

Disturbance of the Seabed by Mobile Fishing Gear: A Comparison to Forest Clearcutting



Les Watling; Elliott A. Norse

Conservation Biology, Vol. 12, No. 6 (Dec., 1998), 1180-1197.

Stable URL:

<http://links.jstor.org/sici?sici=0888-8892%28199812%2912%3A6%3C1180%3ADOTSBM%3E2.0.CO%3B2-4>

Conservation Biology is currently published by Blackwell Publishing.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. 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/journals/black.html>.

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 an independent not-for-profit organization dedicated to creating and preserving a digital archive of scholarly journals. For more information regarding JSTOR, please contact support@jstor.org.

Disturbance of the Seabed by Mobile Fishing Gear: A Comparison to Forest Clearcutting

LES WATLING* AND ELLIOTT A. NORSE†

*Darling Marine Center, University of Maine, Walpole, ME 04573, U.S.A., email watling@maine.maine.edu

†Marine Conservation Biology Institute, 15806 NE 47th Court, Redmond, WA 98052-5208, U.S.A., email enorse@u.washington.edu

Abstract: *Bottom trawling and use of other mobile fishing gear have effects on the seabed that resemble forest clearcutting, a terrestrial disturbance recognized as a major threat to biological diversity and economic sustainability. Structures in marine benthic communities are generally much smaller than those in forests, but structural complexity is no less important to their biodiversity. Use of mobile fishing gear crushes, buries, and exposes marine animals and structures on and in the substratum, sharply reducing structural diversity. Its severity is roughly comparable to other natural and anthropogenic marine disturbances. It also alters biogeochemical cycles, perhaps even globally. Recovery after disturbance is often slow because recruitment is patchy and growth to maturity takes years, decades, or more for some structure-forming species. Trawling and dredging are especially problematic where the return interval—the time from one dredging or trawling event to the next—is shorter than the time it takes for the ecosystem to recover; extensive areas can be trawled 100–700% per year or more. The effects of mobile fishing gear on biodiversity are most severe where natural disturbance is least prevalent, particularly on the outer continental shelf and slope, where storm-wave damage is negligible and biological processes, including growth, tend to be slow. Recent advances in fishing technology (e.g., rockhopper gear, global positioning systems, fish finders) have all but eliminated what were de facto refuges from trawling. The frequency of trawling (in percentage of the continental shelf trawled per year) is orders of magnitude higher than other severe seabed disturbances, annually covering an area equivalent to perhaps half of the world's continental shelf, or 150 times the land area that is clearcut yearly. Mobile fishing gear can have large and long-lasting effects on benthic communities, including young stages of commercially important fishes, although some species benefit when structural complexity is reduced. These findings are crucial for implementation of "Essential Fish Habitat" provisions of the U.S. Magnuson-Stevens Fishery Conservation and Management Act which aim to protect nursery and feeding habitat for commercial fishes. Using a precautionary approach to management, modifying fishing methods, and creating refuges free of mobile fishing gear are ways to reduce effects on biological diversity and commercial fish habitat.*

Perturbaciones del Lecho Marino por Artes de Pesca Móviles: Una Comparación con la Tala Forestal

Resumen: *Los arrastres de fondo y el uso de otras artes de pesca móviles tienen efectos en el lecho marino que se asemejan a la tala total de bosques, que es a su vez una perturbación terrestre reconocida como una de las mayores amenazas a la diversidad biológica y la sustentabilidad económica. Las estructuras en comunidades marinas bénticas son generalmente mucho más pequeñas que aquellas en los bosques, pero la complejidad estructural no es menos importante que la biodiversidad. El uso de artes de pesca móviles quiebra, sepulta y expone animales marinos y estructuras sobre y en el substrato, reduciendo marcadamente la diversidad estructural. Su severidad es burdamente comparable con otras perturbaciones marinas de orden natural o antropogénico. También altera los ciclos biogeoquímicos, de hecho a nivel mundial. La recuperación después de una perturbación es frecuentemente lenta debido a que el reclutamiento es por parches y el crecimiento para alcanzar la madurez toma años, décadas o aún más para algunas especies que forman estructuras. Los arrastres de fondo y dragados son especialmente problemáticos donde el intervalo de retorno*

Paper submitted December 5, 1997; revised manuscript accepted July 1, 1998.

1180

(tiempo entre un evento de dragado o arrastre y otro) es más corto que el tiempo que toma a un ecosistema recuperarse; áreas extensas son arrastradas entre un 100 y 700% por año o más. Los efectos de las artes de pesca móviles en la biodiversidad son más severos cuando las perturbaciones naturales son menos prevalentes, particularmente en las afueras de la plataforma continental y la pendiente, donde el daño del oleaje por tormentas es negligible y los procesos biológicos (incluyendo crecimiento) tienden a ser lentos. Recientes avances en tecnología pesquera (e.g., sistemas de posicionamiento global, detectores de peces) aparentemente tienen todo, pero eliminan lo que de facto fueran refugios contra arrastres. La frecuencia de los arrastres (en porcentaje de la plataforma continental arrastrada por año) es órdenes de magnitud mayor que otras perturbaciones severas al lecho marino, anualmente la cobertura de área es equivalente quizá a la mitad de la plataforma continental marina, o 150 veces el área de tierra que es talada anualmente. Las artes de pesca móviles pueden tener impactos grandes y de larga duración en las comunidades bentónicas, incluyendo estadios jóvenes de peces de importancia comercial, aunque algunas especies se benefician cuando la complejidad estructural es reducida. Estos descubrimientos son cruciales para la implementación de el "hábitat esencial para peces" del Acta de Conservación y Manejo de Pesquerías Magnuson-Stevens de los Estados Unidos y que pretende establecer hábitats de reproducción y alimentación para peces comerciales. El uso de una aproximación precautoria de manejo, la modificación de métodos de pesca y la creación de refugios libres de artes de pesca móviles son formas para reducir los efectos en la diversidad biológica y el hábitat para peces comerciales.

New opinions are always suspected, and usually opposed, without any other reason but because they are not already common.

—John Locke, *An Enquiry Concerning Human Understanding* (1690)

Introduction

Disturbances influence patterns of ecosystem diversity by affecting species composition, spatial structure, and biogeochemistry (Grassle & Sanders 1973; Pickett & White 1985; Huston 1994). Disturbance processes span a wide range of spatial and temporal scales, from the burrowing of individual annelid worms to single treefalls to stand-replacement forest fires to plate tectonics; in general, larger-scale disturbances are rarer. Organisms vary markedly in their resistance and resilience to disturbance. As a result, natural ecosystems are mosaics that reflect their disturbance history and organisms' responses (Huston 1994). Disturbances that humans superimpose on natural disturbance regimes alter community mosaics and form the core of conflicts such that over clearcut logging of the ancient forests of the U.S. Pacific Northwest (Norse 1990). From tropical rainforests to the taiga, clearcutting has become a major issue for conservation biologists, advocates, and policy makers, but there is another comparably severe anthropogenic ecosystem disturbance that is far more prevalent worldwide yet has received little scrutiny: the use of mobile fishing gear—trawls and dredges—to catch bottom-dwelling marine animals (Hutchings 1990; Jones 1992; Dayton et al. 1995). We detail how mobile gear can alter benthic ecosystems, and we compare this disturbance to other marine disturbances and forest clearcutting.

Trawling is a widespread method of catching marine fishes and invertebrates. Individual trawling vessels from

10 m to 130 m long (or, sometimes, pairs of trawlers) fish by pulling large nets through the sea. Midwater or pelagic trawls are used to catch fishes in the water column (e.g., walleye pollock [*Theragra chalcogramma*] in the North Pacific and hoki [*Macruronus novaezelandiae*] off New Zealand). Midwater trawling affects biological diversity by removing portions of target populations and others that are caught incidentally (bycatch), but it causes no long-lasting habitat disturbance as long as the trawl does not touch the bottom. Most trawling (and all dredging, when heavy chain-rigged or hydraulic suction devices are used), however, occurs on the seabed, targeting species such as demersal groundfish (e.g., Atlantic cod [*Gadus morhua*] and plaice [*Pleuronectes platessa*]) on the continental shelves of the North Atlantic, green sea urchins (*Strongylocentrotus droebachiensis*) in nearshore waters of New England, shrimp (*Penaeus*) on the Gulf of Mexico and northern Australian shelves, and scallops (Pectinidae) in the northern and southern hemispheres.

In its first decades, conservation biology has focused mainly on the terrestrial realm (Irish & Norse 1996). So, because human activities in the sea are likely to be less familiar to conservation biologists and because trawling has been likened to clearcutting (McAllister 1995; Levy 1998), we compare these two sources of ecosystem disturbance.

Mobile Fishing Gear

The most widely used towed bottom-fishing gear is the otter trawl (Fig. 1). Its forward motion spreads a pair of otter boards, each weighing tens to thousands of kilograms, that hold the trawl mouth open. The bottom of an otter trawl mouth is a foot rope or ground rope that

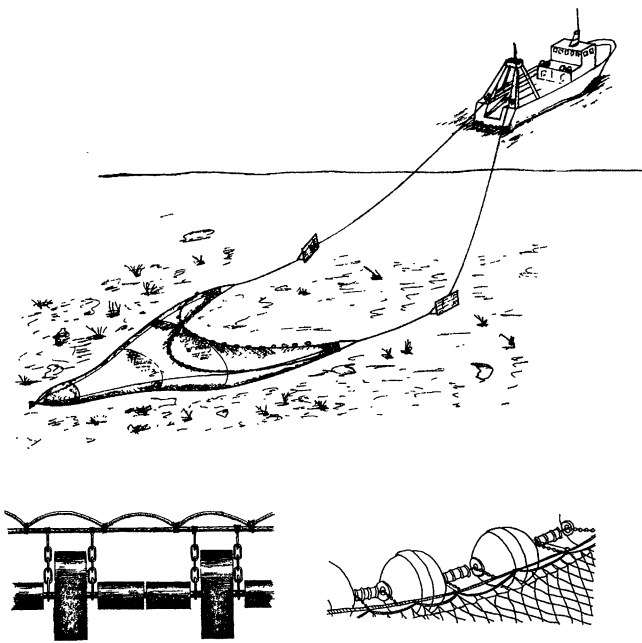


Figure 1. A modern bottom trawl shown in operation on the seabed (top); two types of roller gear applied to the ground rope of the net to aid in trawling over very rough bottom conditions (bottom) (reprinted with permission from Sainsbury 1996).

can bear many heavy (tens to hundreds of kilograms) steel weights (bobbins) that keep the trawl on the seabed. A growing fraction of bottom trawls, called roller trawls or rockhoppers, are armed with large (to 40-cm-diameter) rubber discs or steel bobbins that ride over obstructions such as boulders and coral heads that might otherwise snag the net. Some trawls are armed with tickler chains that disturb the seabed to flush shrimp or fish into the water column to be caught by the net. The constricted posterior netting of a trawl is called the cod end. When filled with tens to thousands of kilograms of marine organisms, rocks, and mud, and dragged for kilometers across the bottom, the cod end, like the otter boards, bobbins, rollers, and tickler chains, can disturb the seabed.

