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Research Priorities for the Next Decade

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HUMAN ALTERATION
OF FOOD WEBS

Research Priorities for Conservation and Management

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MOST NATURAL FOOD WEBS HAVE BEEN ALTERED PROFOUNDLY
through human activities (Botsford et al. 1997; Vitousek et al. 1997; Terborgh
et al. 1999). Human perturbations of food-web interactions result from over-
exploitation of species, particularly top predators; introduction of exotics;
habitat destruction and fragmentation; and changes in resource availability
through alteration of biogeochemical cycles, enhanced loadings of nutrients
and organics, and "subsidies" of natural food webs through waste disposal or
discarded fishery bycatch (see chapters 4, 5, 7, 9). Alterations of resource avail-
ability represent bottom-up perturbations of food-web dynamics, whereas
removal or addition of consumers through hunting, fishing, species introduc-
tions, and habitat alteration represents a top-down perturbation. Top-down
and bottom-up perturbations of natural food webs modify consumer-
resource interactions, with subsequent impacts on population abundances,
community structure and diversity, and ecosystem processes.

Biological conservation and management in the face of human impacts on
whole ecosystems require an understanding of how consumer-resource
interactions control populations and shape communities and a shift from
focusing on single species to taking into account the complexity of ecological
systems and interactions among their components (Lubchenco et al. 1991;

Christensen et al. 1996). This new tendency is exemplified by an increasing recognition among fishery managers that multispecies effects must be considered (NRC 1994; FAO 1997). Traditional, single-species fishery management has often failed to maintain populations of exploited species at sustainable levels (Ludwig et al. 1993). Classic examples include the collapse of the North Sea herring and mackerel stocks (Hempel 1978) and the northern cod (Walters and Maguire 1996). Part of the variability of commercial fish stocks, and the consequent uncertainty about their predicted trajectories, is caused by interactions with other species, which may, in turn, be impacted by harvesting conducted at multiple trophic levels (May et al. 1979; Yodzis 1994; Pauly et al. 1998). The present emphasis on marine reserves as tools for marine conservation and fisheries management exemplifies a shift in focus from an emphasis on single species to more holistic approaches to conservation and management (Roberts and Polunin 1993; Bonsauk 1996; Russ and Alcala 1996; Allison et al. 1998). These new approaches take into account the uncertainty of predictions about the combined effects of environmental variability and human impacts on species assemblages (Clark 1996; Lauck et al. 1998).

Decades of experimental studies have shown dramatic effects of consumer-resource interactions on populations and communities. Bottom-up effects of resources on consumers and top-down effects of consumers on other species in the community include a suite of direct and indirect pathways of interaction. Resource or prey availability controls the rates of population growth of their consumers, whereas predators exert direct effects on their prey abundance, size structure, and spatial distribution (Zaret 1980; Sih et al. 1985). Although even simple predator-prey systems can generate complex dynamics (McCauley et al. 1988), the uncertainty of predictions about resource and predation effects is further increased by responses mediated through other species in the community. Theoretical and empirical studies have shown that predators can influence community structure and diversity through indirect effects (Schoener 1993; Wootton 1993; Menge 1995; Abrams et al. 1996). In theory, there can be an almost unlimited number of different types of indirect effects and resulting dynamics (Hastings and Powell 1991; Abrams 1992), but experimental manipulations have revealed a more limited range of possibilities (Schoener 1993; Menge 1995; Abrams et al. 1996).

Knowledge of the role of consumer-resource interactions in regulating species dynamics and shaping natural communities has important conservation and management implications. Applications include:

- predicting the impacts of enhanced resource availability, predator removal, and species introduction on community structure;
- guiding predator manipulations aimed at decreasing mortality of an endangered or harvested species;

- controlling the abundance of pests and exotics;
- conserving or reintroducing top predators and keystone species with the aim of maintaining diversity or restoring the structure of altered communities through cascading effects;
- controlling the consequences of anthropogenic eutrophication of aquatic ecosystems through manipulation of the food-web structure (biomanipulation); and
- designing reserve networks to conserve whole assemblages and the interactions among their component species.

However, indirect effects and diffuse interactions among multiple species can cause unanticipated changes in community structure and nontarget effects of management interventions. Unraveling the tremendous complexity of the dynamics of multispecies communities is one of the main challenges confronting ecologists, conservation biologists, and environmental managers.

In this chapter, we identify the contributions of ecological studies of food-web interactions to conservation and management, and we highlight promising new research directions. First, we present the ecological theory of consumer-resource interactions and its applications to conservation and management. Second, we review the empirical evidence about the role of top-down and bottom-up forces in influencing the structure and dynamics of ecological communities. Third, we describe the importance of synthesizing experimental and monitoring data to develop generalizations that are more widely applicable, and we provide one example of such synthesis. Then we discuss whether and how to apply what we know about food-web interactions to real-world resource management. Finally, we propose some research priorities for the conservation and management of assemblages of interacting species.

