# PREDATORS, ECOLOGICAL ROLE OF

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## GLOSSARY

**apex predator** An organism that occupies a food web's highest trophic level.

**bottom-up forces** Population-regulating processes based on the availability of food, nutrients, and energy.

**carnivore** An organism that consumes other animals.

**competitionism** The view that competition regulates populations.

**food web** The interconnections among organisms based on diet.

**herbivores** Organisms that feed on plants and other photosynthesizers.

**keystone species** A strong interactor that is relatively rare.

**Lotka–Volterra model** An early equation relating rate of population change to the interplay between competition and predation.

**mesopredator** A small to mid-sized predator.

**nutritionalism** The view that bottom-up forces regulate populations.

**phytoplankton** Microscopic primary producers that live in water column habitats.

**piscivores** Predators that consume fish in aquatic habitats.

**planktivores** Predators that consume zooplankton in aquatic habitats.

**top-down forces** Population-regulating processes that originate from consumer limitation.

**trophic cascades** A chain reaction of top-down interactions across multiple trophic levels.

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*PREDATORS* occur in all of the planet's ecosystems and initiate top-down forces and trophic cascades in many of these. Although evidence for trophic cascades is strongest for aquatic systems, there is increasing evidence that they occur in a variety of terrestrial ecosystems as well. Trophic cascades result in weak or strong plant–herbivore interactions when the respective number of trophic levels is odd or even. Indirect food web effects of trophic cascades, known for lakes and kelp forests, are unstudied in most systems. The loss of large, apex predators from several terrestrial systems has resulted in mesopredator release—the proliferation of moderate-sized predators that commonly reduce or eliminate the smaller vertebrate species. Many dysfunc-

tional ecosystems have developed because of the loss of apex predators. Thus, reserve design and other conservation strategies must be adequate to preserve the apex predators.

# I. INTRODUCTION

The science of ecology has undergone a succession of paradigms on the nature and importance of species interactions, including those between predators and their prey. The earliest view (henceforth termed nutritionalism) was that bottom-up forces (i.e., primary production and the efficiency of energy and material transport upward across trophic levels) regulate populations. Ecosystem ecology was built around this view of nature, which implicitly holds that apex predators, as the end points of energy and material flux, are of minor consequence to ecosystem function. Beginning in the late 1950s and early 1960s, the focus on species interactions changed to competition. In contrast with nutritionalism, competitionism holds that lateral forces within trophic levels regulate population abundance. By this view, predators are no more or less important than any other species. Recently, top-down forces have captured the attention of ecology, thereby legitimizing predators as important ecological entities. Ecologists now recognize that important species interactions follow all three pathways (Fig. 1), often simultaneously and sometimes interactively. Thus, although our focus in this article is on top-down forces generated by apex predators, understanding the ways in which predators influence biodiversity requires a more eclectic view of food webs and species interactions than simply "bottom-up vs top-down."

We begin with a discussion of who the predators are and how they affect populations, communities, and ecosystems. We then present a series of case studies demonstrating the wide range of systems in which predation is an important organizing process, including examples of the unifying concepts and explanations of how they were discovered. This discussion is followed by a theoretical exploration of predation and biodiversity. Next, we discuss the levels of biological organization at which predation can influence biodiversity and develop a conceptual model for how apex predators might influence the location and strength of bottom-up and competitive forces in systems under top-down control. We conclude by considering the needs and opportunities for further research on predators and how predators are likely to figure into the future of conservation biology.

# II. BACKGROUND AND DEFINITIONS

## A. What Are Predators?

Broadly defined, all consumers are predators, thus including all living things except photo- and chemosynthesizers. The carnivorous plants add a minor wrinkle to this dichotomy. Nonetheless, predators would be represented by such diverse functional groups as herbivores, parasites (including microbes and parasitoids), and the immense diversity of invertebrate and vertebrate consumers that hunt and kill their prey. Attempts to define or classify predators based on trophic status, consumer–prey size relationships, or just about any other scheme are similarly problematic. For example, herbivores exist at one end of the trophic-status spectrum and microbes at the other, but it is uncommon for consumers in either group to kill their prey outright. Plants may even benefit from being eaten and a single act of predation by most microbes is of virtually no consequence to their prey because of the prey's immensely greater relative body size. Although herbivores, microbes, and parasites are predators in this broad sense, our focus is on those that kill their prey. Even this restricted definition includes a vast array of species.
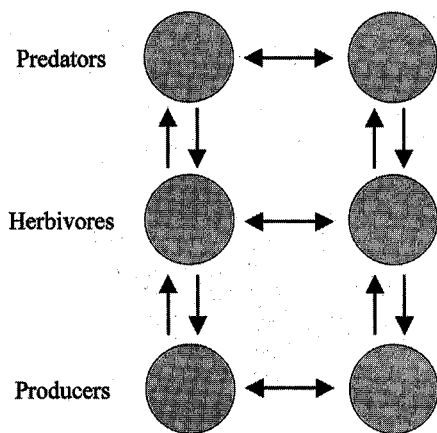


FIGURE 1  A simple stylized food web showing potential interaction pathways. The circles represent species, the downward-pointing arrows represent top-down forces, the upward-pointing arrows represent bottom-up forces, and the double-headed arrows represent competitive interactions. Although real food webs are far more complex, this figure shows the three main ways by which species interact with one another in nature.

## B. Species Interactions

The influence of predators on biodiversity depends first and foremost on direct predator–prey interactions. However, the consequence of predation to communities and ecosystems has less to do with these direct interactions than it does with their indirect effects. Although the direct effects of predation, by definition, are limited to impacts on prey populations, the nature of indirect effects is almost limitless, thus potentially causing populations to increase or decline anywhere in the food web. As will be shown in several of the case studies presented later, such indirect effects may involve long interaction chains, which in turn have broad impacts on associated ecosystems.

