Epibenthic sled samples showed lower biomass, averaging 25%, in trawled areas versus reference sites. Scavenging crabs were observed in trawl tracks after first six hours, and trawl damage to brittle stars and sea urchins was noted. No significant effects of trawling were found for four dominant species of mollusc.	Prena et al. (1996)
Sand; shrimp and macrobenthos	7 months	New South Wales, Australia	Sampled macrofauna before trawling, after trawling, and after commercial shrimp season using Smith McIntyre grab at experimental and control sites. Underwater observations of trawl gear were also made. No detectable changes in macrobenthos were found or observed.	Gibbs et al. (1980)
Soft sediment; scallops and associated fauna	17 months	Port Phillip Bay, Australia	Sampled 3 months before trawling and 14 months after trawling. Most species showed a 20 to 30% decrease in abundance immediately after trawling. Dredging effects generally were not detectable following the next recruitment within 6 months, but some animals had not returned to the trawling site 14 months post trawling.	Currie and Parry (1996)
Bryozoans; fish and associated fauna		Tasman Bay, New Zealand	Review of ecology of the coral-like bryozoan community and changes in fishing gear and practices since the 1950s. Points out the interdependence of fish within this benthic community and that the area was closed to fishing in 1980 because gear had developed that could fish in and destroy the benthic community, thereby destroying the fishery.	Bradstock and Gordon (1983)
Various habitat types diverse tropical fauna	5+ years, ongoing	Northwest Shelf, Australia	Describes a habitat-dependent fishery and an adaptive management approach to sustaining the fishery. Catch rates of all fish and large and small benthos show that in closed areas, fish and small benthos abundance increased over 5 years while large benthos (>25 cm) stayed the same or increased slightly. In trawled areas all groups of animals declined. Found that settlement rate and growth to 25 cm was on the order of 15 years for the benthos.	Sainsbury et al. (1997)

TABLE 5.— (Continued.)

Habitat type; taxa	Time period	Location	Results	Reference
Mudflat; commercial clam cultivation and benthos	7 months	Southeast England	Sampled benthic community on a commercial clam culture site and control area at the end of a two-year growing period, immediately after sampling, and again seven months later. Infaunal abundance was greatest under the clam culture protective netting, but species composition was similar to controls. Harvesting with a suction dredge changed the sediment characteristics and reduced the numbers of individual animals and species. Seven months later the site had essentially returned to the unharvested condition.	Kaiser et al. (1996)
Sand; razor clam and benthos	40 days	Loch Gairloch, Scotland	Compared control and experimentally harvested areas using a hydraulic dredge at 1 day and 40 days after dredging. On day 1 a nonselective reduction in the total numbers of all infaunal species was apparent, but no differences were observed after 40 days.	Hall et al. (1990)
Sand and muddy areas; macrozoobenthos	3 years, ongoing	German Bights	Investigated macrozoobenthos communities around a sunken ship that had been "closed" to fishing for three years. Compared this site with a heavily fished area. Preliminary results showed an increase in polychaetes and the bivalve <i>Tellina</i> in the fished, sandy area. The data did not allow for a firm conclusion regarding the unfished area, but there was some (nonsignificant) increase in species numbers, and some delicate, sensitive species occurred within the protected zone.	Arntz et al. (1994)

over a series of months, for example, in the Bay of Fundy at a high-energy sandy site (Brylinsky et al. 1994; L. Watling, R. H. Findlay, L. M. Mayer, and D. F. Schick, unpublished data). Trawl door marks were visible for 2–7 months, but no sustained significant impact on the benthic community was noted. However, Watling, Findlay, Mayer, and Schick (unpublished data) measured community-level changes caused by scallop dredging at a lower-energy muddy sand location in the Gulf of Maine. They detected a loss in surficial sediments and lowered sedimentary food quality. The subsequent variable recovery of the benthic community over the following 6 months correlated with sedimentary food quality, which was measured as microbial populations, abundance of chlorophyll *a*, and enzyme-hydrolyzable amino acid concentrations. Although some taxa recolonized the impacted areas quickly, the abundances of other taxa

(i.e., cumaceans, phoxocephalid and photid amphipods, nephtyid polychaetes) did not recover until food quality also recovered.

The most consistent pattern in fishing impact studies at shallow depths is the resilience of the benthic community to fishing. Two studies in intertidal depths that involved harvesting worms and clams using suction and mechanical harvesting gear demonstrated a substantial immediate effect on the macrofaunal community. However, from 7 months to 2 years later, the study sites had recovered to prefished conditions (Beukema 1995; Kaiser and Spencer 1996a). Peterson et al. (1987) and Hall et al. (1990) harvested at nearshore subtidal depths bay scallops in a North Carolina sea grass bed and razor clams in a Scottish sea loch (respectively) and found little long-term impact on the benthic community structure except at the most intense level of fishing.



After 40 d, the loch showed no effect of fishing, and in the lightly harvested sea grass bed, with <25% sea grass biomass removal, recovery occurred within a year. In the sea grass bed where harvesting was most extensive, with 65% of the sea grass biomass removed, recovery was delayed for 2 years, and after 4 years preharvesting biomass levels were still not obtained. In a South Carolina estuary, Van Dolah et al. (1991) found no long-term effects of trawling on the benthic community. The study site was assessed before and after the commercial shrimp season and demonstrated variation over time but no trawling effects per se. Other studies of pre and post impacts from mobile gear on shallow sandy to hard bottoms have generally shown similar results (Gibbs et al. 1980; MacKenzie 1982; Currie and Parry 1996) with either no or minimal long-term impact detectable.

Other benthic communities show clear effects that can be related to fishing. Collie et al. (1997) have, for example, characterized disturbed and undisturbed sites on Georges Bank, based on fishing records, and found more individuals, a greater biomass, and greater species richness and diversity in the undisturbed areas. Engel and Kvitek (1998) also found more fish and epifaunal invertebrates in a lightly trawled area compared to a more heavily trawled site over a 3-year period off Monterey, California. Perhaps the most convincing cases of fishing-related impacts on the benthic community are from studies in Northern Ireland, Australia, and New Zealand. Brown (1989) has reported the demise of the horse mussel community in Strangford Loch with the development of the queen scallop fishery. The horse mussel beds were essentially unchanged from 1857 until 1980 when the trawl fishery for scallops was initiated. Along the northwest Australian shelf Bradstock and Gordon (1983); Sainsbury (1987, 1988, 1991); and Sainsbury et al. (1997) describe a habitat-dependent fishery with fish biomass related to the coral-like byzoan community. With the demise of this epifaunal community, there was a shift in fish species composition to less commercially desirable species. In experimentally closed areas there has been a recovery of fish and an increase in the small benthos but, based on settlement and growth of larger epifaunal animals, it may take 15 years for the system to recover. Finally, sampling of fishing grounds along a gradient of fishing effort in the Hauraki Gulf of New Zealand has shown that 15–20% of the variability in the macrofauna com-

munity could be attributed to fishing (Thrush et al., in press). As fishing effort decreased there were increases in the density of large epifauna, in long-lived surface dwellers (with a decrease in deposit feeders and small opportunistic species), and in the Shannon–Weiner diversity index. These results validated most predictions made from small-scale studies, suggesting that there is value in continuing such work. However, where data are available to determine patterns of fishing effort at the scale of fishing grounds, large-scale studies such as this are beneficial for validating predictions from limited experimental work and, most importantly, establishing the range of ecological effects along a gradient of disturbance produced by resource extraction and the variable intensity of impacts from particular harvesting methods. Ultimately, such data can be used to develop strategies for the sustainable harvest of target species while maintaining ecosystem integrity.

#### *Implications for Management*

Clearly the long-term effects of fishing on benthic community structure are not easily characterized. The pattern that does appear to be emerging from the available literature is that communities that are subject to variable environments and are dominated by short-lived species are fairly resilient. Depending on the intensity and frequency of fishing, the impact of such activity may well fall within the range of natural perturbations. In communities that are dominated by long-lived species in more stable environments, the impact of fishing can be substantial and longer term. Studies of Strangford Loch and the Australian shelf show that recovery from trawling will be on the order of decades. In many areas, these two patterns correlate with shallow and deep environments. However, water depth is not the single variable that can be used to characterize fishing impacts. Few studies describe fishing impacts on shallow mud-bottom communities or on deep areas at the edge of the continental shelf. Such sites would be expected to be relatively low-energy zones, similar to areas in Strangford Loch, and might not recover rapidly from fishing disturbances. Studies in these relatively stable environments are required to pattern fishing impacts over the entire environmental range, but, in anticipation of such results, it is suggested that one should expect a tighter coupling between fish production and benthic community structure in the more stable marine environments.