Theory of Consumer-Resource Interactions

Ecological theory has produced a plethora of consumer-resource (i.e., predator-prey) models. One way of classifying these numerous contributions is on the basis of the number of species, or species groups, included in the models. Basic consumer-resource models, such as Lotka-Volterra's, focus on the dynamics of a two-species, enemy-victim system. The predator-prey interaction causes species abundances to cycle, with amplitudes determined by initial population abundances. A suite of biological mechanisms induces stability, including density-dependent (logistic) prey growth, density-dependent predator death rates or predator attack rates (interference among predators), physical refuges for the prey, the presence of an invulnerable life stage for the prey, and external sources of prey or predator recruits (open-system dynamics) (Gurney and Nisbet 1998). In contrast, enrichment is expected to destabilize predator-prey systems (the "paradox of enrichment," Rosenzweig 1971), although there is lit-

tle empirical evidence that real populations show the predicted instability in nutrient-rich environments (see Murdoch et al. 1998). Enemy-victim models such as Lotka-Volterra's and Nicholson-Bailey's, and later modifications of the original equations, have most commonly been applied to terrestrial systems, particularly in biological pest control (Hassell 1978; Murdoch et al. 1985; Waage and Mills 1992; Murdoch and Briggs 1996).

Predator-prey models of the Lotka-Volterra type typically isolate subsets of interacting species from a complex, multispecies ecosystem. Other species in the community are considered part of the environment and are not modeled explicitly. Thus, it is assumed that the dynamics of the target species are determined primarily by strong interactions with its prey or predator, and that links with other species in the community are weaker and less important in determining the system dynamics. However, Lotka-Volterra–type models have also been used to investigate the dynamics of multispecies assemblages. Species that use common resources in similar ways are grouped into trophic levels, which are assumed to act dynamically as populations. This approach was initiated by Hairston, Smith, and Slobodkin (1960) and further developed by Fretwell (1977) and Oksanen et al. (1981).

In Hairston et al.'s classic 1960 paper, food chains are composed of three trophic levels: plants, herbivores, and carnivores. Carnivores control herbivore populations, thereby releasing plants from top-down control and allowing accumulation of "green" biomass. Fretwell (1977) and Oksanen et al. (1981) expanded this approach to examine food-chain length and interactions along productivity gradients. Increasing productivity supports increasing numbers of trophic levels, which subsequently exert a top-down control on their prey and initiate cascading trophic interactions propagating down the food chain. At equilibrium, top-down control produces a stepped pattern of biomass increase along a productivity gradient, where top trophic levels and those even numbers of steps below are resource limited, whereas trophic levels odd numbers of steps below the top are limited by their consumers. Although linear food-chain models were originally developed with terrestrial systems in mind (Hairston et al. 1960; Fretwell 1977; Oksanen et al. 1981), they have been applied most commonly to aquatic systems (Persson et al. 1988, 1992; Crowder et al. 1988; Power 1990; Wootton and Power 1993; Brett and Goldman 1996, 1997).

Similar to linear food-chain models, trophic cascade models (Paine 1980) propose that predator-prey interactions are transmitted through food webs to cause variance in plant biomass and production (Carpenter et al. 1985). Trophic cascades are predation effects across multiple trophic levels resulting in inverse patterns of abundance or biomass across trophic levels of a food web. The trophic cascade hypothesis has been used to explain the ~50 percent

of observed variability in primary production of lakes that could not be attributed to variation in nutrient loading (Carpenter et al. 1985). Trophic cascades are also the basis for management manipulations of lake food webs referred to as biomanipulations (Shapiro et al. 1975; Gulati et al. 1990). Biomanipulation typically involves enhancement of piscivorous fish stocks or removal of planktivorous fish with the goal of decreasing predator control on large herbivorous zooplankton and increasing grazing of the phytoplankton. Thus, successful biomanipulation results in the biological control of one of the consequences of anthropogenic eutrophication, namely increased primary production (Carpenter and Kitchell 1992; Kitchell 1992).

Biological complexities that characterize many food webs can dampen trophic cascades and lead to weak or no top-down control. These include: (1) inedible prey or invulnerable life stages of prey (Murdoch 1966; Ehrlich and Birch 1967; McCauley et al. 1988; Leibold 1989; McQueen 1990; Strong 1992; Abrams 1993; Leibold et al. 1997); (2) complex interactions such as cannibalism, ontogenetic diet shifts, feeding on more than one trophic level (omnivory), and feeding on competitors (intraguild predation) (Mittelbach et al. 1988; Arditi and Ginzburg 1989; Strong 1992; Polis and Strong 1996; Holt and Polis 1997; McCann, Hastings, and Huxel 1998; McCann, Hastings, and Strong 1998); and (3) the fact that most food webs are not closed systems but systems that exchange resources and individuals with adjacent systems through nutrient and detritus input or loss, recruitment processes, and organism migration (Polis and Strong 1996; Polis et al. 1997; Huxel and McCann 1998). Inclusion of the above biological complexities in food-web models generates a range of possible community responses to variation in resource or consumer levels (table 3.1).

Basic consumer-resource and food-chain models focus on the dynamics of subsets of real food webs (figure 3.1). These systems are embedded in a more complex web of interactions (figure 3.2), which may affect the dynamics of the focal consumer-resource system (Polis and Strong 1996; Polis et al. 1997; Yodzis 1998, 2000). Attempts to model all trophic interactions within a community result in an overwhelming amount of possible interaction pathways. Can we safely ignore some of these pathways? Yodzis (1998) has tackled this question using the pelagic marine food web of the Benguela ecosystem, off South Africa (figure 3.2). Inclusion of all documented trophic interactions among the twenty-nine species of the food web yielded 203 direct links and millions of possible indirect pathways of interaction. He quantified the ecosystem response to the removal of one of the top carnivores in the system, South African fur seals, by examining predicted changes in the yield of the main commercial fisheries. This analysis shows that 44 percent of the 203 links can be eliminated from the model without altering the response of fish-