Another type of mobile fishing gear, the beam trawl (Fig. 2), is held open by a steel beam (total aperture 4–12 m) instead of otter boards and is typically fitted with chains, with an empty weight up to 13 tons. Beam trawls can be towed at speeds of up to 14.8 km/hour (Polet et al. 1998). Other towed gear, including scallop, oyster, and crab dredges, consist of steel frames and fiber or metal chain-mesh bags that plow over and through the surface layers of the seabed to sift out target species. These dredges can be so effective at collecting objects in sediments that they were used in 1996 to gather buried debris at the crash site of TWA Flight 800 off Long Island, New York. Bivalve mollusks such as ocean quahogs

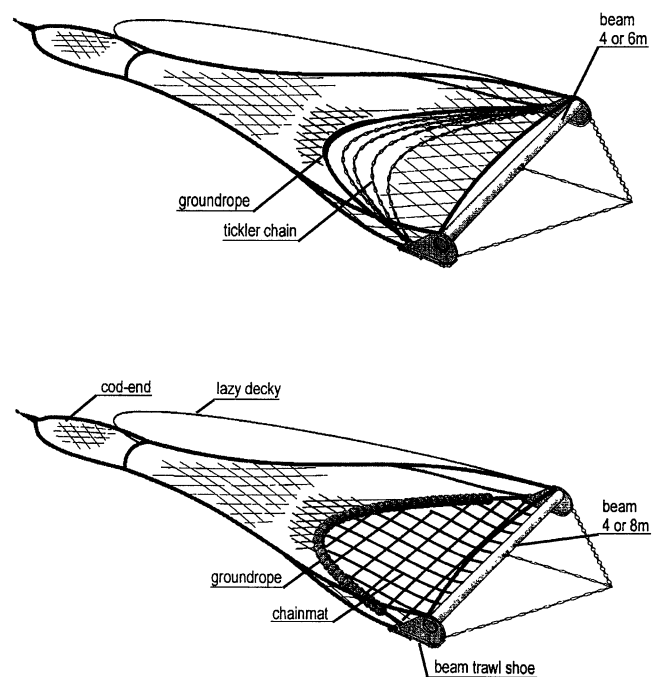


Figure 2. Modern beam trawl designs, showing two ways in which chains are arranged in front of the groundrope. The chains are used to disturb the sand, thus helping to increase the catch of species, such as flatfishes, that live in contact with the bottom (reprinted with permission from Sainsbury 1996).

(*Arctica islandica*) and surf clams (*Spisula solidissima*) are caught by hydraulic dredges that liquefy and suck up large amounts of seabed (Messieh et al. 1991). Continental shelf, slope- and seamount-dwelling anthozoans used for jewelry, such as precious corals (*Corallium* spp.) and black corals (*Antipathes* spp.), are dragged with mobile gear called Italian bars (Risk et al. 1998), tangle nets, and St. Andrew's crosses.

Trawling has a long history, mainly in estuaries, bays, and continental shelf waters at depths from a few to hundreds of meters, but its use accelerated sharply with the introduction of diesel engines in the 1920s (Lindeboom & de Groot 1998). As more continental shelf fish stocks are overfished, the search for new fisheries has extended bottom trawling onto the continental slope to depths of 1400–1829 m (Gordon & Hunter 1994; Merrett & Haedrich 1997). In the last several decades, bottom trawling has also extended from traditional fishing grounds near the margins of industrialized nations such as the North Sea and Georges Bank to waters off developing nations and even the remotest oceanic seamounts of the Southern Ocean (L.W., personal observation). Until the 1980s or early 1990s, many areas were de facto refuges because their numerous obstacles or steep slopes made trawling risky. Recent deployment of rock-hopper trawls, global positioning systems, and fish find-

ers has allowed trawlers to work in previously unfished waters. As a result, trawls or related fishing gear are now used on every kind of bottom type from subpolar to tropical waters.

Unlike clearcutting, most trawling is concealed from view and happens far from traditional study sites, which helps to explain why its effects have been overlooked. This is not a trivial oversight. As on land, biodiversity in the sea is profoundly threatened (Norse 1993; Butman & Carlton 1995). The estuaries, bays, and continental shelves where most trawling occurs, together constituting approximately 7.4% of the sea's area (Sharp 1988), are among the most biologically productive (Koblentz-Mishke et al. 1970; Walsh 1988) and heavily altered (Norse 1993) marine ecosystems. Moreover, trawling might have serious economic consequences: many of the world's fisheries have declined sharply, and trawling has been thought to contribute to diminished fish catches (Messieh et al. 1991), including the commercial extinction of once-bounteous fisheries for haddock (*Melanogrammus aeglefinus*) and cod on the Grand Banks (Canada). There have been protests in Europe against trawling gear since the fourteenth century because of its presumed effects on benthic organisms (de Groot 1984; Berrill 1997). Most studies of trawling effects have focused on the North Sea (e.g., Lindeboom & de Groot 1998; Kaiser, this issue) and tropical Australia (e.g., Sainsbury et al. 1993; International Council for the Exploration of the Sea 1996). It is difficult to explain why there is virtually no scientific literature on the effects of trawling for shrimp in the Gulf of Mexico, one of the world's more heavily trawled areas, nor in U.S. Pacific, Latin American, African, or Asian waters.

Role of Benthic Structures

Gauging the impact of mobile fishing gear requires an understanding of how natural disturbance affects benthic communities (Hall 1994). The sea's geological substratum ranges from massive rocky reefs through boulders, cobbles, pebbles, sands, and muds (silts and clays), reflecting depositional and erosional processes past and ongoing. In general, reefs and coarser clastic substrata are far less common than muds. Reefs and coarse sediments are most prevalent on shallower parts of continental shelves, where storm-generated waves can resuspend and remove finer sediments. Below a few tens of meters depth on the continental shelf and slope, muds are almost universal, except for sand chutes and exposed rocky outcrops in steep-sided submarine canyons or in high-latitude areas where large boulders, cobbles, or pebbles were deposited by icebergs or retreating glaciers and may now occur in deep water. In general, sandy bottoms are the least stable substrata, and their surface is often rippled with waves having periods from

a few centimeters up to a meter, reflecting ongoing or episodic resuspension. Pebbles, cobbles, and boulders are more resistant to resuspension by waves or currents and often remain fixed in ecosystems where sands are repeatedly shifted. At the smaller end of the size spectrum, silt and clay particles in muds are so vulnerable to resuspension and removal that they accumulate mainly in areas with a low frequency of resuspension (e.g., the deep sea) or high supply (estuaries).

On both hard and soft substrates, the structural complexity of benthic ecosystems is further increased by living organisms. A wide variety, including foraminiferans, coralline algae, corals, brachiopods, bryozoans, worms, and mollusks, form structures of shelly calcium carbonate on rocks down to the size of cobbles or even pebbles. Many other organisms, including algae, seagrasses, mangrove trees, sponges, cerianthid anemones, gorgonians, sea pens, phoronids, polychaete worms, amphipod crustaceans, sea urchins, and crinoids, create solid or tubular structures on the seabed.

Although the largest brown algae, giant kelp (*Macrocystis* spp.), can exceed 30 m from holdfasts on the seabed to the sea surface, biogenic structures in marine ecosystems are generally orders of magnitude smaller than in terrestrial forests. Some marine structure-formers can reach similar ages, however (Risk et al. 1998), and are no less important because their scarcity often limits the abundance of many benthic species. Far more than on land, structures that reach even a few centimeters into the water column are heavily used by a diversity of taxa, including post-settlement young of commercially important fish species, for at least three reasons. First, because seawater is far denser than air, gravity is less a deterrent to marine than to terrestrial organisms. Many organisms hover close to seabed structures, a behavior that is scarce in terrestrial species. Second, in contrast to land, where there are few suspension-feeders, a large portion of marine species capture small particles from the passing water. The speed of currents increases dramatically in the first few centimeters above the sediment-water interface (Snelgrove & Butman 1994); therefore, organisms in or on benthic structures have access to faster-moving waters, which can carry larger food particles. Third, dissolved oxygen in the millimeters-thick bottom boundary layer results from diffusion of oxygen from overlying waters and respiration in the sediment below. Oxygen in this thin layer can be eliminated by biological activity (Jørgensen & Revsbech 1985). Thus, a sizable number of benthic organisms must either extend some part of their body into the overlying well-oxygenated waters or climb even small seabed structures to avoid sediment-related anoxia.

As on land, there is also abundant biogenic structure within the substratum (Rhoads 1974). Thick mats of seagrass rhizomes maintain sediment stability in some areas (Orth 1977), and annelid and echiuran worms, bivalve

mollusks, amphipod crustaceans, shrimps, crabs, and fishes (together comprising the infauna) construct long-lived (weeks to years) burrows and tubes in soft sediments that pump oxygen into what would otherwise be an anaerobic environment (Aller 1988; Meyers et al. 1988). The perception that the seabed is a featureless biological desert occurs because people's most common experience of the seabed—on sandy intertidal beaches—represents an anomalous situation where nearly incessant wave pressure largely eliminates long-lived structures. In contrast, the vast majority of the seabed is interrupted and honeycombed with biogenic structures, and this heterogeneity is crucial to benthic ecosystems (e.g., Taylor 1978). MacArthur and MacArthur's (1961) observation—that bird species diversity is positively correlated with forest structural diversity—is even more true of biogenic structures and species in marine benthic ecosystems.

Because most of the sea bottom is essentially level, the major sites of increased surface area for habitation by small invertebrates and post-settlement fishes are structures created by larger organisms. In general, areas of the continental shelf seabed with biogenic structures have higher levels of species diversity than those areas lacking such structures. Coral reefs, among the most rugose marine ecosystems, offer a large surface area and myriad interstices for their exceptional diversity of infauna, epibiota, and associated suprabenthic species (Roberts & Ormond 1987; Reaka-Kudla 1997). In the deep sea, where diversity is generally high, mudballs created by polychaete worms provide habitat for a greater diversity of harpacticoid copepods (Thistle & Eckman 1988), and mounds made by sea cucumbers attract suspension-feeding bivalves, amphipods, and polychaetes (Levinton 1995).