## Effects on Ecosystem Processes

### *Interpretation of Results*

A number of studies indicate that fishing has measurable effects on ecosystem processes, but it is important to compare these effects with natural process rates at appropriate scales. Both primary production and nutrient regeneration have been shown to be affected by fishing gear. These studies are small in scope, and it is difficult to apply small-scale studies at the level of entire ecosystems. Understanding that processes are affected confirms the need to understand the relative changes in vital rates caused by fishing and the spatial extent of the disturbances.

Disturbance by fishing gear in relatively shallow depths (i.e., 30–40 m) can reduce primary production by benthic microalgae. Recent studies in several shallow continental shelf habitats have shown that primary production by a distinct benthic microflora can be a significant portion of overall primary production (i.e., water column plus benthic primary production) (Cahoon et al. 1990, 1993; Cahoon and Cooke 1992). Benthic microalgal production supports a variety of consumers, including demersal zooplankton (animals that spend part of each day on or in the sediment and migrate regularly into the water) (Cahoon and Tronzo 1992). Demersal zooplankton include harpacticoid copepods, amphipods, mysids, cumaceans, and other animals that are eaten by planktivorous fishes and soft-bottom foragers (Thomas and Cahoon 1993).

The effects of fishing were elucidated at Stellwagen Bank in the northwest Atlantic during 1991 and 1994. Measurements showed that a productive benthic microflora existed on the crest of the Bank (Cahoon et al. 1993; Cahoon et al., unpublished data) but that demersal zooplankton was low in comparison to the other shelf habitats and lower than would be expected given the available food supply (Cahoon et al. 1995). Several explanations can be advanced for this anomalously low zooplankton abundance. These include competitive or predatory interactions with meiofauna or the holozooplankton, disturbance by macrobenthos, intense predation by planktivorous fishes, and physical disturbance by mobile fishing gear. Many demersal zooplankters appear to construct and inhabit small burrows or capsules made of accreted or agglutinated sand. These formations provide shelter for demersal zooplankters in a habitat otherwise devoid of structure.

Many small biogenic structures were observed on the sediment surface, and even gentle handling by divers destroyed them easily. Movement by divers and a remotely operated vehicle caused demersal zooplankters to exhibit escape responses. Events that disturb the bottom, particularly such relatively powerful events as storms and towing mobile fishing gear along the sediment surface, must destroy these delicate habitat features. Disturbance of demersal zooplankters may result in increased predation that reduces local populations of zooplankters. Juvenile fish that feed on these taxa may require greater times and longer distances away from benthic shelter sites to forage in the water column to capture prey, exposing themselves to greater predation risk (Walters and Juanes 1993).

Recovery rates of populations of benthic primary producers are not well known. Brylinsky et al. (1994) showed that trawling had significant effects on benthic diatoms, but recovery occurred at all stations after about 30 d. The experimental sites that were trawled were in the intertidal zone in the Bay of Fundy. Trawling occurred during high tides and sampling at low tide. It is important to note that light intensity (and spectral composition) in this experiment was much greater than at sites where trawling normally occurs, that is, where seawater constantly overlays the substrate.

Experimental measurements from scallop dredge and otter trawl impacts off coastal Maine showed that dragging can both resuspend and bury labile organic matter (Mayer et al. 1991). Burial shifts organic matter decomposition and availability from aerobic eucaryotic-microbial pathways to anaerobic pathways. Short-term effects may include shifts from metazoan communities that support harvested species (e.g., meiofauna, polychaetes, flounders) toward anaerobic microbial respiration. Studies by Watling, Findlay, Mayer, and Schick (unpublished data) empirically demonstrate these short-term trends. Longer-term effects of chronic dragging and burial are difficult to predict.

Riemann and Hoffmann (1991) measured the short-term effects of mussel dredging and bottom trawling off Denmark in a shallow coastal marine system. Dredging and trawling increased suspended particulates immediately to 1,361% and 960–1,000%, respectively, above background. Oxygen decreased and nutrients such as ammonia and silicate increased. Dyekjaer et al. (1995) calculated the annual effects of mussel dredging in the same region. The total annual release of suspended particles

during dredging is relatively minor when compared with total wind-induced resuspension. Similarly, the release of nutrients is minor when compared with the nutrient loading from land runoff. However, local effects may be significant when near-bottom dissolved oxygen concentrations are low and reduced substances are resuspended, depending upon the depth of stratification, water flow rates, and the number of dredges operating simultaneously.

Direct movement of fishing gear over and through the sediment surface can change sediment grain size characteristics, change suspended load, and change the magnitude of sediment transport processes. Churchill (1989) showed that trawling could resuspend sediments on the same magnitude as storms and can be the primary factor regulating sediment transport over the outer continental shelf in areas where storm-related currents and bottom stresses are weak. Gear-induced resuspension of sediments can potentially have important impacts on nutrient cycling (Pilskaln et al. 1998). Open continental shelf environments typically receive approximately half of their nutrients for primary production from sediment resuspension and pore water exchange. The nutrients are produced from the microbial-based decay of organic matter and remineralization within sediments. Changes in rates of resuspension from periodic to steady pulses of nutrients (e.g., nitrate fluxes) caused by gear disturbance to the seafloor can shift phytoplankton populations from picoplankton towards diatoms, which may ultimately be beneficial for production of harvested species, although changes in nutrient ratios may stimulate harmful algal blooms.

### *Implications for Management*

The disturbances caused by fishing to benthic primary production and organic matter dynamics are difficult to predict. Semiclosed systems such as bays, estuaries, and fjords are subject to such effects at relatively small spatial scales. Open coastal and outer continental shelf systems can also experience perturbations in these processes. However, the relative rates of other processes (e.g., natural processes) may minimize the effects of fishing disturbances depending upon the level of fishing effort.

Mayer et al. (1991) discuss the implications of organic matter burial patterns in sediments versus soils. Their results are similar to organic matter patterns found in terrestrial soils. Sediments are essen-

tially part of a burial system while soils are erosional. Although gear disturbance can enhance remineralization rates by transforming surficial fungal-dominated communities into subsurface communities with dominant bacterial decomposition processes, burial caused by gear disturbance might also enhance preservation if material is sequestered in anaerobic systems. Given the importance of carbon cycling in estuaries and on continental shelves to the global carbon budget, understanding the magnitude of effects caused by human disturbances on primary production and organic matter decomposition will require long-term studies like those conducted on land.

## **Discussion**

### *Direct Alteration of Food Webs*

In heavily fished areas of the world, it is undebatable that fishing has ecosystem-level effects (Gislason 1994; Fogarty and Murawski 1998) and that shifts in benthic community structure have occurred. The data to confirm that such shifts have taken place are limited at best (Riesen and Reise 1982), but the fact that it has been documented at all is highly significant. If benthic communities change, what are the ecological processes that might bring about such change?

One of these processes involves enhanced food supply resulting from trawl-damaged animals and the discarding of both nonharvested species and offal from fish gutted at sea. The availability of this food source might affect animal behavior and influence survival and reproductive success. There are numerous reports of predatory fishes and invertebrate scavengers foraging in trawl tracks after a trawl passes through an area (Medcof and Caddy 1971; Caddy 1973; Kaiser and Spencer 1994; Evans et al. 1996; Ramsay et al. 1997a, 1997b). The prey available to scavengers is a function of the ability of animals to survive the capture process, which can involve being discarded as unwanted bycatch or passed through or over by the gear (Meyer et al. 1981; Fonds 1994; Rumohr et al. 1994; Santbrink and Bergman 1994; Kaiser and Spencer 1995). Studies in both the Irish and North Seas on the reaction of scavengers to a trawling event, usually involving beam trawling, are the most comprehensive. In the Irish Sea studies focused on the movement of animals over time into experimentally trawled areas at locations that ranged in sediment type from mud to gravel. Results

were found to be habitat dependent (Ramsay et al. 1997a, 1997b) and not always consistent (Kaiser and Ramsay 1997), although the general trends are that the rate of movement of scavengers into a trawled area reflects the mobility of the animals, their sensory abilities, and their behavior (Kaiser and Spencer 1996b). Fish were usually the first to arrive, and slower-moving invertebrates like whelks and starfish, which were also attracted to the area, required a longer time to respond to the availability of damaged or dead prey. That the scavengers are feeding has been documented both by direct diver observations and analysis of stomach contents (see Caddy 1973; Rumohr et al. 1994). Stomach-contents data demonstrate that fish not only feed on discarded or damaged animals and often eat more than their conspecifics at control sites, but they also consume animals that were not damaged but simply displaced by the trawling activity, or even those invertebrates that have themselves responded as scavengers (Kaiser and Spencer 1994; Santbrink and Bergman 1994). Hence the biomass available for consumption from discards and offal are not effecting the community equally but selectively providing additional food resources for those taxa that differentially react to the disturbance created by fishing.