TABLE 3.1. Some Models of Top-Down and Bottom-Up Community Regulation

- *Hairston, Smith, and Slobodkin 1960:* Carnivores control herbivore populations, thereby releasing plants from top-down control and allowing accumulation of "green" biomass.
- *Murdoch 1966; McCauley et al. 1988; Leibold 1989; Strong 1992:* Prey defenses (e.g., inedible prey) dampen top-down effects.
- *Fretwell 1977; Oksanen et al. 1981:* Stepped pattern of biomass accrual along productivity gradients. Top trophic levels and those even numbers of steps below them are resource limited; trophic levels odd numbers of steps below the top one are predator limited.
- *Getz 1984; Arditi and Ginzburg 1989:* Interference among predators prevents their efficient exploitation of resources and leads to no top-down control. Biomass increases with increasing resource levels at all trophic levels. [AUTHOR: Please add Getz 1984 to Literature Cited]
- *Mittelbach et al. 1988:* Ontogenetic diet shifts. Predators cannot track resources because resource increases influence only one life stage, leading to weak top-down effects.
- *McQueen 1990:* Bottom-up control is stronger at base of food web; top-down control is stronger at higher trophic levels. Trophic cascades attenuate before reaching plants.
- *Polis and Strong 1996:* Complex interactions among components of food webs dampen top-down control. Multichannel omnivory can promote top-down regulation when top consumers are subsidized by external resources. Thus, omnivory can both dampen and enhance top-down effects.
- *Leibold et al. 1997:* Species replacement through time (predation selects for defended prey). Weak top-down effects in the long-term.
- *McCann, Hastings, and Strong 1998:* Intratrophic interference affecting consumer population growth rates dampen top-down effects. Increased productivity results in increased plant biomass, whereas consumer biomass shows a modest increase.
- *Huxel and McCann 1998:* Allochtonous resource input weakens top-down control.

Source: Modified from M. E. Power, "Top-Down and Bottom-Up Forces in Food Webs: Do Plants Have Primacy?" *Ecology* 73 (1992): 733–746.

ery yields to seal culling, suggesting that some simplification of the system is possible. Even such simplification leaves 112 direct consumer-resource links potentially influencing the system response to perturbation, still a tremendously complex system. Further modeling and empirical work should determine how much detail is needed to describe the dynamics of whole communities and under what circumstances complex systems yield predictable responses to perturbation (e.g., Terborgh et al. 1999).

Empirical Evidence: How Top-Down and Bottom-Up Forces Influence Ecological Communities

Experiments consisting of altering resource levels and adding or removing consumers have shown that consumer-resource interactions can play a critical role in regulating populations and shaping communities and have eluci-
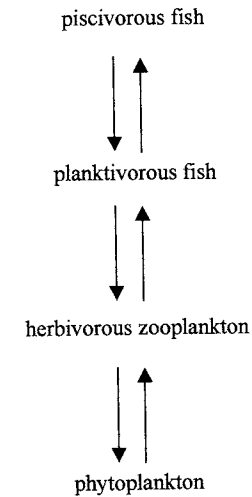
FIGURE 3.1. A simplified food chain comprising four trophic levels: piscivorous fish (e.g., tuna), planktivorous fish (e.g., anchovy), herbivorous zooplankton (e.g., copepod crustaceans), and phytoplankton.

dated direct and indirect mechanisms underlying predation effects (e.g., Sih et al. 1985; Schoener 1993; Wootton 1993; Menge 1995). Unfortunately, controlled manipulative experiments often cannot be conducted over the spatial and temporal scales relevant to biological conservation and management. Despite the difficulty of interpreting observed patterns in the lack of replication and controlled reference conditions, "natural" experiments provide an opportunity to examine the consequences of food-web alterations at large scales (e.g., Terborgh et al. 1999). The alteration of resource availability through nutrient enrichment or food-web subsidies, the widespread decline or loss of top consumers caused by fishing and hunting, and the introduction of predators to new areas are large-scale manipulations of food-web structure and consumer-resource interactions.

