Throughout history, people have preferentially settled along coastlines, and they continue to do so today. Coastal people make up more than half of the total human population, and coastal settlements are transforming marine habitats at a rapid pace. Coastal people have also been long engaged in the extraction of marine resources, mostly animals such as marine mammals, fish, and invertebrates as well as some algae and higher plants (Lotze et al. 2006). The effects of fishing and hunting on marine life forms have now spread from coastal areas to the continental shelves and the open ocean (Watson et al. 2012), and they are beginning to transform the largest ecosystem on Earth, the deep sea (Roberts 2002). While Chapter 8 describes these historical changes in detail, this chapter focuses on the current effects of fishing and habitat alteration on marine communities. In doing so, it examines the role of humans as a top predator (Estes et al. 2011) and ecosystem engineer (Smith 2007) in marine communities.

This chapter treats fishing and habitat degradation together because they represent by far the most dominant human impacts on marine ecosystems. There is little doubt that fishing—which we define here as including all extraction of marine animals and plants—is the human activity that has historically had the most transformative impact on marine communities (Dayton et al. 1995, 1998; Jackson et al. 2001; Lotze et al. 2006; Halpern et al. 2008; Lotze and Worm 2009). The effects of fishing, however, have often occurred in combination with habitat disturbance, either from the fishing gear itself or from other unrelated impacts (Dayton et al. 1995; Watling and Norse 1998). According to a comprehensive analysis of the historical evidence, an estimated 96% of local extinctions in coastal environments involved fishing and hunting and 39% the effects of habitat degradation (Lotze et al. 2006). In 42% of reviewed cases, multiple human impacts were involved. Another study of the factors that drive extinction risk today found that exploitation caused a majority of marine species losses (55%), followed closely by habitat loss (37%), while the remaining losses were linked to invasive species, climate change, pollution, and disease (Dulvy et al. 2003).

Only recently, however, have ecologists begun to study the community-wide effects of fishing and habitat degradation in much detail. Ecological theories and concepts that were developed in terrestrial, freshwater, and coastal ecosystems are now being applied to continental shelf and deep-water habitats. Fisheries-induced trophic cascades, for example, are well known to occur in lakes (Carpenter et al. 1985), rivers (Power 1990), and coastal regions (Estes and Palmisano 1974), but have only recently been described from large offshore marine ecosystems (see review by Baum and Worm 2009). Hence it appears that fisheries that were historically managed with a single-species focus require a much broader community and ecosystem context within which their impacts can be understood and managed. The ecosystem approach to fisheries (EAF)
is a novel management framework that incorporates the manifold interactions among marine organisms and fisheries as well as the cumulative effects of other ocean uses and stressors described in Chapter 19. In this chapter we highlight some of the most important interactions among anthropogenic stressors and the effects they have on the marine environment. It is our conjecture that successful mitigation of human impacts on the marine environment requires a thorough understanding of the scale and magnitude of the effects of fishing and habitat alteration. We will first treat the direct and indirect effects of fishing on community structure, then move on to habitat alteration, and close with an overview of EAF approaches.

Types of Fisheries

Fishing probably remains the most important human impact on marine communities to this day, in part due to the sheer scale of fishing operations. Fisheries operate globally: no major region remains untouched, and less than 2% of ocean area is currently protected in some permanent fashion (Toropova et al. 2010). The total landings of marine species probably approach 100 million metric tons per year (Figure 20.1). This figure includes 78.6 million metric tons of reported landings as of 2009 (FAO 2010) and an estimated 11–26 million metric tons of illegal and unreported landings (Agnew et al. 2009). To put this figure into context, shipping this amount of seafood would require about 2 million standard 20-foot long shipping containers filled to the top. If you were to stack these containers, the column would reach about 5300 km in height, a figure that comes close to the diameter of the planet. This large marine catch contrasts with only 10.3 million metric tons of inland (freshwater fish) landings. Reported landings of both marine and freshwater species have increased more than fivefold from 1950 to 1998 and have thus grown faster than the human population itself. Reported marine landings have declined by 9% since that peak, whereas freshwater landings continue to rise. Apart from the reported and illegal landings, a substantial number of marine organisms are caught as unintentional bycatch. Much of this bycatch is discarded at sea, rather than landed, and is thus rarely recorded. Recent estimates of such discards range around 7 million metric tons, which is down considerably from earlier estimates of 20–27 million metric tons, and may point to some reduction of the discard rate over time (Kelleher 2005), although differences in methodology make these estimates not strictly comparable. Thus, taking into account the uncertainty in estimates of illegal fishing and discards, 100 million metric tons (range 90–130 million) seems a conservative best estimate for total removals of marine life from the ocean by all forms of fishing.

Fishermen employ a wide variety of methods (called fishing “gears”) to capture their intended prey (Figure 20.2). Coastal fisheries often use some form of fish trap, net, or hook-and-line methods. Other methods commonly used are wire fish traps (e.g., in temperate and tropical lobster and reef fish fisheries), bottom longlines (e.g., in coastal groundfisheries), and gill nets (in a wide variety of fisheries). All of these methods are called “fixed gear” because they remain in place while fishing. These methods contrast with “mobile gear,” such as trawls and dredges, which are dragged over the seafloor or through the water column. Bottom trawls and dredges tend to be very efficient at catching fish, but are relatively unselective in doing so, which means that they produce much unwanted bycatch, which is typically discarded dead at sea. On top of these effects on the animals caught, bottom habitats are disturbed and altered by physical contact with the gear. Fixed gear can also produce significant bycatch; gill nets, for example, are controversial because they tend to capture a wide range of animals, including marine mammals, seabirds, and turtles. However, fixed gear typically does not have severe impacts on seafloor habitats. Instead, lost fixed gear can “ghost fish” until the gear disintegrates, thus killing animals that are never harvested. Finally, pelagic (open-water) fishing gear, such as drift nets, seines, and longlines, targets either schooling forage fish and squid or more solitary top predators such as tuna, marlin, swordfish, or sharks. Different gears vary greatly in their effects on different species groups and habitats (Table 20.1).
Over human history, marine fishing has intensified and has spread from coastal and estuarine regions (in the last 5000 years) to continental shelves (in the last 500 years) to the open ocean and deep sea (in the last 50 years; Watson et al. 2012). This spatial expansion and intensification of fishing effort is visualized in Figure 20.3, in which the energy spent fishing per unit area and time is mapped for each decade since 1950. Fishing effort has been rising sharply, and it continues to rise today, although the global catch is slowly declining (Worm and Branch 2012). This declining trend in catch per unit effort (CPUE) is concerning as it is a proxy for declining fish abundance in the water.

Another dimension of the expansion of fishing effort is the increasing mean depth of fishing operations, as deeper waters still harbor some untapped resources. Deep-water communities, however, tend to live beyond the reach of sunlight, which renders them much less productive than the surface communities that fuel more traditional fisheries. This lower productivity translates into lower growth rates, longer life spans, and lower resilience to fishing (Roberts 2002). The final dimension of fisheries expansion is the move to newly exploited species, such as rattails (Macrouridae), sea cucumbers (Holothuroidea), and krill.
(Euphausiacea), thus essentially expanding the fraction of marine biodiversity that is used for human purposes. A recent report estimated that one in four marine fish species is utilized directly by people (FishBase 2013).

The effects that fisheries have on marine communities are a key topic of this chapter, and fall into four categories: First, there are straightforward, direct effects on target fish populations (Figure 20.4A). Direct effects include declines in abundance and biomass as well as shifts in size and age structure. Second, there is “collateral damage” to nontarget (“bycatch”) species that are captured along with the target species and often discarded at sea (Figure 20.4B).

Third, bottom habitats are damaged and transformed to varying degrees by mobile fishing gear such as bottom trawls (Figure 20.4C; see also Table 20.1). Finally, there is a host of indirect effects that arise from removals of marine organisms, typically mediated by species interactions. Indirect effects include mass occurrences of prey populations due to release from their predators (Figure 20.4D), trophic cascades, bottom-up effects of depleting forage fish populations, and the effects of changes in habitat structure on the species that depend on those habitats. In the following sections we will discuss these direct and indirect effects and illustrate them with examples.

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Direct Effects of Fishing on Community Structure

By selectively removing large numbers of individuals, fisheries directly alter the abundance, biomass, and size structure of marine communities. Species composition and diversity are also affected, and some species have been depleted so far as to go locally, or even globally, extinct. These changes are largely due to the selective removal of certain species and size classes (direct effects), but are further amplified by species interactions, which mediate the indirect effects of fishing.

Changes in abundance and biomass

The most immediate effect of removing individuals from a community is a reduction in the abundance of the targeted species, as well as those that are caught as bycatch. This “fishing down” of accumulated biomass is a major manipulation of marine ecosystems, but also a deliberate strategy to move populations away from their carrying capacity. This is desired because a population’s growth rate tends to be higher at low to intermediate abundance than at high abundance, where competition for limited resources may be intense. The so-called surplus production that is generated every year by that reduction in biomass can in theory be skimmed off by fisheries without reducing abundance any further. This principle is called “sustainable yield.” A central dogma of fisheries theory posits that a “maximum sustainable yield” (MSY) will be obtained at a low to intermediate population biomass ($B_{MSY}$; typically 30–50% of what was there before fishing). Outside of fisheries science, it is not often appreciated that this fairly drastic reduction in biomass is a premeditated outcome of fisheries management for maximum yield (Ludwig et al.)
1993). The actual level of biomass reduction, however, varies among communities. The degree to which populations are depleted from their unfi shed biomass depends, among other things, on the history and intensity of exploitation, the effectiveness of management, and the resilience of the species. For species that have a long history of exploitation, average biomass has often declined 80–90% from a pre-fishing baseline (Lotze and Worm 2009). Depleted species include many marine mammals, turtles, seabirds, and large predatory fishes (Figure 20.5).