Kaiser and Spencer (1994) make the comment, as others have before them, that it is common practice for fishermen to re-fish recently fished areas to take advantage of the aggregations of animals attracted to the disturbed benthic community. The long-term effect of opportunistic feeding following fishing disturbances is an area of speculation. In the North Sea, for example, the availability of "extra" food, either from discarded bycatch or as a more direct result of trawling-induced mortality, has been suggested as one reason why the population of dab *Limanda limanda* has increased. Kaiser and Ramsay (1997) argue that the combination of predator and competitor removal by fishing together with an increased food supply has resulted in the increase in the dab population. Obviously the negative effects on the prey organisms themselves are also important and may have an equal but opposite effect on their density. Faunal changes in the North Sea have been noted with major shifts in the composition of the benthic community that can be correlated with trawling. The general decline in populations of hard-bodied animals such as bivalves and heart urchins has been suggested to be the direct result of trawl damage with, one might speculate, this hard-bodied food becoming available to scavengers.

Another process that can indirectly alter food webs is the removal of keystone predators. Removal of herbivorous fishes and invertebrates produced a shift in coral reef communities from coral-invertebrate-dominated systems to filamentous and fleshy algae-dominated systems. (Roberts 1995 provides a synoptic review.) The removal of sea otters from kelp-bed communities in the western Pacific has also had cascading effects on urchin populations and the dynamics of kelp (Duggins 1980; Estes 1996). In the northwest Atlantic, Witman and Sebens (1992) showed that onshore-offshore differences in cod and wolffish *Anarhichas lupus* populations reduced predation pressure on cancerid crabs and other megafauna in deep coastal communities. They suggest that this regional difference in predation pressure is the result of intense harvesting of cod, a keystone predator, with cascading effects on populations of epibenthos (e.g., mussels, barnacles, urchins), which are prey of crabs.

American lobsters have also been considered a keystone predator because they control urchin populations, which in turn control the distribution of kelp (e.g., Mann and Breen 1972; Mann 1982). Communities shifted from kelp dominated to coralline algae dominated under the influence of intense urchin predation, with concomitant shifts in the mobile species that use such habitats. A hypothesis about this shift in communities focused on the role of lobster removals by fishing. Urchins, which are a primary prey of lobsters, had large population increases resulting in greater herbivory on kelp. However, Elner and Vadas (1990) brought the keystone predation hypothesis into question as urchins did not react to lobster predation by forming defensive aggregations and lobster diets were not dominated by urchins. Although understanding the ultimate control of such shifts remains elusive, recent harvesting of urchins has coincided with a return of kelp-dominated habitats. Other processes (e.g., annual variation in physical processes affecting survivorship of recruits, climate change, El Niño, recruitment variability of component species caused by predator-induced mortality) can also result in food web changes. Although it is important to understand all the underlying causes of food web shifts, precautionary management approaches should be considered given the strong inference of human-caused effects in studies focusing on identifying causes of food web shifts.

### *Predicting the Effects of Disturbance*

This review of the literature indicates that fishing, using a wide range of gear, produces measurable impacts. However, most studies were conducted at small spatial scales, and it is difficult to apply such information at regional levels where predictive capabilities would allow fisheries management at an ecosystem scale (Jennings and Kaiser 1998). Studies can be divided into those focused on acute impacts (caused by a single or a small number of tows) and those focused on chronic effects. Although the former type of study is most common and amenable to experimental manipulation, the latter type is most directly applicable in the arena of habitat management. Unfortunately, few long-term monitoring programs allow for an analysis of all the appropriate metrics needed to ascertain the effects of fishing on EFH. Additionally, although there are clear effects on local and regional patterns of biodiversity—an obvious metric needed to monitor the effects of ecosystem-level management—we do not have a good understanding of how communities respond to large-scale disturbances. This level of knowledge is needed to separate responses due to natural variability from responses due to human-caused variability.

Our current understanding of ecological processes related to the chronic disturbances caused by fishing makes results difficult to predict. Disturbance has been widely shown to be a mechanism that shifts communities (Dayton 1971; Pickett and White 1985; Witman 1985; Suchanek 1986). Although a full discussion of this area of ecology is beyond the scope of this review, general models produced from such work are useful for understanding fishing as an agent of disturbance from an ecological perspective. Assumptions regarding the role of fishing in the dynamics of marine communities generally assert that the cessation or reduction of fishing will allow populations and communities to recover to a climax community state, as is the case in long-lived terrestrial plant communities. Succession of communities implies a predictable progression in species composition and abundance (Connell 1989; Bell et al. 1991). Such knowledge of successional patterns would allow managers to predict future marine community states and directly manage EFH. Although direct successional linkages have been found in some communities, others are less predictable.

Two types of patterns in shifts in community states due to disturbance are illustrated in Figure 5. The first model is the traditional successional model where communities change from type A to B to C

and so forth. There are empirical examples of this type of succession in soft substrate benthic communities (e.g., Rhoads et al. 1978). Succession is based on one community of organisms producing a set of local environmental conditions (e.g., enriching the sediments with organic material) that make the environment unsuitable for continued survival and recruitment but are favorable for another community of organisms. Disturbance can move succession back in single or multiple steps, depending on the types of conditions that prevail after the disturbance. The successional stages are predictable based on conditions that result from the organisms themselves or from conditions after a perturbation. The second model of community states is disturbance mediated and lottery based (based on Horn 1976). Empirical studies of such relationships generally examine hard substrate communities (e.g., Dayton 1971; Horn 1976; Sebens 1986; Witman 1987). Shifts in community type are produced by competition and disturbance (e.g., predation, grazing, storms, fishing gear), which can result in shifts toward community types that are often unpredictable because they are based on the pool of recruits available in the water column at the time that niche space is available.

The spatial extent of disturbed and undisturbed communities is a concern in designing and interpreting studies (Pickett and White 1985; Barry and Dayton 1991; Thrush et al. 1994). Single, widely

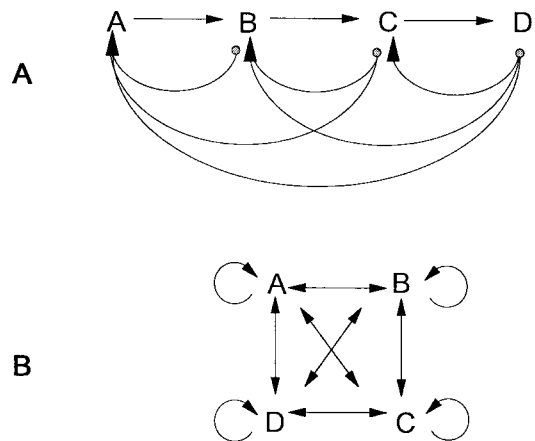


FIGURE 5.—Models of alternative community states. Arrows indicate direction of community shifts. Model A is the successional model, which has relatively predictable shifts in community type. Model B is a lottery-based model, which has more stochastic, nonlinear responses to disturbance.

