What Can Ecology Contribute to Ecosystem-Based Management?

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Abstract

Modern fishing changes the ocean environment in many ways, including disturbing the sea floor, altering the food webs, and shifting many important ecosystem functions. Natural history, oceanographic, habitat, behavior, and ecological information must be integrated to implement meaningful ecosystem-based management. We discuss the urgent need to expand the concept of essential fish habitat to include important food-web relationships. The need for a broader perspective in terms of ecosystem function and the effects of interactive stressors is emphasized to maintain the vitality and resilience of valued ecosystems. Maintenance of multiple ecosystem functions is a key factor in the adaptive capacity of ecosystems to change. We argue that an ecological understanding of resilience embraces uncertainty and encourages multiple approaches to the management of humans such that ecosystem functions are maintained.

INTRODUCTION

Sustainability:
represents the long-term viability of resource use without degradation of biodiversity and concomitant ecosystem services and values

Ecosystem services:
biological, physical, and chemical functions within ecosystems that sustain life and the quality of well-being for humanity

Fisheries, conservation managers, and society face an ongoing dilemma balancing the intrinsic value and use of natural resources. In general, society owns the resources and entrusts managers to protect them for the future. Unfortunately, management often perceives the short-term, immediate, and usually quantifiable financial benefit to outweigh the long-term maintenance of ecosystem goods and services and the intrinsic and future benefits in any ecosystem. Despite the success of environmental impact assessments in the terrestrial realm, enormous impacts of fishing in the marine realm often are ignored.

There is a long history of concern for the broader consequences of fishing, and since the publication of the paper by Dayton et al. (1995), there has been an explosion in both the number and range of studies that address the consequences of disturbance to the seafloor, shifts in community and habitat structure, and loss of ecosystem function. With this and other concerns over the declining fish stocks, changes to the size and structure of marine food webs, impacts of by-catch, and the loss of many of the larger, charismatic, conservation icons (e.g., dolphins, turtles, sharks, albatross), we have seen a shift in focus and a broadening of the scope of marine resource management. Ecological sustainability and ecosystem-based management have become dominant themes in both scientific publications and wider public debates (see Ecosystem-Based Management sidebar below). Finally, we are beginning to see a recognition of the fact that the oceans are not an unfathomable resource with a seafloor composed of vast expanses of featureless and worthless sand and mud and the waters serving as a homogeneous bath.

Indeed, the World Bank teamed up with the Food and Agricultural Organization (FAO) to document the economic justification of fishery reform and estimated the cumulative economic loss over the past three decades to be worth approximately US\$2 trillion (World Bank & FAO 2008). This figure is based on the short-term and direct potential economic benefits and excludes both the impacts and resultant economic losses to recreational fishing, marine tourism, and ecosystem services. The World Bank and FAO report documents sequential overfishing and declining catches (Jackson 2001, Myers et al. 2001, Pauly et al. 1998). But while the report struggles with the economic and policy aspects of recovering this wealth, it seems to argue that fishery reform can recapture a substantial amount of this loss and that sustainable fisheries can create an economic surplus and be a driver of economic growth. This proposed biological recovery focuses on traditional global maximum sustainable yield and carrying capacity concepts, seemingly not recognizing long-standing criticism of these management techniques (Larkin 1977, Ludwig et al. 1993). Of particular concern is the continued sole reliance on single-species management with its focus on recapturing the potential fishery yields of yore, which occurred in ecosystems distinct from those that exist today. As an example of a broader ecological perspective to these economic arguments, which recognizes the wealth of ecosystem services derived from marine ecosystems, the Millennium Assessment (**http://www.millenniumassessment.org/en/index.aspx;** last accessed

ECOSYSTEM-BASED MANAGEMENT

There are many interpretations, but basically this form of management has clear operational goals focused on long-term ecological sustainability. Ecosystem-based management (EBM) recognizes humans as part of the ecosystem and has a commitment to adaptability, accountability, and inclusive decision making. EBM should recognize the dynamic and heterogeneous nature of ecosystems with attention to context and scale and the application of sound ecological models that address complexity and connectivity.
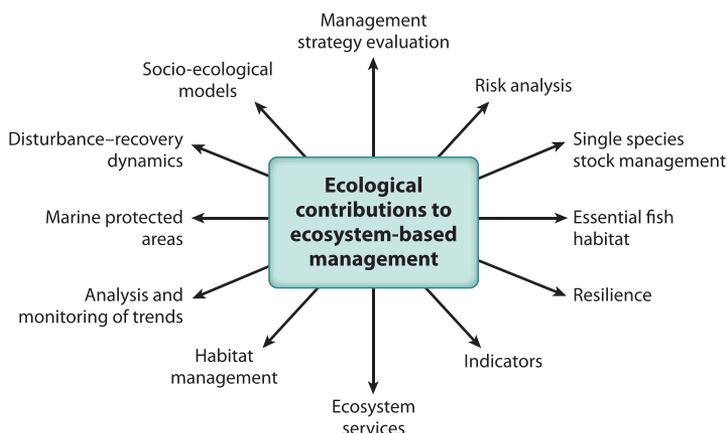
Figure 1

Tools for ecosystem-based management to which ecology contributes. Individual elements are interlinked, but these have been omitted for clarity.

on 22 March 2009) highlights the role of fishing in degradation of the marine environment. Our review emphasizes that shifts in resilience associated with fishing impacts can make recovery a far harder and slower process than those associated with their degradation. We maintain that habitat and ecosystem alteration combined with climate and oceanographic changes have resulted in ecological ratchets that will not easily switch back into the systems that once supported such fishery yields.

Progress toward implementing ecosystem-based management (EBM) and incorporating broader perspectives into fisheries is being made in many countries, albeit slowly. A key problem is illustrated in the summary statement from an International Council for the Exploration of the Sea Symposium that considers incorporating ecosystem objectives into fisheries management. Gislason et al. (2000) concluded that this symposium demonstrated that despite considerable evidence that marine ecosystems have been impacted by fishing there was no consensus on what to do about it. Nevertheless, EBM represents a substantive broadening of the management perspective from traditional stock assessment strategies (**Figure 1**). It does not replace the management of exploited stocks but rather seeks to balance this single action with a range of other important issues. EBM is driven by explicit goals; executed by policies, protocols, and practices; and made adaptable by monitoring and research that is based on our best understanding of the ecological interactions and processes necessary to sustain ecosystem structure and function. EBM is expected to balance the needs and values of society in an inclusive fashion, rather than by focusing on the delivery of benefit to one group of specific resource users. Explicitly, it aims toward the sustainability of ecosystem structures and processes necessary to deliver goods and services.

As a management framework, EBM is a socioecological and political process. Even though many sectarian voices seek to influence decision-making and policy-forming processes, we hope that such decisions are supported by a broad base of the latest scientific data, theory, and expert diagnostic opinion. In this paper, we consider what ecology can contribute to EBM to improve the status of degraded fisheries and ecosystems and broaden the values and scope of decision-making processes.