Habitat structure provides surfaces for feeding and hiding places from predators and is therefore important in regulating population dynamics and species interactions of fish communities, as has been demonstrated for coral reefs, rock reefs, seagrass beds, and kelp beds (e.g., Heck & Orth 1980; Ebeling & Hixon 1991). Much less work has been done in deeper waters of the outer continental shelf. Juveniles of many fish species and other mobile fauna associate with small-scale habitat features (Grimes et al. 1986; Lough et al. 1989; Auster et al. 1994, 1995; Langton et al. 1995; Tupper & Boutilier 1995) such as cobbles, sand ripple crests, biogenic mounds and pits, clam shells, burrows, macroalgae, sponges, and amphipod tubes. The use of these features can be obligatory or facultative to particular life-history stages of a species, but habitat complexity increases the survivorship of individuals by providing cover from predators in species such as Atlantic cod (Gotceitas & Brown 1993; Walters & Juanes 1993) and American lobster (*Homarus americanus*; Wahle 1992a, 1992b; Wahle & Steneck 1992). Lough et al. (1989) found that

the pelagic juvenile stage of Atlantic cod occurs over large areas of Georges Bank, but the subsequent benthic phase juveniles were found only on the gravel habitat of the Northeast Peak. Assuming that cod settle over the whole bank, predation pressure might be responsible for this pattern of differential survival. Off Nova Scotia, Tupper and Boutilier (1995) demonstrated that juvenile cod settle in all habitats (i.e., seagrass, sand, cobble, and rock reef), but survivorship and growth are higher in structurally more complex habitats where the cod can avoid predators. Gregory and Anderson (1997) showed that the youngest cod were cryptically colored and hovered above gravel substrates with low relief, whereas older juveniles seemed to spend more time around individual large boulders.

Life Histories of Structure Formers

The effects of disturbance on benthic ecosystems are determined, in part, by species' life histories. As in forest ecosystems, structural dominants in many marine ecosystems are slow-growing and long-lived. Some sponges, for example, are believed to live 50 years or more (Dayton 1979). Northeast Pacific geoduck (*Panope generosa*) and Atlantic ocean quahog clams are estimated to live up to 146 and 221 years, respectively (Goodwin & Pease 1989; Kraus et al. 1989). A small colony of the gorgonian *Primnoa reseda* from waters between Georges and Browns Banks, Nova Scotia, Canada, was recently estimated to be about 500 years old; larger ones could reach 1500 years (Risk et al. 1998), more than the maximum longevity for Douglas fir (*Pseudotsuga menziesii*) trees (Norse 1990). In the sea, no less than in forests, frequency of disturbance relative to recruitment and growth of structure formers determines the severity of human impact, and slow growth rates of key species make recovery from disturbance a long-term process.

Again, as in forests, where widely varying proportions of species can recover from fire or logging by resprouting, some epifaunal and infaunal species can rebuild their structures after disturbance, but others, such as the tube-dwelling polychaete worm *Amphitrite johnstoni*, cannot (L.W., personal observation). Disturbances that destroy the integrity of burrows or tubes can expose infauna to high risk from predation (Kaiser & Spencer 1994), so recruitment is the only means by which these species can recover after disturbance exposes them. But like many long-lived terrestrial species—such as Douglas fir trees, which generally produce substantial seed crops once every 5–7 years and recruit successfully perhaps once in decades (Norse 1990)—many long-lived marine species do not recruit successfully every year (e.g., Beukema & Essink 1986; Dörjes et al. 1986; Lundälv 1986). The rate of ecosystem recovery after a disturbance that kills structure-forming species can be delayed by slow

recruitment, spatial patchiness of recruitment, and slow post-recruitment growth. As Runkle (1985) noted, a disturbance that is both severe and extensive can result in very long recovery times.

Recolonization and Spatial Scale

Ecosystem resilience in the sea, as on land, is affected by the spatial scale of a disturbance (Sousa 1985). Because so many marine organisms have dispersal stages that live in the plankton for hours to months (usually days or weeks), one might assume that the rate of recolonization after a disturbance would be similar for all patch sizes less than kilometers in diameter. An experiment by Thrush et al. (1996) suggests, however, that even much smaller disturbed areas may show size-dependent recolonization. They defaunated intertidal sand patches of 0.203 m², 0.81 m², and 3.24 m² and sampled for 9 months to assess recovery. They found surprisingly slow recovery after defaunation, particularly in the larger patches. Because the sandflat in the experiment was prone to disturbance by wind-driven waves, sediments were unstable after defaunation removed a dense mat of polychaete tubes, hampering recolonization. This suggests that larger disturbances that destroy organisms that maintain habitat stability are likely to recover very slowly, particularly in wave-disturbed soft bottoms.

Several mechanisms can be invoked to explain slow recolonization of even small patches. First, colonization of patches is affected by patch type: type I patches—those surrounded by undisturbed communities—are colonized both from the perimeter and by dispersed propagules (Connell & Keough 1985; Sousa 1985), whereas type II patches—undisturbed spots surrounded by vast disturbed areas—are the source of colonizers, especially over short distances. Key components of benthic ecosystems, including amphipods, isopods, and other small crustaceans do not have planktonic larvae but have direct development and characteristically short-distance dispersal across the seabed. In addition, in temperate waters at least, production of propagules is seasonal, so disturbed patches may sit for some time before recolonization can occur. Second, disturbance alters the seabed physically and chemically. Watling et al. (unpublished data) have shown that scallop dredging in Maine muddy sand sediments removed the top 4 cm of sediments. They found that this upper sediment layer contains the highest-quality food but is easily resuspended and carried away by mobile fishing gear, so sediment food quality decreases. Several groups of invertebrates did not recolonize the disturbed patch until the food quality had recovered. Third, there are likely to be non-linear changes in recolonization, depending on the aggregation of individual disturbances and the resulting fragmentation of the landscape (Hall et al. 1994).

Adaptation to Disturbance Frequency

The severity of a disturbance can range from damaging only the most sensitive organisms to destruction of all multicellular life. The prevailing disturbance regime and the degree to which it is ameliorated by biotic structures (e.g., tube mats of polychaetes that bind sand grains together) are key factors determining the impact of anthropogenic disturbances (Brylinsky et al. 1994; Kaiser & Spencer 1996). In communities visited by severe disturbances at frequent intervals, only the most resistant or resilient species are likely to be present as adults when the next disturbance occurs. Thus, an event that resuspends the upper 10 cm of sediment in a sandy beach is likely to have minimal effects because organisms living there must have adaptations that confer resistance (such as rapid burrowing) or else must recolonize disturbed areas quickly; organisms lacking these abilities would have been eliminated by previous disturbances. Conversely, communities that rarely experience severe disturbance are likely to lose many species because their selection regimes have not filtered out organisms with low resistance or resilience. In general, the frequency of severe disturbances decreases sharply with increasing depth; continental slopes (except in high relief areas such as submarine canyons, where turbidity currents can occur) have few or no natural agents of severe, large-scale physical disturbance.

Agents of Benthic Disturbance

Agents of benthic disturbance include abiotic processes such as lava flows and volcanic ashfalls, mass-slumping on steep slopes in submarine canyons, wave-generated turbulence, currents generated by tides, winds, or waves, and iceberg scour. Biological disturbance processes include bioturbation—sediment movement by animal burrowing and tunneling—and digging for food by whales, walrus, fishes, and crabs. Anthropogenic disturbances include harbor dredging and dredge disposal, gravel extraction, anchoring and ship grounding, fishing using explosives, muro ami (in which weighted bags smash reef corals to scare fishes from their hiding places so they can be netted by divers), and bottom trawling and dredging.

Although the size, shape, and types (I or II) of disturbed patches (Sousa 1985) affect recolonization and succession after disturbance, a useful first-order estimate of the global impact of a disturbance is the product of severity and frequency. If either is low, then impact overall is low: for example, the global impact of a severe local disturbance is not high if its frequency is low when averaged over the vast area of the world's continental shelves. Severity can be measured as the proportion of

individuals damaged, removed, or killed or by the energetic cost and time required for rebuilding burrows, tubes, or shells. Frequency (analogous to fire frequency in Agee 1993) is the percentage of area disturbed per year. The inverse is what fire ecologists call return interval, the time between successive events at a given place. We can begin to quantify the effects of disturbance on continental shelves worldwide by examining these factors for natural and anthropogenic disturbances.

Natural Disturbances

Very large storm waves can affect the seabed at maximum depths of about 30–40 m, with increased current velocities at 60–70 m (Hall 1994), perhaps even deeper. Wave impacts are most important in the narrow intertidal and shallow subtidal zones, especially near exposed outer coast headlands. For example, Witman (1987) noted that Northwest Atlantic horse mussels (*Modiolus modiolus*) are excluded from depths below 9 m at many wave-exposed sites and that storm-related dislodgment is the most significant source of mortality. Although wave intensity is high during major storms, severity is low because most species living in storm-affected areas are adapted to resisting these events or to recovering quickly. Hurricane-force storms can increase wave pressure in bands hundreds of kilometers wide, but the seabed is physically disturbed mainly in the shallows. The frequency of major storms can vary from several per month along exceptionally stormy coasts to one per century or longer. Averaged over the world's continental shelves, storm frequency is fairly low, and we rate the impact of wave disturbance as low.

Nearshore tidal currents can resuspend and remove all but the largest sediment particles, leaving bottoms of boulders, cobbles, or pebbles. In deeper waters offshore, currents are rarely strong enough to remove even fine, silt-sized particles (Nowell et al. 1981). Where high currents are nearly constant, severity is generally low because organisms are adapted to deal with—and benefit from—currents, and they are seldom lost. As with waves, because of low severity, we rate the impact of current disturbance on benthic communities as low.

Icebergs can plow deep gouges in the seabed as winds and currents move them. They are important agents of disturbance along the coasts of Antarctica, in the Arctic Ocean and even occasionally on the Grand Banks of Newfoundland. Few if any organisms can withstand the tremendous forces icebergs generate. In nearshore Antarctic and Arctic waters, iceberg scour is frequent enough that communities are structurally more complex and more diverse below the depth of scour. The frequency of iceberg scour averaged over the world's continental shelves is very low, however, so impact is low.

Animals moving through marine sediments shift sediment particles through the process of bioturbation,

thereby disrupting the lives of smaller sediment-dwellers. Digging by large, deep-dwelling polychaetes, bivalve mollusks, and thalassinid crustaceans can slow or stop recruitment by covering newly settled larvae repeatedly with layers of sediment. But most sediment movement from bioturbation is extremely local, occurring over a scale of millimeters to a few centimeters (Wheatcroft et al. 1990)—except, perhaps, for the large mounds produced by thalassinid crustaceans (Suchanek 1983). Therefore, although sediment movement rates may be remarkably high (to thousands of litres of sediment shifted annually per square meter), sediment particles and the binding organic matrix are generally not removed, and most animals are not affected by movements of the individual mineral grains. Severity is low because sediment dwellers have time to repair burrows or tubes as other animals are shifting sediment particles. Although frequency can be very high, severity is low, and therefore impact is low.