Human activities result in the production of nutrients and organic matter that can fuel natural food webs and alter abundances and interactions of species or whole trophic levels. In particular, industrial and agricultural activities add to terrestrial systems at least as much fixed nitrogen as all natural sources combined (Vitousek et al. 1997). Nitrogenous compounds from industrial activities, agriculture, and sewage, reach rivers, lakes, and oceans through groundwater and atmospheric discharge. Enhanced nitrogen input generally results in increased primary productivity, decreased biological diversity, and changes in plant community composition in both terrestrial and aquatic ecosystems (Schindler 1974; Tilman 1987; Nixon 1995; Jeffries
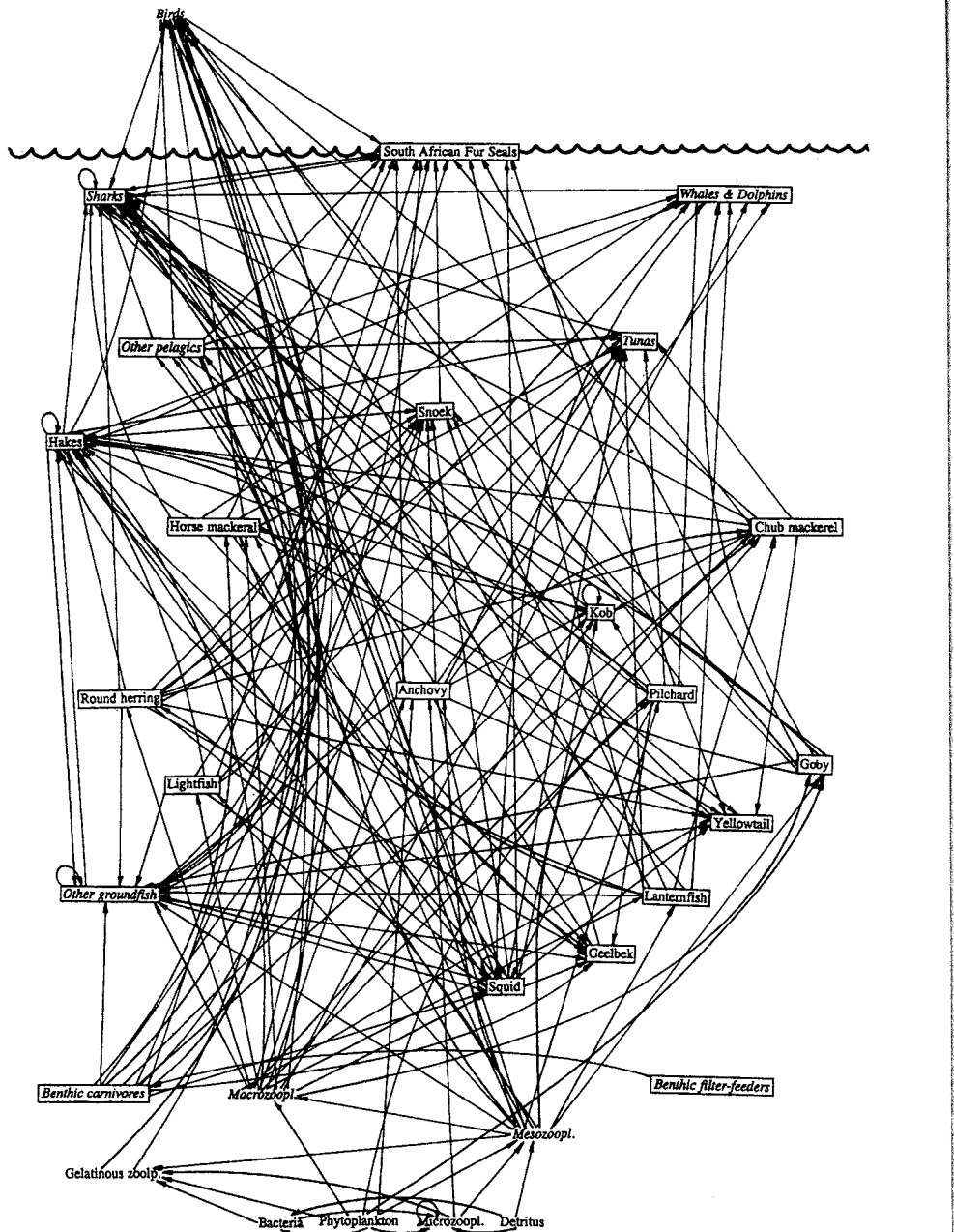
FIGURE 3.2.   The Benguela ecosystem food web (from Yodzis 1998, reproduced with author's permission). The species and species groups are embedded in a complex web of trophic and nontrophic interactions.

and Maron 1997). Such increased primary productivity can support greater abundance and biomass of higher trophic levels (Oksanen et al. 1981; McNaughton et al. 1989). However, anthropogenic nutrient enrichment frequently disrupts food-web interactions, causing ungrazed primary production to accumulate in the focal system or in adjacent ecosystems. The consequences of anthropogenic eutrophication, such as algal and microbial blooms (including toxic species), hypoxic/anoxic conditions of the water column, and mass mortality of fish and invertebrates, are particularly widespread and worrisome in coastal marine ecosystems (Hallegraeff 1993; Turner and Rabalais 1994; Nixon 1995; chapter 7).

A range of human activities produces waste that can subsidize natural food webs. For example, trash dumps and the bycatch discarded by commercial fisheries can provide important resources for scavengers and opportunistic predators, including fish, crabs, seabirds, and raptors (Dayton et al. 1995; Garthe et al. 1996; Blanco 1997), which may in turn control populations of competitors or prey and influence community structure. We still know very little about the impacts of different types of resource subsidies on natural ecosystems, how such impacts vary across spatial scales (from the local effects of waste dumping to the global effects of the alteration of the nitrogen and carbon cycles), and how the enhanced productivity supported by the added resources alters food-web dynamics.

The decline and collapse of top carnivores provide ample evidence that predation can structure aquatic and terrestrial communities (Crowder et al. 1996; Terborgh et al. 1999). One of the best-documented case studies is the sea otter–sea urchin–kelp trophic cascade occurring in North American coastal marine habitats (Estes and Palmisano 1974; Estes et al. 1998). Hunting reduced sea otters to a number of widely scattered remnant populations along the northwestern coast of the United States. The absence of sea otters often is associated with an abundance of sea urchins, which overgraze large benthic algae, including kelps (Estes and Palmisano 1974). In recent years, increased predation by killer whales on sea otters, possibly caused by a decline in the pelagic prey of killer whales, may have led to sea otter decline and increased sea urchin abundance and overgrazing of kelp (Estes et al. 1998). In lakes, experimental or fisheries removal of piscivorous fish can cause trophic cascades, leading to increased abundance of planktivorous fish, alterations of the size structure and species composition of the zooplankton, and increased phytoplankton biomass (Carpenter et al. 1985; Kitchell 1992; Carpenter and Kitchell 1993).