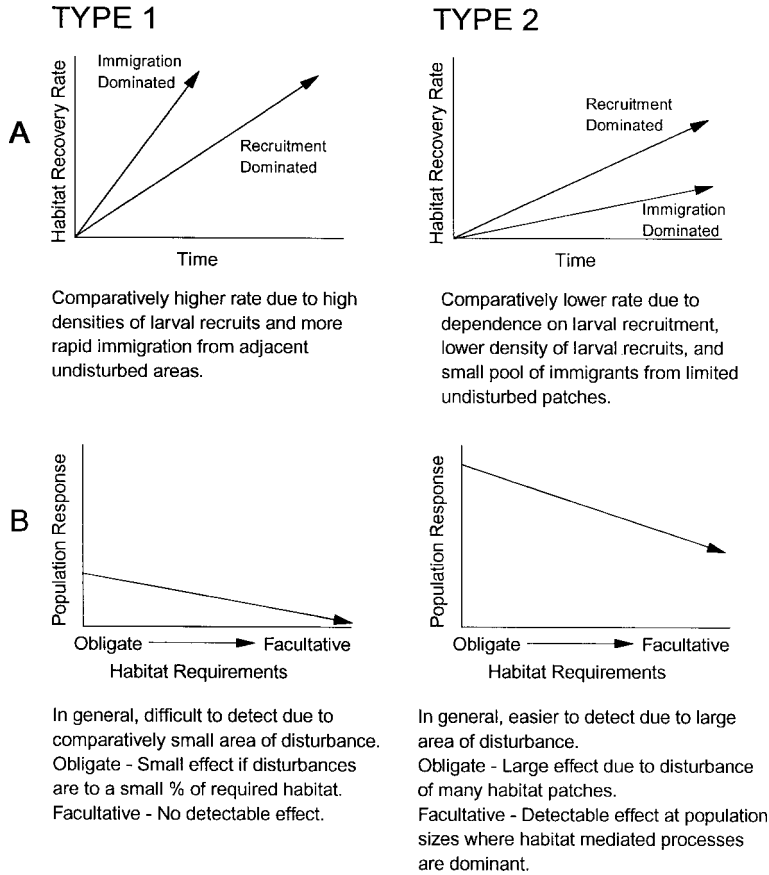


FIGURE 6.—Comparison of biogenic habitat structure and population responses to type-1 and type-2 habitat disturbances.

spaced disturbances may have little overall effect on habitat integrity and benthic communities, and these disturbed areas may show reduced recovery times as a result of immigration of mobile taxa (e.g., polychaetes, gastropods). In the ecological literature this is a type-1 disturbance, where a small patch is disturbed but surrounded by a large unimpacted area. In contrast, type-2 disturbances are those in which small patches of undisturbed communities are surrounded by large areas of disturbed communities. Immigration into such disturbed patches requires large-scale transport of propagules from outside source patches, or significant reproductive output (and high planktonic survival and larval retention) from the small undisturbed patches. Making predictions about the outcome of disturbances even where spatial extent is known is difficult because transport of colonizers (i.e., larvae, juveniles, and adults) depends on oceanographic conditions, larval period, movement rates of juveniles and adults, time of year, and dis-

tance from source. However, as an example of disturbance effects given specific sets of conditions, it is possible to illustrate general trends in the response of biogenic habitat structure to type-1 and type-2 disturbances and population responses based on characteristics of obligate and facultative habitat users (Figure 6). Type-1 disturbances generally have faster recovery rates because they are subject to immigration-dominated recovery in contrast to type-2 disturbances, which are dependent on larval recruitment for recovery. Population responses to such disturbances also are variable. Obligate habitat users have a much greater response to habitat disturbance such that type-1 disturbances would produce substantial small-scale effects but overall population responses would be small. Comparatively, it would be difficult to detect responses from populations of facultative habitat users because of the large areas of undisturbed habitat in type-1 disturbances. However, type-2 disturbances would produce large responses in obligate habitat users

in that a large percentage of required habitat would be affected. Facultative habitat users would have a measurable response at population levels where habitat-mediated processes are important.

The dependence of fish communities on particular habitat features is well represented in the literature on coral reef, kelp forest, and sea grass fish communities (e.g., Heck and Orth 1980; Ebeling and Hixon 1991; Sale 1991). Studies at this particular scale are generally lacking for most harvested taxa on outer continental shelves. One problem in interpreting existing studies is the tendency to compartmentalize the processes that structure these communities and not apply our general knowledge of habitat-mediated processes to other fish assemblages using other habitats. In reality, fish assemblages occur in a continuum along two gradients: one of habitat complexity and the other of environmental variation (Figure 7). Only limited numbers of species and communities have hard (limited) linkages between parts of the food web where gear impacts on prey communities would have obvious and easily measurable effects. Large temperate and boreal marine ecosystems are characterized by soft (flexible) linkages with most species having flexible prey requirements. Measuring effects that can be linked to changes in prey availability and ultimately back to effects of fishing gear will be challenging in these situations. New molecular and stable-isotope techniques offer the possibility for better tracking of trophic transfer of carbon and labeling of the role of particular prey taxa in secondary and tertiary production. The same can be said for effects of structural habitat change. It is difficult to detect signal changes because variability in populations is the cumulative result of many factors. Small-scale field studies producing information on the patterns of survivorship and predator-prey interactions in particular habitats, laboratory tests to determine relative differences in habitat-mediated survivorship under constant predator-prey densities, and numerical modeling to link the small-scale approaches with population-level responses provide the bridge to link small-scale studies to large-scale patterns.

#### *Further Considerations for Management*

Fishing is one of the most widespread human impacts to the marine environment. The removal of fish for human consumption from the world's oceans has effects not only on the target species but also on associated communities. Although the size-specific

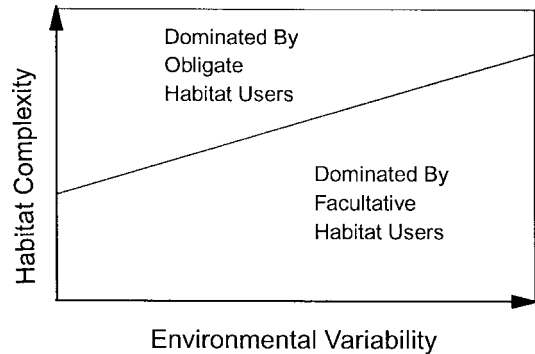


FIGURE 7.—Habitat complexity and environmental variability domain of fish assemblages as it relates to obligate and facultative habitat users. Fish assemblages occur in a continuum along the two gradients.

and species-specific removal of fish can change the system structure, the regions of the continental shelf that are normally fished appear to be fairly resilient. The difficulty for managers is defining the level of resilience—in the practical sense of time and area closures, mesh regulations, or overall effort limits—that will allow for the harvest of selected species without causing human-induced alterations of ecosystem structure to the point that recovery is unduly retarded or community and ecosystem support services are shifted to an alternate state (Steele 1996). Natural variability forms a backdrop against which managers must make such decisions, and, unfortunately, natural variability can be both substantial and unpredictable. The preceding discussion of the impact of fishing on marine communities does not address the role of natural variability directly, but it is apparent that in many of the systems studied there is an inherent resistance to biological change. In the very long term one can expect natural variability to generate regime shifts, but the challenge for natural resource managers is not to precipitate these shifts prematurely or in unintended directions.

Much of the research described herein is not at a scale that directly relates to effects on fish populations and therefore does not link directly to fishery management decisions. The research on fishing gear impacts does offer an indication of the types and direction of changes in benthic communities over large spatial scales as well as confirmation that benthic communities are dynamic and will ultimately compensate for perturbations. However, as observations show, shifts in communities are not necessarily beneficial to the harvested species. The scale of fishing is a confounding factor in management

because systems are being fished to the point where recovery is delayed so long that the economic consequences are devastating. We are currently seeing this pattern in many U.S. fisheries (and many other fisheries worldwide for that matter). Because our knowledge of ecosystem dynamics is still rather rudimentary, managers bear the responsibility of adopting a precautionary approach when considering the environmental consequences of fishing rather than assuming that the extraction of fish has no ecological price and therefore no feedback loop to our nonecologically based economic system.

This review has revealed that primary information is lacking for us to strategically manage fishing impacts on EFH without invoking precautionary measures. The following list identifies three areas where primary data are lacking; improved primary data would allow better monitoring and improved experimentation leading to improved predictive capabilities:

1. *The spatial extent of fishing-induced disturbance.* Although many observer programs collect data at the scale of single tows or sets, fisheries reporting systems often lack this level of spatial resolution. The available data make it difficult to make observations along a gradient of fishing effort to assess the effects of fishing effort on habitat, community, and ecosystem-level processes.
2. *The effects of specific gear types, along a gradient of effort, on specific habitat types.* These data are the first-order needs to allow an assessment of how much effort produces a measurable level of change in structural habitat components and associated communities. Second-order data should assess the effects of fishing disturbance in a gradient of type-1 and type-2 disturbance treatments.
3. *The role of seafloor habitats in the population dynamics of fishes.* Although good time series data often exist for late-juvenile and adult populations and larval abundance, there is a general lack of empirical information (except perhaps for coral reef, kelp bed, and sea grass fishes) on linkages between habitat and survival that would allow modeling and experimentation to predict outcomes of various levels of disturbance.