In some regions, foraging by animals such as California gray whales (*Eschrichtius robustus*) can remove up to 6 m² of the sediment surface in one bite (Oliver & Slattery 1985), whereas fishes and birds can disturb patches on the order of tens of square centimeters (Hall et al. 1994). This type of foraging can be successful only where the bottom supports dense aggregations of prey (amphipod crustaceans of the genus *Ampelisca* in the case of the gray whales). Blue crabs (*Callinectes sapidus*) seeking bivalves and polychaetes dig pits that can be an important source of disturbance where their populations are high (Virnstein 1977). Severity from foraging is high but very local (e.g., near hauling-out sites used by walrus [*Odobenus rosmarus*]), and frequency is low when averaged over the continental shelf. The impact of foraging predators, therefore, is low.

Anthropogenic Disturbances

Dredging of the seabed in harbors and navigation channels completely removes upper sediment layers and resident biota and often redeposits them onto an area of seabed that can differ geologically and biologically. Recolonization of dredged and disposal sites can be rapid, but new colonizers are unlikely to be the same species as the original inhabitants, and it can take years for the dredged site to return to a community composition approximating that of pre-dredge conditions (Rhoads et al. 1978). Further, because harbor sediments are often heavily polluted, this issue is as much one of contaminant dispersal as it is one of physical disturbance. Although severity is high and individual disturbances may be large—tens to hundreds of meters wide along a channel that can be kilometers in length—dredging occurs only in shallow waters; the vast majority of the shelf is never dredged, so frequency is low and impact, overall, is low.

Table 1. Some experimental studies on trawling and dredging impacts on benthic communities.

<i>Gear</i>	<i>Substrate type, depth</i>	<i>Region</i>	<i>Study conditions</i>	<i>Results</i>	<i>Reference</i>
Beam trawl, 2 m	sand, 20 m	southern North Sea	site hauled once; number of tickler chains altered	sessile organisms such as hydroids, tube-making polychaetes, light-shelled bivalves, and echinoids were badly damaged; mobile macrofauna not affected	de Groot & Apeldoorn 1971
Beam trawl, 12 m	sand, well packed, 30 m	southern North Sea	area trawled 3 times; sampling by box core before and immediately after drag	decreased abundance of small heart urchins and various polychaetes; increased abundance of small tellinids and magelonids, possibly due to redistribution in sediment	Bergman & Hup 1992
Beam trawl, 4 m	gravel, cobble, 32 m	Irish Sea	10 hauls with 4-m and 3 with 2-m beam trawl; catches compared	density of sessile epifauna reduced 50%	Kaiser & Spencer 1994
Beam trawl, 4 m	sand, 30 m	Irish Sea	experimental lines trawled 10–20 times	benthos of less mobile sediments showed a 58% reduction in abundance and 50% reduction in species; least abundant species suffered most severe losses	Kaiser & Spencer 1996
Otter trawl, 20-m footrope and 90-kg doors	very fine mud, 20 m	Maine, U.S.A.	site hauled once; sampled 1 day after drag	surface sediment lost	Mayer et al. 1991
Otter trawl	sand, 10 m	New South Wales, Australia	area trawled repeatedly for 1 week; samples before and after trawl by grab	most infauna were rare, making comparisons difficult, but there appeared to be no difference in the faunal composition before and after trawling	Gibbs et al. 1980
Roller-rigged otter trawl	gravel, cobble, 20 m	Georgia, U.S.A.	area trawled once; area surveyed by divers	heavy damage only to barrel sponges; slight damage to octocorals; all recovered after 12 months	Van Dolah et al. 1987
Scallop dredge	muddy sand, 4 m	Maine, U.S.A.	site hauled many times; sampled 3 times over 5 months before drag and 3 times over 9 months after drag	upper 4 cm of sediment lost and sediment coarsened; recovery took 9 months for amino acids, total microbial biomass, total abundances of cumaceans, and phoxocephalid and photid amphipods	L.W. et al., unpublished data
Scallop dredge	sand, 5 m	Scotland	several tows over the same track over 9 days; samples at 1–5 and 9 days	infauna numbers tended to increase with increasing dredge activity, but biomass decreased; sessile polychaetes, heart urchins, and sand eels suffered greatest decreases	Eleftheriou & Robertson 1992
Scallop dredge	poorly sorted mud with shell hash, 8 m	Maine, U.S.A.	site hauled once; sampled 1 day after drag	surface labile organic matter (especially chlorophyll and protein) lost from upper 2 cm, some due to resuspension and some to burial; surface layers also became enriched in anaerobic microbiota	Mayer et al. 1991
Scallop dredge	sand, 24 m	New Zealand	5 parallel tows in experimental site	immediately after dredging, 50% of the macrofauna showed significant abundance reductions; community composition also differed between control and experimental plots; some plots remained different for 3 months	Thrush et al. 1995
Scallop dredge	sand, 15 m	Victoria, Australia	each site towed twice	most species showed reductions of 20–30% in abundance after dredging; recovery strong with seasonal recruitment, although some species had not returned 14 months after impact	Currie & Parry 1996
Hydraulic dredge	silt and clay to silty sand, 2 m	Italy	site dredged nearly completely once	fine sediments were resuspended and removed, resulting in change in grain size; furrows 10 cm deep persisted up to 2 months; all larger macrobenthos were removed by dredging; after 2 months site recolonized by small individuals	Pranovi & Giovanardi 1994

Table 2. Some observational studies on trawled or dredged sites, with inferences being drawn about disturbance mechanism.

<i>Gear</i>	<i>Substrate type, depth</i>	<i>Region</i>	<i>Observations</i>	<i>Reference*</i>
Otter trawl with chains and rollers	sand and cobble, with extensive bryozoan beds, 10–35 m	New Zealand	no trawling in the grounds until synthetic fibers were available; extensive trawling from 1960s to 1970 then destroyed almost all bryozoan beds, considered to be a nursery area for snapper; trawling prohibited in 1980	Bradstock & Gordon 1983
Otter trawls	sand with extensive epibenthic organisms, 50–200 m	Australia, NW shelf	area not trawled until 1959; extensive trawling by Japanese and Taiwanese produced tons of by-catch and resulted in shift of major fish species caught; preferred species associated with epibenthic colonial invertebrates; half of shelf closed to trawling by 1987; recovery is being monitored	Sainsbury 1991; Sainsbury et al. 1993
Otter trawls	gravel bank with mud overlay, 100 m	Gulf of Maine, Jeffreys Bank	extensive sponge community observed in 1987; repeat observations in 1993 showed overturned boulders and reduced cover of sponges; area may be a refuge for juvenile gadoids	Auster et al. 1996; L.W., unpublished data
Scallop dredge and otter trawl	sand, cobble, and shell, 30–40 m	Gulf of Maine, Swans Island	reference and fished sites surveyed by ROV video; epifaunal organisms dominant in reference areas; cover of these species decreased in fished areas	Auster et al. 1996
Scallop dredge and otter trawl	gravel and cobble, 40–90 m	Georges Bank	areas closed to fishing compared with fished sites; compared with the disturbed sites, undisturbed areas had higher numbers of organisms, biomass, species richness and species diversity; undisturbed sites had higher numbers of bushy organisms, making the benthic environment structurally more complex	Collie et al. 1997
Scallop dredge	sand, boulders 80 m	Gulf of Maine, Fippennies Ledge	area fished for scallops showed reduced densities of scallops, polychaetes (<i>Myxicola</i>) and tube-dwelling anemones (<i>Cerianthus</i>) as observed by submersible photos	Langton & Robinson 1990
Scallop dredge	sand	Gulf of Maine, Stellwagen Bank	dredge path and adjacent areas examined with ROV video; dredge path identified as linear strips devoid of benthic microalgae; hydroids were dense in undisturbed area but eliminated from dredge path; shrimp density increased with increased hydroid density outside of dredge path but shrimp absent in dredge path	Auster et al. 1996
Prawn trawl	sand	Gulf of Carpentaria, Australia	areas fished for 20 years were surveyed before and after opening for prawn trawl fishery; numerical abundance of 52 of 82 fish species remained unchanged; 30 taxa changed in abundance, some decreased (benthic) and others (benthic-pelagic) increased; impacts on invertebrates not reported	Harris & Poiner 1991
Prawn and scallop trawls	sand	SW Australia	areas open and closed to trawling were surveyed for bycatch (primarily fish); trawled and untrawled areas not significantly different in their catch; one area, with seagrass and not trawled had very high biodiversity; impact of trawling considered low because the target species live primarily on open sand bottoms	Laurenson et al. 1993

*Sites in all studies chosen have high probability of having been disturbed by fishing activities.

Marine gravel deposits are mined for building, but gravel beds can have high species diversity because the individual sediment particles are quite large and pack loosely, leaving interstitial spaces large enough to be inhabited by infauna. Gravels also offer hard substrate for epibiota. When gravel is mined, severity is great: the entire fauna is removed. Moreover, the pits left by gravel mining operations are large (tens to hundreds of meters), but gravel mining is so localized that the average fre-

quency for the continental shelf is low. The overall impact of this activity is therefore low.

TRAWLING AND DREDGING SEVERITY

Two types of studies have examined effects of mobile fishing gear: (1) experimental studies in which an area of the sea bottom is disturbed by fishing gear and the post-disturbance biota is compared with an undisturbed

nearby area and (2) observational studies in which a fished area is compared with an area that is either off-limits to fishing or where such fishing has not yet commenced. Results from the two types of studies are summarized in Tables 1 and 2. Table 1 contains only those studies where there was evidence of a reasonably undisturbed control site that could be compared to the experimentally trawled site, thereby omitting much published research done in areas where fishing was still occurring.

All experimental studies were done in shallow waters on substrates that are generally hard or clean, that is, with very little silt or clay, or in areas that were not fished because on most bottoms that can be fished control sites are unavailable. Because the bottoms studied are primarily sands, most of these sites either have strong currents or are swept by storm waves. Because these bottoms have infaunal communities dominated by species adapted to frequent physical disturbance, it is hardly surprising that the impacts of trawling and dredging seen in these studies were limited. Even so, each community studied showed the loss of some species, usually the larger-bodied species living buried in the sand. Notably different is the study of Watling et al. (unpublished data) of a muddy sand community subjected to scallop dredging, where exclusion of species from the dredged site due to the loss of low-density, high-quality food particles from the sediment persisted until the food value of the surface layer improved.