Even those contemporary fisheries that are considered well managed can have large effects on biomass, for a major objective in managing for MSY is to remove an ecologically substantial portion (e.g., 50–70%) of the population biomass. Pelagic longline fisheries, for example, did this when spreading across the oceans in the 1950s and 1960s, exploiting large areas of the high seas for the first time. The record from these fisheries allows us to estimate a baseline abundance of species where data from early fishing surveys exist. Ward and Myers (2005), for example, analyzed early longline surveys in the Central Pacific that were designed to literally “test the waters” prior to the development of large-scale commercial fisheries in the region. These survey data were contrasted with data from recent commercial longline fisheries in the same regions. The results are shown in Figure 20.6. The authors observed about a 90% reduction in fish abundance, standardized per 1000 hooks (Ward and Myers 2005), confirming earlier results for pelagic and seafloor-associated fisheries around the world (Myers and Worm 2003). They also documented a large reduction in the mean sizes of fish, as well as a shift from large sharks and tuna (e.g., silky shark, bigeye tuna) to smaller, fast-growing species such as skipjack tuna and pomfrets, which actually increased in abundance (Ward and Myers 2005). Such shifts in size structure are commonly observed; they are discussed in more detail in the next section.

**Changes in size and age structure**

Most fisheries are size selective, which means that they capture individuals across a given size spectrum. Large hooks carrying large bait, for example, select for fish with a large gape (i.e., mouth) size; these tend to be larger and older fish. Mesh size in gill or trawl nets selects for fish of a certain size, but leaves smaller fish to escape. Lobster traps have an opening that allows small and medium-sized lobsters to enter, but large lobsters are spared. In addition, the small lobsters can escape again through the same opening; only medium-sized lobsters remain. Hence fishing pressure is exerted unevenly over different size classes in the community. Within a given species, individual size is correlated with age, and among different species, with other life history attributes such as longevity and growth rate. Thus there is uneven fishing pressure over different
Changes in composition and diversity

The selective removal of certain individuals necessarily alters the composition, and in most cases, the diversity of species in a community. The more skewed the fishing pressure is toward certain species, or species groups, the more pronounced will be the shift in species composition. Typically, a fished community over time will lose species that are particularly vulnerable to the method of fishing used (have high “catchability”) or that have low resilience to additional mortality. Such species include sharks, rays, sea turtles, and marine mammals, most of which are easy to catch, quick to be eradicated, and slow to recover from fishing pressure. The shift from slow-growing to fast-growing species that is so often observed in heavily exploited systems (Jennings and Kaiser 1998) is thus partly a result of the selectivity of fisheries, partly a consequence of differential vulnerability, and partly amplified further by the changes in species interactions discussed on pp. 457–460.

In many cases, this shift in species composition results in a skewing of trophic structure, a phenomenon that has been dubbed “fishing down food webs” (Pauly et al. 1998). Fisheries tend to target high-value species first, and many of these species tend to be large and high up in the food chain. Subsequently, the fishery moves to smaller species, which are typically placed lower in the food chain. “Fishing down” here signifies the serial depletion of successive trophic levels, as can be observed, for example, in the northwestern Atlantic region (Pauly et al. 2001). “Fishing through food webs” is a related phenomenon that entails a successive expansion of effort across the food web without first depleting the top predators (Essington et al. 2006). At a global scale, “fishing through” seems to be more predominant than “fishing down,” but both patterns work to restructure marine food webs on a large scale (Essington et al. 2006; Branch et al. 2010).

Changes in species diversity are also an important consequence of fishing, but they are detected in different ways. Their most basic manifestation is the decline in species richness that occurs when a species goes locally extinct. Sometimes, when a community cannot be fully censused and local extinction cannot be verified, it is more practical to look at the rate at which the species count increases when individuals are randomly sampled. Such “species accumulation curves” give valuable insights into the structure and diversity of communities. For pelagic communities, for example, we can calculate the number of species in a random subsample of the community as it is caught by pelagic longlines. Because of the global reach of this fishing gear and the good records over time, we can derive a global pattern of diversity over time (Figure 20.7).

This method has revealed that the species richness of the pelagic community (here standardized to 50 randomly drawn individuals) is declining over time as more vulnerable species become rare (Worm et al. 2005). This local rarity is caused, at least in part, by the shrinking of species ranges and the local extinction of vulnerable species, such as Atlantic bluefin tuna, across part of their range (Worm and Tittensor 2011).

Another way of looking at changes in diversity is through species–area curves, which track the accumulation of species over increasingly large sampling areas. The species–area relationship is commonly described by the power function $S = ca^z$, where $S$ is the number of species, $A$ the area, $c$ a fitted constant, and $z$ represents the slope in log–log space and hence the rate of accumulation of diversity with area. Although a number of other functional forms have been fitted to species–area data, the power law is the most frequently applied, and the slope parameter $z$ has been applied in terrestrial conservation to estimate extinction rates due to habitat loss (Pimm and Raven 2000) or climate change (Thomas et al. 2004). Detailed analyses of fished and unfished sites in four ocean basins indicate that with increasing fishing pressure, this slope value decreases, which means that the spatial organization of biodiversity is affected by fishing (Tittensor et al. 2007). Changes in species richness, relative abundance, and patch occupancy all appear to contribute to this pattern. Therefore, the species–area curve can be a sensitive indicator of community-level changes in biodiversity.

Finally, changes in diversity are commonly measured with a number of diversity indices, such as the Shannon–Wiener, Margalef’s richness, or Pielou’s evenness index. These indices assume randomized sampling and equal sampling effort between samples, hence they are suited only for the analysis of well-designed sampling studies. Using such designs, De Boer and colleagues (2001) found lower species richness and diversity at a heavily fished tropical estuary than at sites that experienced low fishing pressure. They observed a near-absence of piscivorous predators, and an abundance of small fish, at the heavily fished site, which resulted in low species evenness and high dominance of fewer species at that site (de Boer et al. 2001). Other quasi-experimental studies, most of them
conducted at tropical sites, mirror these observations and indicate large effects of fishing on fish diversity (Jennings et al. 1995; Micheli and Halpern 2005; Tittensor et al. 2007). Consistent with these observations, a general increase in species diversity is observed in areas that have been placed under protection, particularly if they are no-take reserves (Worm et al. 2006).

Extinction risk

Few marine species are known to have been driven to global extinction in modern times (i.e., in the last 500 years or so). The IUCN Red List is considered the most comprehensive source of information on threatened and extinct species (Table 20.2). As of early 2013, a total of 18 marine species were listed as extinct, compared with 226 species in freshwater habitats and 506 species on land. Extinct marine species include mostly birds (8), mammals (4), and molluscs (4). The Steller’s sea cow (Hydrodamalis gigas), Labrador duck (Camptorhynchus labradorius), and eelgrass limpet (Lotitia alveus) are well-known examples. Keep in mind, however, that these animals belong to species groups (marine mammals, birds, and molluscs) to which scientists pay a lot of attention. It is conceivable that significant numbers of marine invertebrates have gone extinct without anyone taking note. But this is likely not true for fishes, which are intensively researched. While a number of freshwater fishes have gone extinct, no truly marine fish species has (one species, the extinct New Zealand grayling, Prototroctes oxyrhynchos, lived in both environments). Yet many marine species, including fishes, have become locally extinct and are globally threatened due to dwindling numbers and declining ranges. According to the IUCN Red List, between 9% (for bony fish) and 38% (for marine mammals) of assessed and non–data deficient species were threatened by extinction (see Table 20.2).
rate of threat is similar to those on land and in freshwater habitats, and it means that extinction risk in the sea is a serious concern across species groups (Dulvy et al. 2003), including most fishes (Reynolds et al. 2005). While slow-growing sharks and rays have long been identified as threatened (Manire and Gruber 1990), even some of the most prolific and wide-ranging species, such as tuna and billfish, have experienced serious declines in stock biomass (Juan-Jordá et al. 2011) and species ranges (Worm and Tittensor 2011), and are therefore considered under threat (Collette et al. 2011).

The risk of extinction is particularly high for large-bodied and slow-growing animals, such as marine mammals, turtles, and chondrichthyan fishes (sharks, rays, skates, and chimaeras). As discussed on p. 455, these species tend to be more vulnerable to most fishing gears (because of their large size), have a lower population abundance overall, and have lower resilience to fishing due to a “slow” life history. Today, reducing fishing mortality for chondrichthyanis, which are not only frequently caught as bycatch, but also targeted directly for the highly valuable shark fin trade, is a major challenge for fisheries management (Worm et al. 2013).

Summary of direct effects

In summary, the direct effects of fishing commonly result in a large reduction of community biomass, particularly for larger and slower-growing species. Some species may even disappear entirely, resulting in local extinctions and a loss of species richness. Typically, we also observe a shift in size and age structure toward smaller and faster-growing size classes and younger ages. These changes tend to increase the productivity of the community, but lead to greater variation and a loss of stability. Direct effects of fishing are compounded by the indirect effects and interaction chains that are discussed in the next section.

Indirect Ecosystem Effects

In this section we highlight how the direct effects of fishing are transmitted through the food web and how they can radically alter species composition, habitat structure, and ecosystem functioning beyond what can be predicted from direct effects.

