



The Impacts of Fisheries on Marine Ecosystems and the Transition to Ecosystem-Based Management

Larry B. Crowder, Elliott L. Hazen, Naomi Avissar, Rhema Bjorkland, Catherine Latanich, and Matthew B. Ogburn

Center for Marine Conservation, Duke University Marine Laboratory, Nicholas School of the Environment, Beaufort, North Carolina 28516; email: lcrowder@duke.edu

Annu. Rev. Ecol. Evol. Syst. 2008. 39:259–78

The *Annual Review of Ecology, Evolution, and Systematics* is online at ecolsys.annualreviews.org

This article's doi:
10.1146/annurev.ecolsys.39.110707.173406

Copyright © 2008 by Annual Reviews.
All rights reserved

1543-592X/08/1201-0259\$20.00

Key Words

artisanal fishing, bycatch, commercial fishing, direct and indirect effects, ecosystem-based management, food webs, habitat effects, interaction webs, recreational fishing

Abstract

Fishing remains one of the largest factors modifying marine ecosystems. Because fisheries constitute only one of many anthropogenic effects, management is shifting from single-species approaches toward ecosystem-based management. Interaction webs are a critical nexus to understand linkages, to model ecosystem change, and to apply management directives. Ecosystem-based management requires consideration of both direct and indirect effects of commercial fisheries. But it must also include impacts of bycatch, recreational fisheries, artisanal fisheries, and environmental change that can be large but unanticipated. Synergistic effects of fishing, environmental variation, and climate change increasingly threaten marine ecosystems and complicate management. Here we review the global effects of fisheries and propose an integrated framework for managing biophysical processes and human ecology. To incorporate the multitude of effects, this emerging approach focuses on the dynamics of interaction webs in a spatially explicit or place-based framework.

Single-species management:

population abundance is assessed for an individual species on the basis of natural mortality, anthropogenic (fishing) mortality, and population reproductive rates

INTRODUCTION

While traditional management of marine fisheries has focused on the widespread declines in targeted species, entire food webs have been significantly altered by overfishing (Jackson et al. 2001, Christensen et al. 2003). Fishing has a variety of direct and indirect effects on food webs in marine ecosystems, with complex and potentially cascading effects. A large portion of fisheries focus on apex predators and are fished at an unsustainable rate (Myers & Worm 2003), whereas forage fisheries such as those on walleye pollock (*Theragra chalcogramma*) or Peruvian anchoveta (*Engraulis ringens*) target strong interactors in the middle of the web and remove prey required by fish, marine mammal, and seabird predators. Fishing not only removes biomass from particular trophic levels in the food web (as one might do in a controlled ecological experiment), but also has indirect effects such as removing nontarget species, altering habitat, modifying behavior, and providing subsidies to scavengers.

Researchers have pointed to fishing as one of the oldest and principal factors modifying marine ecosystems (Jackson et al. 2001). Fishing, in concert with other anthropogenic drivers of change, has resulted in a staggering loss of biodiversity (Worm et al. 2006) and may have unforeseen effects that propagate throughout ecosystems. Recent analyses report that up to 90% of pelagic predators in the sea have been removed by fisheries (Table 1; Myers & Worm 2003). But these claims have been criticized for faulty statistical techniques (Walters 2003) and incomplete analysis of the data (Hampton et al. 2005). More conservative estimates claim the reduction is closer to 50–70% (Hampton et al. 2005), still supporting the evidence of a large-scale decline in pelagic predators. Sibert et al. (2006) analyzed all available data on Pacific tuna fisheries and concluded that fishing has produced substantial impacts on fisheries, with biomass reductions of 9–64%, depending upon the stock.

Although the magnitude of reductions in open-ocean pelagic predators remains controversial, few researchers dispute declines of 90% or more of demersal predators (Christensen et al. 2003, Rose 2004). Friedlander & DeMartini (2002) found that the mean biomass of apex predators on the unfished northwest Hawaiian Islands was more than 260% greater than on the main Hawaiian Islands, where apex predators and other fishes are heavily exploited. Other research has detected rapid, severe declines in coastal and oceanic shark populations in the northwest Atlantic and Gulf of Mexico, with declines as high as 99% for some species (Baum et al. 2003, Baum & Myers 2004, Myers et al. 2007). Direct reductions of top predator biomass cannot be ignored when one assesses fishery impacts, particularly for coastal and demersal fisheries.

Recognizing the difficulties in identifying and managing the direct effects of fisheries, much less the indirect effects and potential ecosystem effects, we suggest that the food web is a key nexus of interactions that must be considered to manage fisheries and to transition to ecosystem-based management (Mangel & Levin 2005). Whereas ecologists recognize the importance of food web theory, keystone species, and the role of strong interactors in ecosystems (Paine 1980, Power et al. 1996, Bascompte et al. 2005), traditional fisheries management has focused on single target species and takes a population-based approach. Although recent directives have emphasized the need to move toward an ecosystem-based approach (Pikitch et al. 2004, McLeod et al. 2005), little agreement exists on how to move forward with implementation. Some have proposed a transition from single-species models to multispecies fisheries models, perhaps including effects of environmental variation, as a reasonable first step (Pikitch et al. 2004). Others advocate dynamic food web models that link system components on the basis of diet data and energetic balances, using models like ECOPATH/ECOSIM (Walters et al. 1997). Implementation of these models is constrained by adequate diet data, but they are also limited because they focus primarily on trophic interactions and biomass transfer, rather than potential strong interactions in the web driven by keystone

Table 1 A subset of recent findings on the effect of fishing on marine food webs^a

Species	Effect(s) of fishing	Study area	Reference
Biomass reduction			
Oceanic whitetip sharks, silky sharks	Declines of 99% and 90%, respectively	Gulf of Mexico	Baum & Myers (2004)
Scalloped hammerhead, white, thresher sharks	Declined more than 75% in past 15 years	Northwest Atlantic	Baum et al. (2003)
Yellowfin tuna	Declined 9–64%	Central Pacific	Sibert et al. (2006)
Apex predators (sharks and jacks)	260% decrease in biomass	Hawaiian Islands	Friedlander & DeMartini (2002)
Large predators	80% reduction in biomass, 90% reduction of top predators	Four continental shelf and nine oceanic systems	Myers & Worm (2003)
Trophic cascades			
Entire food web	Trophic cascade, regime shifts	Black Sea	Daskalov et al. (2007)
Killer whales, sea otters, and entire food web	Prey switching, mesopredator release, and trophic cascade	West Alaskan waters	Estes et al. (1998)
Large elasmobranch predators	Trophic cascade and increased abundance of elasmobranch prey	Northwest Atlantic	Myers et al. (2007)
Fishing down food webs			
Entire food webs	Lowered mean trophic level and declining catch of apex species	48 ecosystems worldwide	Essington et al. (2006)
Various	Decrease in mean ecosystem trophic level	Northwest Atlantic, west Central Atlantic, southeast Pacific, northwest Pacific	Pauly & Palomares (2005)
Various	Declines in mean trophic level of global fisheries	Global	Pauly et al. (1998)
178 species throughout food web	Decrease in mean ecosystem trophic level	Southern European waters	Stergiou et al. (2007)
Rapid evolution			
Atlantic cod	Cod maturing earlier and at smaller body sizes	Northwest Atlantic	Olsen et al. (2005)

^aAlthough the magnitude varies across studies and systems, the effects have been organized into direct biomass reduction, trophic cascades, reduction in overall trophic level i.e., fishing down food webs, and rapid evolution.

species, foundational species, and other strong interactors (Paine 1980). More recently, calls for ecosystem-based management have sought to place fisheries in a larger context including the impacts of environmental variation and multiple stressors driven by human activities (McLeod et al. 2005). Here we advocate focusing on interaction webs as a critical tool for analyzing ecological, environmental, and human interactions. We also suggest a place-based approach to manage the suite of human activities and environmental factors that influence marine ecosystems (**Figure 1**).

Managing the ecosystem effects of fishing will require experimental, hypothesis-based management incorporating food web interactions and climatic drivers. Strong interactors shape the resultant food webs through ecological processes such as predation or competition. When impacted by fisheries, strong interactors can amplify the effects throughout the food web. The effects of fishing can cascade both upward and downward through food webs, resulting in reductions in species diversity, total biomass, and the provision of ecosystem services (Micheli & Halpern 2005).

