



Disturbance to Marine Benthic Habitats by Trawling and Dredging: Implications for Marine Biodiversity

Author(s): Simon F. Thrush and Paul K. Dayton

Source: *Annual Review of Ecology and Systematics*, Vol. 33, (2002), pp. 449-473

Published by: Annual Reviews

Stable URL: <http://www.jstor.org/stable/3069270>

Accessed: 16/07/2008 00:56

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/action/showPublisher?publisherCode=annrevs>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit organization founded in 1995 to build trusted digital archives for scholarship. We work with the scholarly community to preserve their work and the materials they rely upon, and to build a common research platform that promotes the discovery and use of these resources. For more information about JSTOR, please contact support@jstor.org.

DISTURBANCE TO MARINE BENTHIC HABITATS BY TRAWLING AND DREDGING: Implications for Marine Biodiversity

Simon F. Thrush¹ and Paul K. Dayton²

¹*National Institute of Water and Atmospheric Research, PO Box 11-115, Hamilton, New Zealand; email: s.thrush@niwa.cri.nz*

²*Scripps Institution of Oceanography, University of California, San Diego, La Jolla, California 92093-0201; email: pdayton@ucsd.edu*

Key Words fishing, resilience, habitat structure, bioturbation, benthic-pelagic coupling, biocomplexity

■ **Abstract** The direct effects of marine habitat disturbance by commercial fishing have been well documented. However, the potential ramifications to the ecological function of seafloor communities and ecosystems have yet to be considered. Soft-sediment organisms create much of their habitat's structure and also have crucial roles in many population, community, and ecosystem processes. Many of these roles are filled by species that are sensitive to habitat disturbance. Functional extinction refers to the situation in which species become so rare that they do not fulfill the ecosystem roles that have evolved in the system. This loss to the ecosystem occurs when there are restrictions in the size, density, and distribution of organisms that threaten the biodiversity, resilience, or provision of ecosystem services. Once the functionally important components of an ecosystem are missing, it is extremely difficult to identify and understand ecological thresholds. The extent and intensity of human disturbance to oceanic ecosystems is a significant threat to both structural and functional biodiversity and in many cases this has virtually eliminated natural systems that might serve as baselines to evaluate these impacts.

INTRODUCTION

The marine biota is remarkably diverse. There are well over 50 phyla and only one is strictly terrestrial; all the rest have marine representatives. Interestingly, all these phyla had differentiated by the dawn of the Cambrian, almost 600 million years ago, and all evolved in the sea. Since that time the sea has been frozen, experienced extensive anaerobic conditions, been blasted by meteorites, and undergone extensive variations in sea level. Also during this time the continental shelves have been fragmented, reshuffled, and coalesced in such a way that the biotic communities have been exposed to a wide array of environmental conditions. The present diverse

biota reflects the combination of historical events and present physical, chemical, and biological dynamics. We review structural patterns and functional processes important to the perseverance of this ecosystem and discuss the impact of fishing on these patterns and processes.

Whereas great attention has been paid to the decline in species diversity in terrestrial ecosystems, it is apparent that there have also been substantial changes in diversity in aquatic systems, albeit changes that may not be so readily detected. A common perception of marine seafloor biodiversity reflects a disproportionate interest in hard bottoms such as coral reefs, kelp forests, and the rocky intertidal. This bias is understandable because these hard-bottom communities lend themselves to terrestrial comparisons and ecological studies. However, about 70% of the earth's seafloor is composed of marine soft sediments (Wilson 1991, Snelgrove 1999). These soft-sediment habitats can be highly heterogeneous owing to interactions between broad-scale factors (e.g., hydrodynamic and nutrient regimes) and smaller-scale physical and biological features; nonetheless, the apparent three-dimensional habitat structure imposed by this heterogeneity may not be as obvious as that observed on hard-bottom habitats. Although these habitats do not always appear as highly structured as some terrestrial or marine reef habitats, they do support extremely high species diversity (Etter & Grassle 1992, Grassle & Maciolek 1992, Coleman et al. 1997, Gray et al. 1997, Snelgrove 1999). In fact, the organisms that inhabit the sediments create much of the structure in soft-sediment habitats, ranging from the micro-scale changes around individual animal burrows to the formation of extensive biogenic reefs.

As well as adding substantively to the variety of species found on earth, soft-sediment marine organisms have functional roles crucial to many ecosystem processes. The provision of protein for human consumption and the ecosystems that sustain fisheries are clear examples of the products and functions of marine ecosystems that benefit humankind. Other processes in which marine benthos play important roles include their influence on sediment stability, water column turbidity, nutrient and carbon processing, and contaminant sequestering, as well as the provision of pharmaceuticals and nutraceuticals and recreational and amenity values.

There is now good evidence that commercial fishing has a profound effect on marine ecosystems. Although there is a long history of concern about the environmental effects of fishing (Graham 1953, de Groot 1984), it is really only in the past decade or two that ecological research efforts have focused in this arena. In turn this focus has spawned a number of review articles and books that summarize and synthesize the environmental effects of fishing (Dayton et al. 1995, Auster & Langton 1999, Jennings & Kaiser 1998, Watling & Norse 1998, Hall 1999, Kaiser & de Groot 2000). This information has informed the debate over fisheries management and marine conservation, but it also highlights both the challenges and opportunities to test our current understanding of interactions between broad-scale habitat disturbance to seafloor communities and the functioning of benthic ecosystems.

In this review we place studies of the environmental effects of fishing into the context of direct and indirect effects on marine biodiversity. We consider biodiversity to have both structural and functional components. The distribution and abundance patterns of landscapes, habitats, communities, populations, and genotypes form the structural component of biodiversity. Functional components involve mechanisms that drive interactions between species themselves and between them and other components of the environment, as well as other processes generating fluxes of energy and matter. We consider impacts on community structure and physical changes in habitat structure along with functional changes to seafloor ecosystems (benthic-pelagic coupling, nutrient recycling, and biogeochemical processes). Our aim is not to review the literature that addresses the issues of fisheries, marine biodiversity, and the spatial and temporal scales of ecosystem resilience, but to draw together ecological processes and fishing impacts to focus attention on new and integrative research directions.

Scale-Dependant Disturbance

Disturbance regimes play a key role in influencing biodiversity (Connell 1977, Huston 1994). In marine benthic habitats small-scale natural disturbance plays an important role in influencing communities by generating patchiness (Dayton 1994, Hall et al. 1994, Sousa 1984). Many of the small-scale disturbances that impact benthic communities and generate heterogeneity result from the biological activities of organisms that live in or feed on the seafloor. The spatial heterogeneity created by local disturbance events can account for resource patchiness (Thistle 1981, Van Blaricom 1982), and ubiquity of opportunistic species in soft-sediment habitats. Such heterogeneity is an important component of the functioning of ecological systems (Kolasa & Pickett 1991, Legendre 1993, Giller et al. 1994) and has implications for the maintenance of diversity and stability at the population, community, and ecosystem levels (e.g., De Angelis & Waterhouse 1987, Pimm 1991, Loehle & Li 1996).

The fact that natural disturbance is important to soft-sediment communities has led to the suggestion that fishing disturbance can positively effect biodiversity. This application of Connell's (1977) intermediate disturbance hypothesis is not appropriate because this hypothesis is predicated on disturbance as a means of reducing resource monopolization such that diversity is enhanced. Direct competition for food or space, however, has been difficult to demonstrate as an important process in soft sediments, especially over broad spatial scales (Olafsson et al. 1994, Peterson 1979, Wilson 1991). Theoretical consideration of the intermediate disturbance hypothesis demonstrates that the effects of disturbance on multitrophic level systems can, in many situations, have no effect on the coexistence of competitors, as necessitated by the hypothesis, or may even cause a monotonic decline in diversity (Wootton 1998). Furthermore, the intermediate disturbance hypothesis has not been adequately tested over broad spatial scales relevant to fishing disturbance. Thus its application across species, community and habitat types, and over various scales of disturbance and recovery is unfounded.

Spatial heterogeneity in community structure is related to the spatial extent and/or the frequency of disturbance events; for disturbance to create patchiness it must be small relative to the colonization potential of the benthic community, but not so small as to enable the adjacent assemblage to quickly infill the disturbed patch. This concept is encapsulated in a simple ratio-based model of the effect of disturbance on landscapes (Turner et al. 1993). The temporal dimension is considered by the ratio of disturbance interval (time between events) to recovery time, and the spatial dimension is considered by the ratio of size of the disturbed area to size of the habitat. The model simplifies many of the complexities of disturbance-recovery dynamics and the potential for recovery processes to change with scale in a nonlinear fashion. Nevertheless, consideration of these ratios indicates disturbance regimes that, through their frequency, extent, or intensity, could result in catastrophic change across the seafloor landscape. Even such a simple model emphasizes the need to understand the scales of mobility and the processes affecting successful establishment and growth of potential colonists. Typically in soft sediments a wide array of species and life stages are involved in recovery processes within a disturbed patch (Zajac et al. 1998, Zajac 1999, Thrush & Whitlatch 2001, Whitlatch et al. 2002). The ratio model implies that significant threats to the integrity and resilience of marine benthic communities arise when the rate of human-induced change exceeds the rate at which nature can respond. This is particularly likely to occur where habitat structure and heterogeneity are reduced and large areas of habitat have been modified. Slow-growing and -reproducing species will be strongly affected, vastly reducing the potential for such species to reestablish themselves or colonize new areas. The homogenization of habitats and the loss of small-scale patchiness result in the risk of the loss of ecological function and natural heritage values in marine ecosystems.

Fishing as a Disturbance Agent on the Seafloor

Many types of trawls, dredges, and traps are dragged over or sit on the seafloor (Jennings & Kaiser 1998). The type of physical impact the fishing gear has on the seafloor depends on its mass, degree of contact with the seafloor, and the speed at which it is dragged. The way the gear is designed and operated also influences how it interacts with the seafloor and how many species other than the target species the gear removes from the seafloor or damages *in situ* (i.e., by-catch). Not all types of gear are used in all locations, and the impact of the gear depends on the habitat in which it is used.