Resilience: the potential for recovery from disturbance (engineering resilience); a variable that represents the movement of a system within and between stability domains (ecological resilience)

CONFIRMING CHANGE AND BROADENING THE SCOPE OF ASSESSMENT

Meta-analyses: procedures looking for overall effects or how variation in the strength of effects in individual studies can be accounted for by specific broadscale factors

Biological traits analyses: combines natural history information on life history, dispersal, feeding, morphological, and behavioral characteristics of individual species to identify groups of species that contribute to specific ecological functions

One of the problems faced by impact assessments for fisheries has been the need to move from a small-scale and short-term approach, typical of those used for many other impacts, to one that looks at the broadscale of chronic and cumulative impacts (Thrush et al. 1998). Early experimental studies were often interpreted as evidence of weak effects when particular sites failed to detect an impact, although these sites were often located in areas subject to wave disturbance or a long history of fishing disturbance. Early meta-analyses of experimental studies of trawl and dredge disturbance were limited by the range of experiments available (Collie et al. 2000). Meta-analyses are always constrained by the studies available, and there are still strong geographic, depth, and habitat biases, with most funding directed toward temperate and extensively fished areas with comparatively few studies in tropical, polar or shelf break, and deeper habitats (Cryer et al. 2002, Levin & Dayton 2009). Despite these limitations, recent meta-analysis emphasizes the vulnerability of a range of habitat types to trawling and dredging, including areas with gravelly sediments that usually have strong hydrodynamic forcing (Kaiser et al. 2006).

Although the strength of disturbance effects varies with disturbance history and environmental setting, consistent patterns are emerging regarding the loss of large and long-lived organisms, decreases in habitat heterogeneity and species diversity, and the loss of important functional groups (e.g., suspension feeders). In particular, the application of biological traits analysis has both facilitated comparisons across communities and made important links between changes in community structure and function (Bremner et al. 2006a, 2006b). For example, filter-feeding, attached epifaunal organisms and large organisms, in general, tend to show negative correlations with trawling intensity, whereas small infauna and scavengers tend to become more abundant (Tillin et al. 2006). The pattern that emerges from intensive studies in the eastern Bering Sea shows a decrease in the mean size of epifauna organisms associated with chronic trawling disturbance (McConnaughey et al. 2005). Over the long term, a common pattern emerges of the loss of epifauna and large and long-lived organisms such as burrowing urchins, large bivalves, sea pens, and reef-building sabellid polychaetes (Robinson & Frid 2008).

When the larger, rarer, and often sensitive species can be aggregated into groups, specific hypotheses concerning the vulnerability of different community groups to fishing disturbance can be defined and their effects identified. For example, in the northwest Mediterranean, the seafloor is muddy and the benthic community is dominated by small deposit feeders and predator/scavengers. Nevertheless, de Juan et al. (2007) were able to describe differences in community structure between an area fishers avoided owing to the potential for gear loss and a surrounding heavily fished area. More burrowing epifaunal scavengers and motile burrowing infauna were found in the fished area, while the less-disturbed area was characterized by a higher abundance of surface infauna, epifaunal suspension feeders, and predatory fish. These findings illustrate that ecological characterization of the vulnerability of different functional components of the benthic community can lead to the detection of impacts even in areas that are dominated by organisms not normally considered especially sensitive to trawling disturbance.

Recent studies conducted over broad spatial and temporal scales employing biological trait analysis have demonstrated effects in areas with a long history of disturbance. Analysis of a series of historical data sets has revealed substantive changes in the heavily impacted and shallow North Sea, where mechanized fishing has been in operation for over 80 years. These studies can attribute temporal changes in benthic communities to changes in fishing pressure, even though other sources of temporal variability such as changes in productivity were also evident (Callaway et al. 2007, Robinson & Frid 2008). Statistical techniques that allow different sources of variability to

be partialled out or attributed to various factors have been developed and applied in a number of ecological studies: For univariate examples, see Box & Jenkins (1976), Chatfield (1980), and Legendre et al. (1997), and for multivariate examples, see Anderson & Gribble (1998), Borcard & Legendre (1994), Borcard et al. (1992, 2004), and Turner et al. (1999). These types of analyses are essential to identify how different sources of variability, either individually or in combination, affect the emergent broadscale temporal and spatial patterns (Thrush et al. 1998).

EFFECTS ON ESSENTIAL FISH HABITAT

Concerns over the adverse effects of fishing and the inter-relationships between the sustainability of exploited stocks and ecosystem function have resulted in policy initiatives and management actions in a variety of countries. Ecosystem-based fisheries management is predicated on the protection of important ecosystem components, especially essential habitat for all the species impacted by human activities. The legal language regarding essential fish habitat in the U.S. Magnuson-Stevens Fishery Conservation and Management Reauthorization Act (Public Law 109–479) is focused on "those waters and substrate necessary to fish for spawning, breeding, feeding or growth to maturity" for all life stages of all federally managed species in the U.S. Exclusive Economic Zone (R.A. McConnaughey, personal communication). This focus on the specific managed species does not have the breadth of an EBM approach. Most of the literature discussing essential fish habitat focuses on the simplistic geophysical features of the seafloor and ignores many important factors such as biogenic structure and dynamic oceanographic features. At its most simplistic, this approach is akin to defining a terrestrial habitat devoid of vegetation (e.g., rain forest, savannah) or climate (e.g., Mediterranean, arctic). In fact, a wide diversity of habitats exists on the seafloor, and just as in seagrass beds and coral reefs, most of these habitats are defined by resident organisms that structure the sediment and modify interactions across the sediment-water interface. As our ability to view the seafloor improves, we become increasingly aware of the extent and diversity of spatial structure and heterogeneity within these systems.

There are many examples of organisms that are architects of their own habitat. The most familiar are coral reefs, kelp forests, and reefs of filter-feeding bivalves (e.g., oysters and mussels). Less well known but also important are deep-sea sponges, gorgonians, and corals that can be extremely old and that in some cases form deep-water communities that tower more than 40 m above the sea floor, as well as the smaller-scale tube mats, burrow fields, and the many types of foraminiferan gardens (Levin & Dayton 2009, Thrush & Dayton 2002). Yet, trawling tends to homogenize the sediment and simplifies the three-dimensional structure both above and below the sediment-water interface (Gray et al. 2006).

The extensive literature reviewing the effects of fishing on benthic habitats makes the case that essentially all trawling impacts the benthic environment, often in a very serious way (Stevenson et al. 2004). Various habitats and regions with different histories of disturbance are expected to exhibit a variety of responses and magnitude of effects. This implies that we need to understand better the range and diversity of existing habitats, how disturbance is likely to influence their ecosystem function, and therefore ecosystem services, and their recovery potential and resilience (**Figure 2**). Research shows not only that all species have essential or critical habitats, but also that the concept of a habitat is not restricted simply to the physical structures of the seafloor or temperature profiles in the water column. Indeed, this concept must also include the availability of resources (including food) and the natural risk of mortality. Within this broader definition, behaviors involved in foraging and risk avoidance are important components of the natural habitat and may be modified by fishing activities.