## C. Indirect Effects of Predators

An awareness of the indirect effects of predators can be traced back at least to the writings of Charles Darwin, who described an interaction chain leading from cats to mice to bumble bees to clover. Similar early examples were provided by such well-known ecologists as Charles Elton and G. E. Hutchinson. Hairston, Smith, and Slobodkin's (1960) now-classic paper (hereafter HSS) was perhaps the first effort to mold the indirect effects of predation into a conceptual model of trophic interactions and population regulation. HSS recognized four trophic groups—producers, decomposers, herbivores, and predators—and argued that although herbivores are commonly limited by predators, plants, decomposers, and predators are ordinarily limited by resources. The HSS model has weathered the test of time, along the way setting the stage for several conceptual advances, including the importance of top-down forces in population regulation and community organization, the ideas of keystone species and trophic cascades, and a generalized theory of food chain dynamics. Each of these is briefly explained in the following sections.

## D. Top-Down Forces

Bottom-up forces are those passing from producers to consumers, whereas top-down forces are those passing from consumers to producers. As previously mentioned, recognition of top-down regulation dates back to at least Darwin, although it was HSS that introduced the idea in ecology. A Special Features section in the journal *Ecology*, published in 1992, stimulated further interested in the issue, in part by pointing out that top-

down and bottom-up forces need not be competing processes, even though bottom-up forces are necessary for the function of all ecosystems. This realization freed ecologists to imagine a broad potential for the role of predation in nature.

## E. Keystone Species

HSS was followed in the mid-1960s by Robert Paine's highly influential paper on food web complexity and species diversity. Paine argued that predators often selectively consume and thus limit competitively dominant species, thus enhancing species diversity by releasing their subordinates from competitive exclusion. This argument was based on three essential premises: (i) Predators selectively consume the competitively dominant prey; (ii) in so doing, populations of the competitively dominant species are reduced; and (iii) in the absence of predation, the prey guild is limited by interspecific competition. Paine's work captured the interest of community ecologists because it linked the influence of predators to species diversity, and (perhaps most important at the time) it was supported by results from field experiments. His empirical studies of predation by sea stars on mussel bed assemblages were done in the temperate rocky intertidal zone where competition for space can be extreme. This also led to two important developments in ecology: the idea of keystone species and the intermediate disturbance model of species diversity.

The intermediate disturbance model, further refined and generalized by Joseph Connell, holds that species diversity is influenced by the intensity of disturbance (either physical or biological; Fig. 2). When the intensity of disturbance is very high or very low, species diversity is low because the most vulnerable species are eliminated in the former instance and excluded by their competitive dominants in the latter. These limiting conditions are relaxed at intermediate levels of disturbance, thereby elevating species diversity. The notion of keystone species, as envisioned by Paine, applied to cases in which predators were the agents of disturbance. Although the definition of keystone species has broadened, on the one hand, to include other kinds of interactions and grown more restrictive, on the other hand, to exclude the effects of common species, this idea is rooted historically with the indirect effects of predators.

## F. Trophic Cascades

A trophic cascade is the progression of indirect effects by predators across successively lower trophic levels.
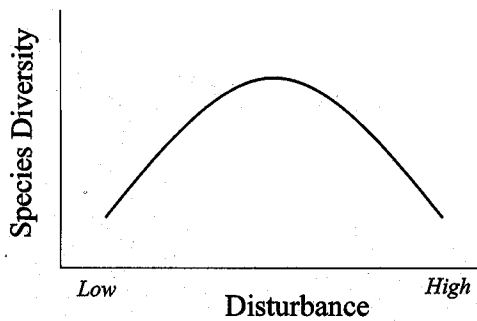
FIGURE 2  The intermediate disturbance model of species diversity. This model is based on the assumption that competitive exclusion occurs in benign systems. Thus, when the intensity of disturbance (including predation) is low, strong competitive interactions by the dominant species reduce species diversity. When the intensity of disturbance is high, species diversity is again low because those species that cannot cope are eliminated. Maximum species diversity occurs at intermediate levels of disturbance—strong enough to prevent competitive exclusion but not so strong as to directly eliminate species.
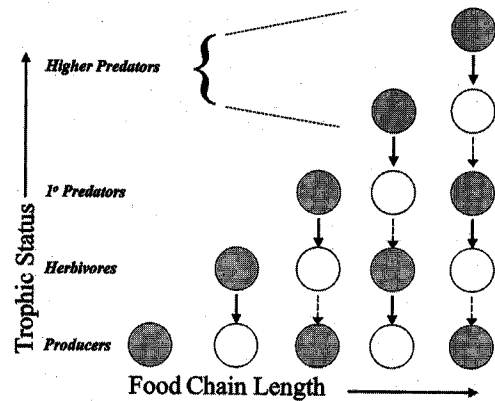


FIGURE 3  A graphical synopsis of Stephen Fretwell's theory of food chain length in systems under top-down control. The circles represent species or groups of species within particular trophic levels: ●, resource limitation; ○, consumer limitation. The sold arrows represent strong interactions, and the dashed arrows represent weak interactions. As food chain length becomes progressively longer, the plant–herbivore interactions alternate between being weak in odd-numbered systems and strong in even-numbered systems.

HSS's proposed relationship between predators, herbivores, and producers was a generalized trophic cascade. Stephen Carpenter and James Kitchell popularized this idea based on the striking influences of predatory fishes on the essential components of lake food chains—from minnows (the predatory fishes' prey) to zooplankton (prey of the minnows) and to phytoplankton (prey of the zooplankton).

## G. Generalized Food Web Theory

A generalized food web theory was developed by Stephen Fretwell to show how predation, trophic cascades, and food chain length combine to predict the strength of plant–herbivore interactions (Fig. 3). To understand this theory, first imagine an ecosystem with producers but no consumers. Lacking consumers, the producers are limited by competition for resources. Adding herbivores creates a two-trophic level system in which the plant populations become limited by herbivory. Adding predators limits herbivore populations, thus releasing the producers from limitation by herbivory and returning them to limitation by resource competition. The progressive increase of trophic complexity cascades downward through the food chain such that plant–herbivore interactions switch from being weak to strong as the respective number of trophic levels alternates between odd and even.