Unfortunately there are limited data on the location and frequency of the area of the seafloor swept by fishing gear. The data available usually are based on broad-scale fisheries management units and not necessarily related to the spatial variation in seafloor habitats or biodiversity. For example, Churchill (1989) summarized trawling effort off the Middle Atlantic Bight, an area of intensive fishing pressure. The range of effort was quite variable along the coast because fishers do not work where there are no fish, but some areas off southern New England were on average

exposed to 200% effort. Another typical fishery in northern California trawled across the same section of seafloor an average of 1.5 times per year, with selected areas trawled as often as 3 times per year (Friedlander et al. 1999). For a scampi fishery on the continental slope off New Zealand (200–600 m water depth), Cryer et al. (2002) calculated that on average about 2100 km² of the seafloor was swept each year by trawlers. The statistics suggest that within the study area trawlers swept about 20% of the upper continental slope each year, although about 80% of all scampi trawls were made in an area of about 1200 km². In some areas the extent and frequency of disturbance can be extreme, Pitcher et al. (2000) identifies one harbor in Hong Kong where every square meter of the seafloor was trawled three times a day. The ecological intensity of response is also determined by the resident species; even low-intensity disturbance can significantly affect sensitive species (Jenkins et al. 2001). The spatial distribution of fishing effort on the seafloor is patchy, reflecting the relative availability of the target species. In some cases refining the scale of measurement reveals higher levels of aggregation of fishing effort (e.g., Pitcher et al. 2000). Actually, we really do not know the global extent of disturbance to the seafloor by fishing. However, the magnitude of exploitation of global fishery resources provides some important clues as to the general extent of disturbance, with about 25–30% of the world's fishery populations overexploited or depleted and a further 40% considered heavily to fully exploited (Pauly et al. 1998). Often the scales of measurement of fishing effort (e.g., tens to hundreds of square kilometers) are difficult to match with ecological effects, as they do not match well with the scales of variability in seafloor ecological communities.

Evaluating the Direct Effects of Habitat Disturbance by Fishing

Many studies have been conducted to assess the direct effects of habitat disturbance by trawling or dredging on benthic communities (Table 1). These studies have been conducted in a variety of habitats and locations, generally in shallow water. We have reviewed a large number of these studies to offer examples from a variety of habitats and locations, rather than attempt a complete list. Our aim is to provide a brief summary of the range of effects observed. We hope this list, as well as previously mentioned reviews, offer the reader an entrée into this literature. There are a number of important issues to consider when summarizing such a diverse array of studies because they encompass a range of intensities and spatial and temporal scales of fishing disturbance. Study designs and assessment approaches are also widely different. We have summarized statistically significant or nonsignificant effects described in the individual papers but refer the reader to Loftis et al. (1991) and Nelder (1999) for comments on "significance." We recommend that readers study papers of interest in detail to assess for themselves the magnitude of ecological effects.

Marine benthic ecosystems are often challenging systems to study, and precise data are rare. Furthermore, the interpretation of results is frequently difficult. For

TABLE 1 Summary of effects on subtidal benthic communities reported in recent assessments of fishing impacts

Effects	Habitats/depths/location	Source
Removal of biogenic and physical habitat structure	Sand, 30 m depth; Northwest Atlantic	Auster et al. 1996
Decreased diversity in trawled plots	Mud, 75 m depth and heavily trawled; 35 m less frequently trawled; Irish Sea	Ball et al. 2000
Decreased density of common echinoderms, polychaetes, and molluscs	Sand, 30 m depth; North Sea	Bergman & Hup 1992
Direct mortality of 5–60% for species following single passage of trawl	Sand/mud, 10–45 m depth; North Sea	Bergman & van Santbrink 2000
Decreased number of organisms, biomass, species richness, species diversity, and biogenic habitat structure	Gravel pavement, 40–80 m depth; Georges Bank; Northwest Atlantic	Collie et al. 1997
6 of 10 common species decreased in abundance	Sand/coarse silt, 10–20 m depth; Port Phillip Bay, Vic., Australia	Currie & Parry 1996
No consistent trends in epifauna or infauna; high site-to-site variability	Sand/coarse silt, 10–20 m depth; Port Phillip Bay, Vic., Australia	Currie & Parry 1999
Decreased abundance of large epifauna and infaunal species abundance	Sand, 10 m depth; Loch Ewe, Scotland	Eleftheriou & Robertson 1992
Higher densities of epifauna in lightly trawled area; higher densities of predator/scavenger worms in heavily trawled area	Sand, 180 m depth; central California	Engel & Kvitek 1998
Large epifauna removed and damaged; boulders displaced	Pebble/cobble/boulder, 200 m depth; Gulf of Alaska	Freese et al. 1999
Temporal trends in community composition differentiate under heavy fishing pressure	Mud, 80 m depth fished and 50 m unfished sites; North Sea	Frid et al. 2000
No detectable changes in macrobenthic fauna	Sand, 10 m depth; Botany Bay, NSW, Australia	Gibbs et al. 1980
Overall decreases in biomass and abundance, but site and time interaction terms make detection of effect difficult	Mud, 73–96 m depth; Gullmarsfjord, Sweden	Hansson et al. 2000
70% reduction of mearl ^a habitat over 4 years	Sand/mud, 6–15 m depth; Firth of Clyde, Scotland	Hall-Spencer & Moore 2000

(Continued)

TABLE 1 (Continued)

Effects	Habitats/depths/location	Source
No significant effects on biomass or production in area of low fishing pressure; under high fishing pressure, significant decrease in biomass and production	High impact site muddy sand 55–75 m depth, low impact site sand 40–65 m; North Sea	Jennings et al. 2001a
Decrease in infaunal and epifaunal biomass, particularly bivalves and burrowing urchins, only detected at high impact site	High impact site muddy sand 55–75 m depth, low impact site sandy 40–65 m; North Sea	Jennings et al. 2001b
Decrease in density of epifauna and diversity in stable sand habitat; no effects detected in unstable sand habitat	2 habitats: one stable sand with rich epifauna, the other mobile sand, 26–34 m depth; Anglesey Bay, Irish Sea	Kaiser & Spencer 1996
Slight changes in community composition in stable habitat; no detectable effects on a number of species or diversity indices in either habitat	2 habitats: one stable sand with rich epifauna, the other mobile sand, 26–34 m depth; Anglesey Bay, Irish Sea	Kaiser et al. 1998
Larger individuals and increased density of epifauna in unfished area	Sand, 18–69 m depth; English Channel	Kaiser et al. 1999
Loss of sessile, emergent, high biomass species, increase in small-bodied infauna	Gravel/sand; Isle of Man, Irish Sea ^b	Kaiser et al. 2000
No effect detected	Sand, 120–146 m depth; Grand Banks of Newfoundland	Kenchington et al. 2001
Trawl reduced density of large epifauna about 15% on each pass; trawl flown 15 cm above seafloor had no detectable impact on large epifauna	50 m depth ^c ; north-west shelf, Australia	Moran & Stephenson 2000
Higher diversity in unfished area; sedentary macrofauna more abundant in unfished sites; mixed response by motile species and infaunal bivalves	Sand, 44–53 m depth; eastern Bering Sea	McConnaughey et al. 2000
Trawls typically removed 5–20% of large benthic fauna	Sand ^b , Great Barrier Reef Region, Australia	Pitcher et al. 2000
Short-term decreases in biomass and abundance of macrofauna; number of taxa showed no immediate effect but increased in trawled area after 7 days	Sand, 24 m depth; Adriatic Sea	Pranovi et al. 2000

(Continued)

TABLE 1 (Continued)

Effects	Habitats/depths/location	Source
Decrease in epifaunal biomass following disturbance; no significant impacts on dominant molluscs	Sand, 120–146 m depth; Grand Banks of Newfoundland	Prena et al. 1999
Decrease in species richness and diversity	Mud, 30–40 m depth; Catalan coast	Sanchez et al. 2000
Decrease in small-scale heterogeneity of sediment texture after trawling	Sand, 120–146 m depth; Grand Banks of Newfoundland	Schwinghamer et al. 1996
Higher numbers of epifauna and diversity, abundance, and biomass of macrofauna outside trawled area	Mud, 200 m depth; Crete	Smith et al. 2000
Changes in community structure, decreased density of common bivalves and polychaetes, increased density of nemerteans	Mud, 60 m depth; Penobscot Bay, Maine	Sparks-McConkey & Watling 2001
Density decreased, effects on number of taxa detected at one site only	Sand, 24 m depth. Mercury Bay, New Zealand	Thrush et al. 1995
Fishing decreased density of burrowing urchins, long-lived surface dwellers, and diversity and increased density of deposit feeders and small opportunists	Varied sediments 1–48% mud, 17–35 m depth; Hauraki Gulf, N.Z.	Thrush et al. 1998
Numbers of species, individuals, and various diversity indices increased in fished area	Mud, 30–35 m depth; Gareloch, Scotland	Tuck et al. 1998
Barrel sponges (<i>Cliona</i>) significantly reduced in abundance but recovered in 12 months	Low relief hard-bottom habitat, 20 m depth; Georgia	Van Dolah et al. 1987
No detectable effect of trawling	Sand, Port Royal (8 m depth) and St. Helena (30 m depth) sounds, S. Carolina	Van Dolah et al. 1991
Species diversity, richness, total number of species decreased with increased fishing effort	Sand, 20–67 m depth; north Irish Sea	Veale et al. 2000
Decrease in numerical dominants and changes in sediment food quality	Silty sand 15 m depth. Damariscotta River, Maine	Watling et al. 2001

^asediments with a surface layer of slow-growing unattached coralline algae.