| Dynamics of change | | Management strategy |
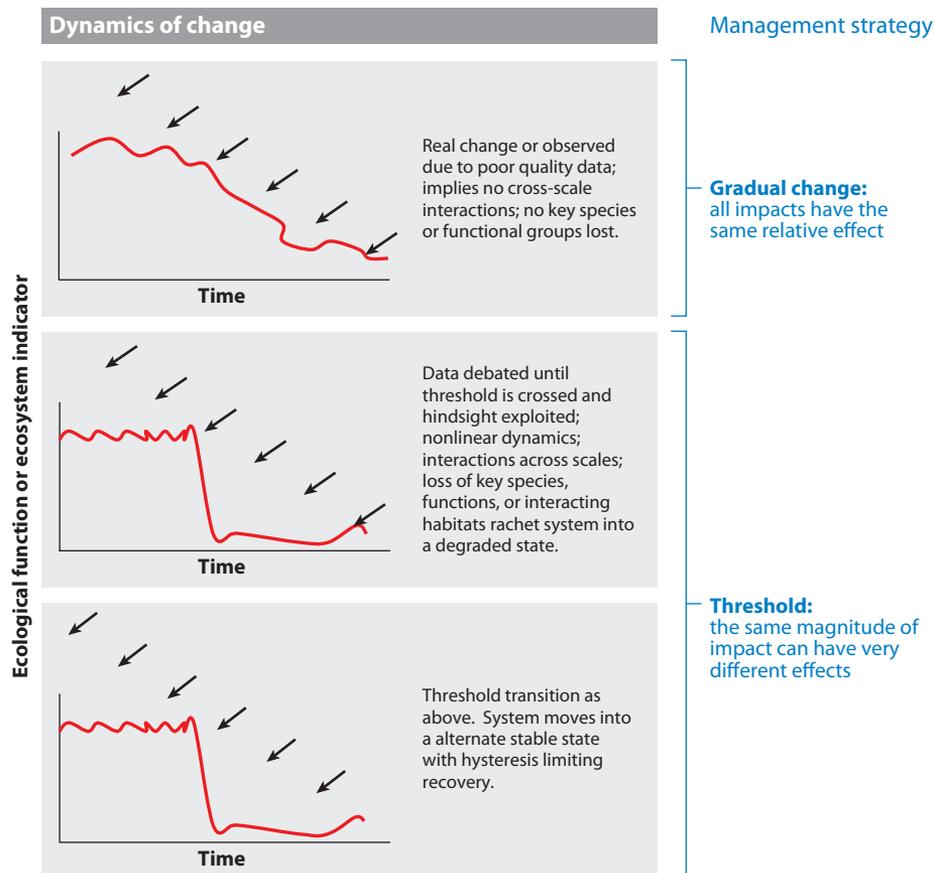
Figure 2

The application of consistent stress does not always lead to consistent ecosystem response. The effects of slow recovery, habitat fragmentation, and shifts in ecosystem function highlight the potential for nonlinear change. Managing ecosystems with thresholds and cumulative effects has profound implications for resource management and conservation.

ECOSYSTEM SERVICES

Bioengineering species fundamentally influence the architectural and functional complexity of the seafloor. These include emergent organisms that modify flow and provide settlement sites and refugia for predators or prey; predators digging into the substratum in search of food (e.g., rays, walrus, fish, crabs, etc.); and organisms creating tubes, burrow mounds, and other manipulations of the sediment. The activities of these benthic marine organisms significantly influence the nature and rate of biogeochemical processes that sustain the biosphere. Microbial species in the sediments drive nutrient and carbon cycling, but this is strongly facilitated by the movement, burrowing, and feeding of infauna and epifauna. These processes highlight important links between seabed and water-column ecosystems that affect nutrient recycling and processing of organic debris (Thrush & Dayton 2002). Such functions represent ecosystem services, i.e., combinations of ecological, physical, and chemical processes from which humans benefit. Benefits to humans can range from the easy to quantify goods such as food production to more intrinsic and nonmonetary values.

Ecosystem services represent a broadening of the valuation of ecological systems by society, including a growing catalog of services from marine ecosystems (Austen et al. 2002, Levin et al. 2001, Myers 1996, National Research Council 2005, Paarlberg et al. 2005, Snelgrove 1998, Wall 2004). The biological traits analyses described in the previous section imply shifts in the functionality of benthic communities. Ecosystem functions often involve the interactions of a number of processes linked via feedback loops (Coco et al. 2006, Lohrer et al. 2004, Pascual & Guichard 2005, Rietkerk & Van de Koppel 2008, Van De Koppel et al. 2001). This makes extensive study difficult and expensive. Nevertheless, links between small-scale, process-based, flux studies and the role of organisms with different sensitivities to fishing disturbance highlight the potential for profound changes in ecosystem services.

The growing literature on the relationships between biodiversity and ecosystem function emphasizes that emergent functions and rates of ecosystem processes not only are a product of the functional traits of individual species but also depend on the interactions between species (Loreau et al. 2001). The view that biodiversity drives function instead of being a product of it is still coming into focus and the reality may not be a simple dichotomy. Most of the empirical studies of biodiversity and ecosystem function from marine systems are conducted in aquaria employing low levels of species diversity and focusing on one ecosystem function variable. Nevertheless, they demonstrate relationships between biodiversity (species richness per se) rather than individual species, which can result in nonadditive responses in a range of ecosystem functions. For example, Emmerson et al. (2001) demonstrated an overall increase in ammonia flux from the sediment with increased infaunal biomass and reduced variability in ecosystem function with increased species richness. One important feature of these experiments is that they often emphasize that the relationship between biodiversity and ecosystem function is idiosyncratic, with individual species playing a disproportionate role in specific ecosystem processes. Waldbusser et al. (2004) extended these earlier studies of organism-sediment-chemical flux interactions to show that functionally more complex assemblages operate in a different way from simple ones. They emphasized that net effects on fluxes and sediment-chemical gradients are not simply the summations of individual species effects.

Although we have a growing recognition of the ecosystem functions that support services derived from seafloor communities, the role of fish is often underestimated. Many demersal fish actively disturb sediments through feeding activities, nesting, and burrow construction. Yahel et al. (2008) recently highlighted the underestimation of the role of fish in affecting benthic-pelagic coupling and geochemical processes. This study of a fjord on the Canadian west coast demonstrates that fish feeding resulted in a distinct nephloid layer significantly affecting the bottom water-oxygen concentration, organic matter remineralization, and nutrient recycling.

The translation of this fundamental ecosystem function—biodiversity research into and an understanding of how ecosystem services are affected by fishing—faces the significant challenge of scaling up. The approach taken by Olsgard et al. (2008) of identifying key species for detailed small-scale study and linking documented rates and processes to changes in the density and distribution of organisms is an advance. The effects of shrimp trawling in Oslofjord demonstrated reductions in the density of large bioturbators. The functional importance of which was demonstrated by mesocosm studies with *Brissopsis lyrifera*, *Nuculana minuta*, *Calocaris macandreae*, and *Amphiura chiajei*, species with different traits affecting the processes involved in nutrient cycling. All four test species enhanced the flux of silica from the sediment, but their effect on dissolved inorganic nitrogen differed: Bulldozing bioturbators (urchins and bivalves) increased the loss of dissolved inorganic nitrogen, whereas bioirrigating species (shrimps and brittlestars) increased the sediment uptake of it (Olsgard et al. 2008). Although this approach is tractable, other approaches to scaling up small-scale experiments are needed because processes can change depending on the scale

of observation. In fact, at broader spatial scales or increased levels of biocomplexity, positive facilitatory interactions emerge (Bruno et al. 2003, Cardinale & Palmer 2002). Such interactions can have a profound influence on community and ecosystem dynamics.

No community or ecosystem has only one functional attribute, and another important scaling challenge is the development of multifunction approaches to biodiversity and ecosystem function (Hector & Bagchi 2007). An important element of the multifunction perspective is the role that species diversity may play in the resilience of communities and ecosystems. In particular, the variability in species traits within functional groups has been highlighted as a key factor in maintaining the adaptive capacity of communities and ecosystems to change (Elmqvist et al. 2003). This is an important attribute on a warming planet with the potential for multifaceted changes affecting coastal and ocean ecosystems.