Next, we summarize many case studies that provide empirical evidence for these theories and concepts. Our presentation is organized around the various systems in which the work was done.

## III. CASE STUDIES

## A. Rocky Shores

Studies of rocky seashores furnish the earliest and some of the most compelling evidence for the effects of predation on communities and ecosystems. The first well-known experimental studies were done by Joseph Connell in Scotland. Connell's work focused mainly on competition between the two barnacles (*Cthamalus stellatus* and *Balanus balanoides*) and predation on these species by the whelk (*Thais lapillus*). This research showed that the upper shore limit of *Cthamalus* was set by physical factors (weather) and the lower limit by competition for space with *Balanus* and predation by *Thais*.

Shortly thereafter, Paine began his studies of predation by the sea star (*Pisaster ochraceous*) in mussel beds along the outer coast of Washington. Paine hypothesized that sea star predation limited the lower distribution of mussels in the mid-littoral zone. This was subsequently confirmed by downward expansion of the mussel bed when the stars were removed. California mussels (*Mytilus californianus*) are the competitive dominants in this system. Predation by sea stars prevents mussels from controlling primary space (the rock

surface), the principal limiting resource in this system, thus permitting other species to coexist within mussel beds. In the absence of predation by sea stars, mussels dominate space, thereby excluding the competitive subordinates and reducing species diversity. Subsequent research has confirmed a similar role for *Pisaster* elsewhere in western North America and for other species of mussels and sea stars elsewhere in the world.

Other predators also influence rocky intertidal communities. Work by Philip Hockey and colleagues demonstrated a trophic cascade among African black oystercatchers (*Haematopus moquini*), herbivorous limpets, and intertidal algae. Succeeding studies of oystercatchers and limpets have confirmed similar interactions in South America, Australia, and western North America. Research in central and southern California further demonstrated how humans perturb the trophic cascade by exploiting owl limpets (*Lottia gigantea*, a large, territorial species) and by causing oystercatchers to abandon their breeding territories. The former effect causes a competitively subordinate guild of small limpets to replace owl limpets as the principal herbivore. The latter effect, induced simply by large numbers of humans being present along rocky shores, transforms the intertidal community from a three- to two-trophic level system. Small limpets come to dominate such areas, in turn reducing the algal cover. These human-caused perturbations probably are responsible for much of the modern-day character of rocky shores in central and southern California.

A final example of predation on rocky shores concerns the loco (*Concholepas concholepas*), a large muricid gastropod that consumes intertidal mussels and is exploited by humans in central and southern Chile. Juan Carlos Castilla excluded humans from a small stretch of shoreline at the Las Cruces Marine Laboratory near Santiago in order to better understand their influence on this system, and as expected loco abundance greatly increased. The more surprising result was a whole scale shift in the intertidal landscape, from one dominated by extensive mussel beds to one largely devoid of mussels. This particular example is noteworthy because it demonstrates (i) how humans can perturb predator-mediated interaction chains with landscape-level consequences, (ii) that reserves can be used effectively both to demonstrate and to mitigate such effects, and (iii) the power of experimental evidence.

## B. Kelp Forests

Kelp forest communities provide several examples of the ecological role of predators. One is that of the sea otter, which was hunted to near extinction in the Pacific maritime fur trade. Following protection in the early 1900s, the process of recovery created a fragmented population distribution within what had been a continuously occupied range. Contrasts between areas with and without sea otters revealed striking differences in kelp forest communities. Areas with sea otters supported lush kelp forests, whereas those without otters were extensively overgrazed by sea urchins, the otter's principal prey. These patterns result from a trophic cascade, driven by sea otter predation on sea urchins, thus releasing kelp beds from sea urchin grazing.

In addition to contributing early empirical support for HSS, the sea otter–kelp forest system provides evidence for a wide range of predator-driven effects beyond those expected from simple trophic cascades. Sea otters influence numerous species by enhancing kelp abundance, thereby providing three-dimensional habitat and fueling increased primary production. This process is especially noteworthy because it shows how bottom-up processes can be altered by the top-down forces of apex predators. Other known or suspected consequences of sea otter predation in kelp forests are summarized in Fig. 4.

Understanding of the sea otter–kelp forest system has several interesting historical dimensions. Faunal remains in Aleut kitchen middens show that sea urchin size distributions during most of Aleut prehistory were similar to those of modern systems lacking sea otters, thus suggesting that aboriginal humans, by limiting sea otters, influenced coastal ecosystems long before modern humans arrived on the scene. Paleontological and biogeographical data provide an even longer time perspective. Because the distribution of sea otters and their recent ancestors was limited to the North Pacific basin, their influence on the evolution of plant–herbivore interactions has been inferred by contrasting plant defense and herbivore resistance between North Pacific and Australasian kelp forests. Australasian kelp forests apparently lacked predators of comparable influence to the sea otter, at least since the Pliocene-Pleistocene. In contrast with North Pacific kelp forests, strong coevolutionary forces between marine plants and their herbivores in Australasia were thus expected, thereby facilitating an arms race between plant defense and herbivore resistance. Marine algae use secondary chemicals as their principal defenses against herbivory, and for this reason the evolutionary hypothesis was put to an initial test by measuring the secondary chemistry of North Pacific and Australasian seaweeds. Phlorotannins (the principal chemical defenses in brown seaweeds) concentrations were approximately an order of
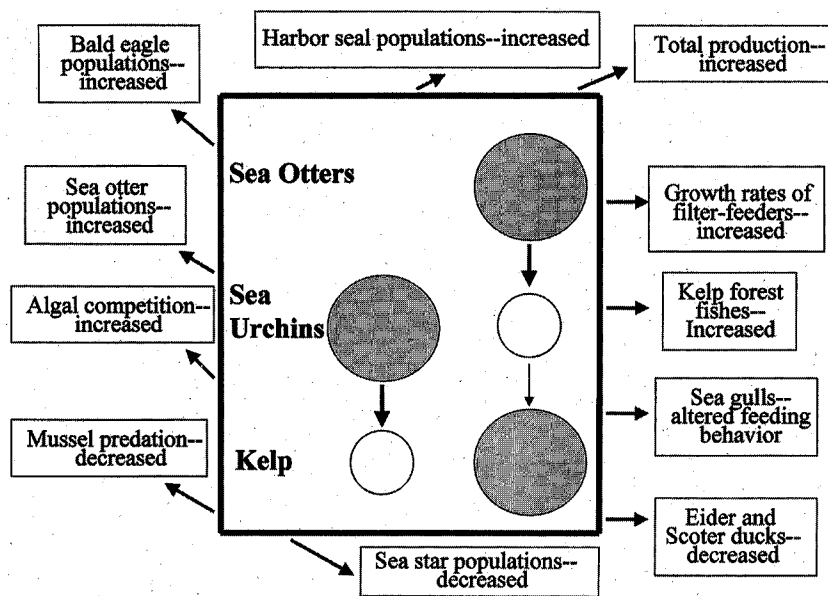
FIGURE 4   A conceptual representation of the direct and indirect effects of trophic cascades in the sea otter–kelp forest system. See the legend to Fig. 3 for explanations of circles and arrows. Some of the known or suspected indirect effects of these two alternate states of kelp forest community organization are shown around the periphery of the central box. See Estes (1996) for further discussion of specific cases (reproduced with permission from Peterson and Estes, 2000).