^bdepth not given.

^csediment type not given.

example, Pitcher et al. (2000) documented the removal of 7 tonnes of epifaunal biomass during experimental trawling, but were unable to detect significant changes by surveying the density of epifauna on the seafloor. Whereas the direct effect of such an impact on benthic communities appears obvious, its magnitude has been difficult to evaluate with regard to other components of the ecosystem. There is often a failure to detect the effect of experimental fishing disturbance in areas exposed to extreme natural disturbance to the seafloor (e.g., storms or very strong tidal flows) (Hall et al. 1990, Brylinsky et al. 1994, Kaiser & Spencer 1996, DeAlteris et al. 1999). Effects are not always consistent across sites, even within studies. Given the variety of experimental designs and habitats studied, these variations in response are far from surprising. Nevertheless these studies emphasize a number of changes in benthic communities including loss of habitat-structuring species, changes in species richness, and loss of large and long-lived organisms.

One of the most conspicuous long-term physical effects of bottom fishing is the homogenization of the substratum and reduced species diversity (Veale et al. 2000). Thus, apart from all the usual difficulties of study design, the history of fishing disturbance can make it impossible to control experimental studies. Some European and Adriatic waters have a long history of fishing by bottom trawling (de Groot 1984, Kaiser & de Groot 2000, Pranovi et al. 2000). Frid et al. (2000) considered reports from the North Sea going back to the 1920s and concluded that fishing practices have changed benthic communities in some parts of the North Sea; in other areas fishing impacts could not be evaluated without a longer time series of data. Aronson (1989, 1990) argued that overfishing has virtually eliminated the evolutionarily new teleost predators, resulting in a rebirth of the Mesozoic-like system dominated by echinoderms and crustacea. Recent analyses of fish predation in the North Sea provide some support for this view (Frid et al. 1999). There is also a long history of transformation of marine coastal ecosystems in the western Atlantic (Steele & Schumacher 2000, Jackson 2001) and eastern Pacific (Dayton & Tegner 1984, Dayton et al. 1998). There are few, if any, unfished habitats with economically exploitable stocks outside the Antarctic region (Dayton et al. 2000). Human disturbances that exceed the rate of natural recovery dynamics have been underway for decades and possibly centuries. Some marine organisms have been driven to extinction by human activities (e.g., the Atlantic gray whale, the great auk). Others are probably close to extinction, for example, the Irish ray (Brander 1981), the barndoor skate (Casey & Myers 1998), and the white abalone (Tegner et al. 1996). A recent review listed 82 species and subspecies of endangered fish in the United States (Musick et al. 2000). Over time, repeated intense disturbance will select for species with appropriate facultative responses, and communities are likely to become dominated by juvenile stages, mobile species, and rapid colonists. Such broad-scale descriptions point to the problem of identifying effects in ecological systems that are potentially already affected. The important point is that the potential for both direct and indirect effects on biodiversity cannot be ignored because of variability in ecological response across such a diverse array

of studies. As always, manipulative experiments are useful but difficult to control properly and limited in scope.

The broader-scale implications of fishing impacts have been inferred from benthic surveys and time-series data (Reise 1982, Holme 1983, Langton & Robinson 1990, Cranfield et al. 1999, Kaiser et al. 2000). One valuable approach to integrating experimental results into broader-scale patterns is to develop iterative procedures and test *a priori* hypotheses with data collected over broad scales. This process can provide good evidence of large-scale change (Thrush et al. 1998). The use of effort data in the rapidly expanding trawl fisheries of the eastern Bering Sea enabled McConnaughey et al. (2000) to contrast areas with different exposure to fishing disturbance and investigate the long-term consequences for benthic communities. They found that the numbers of sedentary epifauna (animals such as anemones, soft corals, sponges, bryozoans, etc.) and diversity and the niche breadth of sedentary taxa decreased with fishing. Mixed patterns of response were apparent for mobile epifauna and infaunal bivalves, suggesting species-specific responses based on life-history characteristics. It is important to note that the clear changes recorded in this study were documented in an area with a high potential for storm-generated wave disturbance, emphasizing the value of carefully designed and analyzed assessments.

The Potential for Functional Changes in Biodiversity

The studies described above provide evidence for direct changes in response to habitat disturbance by fishing, but we must also consider the potential for changes in the functional roles played by organisms, communities, and ecosystems. Usually, as density declines the size of the individuals and their spatial distribution also change; thus, although not biologically extinct, they may be functionally so, being unable to fulfill their natural roles in community and ecosystem function (Dayton et al. 1998).

In soft-sediment habitats the creation of small-scale habitat structure by biogenic features can play key roles in influencing diversity and resilience. Some benthic fishes, such as rays, have an important influence on small-scale habitat structure (Van Blaricom 1982, Levin 1984, Thrush et al. 1994). Organisms that live at the sediment surface or create mounds, tubes, and burrows within it also provide habitat structure and frequently have important roles in the sequestering and recycling processes essential to ecosystem function. Studies listed in Table 1 provide evidence of direct effects on the density and distribution of such organisms; in some cases they are the most susceptible to habitat disturbance by dredging and bottom trawling. As yet, however, there have been no direct assessments of the implications of the loss of these functionally important species to ecosystem function and resilience.

Alteration to marine food webs through changes in the abundance and size distribution of fish populations could have important consequences for benthic communities. Many types of fish prey upon and disturb the seafloor; all rays and

some sharks and bony fishes that make up many important demersal fisheries (e.g., sparids, scorpaenids, labrids, gadoids, pleronectids) are important benthic predators, although their wider ecological role is rarely studied (but see Sala & Ballesteros 1997). Many fishes have life-history characteristics that make them extremely vulnerable to over exploitation, thus highlighting the potential for the role of these animals to be diminished. Jennings et al. (1999) examined long-term trends in the abundance of North Sea demersal fishes and demonstrated that those species that decreased in abundance compared with their nearest relative matured later, grew larger, and had a lower potential for rapid population increase. Many important demersal fish stocks (gadoids, sparids, pleronectids, and scorpaenids) appear to show limited recoverability after over exploitation (Hutchings 2000). We do not have a good understanding of the role of broader community- and ecosystem-level processes in the resilience of fish stocks.

Declining density of a species is usually associated with reductions in both the geographic distribution and the size of individuals. Steele & Schumacher (2000) discussed the implications for marine food webs of historic fish stocks in the Northwest Atlantic possibly being an order of magnitude higher than stocks in the last half of the twentieth century. Density changes of this magnitude could result in a profoundly altered ecosystem. For example, in the Gulf of Maine, the removal of top fish predators through intensive fishing apparently released other predators such as crabs and starfish, thus changing the benthic communities (Witman & Sebens 1992, Steneck 1997). Frid et al. (1999) also provide an example that links changes in the abundance of fish to changes in benthos: Changes in fish biomass in the North Sea appear to have resulted in changes in the taxonomic composition of benthos consumed by fish and an overall increase in predation pressure on benthos. However, such effects are difficult to identify without extensive study; tracking effects through marine foodwebs is difficult because of the inherently complex interactions and weak and indirect effects (Micheli 1999).

Fishing can also directly alter the physical habitat by influencing sediment particle size, resuspension regimes, and biogeochemical flux rates (Churchill 1989, Currie & Parry 1999, Mayer et al. 1991, Palanques et al. 2001). Sediment quality is important because of the intimate relationship between particle size and benthic community structure and function (Gray 1974, Rhoads 1974, Whitlatch 1980, Snelgrove & Butman 1994). One study found significant declines in some organisms (70% for scallops and 20–30% for burrowing anemones and fan worms) owing to a scallop-fishing-induced shift in sediment (organic-rich silty sand to sandy gravel with shell hash) (Langton & Robinson 1990). Caddy (1973) also documented the smothering of suspension feeders as a result of sediment resuspended by fishing. Other effects include modifications to microbial activity (Mayer et al. 1991, Watling et al. 2001), resuspension of contaminants, and increases in benthic/pelagic nutrient flux (Krost 1990). Trawling-induced resuspension of sediments in the Gulf of Maine has been hypothesized to have changed the nature of nutrient supply from the seafloor with potentially ecosystem-wide consequences on phytoplankton growth (Pilkaln et al. 1998).

Habitat-Structuring Organisms, Functions, and Biodiversity

Interactions between hydrodynamic conditions and the benthic habitat drive many of the important processes occurring at the sediment-water interface. The increased drag created by structures protruding into the near-bed water flow and active feeding currents generated by suspension feeders influence localized rates of erosion and deposition (Eckman & Nowell 1984, Frechette et al. 1989, Shimeta & Jumars 1991, Dame 1993, Wildish & Kristmanson 1997). Common benthic suspension feeders include a diverse array of corals, bryozoans, sponges, gorgonians, seapens, echinoderms, brachiopods, and bivalves. Patches of these organisms can further modify hydrodynamics over a wide range of spatial scales, significantly influencing both the vertical and horizontal flux of food and larvae at the seafloor. Both the size of the organisms and the patch are important factors influencing these interactions (Green et al. 1998, Nikora et al. 2002). Bivalves expend high levels of energy drawing water over their gills to feed (Rhodes & Thompson 1993). Thus, suspension-feeding bivalves are capable of actively removing 60–90% of the suspended matter from the horizontal particle flux (Loo & Rosenberg 1989). These bivalves package any particles that are unsuitable for ingestion in mucous and eject them as pseudofeces, thus appreciably influencing the rate of particle deposition to the seafloor (Graf & Rosenberg 1997). These processes create variation in seafloor ecosystems and add to their biodiversity (Cummings et al. 2001, Norkko et al. 2001).