Missing from these experimental studies are those that might be conducted at depths below the storm-wave base or in areas of significant epifaunal growth. A number of the observational studies, on the other hand, were conducted in just those areas where experimental studies would be difficult. In the heavily trawled North Sea, Riesen and Reise (1982) and Reise (1982) noted that the epifauna, especially the large *Sabellaria* reefs, have already been removed. In areas where there has been substantial fishing pressure on bottoms with large epifaunal, colonial invertebrates—especially sponges and cnidarians—there is clear evidence that epifauna were removed by the fishing gear (e.g., Bradstock & Gordon 1983 in New Zealand; Sainsbury 1991 in Western Australia). On Jeffreys Bank in the Gulf of Maine, large sponges disappeared from bottom communities at 100 m depth (Auster et al. 1996) between July 1987 and August 1993. The presence of overturned boulders in 1993 suggests that the cause was mobile fishing gear. In a comparison before and after the start of a large trawl fishery in North-western Australia, Sainsbury (1987, 1988) found that the proportion of commercial fishes in the high-value genera *Lethrinus* (emperors), *Lutjanus* (snappers or seaperch), and *Epinephelus* (groupers or rockcod) dropped from 45–77% of the catch before trawling to 15% afterward. Fishes that are much less prized commercially, including the genera *Nemipterus* (threadfin-bream) and *Saurida* (lizardfishes or grinnings), became far more important.

Sainsbury concluded that the effects of trawling on habitat were most likely responsible because the catch rates of structure-forming sponges and gorgonians had also decreased dramatically. Photographs showed emperors and snappers often associated with sponges, whereas threadfin-bream and lizardfishes were associated with open sandy bottoms. In all the cases in Table 2, evidence for biodiversity loss is seen either as a drop in structure formers in bycatch, a decrease in catch of target species using structurally complex bottoms, or a loss of large structure formers observed from submersibles or remotely operated vehicles.

In areas inhabited by species adapted to being excavated or resuspended, such as sandy beaches or current-swept channels between islands, trawling and similar fishing methods might approximate natural physical disturbances. But the extent of these ecosystems is very limited. Elsewhere, trawling kills seabed organisms by crushing them, by burying them under sediment, and by exposing infauna and under-rock cryptofauna to predators. Bergman et al. (1998) found marked differences in resistance among species in the path of beam and otter trawls in different substrates. For example, a 12-m beam trawl towed on silty sediment killed none of the jack-knife clams (*Ensis* spp.) but 82% of sanguin clams (*Gari fervensis*), and a Norway lobster (*Nephrops norvegicus*) otter trawl on silty sand killed 34–100% of individuals among various groups of smaller benthic crustaceans.

The effects of mobile fishing gear where severe disturbances are naturally rare or absent depend on substrate type. In “hard-bottom” areas, where the seabed consists of various combinations of rocky reefs, boulders, cobbles, and pebbles and there is an abundance of emergent epibiota, mobile fishing gear removes large epifaunal invertebrates such as sponges, cnidarians, and bryozoans and moves boulders along the bottom. This reduces habitat for myriad small species and food for others. Second, on pebbles, sands, and muds, homogenization of the bottom eliminates habitat features important to recruits of the exploited fish populations and to many other species, including ones that commercial fishes eat. Loss of nursery habitat can mean a progressive decline in economically important fisheries. Third, on muddy bottoms, mobile gear passing over and through the upper 10 or so centimeters of the seabed collapse burrows and break the tubes that house small invertebrates. Many of the resident species cannot excavate new burrows or construct new tubes in later life-history stages.

Thus, mobile fishing gear reduces the structural complexity of bottom communities. Hydraulic clam dredging is as severely disturbing as harbor dredging or iceberg scour. Depending on the substratum, community type, and the way trawls are rigged, trawling is not always as severe because it kills only a portion of the megafauna in its path. Use of other mobile gear, such as scallop dredging, falls between hydraulic clam dredging

Table 3. Frequency of trawling in several areas.

<i>Location (area)</i>	<i>Percent trawled annually (years)</i>	<i>Reference</i>
Limfjord, Denmark	200	Riemann & Hoffmann 1991
Irish Sea (3 ICES rectangles)	4, 12, and 50	Kaiser et al. 1996
Southern North Sea	150-200	Lindeboom & de Groot 1998
Georges Bank (37,000 km ²)	21 (1970)	Caddy 1973
Georges Bank (40,806 km ²)	200 to nearly 400 (1976-1991)	Auster et al. 1996
Gulf of Maine (65,013 km ²)	100 (1976-1991)	Auster et al. 1996
Gulf of Maine and Georges Bank, U.S. vessels only	0-450 (1993)	Pilskaln et al. 1998, this issue
Shelf south of Nantucket and Nantucket Shoals, Massachusetts 30 × 30 minute rectangles	up to 413 (1985)	Churchill 1989

and trawling in severity. Overall, we rate the severity of mobile fishing gear as high.

TRAWLING AND DREDGING FREQUENCY

Estimates of trawling and dredging frequency have appeared in a few sources (Table 3). Because the data are of varying quality and several sources are old, these values should be considered rough indicators of disturbance from mobile fishing gear. Estimating the frequency of bottom trawling, the most extensively used mobile gear, as a percentage of the world's continental shelves (which constitute 7.4% of the ocean's area, or 28 million km²) is more difficult because data are few and assumptions can be off the mark. Nonetheless, we can give two estimates. McAllister (1995) assumed that there were 12,000 active trawlers (of 23,000 over 100 tons) towing nets 25 m wide at 5 km/hour for 6 hours a day for 175 days per year, thus covering 1.575 million km² per year. This figure, equivalent to 5.6% of the total area of continental shelf, is too low, in part because it omits the large majority of trawlers, those under 100 tons.

Other data and assumptions can produce a very different estimate. Slavin (1981) noted that in 1978 Mexico's 3000 shrimp trawlers caught 67,000 tons. If shrimp trawlers from other nations caught an equivalent tonnage per boat, then the 1978 world shrimp catch of 1.324 million tons was caught by 59,292 boats. Assuming that shrimpers constituted two-thirds of the world's trawlers, the number of trawlers of all kinds was 88,939 worldwide. Assuming that two-thirds of those were active and that they towed nets 25 m wide at 5 km/hour for 10 hours a day for 200 days per year, then the area they swept annually was 14.8 million km², or 53% of the world's continental shelf area, an order of magnitude higher than McAllister's (1995) estimate. Moreover, this estimate might be too low, for three reasons. First, Pilskaln et al. (this issue) used "realistic estimates" of 40-m trawl track widths and 5.5 km/hour trawl speeds; use of these figures would raise our estimate another 76%. Second, we omitted other towed gear; their inclusion would further raise estimates. Third, because fishing effort and fishing power have increased considerably

since 1978, our estimate likely errs on the low side. Until more reliable data are available, it is reasonable to assume that an area equivalent to the world's continental shelf is swept by trawlers every 2 years. Even if our estimate is high by a factor of two, trawling an area equivalent to the entire world's continental shelf every 4 years is nonetheless a disturbance to the biosphere on a scale that had not previously been imagined. Of course, trawl frequency is unevenly distributed; in an area that is trawled an average of 100% annually, a substantial fraction might not get trawled in a given year, whereas some spots can be trawled an astounding 40,000% annually (Rijnsdorp et al. 1991). Figure 1 in Pilskaln et al. (this issue) hints at the variability in trawling effort in the Gulf of Maine.

Not all trawling occurs on the shelf. As the most accessible fisheries continue to decline, trawlers are focusing increasingly on "underutilized species" of the deeper continental slope and remote oceanic seamounts, such as orange roughy (*Hoplostethus atlanticus*) and grenadiers or rattails (Macrouridae) (Merrett & Haedrich 1997). Deep-water trawling must profoundly alter ecosystems whose species generally are not adapted to resisting or recovering from severe physical disturbances.

In unaltered benthic ecosystems, severe disturbances tend to be low in frequency: they are either large and rare or common but restricted spatially (Connell & Keough 1985). This is also true in forest ecosystems: "Where fires burn frequently, they are seldom highly destructive; infrequent burns, on the other hand, tend to be catastrophic" (Perry 1994). But use of mobile fishing gear is exceptional among agents of disturbance: its effects are severe, yet it occurs at a frequency orders of magnitude higher than other severe disturbances.

Other Effects of Mobile Fishing Gear on Sediments

Mud bottoms comprise sediments with very small mineral grains bound loosely with organic material and associated microorganisms, on and in which live epifaunal and infaunal macroorganisms. Anoxic conditions commonly occur within a few millimeters of the sediment-

water interface, except where pumping by burrow dwellers oxygenates the surrounding sediment. Although the impacts of mobile fishing gear on structural complexity are clear, their effects on sedimentary microenvironments are less certain. Using knowledge of fundamental biological oceanographic processes, we can hypothesize that repeated use of mobile fishing gear has several consequences. First, the homogenization of muddier sediments decreases the sediment-water interface area by collapsing burrows and destroying tubes made by species dwelling within the sediment. This could have consequences for carbon and nitrogen cycling that are presently unknown (Pilskaln et al. 1998, this issue). Second, trawling on the continental shelf south of Georges Bank (Churchill 1989) and in Wilkinson Basin (C. H. Pilskaln, personal communication) results in a much-thickened bottom nepheloid layer of resuspended sediment. When resuspended, organic material with high-quality as food is oxidized to some extent in the water column and settles to the bottom much lower in food value. Diminished availability of high-quality food on the seabed might reduce the species diversity of these muddy bottom areas. Third, the removal of organic material by mobile fishing gear is biogeochemically analogous to the common post-clearcutting practice of broadcast burn or pile-and-burn site preparation, which oxidizes large amounts of slash (remains of logged trees) and forest floor (organic detritus), exporting the ecosystem's nutrients as ash into the atmosphere. Given the high frequency of trawling, the increased resuspension and subsequent oxidation of carbon that would otherwise be buried in sediments could be a significant source of carbon to the water column and atmosphere.

Trawling and dredging for shellfish resuspend large amounts of sediments (Pilskaln et al. 1998, this issue). Riemann and Hoffmann (1991) found short-term increased suspended sediment loads of 960-1361%. The sediment plume and organisms (e.g., polychaetes, amphipods) entrained within it affect water clarity, oxygen content, and the energy relations of organisms living or feeding where the plume interacts with the bottom. High suspended sediment loads in shallow waters affect photosynthesizers in the water column and on the seabed. High suspended sediment loads are associated with shifts in fish communities from domination by visual predators to those that find food by touch and chemosensation, as well as alteration of the benthic community from one dominated by suspension-feeders to one dominated by deposit-feeders. Once deposit-feeders become dominant, they can prevent recovery of suspension-feeders by feeding on and smothering settling larvae (Dayton et al. 1995).