McLaren and Peterson (1994) documented a compelling example of a terrestrial trophic cascade on Isle Royale, Michigan, USA. Wolves control moose populations, which in turn influence tree growth rates. When wolves were

rare, moose abundances increased and the growth rates of balsam fir were depressed. Hunting, combined with habitat destruction and fragmentation, has drastically reduced the abundance and geographical range of many top carnivores, including wolves, bears, coyotes, cougars, lions, and tigers. In North America, reduction or elimination of top predators has resulted in the "mesopredator release" of other small or midsized predators, such as foxes, skunks, raccoons, and feral and domestic cats (Soulé et al. 1988), thereby altering food-web dynamics and community structure. For example, the decline and disappearance of coyotes in landscapes fragmented by development affects the distribution and abundance of smaller carnivores and the persistence of their avian prey (Crooks and Soulé 1999). In suburban areas and parklands of North America, where hunting eliminated top carnivores in the past but is now prohibited, mammals that were part of the top carnivore prey pool, like deer, have increased in numbers, in some cases becoming road hazards and overbrowsing the vegetation (McShea et al. 1997).

In pelagic marine ecosystems, there are many examples of declines of top predators accompanied by species replacement at the same trophic level or in changes of the prey community at the next trophic level. Hunting of blue whales around Antarctica was followed by increased abundance of other species feeding on krill, including minke whales, crab-eater seals, and penguins (Laws 1984; Brownell et al. 1989). On Georges Bank, off the New England coast, small elasmobranchs (mainly dogfish sharks and skates) have increased in abundance following the collapse of the stocks of large gadid fishes such as haddock and cod. This switch in species dominance is likely due to increased prey availability for the elasmobranchs caused by the decline of the piscivorous gadid and flounder species (Fogarty and Murawski 1998). Extensive removal of large sharks off South Africa led to increased abundances of small sharks, on which the large sharks preyed, and to reductions of commercial fish yields (van der Elst 1979). In the North Sea, decline in the herring and mackerel stocks resulted in increased catch of their prey, mostly smaller fish including sand lance, sprat, and Norway pout (Hempel 1978). In contrast, the decline or depletion of some marine apex predators, including great auks, Steller's sea cows, and gray whales, appears to have caused only subtle changes in populations of their prey and competitors (Boersma and Moore in press). In these case studies, it is not known how other food-web components—for example, plankton or benthos—responded to predator decline.

Marine reserves—portions of the coastline protected from fishing and other human disturbance—constitute large-scale human-exclusion experiments. As such, they present an invaluable opportunity to determine the impacts of food-web alterations on marine communities. In the Las Cruces marine reserve, cen-

tral Chile, the predatory gastropod *Concholepas concholepas* ("loco") increased in abundance within the reserve compared to adjacent areas where it was harvested. Increased predation by *Concholepas* on its prey, particularly mussels, led to the almost complete elimination of mussel beds, which were replaced by barnacles and algae (Castilla 1999). Increased abundance of predatory fishes within no-take marine reserves in Spain and East Africa has been linked to increased predation on sea urchins, decreased urchin abundance, changes in population size structure, and a proliferation of fleshy algae (Sala and Zabala 1996; McClanahan et al. 1999).

Introductions of exotic predators provide further evidence of the potential for top-down and bottom-up effects to influence communities and ecosystems. Intentional introductions of fishery species to lakes have had devastating consequences for native communities. The introduction of the peacock bass to Gatun Lake, Panama, led to the loss of several native species of fish and to a simplification of the food web (Zaret and Paine 1973). Similarly, the introduction of the Nile perch to Lake Victoria, East Africa, has profoundly altered the native fish community and caused the loss of many endemic species of cyclid fishes (Barel et al. 1985; Kitchell et al. 1997). The accidental introduction of the ctenophore *Mnemiopsis leidyi,* a consumer of zooplankton and juvenile fish, to the Black Sea has caused further decline and loss of several species of crustacean zooplankton and planktivorous fish in a system already heavily impacted by increased nutrient loading, chemical pollution, and fisheries exploitation (Zaitsev 1992).

The introduction of exotic predators to predator-free islands provides evidence for top-down regulation of some terrestrial communities. For example, the accidental introduction of the brown tree snake to Guam led to the extinction of several species of native birds (Savidge 1987). Similarly, the introductions of foxes to the Alaskan Islands and mangoose to tropical Pacific islands have contributed to the collapse of native fauna (King 1984; Bailey 1993). Exotics may also influence ecosystem processes, altering resource availability for other species and the structure and dynamics of the whole ecosystem. One compelling example is the invasion of the nitrogen-fixing tree *Myrica faya* in Hawaii. The establishment of *Myrica faya* in newly formed volcanic habitats can lead to a rapid increase of the biologically available nitrogen in nutrient-poor volcanic soils, causing dramatic changes of the plant and soil communities and favoring subsequent invasions by non-native organisms (Vitousek and Walker 1989).

Synthesis of Experimental and Monitoring Data

Experimental predator or resource manipulations and large-scale "natural" experiments associated with the decline or introduction of predators, nutrient

enrichment, and food-web subsidies provide crucial information about the types of community changes caused by food-web alterations and point to urgent research priorities for conservation and management.

Fundamental questions concern how commonly different community responses occur and what conditions are more likely to lead to a particular type of community response. Are all systems unique? Can the changes observed in one system be expected in other systems? Syntheses of experimental and monitoring data can produce generalizations about community responses to food-web alterations and yield predictions about the most likely outcomes of future perturbations and management interventions. Unfortunately, the plethora of empirical data documenting food-web effects in experimental and natural systems have rarely been synthesized to test whether general responses exist. For an example of such quantitative synthesis, we focus on generalizations about trophic cascades as one mechanism leading to community changes following the addition or removal of consumers in aquatic ecosystems.