Organisms that live at the sediment surface, as well as the small-scale disturbances created by benthic-feeding predators, can also increase the three-dimensional structure of the habitat. For example, small heterogeneities in sediment topography (e.g., tubes and burrows) and even sparsely distributed epifauna characterize most soft-sediment habitats. Such structure at the sediment-water interface, along with variations in sediment particle size, is positively related to macrobenthic diversity (Thrush et al. 2001). Spatially these small-scale features are often highly variable (e.g., Schneider et al. 1987) and can be important to commercially valuable species (Auster et al. 1995). The sheer vastness of the area covered by such habitats results in an important role for these small-scale features in biogeochemical processes and species and habitat diversity, and it is these elements that are most susceptible to habitat disturbance by dredging and bottom trawling.

Highly structured habitats can provide refuges for both predators and prey. Many studies show significant variations in predator-prey interactions associated with variations in habitat complexity (e.g., Woodin 1978, Ruiz et al. 1993, Irlandi 1994, Skilleter 1994). Habitat structure influences predation rates on fish, particularly juvenile life stages (e.g., Heck & Thoman 1981, Persson & Eklov 1995, Rooker et al. 1998). Topographic complexity can have a significant and positive influence on the growth and survivorship of juvenile life stages of commercially valuable species, often as a result of reduced risk of predation (Tupper & Boutilier 1995, Lindholm et al. 1999). On the Australian northwest shelf, Sainsbury (1988) showed a decrease in the number and variety of epifauna, particularly sponges, collected

over time as by-catch. This reduction was associated with shifts in the fishery from high- to low-value species. A probable explanation was a positive role for epifauna in affecting the survivorship of the commercially valuable fish species. In many cases the habitats damaged by trawling probably constitute very important nursery areas for many species, often including some of the target species of fisheries (Turner et al. 1999).

The importance of habitat-structuring organisms is not restricted to shallow water because shelf-break and seamount habitats can exhibit marvelous levels of habitat complexity generated by biogenic structure. Even the deep-sea basins once considered constant and uniform exhibit high levels of both local biogenic complexity (e.g., Jumars & Eckman 1983, Levin & Gooday 1992) and regional diversity (Levin et al. 2001). Improved technologies and the demand for fish are opening up deep-water habitats to exploitation. Cryer et al. (2002) provide empirical evidence of the large-scale effects of trawling on a deep-water soft-sediment system by demonstrating substantive decreases in the diversity of large benthic invertebrates associated with a continental slope (a depth of 200–600-m) scampi (*Metanephrops challengeri*) fishery. This result emphasizes that the impacts on seafloor communities that have been more readily documented in shallower water are also occurring in deeper water. In these environments effects on biodiversity are likely to be exacerbated because deep-sea communities are generally characterized by life-history adaptations such as slow growth, extreme longevity, delayed age of maturation, and low natural adult mortality, and they exhibit slow rates of recovery from disturbance.

Deep-water corals occur in the upper bathyl zone throughout the world and are under threat from human activity, particularly fishing and oil exploration (Roberts et al. 2000, Rogers 1999). The biology of most of these deep-water coral species is unknown, but they appear to have exceptionally slow growth and low reproductive rates, with individual colonies being hundreds to thousands of years old (e.g., Druffel et al. 1995). These thicket-forming corals are often associated with a diverse fauna, and levels of diversity appear to be similar to those of shallow water tropical coral reefs. Squires (1965) reports the first detection of a deep-water coral structure in the Pacific, at a depth of 320 m on the Campbell Plateau. These coral structures generated about 40-m-high relief on the seafloor. *Lophelia pertusa* is a deep-water coral that occurs in discrete patches hundreds of meters to several kilometers in diameter, and up to 45 m high. Off Norway and the Faeroe Islands *Lophelia* reefs have several hundred species in association, and with the exception of small areas off Norway, most have been heavily damaged (Roberts 1997).

Seamounts too have been the focus of intensive deep-water fisheries. In the southern hemisphere these fisheries were usually initiated to capture orange roughy (*Hoplostethus atlanticus*). When the New Zealand fishery targeting spawning aggregations of orange roughy began, the trawls brought up a great deal of benthic by-catch, but these levels decreased with repeated trawling (Probert et al. 1997). For the orange roughy fishery on seamounts off Tasmania, Koslow et al. (2001)

report tonnes of coralline material brought to the surface in a single trawl when fishing a new area. Surveys confirmed characterizations of changes in benthic communities based on by-catch (de Forges et al. 2000, Koslow et al. 2001). These authors report at least 299 species from a single short seamount cruise near Tasmania; 24–43% of these were new to science. The benthic biomass from fished seamounts was 83% less than from lightly fished or unfished habitats.

Fluxes, Ecosystem Effects, and Biodiversity

Sediments play important roles in transformation and exchange processes of organic matter and nutrients. For example, sediments on marine continental shelves, while occupying only 7% of the area of the planet covered by marine sediments, are responsible for 52% of global organic matter mineralization. Slope sediments (i.e., 200–2000-m depth, 9% area) remineralize another 30% (Middleburg et al. 1997). These disproportionately large contributions to organic matter mineralization reflect the importance of biological activity within marine sediments influencing solute and particle transport. By enhancing the transport of labile particulate organic carbon to subsurface layers within the sediment, organisms stimulate anaerobic degradation and so affect the form and rate at which metabolites are returned to the water column (Herman et al. 1999). The seas above continental shelf environments typically receive one third to half their nutrients for primary production from sediment (Pilskaln et al. 1998). These nutrients are derived from organic matter decay and nutrient remineralization within the sediments, followed by molecular diffusion or biological irrigation back into the water column. The process of sediment manipulation by resident animals (i.e., bioturbation) is the dominant mode of sediment transport in the upper centimeters of oceanic sediments (Middleburg et al. 1997). Solute pumping, burrowing, and feeding increase the area of the sediment-water interface (Aller 1982). Bioturbation affects the stability and composition of marine sediments and influences their role as geochemical sources and sinks (McCall & Tevesz 1982, Marinelli 1994, Bird et al. 1999). Thayer (1983) extensively reviewed estimates of the rate of bioturbation for a wide variety of marine organisms, with rates of sediment reworking ranging from 5×10^{-5} to $2.1 \times 10^6 \text{ cm}^3 \text{ day}^{-1}$ per individual and depths to which sediment was reworked ranging from 0.1 to 400 cm. Larger organisms play a particularly important role in influencing sediment-reworking rates (Thayer 1983, Sandnes et al. 2000). Typically animals increase the particle exchange between water and sediment by a factor of 2 to 10 (Graf 1999).

Direct disturbance of the seafloor enhances the upward flux of nutrients by releasing pore-water nutrients as a pulse, rather than a more steady release controlled by bioturbation (Pilskaln et al. 1998). Fanning et al. (1982) estimated that a storm that imposed sufficient energy on the seafloor to resuspend the top 1 mm of sediment could intermittently augment overlying productivity by as much as 100–200%. This depth of sediment disturbance is much less than what occurs as a result of many types of trawling and dredging. Dredges usually disturb the top 2–6 cm of

sediment, while the doors that hold open trawl nets in the water can plough furrows from 0.2–2 m wide and up to 30 cm deep in the sediment (e.g., Caddy 1973, Jennings & Kaiser 1998, Krost 1990). However, it is not appropriate to equate storm disturbances with fishing because the latter may involve a much higher intensity of disturbance, although its frequency and extent will be highly location dependent.

The rate and efficiency of bioturbation processes are determined by interactions between organisms and between the organisms and their environment. The degree of particle flux enhancement varies with faunal composition and density (Cadee 1979, Thayer 1983) in conjunction with organic carbon flux to the sediment (Legeleux et al. 1994). Interactions between bioturbation and mineralization processes in sediments are highly nonlinear and are characterized by the presence of strong feedback loops between deposit feeders, their food, and their chemical environment (Herman et al. 1999). Variation in large burrow structures and animal activity can result in markedly different biogeochemical fluxes, in terms of both rates and chemicals (Hughes et al. 2000). As well as influencing water column production, bioturbation can also affect the growth of benthic species that use this resource (Weinberg & Whitlatch 1983). Deposit-feeding typically controls the biological mixing of near-shore and, probably, deep-sea sediments. Soetaert et al. (1996) measured and modeled the total flux of ^{210}Pb entering the sediment (used as a marker of particle transport) along a transect from 208–4500 m over the Goban Spur in the northeast Atlantic. Their analysis showed that between 8 and 86% of the particle flux was derived from nonlocal exchange processes (i.e., active pumping/flow through burrows), with these processes most important in shallower waters where trawling is most intense.

Apart from burrowing and actively pumping water and particles through burrows, animals can also influence fluxes by modifying surface sediment topography, which then interacts with sediment boundary water flows. Huettel et al. (1996) demonstrated how shrimp mounds protruding from sandy sediments can alter flow patterns to increase the flux of fine particulate matter into the sediment. Small pressure gradients generated by boundary flow–topography interactions also increase the flux of oxygenated water into the pore waters of sandy sediments, thus increasing the oxic volume of the sediments and affecting biogeochemical processes (Forster et al. 1996, Ziebis et al. 1996).

From these studies it is clear that bioturbation is important in ecosystem functioning. There is some evidence that bioturbation has been a significant factor influencing the evolution and enhancement of marine biodiversity over geological time scales. Regeneration of nitrogen from the seafloor may exceed inputs from freshwater in the coastal zone (Rowe et al. 1975). The faster recycling of nutrients by increased rates of bioturbation over evolutionary time scales may have contributed to the diversity of phytoplankton and zooplankton in the Mesozoic (Thayer 1983). Martin (1996) contends that elevated nutrient levels associated with increased rates of ocean circulation, continental erosion, and bioturbation have played a key role in enhancing the productivity and diversity of marine systems over the Phanerozoic (i.e., essentially post-Precambrian).