Multiple ecosystem functions can be depressed by fishing. Analyzing coastal rocky reef communities, Micheli & Halpern (2005) found increased functional diversity of fish assemblages coinciding with recovery of species diversity in marine reserves. In shelf-deep, soft sediments, the loss of infauna and associated changes in sediment-chemical gradients has been associated with a loss of function (Solan et al. 2004). Danovaro et al. (2008) extended these patterns into the deep sea, demonstrating that relationships between biodiversity and ecosystem properties cannot be fully explained by environmental factors alone.

The growing recognition of the multiple benefits associated with maintaining healthy ecosystems should have a profound influence on decision making in fisheries management (Limburg et al. 2002, Rosenberg & McLeod 2005). Biodiversity-ecosystem function studies require further rigorous evaluation in all marine ecosystems (Levin et al. 2001). However, growing evidence suggests that managers with precautionary mandates (a principle of EBM) must start to encompass these issues, which underpin many of the services for which marine ecosystems are valued by different sectors of society. The challenge now is to take these theoretical and model studies and scale them up to assess their relevance to diverse seafloor ecosystems as well as their dynamics and response to fishing impacts.

CONSIDERATION OF ECOSYSTEM FUNCTION AND INTERACTIVE STRESSORS

Communities and ecosystems respond to cumulative suites of stressors and disturbance factors, and this can have unexpected consequences. Conely et al. (2007) argued that the loss of large infauna due to hypoxia or other disturbances limits the ability of benthic communites to influence organic-matter degradation and nutrient cycling and that this is the reason why major reductions of nutrients to coastal waters have not always resulted in an improvement in eutrophic status. Another example of the role of benthic organisms in broader-scale processes is the recent analysis of the benthic regime shift in part of the North Sea. van Nes et al. (2007) described the different roles of burrowing callianassid shrimps and suspension-feeding brittle stars in influencing the susceptibility of the seabed to wave-induced sediment resuspension. They developed models based on the documented shifts in the dominance of these species that highlight how these two species can reflect fundamentally different regime states. They also discussed the potential for an episode of intense trawling to tip the balance from brittle-star to shrimp dominance.

MAINTAINING THE RESILIENCE OF VALUED ECOSYSTEMS

The fact that ecological systems do not simply track environmental forcing implies a need to provide ecological buffers to change, rather than engineering controls (Gunderson 2000). Resilience

Regime shift: a major change in the functionality of ecological systems that occurs rapidly relative to the length of observed time series

is an important ecological service, offering insurance against regime shifts, and there is increasing evidence of drastic and profound changes in many marine ecosystems (de Young et al. 2008, Hughes et al. 2005, Steele 1998). From an oceanographic perspective, documenting a regime shift implies a change only in environmental forcing, but ecological processes also influence resilience (Scheffer et al. 2001, Scheffer & Carpenter 2003). Tracking such changes in large open ecosystems is difficult, but Litzow et al. (2008) recently used the techniques developed by van Nes & Scheffer (2007) to assess changes in spatial variability as an indicator of alternate stable-state dynamics. For the Gulf of Alaska, where the regime shift was climate related, these authors demonstrated that increased spatial variance occurred one year before the phase shift. In contrast, on the Scotian Shelf, where ecosystem reorganization was attributed to overfishing, a significant increase in variance occurred three years before the transition.

Loss of resilience implies a potential for escalating degradative ecological change as alterations in the disturbance regime impact local and regional changes in ecological communities (Folke et al. 2004). Exactly how common regime shifts or tipping points are or even how common it is for systems to exist in alternative states is still unresolved. But these complex system dynamics have a profound effect on the way we think about predicting change and managing seafloor habitats as well as the impacts of fisheries. For example, if an ecosystem responds in a generally linear fashion to disturbance, then the frequency and extent of disturbance to the seafloor that a specific ecosystem could accommodate is not likely to change greatly from one year to the next. However, if the system is capable of flipping into an alternate state, then the interaction of processes and small changes to the system over a short time frame can lead to a rapid shift from which recovery may be especially slow owing to hysteresis (Scheffer et al. 2001).

INTEGRATING ECOSYSTEM AND HABITAT CHANGE TO DETECT ECOLOGICAL RATCHETS

Nothing in nature is static and natural disturbances are the rule; the resulting heterogeneity is an important component of all ecosystems. Disturbance can involve the removal of high trophic levels, or other functionally important species, with effects that can transform ecosystems. Often, fishing impacts are sufficiently pervasive so as to create a sustained disturbance that eventually depresses the processes that would result in the system's recovery. Such situations can be thought of as ecological ratchets in which a new ecosystem resists recovery such that it can be considered to be an alternative steady state (Birkeland 2004).

Many exploited populations such as sardines, herring, and anchovies mature at a relatively young age, feed low in the food web, and can recover quickly from harvesting. But the habitat of these pelagic species is influenced by the density of predators with much slower recovery rates and that are often also a target for fishers. This can generate profound changes in ecosystem function. Casini et al. (2009) demonstrated such a regime shift in the Baltic: In this case, the collapse of the cod population produced an environment that favored an increase in the abundance of planktivorous sprat, which then interfered with the feeding resources of juvenile cod thereby restricting their recovery. Unfortunately, the less resilient species are often targeted or suffer high levels of incidental mortality (consider marine mammals, sharks, sea turtles, and oceanic birds). For example, the marbled rock cod of the Indian Ocean collapsed in the 1960s and has not recovered, nor has the pelagic armorhead of the Pacific Ocean nor the black-lipped pearl oyster in the northwest Hawaiian Islands, the latter of which yielded hundreds of tons in 1927 (Dayton et al. 2002). The Northern Atlantic cod may represent the best-known example of a robust and heavily fished population that collapsed and has not recovered (Rosenberg et al. 2005). Fishing impacts appear to have resulted in many such ratcheted marine ecosystems. For example,

Hysteresis: used in ecology to represent a change in a system that exhibits alternate stable states, where recovery to previous state is much slower than the previous transition

Ecological ratchets: self-reinforcing processes that degrade ecological structure and function, in favor of an alternative stable state

large-scale trawling in the North Sea has pushed the benthic system into new ecological states that may take centuries to recover (Robinson & Frid 2008). The same is true for the epifauna of heavily trawled sea mounts (Koslow et al. 2001) and deep-water coral and sponge banks, including the oysters and bivalves that once covered our bays (Airoldi et al. 2008, Nichols et al. 1986) and the California abalones, which were once so abundant a diver could collect two tons in one dive (Rogers-Bennett et al. 2002).