These data and research results should allow managers to better strategically regulate where, when, and how much fishing will be sustainable in regards to EFH. Conservation engineering should

play a large role in developing fishing gears that are economical to operate and minimize impacts to environmental support functions.

The ultimate goal of research on fishing impacts is not to retrospectively evaluate what fishing does to the environment but to predict cause and effect given a particular management protocol. This requires applying the conceptual models introduced in this discussion to actual management decisions and, at the same time, increasing our understanding of ecological mechanisms and processes at the level of the fish populations and associated communities. This demands in particular an appreciation of the importance of both the intensity and frequency of fishing impacts. If the objective is maintenance of habitat integrity, fishing should be conducted with an intensity that does not create isolated patches of communities whose progeny are required to recolonize impacted areas. Similarly, the habitat requirements of the harvested species must be taken into account to ensure that harvesting strategies do not disturb habitats more frequently than is required to balance economic as well as ecological sustainability.

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### References

- Able, K. W., M. P. Fahay, and G. R. Shepard. 1995. Early life history of black sea bass, *Centropristis striata*, in the mid-Atlantic Bight and a New Jersey estuary. *Fishery Bulletin* 93:429-445.
- Alexander, A. B., H. F. Moore, and W. C. Kendall. 1914. Otter-trawl fishery. Report of the U.S. Fisheries Commission for 1914, Appendix VI, Washington, D.C.



- Alverson, D. L., M. H. Freeberg, J. G. Pope, and S. A. Murawski. 1994. A global assessment of fisheries bycatch and discards. FAO (Food and Agriculture Organization of the United Nations) Fisheries Technical Paper 339.
- Arntz, W., E. Rachor, and S. Kuhne. 1994. Mid- and long-term effects of bottom trawling on the benthic fauna of the German Bight. Pages 59–74. NIOZ Rapport 1994-11, Netherlands Institute of Fisheries Research, Texel.
- Auster, P. J. 1988. A review of the present state of understanding of marine fish communities. *Journal of Northwest Atlantic Fishery Science* 8:67–75.
- Auster, P. J. 1998. A conceptual model of the impacts of fishing gear on the integrity of fish habitats. *Conservation Biology* 12(6):1198–1203.
- Auster, P. J., R. J. Malatesta, S. C. LaRosa, R. A. Cooper, and L. L. Stewart. 1991. Microhabitat utilization by the megafaunal assemblage at a low relief outer continental shelf site - Middle Atlantic Bight, USA. *Journal of Northwest Atlantic Fishery Science* 11:59–69.
- Auster, P. J., C. A. Griswold, M. J. Youngbluth, and T. G. Bailey. 1992. Aggregations of myctophid fishes with other pelagic fauna. *Environmental Biology of Fishes* 35:133–139.
- Auster, P. J., R. J. Malatesta, and S. C. LaRosa. 1995. Patterns of microhabitat utilization by mobile megafauna on the southern New England (USA) continental shelf and slope. *Marine Ecology Progress Series* 127:77–85.
- Auster, P. J., and eight coauthors. 1996. The impacts of mobile fishing gear on seafloor habitats in the Gulf of Maine (northwest Atlantic): implications for conservation of fish populations. *Reviews in Fisheries Science* 4(2):185–202.
- Auster, P. J., L. Watling, and A. Rieser. 1997a. Comment: The interface between fisheries research and habitat management. *North American Journal of Fisheries Management* 17:591–595.
- Auster, P. J., R. J. Malatesta, and C. L. S. Donaldson. 1997b. Distributional responses to small-scale habitat variability by early juvenile silver hake, *Merluccius bilinearis*. *Environmental Biology of Fishes* 50:195–200.
- Auster, P. J., C. Michalopoulos, P. C. Valentine, and R. J. Malatesta. 1998. Delineating and monitoring habitat management units in a temperate deep-water marine protected area. Pages 169–185 in N. W. Munro and J. H. M. Willison, editors. *Linking protected areas with working landscapes, conserving biodiversity*. Science and Management of Protected Areas Association, Wolfville, Nova Scotia.
- Barry, J. P., and P. K. Dayton. 1991. Physical heterogeneity and the organization of marine communities. Pages 270–320 in J. Kolasa and T. A. Pickett, editors. *Ecological heterogeneity*. Springer-Verlag, New York.
- Bell, S. S., E. D. McCoy, and H. R. Mushinsky. 1991. Habitat structure: the physical arrangement of objects in space. In S. Bell, E. D. McCoy, and H. R. Mushinsky, editors. *Population and community biology series*. Chapman and Hall, New York.
- Bergman, M. J. N., and M. Hup. 1992. Direct effects of beamtrawling on macrofauna in a sandy sediment in the southern North Sea. *ICES Journal of Marine Science* 49:5–11.
- Beukema, J. J. 1995. Long-term effects of mechanical harvesting of lugworms *Arenicola marina* on the zoobenthic community of a tidal flat in the Wadden Sea. *Netherlands Journal of Sea Research* 33:219–227.
- Bradstock, M., and D. Gordon. 1983. Coral-like bryozoan growths in Tasman Bay, and their protection to conserve commercial fish stocks. *New Zealand Journal of Marine and Freshwater Research* 17:159–163.
- Bridger, J. P. 1970. Some effects of the passage of a trawl over the seabed. ICES C.M. 1970/B:10 Gear and Behavior Committee.
- Bridger, J. P. 1972. Some observations on the penetration into the sea bed of tickler chains on a beam trawl. ICES C.M. 1972/B:7.
- Brodeur, R. D. In press. In situ observations of the association between juvenile fishes and scyphomedusae in the Bering Sea. *Marine Ecology Progress Series*.
- Brown, R. A. 1989. Bottom trawling on Strangford Lough: problems and policies. Proceedings reprints, Distress signals, signals from the environment in policy and decision making, May 31–June 2, 1989. Rotterdam, Netherlands.
- Brylinsky, M., J. Gibson, and D. C. Gordon, Jr. 1994. Impacts of flounder trawls on the intertidal habitat and community of the Minas Basin, Bay of Fundy. *Canadian Journal of Fisheries and Aquatic Sciences* 51:650–661.
- Caddy, J. F. 1973. Underwater observations on tracks of dredges and trawls and some effects of dredging on a scallop ground. *Journal of the Fisheries Research Board of Canada* 30:173–180.
- Cahoon, L. B., and J. E. Cooke. 1992. Benthic microalgal production in Onslow Bay, North Carolina. *Marine Ecology Progress Series* 84:185–196.
- Cahoon, L. B., and C. R. Tronzo. 1992. Quantitative estimates of demersal zooplankton abundance in Onslow Bay, North Carolina. *Marine Ecology Progress Series* 87:197–200.
- Cahoon, L. B., R. L. Redman, and C. R. Tronzo. 1990. Benthic microalgal biomass in sediments of Onslow Bay, North Carolina. *Estuarine Coastal and Shelf Science* 31:805–816.
- Cahoon, L. B., G. R. Beretich, Jr., C. J. Thomas, and A. M. McDonald. 1993. Benthic microalgal production at Stellwagen Bank, Massachusetts Bay, USA. *Marine Ecology Progress Series* 102:179–185.
- Cahoon, L. B., M. F. Feeley, and C. F. Jensen. 1995. Quantitative estimates of demersal zooplankton abundance at Stellwagen Bank, Massachusetts Bay. Proceedings of the American Academy of Underwater Sciences. Costa Mesa, California.
- Chopin, F. S., and T. Arimoto. 1995. The condition of fish escaping from fishing gears—a review. *Fisheries Research* 21:315–327.