Implications for Research and Biodiversity Management

We have tried to synthesize the effects of fishing disturbance on the biodiversity of the seafloor by reviewing studies of direct effects and discussing the functional roles of soft-sediment organisms. In doing this we have summarized immediate effects that include changes in species diversity and ecosystem processes, habitat modification, and loss of predators. Because of the high variability within and between studies, there is no single definitive study that adequately describes the range of impacts of fishing disturbance. Nevertheless, there is evidence of effects on seafloor communities that have important ramifications for ecosystem function and resilience.

Whereas gathering good data on the magnitude and extent of disturbance at appropriate spatial scales is important, from both a scientific and management perspective, we have moved beyond the question of what the immediate effect of habitat disturbance by fishing is and now need to focus on the implications of loss of structural and functional biodiversity over various space and timescales. Pitcher (2001) argues that the only hope for fisheries themselves is to move their management to a focus on ecosystem rebuilding. He contends that the goal of sustainable yield of single species in a fishery is a fundamental mistake. The potential for the change in functionally important ecosystem processes leads us to ask very broad questions and test the generality of many fundamental theories. The themes of scale, complexity, resilience, and strong coupling of physical and biological processes in marine benthic ecosystems are pervasive.

We have emphasized the functional roles of marine benthic organisms. To develop this theme further we need a much better understanding of the basic ecology of these species, how their ecosystem roles may be modified by their size, density, and spatial arrangement, and how these characteristics enable them to cope with disturbance. The integration of small-scale variation into broader patterns is important because we should expect threshold effects and nonlinearities in the multispecies biotic and environmental processes that create biodiversity. For example, differences in density and species among a functionally similar group of bioturbators can result in different effects on biodiversity (Widdicombe & Austen 1999, Widdicombe et al. 2000). The potential for different responses of macrobenthic assemblages to the presence of a large epifaunal bivalve under a number of different physical regimes and local species pools has also been demonstrated (Cummings et al. 2001). We must use natural history and environmental information to both design and interpret mechanistic studies because responses are usually scale dependent (Thrush et al. 1999). Standing back from the detail and looking for more general and abstract patterns also provides a basis for revealing emergent phenomena (Brown 1995).

Natural systems have a great deal of structure in time and space, and it is important to identify thresholds of change in this structure and the processes it influences to gauge ecosystem resilience. This means that our predictions of the ecological consequences of human activity in the marine environment require an

understanding of broad-scale forcing functions as well as knowledge of the natural and life-history characteristics of individual species. The removal of small-scale heterogeneity associated with the homogenization of habitats is, by definition, loss of biodiversity. We argue this is important even over the extensive sand- and mud-flats of the seafloor that are often considered "featureless." Spatial mosaics that result from local biological disturbance events, as well as the organisms that create them, can be obliterated by intense broad-scale disturbances. There are winners and losers in the ecological response to any disturbance, but a key issue is understanding ecological heterogeneity and its role in modifying the consequences of habitat disturbance to ecosystem processes. We need to better understand the implications of natural and anthropogenic habitat fragmentation and how it relates to the intensity and frequency of disturbance. Empirical and theoretical studies addressing this issue will need to integrate biogeochemistry, hydrodynamics, and ecology. Site history and the effect of multiple stresses will be particularly important in many areas in order to address the role of the resident species assemblage and environmental context in affecting disturbance-recovery dynamics in fragmented habitats. Once the functionally important components of an ecosystem are missing, it is extremely difficult to identify and understand ecological thresholds that are violated beyond the point of recovery, at which point the anthropogenic disturbances are less obvious. Some knowledge of these issues will be necessary to address the more fundamental question, "At what point are there ecosystem thresholds beyond which recovery is unlikely?" Ecological systems can shift into alternative states as a result of the loss of ecosystem functions, and we must be able to assess the consequences of these shifts in terms of loss of diversity and ecological services (e.g., Carpenter et al. 1999, Scheffer et al. 2001).

ACKNOWLEDGMENTS

We dedicate this review to the memory of Mike Mullin and Mia Tegner for their deep concern for fisheries and related conservation issues. We thank Judi Hewitt, Vonda Cummings, and Bob Whitlatch for comments on the manuscript and Mary Powers and Dan Simberloff for their insightful reviews. FRST CO1804 supported this research.

The Annual Review of Ecology and Systematics is online at
<http://ecolsys.annualreviews.org>

LITERATURE CITED

- Aller RC. 1982. The effects of macrobenthos on chemical properties of marine sediment and overlying water. See McCall & Tevesz, pp. 53–102
- Aronson RB. 1989. Brittlestar beds: low predation anachronisms in the British Isles. *Ecology* 70:856–65
- Aronson RB. 1990. Onshore-offshore patterns of human fishing activity. *Palaios* 5:88–93
- Auster PJ, Langton RW. 1999. The effects of

- fishing on fish habitat. *Am. Fish Soc. Symp.* 22:150–87
- Auster PJ, Malatesta RJ, Langton RW, Watling L, Valentine PC, et al. 1996. The impact of mobile fishing gear on seafloor habitats in the Gulf of Maine (Northwest Atlantic): implications for conservation of fish populations. *Rev. Fish Sci* 4:185–202
- Auster PJ, Malatesta RJ, LaRosa SC. 1995. Patterns of microhabitat utilization by mobile megafauna on the southern New England (USA) continental shelf and slope. *Mar. Ecol. Prog. Ser.* 127:77–85
- Ball BJ, Fox G, Munday BW. 2000. Long- and short-term consequences of a *Nephrops* trawl fishery on the benthos and environment of the Irish Sea. *ICES J. Mar. Sci.* 57:1315–20
- Bergman MJN, Hup M. 1992. Direct effects of beamtrawling in macrofauna in a sandy sediment in the southern North Sea. *ICES J. Mar. Sci.* 49:5–11
- Bergman MJN, vanSantbrink JW. 2000. Mortality in megafaunal benthic populations caused by trawl fisheries on the Dutch continental shelf in the North Sea in 1994. *ICES J. Mar. Sci.* 57:1321–31
- Bird FL, Ford PW, Hancock GJ. 1999. Effects of burrowing macrobenthos on the flux of dissolved substances across the water-sediment interface. *Mar. Freshw. Res.* 50:523–32
- Brander KM. 1981. Disappearance of the common skate, *Raja batis* from the Irish Sea. *Nature* 270:48–49
- Brown JH. 1995. *Macroecology*. Chicago: Univ. Chicago Press. 269 pp.
- Brylinsky M, Gibson J, Gordon DC Jr. 1994. Impacts of flounder trawls on the intertidal habitat and community of the Minas Basin, Bay of Fundy. *Can. J. Fish Aquat. Sci.* 51: 650–61
- Caddy JF. 1973. Underwater observations on tracks of dredges and trawls and some effects of dredging on a scallop ground. *J. Fish. Res. Bd. Can.* 30:173–80
- Cadee GC. 1979. Sediment reworking by the polychaete *Heteromastus filiformis* on a tidal flat in the Dutch Wadden Sea. *Neth. J. Sea Res.* 13:441–54
- Carpenter SR, Ludwig D, Brock WA. 1999. Management of eutrophication for lakes subject to potentially irreversible change. *Ecol. Appl.* 9:751–71
- Casey JM, Myers RA. 1998. Near extinction of a large, widely distributed fish. *Science* 281:690–92
- Churchill JH. 1989. The effect of commercial trawling on sediment resuspension and transport over the Middle Atlantic Bight Continental Shelf. *Cont. Shelf Res.* 9:841–64
- Coleman N, Gason ASH, Poore GCB. 1997. High species richness in the shallow marine waters of southeast Australia. *Mar. Ecol. Prog. Ser.* 154:17–26
- Collie JS, Escanero GA, Valentine PC. 1997. Effects of bottom fishing on the benthic megafauna of Georges Bank. *Mar. Ecol. Prog. Ser.* 155:159–72
- Connell JH. 1977. Diversity in tropical rainforests and coral reefs. *Science* 199:1302–10
- Cranfield HJ, Michael KP, Doonan IJ. 1999. Changes in the distribution of epifaunal reefs and oysters during 130 years of dredging for oysters in Foveaux Strait, southern New Zealand. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 9:461–83
- Cryer M, Hartill B, O'Shea S. 2002. Modification of marine benthos by trawling: towards a generalization for the deep ocean? *Ecol. Appl.* 12: In press
- Cummings VJ, Thrush SF, Hewitt JE, Funnell GA. 2001. Variable effect of a large suspension-feeding bivalve on infauna: experimenting in a complex system. *Mar. Ecol. Prog. Ser.* 209:159–75
- Currie DR, Parry GD. 1996. Effects of scallop dredging on a soft sediment community: a large-scale experimental study. *Mar. Ecol. Prog. Ser.* 134:131–50
- Currie DR, Parry GD. 1999. Impacts and efficiency of scallop dredging on different soft substrates. *Can. J. Fish Aquat. Sci.* 56:539–50
- Dame RF, ed. 1993. *Bivalve Filter Feeders in Estuarine and Coastal Ecosystem Processes*, Vol. G 33. Berlin: Springer-Verlag. 579 pp.
- Dayton PK. 1994. Community landscape: scale