The relationships between trophic cascades and habitat emphasize the importance of synthesizing ecosystem and habitat studies. Whereas our focus in this review is on changes to seafloor communities and ecosystems, an extensive literature documents changes in the size structure, trophic relationships, and species composition in marine food webs as a result of fishing pressure. For example, Ward & Myers (2005) reviewed long-line surveys showing tenfold declines in catch rates of large predators coincident with up to 100-fold increases in pelagic stingrays. In many cases, these ecological ratchets may be related to long-term benthic shifts resulting from trawling. Many fish interact directly with the seafloor by feeding on benthic species (**Figure 3**), depositing egg masses, or seeking shelter from predators (particularly for juvenile life stags). Trophic changes in the water column can impact the benthic food webs just as structural and ecosystem changes on the seafloor can have serious impacts on pelagic species. For example, the impact of declines in cod stocks and other large predatory fish on the Scotian Shelf has cascaded down to influence the populations of shrimps, crabs, and other benthic predatory scavengers and nutrient dynamics (Frank et al. 2005). In fact, this increase in the abundance of benthic crustaceans where cod stocks have declined appears to be a common phenomenon in the North Atlantic even when environmental conditions vary (Ward & Myers 2003, 2005). These broad-scale patterns are supported by detailed observations, and small-scale exclusion experiments have demonstrated that crabs, shrimp, and other predatory crustaceans increased in density concomitant with the collapse of the cod fishery in Newfoundland. Once these alternative predators are established, they assume a new and important role structuring the benthic community (Quijon & Snelgrove 2005).

Richardson et al. (2009) reviewed examples of jellyfish outbreaks worldwide resulting from human-induces stresses, mostly from badly managed fishing; many of these outbreaks represent fast and important ecological ratchets such as those discussed in this review. We speculate that the widespread explosion of the jellyfish *Cyanea capillata* in the Bering Sea may be associated with a fishing-induced benthic-pelagic impact. There is certainly spatial concordance between the area of jellyfish abundance noted by Brodeur et al. (2008) and the trawling effort recorded. Jellyfish are efficient pelagic predators and because *Cyanea* can become very large, as they grow they filter various-sized organisms, thereby affecting several pelagic food webs. Moreover, the sexual stage of these jellyfish produces larvae that must settle and survive on the seafloor to metamorphose into a polyp stage that asexually produces large numbers of jellyfish. We hypothesize that large-scale trawling has shifted the community structure to the extent that benthic interactions no longer constrain the polyp stage. Eventually, the system may ratchet into one in which jellyfish play functional roles that impact the entire ecosystem.

Randall (1965, 1967) demonstrated the importance of physical structure as a refuge from predation. Having observed grazed halos in turtle-grass beds around reefs, he tested the hypothesis that these grazed areas reflected herbivore ambits from the protection of reefs by artificially extending the reefs. This simple experiment introduced the concept of the "zone of fear" as it demonstrated that the grazed areas moved out only as far as the herbivores dared to risk predation (**Figure 4**). Grabowski & Kimbro (2005) extended this idea and offered a brilliantly clear and simple example of the important role that refugia provided by habitat structure plays in modifying trophic interactions. In their example, toadfish consume mud crabs that are effective predators of juvenile oysters. Clever experimentation with habitat refugia showed that oyster

Trophic cascade: occurs when predators suppress the abundance of their prey on the next lower trophic level, which in turn releases lower trophic levels from predation pressure

a Former state
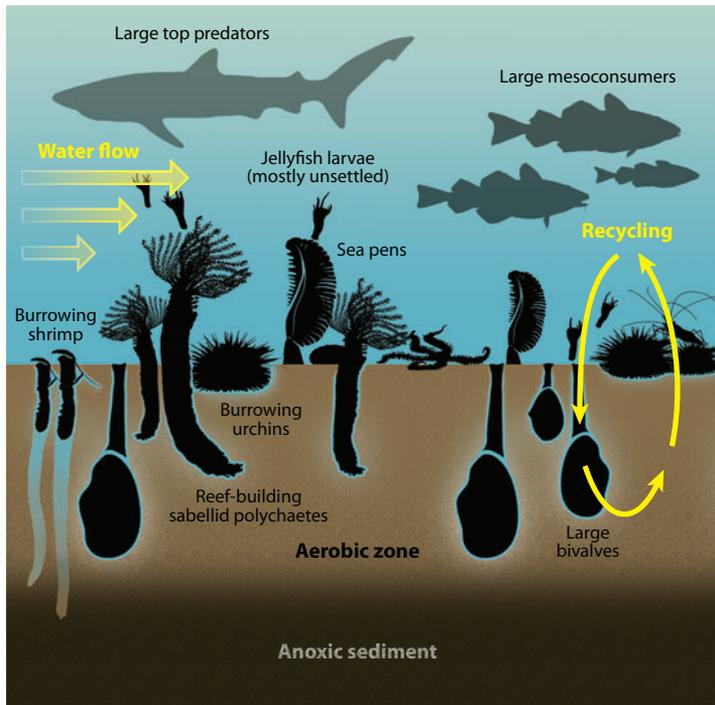
b More fished world
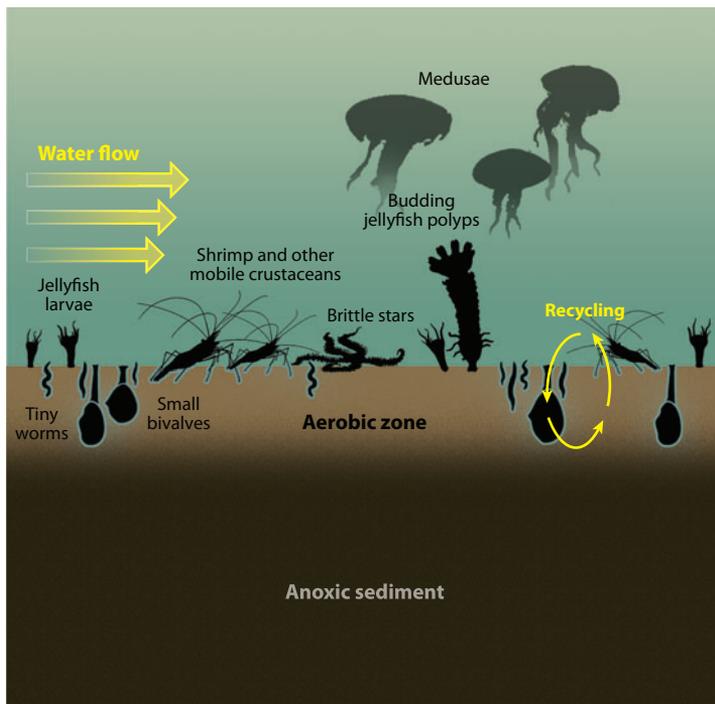
Figure 3