Place-based management: the management of multiple ocean resources (e.g., fisheries, tourism, transport, oil exploration) in concert through the use of a spatially explicit approach

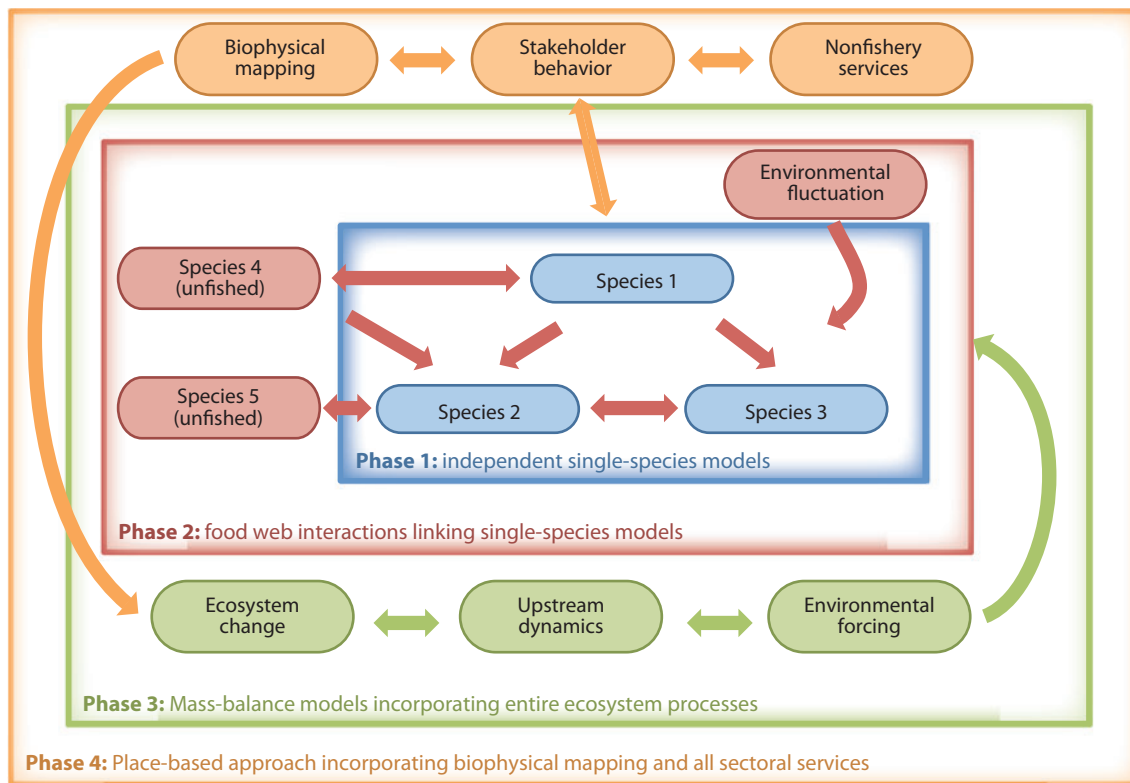


Figure 1

Thematic representation of ecosystem-based management transitioning from single-species management. Arrows indicate linkages; the colors represent the phase at which linkages are included in management. Phase 1 includes traditional single-species management based on maximum sustainable yield (species 1–3). Phase 2 incorporates interaction among species, including un-fished top predators and competitors (species 4–5) while also including the effects of fine-scale environmental variability (e.g., El Niño). Phase 3 includes mass-balance models with long-term climate forcing, ecosystem changes (e.g., regime shifts), and interacting ecosystems (e.g., watersheds). Phase 4 adds a spatial framework including the social, economic, and institutional structures governing all the sectoral ecosystem services.

One recent hypothesis is that food webs with strong interactors and high specialization (e.g., low omnivory) are most susceptible to fisheries-driven collapse and that more complex webs include functional redundancy and promote resilience (Bascompte et al. 2005). Marine food webs vary greatly from three trophic levels with low diversity (e.g., Antarctic plankton → krill → whales) to complex tropical systems (249 trophic groups in the Caribbean) (Bascompte et al. 2005). Healthy ecosystems are buffered from collapse by having food webs with increased connectance (interactions among species) and high functional diversity (species per trophic level) (McCann 2000), but they also provide ecosystem services (i.e., the benefits obtained by humans) (Millenium Ecosystem Assessment 2005). Recent reviews have summarized potential mechanisms such as trophic cascades and predatory or competitive release behind these ecosystem effects (Carpenter and Kitchell 1998, Dayton et al. 2002, Chuenpagdee et al. 2003, Rose & Cowan 2003, National Research Council 2006), but it is important to extend our understanding of fisheries effects beyond those of commercial fisheries. In this paper, we assess the literature on the indirect effects of commercial fishing, including habitat and ecosystem effects of fishing, but moreover we propose that ecosystem approaches must also incorporate effects of nontarget removals (bycatch) and recreational

Commercial fisheries: often characterized by large boats, large catches, and a high amount of export; income-driven fishing fleets

Nontarget catch: any organism landed without being targeted by fishers and used for consumption or sale

and artisanal fisheries. Ecosystem management tools vary in complexity and the extent of data required. The ideal approach must balance the available data with the predictive capacity, yet must evolve as more data and computational power become available.

DIRECT AND INDIRECT EFFECTS OF FISHERIES ON MARINE FOOD WEBS

Commercial fisheries have led to dramatic changes in marine food webs by direct removal of key food web components. Fishing pressure continues to shift toward lower trophic levels as apex predators decline; this process is termed fishing down marine food webs (Pauly et al. 1998, Pauly & Palomares 2005). The development of fisheries targeting lower trophic level species can further reduce the mean trophic level of harvested fishes (Essington et al. 2006). Increased fishing of forage species, commonly planktivorous fishes, can also lead to user conflicts, such as those between commercial and recreational interests in menhaden (*Brevoortia tyrannus*) (Richards & Rago 1999) or between fisheries and protected species, for example, groundfish use between fisheries and Steller sea lions. Menhaden are fished commercially along the east coast of the United States for fish meal and oil and are also an important prey item of sport fish such as striped bass (*Morone saxatilis*).

The hypotheses of fishing down and fishing through marine food webs are supported by direct evidence from experimental fishing trials that resulted in altered mean trophic levels (Stergiou et al. 2007). Researchers compared fishing gear effects on mean trophic level of catch and found that longlines with large hooks selectively remove the highest trophic levels, leading to the highest potential ecosystem effects (Stergiou et al. 2007). Friedlander & DeMartini (2002) suggest that harvesting of top predators may have reduced consequences if lower trophic levels are extracted in equal proportions, effectively slicing off the side of the trophic triangle instead of decapitating it. But this is rarely the case. The much more common pattern is the disproportionate removal of large predators. For example, unfished areas in the northwest Hawaiian Islands are 50–60% apex predators by biomass as opposed to 2–3% in the main Hawaiian Islands. Food web alterations can result in trophic cascades, regime shifts, or, in the worst case, ecosystem collapse (Mangel & Levin 2005, National Research Council 2006, Worm et al. 2006). Using a variety of analyses, including time series data on abundance, diet data, and results from experimental predator exclosures, Myers et al. (2007) describe a possible trophic cascade that they attribute to large declines in predatory sharks (approaching 90%) in the northwest Atlantic. Concurrently, there was a dramatic increase in the abundance of cownose rays (*Rhinoptera bonasus*), which through predation may have played a role in the collapse of the bay scallop (*Argopecten irradians*) fishery. Although this study relied primarily on correlations among these observed trends, the investigators suggest a dynamic that clearly would be missed from a single-species perspective.

In diverse systems, alternative species can increase in abundance and occupy the niche made available by species removal (Pace et al. 1999). One example from terrestrial systems showed an increase in mid-level predators (feral cat, opossum, and raccoon) with a decrease in coyotes due to habitat fragmentation (Crooks & Soule 1999). This increased abundance of mid-level predators following a reduction of apex predators is termed mesopredator release and can have cascading effects through the food web. The food web can shift from top-down control to bottom-up control, as is common in Caribbean coral reef systems with the loss of grazers (Newman et al. 2006). When previously complex food webs are simplified, ecosystems may collapse and can be difficult, if not impossible, to recover. The best example of this is algal domination of Caribbean reefs after the collapse of the herbivorous urchin *Diadema antillarum* due to a disease outbreak (Bellwood et al. 2004); this event likely occurred because other herbivores, including a suite of herbivorous reef

Bycatch: any organism landed, directly wounded, or killed without being targeted by fishers; can be landed or discarded

Recreational fisheries: anglers without a commercial license practicing catch and release or landing fish for personal use; not required for subsistence

Artisanal fisheries: mainly subsistence fisheries making short trips from land with catch primarily for local consumption; also referred as small-scale fisheries

Top-down control: when a food web's structure and population dynamics are regulated by top predators

Bottom-up control: when a food web's structure and population dynamics are regulated by nutrients and primary production

fishes, had been depleted. Another example includes the shifts in fish community composition following the collapse of North Atlantic cod—increases in small predators, including dogfish sharks, may contribute to the delayed recovery of cod populations (Bundy & Fanning 2005).

Overfishing of apex predators can result in a direct increase in the abundance of their prey, potentially altering the remaining food web. For example, in the Black Sea before large-scale fisheries were prevalent, predator numbers were controlled by variability in system productivity. After large-scale depletion of apex predators (piscivorous fish, including mackerel, *Scomber scomber*) in the 1960s and 1970s, a trophic cascade resulted in increased abundance of planktivorous fish, subsequent decreases in zooplankton, and an increase in phytoplankton. The altered food web supported an outbreak of gelatinous planktivores that now dominate the ecosystem (Daskalov et al. 2007), a pattern common in disturbed ecosystems.

Harvesting forage fish from the middle of the food web can decrease prey availability to top predators, as evidenced with a number of marine mammal populations (DeMaster et al. 2006). A pertinent example is of wasp-waist dynamics, in which, rather than top-down or bottom-up control, abundances of planktivores control primary production and top predator numbers. Examples include the highly productive Peruvian upwelling system. Abundances of sardines (*Sardinops sagax*) and anchovies (*E. ringens*) cycle on the basis of the strength of upwelling, strongest in cooler La Niña years and weakest in warmer El Niño years, driving the distribution of top predators—a trend echoed by fishery landings (Bakun & Broad 2003). Many top predators such as sea lions (*Otaria flavescens*) have faced decreased recruitment and survival in less productive years as a result of these combined effects (Soto et al. 2004).

Fishing can also alter ecological processes such as habitat selection and mating behavior of their prey. For example, kelp perch (*Brachyistius frenatus*) change their behavior in response to predation pressure; in the absence of their predators, kelp bass (*Paralabrax clatbratus*), kelp perch select habitats and activity patterns different from those when predators are present (Anderson 2001). Changes in mate selection and mating behavior are also likely influenced by predation risk, as has been observed in marine species including the bicolor damselfish (*Stegastes partitus*) (Figueira & Lyman 2007). These effects may be minor compared with the effects of direct removal but can hamper recovery and further accelerate declining ecosystems.