- Churchill, J. H. 1989. The effect of commercial trawling on sediment resuspension and transport over the Middle Atlantic Bight continental shelf. *Continental Shelf Research* 9:841–864.
- Collie, J. S., G. A. Escanero, L. Hunke, and P. C. Valentine. 1996. Scallop dredging on Georges Bank: photographic evaluation of effects on benthic fauna. ICES C.M. 1996/Mini:9.
- Collie, J. S., G. A. Escanero, and P. C. Valentine. 1997. Effects of bottom fishing on the benthic megafauna of Georges bank. *Marine Ecology Progress Series* 155:159–172.
- Colvocoresses, J. A., and J. A. Musick. 1984. Species associations and community composition of Middle Atlantic Bight continental shelf demersal fishes. *Fishery Bulletin* 82:295–313.
- Connell, J. H. 1989. Change and persistence in some marine communities. Pages 339–352 in A. J. Gray, M. J. Crawley, and P. J. Edwards, editors. *Colonization, succession and stability. The 26th symposium of the British Ecological Society*. Blackwell Scientific Publications Scientific Publishers, Oxford.
- Currie, D. R., and G. D. Parry. 1994. The impact of scallop dredging on a soft sediment community using multivariate techniques. *Memoirs of the Queensland Museum* 36:316–326.
- Currie, D. R., and G. D. Parry. 1996. Effects of scallop dredging on a soft sediment community: a large-scale experimental study. *Marine Ecology Progress Series* 134:131–150.
- Cushing, D. H. 1975. *Marine ecology and fisheries*. Cambridge University Press, Cambridge and New York.
- Dayton, P. K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs* 41:351–389.
- Dayton, P. K., S. F. Thrush, M. T. Agardy, and R. J. Hofman. 1995. Environmental effects of marine fishing. *Aquatic Conservation: Marine and Freshwater Ecosystems* 5:205–232.
- de Groot, S. J. 1984. The impact of bottom trawling on benthic fauna of the North Sea. *Ocean Management* 9:177–190.
- Duggins, D. O. 1980. Kelp beds and sea otters: an experimental approach. *Ecology* 61:447–453.
- Dyckjaer, S. M., J. K. Jensen, and E. Hoffmann. 1995. Mussel dredging and effects on the marine environment. ICES C.M. 1995/E:13.
- Ebeling, A. W., and M. A. Hixon. 1991. Tropical and temperate reef fishes: comparison of community structures. Pages 509–563 in P. F. Sale, editor. *The ecology of fishes on coral reefs*. Academic Press, New York.
- Eleftheriou, A., and M. R. Robertson. 1992. The effects of experimental scallop dredging on the fauna and physical environment of a shallow sandy community. *Netherlands Journal of Sea Research* 30:289–299.
- Elnor, R. W., and R. L. Vadas. 1990. Inference in ecology: the sea urchin phenomenon in the Northwest Atlantic. *American Naturalist* 136:105–108.
- Engel, J., and R. Kvitek. 1998. Impacts of otter trawling on a benthic community in Monterey Bay National Marine Sanctuary. *Conservation Biology* 12:1204–1214.
- Eno, N. C., D. S. MacDonald, and S. C. Amos. 1996. A study on the effects of fish (crustacea/mollusc) traps on benthic habitats and species. Final report to the European Commission.
- Estes, J. A. 1996. The influence of large, mobile predators in aquatic food webs: examples from sea otters and kelp forests. Pages 65–72 in S. P. R. Greenstreet and M. L. Tasker, editors. *Aquatic predators and their prey*. Blackwell Scientific Publications Scientific, Oxford.
- Evans, P. L., M. J. Kaiser, and R. N. Hughes. 1996. Behavior and energetics of whelks, *Buccinum undatum* (L.), feeding on animals killed by beam trawling. *Journal of Experimental Marine Biology and Ecology* 197:51–62.
- FAO (Food, and Agriculture Organization of the United Nations). 1997. Review of the state of world fishery resources: marine fisheries. FAO Fisheries Circular No. 920.
- Fogarty, M. J., and S. A. Murawski. 1998. Large-scale disturbance and the structure of marine systems: fishery impacts on Georges Bank. *Ecological Applications* 8(1) Supplement:S6–S22.
- Fonds, M. 1994. Mortality of fish and invertebrates in beam trawl catches and the survival chances of discards. Pages 131–146. NIOZ Rapport 1994-11, Netherlands Institute for Fisheries Research, Texel.
- Fonseca, M. S., G. W. Tanyer, A. J. Chester, and C. Foltz. 1984. Impact of scallop harvesting on eelgrass (*Zostera marina*) meadows: implications for management. *North American Journal of Fisheries Management* 4:286–293.
- Freese, L., P. Auster, J. Heifetz, and B. Wing. In press. Effects of trawling on sea floor habitat and associated invertebrate taxa in the Gulf of Alaska. *Marine Ecology Progress Series*.
- Gabriel, W. L. 1992. Persistence of demersal fish assemblages between Cape Hatteras and Nova Scotia, northwest Atlantic. *Journal of Northwest Atlantic Fisheries Science* 14:29–46.
- Gabriel, W. L., and A. V. Tyler. 1980. Preliminary analysis of Pacific coast demersal fish assemblages. *Marine Fisheries Review* 42(3-4):83–88.
- Gaspar, M. B., C. A. Richardson, and C. C. Monteiro. 1994. The effects of dredging on shell formation in the razor clam *Ensis siliqua* from Barrinha, southern Portugal. *Journal of the Marine Biological Association of the United Kingdom* 74:927–938.
- Gibbs, P. J., A. J. Collins, and L. C. Collett. 1980. Effect of otter prawn trawling on the macrobenthos of a sandy substratum in a New South Wales estuary. *Australian Journal of Marine and Freshwater Research* 31:509–516.
- Gislason, H. 1994. Ecosystem effects of fishing activities in the North Sea. *Marine Pollution Bulletin* 29(6-12):520–527.
- Gotceitas, V., and J. A. Brown. 1993. Substrate selection by juvenile Atlantic cod (*Gadus morhua*): effects of predation risk. *Oecologia* 93:31–37.