Top-down effects and trophic cascades

Top-down effects arise from the effects of exploitation on higher-trophic-level species such as marine mammals, sharks, and other large fishes. If these effects are transmitted across two or more trophic levels, we call this interaction chain a trophic cascade. One of the classic examples involved the historical exploitation of sea otters (Enhydra lutris) in the Aleutian Islands of Alaska for their valuable pelts (Estes and Palmisano 1974). The demise of otters led to a proliferation of their favorite prey, sea urchins, a phenomenon called prey release. As urchin numbers increased, the lush kelp forests that graced these shores disappeared due to the strong grazing pressure. This trophic cascade reversed when sea otters were protected from exploitation and increased in numbers. It reversed once again, if only locally, in areas where killer whales (Orcinus orca) learned to prey on sea otters, again reducing their numbers, causing urchins to multiply and remove the kelp (Estes et al. 1998). This prey switching by killer whales was hypothesized to have been linked to the precipitous decline of Steller’s sea lions (Eumetopias jubatus) in the area. Some observers linked the decline in sea lions to the overfishing of their prey species (Atkinson et al. 2008). Others hypothesized that it was caused by killer whale predation when the whales were forced to switch from cetaceans to pinnipeds in the wake of industrial whaling (Springer et al. 2003). Although the exact mechanisms are still debated, this example illustrates the complex pathways through

<table>
<thead>
<tr>
<th>TABLE 20.2 Threat status of marine animals</th>
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<tr>
<td>IUCN CLASSIFICATION</td>
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<tr>
<td>----------------------</td>
</tr>
<tr>
<td>Extinct (EX)</td>
</tr>
<tr>
<td>Critically endangered (CR)</td>
</tr>
<tr>
<td>Endangered (EN)</td>
</tr>
<tr>
<td>Vulnerable (VU)</td>
</tr>
<tr>
<td>Near threatened (NT)</td>
</tr>
<tr>
<td>Least concern (LC)</td>
</tr>
<tr>
<td>Data deficient (DD)</td>
</tr>
<tr>
<td>Total</td>
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<tr>
<td>Percentage threatened (excluding DD species)</td>
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</table>

Source: IUCN 2013.
which the depletion of particular target species high in the food chain can affect lower trophic levels, leaving the entire ecosystem changed.

There is now strong evidence for cascading effects from fishing in coastal and shelf seas (Baum and Worm 2009). Large apex predators can have powerful effects on so-called mesopredators. These smaller carnivores are often kept in check by larger predators such as sharks. One study from the U.S. east coast examined the trend of large sharks (for example, blacktip \([\text{Carcharhinus limbatus}]\), hammerhead \([\text{Sphyrna spp.}]\), and dusky sharks \([\text{C. obscurus}]\)) declining in fisheries surveys since the 1970s and the coincident increase in prey species in the same surveys (Figure 20.8). These prey include smaller shark species (such as the Atlantic sharpnose shark \([\text{Rhizoprionodon terraenovae}]\)) and rays, most conspicuously the cownose ray (\([\text{Rhinoptera bonasus}]\); see Figure 20.4D), which increased more than tenfold over 30 years to an estimated 40 million individuals. This increase, in turn, coincided with the collapse of some coastal shellfish populations. Experiments showed clearly that much of the shellfish demise was due to excessive predation by cownose rays. This chain of events indicated a trophic cascade from sharks to rays to shellfish, an unintended consequence of the regional depletion of sharks (Myers et al. 2007).

There is some debate over the plausibility of the rapid population increase in cownose rays, and other elasmobranch prey species, in the surveys. Some of the increase observed in the surveys may be explained by the movement of rays into surveyed coastal areas. This explanation hints at “risk effects,” meaning that the risk of shark predation can be enough of a deterrent to scare prey species away from habitats where sharks are present (Heithaus et al. 2012). If sharks are fished out, these risk effects diminish, and the behavior of prey populations is altered. Observational and experimental work has indicated that such risk effects on the ecosystem can be at least as important as the release of prey species from predator-induced mortality (Heithaus et al. 2008).

Another class of top-down interactions arises from so-called trophic triangles that can lead to a reversal of the roles of predator and prey (Walters and Kitchell 2001; Minto and Worm 2012). A well-documented example (Figure 20.9) involves the Atlantic cod (\([\text{Gadus morhua}]\)), a large predatory fish that preys heavily on benthic invertebrates such as various species of shrimp, crabs, and young lobsters (\([\text{Homarus americanus}]\) as well as on small pelagic fishes (herring [\(\text{Clupea harengus}\)], capelin [\(\text{Mallotus villosus}\)], and sand lance [\(\text{Ammodromes americanus}\)], for example). As cod stocks were depleted by industrialized fishing, a concomitant increase in most of their prey populations was observed (Frank et al. 2007). Following the collapse of most cod stocks in the northwestern Atlantic, shrimp and lobster stocks soared and supported lucrative fisheries (Worm and Myers 2003; Boudreau and Worm 2010). Small pelagics also exploded in abundance, rising from an estimated 2 to 12 million metric tons on the Scotian Shelf in eastern Canada (Frank et al. 2011). Some pelagics, such as herring, are known to prey on cod eggs and larvae (Köster and Möllmann 2000). There appears to be a general link between the abundance of herring and the survival of cod up to the age at which they are first fished (Minto and Worm 2012). Thus, when cod abundance is high, the species “cultivates” the ecosystem to be favorable for its own offspring by cropping the predators of its larvae. If cod abundance is low, herring do the same.
by reducing the larval survival of cod, their main enemy. This phenomenon may partly explain the observed non-recovery of cod on the Scotian Shelf during the 1990s, which occurred in the absence of fishing (see Figure 20.9). Only after herring stocks outstripped their own food supply and crashed did cod and other large groundfish begin to recover (Frank et al. 2011). The effects of herring also extended to their main prey item, copepod zooplankton, and thus to phytoplankton in a classic four-level trophic cascade (Frank et al. 2005). Similar cascades have now been documented in the Baltic (Casini et al. 2009) and Black Seas (Daskalov 2002) and may be a dominant feature of heavily exploited shelf sea ecosystems (Frank et al. 2007; Baum and Worm 2009).

An important unanswered question, however, is whether pelagic communities in the open ocean, which covers two-thirds of the planet’s surface, are similarly altered by fishing. Undoubtedly, the abundance of large predators, such as tuna, billfish, and sharks, has plummeted across most of the world’s oceans (Myers and Worm 2003; Juan-Jordá et al. 2011; Worm et al. 2013). There is some evidence of a release of mesopredators where detailed survey data exist (e.g., Ward and Myers 2005; Myers et al. 2007). But there is little evidence available that would support a trophic cascade (Baum and Worm 2009). One study in the northeastern Pacific indicated striking year-to-year inverse correlations between pink salmon abundance, zooplankton, and phytoplankton concentrations, respectively (Shiomoto et al. 1997). Yet, scientists are still unclear as to what the broader consequences of depleting large, mobile predators in the open ocean are. One possibility is that the complexity of marine pelagic food webs dampens any deterministic effects that are transmitted from the fishing of top predators. It was shown experimentally that there are two counteracting food chains leading from fish to phytoplankton (Stibor et al. 2004): a three-level chain, from fish to copepod zooplankton to larger phytoplankton, and a four-level chain, from fish to zooplankton to protozoans to smaller phytoplankton, occur side by side. When fish are depleted, the three-level chain leads to a decrease in larger phytoplankton, while the four-level chain causes an increase in smaller phytoplankton (Stibor et al. 2004). Net effects on total phytoplankton biomass may thus be small, even when large changes in fish abundance occur. How these complex interactions play out in the real ocean, however, remains unresolved.

**Bottom-up effects**

Fisheries not only alter marine ecosystems from the top, but also exert their effects from the bottom of the food chain when low-trophic-level “forage” species are fished. These species include small pelagic fishes such as herring, sardines, and anchovies as well as invertebrates such as squid, shrimp, and krill. Taken together, such
forage species contribute about 30% of total global fisheries production and hence contribute substantially to our food supply. These forage species are also important food sources for marine mammals, seabirds, and larger fish and are seen as important conduits for channeling photosynthetic energy from plankton to higher trophic levels. Recent analyses indicate that low trophic levels are just as heavily depleted, on average, as higher trophic levels (Pinsky et al. 2011) despite their greater productivity. The reason for this is that they are typically fished at higher rates, which compensates for their faster growth potential.

The bottom-up effects of depleting forage species on higher trophic levels can be substantial. A comprehensive modeling study of five ecosystems with large forage fisheries concluded that fishing these species for MSY will have severe effects on other species, most strongly on marine mammals and seabirds (Smith et al. 2011). In Peru, where the largest single-species fishery on Earth pursues the Peruvian anchoveta (Engraulis ringens), a drastic decline of seabirds—cormorants (Phalacrocorax bougainvillii), boobies (Sula variegata), and pelicans (Pelecanus thagus)—was observed following the expansion of the fishery (Jahncke et al. 2004). When the ecological roles of anchoveta, birds, and fishermen were modeled, the magnitude of fishing effects on seabirds became apparent (Figure 20.10). Similarly, the carrying capacity of African penguins (Spheniscus demersus) in the Benguela upwelling ecosystem off South Africa was reduced by food competition from fisheries (Crawford et al. 2007). Overall, effects on higher trophic levels are predicted to be particularly severe in fisheries targeting abundant species that are highly connected in the food web, including anchovies, krill, and small pelagic fishes. As such, the appropriate level of fishing on forage species is an important question for ecosystem management (see p. 471, Reference points for management).

**Effects on ecosystem functioning**

The effects of changes in biomass, changes in species composition, and diversity loss on ecosystem functioning can be substantial. As discussed on pp. 454–455, the observed shift toward smaller species and individuals entails an increase in growth rates and in turnover of biomass. Such changes are partly intended by fisheries managers in order to increase sustainable harvest rates. However, these changes also tend to make the ecosystem more vulnerable to environmental fluctuations and may decrease temporal stability (Hsieh et al. 2006). A decline in diversity, either within a species or across the community, has a similar effect, largely due to the loss of response diversity—the collective sum of species traits that can help the community cope with variable environmental conditions (Elmqvist et al. 2003; Schindler et al. 2010). Loss of biomass and diversity also often entail a long-term loss of productivity (Tilman et al. 2012). This loss results in a reduced flow of ecosystem goods and services, such as fisheries yield. Other services, such as the maintenance of water quality and the recycling of nutrients, are often similarly compromised, depending on the particular species that have been depleted or lost (Worm et al. 2006). Fortunately, these changes appear reversible. Where marine ecosystems have been effectively protected, community biomass, diversity, productivity, and stability all tend to increase in a similar fashion (Worm et al. 2006), often within a decade or less (Halpern and Warner 2002).