Researchers are now finding that size-selective fishing can have population-level effects on marine species and that intense selection can alter the genetic composition of fished populations. Evolutionary change occurs in populations exposed to relatively short-term selection pressures, including fishing (Law 2007). Olsen et al. (2005) noted that Northern cod (*Gadus morhua*) appeared to mature earlier and at smaller body size in response to years of size-selective fishing. Observing these trends could provide managers with warning signs before a population crashes (Olsen et al. 2005). Silverside minnows (*Menidia menidia*) that were size-selectively harvested over multiple generations in the lab showed genetic changes toward slower-growing individuals (Conover & Munch 2002). Such changes in populations may not be reversible, suggesting that an evolutionary perspective is needed in fisheries management (e.g., the protection of both juvenile and the largest individuals, termed slot limits) if we are to protect species and maximize yields (Conover & Munch 2002, Hughes et al. 2005, Law 2007).

The impact that fishing a particular species has on its ecosystem depends on the life history of that species, the extent of removal, the potential for density-dependent compensation, its role in the community, and the functional redundancy therein (National Research Council 2006). These effects are complicated by natural phenotypic plasticity, variation in animal behavior, prey switching, ontogenetic shifts in diet, species diversity, and numerical versus aggregated responses of prey (Anderson 2001). Whether food web alterations have long-term ecosystem-wide effects also depends on the ability of the fished species to recover (Jackson et al. 2001, Caddy & Agnew

2004). If no other species has taken over the niche in their absence, their prey base is still intact, and there are no compensatory effects barring recovery, temporary removal of a species may not have significant long-term consequences. The system may be able to shift back to a previous state, adapt to the new conditions, or alternate between different stable states (Daskalov et al. 2007).

Unfortunately, few examples exist of successful recovery of heavily exploited fishes. For example, the North Atlantic swordfish recovery was successful because depletion was not excessive (stock was at 70% of maximum sustainable yield), recovery time was relatively short (10 years), and the fishing fleets cooperated in management, a feat simplified by their similarities and shared incentives (Caddy & Agnew 2004). Otherwise, evidence for recovery of long-lived, slowly maturing top predators is limited and dependent on many factors, both biological and political (Caddy & Agnew 2004, Hutchings & Reynolds 2004).

POTENTIAL ECOSYSTEM EFFECTS OF NONTARGET (BYCATCH) CATCH

In the process of fishing, target and nontarget species can be inadvertently killed, injured, or otherwise incapacitated, but not retained. This is referred to as bycatch. Nontarget species retained by fishers should be considered catch. For some marine megafauna such as loggerhead turtles (*Caretta caretta*), bycatch mortality encompasses nearly all of their fishing-related mortality. From a population dynamics perspective, bycatch-associated mortality is indistinct from a directed mortality (Cook 2003, Kelleher 2005). The challenges to determining possible higher-order impacts on marine ecosystems are similar for bycatch and target species (Lewison et al. 2004), but even less information regarding the magnitude of removals is available. Life history characteristics can be better predictors of fishing impact than can trophic level (Jennings et al. 2002), and when bycatch species are slower growing and later maturing than target catch, their removals can exceed mortality limits before mortality limits of target populations are reached, placing bycatch taxa at risk of inadvertent overexploitation in even well-managed fisheries (Heppell et al. 2005).

Seabirds, sea turtles, marine mammals, and chondrichthyans are among the most bycatch sensitive of the long-lived taxa (Lewison et al. 2004, Lewison & Crowder 2007). Chondrichthyans (sharks, rays, and chimaeras) are common in bycatch and are increasingly retained in many fisheries. Global reported landings have increased steadily since 1984, but their total catch may be twice the reported landings, and the evidence suggests global declines in abundance (Baum et al. 2003, Myers & Worm 2003). An examination of the incidental capture of elasmobranchs in one of Australia's prawn fisheries estimated that elasmobranchs composed 65% of the bycatch of that fishery (Stobutzki et al. 2002).

Many sea turtle populations are significantly reduced from historical numbers, and some populations continue to decline. An estimated 200,000 loggerhead (*C. caretta*) and 50,000 leatherback (*Dermochelys coriacea*) sea turtles are taken annually as bycatch in pelagic longlines (Lewison et al. 2004). Information on bycatch of endangered sea turtles in artisanal fisheries is relatively limited but growing (Lum 2006, Peckham et al. 2007).

Researchers recently estimated that more than 650,000 marine mammals are taken in fisheries each year (Read et al. 2006). The vaquita (*Phocoena sinus*) is in a critical situation (Jaramillo-Legorreta et al. 2007). A minimum estimate of mortality of this porpoise in gillnets in Baja, Mexico, is 39 animals per year, more than 17% of the most recent estimate of the vaquita's population (D'Agrosa et al. 2000). Hector's dolphin (*Cephalorhynchus hectori*) is also critically threatened by bycatch, and bycatch is a factor in the continued failure to recover the Mediterranean monk seal (*Monachus monachus*) and the North Atlantic right whale (*Eubalena glacialis*) populations (Read et al. 2006).

Populations of northeastern offshore spotted dolphins *Stenella attenuata attenuata* and eastern spinner dolphins *Stenella longirostris orientalis* were dramatically reduced by bycatch in purse seine fisheries for tuna in the eastern tropical Pacific. Although their annual mortality in this fishery has been reduced by two orders of magnitude, they have not recovered. Potential hypotheses for this lack of recovery include (a) dolphin bycatch is higher than reported, (b) the effects of the tuna fishery are not limited to direct mortality, (c) a regime shift has reduced dolphin habitat, and (d) recovery expectations were unrealistic. The last hypothesis reflects the deficiency of single-species models that do not take into account the ecosystem effects, including the unknown effects of the large-scale removal of tuna populations (Gerrodette & Forcada 2005).

The seabirds most threatened due to bycatch include albatrosses, petrels, and shearwaters (Tasker et al. 2000). Albatrosses are captured primarily in longline fisheries, and shearwaters and auks are most often captured in gillnets. More than 44,000 wandering albatross are caught annually in Japanese longlines in the Southern Ocean (Brothers et al. 1999). Population viability analysis shows that incidental capture of Humboldt penguins (*Spheniscus humboldti*) in a small-scale driftnet fishery in Peru is unsustainable (Majluf et al. 2002).

Finfish bycatch includes both nonmarketable individuals (juveniles, prohibited size/length classes) of economically important species as well as unwanted species and therefore impacts all fish populations. The most recent estimate for global discards is 7.3 million tonnes (t), compared with 78 million t of landings (Kelleher 2005). Although not directly comparable to the first global estimates (Alverson et al. 1994), the revised estimate represents a considerably smaller quantity than the previous assessment of 27 million t. The explanations for the decline in reported finfish bycatch include (a) an increasing amount of former bycatch that is retained as catch, (b) effective implementation of bycatch reduction devices in fishing gear or other changes in fishing practice, and (c) reduced reporting of bycatch as the issue increased in conservation concern.

This global estimate of finfish bycatch also masks tremendous regional and fishery-specific variation. Shrimp and demersal finfish trawlers represent more than 50% of total estimated discards, but only 22% of total recorded catch (Kelleher 2005). Of these, tropical shrimp trawlers have the highest discard rate (27%). The regions with the highest estimates of discarded biomass are the northeast Pacific and the northwest Atlantic, accounting for 40% of the global estimate. The total annual quantity of discards and offal from gutted fish in the North Sea has been estimated at 70,000 t of offal, 120,000 t of groundfish, 200,000 t of flatfish, and 180,000 t of benthic invertebrates (Tasker et al. 2000). Discard rates for U.S. fisheries are on the high end (Harrington et al. 2005). In the United States, crustaceans and demersal finfish constitute more than 86% of the discarded material. Shrimp trawling and demersal finfish fishery account for 75% of discard material by weight.

Discarded bycatch and offal represent important inputs into the marine environment. Discards alter community composition and distribution patterns by providing food subsidies to a variety of scavenging species as well as initiating physico-chemical changes that can produce ecosystem-wide changes. In some cases, discards are viewed as beneficial—examples include the Gulf of Mexico shrimp fishery and the blue crab fishery in the Mid-Atlantic states. But bacterial decomposition of uneaten prey can exacerbate low-oxygen waters in these areas.

The ecological impact of energy subsidies to scavengers is gaining increased attention. The major consumers of discarded material include benthic invertebrates, teleost fishes, sharks, seabirds, and some delphinids. Discards and offal are food sources for seabirds with scavenging behavior, including gannets, fulmars, gulls, and kittiwakes (Camphuysen & Garthe 1997). Many large marine vertebrates (delphinids, sea turtles, and sharks) are attracted to forage on discards and escaping fish. If the species influenced are strong interactors, then the effects of this subsidy may be far-reaching. Overall, discards may indirectly stabilize ecosystems by dampening the propagation of top-down or bottom-up controls through the food web (Chassot et al. 2005). But the majority of

bycatch species at risk are top predators, so examples of ecosystem effects such as mesopredator release [e.g., increased cownose ray abundance and decreased bay scallop harvests (Myers et al. 2007)] or habitat degradation [e.g., bycatch of algal grazers combined with predatory release of coral consumers (Bellwood et al. 2004)] may be more frequent.