magnitude greater in Australasian algae and North Pacific herbivores were more strongly deterred by these compounds than were their Southern Hemisphere counterparts. These evolutionary responses to predation probably explain why Northern Hemisphere kelp forests have been so devastated by sea urchin grazing following decimation of their predators.

The sea otter–kelp forest system changed remarkably in recent years as killer whales entered the coastal ecosystem and began preying intensively on sea otters after their normal prey populations (seals and sea lions) declined. Since the early 1990s, killer whale predation has driven otter numbers downward by approximately an order of magnitude across large areas of western Alaska. The consequent reduction in sea otter predation has caused sea urchin numbers to increase and kelps to decline (Fig. 5). This example illustrates that predator–prey interactions, acting through trophic cascades, influence herbivore–plant interactions in a manner consistent with the predictions described earlier for odd-vs even-numbered food chains (Fig. 4). It further indicates a role for predators in linking ecosystems over large areas.

Sea urchins have deforested kelp beds in the Gulf of Maine. Early reports attributed this to the overfishing of American lobsters (*Homarus americanus*), a pur-

ported ecological analog of the sea otter. However, this explanation is in doubt because the lobster fishery is apparently at an all-time high. Atlantic cod (*Gadus morhua*) also prey on a variety of benthic species, including urchins and lobsters, and the well-known collapse of cod populations may have influenced both lobsters and kelp forests in the Gulf of Maine.

Predation by sheephead (*Semicossyphus pulcher*, a benthic feeding fish) and spiny lobsters (*Panulirus interruptus*) is thought to limit sea urchins in warm-temperate kelp forests of southern California. Sea otters also occurred in this system, but deforestation events in this area did not occur until long after the otter's demise. The alternative urchin predators may explain the difference. As humans have progressively depleted these predators in recent decades through commercial and recreational fisheries, deforestation has become an increasing problem.

In the Southern Hemisphere, predation by rock lobsters (*Jasus lalandii*) in South Africa limits predatory whelks, in turn releasing subtidal mussel beds from limitation by whelk predation. A remarkable predator–prey role reversal occurred in this system following the extirpation of lobsters from several small islands. Whelk populations increased substantially in the lobsters' absence, thus transforming the reef from a mussel bed
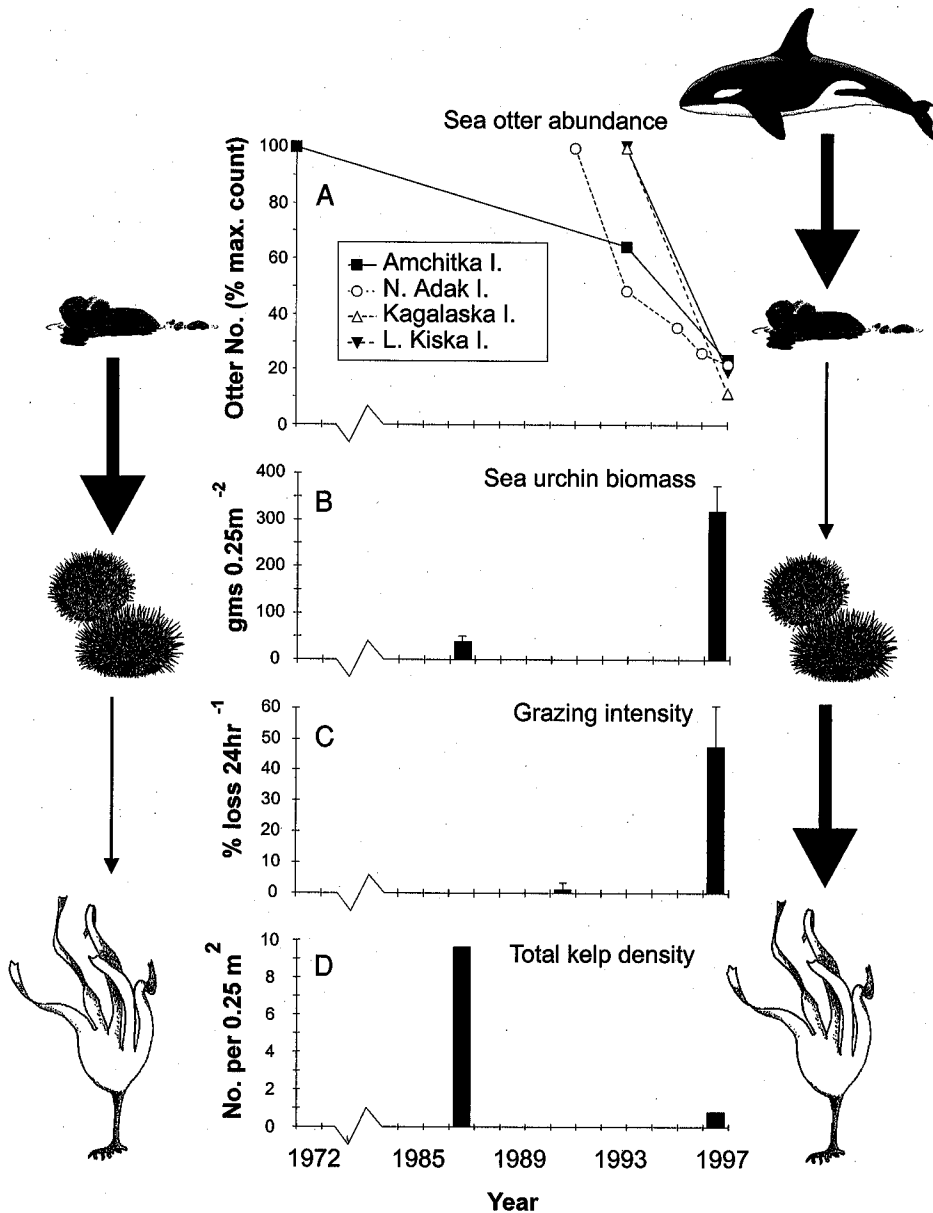
FIGURE 5 (A) Changes in sea otter abundance over time at several islands in the Aleutian archipelago and concurrent changes in (B) sea urchin biomass, (C) grazing intensity, and (D) kelp density measured from kelp forests at Adak Island, Alaska. Error bars in B and C indicate 1 SE. The proposed mechanisms of change are portrayed in the marginal cartoons: The one on the left shows how the kelp forest ecosystem was organized before the sea otter's decline and the one on the right shows how this ecosystem changed with the addition of killer whales as an apex predator. Thick arrows represent strong trophic interactions, and thin arrows represent weak interactions (reproduced with permission from Estes et al., 1998).