- Guillén, J. E., A. A. Ramos, L. Martínez, and J. Sánchez Lizaso. 1994. Antitrawling reefs and the protection of *Posidonia oceanica* (L.) meadows in the western Mediterranean Sea: demands and aims. *Bulletin of Marine Science* 55(2-3):645-650.
- Hall, S. J. 1994. Physical disturbance and marine benthic communities: life in unconsolidated sediments. *Oceanography and Marine Biology: An Annual Review* 32:179-239.
- Hall, S. J., D. J. Basford, and M. R. Robertson. 1990. The impact of hydraulic dredging for razor clams *Ensis* sp. on an infaunal community. *Netherlands Journal of Sea Research* 27:119-125.
- Hall, S. J., M. R. Robertson, D. J. Basford, and S. D. Heaney. 1993. The possible effects of fishing disturbance in the northern North Sea: an analysis of spatial patterns in community structure around a wreck. *Netherlands Journal of Sea Research* 31:201-208.
- Harper, D. E., Jr., and S. H. Hopkins. 1976. The effects of oyster shell dredging on macrobenthic and nektonic organisms in San Antonio Bay. Pages 232-279 in A. H. Bouma, editor. *Shell dredging and its influence on Gulf coast environments*. Gulf Publishing Company, Houston.
- Heck, K. L. Jr., and R. J. Orth. 1980. Seagrass habitats: the roles of habitat complexity, competition and predation in structuring associated fish and motile macroinvertebrate assemblages. Pages 449-464 in V. S. Kennedy, editor. *Estuarine perspectives*. Academic Press, New York.
- Holme, N. A. 1983. Fluctuations in the benthos of the western English Channel. *Oceanol. Acta* XX:121-124.
- Horn, H. S. 1976. Succession principles and applications. Pages 187-204 in R. M. May, editor. *Theoretical ecology*. WB Saunders, Philadelphia.
- Hutchings, P. 1990. Review of the effects of trawling on macrobenthic epifaunal communities. *Australian Journal of Marine and Freshwater Research* 41:111-120.
- ICES (International Council for the Exploration of the Sea). 1988. Report of the study group on the effects of bottom trawling. *ICES C.M.* 1988/B:56.
- ICES (International Council for the Exploration of the Sea). 1992. Report of the working group on ecosystem effects of fishing activities. Copenhagen, 7-14 Apr. 1992. *ICES C.M.* 1992/G:11 Ref.: Session T.
- ICES (International Council for the Exploration of the Sea). 1996. Report of the working group on ecosystem effects of fishing activities. *ICES Headquarters*, 13-21 Mar. 1996. *ICES CM 1996/Assess/Env:1 Ref.: Session G*.
- Industrial Science Division. 1990. The impact of commercial trawling on the benthos of Strangford Lough. Interim Report No. TI/3160/90. Industrial Science Division, 17 Antrim Rd., Lisburn, Co., Antrim B128 3AL.
- Jennings, S., and M. J. Kaiser. 1998. The effects of fishing on marine ecosystems. *Advances in Marine Biology* 34.
- Jones, J. B. 1992. Environmental impact of trawling on the seabed: a review. *New Zealand Journal of Marine and Freshwater Research* 26:59-67.
- Kaiser, M. 1996. Starfish damage as an indicator of trawling intensity. *Marine Ecology Progress Series* 134:303-307.
- Kaiser, M. J., and B. E. Spencer. 1994. Fish scavenging behavior in recently trawled areas. *Marine Ecology Progress Series* 112:41-49.
- Kaiser, M. J., and B. E. Spencer. 1995. Survival of by-catch from a beam trawl. *Marine Ecology Progress Series* 126:31-38.
- Kaiser, M. J., and B. E. Spencer. 1996a. The effects of beam-trawl disturbance on infaunal communities in different habitats. *Journal of Animal Ecology* 65:348-358.
- Kaiser M. J., and B. E. Spencer. 1996b. Behavioural responses of scavengers to beam trawl disturbance. Pages 116-123 in S. P. R. Greenstreet and M. L. Tasker, editors. *Aquatic predators and their prey*. Blackwell Scientific Publications, Oxford.
- Kaiser M. J., and K. Ramsay. 1997. Opportunistic feeding by dabs within areas of trawl disturbance: possible implications for increased survival. *Marine Ecology Progress Series* 152:307-310.
- Kaiser, M. J., D. B. Edwards, and B. E. Spencer. 1996. Infaunal community changes as a result of commercial clam cultivation and harvesting. *Aquatic Living Resources* 9:57-63.
- Kaiser, M. J., and six coauthors. In press. Changes in megafaunal benthic communities in different habitats after trawling disturbance. *ICES Journal of Marine Science*.
- Kroger, R. L., and J. F. Guthrie. 1972. Effect of predators on juvenile menhaden in clear and turbid estuaries. *Marine Fisheries Review* 34:78-80.
- Langton, R. W. 1994. Fishing effects on demersal fish habits. In R. W. Langton, J. B. Pearce, and J. A. Gibson, editors. *Selected living resources, habitat conditions and human perturbations of the Gulf of Maine*. NOAA (National Oceanic and Atmospheric Administration) Technical Memorandum NMFS-NE-106.
- Langton, R. W., P. J. Auster, and D. C. Schneider. 1995. A spatial and temporal perspective on research and management of groundfish in the northwest Atlantic. *Reviews in Fisheries Science* 3:201-229.
- Langton, R. W., R. S. Steneck, V. Gotceitas, F. Juanes, and P. Lawton. 1996. The interface between fisheries research and habitat management. *North American Journal of Fisheries Management* 16:1-7.
- Lindholm, J., M. Ruth, L. Kaufman, and P. Auster. 1998. A modeling approach to the design of marine refugia for fishery management. Pages 138-168 in N. W. Munro and J. H. M. Willison, editors. *Linking protected areas with working landscapes, conserving biodiversity*. Science and Management of Protected Areas Association, Wolfville, Nova Scotia.

- Lough, R. G., and six coauthors. 1989. Ecology and distribution of juvenile cod and haddock in relation to sediment type and bottom currents on eastern Georges Bank. *Marine Ecology Progress Series* 56:1–12.
- MacDonald, D. S., M. Little, N. C. Eno, and K. Hiscock. 1996. Disturbance of benthic species by fishing activities: a sensitivity index. *Aquatic Conservation: Marine and Freshwater Ecosystems* 6:257–268.
- MacKenzie, C. L., Jr. 1982. Compatibility of invertebrate populations and commercial fishing for ocean quahogs. *North American Journal of Fisheries Management* 2:270–275.
- Magorrian, B. H. 1995. The impact of commercial trawling on the benthos of Strangford Lough. Doctoral dissertation. The Queen's University of Belfast, Northern Ireland.
- Mann, K. H. 1982. Kelp, sea urchins and predators: a review of strong interactions in rocky subtidal systems of eastern Canada, 1970–1980. *Netherlands Journal of Sea Research* 16:414–423.
- Mann, K. H., and P. A. Breen. 1972. The relation between lobster abundance, sea urchins, and kelp beds. *Journal of the Fisheries Research Board of Canada* 29:603–605.
- Mayer, L. M., D. F. Schick, R. H. Findlay, and D. L. Rice. 1991. Effects of commercial dragging on sedimentary organic matter. *Marine Environmental Research* 31:249–261.
- Medcof, J. C., and J. F. Caddy. 1971. Underwater observations on the performance of clam dredges of three types. *ICES C.M.* 1971/B:10.
- Messieh, S. N., T. W. Rowell, D. L. Peer, and P. J. Cranford. 1991. The effects of trawling, dredging and ocean dumping on the eastern Canadian shelf seabed. *Continental Shelf Research* 11(8-10):1237–1263.
- Meyer T. L., R. A. Cooper, and K. J. Pecci. 1981. The performance and environmental effects of a hydraulic clam dredge. *Marine Fisheries Review* 43(9):14–22.
- Moser, M. L., P. J. Auster, and J. B. Bichy. 1998. Effects of mat morphology on large *Sargassum*-associated fishes: observations from a remotely operated vehicle (ROV) and free-floating video camcorders. *Environmental Biology of Fishes* 51:391–398.
- Murawski, S. A. 1993. Climate change and marine fish distributions: forecasting from historical analogy. *Transactions of the American Fisheries Society* 122:647–658.
- Murawski, S. A., and F. M. Serchuk. 1989. Environmental effects of offshore dredge fisheries for bivalves. *ICES 1989 Statutory Meeting*. The Hague, Netherlands.
- National Research Council. 1994. Improving the management of U.S. marine fisheries. National Academy Press, Washington, D.C.
- National Research Council. 1995. Understanding marine biodiversity: a research agenda for the nation. National Academy Press, Washington, D.C.
- Overholtz, W. J., and A. V. Tyler. 1985. Long-term responses of the demersal fish assemblages of Georges Bank. *Fishery Bulletin* 83:507–520.
- Pearson, T. H., A. B. Josefsen, and R. Rosenberg. 1985. Petersen's benthic stations revisited. I. Is the Kattagatt becoming eutrophic? *Journal of Experimental Marine Biology and Ecology* 92:157–206.
- Peters, D. S., and F. A. Cross. 1992. What is coastal fish habitat? Pages 17–22 in R. H. Stroud, editor. *Stemming the tide of coastal fish habitat loss*. Marine recreational fisheries, volume 14. National Coalition for Marine Conservation, Savannah, Georgia.
- Peterson, C. H., H. C. Summerson, and S. R. Fegley. 1983. Relative efficiency of two clam rakes and their contrasting impacts on seagrass biomass. *Fishery Bulletin* 81:429–434.
- Peterson, C. H., H. C. Summerson, and S. R. Fegley. 1987. Ecological consequences of mechanical harvesting of clams. *Fishery Bulletin* 85(2):281–298.
- Phoel, W. C. 1986. Community structure of demersal fishes on the inshore U.S. Atlantic continental shelf: Cape Ann, Massachusetts to Cape Fear, North Carolina. Doctoral dissertation. College of William and Mary, Gloucester Point, Virginia.
- Pickett, S. T. A., and P. S. White, editors. 1985. The ecology of natural disturbance and patch dynamics. Academic Press, New York.
- Pilskaln, C. H., J. H. Churchill, and L. M. Mayer. 1998. Resuspension of sediment by bottom trawling in the Gulf of Maine and potential geochemical consequences. *Conservation Biology* 12(6):1223–1224.
- Prena, J., T. W. Rowell, P. Schwinghamer, K. Gilkinson, and D. C. Gordon, Jr. 1996. Grand Banks otter trawling impact experiment: site selection process, with a description of macrofaunal communities. Canadian Technical Report of Fisheries and Aquatic Sciences 2094.
- Ramsay, K., M. J. Kaiser, and R. N. Hughes. 1996. Changes in hermit crab feeding patterns in response to trawling disturbance. *Marine Ecology Progress Series* 144:63–72.
- Ramsay, K., M. J. Kaiser, and R. N. Hughes. 1997a. Responses of benthic scavengers to fishing disturbance by towed gear in different habitats. *Journal of Experimental Marine Biology and Ecology* 224:73–89.
- Ramsay, K., M. J. Kaiser, P. G. Moore, and R. N. Hughes. 1997b. Consumption of fisheries discards by benthic scavengers: utilization of energy subsidies in different marine habitats. *Journal of Animal Ecology* 66:884–896.
- Reise, K. 1982. Long-term changes in the macrobenthic invertebrate fauna of the Wadden Sea: are polychaetes about to take over? *Netherlands Journal of Sea Research* 16:29–36.
- Reiswig, H. M. 1973. Population dynamics of three Jamaican Demospongiae. *Bulletin of Marine Science* 23:191–226.