INTEGRATED FOOD WEB EFFECTS OF COMMERCIAL FISHING

The strongest ecosystem impacts of commercial fisheries are from mobile fishing gears that contact the bottom, taking target and nontarget species and damaging benthic habitat. Bottom gears include otter trawls and beam trawls that primarily target bottom-dwelling fish or shrimp and dredges that remove scallops, oysters, crabs, and other animals from surface sediment (Watling & Norse 1998). Stationary bottom gears such as traps, pots, bottom gillnets, and bottom longlines also damage benthic habitats by crushing organisms where they contact the bottom and by dragging during storms (Chuenpagdee et al. 2003). Pelagic gears, including midwater trawls, pelagic longlines, and purse seines, impact ecosystems primarily by removing target and nontarget species from food webs (Chuenpagdee et al. 2003).

Habitat destruction, loss of refuge, and subsequent reductions in survival are fundamental ecosystem impacts of mobile bottom gears. Mobile gears reduce heterogeneity and structural complexity in both hard- and soft-bottom habitats that provide refuge for target and nontarget species (Turner et al. 1999). Because they are often slow growing and long-lived, structure-forming species decrease in abundance and require long recovery periods when fishermen move into new areas (Turner et al. 1999, Kaiser et al. 2006). Soft-sediment habitats are often ignored as examples of ecosystems impacted by commercial fisheries, but these habitats support high biodiversity and cover more than 70% of the seafloor, making it essential to consider ecosystem impacts in these areas (Thrush & Dayton 2002). With each square meter of bottom in the Gulf of Mexico trawled up to seven times per year, this disturbance results in community shifts toward rapid colonizers (Watling & Norse 1998).

Food web alterations have cascading effects that affect other food web components and can lead to regime shifts in marine ecosystems. The removal of herbivorous and predatory species has resulted in regime shifts affecting ecosystems from coral reefs to the open ocean (Folke et al. 2004). The Gulf of Maine in the western North Atlantic has undergone two fishery-induced regime shifts over the past 100 years (Steneck et al. 2004). The collapse of cod and other dominant benthic fish species in the late 1980s and early 1990s coincided with increases in macroinvertebrates and phytoplankton but decreases in large zooplankton, resulting in a four-step trophic cascade and a highly altered ecosystem (Frank et al. 2005). Shrimp and crab fisheries that replaced groundfish fisheries have attained a higher monetary value, but the ecological damage leading to the development of low-trophic-level fisheries is not considered desirable (Frank et al. 2005). Contrary to the trophic cascade proposed by Frank et al. (2005), salinity changes in the Gulf of Maine due to Arctic sea ice melting are suggested to have caused a bottom-up-driven regime shift in phytoplankton and zooplankton (Greene & Pershing 2007). Because both anthropogenic drivers of change and climatic change act in concert on marine ecosystems, it is difficult to apportion causality to drivers of regime shifts.

Discerning the effects of commercial fisheries has proven difficult in cases in which regime shifts and climate change may also alter marine ecosystems. Steller sea lions have declined by 80% in the western Gulf of Alaska since the 1970s. Hypotheses for this decline have included nutritional stress, disease, competition for commercial target species, and prey switching by killer whales (DeMaster & Atkinson 2002, National Research Council 2002). Although some or all of these processes may have affected populations, the individual hypotheses do not provide satisfactory explanations of the

Ecosystem function: ecological processes such as migration and predation, including food webs with multiple trophic levels, functional duplicity, and high connectivity. From a human perspective, ecosystem services (seafood, tourism, transport) are sustained

observed population trends (Trites et al. 2007). Archaeological evidence of historical population fluctuations and ecosystem modeling studies have suggested that the ultimate cause of the Steller sea lion decline may have been climate-induced, basin-wide ecosystem changes (Trites et al. 2007), but this is contrary to the evidence that the symptoms more likely reflect a top-down effect rather than a bottom-up effect (National Research Council 2002). This case highlights the importance of considering multiple interacting hypotheses and potential compounding effects when managing target and nontarget species.

As shelf fisheries have become fully or overexploited, there has been a shift to deeper waters to sustain catch and profits. This shift may not prove sustainable when it reaches deep sea and seamount ecosystems owing to their low productivity. These ecosystems are notable in that both structure-forming and target species are exceptionally long-lived and slow growing (Koslow et al. 2000, Devine et al. 2006). Seamounts, in particular, are often isolated and harbor many endemic species that have suffered severe population declines over a very short period (Koslow et al. 2000). Declines in five deep sea fisheries in the northwest Atlantic were 87–98% over a 17-year period, sufficient to list them as critically endangered on the basis of International Union for Conservation of Nature (IUCN) criteria (Devine et al. 2006).

Measuring the ecosystem effects of fishing is a daunting task because many abiotic, ecological, and anthropogenic factors act in synergy. The development of marine food web models such as Ecopath/Ecosim has allowed fisheries ecologists to assess the anthropogenic impacts on marine ecosystems that are too large and complex for experimental studies (Christensen & Walters 2004). Mass-balance models have been extremely successful in modeling potential ecosystem impacts of various fisheries management approaches (Walters et al. 2005) as well as modeling complex food web and spatial interaction effects (Walters & Christensen 2007). Variability in climate forcing can propagate up food webs to affect higher trophic levels in the North Pacific (Megrey et al. 2007), although explaining predicted biological responses to climate forcing can be difficult.

Widespread use of single-species harvesting policies based on maximum sustainable yield can lead to the removal of a suite of top predators and extensive loss of ecosystem function (Walters et al. 2005). Other models suggest that variability in oceanographic processes is more important than dispersal in the design of marine protected areas for large pelagic species (Martell et al. 2005) and that changing the set depth and using circle hooks in Pacific longline fisheries may be more effective than effort reduction in protecting marlin and shark populations (Kaplan et al. 2007). Despite these advances, applying robust models to improve ecosystem-based management of commercial fisheries will require investment in the collection of sufficient biological and environmental data as well as extensive model validation exercises.

FOOD WEB EFFECTS OF MARINE RECREATIONAL FISHERIES

Recreational angling is a diverse and lucrative industry responsible for an estimated 12% of global landings (Cooke & Cowx 2004). Worldwide, approximately 11.5% of the population participates in recreational fisheries, landing in excess of 10 million t of fish per year (Cooke & Cowx 2004). Angling is characterized as fishing for leisure, rather than for subsistence or profit, and includes traditional hook-and-line angling as well as trapping, gigging, netting, and spear and dive fishing. The rate of participation in recreational fisheries varies widely by country, as does the percentage of catch retained for consumption (Cooke & Cowx 2004). Although the actions of a single recreational fisherman may seem insignificant, the cumulative impact of millions of recreational anglers may have a profound effect on freshwater and marine environments (Coleman et al. 2004). Although recreational landings represent only a fraction of the U.S. total [4% in 2002 (Coleman et al. 2004)], recreational anglers land a disproportionate percentage of “species of concern” (Coleman et al.

2004). Recreational landings exceed commercial harvests in some areas, particularly near major cities and popular tourist destinations (McPhee et al. 2002).

The potential ecological effects of recreational fishing at the population level are comparable to those of commercial harvest, including localized depletion, growth and recruitment overfishing, reduced biomass, the disruption of compensatory mechanisms, and truncated size and age distributions. Anglers tend to concentrate their effort in more accessible nearshore habitats, sometimes leading to the exploitation of immature life stages (McPhee et al. 2002, Cooke & Cowx 2004). But many anglers target larger and often older trophy fish, removing the most reproductively valuable individuals from a population (Birkeland & Dayton 2005).

Managers of recreational fisheries use many of the same management strategies applied to commercial fisheries, including size limits, gear restrictions, possession limits, and area closures. Captured fish that cannot legally be kept are presumably released alive and unharmed, a practice referred to as catch-and-release (C&R) fishing. A broad definition of C&R fishing therefore includes any fishing activity involving the voluntary or regulatory release of captured fish. Although release rates vary by species, an estimated 60% of all the fish now landed recreationally are released (Cooke & Cowx 2006), up from ~34% in 1981 (Bartholomew & Bohnsack 2005).

Recreational and commercial fisheries are fundamentally different and present distinct management challenges. Unlike most commercial fisheries, recreational fisheries remain open access (McPhee et al. 2002), and although most U.S. states issue saltwater fishing licenses, there is generally no mechanism to limit total effort, making it difficult to regulate or reduce takes. In many regions, recreational fisheries lack consistent data collection on effort, landings, discards, and expenditures (McPhee et al. 2002). In the United States, the National Marine Fisheries Service currently uses telephone and intercept surveys to gather data. But the high volume and diffuse nature of angler effort present sampling challenges, making it difficult for managers to monitor trends in real time.

Recreational anglers are driven by entirely different motivations than their commercial counterparts. Managers often suffer from the mistaken assumption that recreational fisheries are self-regulating and that anglers will exit the fishery if the fishing experience somehow declines in quality. But if anglers are willing to tolerate low catch rates, recreational fishers may be more likely to exploit fisheries to the point of collapse. Because recreational fisheries target a narrow trophic level (e.g., Stergiou et al. 2007), they may have a higher likelihood of food web effects than do less selective fisheries (Friedlander & DeMartini 2002).

FOOD WEB EFFECTS OF ARTISANAL, SMALL-SCALE FISHERIES

The United Nations Food and Agriculture Organization (FAO) glossary defines artisanal fisheries as traditional fisheries involving fishing households (as opposed to commercial companies), using relatively small amount of capital and energy, relatively small fishing vessels (if any), making short fishing trips, close to shore, mainly for local consumption. In practice, definition varies between countries, e.g., from gleaning or a one-man canoe in poor developing countries, to more than 20-m. trawlers, seiners, or long-liners in developed ones. Artisanal fisheries can be subsistence or commercial fisheries, providing for local consumption or export. They are sometimes referred to as small-scale fisheries (FAO 2006).

Artisanal fisheries outnumber industrial fisheries by a wide margin, even after one accounts for differences in categorizing fishers. An estimated 99% of the 51 million fishers worldwide are artisanal (Berkes et al. 2001).