into a kelp forest. In an effort to reestablish lobsters and their associated role as the system's dominant predator, a large number of lobsters were relocated to one of the islands. However, the whelks had become so abundant that they attacked the lobsters in mass, killing all of them within hours of the translocation. This surprising case study demonstrates how a density-dependent role reversal between predator and prey can generate alternate stable-state communities.

These several examples from kelp forest systems

have shown that predators can shape populations and communities on ecological timescales and life history characters on evolutionary timescales. Comparative studies of sea urchins in tropical and temperate reef systems also suggest that predators influence their prey's behavior in complex ways. In warm temperate/tropical systems, sea urchins commonly retreat to protective cracks and crevices within the reef during daylight hours in order to avoid being eaten by diurnally active benthic predatory fishes. Fishes quickly attack urchins removed from their refuges during the day and placed on exposed habitats. Similar patterns have been shown for a variety of warm temperate and tropical systems in which benthic predatory fishes occur. However, the nature of urchin behavior appears to differ between species whose evolutionary histories are rooted in tropical vs temperate environments. Tropical species tend to display diel sheltering as a fixed behavior, regardless of ecological context, whereas the sheltering behavior is plastic in temperate species depending on whether predatory fishes are present or absent. The explanation for this difference in plasticity may lie in the fact that tropical urchins have long been subject to predation by diurnally active fishes, whereas temperate urchins have come into contact with benthic predatory fishes more recently, and then only at the warm margins of their geographical ranges.

## C. Lakes

Studies of freshwater lakes provide some of the clearest and best known evidence for trophic cascades. There are two main reasons for the quality of this evidence. Lakes, as discrete and recurrent entities, are well suited for comparative and experimental studies. Furthermore, the producers and herbivores (especially phytoplankton and zooplankton) have very short generation times, thereby making population-level responses to perturbations rapid enough for scientists to observe and document.

Some of the earliest evidence for the influence of predation in lake systems comes from Brooks and Dodson's analysis of New England lakes. These researchers showed that in the absence of planktivorous fishes, zooplankton assemblages were dominated by species with large body size because of their increased foraging efficiency and competitive superiority over small species. In lakes with planktivorous fishes, the composition of the plankton shifted toward small body size due to the influence of size-selective predation. This example was followed by Zaret and Paine's report on the cascad-

ing influences of introduced peacock bass (*Cichla ocellaris*) to Lake Gatun, Panama. Peacock bass, a cichlid native to the Amazon River, was first introduced to Lake Gatun in 1965 for sport fishing and consumption. These introduced predators are voracious piscivores and they caused a remarkable series of food web effects as the bass population grew and spread across Lake Gatun. The immediate influence was a rapid and extreme reduction of planktivorous minnows, thus causing zooplankton populations, including that of mosquito larvae, to increase. This example added two interesting dimensions to the understanding of lake systems. One is the strength of influence by an exotic predator on naïve prey, with broad-ranging indirect effects across the lake and surrounding terrestrial systems. In addition to the top-down effects described previously, the reduced populations of planktivorous minnows negatively impacted other apex predators, including several species of aquatic birds and predatory fishes. Another dimension is the potential impact on human health, in this case resulting from an increased threat of malaria because of increased mosquito populations. Similar examples of broad-ranging influences by exotic predators are known for many other lake systems throughout the world.