Resuspension of buried organic material by trawlers increases oxygen demand in the water column; in areas where dissolved oxygen is already limiting, this increase could significantly affect plankton and nekton species

composition, even contributing to the growth of anoxic areas such as "the dead zone" in the Gulf of Mexico. Indeed, it could be a substantial unaccounted source of atmospheric carbon dioxide. In polluted areas, resuspension can also increase exposure of water column and benthic species to toxic materials adsorbed on sediment grains which were previously sequestered in the sediment. Resuspended sediment and pore water can also add to the nutrient loading of the water, perhaps triggering phytoplankton blooms.

Trawling and Clearcutting

Trawling disturbs the seabed in ways that can be compared to terrestrial disturbances. Like surface mining, it displaces large amounts of surface organic material, but it doesn't necessarily kill all macroscopic life. Like plowing, it disturbs the upper several centimeters of substrate at return intervals of years or months; but it is not conducted on private lands where harvested species are reseeded but in areas that are under public ownership and considered "natural." It is more similar to clearcutting (Table 4), but there is one great difference: whereas forest loss is estimated at 100,000 km² per year worldwide (Food and Agriculture Organization of the United Nations [FAO] 1995), the area trawled annually is about 150 times as great. The FAO's estimate of annual worldwide forest loss, however alarming, is smaller than the combined area of Georges Bank and the Gulf of Maine (Auster et al. 1996), which is trawled each year.

Mobile Fishing Gear as a Conservation Issue

Since the dimensions of the biological diversity crisis became clear (Myers 1979; Lovejoy 1980; Norse & McManus 1980), biologists have told decision makers and the public that physical disturbance—particularly habitat loss from forest clearcutting—is the leading cause of biological diversity loss. Until this decade, however, biodiversity loss in the sea was largely overlooked, with the scant attention focused mainly on the important threats of overexploitation of fisheries and pollution. Now, with growing understanding that marine biodiversity is imperiled, we have shown that the sea is experiencing physical alteration from bottom trawling and other towed fishing gear on a scale that was not previously appreciated. The use of mobile fishing gear, whose effects resemble those of clearcutting, occurs at a rate two orders of magnitude higher than forest loss worldwide. With the possible exception of agriculture, we doubt that any other human activity physically disturbs the biosphere to this degree. The lack of scrutiny of bottom trawling until now is indicative of the mis-

Table 4. A comparison of the impacts of forest clearcutting and trawling of the seabed.*

<i>Impact</i>	<i>Clearcutting</i>	<i>Bottom trawling</i>
Effects on substratum	exposes soils to erosion and compresses them	overturns, moves, and buries boulders and cobbles, homogenizes sediments, eliminates existing microtopography, leaves long-lasting grooves
Effects on roots or infauna	stimulates, then eliminates, saprotrophs that decay roots	crushes and buries some infauna; exposes others, thus stimulating scavenger populations
Effects on emergent biogenic structures and structure formers	removes or burns snags, down logs, and most structure-forming species aboveground	removes, damages, or displaces most structure-forming species above sediment-water interface
Effects on associated species	eliminates most late-successional species and encourages pioneer species in early years to decades	eliminates most late-successional species and encourages pioneer species in early years to decades
Effects on biogeochemistry	releases large pulse of carbon to atmosphere by removing and oxidizing accumulated organic material; eliminates nitrogen fixation by arboreal lichens	releases large pulse of carbon to water column and atmosphere by removing and oxidizing accumulated organic material; increases oxygen demand
Recovery to original structure	decades to centuries	years to centuries
Typical return time	40–200 years	40 days to 10 years
Area covered per year globally	~0.1 million km ² (net forest and woodland loss)	~14.8 million km ²
Latitudinal range	subpolar to tropical	subpolar to tropical
Ownership of areas where it occurs	private and public	public
Published scientific studies	many	few
Public consciousness	substantial	very little
Legal status	activity increasingly modified to lessen impacts or not allowed in favor of alternative logging methods and preservation	activity not allowed in a few areas

*Sources include Norse (1990), Food and Agriculture Organization (1995), and discussions at the 1996 trawling workshop of the Marine Conservation Biology Institute.

match between humankind's environmental impacts and priorities.

An activity that each year severely disturbs an area of seabed as large as Brazil, the Congo, and India combined must affect the structure, species composition, and biogeochemistry of benthic ecosystems on both local and global scales. It is disheartening that scientists have not yet done the research necessary to determine whether trawling has caused large numbers of extinctions, and that sequential overfishing, improved technologies, and the lack of marine protected areas make it difficult or impossible to find suitable control areas.

Our marine conservation ethic is far less advanced than our land ethic. For example, recent decades have seen a dramatic change in attitude in many countries about killing apex predators such as tigers, wolves, and eagles, whereas there has been much less concern about killing sharks, tunas, and marlin. In the United States (SeaWeb 1996) and many other countries, public concern about maintaining marine biodiversity seems to be increasing but has not yet become deep or pervasive. But even in the face of compelling evidence for concern about the effects of trawling on benthic biodiversity, the

pivotal question for many people will be economic: how does trawling affect fisheries? In Australia, on the other hand, perhaps because of a widespread acceptance that its biodiversity is truly unique, there is a more balanced view. Recently, for example, the president of the South East Trawl Fishing Industry Association proposed a voluntary interim closure of a 370-km² region of seamounts south of Tasmania until a biodiversity assessment could be made (The Australian, Sydney, 9 June 1998:8).

Like clearcutting, use of mobile fishing gear does not eliminate biological activity. Rather, it converts ecosystems dominated by disturbance-intolerant equilibrium species to ones dominated by disturbance-tolerant opportunistic species. In general, trawling undermines fisheries for species that benefit from complex benthic structure. For fishes that do not need benthic structure, however, some trawling is likely to increase their populations by encouraging opportunistic prey species or reducing disturbance-intolerant competitors. Thus, increasingly, trawled seabeds might have fewer sabellariid polychaete reefs but more cirratulid and capitellid polychaetes, fewer sponges and gorgonians but more penaeid shrimps and brittle stars, fewer groupers and snap-

pers, but more threadfin-bream and lizardfishes, fewer cod but more plaice. In general, where structure-forming species have life spans of years or more but the chronic disturbance of trawling occurs at shorter return intervals, benthic succession will not proceed to climax and fish communities that need a structurally complex seabed will disappear. A terrestrial analogue is the change in animal species when virgin forest is converted to cattle pasture. Thus, trawling could prevent recovery of diminished fish stocks, such as Georges Bank and Grand Banks Atlantic cod, whose juvenile stages have higher survivorship in structurally complex habitats, but it can benefit fisheries for some other species. This kind of anthropogenic change—which foresters call “type conversion”—has occurred in an intensively trawled off-shore area in the Irish Sea, of which Lindeboom and de Groot (1998) say “[t]he present species-poor and low biomass fauna may represent an artificial man-made community adapted to the regular fishing disturbance experienced at this site.” They conclude that “if trawling intensity remains high, these communities may never recover.”

At present, people trawl almost anywhere they want, and the sea’s equivalents of ancient forests are becoming cattle pastures by default, not by design. Merrett and Haedrich (1997) put it this way: “there still seems to be a general frontier mentality that operates in high-seas fisheries.” Governments generally do not apply the precautionary principle to the sea; individuals and corporations do what they wish unless some governing authority demonstrates conclusively that they should not, decides to prohibit the activity, and enforces its prohibition. As highly structured benthic ecosystems and fisheries continue to decline, fishery managers must make more conscious choices about the mix of disturbance-intolerant communities (including fishes) and disturbance-tolerant ones under their jurisdiction.

In general, fisheries managers regulate the use of varying kinds of fishing gear by trying to determine the influence of the gear on the population parameters of target species. When disputes arise, the common response has been to look at the issue as a “gear conflict.” This is especially true for mobile fishing gear, which were not used on hard bottoms in northern waters such as the Gulf of Maine, the Grand Banks, and the Bering Sea until the mid-1980s. Rather, those ecosystems were typically fished with hook and line gear, which has far less physical impact on the bottom community. As the fishing industry developed rockhopper trawls, topographically rough bottoms were no longer unfishable, and longline fishermen saw their fishing grounds produce progressively fewer fish. The response from the New England Fishery Management Council, as an example, has been to consider the complaints of the long-liners under the rubric of gear conflict, thus escaping the need to look at the more fundamental question of whether trawling is

reducing the economic value of the fisheries overall as a result of reduced habitat complexity, or the even broader question of what trawling is doing to biological diversity.

Typically, people who catch and process fish have been considered the primary stakeholders in this conflict, and decisions have often been driven by short-term economic factors. Because of the long-term—even irreversible—changes that mobile fishing gear can bring to benthic communities, all those with an interest in the sea’s biological diversity and integrity should consider themselves stakeholders in this debate. In the U.S. Pacific Northwest, the political decisions that governed logging of ancient forests on federal lands began to change in the late 1980s, when citizens beyond Northwest timber towns became aware and involved. Examining the use of mobile fishing gear from the viewpoint of a broader group of stakeholders might produce very different solutions. To serve the public interest, meaningful input on managing the seabed has to involve people with interests broader than fisheries alone.

Recent developments suggest that concern about fishing effects is increasing in the United States. The recently reauthorized Magnuson-Stevens Fishery Conservation and Management Act (National Marine Fisheries Service 1997) contains provisions for the first time that require regional Fishery Management Councils to identify essential fish habitat (EFH), which is “those waters and substrate necessary to fish for spawning, breeding, feeding, or growth to maturity.” This law requires the National Marine Fisheries Service and the Fishery Management Councils to identify “activities with known or potential adverse effects on EFH,” and it allows them to impose fishing-gear restrictions or to close areas to fishing.

Still, management of the living resources of the U.S. seabed is effectively controlled by the Department of Commerce’s National Marine Fisheries Service, which is responsible for determining which aspects of the habitat are important for fish production. We have seen, however, that some benthic communities can have productive fisheries in the face of continual physical disturbance by mobile fishing gear. The question, therefore, is who is responsible for maintaining the overall biodiversity of the seabed. To date, maintenance of biodiversity has hardly been a priority of fisheries managers.

Some management options could stem the loss of biodiversity and fisheries dependent on benthic structure, could benefit all fishers and consumers in the longer term, and could minimize the short-term economic harm to trawlers and dredgers:

- (1) Using a precautionary approach to management: the burden of proof should rest with those who would alter the sea’s biodiversity and integrity. This might lead to lessened use of mobile fishing gear in structurally complex benthic ecosystems.

- (2) Matching fishing gear types to the disturbance-

vulnerability of the seabed, thus minimizing the long-term impacts of all types of gear. This most likely would give preference to some gear types over others in each bottom type but would maintain species diversity and fisheries production in each.

(3) Establishing “no trawling zones” in a portion of all continental shelf and slope ecosystems, allowing the recovery of benthic communities to their pre-trawling state. Such reserves would offset, to some extent, the loss of de facto reserves in areas that could not previously be fished with mobile gear and where commercially important fishes were more abundant. This would provide crucial information on the effects of mobile gear and requirements for sustainable fisheries over the long term.