Trophic cascades (predation effects across multiple trophic levels resulting in inverse patterns of abundance or biomass across a food web) have received much attention for their potential to spread alterations in consumer levels across an entire food web. Thus, loss or introduction of predators may impact the whole community through cascading trophic interactions. In addition, trophic cascades have management applications as a means of controlling the productivity and biomass of the phytoplankton in waters subject to anthropogenic nutrient loading (Shapiro et al. 1975; Gulati et al. 1990; Kitchell 1992).

Trophic cascades have been documented in a variety of terrestrial and aquatic ecosystems, including temperate and tropical reefs, rocky intertidal communities, streams, lakes, and terrestrial insect communities in the tropics (Power 1990; Wootton 1995; Spiller and Schoener 1994; Hixon 1997; Letourneau and Dyer 1998; Pace et al. 1999; Pinnegar et al. 2000; and references in the preceding "Empirical Evidence" section). Most documented cascades occur among a few of the species in the community, particularly in terrestrial systems (Polis 1999; Persson 1999). However, trophic cascades influencing the structure and dynamics of whole communities occur in aquatic ecosystems (e.g., Estes and Palmisano 1974; Power 1990; Carpenter and Kitchell 1993; Shiomoto et al. 1997; Estes et al. 1998). Thus, food-web alterations can initiate cascading trophic interactions influencing the structure of aquatic communities. How commonly do trophic cascades occur, and in what conditions are they more likely to occur?

Syntheses conducted in lakes, marine pelagic ecosystems, and rocky intertidal communities indicate that trophic cascades are uncommon in those systems. In a meta-analysis of predator (fish) manipulations conducted in lakes, Brett and Goldman (1997) found that fish exerted a strong control on their

prey, the zooplankton, but phytoplankton biomass exhibited weak responses to fish manipulation. In a more extensive analysis, phytoplankton responded strongly to fish manipulation in approximately one-third of fifty-four enclosure or pond experiments and showed weak responses in the others (Brett and Goldman 1996).

Meta-analyses of data from manipulations of nutrients and consumers conducted in marine mesocosms and long-term monitoring of nutrients, phytoplankton, zooplankton, and zooplanktivorous fish abundance in open pelagic ecosystems indicated that trophic cascades are uncommon in marine pelagic food webs (Micheli 1999). In particular, of the twenty open marine systems included in this analysis, only one exhibited an inverse pattern in biomass across three trophic levels. A ten-year time series of phytoplankton, zooplankton, and a planktivorous predator, the pink salmon *Oncorhynchus gorbuscha,* from the subarctic Pacific Ocean showed that interannual variation in salmon abundance was inversely related to zooplankton biomass and positively related to phytoplankton biomass (Shiomoto et al. 1997).

In general, year-to-year fluctuations in zooplankton biomass were negatively correlated with fish, indicating that fish predation may control zooplankton biomass. In contrast, the zooplankton and the phytoplankton were not significantly correlated, indicating that fish predation does not commonly control the biomass of primary producers in these pelagic ecosystems (Micheli 1999). An important implication is that biomanipulations are unlikely to control phytoplankton production and biomass in the coastal marine environment. Reductions of anthropogenic nutrient loading to coastal waters may be the only means of controlling marine eutrophication.

Whole-lake experiments suggest that trophic cascades may be enhanced under nutrient-rich conditions (Pace et al. 1999). This result has important implications because most aquatic systems are subjected to simultaneous food-web alterations, through fishing and introduction of exotic species, and to increased nutrient loading from agricultural activities and coastal development. Food-web manipulations conducted in marine mesocosms suggest that nutrient enrichment may favor trophic cascades also in marine food webs. Overall, there was a statistically significant increase in phytoplankton biomass following the addition of planktivorous fishes in mesocosms enriched with nitrogen but not in mesocosms with no nutrients added (Micheli 1999). However, patterns from open marine systems do not support this hypothesis: the only system where trophic cascades occurred had the lowest productivity among the twenty systems in the data set (Micheli, unpublished data).

In a survey of direct and indirect effects in experimental manipulations of twenty-three marine rocky intertidal food webs, Menge (1995) found that indirect effects accounted for a large proportion of the community changes caused by manipulations (24 to 61 percent, mean ≈ 40 percent). Nearly half of all indirect effects (total = 565) resulted from manipulations of predators. In

these food webs, 6.5 percent of all indirect effects were trophic cascades. The most frequent types of indirect effects were keystone predation (when a predator's consumption of a prey increases the abundance of the prey competitors: 35 percent of all indirect effects) and apparent competition (when species share a common predator and increased abundance of one species enhances predation on the other species: 25 percent).

In conclusion, trophic cascades can have important effects on community structure and species dynamics (see the "Empirical Evidence" section) but appear to be more common in some ecosystem types—such as shallow marine benthic communities, small lakes, and vertebrate terrestrial systems—and in the presence of intense anthropogenic disturbance (Carpenter et al. 1985; Terborgh et al. 1999; Pinnegar et al. 2000). Our present perception may reflect biases in the focus and time frames of the studies conducted to date. For example, shallow benthic marine communities are more accessible and amenable to experimental manipulations than offshore pelagic ecosystems (Pinnegar et al. 2000). In addition, large terrestrial and aquatic predators have been decimated through hunting, fishing, and habitat destruction long before the start of the monitoring programs and ecological studies with which we are attempting to detect the community consequences of predator removal (e.g., Jackson 1997). Determining what conditions lead to trophic cascades, how commonly they occur in different types of ecosystems, and the temporal and spatial scales at which food-web perturbations alter community structure and interactions is an important research priority.