- and stability in hard bottom marine communities. See Giller et al. 1994, pp. 289–332
- Dayton PK, Sala E, Tegner MJ, Thrush S. 2000. Marine reserves: parks, baselines and fishery enhancement. *Bull. Mar. Sci.* 66:617–34
- Dayton PK, Tegner MJ. 1984. The importance of scale in community ecology: a kelp forest example with terrestrial analogs. In *A New Ecology: Novel Approaches to Interactive Systems*, ed. PW Price, CN Slobodchikoff, WS Gaud, pp. 457–83. New York: Wiley & Sons. 515 pp.
- Dayton PK, Tegner MJ, Edwards PB, Riser KL. 1998. Sliding baselines, ghosts, and reduced expectations in kelp forest communities. *Ecol. Appl.* 8:309–22
- Dayton PK, Thrush SF, Agardy TM, Hofman RJ. 1995. Environmental effects of fishing. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 5:205–32
- DeAlteris J, Skrobe L, Lipsky C. 1999. The significance of seafloor disturbance by mobile fishing gear relative to natural processes: a case study in Narragansett Bay, Rhode Island. *Am. Fish Soc. Symp.* 22:224–37
- De Angelis DL, Waterhouse JC. 1987. Equilibrium and nonequilibrium concepts in ecological models. *Ecol. Monogr.* 57:1–21
- de Forges BR, Koslow JA, Poore GCB. 2000. Diversity and endemism of the benthic seamount fauna in the southwest Pacific. *Nature* 405:944–47
- de Groot SJ. 1984. The impact of bottom trawling on benthic fauna of the North Sea. *Ocean Manag.* 9:177–90
- Druffel ERM, Griffin S, Witter A, Nelson E, Southon J, et al. 1995. *Gerardia*: bristlecone pine of the deep-sea? *Geochem. Cosmochim. Acta* 59:5031–36
- Eckman JE, Nowell AR. 1984. Boundary skin friction and sediment transport about an animal-tube mimic. *Sedimentology* 31:851–62
- Eleftheriou A, Robertson MR. 1992. The effects of experimental scallop dredging on the fauna and physical environment of a shallow sandy community. *Neth. J. Sea Res.* 30:289–99
- Engel J, Kvitek R. 1998. Impacts of otter trawling on a benthic community in Monterey Bay National Marine Sanctuary. *Conserv. Biol.* 12:1204–14
- Etter RJ, Grassle F. 1992. Patterns of species diversity in the deep sea as a function of sediment particle size diversity. *Nature* 360:576–78
- Fanning KA, Carder KL, Betzer PR. 1982. Sediment resuspension by coastal waters: a potential mechanism for nutrient re-cycling on the ocean's margins. *Deep-Sea Res.* 29:953–65
- Forster S, Huettel M, Ziebis W. 1996. Impact of boundary layer flow velocity on oxygen utilisation in coastal sediments. *Mar. Ecol. Prog. Ser.* 143:173–85
- Frechette M, Butman CA, Geyer WR. 1989. The importance of boundary-layer flows in supplying phytoplankton to the benthic suspension feeder, *Mytilus edulis* L. *Limnol. Oceanogr.* 34:19–36
- Freese L, Auster PJ, Heifetz J, Wing BL. 1999. Effects of trawling on seafloor habitat and associated invertebrate taxa in the Gulf of Alaska. *Mar. Ecol. Prog. Ser.* 182:119–26
- Frid CLJ, Hansson S, Ragnarsson SA, Rijnsdorp A, Steingrimsdottir SA. 1999. Changing levels of predation on benthos as a result of exploitation of fish populations. *Ambio* 28:578–82
- Frid CLJ, Harwood KG, Hall SJ, Hall JA. 2000. Long-term changes in the benthic communities on North Sea fishing grounds. *ICES J. Mar. Sci.* 57:1303–9
- Friedlander AM, Boehlert GW, Field ME, Mason JE, Gardner JV, Dartnell P. 1999. Side-scan sonar mapping of benthic trawl marks on the shelf and slope off Eureka, California. *Fish. Bull.* 97:786–801
- Gibbs PJ, Collins AJ, Collett LC. 1980. Effect of otter prawn trawling on the macrobenthos of a sandy substratum in a New South Wales estuary. *Aust. J. Mar. Freshw. Res.* 31:509–16
- Giller PS, Hildrew AG, Raffaelli D. 1994. *Aquatic Ecology: Scale, Pattern and Process*. Oxford: Blackwell Sci. 649 pp.

- Graf G. 1999. Do benthic animals control the particle exchange between bioturbated sediments and benthic turbidity zones? See Gray et al. 1999, pp. 153–59
- Graf G, Rosenberg R. 1997. Bioresuspension and biodeposition: a review. *J. Mar. Syst.* 11:269–78
- Graham M. 1953. Effect of trawling on animals of the sea bed. *Deep-Sea Res.* 3:1–6
- Grassle JF, Maciolek NJ. 1992. Deep-sea species richness: regional and local diversity estimate from quantitative bottom samples. *Am. Nat.* 1992:313–41
- Gray JS. 1974. Animal-sediment relationships. *Oceanogr. Mar. Biol. Annu. Rev.* 12:707–22
- Gray JS, Ambrose W Jr, Szaniawska A, eds. 1999. *Biogeochemical Cycling and Sediment Ecology*. Dordrecht, The Netherlands: Kluwer Academic. 236 pp.
- Gray JS, Poore GCB, Uglund KI, Wilson RS, Olsford F, Johannessen O. 1997. Coastal and deep-sea benthic diversities compared. *Mar. Ecol. Prog. Ser.* 159:97–103
- Green MO, Hewitt JE, Thrush SF. 1998. Seafloor drag coefficients over natural beds of horse mussels (*Atrina zelandica*). *J. Mar. Res.* 56:613–37
- Hall SJ. 1999. *The Effects of Fisheries on Ecosystems and Communities*. Oxford: Blackwell Sci. 274 pp.
- Hall SJ, Basford DJ, Robertson MR. 1990. The impacts of hydraulic dredging for razor clams *Ensis* sp. on an infaunal community. *Neth. J. Sea Res.* 27:119–25
- Hall SJ, Raffaelli D, Thrush SF. 1994. Patchiness and disturbance in shallow water benthic assemblages. See Hildrew et al. 1994, pp. 333–75
- Hall-Spencer JM, Moore PG. 2000. Scallop dredging has profound, long-term impacts on maerl habitats. *ICES J. Mar. Sci.* 57:1407–15
- Hansson M, Lindegarh M, Valentinsson D, Ulmestrand M. 2000. Effects of shrimp-trawling on abundance of benthic macrofauna in Gullmarsfjorden, Sweden. *Mar. Ecol. Prog. Ser.* 198:191–201
- Heck KLJ, Thoman TA. 1981. Experiments on predator-prey interactions in vegetated aquatic habitats. *J. Exp. Mar. Biol. Ecol.* 53:125–34
- Herman PMJ, Middelburg JJ, VandeKoppel J, Heip CHR. 1999. Ecology of estuarine macrobenthos. *Adv. Ecol. Res.* 29:195–231
- Holme NA. 1983. Fluctuations in the benthos of the Western Channel. *Oceanol. Acta, Proc. 17th Eur. Mar. Biol. Symp.* pp. 121–24. Elsevier. 225 pp.
- Huettel M, Ziebis W, Forster S. 1996. Flow-induced uptake of particulate matter in permeable sediments. *Limnol. Oceanogr.* 41:309–22
- Hughes DJ, Atkinson RJA, Ansell AD. 2000. A field test of the effects of megafaunal burrows on benthic chamber measurements of sediment-water solute fluxes. *Mar. Ecol. Prog. Ser.* 195:189–99
- Huston MA. 1994. *Biological Diversity: The Coexistence of Species on Changing Landscapes*. Cambridge: Cambridge Univ. Press. 681 pp.
- Hutchings JA. 2000. Collapse and recovery of marine fishes. *Nature* 406:882–85
- Irlandi EA. 1994. Large- and small-scale effects of habitat structure on rates of predation: how percent coverage of seagrass affects rates of predation and siphon nipping on an infaunal bivalve. *Oecologia* 98:176–83
- Jackson JBC. 2001. What was natural in the coastal oceans? *Proc. Natl. Acad. Sci. USA* 98:5411–18
- Jenkins SR, Beukers-Stewart BD, Brand AR. 2001. Impact of scallop dredging on benthic megafauna: a comparison of damage levels in captured and non-captured organisms. *Mar. Ecol. Prog. Ser.* 215:297–301
- Jennings S, Dinmore TA, Duplisea DE, Warr KJ, Lancaster JE. 2001a. Trawling disturbance can modify benthic production processes. *J. Anim. Ecol.* 70:459–75
- Jennings S, Greenstreet SPR, Reynolds JD. 1999. Structural change in an exploited fish community: a consequence of differential fishing effects on species with contrasting life histories. *J. Anim. Ecol.* 68:617–27