Numerous reports from various lake systems throughout the world show that altered populations of apex predators result in altered food webs. The essential players in these lake systems include four main groups of organisms: phytoplankton, herbivores, planktivores, and piscivores. The relationship of the first three of these to piscivore abundance, explained by cascading trophic interactions, is shown in Fig. 6. The evidence for these interactions comes from a variety of areas and approaches. Early insights were provided by contrasts among lakes in which piscivore populations varied serendipitously but for unknown reasons. There are many such examples from tropical and temperate lake systems in both the New and Old Worlds. Additional evidence that these patterns are caused by trophic cascades has come from the results of microcosm experiments, by tracking changes associated with the fortuitous extinction or reintroduction of piscivores into particular lakes through time, and recently by whole-lake experiments in which the piscivores were purposely added or removed. Although the details vary depending on such factors as food chain length and the nature of particular species, the overall view of food web dynamics in lake ecosystems is remarkably uniform, especially the importance of apex predators and trophic cascades.
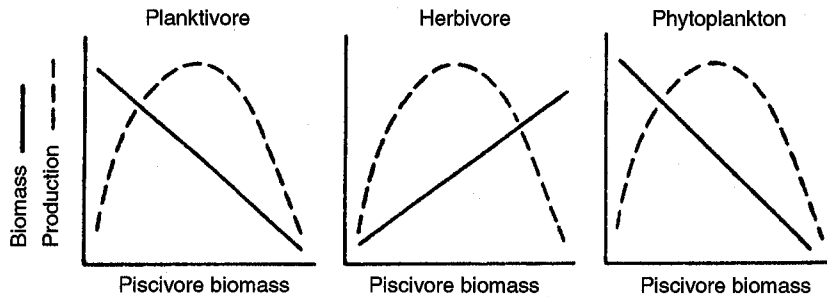
FIGURE 6 Piscivore biomass in relation to biomass (solid line) and production (dashed line) of vertebrate zooplanktivores, large herbivores, and phytoplankton in lake systems (reproduced with permission from Carpenter *et al.*, 1993).

## D. Rivers and Streams

Experimental work in rivers and streams has demonstrated important influences of predation on both food web structure and the life history of prey populations. The structure and dynamics of river food webs are grossly similar to those described for lakes, the main differences being that rivers are episodically disturbed by changes in water flow and they depend less on waterborne phytoplankton and zooplankton. Both fishes and birds are important apex predators in river food webs, and like lakes, many river food webs are strongly influenced by trophic cascades. The experimental exclusion of these predators from a variety of tropical and temperate river systems by Mary Power and colleagues provided several novel dimensions to the understanding of predation and trophic cascades. The manipulation of predatory fishes and other consumers provided consistent evidence for top-down forces and exclusion of birds has revealed depth-related gradients in the outcomes of trophic cascades. These findings show that the influence of predators on food webs can be strongly influenced by prey refuges, which in turn can vary across habitat gradients. Another important contribution of the riverine studies is that they have been done in systems that deviate in food chain length, thus providing the first experimental evidence that the strength of plant–herbivore interactions varies predictably between odd- and even-numbered food chains. Work by Sih and colleagues in streams of the eastern United States also shows how the risk of predation can influence the interplay between feeding and reproductive behavior in several prey species.

The pioneering work of Endler and Reznick on Trinidadian guppies provides some of the strongest and most comprehensive evidence for the selective effects of predation. The risk of predation to guppies by various larger fish species varies within and among streams, and a variety of life history characters, color patterns, and features of guppy mating systems covary accordingly. By manipulating predator populations and translocating guppies among habitats, these researchers demonstrated rapid selective responses to altered risks of predation.

## E. Oceanic Systems

Although the oceans dominate our biosphere and provide critical ecosystem services in such diverse forms as food production and climate control, little is known about the role of apex predators in the open sea. One reason is that the open sea and its associated seafloor habitat present serious logistical challenges to studies of any kind. Furthermore, many ocean ecologists still embrace the view that bottom-up processes are the main drivers of biological pattern in ocean ecosystems. Although bottom-up forcing in the sea is clearly important, this does not preclude top-down effects, which might be expected for several reasons. One is that strong predator-induced effects occur broadly in lakes and the general structures of ocean food webs (from phytoplankton to zooplankton to. planktivores–piscivores) are similar to those of lakes. A second is that nowhere else on the planet are predators so abundant, as witnessed by the vast schools of marine mammals, seabirds, and predatory fishes. Despite this, we are aware of but one example of an oceanic trophic cascade. Pink salmon (*Oncorhynchus gorbuscha*) populations in the North Pacific fluctuate on a 2-year cycle. During years when pink salmon are abundant, zooplankton are depressed and phytoplankton are abundant, whereas during years when pink salmon are rare, zooplankton are abundant

and phytoplankton are relatively rare. Another potential example of predation in the open sea resulted when the blue, fin, sei, and minke whales were decimated by the whaling industry. This reduction in the great whales may have released Antarctic krill populations from limitation by predation, in turn elevating the carry capacities of other krill-feeders—pinnipeds, penguins, and perhaps additional groups of consumers. Increased growth rates and reduced age of first reproduction of seals and whales after the depletion of great whales from Antarctica have been interpreted as evidence for such effects.

Predation by gray whales (*Eschrictius robustus*) and walruses (*Odobenus rosmarus*) has important effects on seafloor systems. Gray whales influence these systems by resuspending sediments and consuming ampeliscid amphipods. Furrows formed by the whales in the soft benthos are colonized by scavenging lysianassid amphipods, serve to accumulate detritus, and thus facilitate a local detritus-based food web. Walruses further impact these systems by consuming clams and other large infauna, in turn attracting predatory and detritivorous sea stars.

Although evidence from food web dynamics for a role by apex predators in the open sea is spotty at best, behavioral patterns of various prey species suggest strong predator–prey interactions. For example, krill and other large zooplankters typically undergo diel vertical migrations that take them beyond the foraging range of marine birds and mammals during daylight hours. Many species of forage fish and zooplankton form dense swarms, which probably reduce their likelihood of being consumed by predators that must search for and capture individual prey. Pagophillic (ice-loving) pinnipeds in the Arctic and Antarctica also provide a commanding case. In the Arctic, where polar bears and humans are both important predators, pinnipeds flee from the ice to water at signs of danger. In Antarctica, where the threat of predation is much greater in the water (from killer whales and leopard seals) than it is on the ice, the pinnipeds do not display such extreme flight behavior and often are nearly oblivious to potential disturbances when hauled out.