- Rhoads, D. C., P. L. McCall, and J. Y. Yingst. 1978. Disturbance and production on the estuarine seafloor. *American Scientist* 66:557–586.
- Riemann, B., and E. Hoffmann. 1991. Ecological consequences of dredging and bottom trawling in the Limfjord, Denmark. *Marine Ecology Progress Series* 69:171–178.
- Riesen, W., and K. Reise. 1982. Macrobenthos of the subtidal Wadden Sea: revisited after 55 years. *Helgoländer Meeresunters* 35:409–423.
- Rijnsdorp, A. D., A. M. Buijs, F. Storbeck, and E. Visser. 1996. Micro-scale distribution of beam trawl effort in the southern North Sea between 1993 and 1996 in relation to the trawling frequency of the sea bed and the impact on benthic organisms. ICES CM 1996/Mini 11 Mini-Symposium Ecosystem Effects Fisheries.
- Roberts, C. M. 1995. Effects of fishing on the ecosystem structure of coral reefs. *Conservation Biology* 9:988–995.
- Rumohr, H., and P. Krost. 1991. Experimental evidence of damage to benthos by bottom trawling with special reference to *Artica islandica*. *Meeresforsch* 33:340–345.
- Rumohr, H., H. Schomann, and T. Kujawski. 1994. Environmental impact of bottom gears on benthic fauna in the German Bight. Pages 75–86. NIOZ Rapport 1994-11, Netherlands Institute for Fisheries Research, Texel.
- SAFMC (South Atlantic Fishery Management Council). 1991. Amendment 4 (gear restrictions and size limits), regulatory impact review, initial regulatory flexibility analysis and environmental assessment for the fishery management plan for the snapper grouper fishery of the south Atlantic region. SAFMC, Charleston, South Carolina.
- Sainsbury, K. J. 1987. Assessment and management of the demersal fishery on the continental shelf of north-western Australia. Pages 465–503 in J. J. Polovina and S. Ralston, editors. *Tropical snappers and groupers: biology and fisheries management*. Westview, Boulder, Colorado.
- Sainsbury, K. J. 1988. The ecological basis of multispecies fisheries and management of a demersal fishery in tropical Australia. Pages 349–382 in J. A. Gulland, editor. *Fish population dynamics*, 2nd edition. John Wiley and Sons, London.
- Sainsbury, K. J. 1991. Application of an experimental approach to management of a demersal fishery with highly uncertain dynamics. *ICES Marine Science Symposium* 193:301–320.
- Sainsbury, K. J., R. A. Campbell, R. Lindholm, and A. W. Whitelaw. 1997. Experimental management of an Australian multispecies fishery: examining the possibility of trawl-induced habitat modification. Pages 107–112 in E. K. Pikitch, D. D. Huppert, and M. P. Sissenwine, editors. *Global trends: fisheries management*. American Fisheries Society, Symposium 20, Bethesda, Maryland.
- Sale, P. F., editor. 1991. *The ecology of fishes on coral reefs*. Academic Press, New York.
- Santbrink, J. W., and M. J. N. Bergman. 1994. Direct effects of beam trawling on macrofauna in a soft bottom area in the southern North Sea. Pages 147–178. NIOZ Rapport 1994-11, Netherlands Institute for Fisheries Research, Texel.
- Sebens, K. P. 1986. Community ecology of vertical rock walls in the Gulf of Maine, U.S.A.: small-scale processes and alternative community states. Pages 346–371 in P. G. Moore and R. Seed, editors. *The ecology of rocky coasts*. Hodder and Stoughton Press, Kent, UK.
- Smith, E. M., and 15 coauthors. 1985. A study of lobster fisheries in the Connecticut waters of Long Island Sound with special reference to the effects of trawling on lobsters. Connecticut Department of Environmental Protection, Marine Fisheries Program, Hartford.
- Sogard, S. M., and K. W. Able. 1991. A comparison of eelgrass, sea lettuce macroalgae, and marsh creeks as habitats for epibenthic fishes and decapods. *Estuarine Coastal and Shelf Science* 33:501–519.
- Steele, J. H. 1996. Regime shifts in fisheries management. *Fisheries Research* 25:19–23.
- Suchanek, T. H. 1986. Mussels and their role in structuring rocky shore communities. Pages 70–96 in P. G. Moore and R. Seed, editors. *The ecology of rocky coasts*. Hodder and Stoughton Press, Kent, UK.
- Szedlmayer, S. T., and J. C. Howe. 1997. Substrate preference in age-0 red snapper, *Lutjanus campechanus*. *Environmental Biology of Fishes* 50:203–207.
- Thomas, C. J., and L. B. Cahoon. 1993. Stable isotope analyses differentiate between different trophic pathways supporting rocky-reef fishes. *Marine Ecology Progress Series* 95:19–24.
- Trush, S. F., R. D. Pridmore, and J. E. Hewitt. 1994. Impacts on soft-sediment macrofauna: the effects of spatial variation on temporal trends. *Ecological Applications* 4:31–41.
- Trush, S. F., J. E. Hewitt, V. J. Cummings, and P. K. Dayton. 1995. The impact of habitat disturbance by scallop dredging on marine benthic communities: what can be predicted from the results of experiments? *Marine Ecology Progress Series* 129:141–150.
- Trush, S. F., and eight coauthors. In press. Disturbance of the marine benthic habitat by commercial fishing: impacts at the scale of the fishery. *Ecological Applications*.
- Tupper, M., and R. G. Boutilier. 1995. Effects of habitat on settlement, growth, and postsettlement survival of Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences* 52:1834–1841.
- Valentine, P. C., and E. A. Schmuck. 1995. Geological mapping of biological habitats on Georges Bank and Stellwagen Bank, Gulf of Maine region. Pages 31–40 in *Applications of side-scan sonar and laser-line systems in fisheries research*. Alaska Department of Fish and Game, Special Publication 9.

- Van Dolah, R. F., P. H. Wendt, and N. Nicholson. 1987. Effects of a research trawl on a hard bottom assemblage of sponges and corals. *Fisheries Research* 5:39–54.
- Van Dolah, R. F., P. H. Wendt, and M. V. Levisen. 1991. A study of the effects of shrimp trawling on benthic communities in two South Carolina sounds. *Fisheries Research* 12:139–156.
- Walters, C. J., and F. Juanes. 1993. Recruitment limitation as a consequence of natural selection for use of restricted feeding habitats and predation risk taking by juvenile fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 50:2058–2070.
- Watling, L., and E. A. Norse. 1998. Disturbance of the seabed by mobile fishing gear: a comparison to forest clearcutting. *Conservation Biology* 12(6):1180–1197.
- Witbaard, R., and R. Klein. 1994. Long-term trends on the effects of the southern North Sea beamtrawl fishery on the bivalve mollusc *Arctica islandica* L. (Mollusca, bivalvia). *ICES Journal of Marine Science* 51:99–105.
- Witman, J. D. 1985. Refuges, biological disturbance, and rocky subtidal community structure in New England. *Ecological Monographs* 55:421–445.
- Witman, J. D. 1987. Subtidal coexistence: storms, grazing, mutualism, and the zonation of kelp and mussels. *Ecological Monographs* 57:167–187.
- Witman, J. D., and K. P. Sebens. 1985. Distribution and ecology of sponges at a subtidal rock ledge in the central Gulf of Maine. Pages 391–396 *in* K. Rutzler, editor. *New perspectives in sponge biology*. Smithsonian Institution Press, Washington, D.C.
- Witman, J. D., and K. P. Sebens. 1992. Regional variation in fish predation intensity: a historical perspective in the Gulf of Maine. *Oecologia* 90:305–315.
- Witman, J. D., J. J. Leichter, S. J. Genovese, and D. A. Brooks. 1993. Pulsed phytoplankton supply to the rocky subtidal zone: influence of internal waves. *Proceedings of the National Academy of Sciences of the United States of America* 90:1686–1690.