Ecological ratchets tighten their grip on marine ecosystems. Loss of top predators and habitat destruction removes environmental heterogeneity created by large and old organisms and decreases the depth and extent of sediment bioturbation and bioirrigation.
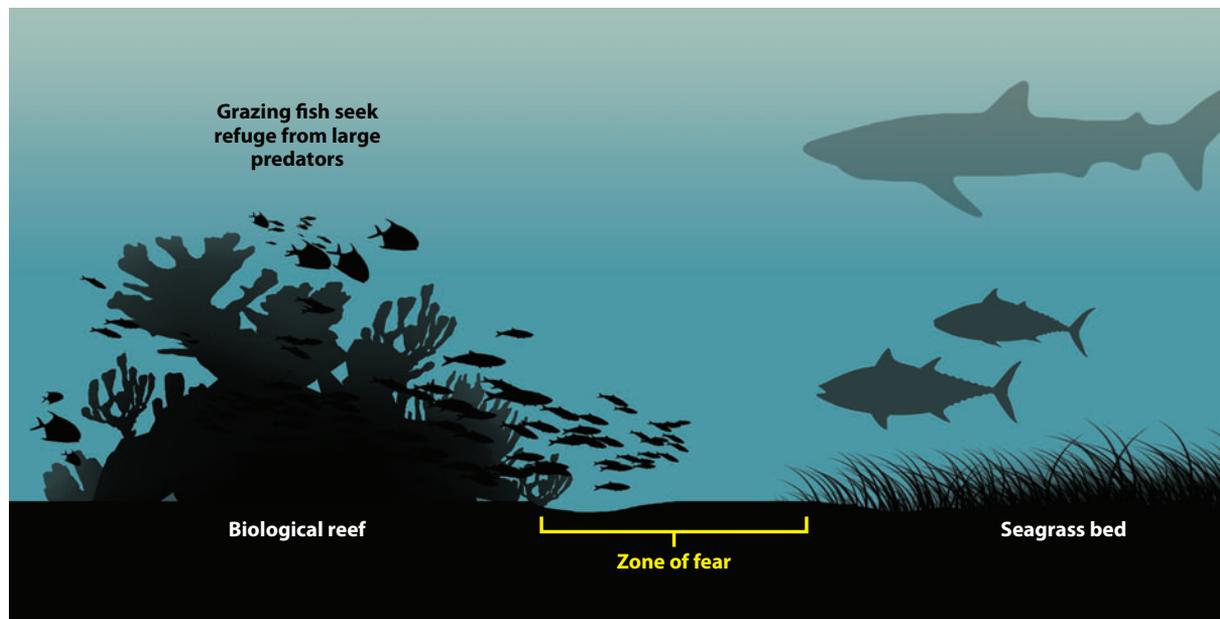
Figure 4

The zone of fear: Loss of biogenic habitats that provide refugia from large roaming predators affects the risks faced by intermediate-level predators, influencing behavior, time allocation, fitness, and the role of intermediate predators in community dynamics.

survivorship increased because of density-mediated effects that resulted from the toadfish killing the crabs. However, approximately 96% of the enhanced oyster survival was a result of trait-mediated predator-avoidance behavior by the crab in which the crab stayed in the refugia—a modern example of the Randall effect. Grabowski et al. (2008) makes a convincing argument that, although direct cascade effects of top predators and mesoconsumers are real and important, in many cases behavioral responses to the risk of the predation are even more important.

Myers et al. (2007) summarized a series of direct and indirect responses to the loss of large coastal sharks first demonstrated by Baum et al. (2003). In this case, the removal of the large elasmobranch-eating sharks enabled a sharp rise in the population of cow-nosed rays. As their population increased, the rays moved into areas that had previously been too risky to inhabit when sharks were present, which in turn devastated the bay bivalve populations. Another interesting example of the importance of understanding behavioral biology can be found in a recent study made possible via the tagging and detailed analysis of two subpopulations of sea otters (Johnson et al. 2009). Although a common response to limiting resources, foraging specialization is hard to document. However, because the diets of these otters were well known, the study found that those animals with search images for the preferred abalone prey were much more resistant to a disease that caused significant mortality to those otters consuming suboptimal prey.

Heithaus et al. (2008) reviewed these and other examples of trophic cascades and risk-averse behavior by meso-consumers that have resulted in profound changes to the ecosystems. These changes result after the top predators are functionally removed from the ecosystem, and they are mediated by community interactions involving species released from predator control—or, importantly, the perceived risk of predation. Another illustrative example involves Alaskan harbor seals whose perception of the risk of sleeper shark predation results in a refugia for fish that

coexist with the sharks. Heithaus et al. (2008) also provided other examples of complicated direct and indirect effects of predators and emphasized that predicting the community and ecosystem consequences of predator removal depends on detailed appreciation of the selectivity and foraging flexibility along with the perceived risks of predation integrated with the community roles of prey. The potential for links with broader changes in marine food webs highlights the potential for strong nonlinear dynamics and the potential that thresholds in the delivery of ecosystem function, habitat structure, and biodiversity may be crossed. Although challenging, if we wish to assess the risk of abrupt but potentially drastic changes as well as manage to maintain or enhance the broad range of values of marine ecosystems, then an ecosystem approach is necessary (Scheffer & Carpenter 2003).

ON PELAGIC HABITATS

Many forget that the pelagic realm also has a great deal of spatial and temporal structure and that many pelagic species have species-specific preferences for various meso-scale physical features of the ocean. Seasonal and interannual patterns are complex, and although species-specific relations tend to remain stable over time, distribution patterns co-vary with preferred habitats (Balance et al. 2006). In many cases, the relationships are not with specific physical features but with combinations of variables along complex gradients. These multifaceted relationships involving oceanography, migration for reproduction, or tracking of preferred habitat or prey can be masked by changes resulting from fishing.

Animals have strong behavioral patterns, including those associated with foraging in the ever-present zone of fear. In this context, schooling offers a temporary but effective defense against predators, which, in turn, have evolved tactics to deal with schooling prey (Bullis 1961). Complex oceanographic phenomena such as an oxygen minimum zone may act as a spatial refuge for squid from visual-foraging predatory fish, but not from diving mammals. Squid and other pelagic species also avoid visual predators by staying below the photic zone during the day and moving up to feed at night. In doing so, they remain vulnerable to mammals that use sonar as well as to fish with good eyesight. Their response when encountering predators is to form a tight school that the predators often force to the surface, where they represent a critical resource for oceanic birds (Hebshi et al. 2008). It is likely that a pelagic ecological ratchet has occurred in which the depletion of some 90% of the large fish from the ocean has released their former prey to alternative predators such as squid and marine mammals. If this is true, then there are important implications for sea birds as well as the recovery of large fish such as sharks and billfish. Baum & Worm (2009) reviewed many examples of cascading top-down effects resulting from the reduced functional roles of oceanic predators. If we are to understand the important functional ties in such relationships, we need to integrate natural history and predator-prey behavioral interactions with information about the spatial and temporal oceanographic patterns.

PROGRESS TOWARD DEVELOPING INDICATORS OF THE EFFICACY OF ECOSYSTEM-BASED MANAGEMENT

Recognition of the dynamic character of ecosystems and the importance of assessing the efficacy of management actions are important components of EBM. Pikitch et al. (2004) outlined the main elements of ecosystem-based fisheries management to include (*a*) avoiding the degradation of ecosystems, (*b*) minimizing the risk of irreversible change, (*c*) obtaining long-term socioeconomic benefits from fishing, and (*d*) adopting a precautionary approach to uncertainty. These elements require a strong underpinning by ecological research, in particular, to address the consequences of

habitat disturbance across seafloor landscapes, to understand ecosystem function and resilience, and to improve societal understanding of the broad values of marine ecosystems to assess and define more fully the related socioeconomic benefits.

The need to define explicit goals and monitor the efficacy of EBM actions has led to the additional need to define environmental standards, baselines, and monitor indicators to give feedback to managers and society. The development of such tools for management must be done in a manner that is cognizant of the fact that many of the continental shelves around the world have a long history of human impact (Jackson 2001, Lotze et al. 2006, Lotze & Milewski 2004) and continue to change (e.g., Yeung & McConnaughey 2006). Intense disturbance selects for species with appropriate responses. As a result, benthic communities become dominated by small, mobile species and rapid colonists, and we lose track of natural biodiversity. Equally important, ecosystems are dynamic and may not respond to disturbance in a simple monotonic fashion, but instead exhibit threshold-type responses (de Young et al. 2008). This means that benchmarks and baselines must be carefully considered. Thus, ecological insight is currently our best option to assess the risk of threshold-type responses and ecological ratchets (Duarte et al. 2009). Monitoring approaches need to be ecologically sound and broad-based, as well as practical, and include appropriate indicators of ecological status. This challenge is made all the more difficult because of the lack of controls or defined gradients of disturbance that have not been historically built into fisheries management strategies (Gray et al. 2006). Despite these limitations, our growing knowledge of chronic and cumulative impacts of fishing and the application of indicators based on functional traits can be developed even for systems that have an extensive history of exploitation (de Juan et al. 2009).