**Summary of indirect effects**

In summary, fishing can have a host of indirect effects on the ecosystem that are largely mediated by changes in species interactions. The depletion of top predators can lead to cascading top-down effects; this has been shown for a number of coastal and continental shelf ecosystems. In some cases, this change in top-down control can reverse the roles of predators and prey and lead to new food web configurations and dominance patterns. Fishing low-trophic-level species such as small forage fish, krill, or squid can also change food webs from the bottom up. Effects on seabirds and marine mammals, which rely heavily on particular forage species for survival, tend to be particularly pronounced. Both direct and indirect effects of fishing affect the functioning of marine ecosystems, which can exhibit a decline in productivity and stability in the wake of overexploitation. Evidence so far suggests that many of these changes are reversible with proper management. In the next section we will discuss in detail another class of impacts that can arise from fishing or from other activities that alter or destroy marine habitats.

![Figure 20.10](460.png)
Habitat Loss and Alteration

Some fishing practices, among other human activities, degrade or destroy marine habitat. These impacts on habitats can have manifold ecological effects because most marine species depend on specific habitats at certain stages in their life history. Suitable substrates for larval settlement, nurseries for juveniles, and foraging and spawning grounds for adults are examples of essential habitats required for survival. Such habitats may include soft sediments, which cover 80% of world’s seafloor, rocky outcrops, or biogenic habitats such as salt marshes, seagrass meadows, kelp forests, coral reefs, shellfish beds, or mangroves. Habitat loss, modification, and fragmentation are major threats to marine biodiversity (Sih et al. 2000; Dulvy et al. 2003; Lotze et al. 2006) and compromise the provision of ecosystem services (Worm et al. 2006), including fisheries. Thus habitat protection is a major objective of marine conservation and management, and restoration is emerging as an effective way of replacing lost or degraded habitat. For marine ecologists, these applied objectives also present opportunities to test and apply ecological theory, estimate the ecological risks of habitat-degrading activities, and assess the success of conservation and restoration. This section will discuss and quantify the loss of marine habitats, showing how this loss can influence marine communities through direct and indirect effects.

Fishery-related habitat disturbance

Fishing affects mainly benthic (seafloor) habitat, as pelagic and ice-associated habitats are highly dynamic by nature and thus usually recover quickly from disturbance. Fishing has a larger direct impact on marine benthic habitats than any other natural or anthropogenic disturbance, except perhaps hurricanes and “dead zones” caused by hypoxia (Kaiser et al. 2002; Figure 20.11). Most fishery-related impacts are associated with mobile fishing gear, primarily bottom trawls and dredges that are dragged across the seafloor. Individual patches of seafloor heavily impacted by trawling range in size from 25 to 2400 km² (NRC 2002), and an estimated 75%—or 20 million km²—of the world’s continental shelf area has been trawled or dredged at least once (Halpern et al. 2008). Large sections off the northeastern United States are trawled 3–7 times per year (Auster and Langton 1999), and 35% of the Baltic Sea and 71% of the Danish North Sea are trawled at least once a year (Thrush and Dayton 2002). Thus there is a very high probability that any patch of seafloor near fishing harbors has been trawled or dredged at some point in time. Such is the case because humans have pulled trawl nets across the seafloor for over 2000 years, first from small dugout canoes, then from sailing vessels, and now from diesel-powered boats 10–100 m in length.

Modern trawl nets are 10–25 m wide and are used primarily to catch flatfish (e.g., halibut and sole), other groundfish (rockfish, lingcod, hake, or cod), shrimp, and sometimes crabs. Beam trawls have a net attached to a rigid beam that is pulled along above the seafloor. The beams have so-called “tickler” chains that bounce along the substrate, scaring benthic animals off the bottom and into the net. Otter trawls use two wing-shaped steel or wooden boards (or doors) as foils that pull the funnel-shaped net open, but also carve furrows in sediments or resuspend them (see Figure 20.4C). The ground gear—trawl doors, ground ropes, and net—of the largest otter trawls are 200 m long, and when dragged across the bottom can cause lasting damage to bottom communities. Dredges cause even greater damage because they are engineered to dig into the substrate to dislodge animals—mostly bivalves, but also crabs, finfish, and echinoderms. Like trawls, dredges often take significant bycatch. Hydraulic dredging, in which water is injected into the sediment to liquefy it and dislodge deep-burrowing shellfish, can radically disturb sandy bottom sediments, remove submerged aquatic vegetation, and cover surrounding communities with resuspended sediments over large areas (NRC 2002). A suite of other fishing practices, including the setting of pots and traps and bottom long-lining, can also disturb seafloor habitat, either when lines and cables are dragged across the seafloor during normal fishing operations or when the fishing gear sits (or is lost) on the bottom (Donaldson et al. 2010). Particularly destructive forms of artisanal fishing involve the use of explosives or poison to extract fish from complex reef habitats, causing lasting damage to the three-dimensional structure of reef-building corals.

Other forms of habitat disturbance

Marine habitats are affected by a multitude of other human activities. Major threats are the loss of coastal...
wetlands due to land reclamation, coastal development, pollution, and eutrophication. Sedimentation from terrestrial runoff, beach development, and dredging are threats to nearby rocky shore habitats and coral reefs. Species invasions, shipping, and tourism can cause further disruption. Aquaculture, which is the world’s most rapidly growing food sector, also entails practices that degrade or destroy coastal habitat, as, for example, when mangroves are replaced by shrimp farms (Naylor et al. 2000). Coral and other biogenic reefs are also affected by ocean acidification, as much of their biogenic structure is formed from aragonite or calcium carbonate, which is pH-sensitive. Some intertidal and nearshore habitats are threatened by global climate change, especially by rising sea level. On continental shelves and slopes and in the deep sea, habitats and their ecological communities are perturbed by oil exploration and extraction, mineral mining, the dumping of human waste and debris, and the laying of communication cables. More recently, the deep-sea benthic environment has been proposed as a dumping ground for anthropogenic CO₂. As a result of all these activities, the marine environment is becoming less heterogeneous and less dominated by structurally complex physical and biogenic habitat.

Many habitats experience natural disturbances as well as human impacts, and it is sometimes very challenging to separate the relative effects of each. Ecologists typically apply survey sampling, experiments, or a combination of both. Meta-analyses of existing data, including historical records and data from other disciplines, such as anthropology (Lotze et al. 2006) and paleontology (Pandolfi et al. 2003), are used to address the effects of human activities over large temporal and spatial scales. Measuring the ecological effects of a single, unperturbed disturbance, such as the construction of an airport on a remote coral reef or the mineral mining of an isolated hydrothermal vent, presents an additional set of challenges that cannot be addressed by conventional approaches. For these cases, powerful Before–After/Control–Impact (BACI) assessment designs have been developed (Schmitt and Osenberg 1996). These designs include a series of samples, paired between impact and control sites, taken over time before and after the planned disturbance (i.e., BACIPS). The most complete ecological impact assessment designs include ecological risk modeling. As such, computer-simulated experiments on potential impacts, based on the best available information, are combined with BACIPS sampling designs and follow-up experiments that test specific hypotheses about community impacts (Peterson and Bishop 2005). These research approaches have been used to unravel the direct and indirect effects of habitat disturbances.

**Direct effects of fisheries on benthic habitats**

Habitat alteration by fishing gear is perhaps the largest, yet least understood, threat to marine habitat because much of it remains unobserved. Most areas had been trawled or otherwise fished historically before adequate baseline data were collected (Jackson 2001; Jackson et al. 2001). In addition, the large spatial scale of fishing (see Figure 20.11) exceeds our ability to observe and monitor it. For example, most of the Gulf of Maine was trawled or dredged for scallops between 1990 and 1994 (Auster and Langton 1999). This large extent of fishing also makes it difficult to select lightly fished areas, let alone ecologically similar unfished areas, as controls for impact studies. Finally, detecting the ecological effects of fishing is difficult in habitats that are disturbed naturally, especially by storms or large wave events, which can substantially affect benthic communities, even in waters up to 1000 m deep (NRC 2002). Nevertheless, studies conducted over the past 40 years provide insight into the many ecologically important effects of habitat-disturbing fishing practices.

Despite the logistical difficulties of assessing the effects of fishing, and despite evidence for high site-to-site variation, it is clear that some fishing practices have substantial direct effects on benthic communities. These effects include (1) removal of biogenic and physical habitat structure, which reduces the physical complexity of benthic communities, (2) direct mortality, leading to decreases in the abundance, biomass, and diversity of species, (3) increased abundance of mobile predators and scavengers that feed on organisms injured or killed by fishing gear, (4) reduction in the average size and life span of benthic organisms, (5) increased abundance of small-bodied invertebrate species, and (6) a decrease (or sometimes increase) in the secondary production of benthic invertebrates and fishes in the affected area. Evidence for these effects was assembled in a series of review papers (Watling and Norse 1998; Collie et al. 2000; Kaiser et al. 2002; Kaiser et al. 2006; Crowder et al. 2008), in which the authors synthesized results from hundreds of peer-reviewed scientific studies, conducted mainly in relatively shallow soft-substrate habitats. Impacts on corals and other habitat-forming species entail additional ecological effects.

Fishing alters the physical characteristics of soft-sediment habitats by reducing the small-scale heterogeneity and topography created by large burrowing infauna and demersal fishes, such as rays. Results from trawling studies are consistent with general ecological theory on the effects of physical disturbance on benthic community structure (Peterson and Estes 2001). The theory states that the effects of intensive or frequent disturbance should be greatest in communities that normally experience low levels of disturbance. Such communities are dominated by larger and older organisms that have long generation times, and thus a relatively low capacity to recover from disturbance. Relatively undisturbed communities are often referred to as late-successional communities because they have gone through a sequence, or succession, of natural species replacements following prior disturbance. This successional process usually entails the replacement of weak competitors for space or other resources with strong competitors.
as well as the establishment of species due to positive interactions, such as mutualism and facilitation, especially by foundation species that create habitat (Bruno and Bertness 2001).