Classifying fishers and fishing operations is difficult, and the interchangeable use of artisanal with “small-scale” (an even more relative descriptor) may contribute to the difficulties in assessing

the impacts of these fisheries. First, multigear use, in a variety of local conditions, can complicate and confound data collection and analysis. Second, isolating the specific impacts of such fisheries in the nearshore marine environment is difficult because fishing occurs synoptically with other economic activities (including commercial fisheries, shipping, tourism, and mining), all of which affect water quality, nursery habitat, and pollution loading and can alter the composition and functioning of the adjacent marine ecosystems (Gomez et al. 2006). In some cases, the impacts of commercial and artisanal activities are not independent. Artisanal fishing can amplify the effects of commercial fishing if both artisanal and industrial fleets sequentially target a single stock, as in the red grouper fishery in the Gulf of Mexico (Burgos & Defeo 2004). Billfish fisheries in the tropical Pacific exhibit similar overlap with commercial, recreational, and artisanal fisheries all targeting these migratory stocks (Uozumi 2003).

Certain fisheries (gillnets, trap fisheries, hand harvests) are almost exclusively conducted by artisanal and small-scale fishers and dominate removals in shallow-water systems. These relatively unselective gears catch a diversity of species (Ambrose et al. 2005), including juveniles of nontarget species. Retention of nontarget catch is an important component of the economic viability of these operations in the tropics, so these fisheries often have low discard ratios (e.g., a 6.5% discard ratio was reported by Mangi & Roberts 2006).

No-fishing zones or marine reserves offer some insights into the impacts of artisanal fishing. Much of the information on the effects of artisanal fishing on community assemblage and food web relationships has been gathered from tropical systems, including the Indian Ocean (e.g., Jennings & Polunin 1997) and the Caribbean (e.g., Hawkins & Roberts 2004). Miller et al. (2007) provide a case study of coral reef ecosystems around Navassa Island in the Caribbean. Navassa's relative isolation from other anthropogenic impacts provided an opportunity to examine the impact of an escalating artisanal fishery by mainland Haitian fishers. The reef fish assemblage underwent a rapid shift in community structure, characterized by depletion of piscivorous fish. Evidence for a similar phenomenon was also obtained by analyses of catch and effort studies in Eritrea (Tsehaye et al. 2007). Tsehaye et al. (2007) concluded that "reef-associated demersal fishes are highly vulnerable to fishing and can decline even at the early stages of the fisheries." In comparing Caribbean coral reefs subjected to a range of fishing pressures, Hawkins & Roberts (2004) suggest that the ability of herbivorous fish to control algal overgrowth after the loss of key grazers (e.g., sea urchins) is reduced in intensively fished areas. Similar cascading, ecosystem-level effects are observed in the Galapagos Islands, where highly fished areas have higher abundance of urchins and encrusting algae (Sonnenholzner et al. 2007). Heavily fished areas in the intertidal flats of Inhaca Island, Mozambique, exhibited lower catch rates, a lower proportion of piscivorous fish, an increased proportion of small fish, and a decrease in species diversity (de Boer et al. 2001).

The impact of large numbers of small-scale fishers can be rapid and similar in magnitude to that of commercial fisheries. Bycatch of loggerhead sea turtles (*C. caretta*) in just two small-scale fisheries in Baja California Sur, Mexico, is comparable to that taken in the entire industrial longline fleet in the North Pacific (Peckham et al. 2007). The Franciscana dolphin (*Pontoporia blainvillei*) in the southwest Atlantic is predicted to suffer a population crash within 30 years if incidental kills in gillnets are not halted or reduced (Kinas 2002).

Although artisanal fisheries typically do not operate crushing or habitat-altering gear, they can damage key structure-forming organisms. Studies evaluating environmental impacts of artisanal fishing gear on coral reef ecosystems in the multigear fishery of southern Kenya found that fishers using beach seines, spears, and gillnets caused the most direct physical damage to corals (Mangi & Roberts 2006).

The heterogeneity and complexity (Tzanatos et al. 2006) of small-scale fisheries provide challenges to assessing their impacts and contrast directly with large commercial fishing operations.

Consequently, mitigation of the impacts of artisanal fisheries proves challenging and may be region and/or gear specific (Tzanatos et al. 2006). Small-scale fisheries clearly alter community structure and trophic relationships, but the general direction and processes do not differ from those of other sectors of the fishing community. Artisanal fisheries may be somewhat unique with respect to (a) predominance in the inshore zones, (b) multispecies catch and low discard ratios, and consequently (c) low provision of subsidies to other marine fauna. Better management of postharvest losses could reduce the demand and subsequent rate of removals (FAO 2006). Where artisanal fisheries overlap with intrinsically vulnerable taxa such as sea turtles or marine mammals, a large number of small-scale fishers can rival the impact of commercial fisheries and can generate rapid declines.

CUMULATIVE EFFECTS OF ANTHROPOGENIC ACTIVITIES ON MARINE FOOD WEBS

Most marine systems are adapted to natural levels of disturbance, but oceans are subject to increasing, cumulative, and synergistic effects of both natural and anthropogenic factors that threaten their resilience (Figure 2; Halpern et al. 2008). Coastal food webs are at risk from the effects of

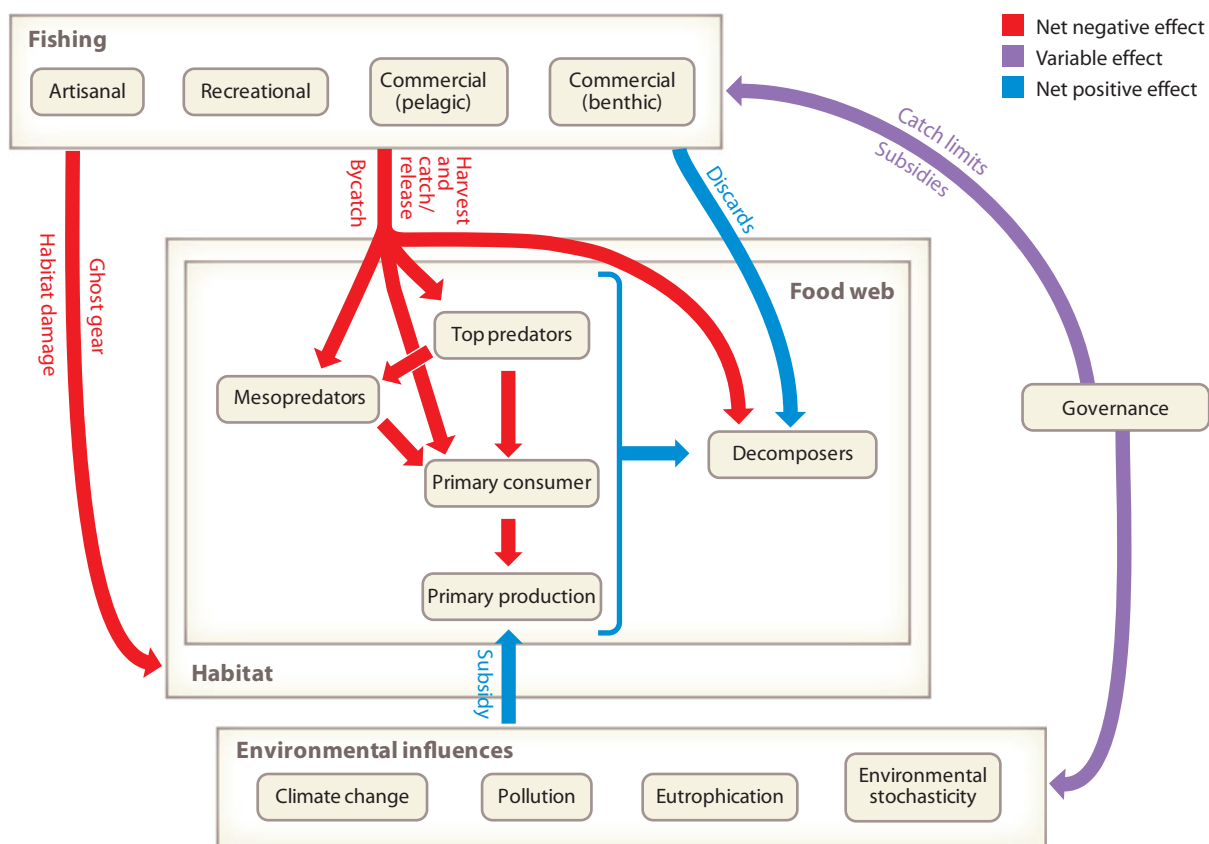


Figure 2

Diagram of the ecosystem and food web effects of fishing. Fisheries increase subsidies to primary production through eutrophication. Fishing directly affects predominantly the upper trophic levels as well as the supporting habitat. Governance regulates both top-down and bottom-up anthropogenic influences.

Table 2 Fisheries effort by type of fisher in the United States and world (from NMFS 2006)

	Fishery subsector		
	Large scale	Recreational landings	Recreational releases
World catch (tonnes)	141,400,000	N/A	N/A
U.S. catch (tonnes)	5,400,000	117,000	144,000

multiple stressors owing to being proximate to and downstream from human activities and to the prolonged timescale of degradation (Lotze et al. 2006). Although previous research has focused on the ecosystem effects of commercial fisheries, the additional effects of bycatch and artisanal and recreational fisheries can further exacerbate a degraded food web, particularly where their effects interact. In 2006, recreational fisheries in the United States focused on apex predators and were responsible for 2.2% of all landings; the number of fish caught and released was even larger (Table 2). Artisanal fisheries also play a larger role than do industrial fisheries. In the Indian Ocean, artisanal fisheries landed 200,000 tons more than did commercial fisheries in 2006 (Table 3). There are more than 4 times more artisanal vessels and more than 2.5 times more participants in artisanal fisheries compared with large-scale commercial fisheries. Although the large number of participants and vessels makes monitoring more difficult, their impact on the ecosystem cannot be overlooked.