- Jennings S, Kaiser MJ. 1998. The effects of fishing on marine ecosystems. *Adv. Mar. Biol.* 34:203–314
- Jennings S, Pinnegar JK, Polunin NVC, Warr KJ. 2001b. Impacts of trawling disturbance on the trophic structure of benthic invertebrate communities. *Mar. Ecol. Prog. Ser.* 213:127–42
- Jumars PA, Eckman JE. 1983. Spatial structure within deep-sea benthic communities. In *The Sea*, ed. GT Rowe, pp. 399–451. New York: Wiley & Sons. 569 pp.
- Kaiser MJ, de Groot SJ, eds. 2000. *The Effects of Fishing on Non-Target Species and Habitats*. Oxford: Blackwell Sci. 416 pp.
- Kaiser MJ, Edwards DB, Armstrong PJ, Radford K, Lough NEL, et al. 1998. Changes in megafaunal benthic communities in different habitats after trawling disturbance. *ICES J. Mar. Sci.* 55:353–61
- Kaiser MJ, Ramsay K, Richardson CA, Spence FE, Brand AR. 2000. Chronic fishing disturbance has changed shelf sea benthic community structure. *J. Anim. Ecol.* 69:494–503
- Kaiser MJ, Spence FE, Hart PJB. 1999. Fishing-gear restrictions and conservation of benthic habitat complexity. *Conserv. Biol.* 14:1512–25
- Kaiser MJ, Spencer BE. 1996. The effects of beam-trawl disturbance on infaunal communities in different habitats. *J. Anim. Ecol.* 65:348–58
- Kenchington ELR, Prena J, Gilkinson KD, Gordon DC, MacIsaac K, et al. 2001. Effects of experimental otter trawling on the macrofauna of a sandy bottom ecosystem on the Grand Banks of Newfoundland. *Can. J. Fish Aquat. Sci.* 58:1043–57
- Kolasa J, Pickett STA. 1991. *Ecological Heterogeneity*. New York: Springer-Verlag. 332 pp.
- Koslow JA, Gowelett-Holmes K, Lowry JK, O'Hara T, Poore GCB, Williams A. 2001. Seamount benthic macrofauna off southern Tasmania: community structure and impacts of trawling. *Mar. Ecol. Prog. Ser.* 213:111–25
- Krost P. 1990. The impact of otter-trawl fishery on nutrient release from the sediment and macrofauna of Kieler Bucht (Western Baltic). *Ber. Inst. Meereskd. Nr.* 200:167
- Langton RW, Robinson WE. 1990. Faunal association on scallop grounds in the Western Gulf of Maine. *J. Exp. Mar. Biol. Ecol.* 144:157–71
- Legeleux F, Reyss J-L, Schmidt S. 1994. Particle mixing rates in sediments of the north-east tropical Atlantic: evidence from $^{210}\text{Pb}_{\text{xs}}$, ^{137}Cs , $^{228}\text{Th}_{\text{xs}}$ and $^{234}\text{Th}_{\text{xs}}$ downcore distributions. *Earth Planet Sci. Lett.* 128:545–62
- Legendre P. 1993. Spatial autocorrelation: trouble or new paradigm? *Ecology* 74:1659–73
- Levin LA. 1984. Life history and dispersal patterns in a dense infaunal polychaete assemblage: community structure and response to disturbance. *Ecology* 65:1185–200
- Levin LA, Etter RJ, Rex MA, Cooday AJ, Smith CR, et al. 2001. Environmental influences on regional deep-sea species diversity. *Annu. Rev. Ecol. Syst.* 32:51–93
- Levin LA, Gooday AJ. 1992. Possible roles for xenophyophores in deep-sea carbon cycling. In *Deep-Sea Food Chains and the Global Carbon Cycle*, ed. GT Rowe, V Pariente, pp. 93–104. The Netherlands: Kluwer Academic. 410 pp.
- Lindholm JB, Auster PJ, Kaufman LS. 1999. Habitat-mediated survivorship of juvenile (0-year) Atlantic cod *Gadus morhua*. *Mar. Ecol. Prog. Ser.* 180:247–55
- Loehle C, Li B-L. 1996. Habitat destruction and the extinction debt revisited. *Ecol. Appl.* 6:784–89
- Loftis JC, McBride GB, Ellis JC. 1991. Considerations of scale in water quality monitoring and data analysis. *Water Res. Bull.* 27:255–64
- Loo L-O, Rosenberg R. 1989. Bivalve suspension-feeding dynamics and benthic-pelagic coupling in an eutrophicated marine bay. *J. Exp. Mar. Biol. Ecol.* 130:253–76
- Marinelli RL. 1994. Effects of burrow ventilation on activities of a terebellid polychaete and silicate removal from sediment pore waters. *Limnol. Oceanogr.* 39:303–17
- Martin RE. 1996. Secular increase in nutrient levels through the phanerozoic: implications

- for productivity, biomass and diversity of the marine biosphere. *Palaios* 11:209–19
- Mayer LM, Schick DF, Findlay RH, Rice DL. 1991. Effects of commercial dragging on sedimentary organic matter. *Mar. Environ. Res.* 31:249–61
- McCall PL, Tevesz MJS, eds. 1982. *Animal-Sediment Relations: The Biogenic Alteration of Sediments*. New York: Plenum. 351 pp.
- McConnaughey RA, Mier KL, Dew CB. 2000. An examination of chronic trawling effects on soft-bottom benthos of the eastern Bering Sea. *ICES J. Mar. Sci.* 57:1377–88
- Micheli F. 1999. Eutrophication, fisheries and consumer-resource dynamics in marine pelagic ecosystems. *Science* 285:325–26
- Middleburg JJ, Soetaert K, Herman PMJ. 1997. Empirical relationships for use in global diagenetic models. *Deep-Sea Res.* 44:327–44
- Moran MJ, Stephenson PC. 2000. Effects of otter trawling on macrobenthos and management of demersal scalefish fisheries on the continental shelf of north-western Australia. *ICES J. Mar. Sci.* 57:510–16
- Musick JA, Harbin MM, Berkeley SA, Burgess GH, Eklund AM, et al. 2000. Marine, estuarine, and diadromous fish stocks at risk of extinction in North America (exclusive of Pacific salmonids). *Fisheries* 25:6–30
- Nelder JA. 1999. Statistics for the millennium: from statistics to statistical science. *Statistician* 48:257–69
- Nikora V, Green MO, Thrush SF, Hume TM, Goring DG. 2002. Structure of the internal boundary layer over a patch of horse mussels (*Atrina zelandica*) in an estuary. *J. Mar. Res.* 60:121–50
- Norkko A, Hewitt JE, Thrush SF, Funnell GA. 2001. Benthic-pelagic coupling and suspension feeding bivalves: linking site-specific sediment flux and biodeposition to benthic community structure. *Limnol. Oceanogr.* 46:2067–72
- Olafsson EB, Peterson CH, Ambrose WGJ. 1994. Does recruitment limitation structure populations and communities of macroinvertebrates in marine soft sediments: the relative significance of pre- and post-settlement processes. *Oceanogr. Mar. Biol. Annu. Rev.* 32:65–109
- Palanques A, Guillen J, Puig P. 2001. Impact of bottom trawling on water turbidity and muddy sediment of an unfished continental shelf. *Limnol. Oceanogr.* 46:1100–10
- Pauly D, Christensen V, Dalsgaard J, Froese R, Torres F Jr. 1998. Fishing down marine food-webs. *Science* 279:860–3
- Persson L, Eklöv P. 1995. Prey refuges affecting interactions between piscivorous perch and juvenile perch and roach. *Ecology* 76:70–81
- Peterson CH. 1979. The importance of predation and competition in organising the intertidal epifaunal communities of Barnegat Inlet, New Jersey. *Oecologia* 39:1–24
- Pilskaln CH, Churchill JH, Mayer LM. 1998. Resuspension of sediments by bottom trawling in the Gulf of Maine and potential geochemical consequences. *Conserv. Biol.* 12:1223–24
- Pimm SL. 1991. *The Balance of Nature: Ecological Issues in the Conservation of Species and Communities*. Chicago/London: Univ. Chicago Press. 434 pp.
- Pitcher CR, Poiner IR, Hill BJ, Burrige CY. 2000. Implications of the effects of trawling on sessile megazoobenthos on a tropical shelf in northeastern Australia. *ICES J. Mar. Sci.* 57:1359–68
- Pitcher TJ. 2001. Fisheries managed to rebuild ecosystems? Reconstructing the past to salvage the future. *Ecol. Appl.* 11:601–17
- Pitcher TJ, Watson R, Haggan N, Guenette S, Kennish R, et al. 2000. Marine reserves and the restoration of fisheries and marine ecosystems in the South China Sea. *Bull. Mar. Sci.* 66:543–66
- Pranovi F, Raicevich S, Franceschini G, Farrace MG, Giovanardi O. 2000. Rapido trawling in the northern Adriatic Sea: effects on benthic communities in an experimental area. *ICES J. Mar. Sci.* 57:517–24
- Prena J, Schwinghammer P, Rowell TW, Gordon DC Jr, Gilkinson KD, et al. 1999. Experimental otter trawling on a sandy bottom ecosystem of the Grand Banks of

- Newfoundland: analysis of the trawl bycatch and effects on epifauna. *Mar. Ecol. Prog. Ser.* 181:107–24
- Probert PK, McKnight DG, Grove SL. 1997. Benthic invertebrate bycatch from a deep-water trawl fishery, Chatham Rise, New Zealand. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 7:27–40
- Reise K. 1982. Long-term changes in the macrobenthic invertebrate fauna of the Wadden sea. *Neth. J. Sea Res.* 16:29–36
- Rhoads DC. 1974. Organism-sediment relations on the muddy seafloor. *Oceanogr. Mar. Biol. Annu. Rev.* 12:263–300
- Rhodes MC, Thompson RJ. 1993. Comparative physiology of suspension feeding in living brachiopods and bivalves: evolutionary implications. *Paleobiology* 19:322–34
- Roberts JM, Harvey SM, Lamont PA, Gage JD, Humphery JD. 2000. Seafloor photography, environmental assessment and evidence for deep-water trawling on the continental margin west of the Hebrides. *Hydrobiologia* 441:173–83
- Roberts M. 1997. Coral in deep water. *New Sci.* 155:40–43
- Rogers AD. 1999. The biology of *Lophelia pertusa* (Linnaeus 1758) and other deep-water reef forming corals and impacts from human activities. *Int. Rev. Hydrobiol.* 84:315–406
- Rooker JR, Holt GJ, Holt SA. 1998. Vulnerability of newly settled red drum (*Scianops ocellatus*) to predatory fish: Is early-life survival enhanced by seagrass meadows? *Mar. Biol.* 131:145–51
- Rowe GT, Clifford CH, Smith KL Jr, Hamilton PL. 1975. Benthic nutrient regeneration and its coupling to primary productivity in coastal waters. *Nature* 255:215–17
- Ruiz GM, Hines AH, Posey MH. 1993. Shallow water as a refuge habitat for fish and crustaceans in non-vegetated estuaries: an example from Chesapeake Bay. *Mar. Ecol. Prog. Ser.* 99:1–16
- Sainsbury KJ. 1988. The ecological basis of multispecies fisheries and management of a demersal fishery in tropical Australia. In *Fish Population Dynamics: The Implications for Management*, ed. JA Gulland, pp. 349–82. New York: Wiley. 351 pp.
- Sala E, Ballesteros E. 1997. Partitioning of space and food resources by three fish of the genus *Diplodus* (Sparidae) in a Mediterranean rocky infralittoral ecosystem. *Mar. Ecol. Prog. Ser.* 152:273–83
- Sanchez P, Demestre M, Ramon M, Kaiser MJ. 2000. The impact of otter trawling on mud communities in the northwestern Mediterranean. *ICES J. Mar. Sci.* 57:1352–58
- Sandnes J, Forbes T, Hansen R, Sandnes B, Rygg B. 2000. Bioturbation and irrigation in natural sediments, described by animal-community parameters. *Mar. Ecol. Prog. Ser.* 197:169–79
- Scheffer M, Carpenter S, Foley JA, Folke C, Walker B. 2001. Catastrophic shifts in ecosystems. *Nature* 413:591–96
- Schneider DC, Gagnon JM, Gilkinson KD. 1987. Patchiness of epibenthic megafauna on the outer Grand Banks of Newfoundland. *Mar. Ecol. Prog. Ser.* 39:1–13
- Schwinghamer P, Guigne JY, Siu WC. 1996. Quantifying the impact of trawling on benthic habitat structure using high resolution acoustics and chaos theory. *Can. J. Fish Aquat. Sci.* 53:288–96
- Shimeta JS, Jumars PA. 1991. Physical mechanisms and rates of particle capture by suspension feeders. *Oceanogr. Mar. Biol. Annu. Rev.* 29:191–257
- Skilleter GA. 1994. Refuges from predation and the persistence of estuarine clam populations. *Mar. Ecol. Prog. Ser.* 109:29–42
- Smith CJ, Papadopoulou KN, Diliberto S. 2000. Impact of otter trawling on an eastern Mediterranean commercial trawl fishing ground. *ICES J. Mar. Sci.* 57:1340–51
- Snelgrove PVR. 1999. Getting to the bottom of marine biodiversity: sedimentary habitats—ocean bottoms are the most widespread habitat on Earth and support high biodiversity and key ecosystem services. *Bioscience* 49:129–38
- Snelgrove PVR, Butman CA. 1994. Animal-sediment relationships revisited: cause