## F. Boreal/Temperate Forests

Although terrestrial biotas of the New World once contained numerous large mammalian carnivores, the potential ecological significance of these predators was unknown until recently. There are at least five reasons for the prolonged state of ignorance. One is that the largest of these creatures—gray wolves and grizzly bears—were all but exterminated in the United States and Mexico well before modern ecological research had taken form. Second, even if large carnivores have been able to persist in the face of direct persecution, they are extremely difficult animals to study due to their low densities, nocturnality, secretive habits, aggressive behavior, and wariness of humans. Third, just as ocean ecologists have downplayed the importance of predators in the open sea, many wildlife ecologists have tended to be skeptical about the importance of predation in population regulation, and this topic has been hotly debated in the wildlife literature. In a famous example, Rasmussen, Leopold, and then HSS attributed an irruption of mule deer on the Kaibab Plateau, subsequent overgrazing, and the eventual mass starvation of the deer herd to the extermination of gray wolves and other large predators, but Caughley later attempted to debunk this explanation. Fourth, the long generation times of key players (decades to centuries for trees; multiple years to decades for ungulates and carnivores) and the large areas required for the measurement or manipulation of their representative populations make rigorous study of the top-down effect of apex predators very challenging. Finally, political, social, ethical, and legal issues have dissuaded many scientists from studying large mammals.

Despite these difficulties, there are indications of top-down effects by large predators in boreal forests. McLaren and Peterson used historical information on wolf and moose abundance, together with growth ring measurements from balsam fir, as evidence for a trophic cascade at Isle Royale in Lake Superior (Fig. 7). Wolf numbers have fluctuated substantially throughout the twentieth century, apparently in large measure because of demographic factors related to their small population size. Inverse changes in moose numbers followed wolf population fluctuations, thus suggesting regulation by wolf predation. Direct measures of herbivory were unavailable. However, the distance between annual tree rings in balsam fir showed that sapling growth rates were lower when moose were abundant than when moose were rare.

## G. Fragmented Coastal Scrub Habitats

Although experimental manipulation of terrestrial carnivores is exceedingly difficult, fragmented habitats can provide valuable, large-scale, ecological experiments to rigorously explore the top-down effects of mammalian predators. Large carnivores are particularly vulnerable to local extinction in fragmented landscapes due to large ranges and resource requirements, low population
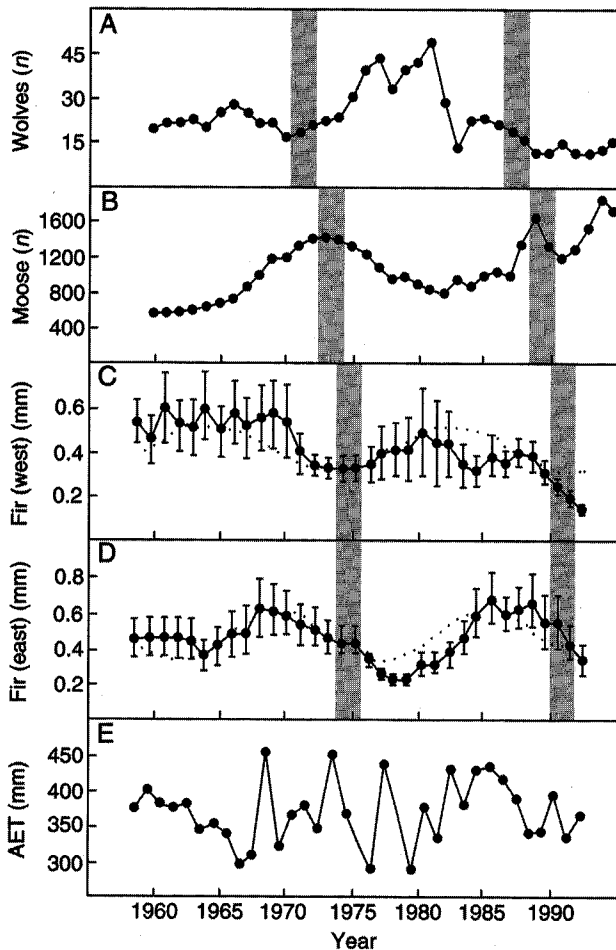
FIGURE 7 The trophic system on Islae Royale, reconstructed for 1958–1994. (A) Wolf abundance calculated from aerial surveys; (B) moose abundance calculated from skeletal remains and aerial surveys; mean ring-width indices for balsam fir from the west (C) and east (D) ends of Isle Royale; and (E) actual evapotranspiration from April to October, a measure of water availability during the growing season. The shaded areas highlight intervals of forage suppression that the authors believe are closely tied to periods of elevated moose density, which in turn follow periods of low wolf density (reproduced with permission from McLaren and Peterson, 1994).

non has been implicated in the extinction of prey species worldwide.

In coastal southern California, intensive urbanization during the past century has destroyed most of the native coastal sage scrub and chaparral habitats, creating a "hot spot" of endangerment and extinction in the region and leaving undeveloped canyons dissecting coastal mesas to function as habitat islands immersed within a matrix of inhospitable urban habitat. Michael Soulé proposed the mesopredator release hypothesis as a possible mechanism to explain the rapid disappearance of scrub-breeding birds from the habitat fragments. He predicted that the decline of the most common large predator (coyote) would result in the ecological release of native (striped skunk, raccoon, and gray fox) and exotic (domestic cat and opossum) mesopredators, and that increased predation by these particularly effective avian mesopredators would result in higher mortality and extinction rates of scrub-breeding birds.

To test this prediction, Crooks and Soulé exploited a serendipitous ecological experiment—spatial and temporal variation in the distribution and abundance of coyotes among these urban habitat fragments—to investigate direct and indirect effects of this top predator on community structure. In accordance with the mesopredator release hypothesis, lower visitation rates of coyotes in small, isolated remnants resulted in elevated numbers and activity of urban mesopredators. Coyotes directly preyed on some mesopredator species; for example, domestic cats were found in approximately 20% of coyote scats in the fragments. Mesopredators temporally avoided coyotes as well. In fragments that coyotes visited episodically during the course of the study, mesopredator activity increased when coyotes were absent. As predicted, scrub bird diversity was lower in fragments with fewer coyotes and more mesopredators, even after accounting for the positive effect of fragment area and the negative effect of fragment age on bird persistence.