Conclusions

There is ample experimental and correlative evidence that consumer-resource interactions play an important role in regulating population dynamics, community structure, and diversity. Potential applications include:

- predicting the impacts of food-web alterations on population and community dynamics;
- conserving top predators and keystone species, preventing competitive displacement of species, and maintaining diversity;
- manipulating consumers and resources to restore community structure and ecosystem processes;
- conserving species or species groups that effectively control pests and exotic invaders;
- designing reserve networks to conserve whole assemblages and the interactions among their component species; and
- controlling anthropogenic eutrophication of aquatic ecosystems through biomanipulation of food webs.

Do we know enough about bottom-up and top-down regulation of natural communities to predict change and implement these conservation and management strategies successfully?

Theory and data indicate that there is considerable indeterminacy about the type, magnitude, and direction of community changes following food-web alterations. Perturbations caused by the addition or removal of a resource or of a consumer species can cause both direct and indirect effects and result in a large suite of possible outcomes (Bender et al. 1984; Yodzis 1988; Abrams 1993; Wootton 1993). Because of the inherent variability of ecological processes and the fragmentary data available, we will never be able to fully explain and predict species dynamics and community change. Management of species and ecosystems in the face of uncertainty requires implementation of the precautionary principle (FAO 1995; Lauck et al. 1998) and of adaptive management (Walters 1986; Parma et al. 1998). Uncertainty about the consequences of food-web alterations in complex, multispecies communities is an additional reason to use precautionary and adaptive approaches in conservation and management. Nevertheless, a better understanding of processes structuring communities, including food-web interactions, could only help reduce some of the uncertainty.

Perhaps the main challenge in applying food-web research to conservation is how to deal with the multitude of possible direct and indirect pathways of interactions among species. One approach is to focus on subsets of species linked through strong interactions and weakly linked to other species in the system (community "modules," Holt 1996). Simplifying complex communities to smaller subsets of strong interactors that largely drive community dynamics allows a mechanistic understanding of consumer-resource interactions and has a strong theoretical basis in a plethora of predator-prey models. However, we still know very little about the relative frequencies of strong and weak interactions in natural communities (Power et al. 1996). Direct quantification of interaction strength in two marine and one terrestrial community indicated that most interactions were weak, with a few strong interactions (Paine 1992; Power et al. 1996), but broader comparisons are needed before any generalization is possible.

The presence of strong interactors within communities, such as keystone predators, has potentially broad applicability in conservation because it allows focusing monitoring and management on key species that regulate the structure and diversity of the whole community. To date, there are no general guidelines about the traits that characterize keystones or the types of communities where they are more likely to occur (Mills et al. 1993; Power et al. 1996). Identifying the species that are strong interactors in different communities, as well as the context where species are most likely to be strong interactors, is an

important research priority for the coming decade. However, ample evidence suggests that the top predators targeted by hunting and fishing tend to exert strong top-down effects and that immediate action should be taken to protect top predators and prevent further disruption of natural food webs.

Attempts to model, manipulate, or measure all possible interactions in a food web quickly exceed data availability and our ability to relate community patterns to the processes that underlie them. Aggregation of species into trophic levels is one means of simplifying complex communities while including multiple species, but it can overlook important biological complexities. For example, intratrophic interference, nontrophic interactions, and long-term species replacement result in community patterns that are not predicted by linear food-chain models (table 3.1). Models of intermediate complexity and determination of what key processes should be included for different ecosystems seem the most promising research directions for producing theory and guidelines for conservation and management. The added realism renders models less general but more applicable to particular systems (Murdoch and Briggs 1996).

The community-wide consequences of fishery collapses, loss of top carnivores from terrestrial systems, introduction of exotic species, and anthropogenic nutrient enrichment of ecosystems indicate that the removal or addition of consumers and resources generally influences prey at the next lower trophic level and the species that directly use the resource. Frequently, species replacement occurs within a trophic level. In some cases, effects can also influence the whole community through trophic and nontrophic interactions cascading through the food web. Establishing the generality of these trends and identifying the key processes underlying community responses to food-web perturbations are urgent research priorities.

Research Priorities

The following priorities and their components are outlined in box 3.1.

Produce Generalizations about Species and Community Responses to Food-Web Alteration

Theory and experiments have shown that food-web alterations influence communities through a range of direct and indirect pathways of interactions, which result in a large suite of possible outcomes (Bender et al. 1984; Yodzis 1988; Abrams 1993; Wootton 1993). Yet recent syntheses of data suggest that some generalization may be possible. In freshwater and marine pelagic food webs, alterations of resource and consumer levels cause similar general patterns of community change (Brett and Goldman 1996, 1997; Micheli 1999). In marine rocky intertidal food webs, experimental manipu-

lations caused several types of indirect effects, but approximately 60 percent of indirect effects were either keystone predation or apparent competition (Menge 1995). "Natural" experiments provided by the variation in space and time of human impacts (e.g., Estes et al. 1998; Crooks and Soulé 1999; Terborgh et al. 1999) represent invaluable opportunities to examine food-web responses to bottom-up and top-down forces over large scales and compare responses across systems. Syntheses of existing data may produce generalizations about community responses to food-web alterations and generate predictions about the likelihood of different effects of future perturbations or management interventions.