One pragmatic argument concerning the development of indicators for EBM is the potential difficulty of monitoring the vast areas of the planet in which fisheries are persecuted. An approach is to develop indicators based on data already being gathered for traditional fisheries management. Link et al. (2002) investigated a range of abiotic, biotic, and human metrics for the northeast U.S. continental shelf ecosystem, a comparatively data-rich ecosystem. Their analysis offers a note of caution in the definition and interpretation of a minimal suit of indicators. They emphasized the need for a diverse array of indicators to characterize ecosystem status, highlighting that such indicators cannot easily be treated as analogs of the indicators used in single-species fisheries management. They also called for the development of mechanistic or analytical models of key ecosystem processes. Another pragmatic approach is to develop indicators from models of ecosystem performance (Fulton et al. 2005). Fisheries research has a strong tradition of developing population-exploitation models. But now, broadening the scope of the information needed to underpin a more ecosystem-based approach to management, new modeling approaches are being developed. For example, a model developed for the North Sea demonstrated current ecosystem performance as a 56% reduction in biomass and 21% reduction in productivity compared with a theoretical unfished situation (Hiddink et al. 2006). Although this model simplifies many potentially important ecological interactions in seafloor communities and potentially underestimates the magnitude of effects, it does illustrate that fishing is not the same as farming, and trawlers and dredges tilling the seafloor is not enhancing productivity.

As the range of interest and stakeholder groups involved in fisheries management increases, there is growing pressure to ensure effective management of ecosystems that balance conservation with ecologically sustainable management. Smith et al. (2007) pointed out that the policy and management initiatives to implement EBM have outstripped scientific knowledge and the development of management tools—science needs to catch up! This necessitates the implementation of risk-assessment procedures to account for uncertainty (Burgman 2005). More explicitly, the focus of traditional fisheries models has been expanded through procedures such as management strategy evaluation (MSE), which seeks to dynamically link potential management actions to environmental

outcomes and also incorporates the objectives of monitoring and assessment (Sainsbury et al. 2000). For example, Ellis et al. (2008) examined the consequences of a range of management options for the Torres Strait trawl fishery to highlight that the greatest benefit to both fishery and ecosystem can be derived from effort restrictions. This strategy emphasizes the link between conservation areas and ecological management of the interconnecting habitats. Nevertheless, although such decision-supporting tools attempt to encapsulate uncertainty, more ecological information on key rates, processes, and feedbacks is needed. For example, in the MSE of Ellis et al. (2008, table 1), benthic community recovery rates even for large organisms were defined as less than one year. This rate is exceedingly fast compared with the settlement, growth, and community dynamics of sponges, bryozoans, compound ascidians, and, in fact, most of the large metazoans that structure most benthic communities. Such recovery rates beg the question of how recovery is defined (in terms of density as well as an organism's age, size, or function). Recovery rates of less that one year are unbelievably fast compared with the summary from recent meta-analysis of fishing impact studies (Kaiser et al. 2006) and rates apparent in small-scale defaunation experiments of relatively simple intertidal communities (Beukema et al. 1999; Thrush et al. 2008, 1998; Volkenborn et al. 2009).

In developing MSE, it is appropriate to consider the output from a range of models of intermediate complexity rather than a single highly complex one. The advantage of MSE is that it makes many assumptions and interconnections between ecosystem components explicit so that they can be considered by all participants in the decision-making process. Assessing the robustness of different management strategies to alternatives by considering alternative models is an advance, but there is no guarantee that they will be robust to a wider set of uncertainties and models. Ecological complex systems models developed to investigate the interactions of processes operating across scales emphasize the potential interconnected nature and nonlinearity of ecological systems.

MARINE PROTECTED AREAS AS AN INTEGRAL PART OF ECOSYSTEM-BASED MANAGEMENT

This review focuses on and attempts to integrate EBM with protection of essential fish habitat. In the coastal regions of many countries, marine protected areas have proliferated as a conservation measure. These areas have become popular due to the growing recognition of the effects that commercial and recreation fishing can have on coastal ecosystems. These areas are often small, represent a very low proportion of coastal habitat, and are often poorly interconnected. Nevertheless, when carefully managed, they can be beneficial (Abesamis & Russ 2005, Babcock et al. 1999, Castilla & Fernandez 1998). There is an extensive literature on the design and networking of marine protected areas (Elkin & Possingham 2008, Fraschetti et al. 2009, Jennings 2009, Leslie et al. 2003, Roberts et al. 2003). However, even if reserves are well managed and policed (see van Gils et al. 2006 for an example of potential problems), coastal MPAs cannot protect resident communities from all anthropogenic disturbances (e.g., land-derived contaminants) and thus are insufficient protection alone (Allison et al. 1998). If policy agencies set targets of a representative 10–20% of a particular type of habitat or marine zone to be set aside, then we must still effectively manage the other 80–90%.

Nevertheless, MPAs represent an important tool in the arsenal of management options for EBM. MPAs do not replace traditional management tools, but they contribute in two important ways. First, MPAs are useful for both EBM and essential fish habitat, allowing our best insight into natural relationships. Appropriate management must have a fundamental understanding of the ecological conditions in the absence, or at least reduction, of fishing pressure. Second, they can help traditional management for species that depend on Allee effects and breeding aggregations.

Allee effects: at low population densities, a species exhibits especially low fitness and survivorship

Protecting breeding aggregations seems obvious, but it has proved difficult. For species with ambits small enough to be contained in the reserves, protection allows the bigger fish to survive, and this is important to both larval production and the gene pool that can be selected to shift to small, faster-maturing individuals.

THE PAST IS PAST AND THE FUTURE IS OURS TO PROTECT

In this review, we try to illustrate briefly the legacy of ecological and natural history information that can be used to advance the implementation of EBM. Furthermore, it is important that we remember the lessons of early ecologists such as Gause, Park, Errington, and Huffaker, who demonstrated the stabilizing effects of heterogeneity and refuges from predation. In addition to the physical habitats understood in the benthos, we must also consider important habitat structure in the pelagic realm that offers real, if temporary, refuge from predation. The loss of critical habitats is the primary factor responsible for species extinctions and the global decline in species diversity. Protecting the habitats from human-induced disturbance is a critical responsibility we have to the future. Many comprehensive reviews have documented the impacts of fishing on the benthic habitats around the world. The growing literature consistently reports immediate decreases in species richness and diversity and a marked reduction in habitat complexity (Thrush & Dayton 2002).