Ecosystems such as the Chesapeake Bay have faced large-scale collapse owing to the synergism of increased harvest of oysters (*Crassostrea virginica*), high levels of eutrophication, broad-scale hypoxia, and increased water temperatures (Jackson et al. 2001). These conditions have led to toxic dinoflagellate blooms and fish kills. Coastal properties are left with tons of rotting fish, and coastal food webs are impaired. Unfortunately, numerous recovery attempts have had little effect on oyster populations or overall water quality, but successful recovery of striped bass still provides hope for future efforts (Boesch 2006). Owing to the multiple inputs (land, river, sea) and actors in the system (watershed to estuary), coastal systems will continue to face synergistic effects from harvest, nutrient loading, and global change (Lotze et al. 2006).

Synergistic effects require management strategies that deal with the entire ecosystem, through food webs and other drivers of change, including global change. The global decline in marine ecosystems has stimulated expansion into new fields of inquiry, including historical ecology (Jackson et al. 2001) and resilience theory (McLeod & Leslie 2008). New approaches are needed to ensure that ecological baselines sufficiently account for historical influences, scale in space and time, multiplicity of natural and anthropogenic impacts to the environment, and the human component of marine ecosystems (Shackeroff et al. 2008).

FISHING, MARINE ECOSYSTEMS, AND THE TRANSITION TO ECOSYSTEM-BASED MANAGEMENT

How can we address the impacts of diverse fisheries in the context of other anthropogenic and naturally driven variation in marine ecosystems? Three recent assessments (Pew Oceans Commission 2003, U.S. Commission on Ocean Policy 2004, Millenium Ecosystem Assessment 2005) call for

Table 3 Fisheries effort by type of fisher in the Indian Ocean (from FAO 2006)

	Fishery subsector		
	Large scale	Small scale	Recreational
Number of participants	1,600,000	4,300,000	90,000
Total landings (tonnes)	4,000,000	4,200,000	N/A
Number of vessels	73,000	313,000	N/A

a dramatic shift in ocean policy, from management of individual sectoral activities, like fisheries, toward ecosystem-based management (Crowder et al. 2006). Ecosystem-based management is “an integrated approach to management that considers the entire ecosystem, including humans” (McLeod et al. 2005). However, a practical framework for implementation of marine ecosystem-based management is still emerging.

Although there are ecosystem approaches to managing fisheries that are not necessarily place based (e.g., Pikitch et al. 2004), and a variety of food web modeling approaches provide insights regarding food web dynamics under exploitation (Walters et al. 1997), marine ecosystems are inherently place based (McLeod et al. 2005, Crowder et al. 2006, Young et al. 2007). Moreover, social, cultural, economic, and political attributes overlay these biophysically defined places. Thus, approaches that integrate natural and social scientific perspectives on defining and managing places at sea are necessary to overcome uncontrolled, cumulative impacts of fisheries and other anthropogenic effects (Shackeroff et al. 2008). Although consensus has arguably been reached on the definition and goals of ecosystem-based management, the slow progress toward implementation leaves few concrete examples of success. Historically, fishing communities in Hawaii succeeded in managing their local ecosystem from mountains, through watersheds, to fishery harvest before globalization increased participants and altered perspectives (Shackeroff et al. 2008).

Analysts are beginning to agree that the escalating crisis in marine ecosystems is in large part a failure of governance (Crowder et al. 2006). All the recent assessments have called for a transition from managing sectoral activities, including fisheries, toward ecosystem-based management. Environmentalists have sought to implement marine reserves to maintain the structure and function of marine ecosystems. But this too is a sectoral approach. Traditional single-species management has a clearer recovery goal, specifically the maintenance of a certain spawning stock biomass. But it is more difficult to define recovery goals in an ecosystem framework.

Place-based management and marine spatial planning (MSP) can provide a far more promising approach to implementing ecosystem-based management (Young et al. 2007). Rather than individual sectoral agencies managing their activities everywhere, responsible sectoral authorities could work together to manage all the human activities in a place. These places might align with ecosystem boundaries, socioeconomic boundaries, and/or jurisdictional boundaries. In practice, management always occurs in a delimited space, with processes that cross management boundaries.

The biophysical component of marine ecosystems provides the basic template on which all human activities, including fisheries, occur and that various forms of governance regulate. Approaches to MSP and ocean zoning consider basic ecological concepts so that human activities can be conducted in ways that provide sustainable ecosystem services on which people depend and maintain resilient ecosystems that can respond to environmental change.

Rather than discarding successful single-species management techniques, some argue that we can use our current tools in the context of the larger ecosystem (Hilborn et al. 2003). Multispecies fisheries models consist of aggregated single-species models for species harvested in concert or can include predator-prey interactions (Hollowed et al. 2000). Mass-balance models can incorporate environmental variability, human behavior, and complex species relationships to predict ecosystem change but also require additional expertise and parameterization (Walters & Christensen 2007). But as model complexity increases, data requirements also increase, so we suggest an adaptive approach centered on food web interactions that adds complexity as data become available (**Figure 1**).

Place-based management of marine ecosystems requires a hierarchy of management practices starting at the most general level with the concept of ecosystem-based management and moving toward the development of an integrated approach that accords priority to the maintenance of healthy, biologically diverse, productive, and resilient ecosystems. Multiple spatial and temporal scales must be explicit in planning to ensure that management units overlies relevant ecological

processes and ultimately stakeholder uses; there is no single correct scale for MSP. The key to success in place-based management of marine ecosystems is to design governance systems that align the incentives of stakeholders, in this case fishermen, with the objectives of management (Hilborn et al. 2003). MSP that fully incorporates the underlying ecosystem template and explicitly integrates the socioeconomic and governance overlays can form the basis for adequate protection of marine ecosystems and the sound use of marine resources, including fisheries.

DISCLOSURE STATEMENT

The authors are not aware of any biases that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

We thank the other participants in the Fisheries Ecology course for their insights and discussion as well as the reviewers and editors of this manuscript. L.B.C. was supported by the Gordon and Betty Moore Foundation during the development of this manuscript.

LITERATURE CITED

- Alverson DL, Freeberg MH, Pope JG, Murawski SA. 1994. *A global assessment of fisheries bycatch and discards. Rep. 339*, FAO Fish. Tech. Pap., Rome
- Ambrose EE, Solarin BB, Isebor CE, Williams AB. 2005. Assessment of fish by-catch species from coastal artisanal shrimp beam trawl fisheries in Nigeria. *Fish. Res.* 71:125–32
- Anderson TW. 2001. Predator responses, prey refuges, and density-dependent mortality of a marine fish. *Ecology* 82:245–57
- Bakun A, Broad K. 2003. Environmental ‘loopholes’ and fish population dynamics: comparative pattern recognition with focus on El Niño effects in the Pacific. *Fish. Oceanogr.* 12:458–73
- Bartholomew A, Bohnsack JA. 2005. A review of catch-and-release angling mortality with implications for no-take reserves. *Rev. Fish Biol. Fish.* 15:129–54
- Bascompte J, Melian CJ, Sala E. 2005. Interaction strength combinations and the overfishing of a marine food web. *Proc. Natl. Acad. Sci. USA* 102:5443–47
- Baum JK, Myers RA. 2004. Shifting baselines and the decline of pelagic sharks in the Gulf of Mexico. *Ecol. Lett.* 7:135–45
- Baum JK, Myers RA, Kehler DG, Worm B, Harley SJ, Doherty PA. 2003. Collapse and conservation of shark populations in the Northwest Atlantic. *Science* 299:389–92
- Bellwood DR, Hughes TP, Folke C, Nystrom M. 2004. Confronting the coral reef crisis. *Nature* 429:827–33
- Berkes F, Mahon R, McConney P, Pollnac R, Pomeroy R. 2001. *Managing Small-Scale Fisheries: Alternative Directions and Methods*. Ottawa: Int. Dev. Res. Cent. 250 pp.
- Birkeland C, Dayton P. 2005. The importance in fishery management of leaving the big ones. *Trends Ecol. Evol.* 20:356–58
- Boesch DF. 2006. Scientific requirements for ecosystem-based management in the restoration of Chesapeake Bay and Coastal Louisiana. *Ecol. Eng.* 26:6–26
- Brothers NP, Cooper J, Lokkeborg S. 1999. *The incidental catch of seabirds by longline fisheries: worldwide review and technical guidelines for mitigation. Rep. 937*, FAO, Rome
- Bundy A, Fanning P. 2005. Can Atlantic cod (*Gadus morhua*) recover? Exploring trophic explanations for the nonrecovery of the cod stock on the eastern Scotian Shelf, Canada. *Can. J. Fish. Aquat. Sci.* 62:1474–89
- Burgos R, Defeo O. 2004. Long-term population structure, mortality and modeling of a tropical multi-fleet fishery: the red grouper *Epinephelus morio* of the Campeche Bank, Gulf of Mexico. *Fish. Res.* 66:325–35
- Caddy JF, Agnew DJ. 2004. An overview of recent global experience with recovery plans for depleted marine resources and suggested guidelines for recovery planning. *Rev. Fish Biol. Fish.* 14:43–112