Determine Level of Resolution of Community Representation

There is an urgent need to determine how much detail is necessary to detect change and predict community dynamics in the face of environmental variability and human impacts. The difficulty and costs of modeling and monitoring species dynamics and interactions within complex food webs increase quickly with increasing resolution of models and sampling. Some form of simplification is necessary. This is typically achieved by focusing on small groups of interacting species or by lumping species into trophic levels or functional groups. Simulations, resampling of existing data, and investigation of the effects of aggregating species-level data into broader categories are promising avenues for determining how much detail can be omitted from food-web models and for producing guidelines for monitoring multispecies assemblages (e.g., Frost et al. 1995; Cottingham and Carpenter 1998; Yodzis 1998).

Understand the Effects of Nutrient and Organic Enrichment of Ecosystems

The availability of resources to species at all trophic levels of natural food webs is altered through a variety of human activities. Human alteration of the availability of nutrients, detritus, and prey to producers and consumers is a widespread phenomenon, but it includes a variety of types of alteration, occurring over local to global scales. Determining how different types and scales of subsidies influence food-web interactions, community structure, and ecosystem processes is an urgent research priority in the face of the ever increasing human production of pollutants and waste.

Link Pattern and Process to Understand Mechanisms Underlying Food-Web Dynamics

A better understanding of the processes underlying observed community dynamics would greatly improve conservation and management of aquatic

BOX 3.1. **Research Priorities for**
Food-Web Conservation and Management

Produce Generalizations about Species and Community
Responses to Food-Web Alteration

*1. Characterize community responses to food-web alterations and determine which conditions are more likely to lead to a particular type of community response.
2. Determine unique vs. general responses to food-web perturbation.
3. Relate the strength and effects of consumer-resource interactions to environmental gradients in productivity and disturbance.
4. Explore how systems of increasing complexity respond to perturbation and determine under what circumstances complex systems may yield predictable responses to perturbation.
5. Investigate the separate and joint effects of different types of food-web perturbations.

Determine Level of Resolution of Community Representation

*1. Determine how many species and interactions can be omitted from monitoring and models and what level of aggregation still allows accurate representation of community dynamics.
2. Establish the relative frequencies of strong and weak interactions in natural ecosystems.
3. Investigate what traits characterize strong interactors and keystone species.

Understand the Effects of Nutrient and Organic Enrichment
of Ecosystems

*1. Determine how different types of subsidies influence food-web interactions, community structure, and ecosystem processes.

2. Investigate how nutrient and organic matter subsidies influence food-web dynamics in ecosystems already subjected to other perturbations, including overexploitation, habitat degradation, and climate change.
3. Explore how the effects of food-web subsidies vary between natural sources (e.g., oceanic upwelling, litter fall, bird guano) and anthropogenic sources (e.g., sewage and fertilizers, urban waste, discarded fisheries bycatch).
4. Evaluate how the effects of resource alteration vary among local, regional, and global scales.

Link Pattern and Process to Understand
Mechanisms Underlying Food-Web Dynamics

1. Link alternative models of consumer-resource interactions to observed patterns of community change.
*2. Develop models that include the influence of human activities on community and ecosystem dynamics and explore alternative conservation and management scenarios before they are implemented.

Determine Scale of Interactions and Food-Web Boundaries

*1. Determine the relevant food-web components influencing community structure and diversity.
*2. Investigate the effects of the movement of energy, matter, and organisms across community and ecosystem boundaries on food-web dynamics.
*3. Establish the temporal and spatial scales over which community change can be detected.
4. Explore how local, regional, and global food-web perturbations influence each other.

Note: Asterisks denote the six highest priorities for the current decade.

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ecosystems. One approach is to develop mechanistic models that represent alternative views of the processes driving food-web dynamics, and to compare model predictions to observed patterns. Confidence in alternative models is built through comparisons of model predictions to data, thereby linking observed patterns of community change to specific mechanisms of consumer-resource interactions. For example, Shea et al. (1998) proposed testing alternative process-based models against population time series to improve population management in conservation, fisheries management, and pest control. Similarly, Kendall et al. (1999) combined mechanistic models and time-series statistical models to elucidate the processes underlying population cycles. McCann, Hastings, and Strong (1998) compared predic-

tions of food-web models that include different forms of interference among consumers to patterns of biomass change at different trophic levels of lake food webs. Modeling also can be used to simulate scenarios that cannot be simultaneously realized in practice, allowing exploration of the effects of species addition and deletion, of single vs. multiple perturbations, and of different management strategies.

Determine Scale of Interactions and Food-Web Boundaries

A largely unexplored area is that of how delimiting food webs and ecosystems using different criteria and over different spatial and temporal scales may influence conclusions about the community and ecosystem conse-

quences of food-web interactions (e.g., Polis et al. 1997). For example, our understanding of above-ground plant-insect interactions and marine plankton dynamics was dramatically changed by including soil (Strong 1999) and microbial (Pomeroy 1974) communities in these food webs. Similarly, the dynamics of intertidal marine communities and terrestrial communities on small islands are largely influenced by oceanic input of larvae (Roughgarden et al. 1988) and detritus (Bustamante et al. 1995; Polis and Hurd 1996). Historical and paleontological data indicate that coral reef communities have been impacted and modified by fishing and other human activities well before the start of the monitoring programs with which we attempt to detect temporal change (Jackson 1997). Scale and boundary issues are relevant to a suite of conservation and management applications, such as designing networks of reserves, managing watersheds and coastal areas, and determining whether species assemblages are being modified by human disturbances. Tackling scale issues will require conducting research at multiple scales, using a diverse set of perspectives and approaches, and establishing interdisciplinary collaborations.

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