(4) Educating the public about the nature of the seabed and its importance for biodiversity, including its role in supporting fisheries.

(5) Ensuring opportunities for more sectors of society (beyond fishing interests) to influence the policy-making process and to hold positions of authority, in recognition that all of us are stakeholders when it comes to publicly owned marine resources.

Conclusions

Mobile fishing gear exceeds other natural and anthropogenic disturbances on the marine continental shelf and slope. By crushing, burying, and exposing benthic organisms to predation and by altering sediment and water-column biogeochemistry, trawling and dredging disrupt the structure of benthic communities from high latitudes to the tropics in ever-deeper waters. Many marine species, including the young of commercially caught fishes, use lithic and biogenic structures to avoid predation, so loss of these structures due to use of mobile fishing gear could be a major factor—in addition to overfishing—underlying diminishing demersal fish stocks worldwide. Indeed, trawling and other mobile fishing gear have effects resembling a disturbance—forest clearcutting—that has generated far more comment yet occurs on a scale two orders of magnitude smaller than use of mobile fishing gear. Thanks to improvements in fishing technologies and inadequate regulation, there are few places in the world’s continental shelves with commercially valuable fishery resources that have not been trawled or dredged. Given the rapid, progressive collapse of commercial fish stocks and the less-noticed but even more worrisome loss of biodiversity worldwide, it seems prudent to devote more resources to understanding the effects of mobile fishing gear and to act decisively to ameliorate their impacts on commercial fishery resources and other species comprising the world’s marine biodiversity.

Acknowledgments

We thank the participants and observers of the workshop on the Effects of Bottom Trawling on Marine Ecosystems for providing insights and references. Darling Marine Center staff and students, particularly C. Chisholm and A. Palma, provided crucial logistical support and served as rapporteurs. The workshop and this paper could not have happened without dedicated financial support to the Marine Conservation Biology Institute (MCBI) from the Curtis and Edith Munson Foundation, the Natural Resource Defense Council, and three components of the National Oceanic and Atmospheric Administration—Auke Bay Fisheries Laboratory of the National Marine Fisheries Service, Stellwagen Bank National Marine Sanctuary, and the Office of Strategic Policy and Planning—nor without general support to MCBI from the Heart of America Fund, Sun Hill Foundation, Rockefeller Brothers Fund, Bullitt Foundation, Geraldine R. Dodge Foundation, Educational Foundation of America, Horizons Foundation, Surdna Foundation, Bay Foundation, DuPont, New England Biolabs, E. Stanley, A. Rowland, B. Cohn, and two anonymous funders. We completed this paper while serving as Pew Fellows in Marine Conservation, and we thank the Center for Marine Conservation, where E.A.N. planned the workshop, and C. Green, E. Linen, J. Schorr, T. Steiner, A. Tinker, and E. Bertson, who provided valuable information. Drafts of the paper benefited greatly from critical reviews by P. Auster, M. Kaiser, S. Thrush, P. Valentine, D. Gordon, and A. Mathews-Amos. The figures are the work of S. Gerken. This is Marine Conservation Biology Institute contribution 17.

Literature Cited

- Agee, J. K. 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington, D.C.
- Aller, R. C. 1988. Benthic fauna and biogeochemical processes in marine sediments: the role of burrowing structures. Pages 301–338 in T. H. Blackburn and J. Sorensen, editors. Nitrogen cycling in coastal marine environments. Wiley and Sons, New York.
- Auster, P. J., R. J. Malatesta, and C. L. S. Donaldson. 1994. Small-scale habitat variability and the distribution of postlarval silver hake, *Merluccius bilinearis*. Pages 82–86 in D. Stevenson and E. Braasch, editors. Gulf of Maine habitat: workshop proceedings. Sea grant report UNHMP-T/DR-SG-94-18. University of Maine, Orono.
- 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., R. J. Malatesta, R. W. Langton, L. Watling, P. C. Valentine, C. L. S. Donaldson, E. W. Langton, A. N. Shepard, and I. G. Babb. 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* 4:185–202.
- Bergman, M. J. N., and M. Hup. 1992. Direct effects of beamtrawling on macrofauna in a sandy sediment in the southern North Sea. *International Council for the Exploration of the Sea Journal of Marine Science* 49:5–11.

- Bergman, M. J. N., B. Ball, C. Bijleveld, J. A. Craymeersch, B. W. Munday, H. Rumohr, and J. W. van Santbrink. 1998. Direct mortality due to trawling. Pages 167-184 in H. J. Lindeboom and S. J. de Groot, editors. Impact II. The effects of different types of fisheries on North Sea and Irish Sea benthic ecosystems. Netherlands Institute for Sea Research, Texel, Netherlands.
- Berrill, M. 1997. The plundered seas: can the world's fish be saved? Sierra Club Books, San Francisco.
- Beukema, J. J., and K. Essink. 1986. Common patterns in the fluctuations of macrozoobenthic species living at different places on tidal flats in the Wadden Sea. *Hydrobiologia* 142:199-207.
- Bradstock, M., and D. P. Gordon. 1983. Coral-like bryozoan growths in Tasman Bay, and their protection to conserve local fish stocks. *New Zealand Journal of Marine and Freshwater Research* 17:159-163.
- 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 Science* 51:650-661.
- Butman, C. A., and J. T. Carlton, editors. 1995. Understanding marine biodiversity: a research agenda for the nation. National Academy Press, Washington, D.C.
- 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.
- 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, and P. C. Valentine. 1997. Effects of bottom fishing on the benthic megafauna of Georges Bank. *Marine Ecology Progress Series* 155:159-172.
- Connell, J. H., and M. J. Keough. 1985. Disturbance and patch dynamics of subtidal marine animals on hard substrata. Pages 125-147 in S. T. A. Pickett and P. S. White, editors. The ecology of natural disturbance and patch dynamics. Academic Press, New York.
- 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.
- Dayton, P. K. 1979. Observations of growth, dispersal, and population dynamics of some sponges in McMurdo Sound, Antarctica. Pages 271-282 in C. Levy and N. Boury-Esnault, editors. *Biologie des Spongiaires*. Centre Nationale Recherche Scientifique, Paris.
- 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.
- de Groot, S. J., and J. M. Apeldoorn. 1971. Some experiments on the influence of the beam-trawl on the bottom fauna. Report 1971/B: 2. International Council for the Exploration of the Sea, Copenhagen, Denmark.
- Dörjes, J., H. Michaelis, and B. Rhode. 1986. Long-term studies of macrozoobenthos in intertidal and shallow subtidal habitats near the island of Norderney (East Frisian coast, Germany). *Hydrobiologia* 142:217-232.
- 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.
- Food and Agriculture Organization of the United Nations. 1995. Forest resources assessment 1990: global synthesis. Forestry report 124. Rome.
- 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.
- Goodwin, C. L., and B. Pease. 1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Pacific Northwest). Pacific geoduck clam. Biological report. U.S. Fish and Wildlife Service.
- Gordon, J. D. M., and J. E. Hunter. 1994. Study of the deep-water fish stocks to the west of Scotland. Volume 2. Appendices 1994. Report presented to Highlands and Islands Enterprise and other sponsors. Oban, Scotland, United Kingdom.
- Gotceitas, V., and J. A. Brown. 1993. Substrate selection by juvenile Atlantic cod (*Gadus morhua*): effects of predation risk. *Oecologia* 93:31-37.
- Grassle, J. F., and H. L. Sanders. 1973. Life histories and the role of disturbance. *Deep Sea Research* 20:289-299.
- Gregory, R. S., and J. T. Anderson. 1997. Substrate selection and use of protective cover by juvenile Atlantic cod *Gadus morhua* in in-shore waters of Newfoundland. *Marine Ecology Progress Series* 146:9-20.
- Grimes, C. B., K. W. Able, and R. S. Jones. 1986. Tilefish, *Lopholatilus chamaeleonticeps*, habitat, behavior, and community structure in mid-Atlantic and southern New England waters. *Environmental Biology of Fishes* 15:273-292.
- Hall, S. J. 1994. Physical disturbance and marine benthic communities: life in unconsolidated sediments. *Oceanography and Marine Biology Annual Review* 32:179-239.
- Hall, S. J., D. Raffaelli, and S. F. Thrush. 1994. Patchiness and disturbance in shallow water benthic assemblages. Pages 333-375 in P. S. Giller, A. G. Hildrew, and D. Raffaelli, editors. *Aquatic ecology: scale, pattern, and process*. Blackwell Scientific Publications, Oxford, United Kingdom.
- Harris, A. N., and I. R. Poiner. 1991. Changes in species composition of demersal fish fauna of Southeast Gulf of Carpentaria, Australia, after 20 years of fishing. *Marine Biology* 111:503-519.
- 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.
- Huston, M. A. 1994. Biological diversity: the coexistence of species on changing landscapes. Cambridge University Press, Cambridge, United Kingdom.
- Hutchings, P. 1990. Review of the effects of trawling on macrobenthic epifaunal communities. *Australian Journal of Marine and Freshwater Research* 41:111-120.
- International Council for the Exploration of the Sea. 1996. Report of the Working Group on Ecosystem Effects of Fishing Activities, 13-21 March 1996. Copenhagen, Denmark.
- Irish, K. E., and E. A. Norse. 1996. Scant emphasis on marine biodiversity. *Conservation Biology* 10:680.
- Jones, J. B. 1992. Environmental impact of trawling on the seabed: a review. *New Zealand Journal of Marine and Freshwater Research* 26: 59-67.
- Jørgensen, B. B., and N. P. Revsbech. 1985. Diffusive boundary layers and the oxygen uptake of sediments and detritus. *Limnology and Oceanography* 30:111-122.
- Kaiser, M. J. 1998. Fishing effort data independent indicators of disturbance: an important link in determining long-term change in marine communities. *Conservation Biology* 12:1230-1235.
- Kaiser, M. J., and B. E. Spencer. 1994. Fish scavenging behaviour in recently trawled areas. *Marine Ecology Progress Series* 112:41-49.
- Kaiser, M. J., and B. E. Spencer. 1996. The effects of beam-trawl disturbance on infaunal communities in different habitats. *Journal of Animal Ecology* 65:348-358.
- Kaiser, M. J., et al. 1996. Benthic disturbance by fishing gear in the Irish Sea: a comparison of beam trawling and scallop dredging.