- Camphuysen K, Garthe S. 1997. An evaluation of the distribution and scavenging habits of northern fulmars (*Fulmarus glacialis*) in the North Sea. *ICES J. Mar. Sci.* 54:654–83
- Carpenter SR, Kitchell J. 1998. The trophic cascade in lakes. *Biol. Conserv.* 83:233–34
- Chassot E, Gascuel D, Colomb A. 2005. Impact of trophic interactions on production functions and on the ecosystem response to fishing: a simulation approach. *Aquat. Living Resour.* 18:1–13
- Christensen V, Guenette S, Heymans JJ, Walters CJ, Watson R, et al. 2003. Hundred-year decline of North Atlantic predatory fishes. *Fish Fish.* 4:1–24
- Christensen V, Walters K. 2004. Ecopath with Ecosim: methods, capabilities and limitations. *Ecol. Model.* 172:109–39
- Chuenpagdee R, Morgan LE, Maxwell SM, Norse EA, Pauly D. 2003. Shifting gears: assessing collateral impacts of fishing methods in US waters. *Front. Ecol. Environ.* 1:517–24
- Coleman FC, Figueira WF, Ueland JS, Crowder LB. 2004. The impact of United States recreational fisheries on marine fish populations. *Science* 305:1958–60
- Conover DO, Munch SB. 2002. Sustaining fisheries yields over evolutionary time scales. *Science* 297:94–96
- Cook R. 2003. The magnitude and impact of by-catch mortality by fishing gear. In *Responsible Fisheries in the Marine Environment*, ed. M Sinclair, G Valdimarsson, pp. 219–33. Rome, Italy: FAO/CABI
- Cooke SJ, Cowx IG. 2004. The role of recreational fishing in global fish crises. *BioScience* 54:857–59
- Cooke SJ, Cowx IG. 2006. Contrasting recreational and commercial fishing: searching for common issues to promote unified conservation of fisheries resources and aquatic environments. *Biol. Conserv.* 128:93–108
- Crooks KR, Soule ME. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. *Nature* 400:563–66
- Crowder LLB, Osherenko GG, Young OOR, Airamé SS, Norse EEA, et al. 2006. Sustainability. Resolving mismatches in U.S. ocean governance. *Science* 313:617–18
- D'Agrosa C, Lennert-Cody CE, Vidal O. 2000. Vaquita bycatch in Mexico's artisanal gillnet fisheries: driving a small population to extinction. *Conserv. Biol.* 14:1110–19
- Daskalov GM, Grishin AN, Rodionov S, Mihneva V. 2007. Trophic cascades triggered by overfishing reveal possible mechanisms of ecosystem regime shifts. *Proc. Natl. Acad. Sci. USA* 104:10518–23
- Dayton PK, Thrush S, Coleman FC. 2002. *Ecological Effects of Fishing in Marine Ecosystems of the United States*. Arlington, VA: Pew Oceans Comm.
- de Boer WF, van Schie AMP, Jocene DF, Mabote ABP, Guissamulo A. 2001. The impact of artisanal fishery on a tropical intertidal benthic fish community. *Environ. Biol. Fishes* 61:213–29
- DeMaster DP, Atkinson S, eds. 2002. *Steller Sea Lion Decline: Is It Food II: Proceedings of the Workshop Is It Food II, Alaska SeaLife Center and Univ. Alaska Sea Grant AK-SG-02-02, Seward, Alaska, May, 2001*
- DeMaster DP, Trites AW, Clapham P, Mizroch S, Wade P, et al. 2006. The sequential megafaunal collapse hypothesis: testing with existing data. *Progr. Oceanogr.* 68:329–42
- Devine JA, Baker KD, Haedrich RL. 2006. Fisheries: Deep-sea fishes qualify as endangered. *Nature* 439:29
- Essington TE, Beaudreau AH, Wiedenmann J. 2006. Fishing through marine food webs. *Proc. Natl. Acad. Sci. USA* 103:3171–75
- Estes JA, Tinker MT, Williams TM, Doak DF. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science*. 5388:473–76
- FAO. 2006. *The State of World Fisheries and Aquaculture*. FAO, Rome (also available at <ftp://ftp.fao.org/docrep/fao/009/a0699e/a0699e.pdf>) 162 pp.
- Figueira WF, Lyman S. 2007. Context-dependent risk tolerance of the bicolor damselfish: courtship in the presence of fish and egg predators. *Anim. Behav.* 74:329–36
- Folke C, Carpenter S, Walker B, Scheffer M, Elmqvist T, et al. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. *Annu. Rev. Ecol. Evol. Syst.* 35:557–81
- Frank KT, Petrie B, Choi JS, Leggett WC. 2005. Trophic cascades in a formerly cod-dominated ecosystem. *Science* 308:1621–23
- Friedlander AM, DeMartini EE. 2002. Contrasts in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian islands: the effects of fishing down apex predators. *Mar. Ecol. Prog. Ser.* 230:253–64
- Gerrodette T, Forcada J. 2005. Non-recovery of two spotted and spinner dolphin populations in the eastern tropical Pacific Ocean. *Mar. Ecol. Prog. Ser.* 291:1–21

- Gomez S, Lloret J, Demestre M, Riera V. 2006. The decline of the artisanal fisheries in Mediterranean coastal areas: the case of Cap de Creus (Cape Creus). *Coast. Manag.* 34:217–32
- Greene CH, Pershing AJ. 2007. Climate drives sea change. *Science* 315:1084–85
- Halpern BS, McLeod KL, Rosenberg AA, Crowder LB. 2008. Managing for cumulative impacts in ecosystem-based management through ocean zoning. *Ocean Coast. Manag.* 51:201–11
- Hampton J, Sibert JR, Kleiber P, Maunder MN, Harley SJ. 2005. Fisheries: decline of Pacific tuna populations exaggerated? *Nature* 434:E1–2
- Harrington JM, Myers RA, Rosenberg AA. 2005. Wasted fishery resources: discarded by-catch in the USA. *Fish Fish.* 6:350–61
- Hawkins JP, Roberts CM. 2004. Effects of artisanal fishing on Caribbean coral reefs. *Conserv. Biol.* 18:215–26
- Heppell SS, Heppell SA, Read AJ, Crowder LB. 2005. Effects of fishing on long-lived marine organisms. In *Marine Conservation Biology*, ed. EA Norse, LB Crowder, pp. 211–31. Washington, DC: Island Press
- Hilborn R, Branch TA, Ernst B, Magnusson A, Minte-Vera CV, et al. 2003. State of the world's fisheries. *Annu. Rev. Environ. Resour.* 28:359–99
- Hollowed AB, Bax N, Beamish R, Collie J, Fogarty M, et al. 2000. Are multispecies models an improvement on single-species models for measuring fishing impacts on marine ecosystems? *ICES J. Mar. Sci.* 57:707–19
- Hughes TP, Bellwood DR, Folke C, Steneck RS, Wilson J. 2005. New paradigms for supporting the resilience of marine ecosystems. *Trends Ecol. Evol.* 20:380–86
- Hutchings JA, Reynolds JD. 2004. Marine fish population collapses: consequences for recovery and extinction risk. *BioScience* 54:297–309
- Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293:629–38
- Jaramillo-Legorreta A, Rojas-Bracho L, Brownell RL Jr, Read AJ, Reeves RR, et al. 2007. Saving the Vaquita: immediate action, not more data. *Conserv. Biol.* 21:1653–55
- Jennings S, Greenstreet S, Hill L, Piet G, Pinnegar J, Warr KJ. 2002. Long-term trends in the trophic structure of the North Sea fish community: evidence from stable-isotope analysis, size-spectra and community metrics. *Mar. Biol.* 141:1085–97
- Jennings S, Polunin NVC. 1997. Impacts of predator depletion by fishing on the biomass and diversity of nontarget reef fish communities. *Coral Reefs* 16:71–82
- Kaiser MJ, Clarke KR, Hinz H, Austen MCV, Somerfield PJ, Karakassis I. 2006. Global analysis of response and recovery of benthic biota to fishing. *Mar. Ecol. Prog. Ser.* 311:1–14
- Kaplan IC, Cox SP, Kitchell JF. 2007. Circle hooks for Pacific longliners: not a panacea for marlin and shark bycatch, but part of the solution. *Trans. Am. Fish. Soc.* 136:392–401
- Kelleher K. 2005. *Discards in the world's marine fisheries: an update. Rep. FAO Tech. Pap. No. 470*, FAO, Rome, Italy
- Kinas PG. 2002. The impact of incidental kills by gill nets on the Franciscana dolphin (*Pontoporia blainvillei*) in southern Brazil. *Bull. Mar. Sci.* 70:409–21
- Koslow JA, Boehlert GW, Gordon JDM, Haedrich RL, Lorange P, Parin N. 2000. Continental slope and deep-sea fisheries: implications for a fragile ecosystem. *ICES J. Mar. Sci.* 57:548–57
- Law R. 2007. Fisheries-induced evolution: present status and future directions. *Mar. Ecol. Prog. Ser.* 335:271–77
- Lewis RL, Crowder LB. 2007. Putting longline bycatch of sea turtles into perspective. *Conserv. Biol.* 21:79–86
- Lewis RL, Crowder LB, Read AJ, Freeman SA. 2004. Understanding impacts of fisheries bycatch on marine megafauna. *Trends Ecol. Evol.* 19:598–604
- Lotze HK, Lenihan HS, Bourque BJ, Bradbury RH, Cooke RG, et al. 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science* 312:1806–9
- Lum LL. 2006. Assessment of incidental sea turtle catch in the artisanal gillnet fishery in Trinidad and Tobago, West Indies. *Appl. Herpetol.* 3:357–68
- Majluf P, Babcock EA, Riveros JC, Schreiber MA, Alderete W. 2002. Catch and bycatch of sea birds and marine mammals in the small-scale fishery of Punta San Juan, Peru. *Conserv. Biol.* 16:1333–43
- Mangel M, Levin P. 2005. Regime, phase and paradigm shifts: making community ecology the basic science for fisheries. *Philos. Trans. R. Soc. London Ser. B* 360:95–105
- Mangi SC, Roberts CM. 2006. Quantifying the environmental impacts of artisanal fishing gear on Kenya's coral reef ecosystems. *Mar. Pollut. Bull.* 52:1646–60