When benthic communities are disturbed intensely or frequently, late-successional species are usually replaced by highly mobile demersal fishes and invertebrates (Lenihan and Micheli 2001). These animals include scavenging organisms, such as crabs, shrimp, amphipods, and gastropods, that attack organisms displaced or damaged by the passing fishing gear. Moderately disturbed areas, or areas that are recovering from disturbance, sometimes attract high abundances of predatory or scavenging groundfish species—a pattern that can produce higher fishery yields on fishery-disturbed bottoms than in nearby unfished areas (Kaiser et al. 2002). Highly disturbed communities are usually composed of small, shallow-burrowing infaunal species that are rapid colonizers because they either have plentiful pelagic larvae or are brooding species with short generation times. The early colonizers, or “opportunistic species,” are dominated by various wormlike invertebrates, especially nematodes, oligochaetes, and some species of polychaete worms (Lenihan and Oliver 1995). Many opportunistic species are small and soft-bodied. They tend to be poor competitors for space and are readily eaten by predators, including flatfish and larger amphipod crustaceans. However, these opportunistic species also tend to show high tolerance for hypoxia, which can occur where physical disturbances create a pitted, furrowed, or trenched seafloor that accumulates fine sediments and rotting organic matter. Such hypoxic patches often form on seafloor disturbed by trawl doors and dredges or naturally by sediment slumps and iceberg scours (Lenihan and Micheli 2001). Similar opportunistic species are found in polluted areas, especially those associated with oil spills and sewage outfalls, because these chemical disturbances introduce other forms of organic enrichment that lead to sediment hypoxia (Lenihan et al. 2003).

The degree to which a benthic community is modified by mobile, bottom-disturbing fishing gear usually scales with the intensity of fishing disturbance (e.g., the number of times an area has been trolled), the level of background natural disturbance, and the type of bottom substrate. Figure 20.12 shows a conceptual model of the relative change in community composition—for example, the relative loss of large epifauna or macroalgae—as it relates to these three factors. Habitats consisting of unconsolidated sediments that experience high rates of natural disturbance can have more subtle responses to trawling than habitats characterized by boulders or pebbles (Kenchington et al. 2001). Animals that live in unconsolidated sediments in high-disturbance regimes, such as sand flats near wave-swept beaches, are adapted to periodic sediment resuspension and smothering like that caused by mobile bottom gear. Such communities are often dominated by opportunistic species and tend to not change much when fished. In contrast, epifaunal communities that help stabilize sediments, communities of reef-forming foundation species, and other communities in habitats that experience low rates of natural disturbance—for example, in deep-sea muds—are particularly vulnerable to fishing. Ultimately, fishing disturbance influences community composition and structure by changing the demographic rates of individual organisms—that is, by increasing per capita rates of mortality or emigration or decreasing reproduction or immigration rates.

Some of the strongest direct effects of fishing are related to the removal, killing, or disturbance of so-called foundation species (sensu Dayton 1972), such as corals, kelps, seagrasses, or oysters. These species create complex three-dimensional structure that provides habitat for many other species. Some predators, such as sea otters, indirectly maintain foundation species by influencing benthic community composition through top-down cascades (see p. 457, Top-down effects and trophic cascades). Foundation species are sometimes also referred to as ecosystem engineers (Jones et al. 1994) because they build ecosystem structure. Protecting and restoring foundation species is an effective way to conserve the structure and functioning of marine communities (Coleman and Williams 2002; Byers et al. 2006).
A particularly crude direct disturbance of highly sensitive foundation species is caused by “blast” and poison fishing on coral reefs. These destructive forms of fishing are practiced mainly in eastern Africa, Indonesia, the Philippines, Thailand, and other Southeast Asian countries (Fox et al. 2005). An estimated 36% of the world’s reefs are already overexploited by overfishing. The additional stress of destructive fishing practices has placed 56% of the coral reefs in Southeast Asia at risk of collapse (Burke et al. 2002). Blast fishing is done cheaply with dynamite or homemade fertilizer bombs that kill large numbers of fish, which are skinned off the surface or collected from the bottom by divers. These explosions also destroy the physical structure created by hard corals, which is critical in maintaining high fish diversity and coral populations resilient to bleaching (Lenihan et al. 2011) and crown-of-thorns sea star (Acanthaster planci) outbreaks (Kay et al. 2011). On average, a 1 kg beer-bottle bomb can leave a rubble crater approximately 1 to 2 m in diameter, killing 50–80% of the coral in that area. It can take many decades for the physical structure of the reef to rebuild, not only because corals grow slowly, but also because the rubble and sediment created by the blast inhibits coral recruitment and growth, thus impeding recovery (Fox and Caldwell 2006). Poison fishing is used mainly to capture live fish for the aquarium and food trades. Most of these fish are sold in Asian restaurants, where live fish are prized for their freshness. Fishermen using this method dive down to the reef and squirt poisons, usually sodium cyanide or bleach, into reef crevices to stun fish, making them easy to catch. These poisons bleach or kill corals and cause lasting damage to the reef habitat (Sadovy et al. 2003).

Another example of damage to foundation species is the dredge harvesting of oysters, as practiced in Atlantic and Gulf Coast estuaries of the United States. This form of fishing flattens otherwise tall biogenic oyster reefs that are inhabited by over 300 fish and invertebrate species (Lenihan and Peterson 2004). An estimated 90% of oyster habitat has been destroyed globally (Beck et al. 2011), mainly by destructive harvesting that began many centuries ago (Lotze et al. 2006). Similarly, clam dredging in seagrass beds negatively affects the habitat-building species Zostera marina in North Carolina (Peterson et al. 1987). By comparing fish and unfished seagrass patches, Peterson and colleagues demonstrated that clam dredging substantially increased seagrass mortality, either by direct damage and dislocation or indirectly by resuspending sediment. The loss of seagrass resulted in a long-term decrease in the abundance of macroinvertebrates, including scallops, shrimp, whelks, and blue crabs. Dredging also caused a decrease in the species richness of soft-sediment infauna and a reduction in the local populations of seagrass-associated fishes, such as weakfish, croaker, and pigfish. Many of these species are economically valuable in fisheries as well as functionally important consumers in estuarine food webs (Beck et al. 2001). The application of ecological experimentation to assess the effects of clam dredging led eventually to regulations in most U.S. states that prevent dredging of seagrass beds.

Habitat degradation caused by fishing and related ecological impacts now occur in very deep water. Prior to about 1950, bottom-fishing was restricted to less than 200 m but extended onto the continental slopes and deep sea, in water as deep as 3000 m, with the introduction of large factory trawlers. Fisheries for orange roughy (Hoplostethus atlanticus), armourhead (Pseudopentaceros wheeleri), thornyheads (Sebastolobus spp.), alfonsino (Beryx splendens), oreos (Pseudocyttus maculatus, Allocyttus niger) and grenadiers (Coryphaenoides spp.) have often been unsustainable (Ramirez-Llodra et al. 2011), and substantial effects on deep-water benthic habitats have been reported from the few studies that have been conducted (e.g., Althaus et al. 2009). Deep-water trawling can affect bottom communities by disturbing sediment, removing infauna, and damaging foundation species. Trawling on continental slopes is a major source of sediment deposition and burial of deep-water communities (Puig et al. 2012). Sediment resuspension and transport rates during trawling for deep-water shrimp (Aristeus antennatus) were sampled near the mouth of a submarine canyon in the northwestern Mediterranean Sea and compared with data from periods without trawling. Trawling caused a dramatic increase in downslope turbidity currents and dynamic sedimentation on the deep canyon floor. Based on their synthesis of worldwide patterns of bottom fishing on continental slopes, Puig and colleagues estimated that trawl-related sediment disturbance, or “deep-sea plowing,” now accounted for a major portion of habitat destruction on, and near the base of, continental slopes (Puig et al. 2012).

On a global scale, most deep-sea bottom trawling happens on sedimentary slopes, but smaller, highly vulnerable habitats and communities located on seamounts and cold-water seeps are also trawled, with large effects on associated communities. The effects of trawling on deep-sea benthic communities can be especially severe because their productivity is generally low and because many of the organisms are long-lived, with slow population growth rates. These factors, combined with the isolation of many seamounts, greatly reduce the resilience of deep-water communities to fishing disturbances. One of the most severe effects of deep-sea fishing is the removal of foundation species, such as deep-water corals (Figure 20.13) and sponges, which provide habitat and refuge for other species (Morato et al. 2006; Althaus et al. 2009).

**Effects of other habitat-degrading activities**

Many human activities other than fishing have direct effects on communities by destroying, degrading, or fragmenting marine habitat. Most of these effects result from our activities on land. One important example is sedimentation resulting from deforestation, land development,
Figure 20.13  Trawl fishing for orange roughy (*Hoplostethus atlanticus*) has affected habitat-forming stony coral (*Solenosmilia variabilis*) across replicate seamounts located south of Tasmania. Photographic samples of coral beds were taken from ROVs over seamounts that had never been trawled, where trawling had ceased 15–20 years before the study, and where trawling has continued. The trawled areas sustained thousands of trawl sets over relatively small areas across the tops of seamounts. (After Althaus et al. 2009; courtesy of Alan Williams/CSIRO Marine Research.)

reclamation of wetlands, and industrial and municipal discharges. While some activities, especially dam building, can reduce sediment inputs from rivers, effectively starving wetlands and beaches of building materials, many marine habitats are threatened by too much sediment. Natural processes such as river discharge, erosion of cliffs, and the resuspension and transport of marine sediments deliver sediments to coastal areas, producing large expanses of soft-sediment bottoms in estuaries, on beaches, and on continental margins. About 10% of the deep sea is covered by natural land-based sediments that flow off the continental shelves and downslope to deep water (Kennett 1982). The remainder of deep-sea sediment originates mainly from the deposition of biogenic matter, especially phytoplankton and zooplankton parts, marine snow, and other particles produced in the euphotic zone. Over the last few decades, however, there has been a substantial increase in the deposition of human-induced sediment in coastal waters and a related increase in turbidity (Airoldi 2003). Unprecedented rates of sedimentation result from deforestation when land is cleared for timber, agriculture, or urban development. Other direct inputs of sediment come from industrial and municipal discharges; the construction of roads, bridges, and tunnels; dredging for navigation; replenishment of beaches; and the removal of wetlands and mangroves for aquaculture. Human activities also affect the supply of sediments to coastlines in indirect ways, such as by accelerating natural soil erosion; by removing important foundation species, such as salt marsh grasses, seagrasses, and oysters, that can control the distribution of sediment; and by modifying the coastline and river catchments, thus changing hydrodynamic and bottom characteristics (Airoldi 2003). For example, about 70% of the wetlands of Europe have been removed, and much of the coastline is now armored or otherwise protected from sea level rise (Airoldi and Beck 2007). This change has resulted in a large increase in the rate of sediment transport along shorelines.