- Aquatic Conservation: Marine and Freshwater Ecosystems 6:269-285.
- Koblentz-Mishke, O. J., V. V. Valkovsinky, and J. C. Kabanova. 1970. Plankton primary production of the world oceans. Pages 189-193 in W. S. Wooster, editor. Scientific exploration of the South Pacific. National Academy of Sciences Press, Washington, D.C.
- Kraus, M. G., B. F. Beal, and S. R. Chapman. 1989. Growth rate of *Arctica islandica* Linne: a comparison of wild and laboratory-reared individuals. *Journal of Shellfisheries Research* 8:463.
- Langton, R. W., and W. E. Robinson. 1990. Faunal association on scallop grounds in the Western Gulf of Maine. *Journal of Experimental Marine Biology and Ecology* 144:157-171.
- 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.
- Laurenson, L. J. B., P. Unsworth, J. W. Penn, and R. C. J. Lenanton. 1993. The impact of trawling for saucer scallops and western king prawns on the benthic communities in coastal waters off southwestern Australia. Report 100. Fisheries Department of Western Australia Fisheries Research, Perth, Western Australia.
- Levinton, J. S. 1995. *Marine biology: function, biodiversity, ecology*. Oxford University Press, New York.
- Levy, S. 1998. Watery wastelands. *New Scientist* 158:40-44.
- Lindeboom, H. J., and S. J. de Groot, editors. 1998. Impact II. The effects of different types of fisheries on North Sea and Irish Sea benthic ecosystems. Netherlands Institute for Sea Research, Texel, The Netherlands.
- Lough, R. G., P. C. Valentine, D. C. Potter, P. Auditore, G. R. Bolz, J. D. Neilson, and R. I. Perry. 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.
- Lovejoy, T. 1980. Changes in biological diversity. Pages 327-332 in Council on Environmental Quality and U.S. Department of State. The global 2000 report to the President. Volume 2, the technical report. U.S. State Department, Washington, D.C.
- Lundälv, T. 1986. Detection of long-term trends in rocky sublittoral communities: representativeness of fixed sites. Pages 329-345 in P. G. Moore and R. Seed, editors. *Ecology of rocky coasts*. Columbia University Press, New York.
- MacArthur, R. H., and J. W. MacArthur. 1961. On bird species and diversity. *Ecology* 42:594-98.
- Mayer, L. M., D. F. Schick, R. H. Findlay, and D. L. Rice. 1991. Effects of commercial dragging on sediment organic matter. *Marine Environmental Research* 31:249-261.
- McAllister, D. E. 1995. Status of the world ocean and its biodiversity. *Sea Wind* 9:1-72.
- Merrett, N. R., and R. L. Haedrich. 1997. *Deep-sea demersal fish and fisheries*. Chapman & Hall, New York.
- Messiah, 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 continental shelf seabed. *Continental Shelf Research* 11:1237-1263.
- Meyers, M. B., E. N. Powell, and H. Fossing. 1988. Movement of oxybiotic and thiobiotic meiofauna in response to changes in pore-water oxygen and sulfide gradients around macro-infaunal tubes. *Marine Biology* 98:395-414.
- Myers, N. 1979. *The sinking ark: a new look at the problem of disappearing species*. Pergamon Press, New York.
- National Marine Fisheries Service. 1997. Proposed rule. Magnuson Act Provisions: essential fish habitat (EFH). *Federal Register* 62:19723-19732.
- Norse, E. A. 1990. *Ancient forests of the Pacific Northwest*. Island Press, Washington, D.C.
- Norse, E. A., editor. 1993. *Global marine biological diversity: a strategy for building conservation into decision making*. Island Press, Washington, D.C.
- Norse, E. A., and R. E. McManus. 1980. Ecology and living resources: biological diversity. Pages 31-80 in *Environmental quality 1980: the eleventh annual report*. Council on Environmental Quality, Washington, D.C.
- Nowell, A. R. M., P. A. Jumars, and J. E. Eckman. 1981. Effects of biological activity on the entrainment of marine sediments. *Marine Geology* 42:133-153.
- Oliver, J. S., and P. N. Slattery. 1985. Destruction and opportunity on the sea floor: effects of gray whale feeding. *Ecology* 66:1965-1975.
- Orth, R. J. 1977. The importance of sediment stability in seagrass communities. Pages 281-300 in B. C. Coull, editor. *Ecology of marine benthos*. University of South Carolina Press, Columbia.
- Perry, D. A. 1994. *Forest ecosystems*. Johns Hopkins University Press, Baltimore.
- 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. Frequency of bottom trawling in the Gulf of Maine and speculations on the geochemical consequences. *Conservation Biology*, 12:1223-1229.
- Polet, H., B. Ball, T. Kujawski, B. W. Munday, H. Rumohr, and I. Tuck. 1998. Fishing gears used by different fishing fleets. Pages 83-119 in H. J. Lindeboom and S. J. de Groot, editors. *Impact II. The effects of different types of fisheries on North Sea and Irish Sea benthic ecosystems*. Netherlands Institute for Sea Research, Texel, Netherlands.
- Pranovi, F., and O. Giovanardi. 1994. The impact of hydraulic dredging for short-necked clams, *Tapes* spp., on an infaunal community in the lagoon of Venice. *Scientia Marina* 58:345-353.
- Reaka-Kudla, M. L. 1997. The global biodiversity of coral reefs: a comparison with rain forests. Pages 83-108 in M. L. Reaka-Kudla, D. E. Wilson, and E. O. Wilson, editors. *Biodiversity II: understanding and protecting our biological resources*. Joseph Henry Press, Washington, D.C.
- 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.
- Rhoads, D. C. 1974. Organism-sediment relationships on the muddy sea floor. *Oceanography and Marine Biology Annual Review* 12:263-300.
- Rhoads, D. C., P. L. McCall, and J. Y. Yingst. 1978. Disturbance and production on the estuarine seafloor. *American Scientist* 66:577-586.
- 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. *Helgolander Meeresuntersuchungen* 35:409-423.
- Rijnsdorp, A., P. Groot, and F. van Beek. 1991. The micro distribution of beam trawl effort in the southern North Sea. Committee Meeting 1991/G:49. International Council for the Exploration of the Sea, Copenhagen, Denmark.
- Risk, M. J., D. E. McAllister, and L. Behnken. 1998. Conservation of cold- and warm-water seafans: threatened ancient gorgonian groves. *Sea Wind* 12(1):2-21.
- Roberts, C. M., and R. F. G. Ormond. 1987. Habitat complexity and coral reef fish diversity and abundance on Red Sea fringing reefs. *Marine Ecology Progress Series* 41:1-8.
- Runkle, J. R. 1985. Disturbance regimes in temperate forests. Pages 17-33 in S. T. A. Pickett and P. S. White, editors. *The ecology of natural disturbance and patch dynamics*. Academic Press, New York.
- Sainsbury, J. C. 1996. *Commercial fishing methods, an introduction to vessels and gears*. 3rd edition. Fishing News Books, Oxford, United Kingdom.
- Sainsbury, K. J. 1987. Assessment and management of the demersal fishery on the continental shelf of northwestern Australia. Pages 465-503 in J. J. Polovina and S. Ralston, editors. *Tropical snappers and groupers: biology and fisheries management*. Westview Press, 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. Wiley, New York.
- Sainsbury, K. J. 1991. Application of an experimental approach to management of a tropical multispecies fishery with highly uncertain dynamics. *International Council for the Exploration of the Sea Marine Science Symposium* 193:301-320.
- Sainsbury, K. J., R. A. Campbell, and A. W. Whitelaw. 1993. Effects of trawling on the marine habitat on the North West Shelf of Australia and implications for sustainable fisheries management. Pages 137-145 in D. A. Hancock, editor. *Sustainable fisheries through sustaining fish habitat*. Australian Society for Fish Biology workshop. Australian Government Publishing Service, Canberra.
- SeaWeb. 1996. Presentation of findings from a nationwide survey and focus groups. SeaWeb, Washington, D.C.
- Sharp, G. D. 1988. Fish populations and fisheries: their perturbations, natural and man-induced. Pages 155-202 in H. Postma and J. J. Zijlstra, editors. *Continental shelves, ecosystems of the world* 27. Elsevier Science Publishers, Amsterdam.
- Slavin, J. W. 1981. Utilization of the shrimp by-catch. Pages 21-28 in *Fish by-catch—bonus from the sea*. IDRC-198e. Food and Agriculture Organization of the United Nations and International Development Research Centre, Ottawa, Canada.
- Snelgrove, P. V. R., and C. A. Butman. 1994. Animal-sediment relationships revisited: cause versus effect. *Oceanography and Marine Biology Annual Review* 32:111-177.
- Sousa, W. P. 1985. Disturbance and patch dynamics on rocky intertidal shores. Pages 101-124 in S. T. A. Pickett and P. S. White, editors. *The ecology of natural disturbance and patch dynamics*. Academic Press, New York.
- Suchanek, T. H. 1983. Control of seagrass communities and sediment distribution by *Callinassa* (Crustacea, Thalassinidea) bioturbation. *Journal of Marine Research* 41:281-298.
- Taylor, J. 1978. Present day. Pages 352-364 in W. S. McKerrow, editor. *The ecology of fossils, an illustrated guide*. The MIT Press, Cambridge, Massachusetts.
- Thistle, D., and J. Eckman. 1988. Response of harpacticoid copepods to habitat structure at a deep-sea site. *Hydrobiologia* 167-168:143-149.
- Thrush, 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.
- Thrush, S. F., R. B. Whitlatch, R. D. Pridmore, J. E. Hewitt, V. J. Cummings, and M. R. Wilkinson. 1996. Scale-dependent recolonization: the role of sediment stability in a dynamic sandflat habitat. *Ecology* 77: 2472-2487.
- 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.
- 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.
- Virnstein, R. W. 1977. The importance of predation by crabs and fishes on the benthic infauna in Chesapeake Bay. *Ecology* 58:1199-1217.
- Wahle, R. A. 1992a. Substratum constraints on body size and the behavioral scope of shelter use in the American lobster. *Journal of Experimental Marine Biology and Ecology* 159:59-75.
- Wahle, R. A. 1992b. Body-size dependent anti-predator mechanisms of the American lobster. *Oikos* 65:52-60.
- Wahle, R. A., and R. S. Steneck. 1992. Habitat restrictions in early benthic life: experiments on habitat selection and in situ predation with the American lobster. *Journal of Experimental Marine Biology and Ecology* 157:91-114.
- Walsh, J. J. 1988. *On the nature of continental shelves*. Academic Press, New York.
- Walters, C., 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.
- Wheatcroft, R. A., P. A. Jumars, C. R. Smith, and A. R. M. Nowell. 1990. A mechanistic view of the particulate biodiffusion coefficient: step lengths, rest periods and transport directions. *Journal of Marine Research* 48:177-207.
- Witman, J. D. 1987. Subtidal coexistence: storms, grazing, mutualism, and the zonation of kelp and mussels. *Ecological Monographs* 57: 167-187.