Given the emerging patterns of the loss of large and long-lived organisms, decreases in habitat heterogeneity as well as species diversity and function, we consider that a range of ecological knowledge should be used to underpin the expansion of the resource manager's toolbox to implement EBM more fully. Habitat and ecosystem alteration combined with climate and oceanographic changes have resulted in ecological ratchets that constrain recovery. We highlight a potential for escalating degradative ecological change as alterations in the disturbance regime further impact ecosystem dynamics (**Figure 5**). As ecological ratchets tighten their grip on marine ecosystems owing to the interactions of trophic cascades, habitat-mediated effects on predator refugia, and loss of ecosystem services, the consequences have a profound effect on the way we think about managing seafloor habitats and fisheries impacts.

The evidence of the profound, though unintended, consequences of fishing condemns single-species assessment as the only tool for fisheries management. However, there has been progress toward the implication of broader ecosystems-based perspectives. Fluharty (2005) reviewed a pragmatic approach to exploring an ecosystem approach to management defined as "using what is known about the ecosystem to manage fisheries." He recognized that managers are not employing the currently available ecological knowledge. In particular, maintaining the adaptive capacity of communities and ecosystems to change is a challenge requiring the application and scale-up of fundamental and theoretical research to diverse seafloor ecosystems and their dynamics and response to fishing impacts. Embracing uncertainty and using multiple approaches to develop lines of evidence is a radical departure from stock assessment, and we argue that ecology can make a significant advance in expanding the toolbox for fisheries managers. Effective communication and information uptake from both the research and management communities is essential (Arkema et al. 2006).

As a management framework, we might expect the implementation of EBM to be inhibited by social and management structures that enforce lock-in and path dependency (Scheffer & Westley 2007). We need to find the appropriate tipping points or policy regime shifts. The debate has clearly moved from assertions that there is no impact of fishing to an acceptance of the problem and a focus on defining its magnitude in different locations and seeking solutions from a policy and management perspective. Unfortunately, often strongly divergent views, common to fisheries problems, can subvert communication, conversation, and consensus building
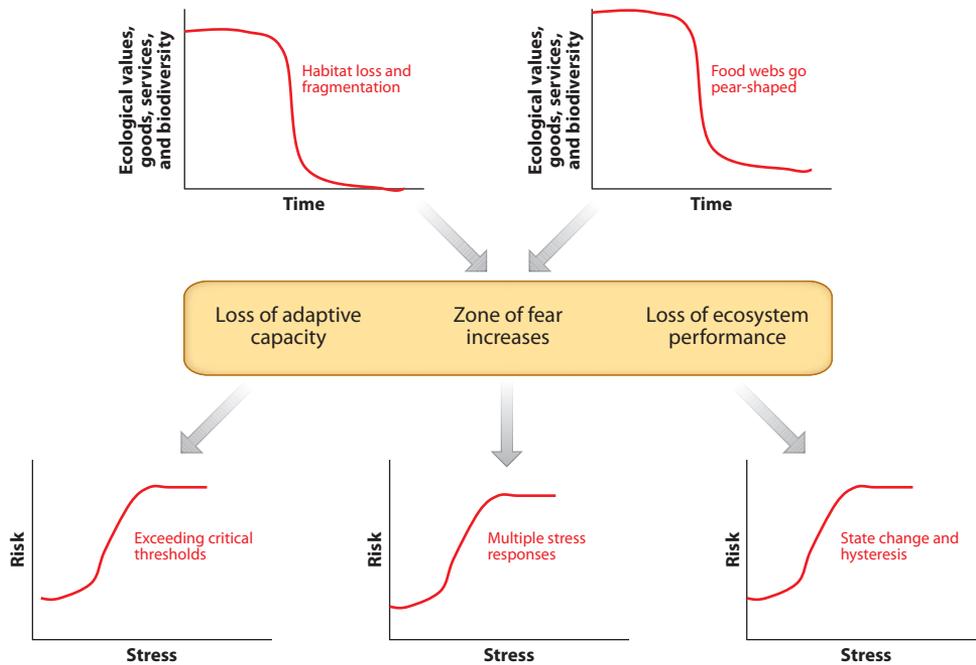
Figure 5

Habitat destruction and fragmentation, the functional loss of high trophic level species, and the microbialization of food webs are prone to threshold responses leading to a loss of adaptive capacity, behavior-mediated changes in predation, and loss of ecosystem performance. These features increase the threat of cumulative or multiple-stressor effects and the risk of low recovery potential.

(LeHeron et al. 2008). For example, it seems that dynamic multispecies management has resulted in separate groups of specialists with variously overlapping ecosystem approaches. On the habitat side are benthic ecologists worried about protecting the structural aspects of the benthos, whereas those interested in trophodynamics often focus on water-column processes. We believe that there is sufficient overlap for both groups to profit from merging habitat and food-web perspectives into a systemic ecosystem-based approach that integrates benthic-pelagic coupling. We need to acknowledge the difficulties in computing all aspects of complex ecological problems (Carpenter et al. 2009). EMB includes the development of institutional frameworks that facilitate inclusive behaviors and an appreciation of others' expertise when confronting the questions at hand. The science and wisdom of ecological science must continue to play an increasing role in the improved valuation, resource management, and conservation of our coasts and oceans.

SUMMARY POINTS

1. There is now clear evidence of serious changes to the structure and function of marine ecosystems as a result of fishing.

2. In response to our growing scientific knowledge of these impacts and public concern, many resource-management agencies are endeavoring to implement elements of EBM. Such inclusive management strategies require a broad-based understanding of potential ecological responses.

3. Trophic cascades in marine ecosystems are typically regarded as a process solely related to changes in food-web structure. However, we are beginning to integrate habitat information to define important links between risk aversion by prey and predator responses, thus linking trophic shifts and habitat destruction.

4. Basic ecological research on ecosystem functions and biodiversity-ecosystem function relationships needs to be extended and scaled-up to broaden our understanding of the linkages between ecosystem functions and services. Many ecosystem services are directly relevant to fisheries management as they underpin productivity, sustainability, and recovery following disturbance.

5. Managing for functional resilience draws attention to ecological dynamics across scales of space and time. It also quantitatively links the dynamics of ecosystem state and the dynamics of use and values. Until our ability to predict shifts in resilience improves, management and policy should focus on insurance and capacity maintenance, emphasizing the need to provide ecological buffers to change, rather than traditional fisheries management controls.

FUTURE ISSUES

There is tremendous potential for ecological research to contribute to the implementation of EBM strategies for fisheries. Building on current advances, new research is needed to advance functionally focused research; develop appropriate biophysical models; and integrate this research into policy, management, and decision making. In particular, we identify seven interacting themes:

1. Extension of effects studies to represent all habitats (e.g., polar and tropic) and inclusion of processes operating on shelf and deeper depths.

2. Scaling-up of biodiversity-ecosystem function studies in terms of space, time, and scales of biological organization to develop models defining the risks of degradation of ecosystem services and the loss of values.

3. Development of an appropriate suite of ecological indicators to test the efficacy of management and to create dynamic frameworks against which improvements in marine ecosystems can be judged.

4. Development of frameworks to define multiple stressor effects so that risks associated with fishing can be understood relative to and interacting with other stressors.

5. Improved understanding, via recognition of key processes and feedbacks, of the limits of resilience in valued ecosystems.

6. Advancement of MSE-type models, in particular, to ensure that they address key ecological questions and are parameterized by appropriate ecological data and knowledge of functional relationships.

7. Development of socioecological models to facilitate translation and define key feedbacks between ecological systems responses and broad societal responses.

DISCLOSURE STATEMENT

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Errata

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