Dramatic negative ecological effects of enhanced sedimentation have been observed in estuaries (Cooper and Brush 1991), mangroves (Ellison 1998), seagrass beds (Vermaat et al. 1997), beaches (Bishop et al. 2006), coral reefs (Rogers 1990), and rocky shores (Airoldi 2003). For example, sedimentation affects the composition, structure, and dynamics of rocky coast assemblages by burying, scouring, or otherwise modifying the characteristics of bottom surfaces as well as by interfering with physical (e.g., hydrodynamics) and biological (e.g., bioturbation) processes (Airoldi 2003). Enhanced deposition of sand, silt, or other loose material on rocky substrates can prevent the settlement of larvae of hard-substrate organisms, such as macroalgae or sessile invertebrates, because they usually choose not to settle in patches of soft substrate. Larvae are often smothered when they settle on clean substrates that later experience sedimentation, which increases mortality and can reduce recruitment. Sediment loading also increases the mortality of adults; for example, by smothering coral polyps (Fabricius and Wolanski 2000), giant kelp (*Macrocystis pyrifera*; Reed et al. 1988), oysters (Lenihan and Peterson 1998), or other foundation species, thereby affecting many associated species. Enhanced sedimentation can also reduce the growth rates of sessile filter and suspension feeders, such as mussels and oysters, and it can reduce light availability for macroalgae (Konar and Roberts 1996) and symbiotic algae within corals.

In some cases, communities can control sedimentation. For example, giant kelp forests, mangroves, and seagrasses can trap sediment and reduce the downstream rate of sediment deposition, while some mobile invertebrates, such as salt marsh snails, can bulldoze sediments, thus clearing patches of hard substrate to the benefit of other species (Bertness 1984). For the most part, however, sedimentation controls community composition and structure. In fact, burial and scour, as well as the reduced availability of light and oxygen (and related increases in toxic hydrogen sulfide), often change communities on rocky shores.
by removing late-successional, large-bodied, and long-lived species, and sometimes foundation species that provide complex structural habitat for co-inhabitants. These species are then replaced by communities of opportunistic flora and fauna, which on rocky coasts are often species of Ulva and other turf-like macroalgae, Phyllospadix (a vascular plant), Anthopleura spp. and other anemones, Tre troublea barnacles, and Phragmatopoma worms. These species replace less tolerant fauna, such as Mytilus mussels and Semibalanus barnacles, and flora, including Ascophyllum, Porphyra, Gelidium, Mesophyllum, and Palmaria (Airoldi 2003). Consequently, sediment deposition brings about fairly predictable community impacts.

Away from coastal and shelf waters, deep-sea communities are affected by many human activities other than fishing, habitat degradation, and sedimentation, which may interact in reshaping these fragile communities on a large scale (Figure 20.14). For 150 years, steamships crisscrossed the seas, dumping pieces of burnt coal, called clinker, over the side, much of it in deep water. Clinker now represents an estimated 50% of the hard substrate available for attachment by brachiopods and anemones, such as Phellactis robusta, across huge expanses of the abyssal plain (Ramirez-Llodra et al. 2011). Along with glacially deposited stones, clinker is an abundant hard-substrate habitat on continental slopes and in deep-water canyons. Like other materials that we dump into the deep sea, including unexploded weapons and low-grade radioactive, pharmaceutical, and chemical waste, clinker is toxic to some species. Littering from boats, a practice outlawed by the 1972 Convention on the Dumping of Wastes at Sea, continues illegally at an estimated rate of about 6.4 million metric tons per year, depositing wood, furniture, fruits and vegetables, meat scraps, milk cartons, naval debris, and plastic bags, bottles, and scraps, most of which degrade slowly into smaller, sometimes more harmful fragments. About 36 million metric tons of human sewage was dumped from barges off the eastern United States between 1979 and 1992, much of it containing toxic material (Van Dover et al. 1992).

Other deep-sea disturbances that are likely to increase in the near future include mining for metal-rich manganese nodules, cobalt-rich crusts on seamounts, and polynuclastic sulfide deposits at hydrothermal vents (Ramirez-Llodra et al. 2011). These various hard substrates are critical habitat for communities of species composed of vestimentiferan worms, mussels, eels, crabs, and limpets (Micheli et al. 2002). Manganese nodules, for example, provide important hard-substrate habitat for the recruitment of epifauna found beneath ocean regions of low and moderate productivity. These deep-sea communities are often separated by long distances from other assemblages, which reduces their capacity to recolonize after a disturbance. More recently, deep sediments have been used as storage space for CO$_2$ and methane, and carbon capture and storage (CCS) plants operating in the Barents Sea and North Sea already store about 700,000 metric tons of CO$_2$ per year in the seafloor at depths of 320–1000 m. CCS is based on the fact that carbon dioxide and methane form stable, solid crystalline structures at high pressure and low temperature. Carbon dioxide can also be disposed of as a liquid directly onto the seabed. Experiments to assess the ecological effects of deep-sea CCS have detected low oxygen and pH levels in surface sediments and near-bottom water. These highly stressful chemical conditions kill infaunal macroinvertebrates and meiofauna and cause scavenging species of amphipods and fish to avoid these areas (Barry et al. 2005; Thistle et al. 2005).

Deep-sea oil exploration, exploitation, and spills have become a major concern following the 2010 Deepwater Horizon oil well blowout in the Gulf of Mexico that released close to 5 million barrels of oil (780,000 m$^3$), the largest accidental spill in human history. The oil not only covered or otherwise killed an immense number of benthic and near-bottom animals, as well as many animals and plants along the Gulf coastline, but also reduced ox-
ygen to harmful levels for many deep-sea organisms as aerobic bacteria metabolized the huge volume of oil. Toxic oil dispersants, used in massive amounts, were also implicated in the death of many marine organisms (Peterson et al. 2012). Like most environments, the deep sea is subject to a growing multitude of human impacts that sometimes cause synergistic effects (see Figure 20.14), such as deepwater hypoxia in the Gulf of Mexico caused by the combination of oil spills and the runoff of nutrients and organic-rich sediment from the Mississippi River.

**Indirect effects of habitat degradation**

Habitat degradation and destruction can cause a complex array of indirect effects on communities, many of which we are just beginning to detect and understand. Here we present a set of representative examples related to sedimentation on rocky shores, predator outbreaks on coral reefs, and fishing impacts on salt marshes. These examples highlight the marked resilience of some marine communities when impacted by catastrophic natural and human-induced habitat disturbances.

Indirect effects accompany many of the direct effects of sedimentation on rocky coastlines described on p. 465. These effects include the facilitation of sediment-tolerant turf algae that provide habitat for many infaunal invertebrates, as well as colonization space for *Pachythione* sea cucumbers, voracious filter feeders that can prevent the reestablishment of upright macroalgal species by filtering out algal spores long after the cessation of sediment deposition (Rassweiler et al. 2010). The establishment of massive colonies of these turf-dwelling echinoderms leads to the permanent loss of upright macroalgae, especially *Gelidium*. Those macroalgae provide habitat for benthic amphipods, the major food item of reef fishes such as surf perches (Okamoto et al. 2012). Other indirect effects of sedimentation result from periodically intensified sediment scouring events that remove patches of turf algae, thus providing recruitment substrate for macroalgae (Airoldi 2003). This is an example of community resilience due to positive feedbacks within food webs caused, in this case, by additional physical disturbance.

Other examples of community resilience and hysteresis (i.e., the existence of different stable states under similar environmental parameters) come from research on coral reefs and salt marshes. Coral reefs are decimated periodically by natural disturbances, especially bleaching events, storms, and localized outbreaks of coralivores. The frequency of severe storms may be increasing as a consequence of global climate change (Tudhope et al. 2001; but see Cobb et al. 2013), and the frequency of coral-eating crown-of-thorns sea star outbreaks has been increasing as well, possibly due to the combined effects of fishing of the sea star’s predators and increasing nutrient inputs that may benefit its larvae (De’ath et al. 2012). In many circumstances, when corals are killed by bleaching, storms, or sea star predation, macroalgal communities become established that prevent or greatly slow the recovery of corals, especially on reefs where humans fish intensively for herbivores (Hughes 1994). Hysteresis occurs when coral populations fail to recover after the disturbance and the reef communities become dominated by macroalgae instead. However, Adam and colleagues (2011) recently reported work from Moorea, French Polynesia, showing that abundant herbivores, particularly parrotfishes, can control macroalgae and thereby speed the recovery of corals. Herbivory clears substrate for the settlement of coral larvae and prevents the overgrowth of juvenile corals by rapidly growing algae. These positive feedbacks of herbivore populations—in this case promoted by nearby healthy lagoon habitats that act as parrotfish nurseries—enhance the resilience of coral reefs by preventing hysteresis. Interestingly, Tahitians have a tradition of protecting parrotfishes from fishing during crown-of-thorns outbreaks because they understand, through a long history of direct observation, that parrotfishes are important to coral recovery (Kirch and Dye 1979).