- versus effect. *Oceanogr. Mar. Biol. Annu. Rev.* 32:111–77
- Soetaert K, Herman PMJ, Middleburg JJ, Heip C, deStigter HS, et al. 1996. Modeling ^{210}Pb -derived mixing activity in ocean margin sediments: diffusive versus nonlocal mixing. *J. Mar. Res.* 54:1207–27
- Sousa WP. 1984. The role of disturbance in natural communities. *Annu. Rev. Ecol. Syst.* 15:353–91
- Sparks-McConkey PJ, Watling L. 2001. Effects on the ecological integrity of a soft-bottom habitat from a trawling disturbance. *Hydrobiologia* 456:73–85
- Squires DF. 1965. Deep-water coral structure on the Campbell Plateau, New Zealand. *Deep-Sea Res.* 12:785–88
- Steele JH, Schumacher M. 2000. Ecosystem structure before fishing. *Fish. Res.* 44:201–5
- Steneck RS. 1997. Fisheries-induced biological changes to the structure and function of the Gulf of Maine. In *Proc. Gulf of Maine Ecosys. Dynamics Scientific Symp. and Workshop. RARGOM Rep., 91-1. Regional Assoc. for Res. on the Gulf of Maine*, ed. GT Wallace, EF Braasch, pp. 151–65. Hanover, NH: Maine/New Hampshire Sea Grant Progr.
- Tegner MJ, Basch LV, Dayton PK. 1996. Near extinction of an exploited marine invertebrate. *TREE* 11:278–80
- Thayer CW. 1983. Sediment-mediated biological disturbance and the evolution of marine benthos. In *Biotic Interactions in Recent and Fossil Benthic Communities*, ed. MJS Tevesz, pp. 479–625. New York/London: Plenum
- Thistle D. 1981. Natural physical disturbances and the communities of marine soft bottoms. *Mar. Ecol. Prog. Ser.* 6:223–28
- Thrush SF, Hewitt JE, Cummings VJ, Dayton PK. 1995. The impact of habitat disturbance by scallop dredging on marine benthic communities: What can be predicted from the results of experiments? *Mar. Ecol. Prog. Ser.* 129:141–50
- Thrush SF, Hewitt JE, Cummings VJ, Dayton PK, Cryer M, et al. 1998. Disturbance of the marine benthic habitat by commercial fishing: impacts at the scale of the fishery. *Ecol. Appl.* 8:866–79
- Thrush SF, Hewitt JE, Funnell GA, Cummings VJ, Ellis J, et al. 2001. Fishing disturbance and marine biodiversity: the role of habitat structure in simple soft-sediment systems. *Mar. Ecol. Prog. Ser.* 221:255–64
- Thrush SF, Lawrie SM, Hewitt JE, Cummings VJ. 1999. The problem of scale: uncertainties and implications for soft-bottom marine communities and the assessment of human impacts. See Gray et al. 1999, pp. 195–210
- Thrush SF, Pridmore RD, Hewitt JE, Cummings VJ. 1994. The importance of predators on a sandflat: interplay between seasonal changes in prey densities and predator effects. *Mar. Ecol. Prog. Ser.* 107:211–22
- Thrush SF, Whitlatch RB. 2001. Recovery dynamics in benthic communities: balancing detail with simplification. In *Ecological Comparisons of Sedimentary Shores*, ed. K Reise, pp. 297–316. Berlin: Springer-Verlag. 384 pp.
- Tuck ID, Hall SJ, Robertson MR, Armstrong E, Basford DJ. 1998. Effects of physical trawling disturbance in a previously unfished sheltered Scottish sea loch. *Mar. Ecol. Prog. Ser.* 162:227–42
- Tupper M, Boutilier RG. 1995. Effects of habitat on settlement, growth and postsettlement survival of Atlantic cod (*Gadus morhua*). *Can. J. Fish Aquat. Sci.* 52:1834–41
- Turner MG, Romme WH, Gardner RH, O'Neill RV, Kratz TK. 1993. A revised concept of landscape equilibrium: disturbance and stability on scaled landscapes. *Landscape Ecol.* 8:213–27
- Turner SJ, Thrush SF, Hewitt JE, Cummings VJ, Funnell G. 1999. Fishing impacts and the degradation or loss of habitat structure. *Fish Manag. Ecol.* 6:401–20
- Van Blaricom GR. 1982. Experimental analysis of structural regulation in a marine sand community exposed to oceanic swell. *Ecol. Monogr.* 52:283–305

- Van Dolah RF, Wendt PH, Levisen MV. 1991. A study of the effects of shrimp trawling on benthic communities in two South Carolina sounds. *Fish Res.* 12:139–56
- Van Dolah RF, Wendt PH, Nicholson N. 1987. Effects of a research trawl on a hard-bottom assemblage of sponges and corals. *Fish Res.* 5:39–54
- Veale LO, Hill AS, Hawkins SJ, Brand AR. 2000. Effects of long-term physical disturbance by commercial scallop fishing on subtidal epifaunal assemblages and habitats. *Mar. Biol.* 137:325–37
- Watling L, Findlay RH, Mayer LM, Schick DF. 2001. Impact of a scallop drag on the sediment chemistry, microbiota, and faunal assemblages of a shallow subtidal marine benthic community. *J. Sea Res.* 46:309–24
- Watling L, Norse EA. 1998. Disturbance of the seafloor by mobile fishing gear: a comparison to forest clear cutting. *Conserv. Biol.* 12:1180–97
- Weinberg JR, Whitlatch RB. 1983. Enhanced growth of a filter-feeding bivalve by a deposit-feeding polychaete by means of nutrient regeneration. *J. Mar. Res.* 41:557–69
- Whitlatch RB. 1980. Patterns of resource utilization and co-existence in marine intertidal deposit-feeding communities. *J. Mar. Res.* 38:743–65
- Whitlatch RB, Lohrer AM, Thrush SF. 2002. Scale-dependent recovery of the benthos: effects of larval and post-larval stages. In *Organism-Sediment Workshop*, ed. R Aller, J Aller, SA Woodin, pp. 181–98 Columbia: Univ. SC. 403 pp.
- Widdicombe S, Austen MC. 1999. Mesocosm investigation into the effects of bioturbation on the diversity and structure of a subtidal macrobenthic community. *Mar. Ecol. Prog. Ser.* 189:181–93
- Widdicombe S, Austen MC, Kendall MA, Warwick RM, Jones MB. 2000. Bioturbation as a mechanism for setting and maintaining levels of diversity in subtidal macrobenthic communities. *Hydrobiologia* 440:369–77
- Wildish D, Kristmanson D. 1997. *Benthic Suspension Feeders and Flow*. Cambridge: Cambridge Univ. Press. 422 pp.
- Wilson WH. 1991. Competition and predation in marine soft-sediment communities. *Annu. Rev. Ecol. Syst.* 21:221–41
- Witman JD, Sebens K. 1992. Regional variation in fish predation intensity: a historical perspective in the Gulf of Maine. *Oecologia* 90:305–15
- Woodin SA. 1978. Refuges, disturbance and community structure: a marine soft-bottom example. *Ecology* 59:274–84
- Wootton JT. 1998. Effects of disturbance on species diversity: a multitrophic perspective. *Am. Nat.* 152:803–25
- Zajac RN. 1999. Understanding the sea floor landscape in relation to impact assessment and environmental management in coastal marine sediments. See Gray et al. 1999, pp. 211–27
- Zajac RN, Whitlatch RB, Thrush SF. 1998. Recolonisation and succession in soft-sediment infaunal communities: the spatial scale of controlling factors. *Hydrobiologia* 376:227–40
- Ziebis W, Huettel M, Forster S. 1996. Impact of biogenic sediment topography on oxygen fluxes in permeable seafloors. *Mar. Ecol. Prog. Ser.* 140:227–37