- Martell SJD, Essington TE, Lessard B, Kitchell JF, Walters CJ, Boggs CH. 2005. Interactions of productivity, predation risk, and fishing effort in the efficacy of marine protected areas for the central Pacific. *Can. J. Fish. Aquat. Sci.* 62:1320–36
- McCann K. 2000. The diversity–stability debate. *Nature* 405:228–33
- McLeod KL, Leslie H. 2008. *Managing for Resilience: New Directions in Marine Ecosystem-Based Management*. Washington, DC: Island Press
- McLeod KL, Lubchenco J, Palumbi SR, Rosenberg AA. 2005. *Scientific Consensus Statement on Marine Ecosystem-Based Management*. Washington, DC: Commun. Partnersh. Sci. Sea
- McPhee D, Leadbitter D, Skilleter G. 2002. Swallowing the bait: Is recreational fishing in Australia ecologically sustainable? *Pac. Conserv. Biol.* 8:40–51
- Megrey BA, Rose KA, Ito S, Hay DE, Werner FE, et al. 2007. North Pacific basin-scale differences in lower and higher trophic level marine ecosystem responses to climate impacts using a nutrient-phytoplankton-zooplankton model coupled to a fish bioenergetics model. *Ecol. Model.* 202:196–210
- Micheli F, Halpern BS. 2005. Low functional redundancy in coastal marine assemblages. *Ecol. Lett.* 8:391–400
- Millennium Ecosyst. Assess. 2005. *Ecosystems and Human Well-Being*. Washington, DC: Island Press. 549 pp.
- Miller MW, McClellan DB, Wiener JW, Stoffle B. 2007. Apparent rapid fisheries escalation at a remote Caribbean island. *Environ. Conserv.* 34:92–94
- Myers RA, Baum JK, Shepherd TD, Powers SP, Peterson CH. 2007. Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science* 315:1846–50
- Myers RA, Worm B. 2003. Rapid worldwide depletion of predatory fish communities. *Nature* 423:280
- Natl. Res. Counc. 2002. *A Century of Ecosystem Science: Planning Long-Term Research in the Gulf of Alaska*. Washington, DC: Natl. Acad. Press. 94 pp.
- Natl. Res. Counc. 2006. *Dynamic Changes in Marine Ecosystems: Fishing, Food Webs and Future Options*. Washington, DC: Natl. Acad. Press. 153 pp.
- Newman MJH, Paredes GA, Sala E, Jackson JBC. 2006. Structure of Caribbean coral reef communities across a large gradient of fish biomass. *Ecol. Lett.* 9:1216–27
- Olsen E, Lilly GR, Heino M, Morgan MJ, Brattey J, Dieckmann U. 2005. Assessing changes in age and size at maturation in collapsing populations of Atlantic cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.* 62:811–23
- Pace ML, Cole JJ, Carpenter SR, Kitchell JF. 1999. Trophic cascades revealed in diverse ecosystems. *Trends Ecol. Evol.* 14:483–88
- Paine RT. 1980. Food webs: linkage, interaction strength and community infrastructure. The third Tansley Lecture. *J. Anim. Ecol.* 49:667–85
- Pauly D, Christensen V, Dalsgaard J, Froese R, Torres F. 1998. Fishing down marine food webs. *Science* 279:860–63
- Pauly D, Palomares ML. 2005. Fishing down marine food web: It is far more pervasive than we thought. *Bull. Mar. Sci.* 76:197–211
- Peckham SH, Diaz DM, Walli A, Ruiz G, Crowder LB, Nichols WJ. 2007. Small-scale fisheries bycatch jeopardizes endangered Pacific loggerhead turtles. *PLoS One* 2:e1041
- Pew Oceans Comm. 2003. *America's Living Oceans: Charting a Course for Sea Change. A Report to the Nation*. Arlington, VA: Pew Oceans Comm.
- Pikitch EEK, Santora CC, Babcock EEA, Bakun AA, Bonfil RR, et al. 2004. Ecosystem-based fishery management. *Science* 305:346–47
- Power ME, Tillman D, Estes JA, Menge BA, Bond WJ, et al. 1996. Challenges in the quest for keystones. *BioScience* 8:609–20
- Read AJ, Drinker P, Northridge S. 2006. Bycatch of marine mammals in US and global fisheries. *Conserv. Biol.* 20:163–69
- Richards RA, Rago PJ. 1999. A case history of effective fishery management: Chesapeake Bay striped bass. *North Am. J. Fish. Manag.* 19:356–75
- Rose GA. 2004. Reconciling overfishing and climate change with stock dynamics of Atlantic cod (*Gadus morhua*) over 500 years. *Can. J. Fish. Aquat. Sci.* 61:1553–57
- Rose KA, Cowan JH. 2003. Data, models, and decisions in U.S. marine fisheries management: lessons for ecologists. *Annu. Rev. Ecol. Evol. Syst.* 34:127–51

- Shackleroff JS, Hazen EL, Crowder LB. 2008. Status and drivers of change in coupled social-ecological marine systems. In *Managing for Resilience: New Directions in Marine Ecosystem-Based Management*, ed. KL McLeod, H Leslie. In press. Washington, DC: Island
- Sibert J, Hampton J, Kleiber P, Maunder M. 2006. Biomass, size, and trophic status of top predators in the Pacific Ocean. *Science* 314:1773–78
- Sonnenholzner JI, Ladah LB, Lafferty KD. 2007. Cascading effects of fishing on Galapagos rocky reef communities. *Mar. Ecol. Prog. Ser.* 343:77–85
- Soto KH, Trites AW, Arias-Schreiber M. 2004. The effects of prey availability on pup mortality and the timing of birth of South American sea lions (*Otaria flavescens*) in Peru. *J. Zool.* 264:419–28
- Steneck RS, Vavrinc J, Leland AV. 2004. Accelerating trophic-level dysfunction in kelp forest ecosystems of the western North Atlantic. *Ecosystems* 7:323–32
- Stergiou KI, Moutopoulos DK, Hernando JAC, Hernando JA, Erzini K. 2007. Trophic signatures of small-scale fishing gears: implications for conservation and management. *Mar. Ecol. Prog. Ser.* 333:117–28
- Stobutzki IC, Miller MJ, Heales DS, Brewer DT. 2002. Sustainability of elasmobranchs caught as bycatch in a tropical prawn (shrimp) trawl fishery. *Fish. Bull.* 100:800–21
- Tasker ML, Camphuysen CJ, Cooper J, Garthe S, Montevecchi WA, Blaber SJM. 2000. The impacts of fishing on marine birds. *ICES J. Mar. Sci.* 57:531–47
- Thrush SF, Dayton P. 2002. Disturbance to marine benthic habitats by trawling and dredging: implications for marine biodiversity. *Annu. Rev. Ecol. Syst.* 33:449–500
- Trites AW, Miller AJ, Maschner HDG, Alexander MA, Bograd SJ, et al. 2007. Bottom-up forcing and the decline of Steller sea lions (*Enmetopias jubatas*) in Alaska: assessing the ocean climate hypothesis. *Fish. Oceanogr.* 16:46–67
- Tsehaye I, Machiels MAM, Nagelkerke LAJ. 2007. Rapid shifts in catch composition in the artisanal Red Sea reef fisheries of Eritrea. *Fish. Res.* 86:58–68
- Turner SJ, Thrush SF, Hewitt JE, Cummings VJ, Funnell G. 1999. Fishing impacts and the degradation or loss of habitat structure. *Fish. Manag. Ecol.* 6:401–20
- Tzanos E, Dimitriou E, Papaharisis L, Roussi A, Somarakis S, Koutsikopoulos C. 2006. Principal socio-economic characteristics of the Greek small-scale coastal fishermen. *Ocean Coast. Manag.* 49:511–27
- Uozumi Y. 2003. Historical perspective of global billfish stock assessment. *Mar. Freshw. Res.* 54:555–65
- U.S. Comm. Ocean Policy. 2004. *Preliminary Report of the U.S. Commission on Ocean Policy, Governor's Draft*. Washington, DC: U.S. Comm. Ocean Policy
- Walters C, Christensen V, Pauly D. 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. *Rev. Fish Biol. Fish.* 7:139–72
- Walters CJ. 2003. Folly and fantasy in the analysis of spatial catch rate data. *Can. J. Fish. Aquat. Sci.* 60:1433–36
- Walters CJ, Christensen V. 2007. Adding realism to foraging arena predictions of trophic flow rates in Ecosim ecosystem models: shared foraging arenas and bout feeding. *Ecol. Model.* 209:342–50
- Walters CJ, Christensen V, Martell SJ, Kitchell JF. 2005. Possible ecosystem impacts of applying MSY policies from single-species assessment. *ICES J. Mar. Sci.* 62:558–68
- Watling L, Norse E. 1998. Disturbance of the seabed by mobile fishing gear: a comparison to forest clearcutting. *Conserv. Biol.* 12:1180–97
- Worm B, Barbier EB, Beaumont N, Duffy JE, Folke C, et al. 2006. Impacts of biodiversity loss on ocean ecosystem services. *Science* 314:787–90
- Young OR, Osherenko G, Ogden J, Crowder LB, Ogden J, et al. 2007. Solving the crisis in ocean governance: place-based management of marine ecosystems. *Environment* 49:20–32