Indirect effects of recreational fishing on habitats have been demonstrated in New England salt marshes (see Chapter 11). There, intensive recreational fishing of predatory fish and crabs led to increases in populations of their prey, including *Sesarma reticum*, a native herbivorous crab that grazes on cordgrass, the foundation species in these marshes. Fishery-related increases in *Sesarma*, in turn, led to a massive die-off of cordgrass caused by enhanced grazing rates (Figure 20.15). Nearly 40% of this foundation species disappeared across New England salt marshes, and up to 90% in some extreme cases (Coverdale et al. 2013). The die-off of cordgrass led to more indirect effects because its disappearance exposed peat-rich banks to heat stress and desiccation that prevented cordgrass recruitment and therefore recovery (Altieri et al. 2013). This cycle of marsh desertification was partly reversed when the peat banks finally eroded, in part due to the influence of bioturbating animals, thus creating mud patches that cordgrass could colonize. Once cordgrass was reestablished, a positive feedback occurred where small cordgrass patches engineered zones of reduced physical stress, largely through shading and moisture retention, which led to the subsequent expansion of cordgrass populations. Further recovery of cordgrass was also facilitated by the introduction of *Carcinus maenas*, a predatory crab, which reduced local abundances of *Sesarma* through risk-induced escape behavior (Bertness and Coverdale 2013). These examples illustrate how facilitation and consumer interactions can influence community resilience and recovery from habitat disturbance in positive ways.

**Summary: Effects of habitat degradation**

In summary, the direct effects of habitat degradation are reduced habitat complexity, biomass, species richness, biodiversity, and productivity. Habitat degradation is also an important cause of local extinctions. Some habitat types exhibit resilience to human perturbations, while others are...
more vulnerable and take longer to recover. Vulnerability is often a function of the natural disturbance regime and the longevity of the foundation species. Fishing causes large-scale, intense habitat disturbance on much of the seafloor, including parts of the deep sea. The greatest impacts result from mobile fishing gear, such as bottom trawls and dredges. Destructive coral and oyster reef fishing also reduces species abundance and diversity. The largest threats to marine habitats are in the deep sea, due to its inherent vulnerability, and near coastlines, due to additional habitat degradation caused by pollution, sedimentation, land reclamation, and urban development.

A diverse array of indirect ecological effects result from habitat loss, degradation, and fragmentation. Habitat degradation can increase physical stress, thereby excluding some species and attracting others, including non-native predators, grazers, or parasites. Habitat degradation can also cascade through marine communities by exposing organisms to multiple environmental stressors that generate synergistic negative effects. Habitat fragmentation reduces local resource availability, enhances encounter rates between predator and prey species, and reduces population connectivity. Negative feedbacks can enhance cascades of effects leading to community hysteresis. However, positive feedbacks can enhance community recovery, and thus resilience. Understanding and recognizing positive feedbacks leads to better environmental practices, and perhaps greater success in marine conservation and restoration. The effects of habitat degradation are sometimes alleviated or reversed by habitat restoration, as described in the next section.

**Habitat restoration**

Habitat restoration is used to compensate for habitat degradation or loss, to recover marine resources, and to conserve habitat-dependent populations and communities (Thayer 1992). Well-established examples of reversing habitat degradation and loss include the restoration of seagrass by reseeding (Bell et al. 2008), of salt marsh and mangroves through hydrological engineering (Lewis 2005), and of surfgrass by transplanting sprigs (Bull et al. 2004). Restoring coral reefs destroyed by blast fishing has proved possible by outplanting rocky substrates for coral settlement (Fox et al. 2005). However, this method, along with coral “gardening,” in which coral fragments or colonies are collected from wild populations and transplanted, is expensive and not as effective as protecting corals from destructive fishing in the first place (Haisfield et al. 2010). In fact, coral populations sometimes display a high capacity for recovery from catastrophic disturbance, especially when herbivorous fish are able to suppress macroalgal overgrowth of coral recruits (Adam et al. 2011). These general examples highlight the successful recovery and restoration of foundation species, which in turn promote associated communities (Thayer 1992). Next we discuss two specific examples that emphasize how positive ecological feedbacks enhance restoration success and benefit marine communities.

In many regions, oyster reef restoration is necessary to sustain oyster fisheries and other ecosystem services, such as the maintenance of decent water quality and provision of habitat. Dredge harvesting of oysters has decimated populations and degraded reef habitats by reducing vertical structure (Beck et al. 2011). Such “flattened” reefs have...
become more prone to sedimentation and bottom-water hypoxia (Lenihan and Peterson 1998). The enhancement of oyster reefs is usually achieved by adding oyster shells to rebuild reef structure, which boosts oyster recruitment and enhances reef quality. In addition, reef restoration in marine reserves appears to increase oyster larval supply and subsequent recruitment on reefs in fished areas (Powers et al. 2009). Reef restoration also attracts a large variety of estuarine fishes that prey on reef invertebrates, primarily amphipods, mud crabs, and shrimp (Figure 20.16). According to an economic analysis, restored reefs are even more valuable for their production of commercial fish than for their production of oysters (Grabowski et al. 2012).

As oysters settle and grow, they create increasingly large and physically complex reefs that attract greater numbers of benthic predators, including blue crabs (Callinectes sapidus) and oyster toadfish (Opsanus tau; Lenihan et al. 2001). Increased abundance of these predators leads to reduced predation on oysters by mud crabs (Panopeus herbstii), via both direct predation on mud crabs and risk effects (Grabowski 2004). The improvement in reef structure thus increases oyster recruitment and growth, which generates habitats that benefit predators, which indirectly protect oyster populations. Such positive feedbacks have provided the ecological underpinnings for successful large-scale oyster restoration efforts (Schulte et al. 2009).

Forests of giant kelp (Macrocystis pyrifera) have also been restored, with positive effects on kelp and the many species that depend on this highly productive foundation species. One of the largest marine restoration projects in history is under way in southern California near the city of San Clemente. Operation of the San Onofre Nuclear Generating Station since 1983 led to the disappearance of a giant kelp forest near the plant. Nearly 74 ha of kelp forest vanished as the plant drew in and then discharged 6.3 million liters of seawater per minute to cool the nuclear reactors (Reed et al. 2006). The turbid discharge water severely reduced water clarity on rocky reefs, which led to a dramatic loss of kelp.

The kelp restoration effort entailed construction of multiple artificial patch reefs, built with discarded cement and quarry rock, which covered an area of 61 ha just beyond the zone of reduced water clarity. Operation of the nuclear power plant is under way, but the kelp restoration effort has continued. Within 2 years, most of the replicate artificial reefs supported thick stands of giant kelp as well as a large number of kelp forest invertebrates and fishes. As the kelp grew taller, it reduced light penetration to the benthos, thus inhibiting the growth of understory macroalgae that compete with it for space and prevent giant kelp recruitment (Reed et al. 2004). On some reefs, however, sea fans (Muricea californica) recruited in high abundance, preventing kelp recruitment by filtering spores before they settled. By trapping sediments, sea fans and neighboring understory algae also reduced the survival of the few kelp recruits that managed to establish. Sea fans dominated many of the patch reefs for several years until a large storm caused intense sand scour that killed the sea fans. Reefs once dominated by sea fans were quickly recolonized by giant kelp. This example illustrates that the success of habitat
restoration is often dependent not only on good engineering—in this case, well-designed artificial reefs—but also on an element of ecological good luck. Episodic events, such as sea fan recruitment and physical disturbance, can temporarily alter the trajectory of habitat restoration. Positive feedbacks, such as the inhibition of competitors by the kelp itself, help to ensure the persistence of restored habitats. These examples illustrate some of the challenges and benefits of habitat restoration, which is now an important tool for marine ecosystem-based management.

**Synthesis: The Ecosystem Approach to Fisheries Management**

From all the evidence discussed in this chapter emerges the pressing question of how to balance fishing and other ocean use with the conservation of marine resources and their supporting ecosystems. There have been long-standing efforts to get this right for individual target species (Garstang 1900; Beverton and Holt 1957; Ludwig et al. 1993), but more recently our focus has shifted toward an ecosystem approach to fisheries (EAF; Garcia et al. 2003; Pikitch et al. 2004; Crowder et al. 2008). In this section we first examine in more detail the concept of overfishing, how it is traditionally defined and quantified, and how it might be reexamined from an ecosystem perspective. Then we consider the trade-offs, the cumulative effects, and ultimately the societal choices that will guide the sustainable management of marine ecosystems in an uncertain future.

**What is overfishing?**

A population or an ecosystem that suffers severely from the effects of fishing is said to be overfished. Overfishing is driven by the exploitation rate $U$, which denotes the proportion of the fishable biomass $B$ that is taken out every year as catch $C$; that is, $U = C/B$. From a single-species management perspective, a population is being overfished when the exploitation rate $U$ exceeds the long-term sustainable rate $U_{MSY}$. If this continues for some time, the population biomass will decline below the biomass $B_{MSY}$ that is predicted to produce maximum sustainable yield. Such a population is biologically overfished. Currently, about two in three fish populations that are scientifically assessed have been overfished according to this definition, and about half of those populations are being driven down even more by further overfishing (Worm et al. 2009). The availability of a scientific assessment should in principle enable managers to avoid overfishing in the first place, yet it has failed to do so in many cases. One key problem with the MSY approach is that the exact point of maximum sustainable yield is often difficult to determine in a variable environment, as there are uncertain estimates of fish biomass, population structure, and life history attributes. In a management context, that uncertainty can be used by special interests to push for larger catches, which deplete biomass even further. In addition, there is illegal, unreported, and unregulated (IUU) fishing that leads to lower biomass than the management target. The result of this pattern is that many populations and entire fish communities have been depleted far below the biomass that would produce maximum sustainable yield (Worm et al. 2009; Hutchings et al. 2010). Fish stocks that are not being scientifically assessed are especially at risk (Costello et al. 2012). An analysis of catch levels and life history attributes suggests that unassessed stocks are fished at a higher rate and depleted further, on average, than assessed stocks. This is particularly true for smaller inshore stocks that are important to coastal communities and artisanal fisheries. While many assessed stocks have been stable or even increasing in abundance in recent years, unassessed stocks continue to decline (Costello et al. 2012). Since assessed stocks are mostly based in wealthy, developed countries, these recent trends indicate a growing divide between rich and poor parts of the world in terms of the sustainability of their fisheries resources, and by inference, the health of their marine ecosystems (Worm and Branch 2012).

**Ecosystem overfishing**

While there is little debate about what constitutes an overfished population, there is much less clarity about the overfishing of ecosystems. Clearly there is a need for a novel framework for considering the effects of fishing on nontarget species, habitats, and food web structure. In a comprehensive review on the topic of ecosystem overfishing, many definitions were extracted from the published literature (Murawski 2000). While those definitions focused on different aspects of overfishing, they converged on a number of common themes, from which a number of overfishing symptoms could be derived. An ecosystem is thought of as overfished when the effects of catches and discards, as well as the effects on habitats, meet one or more of the following conditions (Murawski 2000):

- **Biomass** of one or more system components falls below minimum biologically acceptable limits, such that recruitment and recovery prospects are significantly impaired.
- **Prey species** are harvested to an extent that impairs the long-term viability of non-resource species such as marine mammals, turtles, or seabirds.
- **Biodiversity** of communities or populations declines significantly as a result of sequential depletion of stocks.
- **Variability** over time increases due to selective harvesting and increasing exploitation rates.
- **Resilience** of the ecosystem declines as a result of fishing-related changes to species composition, size structure, and age structure.
- **Economic and social benefits** decline due to overharvesting.

Where these criteria are used for management, they result in significantly more conservative management than if every species were managed in isolation. Species interactions
are accounted for and the sustainability of nontarget foundation species (many of which may require enforcement of a very low mortality rate) is also kept within safe limits.

**Reference points for management**

To operationalize the concept of overfishing for decision making, managers require clear decision rules that indicate when a harvest strategy is safe and when it is not. The question, from a management point of view, is rarely “Should fishing take place?” but more commonly “How much fishing is sustainable?” Ideally, there is a so-called reference point beyond which fishing must cease in order to rebuild the population, or ecosystem, to more desirable states. Again, reference points are easily implemented from a single-species perspective. If the objective were to maximize food supply from the oceans, every target species would be scientifically assessed and fished at MSY. The operational reference points would be the $B_{MSY}$ and $U_{MSY}$ that (if perfectly enforced) should ensure long-term sustainability with maximum yield. The problem with this strategy is that it would still result in overfishing from an ecosystem perspective, as species interactions such as those between forage fishes and predators would not be taken into account.

To fix this problem, we can consider the multispecies maximum sustainable yield, or MMSY (Figure 20.17). This parameter is based on a multispecies model of the fished community that includes all species that are captured as target species or bycatch. Just as for single species, one can plot the long-term sustainable catch as a function of the community exploitation rate. The MMSY occurs where the yield across all species taken together is maximized. Although this strategy brings us one step closer to a true ecosystem approach, there are still large reductions in total biomass, declines in the average size of fish, and most importantly, a steep increase in collapsed species, even under optimal MMSY-based harvesting. From the perspective of total yield, this strategy makes sense, but from a conservation perspective it would be disastrous! Thus there is a trade-off between the degradation of the ecosystem and the extraction of biomass for human consumption.

Figure 20.17 also indicates, however, that a large reduction in the exploitation rate (say, to 50% of $U_{MMSY}$), would cause only about a 15–20% reduction in total yield, but an almost tenfold reduction in the proportion of collapsed species. Biomass would be predicted to double under this scenario, and size structure would be restored to more natural levels as well. Interestingly, such a conservative harvest strategy also makes more economic sense. Halving the exploitation rate would also cut the cost of harvest-
It should be noted that this strategy does not yet incorporate the effects of fishing on habitats, and that additional measures are needed to preserve some of the most vulnerable bycatch species, such as sharks and sea turtles. For these aspects of ecosystem management, gear regulations and modifications, as well as spatial management measures, are required. Bycatch of sea turtles in shrimp trawls, for example, was largely addressed through a modification of the fishing gear. Turtle excluder devices, which include a sorting grid and escape hatch fitted to the front of the trawl, allowed turtles to survive capture in a trawl. Other such gear modifications for reducing bycatch are devices to “shoot” pelagic longlines into the water without exposing the bait to surface-feeding seabirds such as albatrosses. Similarly, an “eliminator trawl” that hovers above the seafloor reduces cod bycatch in groundfish trawls while capturing more prolific haddock and reduces seafloor impacts at the same time. Replacement of destructive fishing practices, such as handpicking of oysters using scuba gear rather than dredge harvesting, also helps conserve habitat and increase harvesting efficiency (Lenihan and Peterson 2004). These ecosystem management measures are all, in effect, aimed at protection of vulnerable bycatch species or habitats.

Spatial management is another key element of ecosystem management. It includes the use of time-area closures and marine protected areas (MPAs) to protect certain species or habitats. Spatial management takes different ocean uses into account and protects particular habitats from fishing or other impacts. Protected areas may exclude certain forms of fishing (or other uses such as oil and gas drilling) that are deemed damaging to sensitive habitats, such as coral reefs, sponge beds, or other biogenic structures. Or they may exclude all uses, as in marine reserves, which allow for the full recovery of species within their boundaries and may act as a reference site and refuge for even the most sensitive species. A detailed review of marine spatial planning and marine protected areas is found in Chapter 21.

**Figure 20.18** Modeling of trade-offs in the management of forage fish. Yield is shown as a proportion of maximum sustainable yield (MSY) of low-trophic-level forage fish species. The ecological impact of taking that yield is measured as the proportion of other ecological groups whose biomass varied by more than 40%. Shaded zones show 95% confidence limits derived from running different ecosystem models. (After Smith et al. 2011.)
Summary of ecosystem-based fisheries approaches

In summary, the ecosystem approach to fisheries takes into account the direct and indirect effects of fishing on target species as well as on the ecosystem at large. As such, it does not strictly replace, but widens the mandate of traditional single-species management by recognizing the complex interactions among different species, fisheries, and other ocean uses. There are a number of approaches to avoid overfishing from an ecosystem perspective, all of which result in more conservative exploitation rates than single-species management does. A robust ecosystem-based harvest strategy appears to center around much lower exploitation rates than previously aimed for, probably about half of MSY or MMSY. Such a strategy would rebuild biomass across the community, restore size structure, and reduce the number of collapsed or heavily depleted stocks. It would also entail significant economic benefits, as the costs of fishing would be reduced and profits increased. Gear modifications and spatial management approaches, including marine protected areas, would augment such a harvest strategy and deal with the protection of habitats and sensitive bycatch species.

Conclusions and Future Directions

In this chapter we have summarized what is known about the effects of fishing and habitat degradation on marine communities from salt marshes to the open ocean. There is little doubt that fishing and other forms of exploitation, often in combination with habitat degradation, represent a major threat to marine populations and ecosystems. Overfishing has been widespread throughout human history and has dramatically altered marine ecosystems. Even low levels of fishing tend to have powerful effects on community structure by reducing the biomass and abundance of target and bycatch species and by changing the size and age structure of communities toward smaller, younger, and faster-growing species. Fishing or hunting of marine predators often has profound top-down effects via release of mesopredators or herbivores that can cascade through the food web. These indirect effects are well understood in coastal and benthic ecosystems, but remain less clear in open-ocean food webs. Transmission of top-down effects through the food web occurs both through direct consumption and through risk effects, resulting in “fear-released” systems. The relative importance of these mechanisms and their long-term effects requires further study. Low-trophic-level fisheries, which are increasing in many parts of the world, can have severe indirect effects on populations of predators such as marine mammals and seabirds. Despite all these changes, few global extinctions have yet been documented in the marine environment, and recovery of populations and ecosystems typically occurs when the effects of fishing are brought under control.

Some fishing practices, such as trawling, dredging, poisoning, and dynamiting, degrade or destroy habitat formed by biogenic reefs, epifaunal assemblages, and soft-sediment communities. Benthic disturbance caused by bottom trawling is exceeded in spatial scale only by massive oxygen dead zones, yet trawl scars can take longer to recover. Reducing physical habitat complexity or removing ecosystem engineers can affect community composition and structure by reducing the abundance, biomass, and species diversity of resident fauna, changing community patchiness, and shifting communities from higher to lower trophic complexity. Disturbances modify hydrodynamic, geochemical, and sedimentary habitat conditions and can reduce community production and the provision of ecosystem services. Habitats can recover from fishing disturbance, but its indirect effects can slow recovery, sometimes generating hysteresis and thus alternative stable states.

Ecosystem approaches to fisheries aim to avoid these deleterious effects of fishing and habitat degradation on marine communities and food webs. Such approaches are now widely mandated. Although there is no unifying definition of EAF, or even a coherent system for evaluating the success of EAF approaches, there are some clear indicators of overfishing that can guide more sustainable management practices. These practices include substantially reduced harvest rates in combination with special measures to reduce bycatch and preserve habitats. With the shift toward an ecosystem approach, we actually observe declining exploitation and fair prospects for rebuilding across much of the developed world. Other regions and stocks, however, appear to be declining ever further as they are subjected to continuing unsustainable practices. Marine community ecologists are shifting their focus from documenting impacts toward understanding the prerequisites for the rebuilding of depleted populations and the recovery of damaged ecosystems. Expanding the traditional focus on the Northern Hemisphere to heavily impacted regions in the developing world may be an important frontier for applied ecological research in the twenty-first century.

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LITERATURE CITED


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