The top-down effect of coyotes on cats seems to have had the strongest impact on the decline and extinction of scrub-breeding birds in the urban fragments. Unlike wild predators, domestic cats are recreational hunters. Maintained well above carrying capacity by nutritional subsidies from their owners, they continue to kill even when prey populations are low. Using data on cat densities and predation rates, Crooks and Soulé estimated that cats surrounding a moderately sized fragment return approximately 840 rodents, 525 birds, and 595 lizards to residences per year. Such high levels of predation appear to be unsustainable for many small vertebrate populations. For example, existing population

densities, and direct persecution by humans. Larger carnivores can depress populations of smaller mammalian carnivores, or "mesopredators," through direct predation, resource competition, and interference competition, including spatial and temporal avoidance. Consequently, the decline and disappearance of dominant carnivores in fragmented systems may lead to the ecological release of smaller predators that in turn threaten birds and other vertebrates. This process has been labeled "mesopredator release" and the phenome-

sizes of some birds do not exceed 10 individuals in small to moderately sized fragments, so even modest increases in predation pressure from mesopredators may quickly drive native prey species to extinction. Extinctions of scrub-breeding birds are frequent and rapid; at least 75 local extinctions may have occurred in these fragments during the past century. Overall, this example illustrates that trophic cascades generated by the disappearance of an apex predator can combine with other fragmentation effects to influence species diversity in terrestrial systems.

## H. Midcontinent North American Prairies

The top-down effect of coyotes is evident in other systems as well. Historically, coyotes were generally confined to open plains and arid regions of western North America. The eradication of wolves from most of the continental United States in the late 1800s and early 1900s likely facilitated the expansion of coyote populations. Currently, predator control efforts in the United States are directed primarily at coyotes, and lethal and nonlethal measures have resulted in at least temporary coyote declines in some areas. In the Prairie Pothole Region of the North American midcontinent, coyote population reduction is considered one of the principal causes of increases in red fox populations starting in the 1930s; other carnivore species have been shown to increase in areas of coyote control as well. Although coyotes will kill red foxes, spatial and temporal avoidance, behavioral exclusion, and territorial shifting are likely the primary mechanisms by which coyotes reduce fox populations.

Red foxes are the most important predators on nesting ducks and their eggs and offspring in the prairie region. The ecological release of red foxes following coyote control has therefore resulted in increased predation on ground-nesting dabbling ducks, most notably mallards. Predation accounts for more than 70% of nest failures in these duck species, and in some areas intense predation on eggs, ducklings, and hens has been sufficiently intense to depress recruitment below replacement levels. Predation has resulted not only in population declines of duck species in the Prairie Pothole Region but also in altered population composition and skewed sex ratios.

Interestingly, since the mid-1970s, coyote populations have begun to rebound in parts of the Prairie Pothole Region due to restrictions in control and fur harvest methods and to reduced commercial value of fur. In these areas, expanding coyote populations have contributed to reduced red fox activity and higher duck

nest success; overall nest success in sites where coyotes are the principal canid is nearly twice as high as that in areas where red foxes dominate. Overall, the excellent series of studies by Sargeant and colleagues in the Prairie Pothole Region highlight the changes in the canid predator assemblage in North America during the past century and emphasize the top-down community-level effects generated by these dynamic canid–canid interactions.

## I. Tropical Forests

Some of the most dramatic evidence for top-down control by apex predators comes from research by John Terborgh and colleagues in New World tropical forests. Terborgh's vision of top-down control in this system stems from a contrast between Barro Colorado Island, in the Panama Canal, and Cocha Cashu Biological Station in Peru's Manu National Park. Although the two sites are similar in climate and native biota, Barro Colorado Island, because of its small size and isolation from other forest habitat, lost its apex predators (jaguars, pumas, and harpy eagles) shortly after construction of the Panama Canal. Barro Colorado Island currently supports notably higher densities of herbivorous mammals, such as agoutis, coatimundis, sloths, and howler monkeys, than does Cocha Cashu—differences attributed to the loss of predators from Barro Colorado Island. These ideas are now being put to a more rigorous test by using recently formed habitat fragments—the islands of Lago Guri in Venezuela—as a large-scale ecological experiment. The Caroni Valley of east-central Venezuela, once a vast, unbroken forest, was substantially altered by the 1986 creation of a hydroelectric impoundment. Within this 120-km-long by 70-km-wide reservoir, Lago Guri, the emergent hilltops became islands—isolated fragments of tropical forest that varied in size and distance from the shoreline border of unbroken forest. Although the larger islands retain nearly complete vertebrate faunas, the smaller islands lost up to 90% of the native vertebrate species, including all of the large vertebrate predators. Resulting changes in the forest system have been swift and sensational. Populations of herbivore species such as leaf-cutter ants, howler monkeys, iguanas, and rodents (all seed predators or herbivores) have increased by from one to three orders of magnitude. Indirect impacts on producers have been equally dramatic. Fewer than 5 of approximately 6070 native tree species are continuing to successfully reproduce, thus suggesting that highly impoverished floras will result from the loss of predators.

This particular example illustrates two important

points. First, predators often exert crucial roles in maintaining local species diversity. Terborgh's data indicate that the majority of tree species will eventually be lost from these islands systems, largely because of the loss of predators. This example, together with the Crooks–Soulé study of fragmented coastal scrub habitats, also serves to remind us of the power of ecological experiments and the importance of scale (space and time) in designing studies on the role of apex predators in nature. It is highly unlikely that any amount of study of unperturbed terrestrial systems could have demonstrated the magnitude and breadth of effect by relatively rare apex predators. However, anthropogenically disturbed systems, such as fragmented landscapes, offer unique opportunities to understand the complex trophic interactions generated by large carnivores.

## J. Exotic Predators on Islands

Perhaps nowhere is the top-down effect of predation on biodiversity so apparent as with the introduction of nonnative predators onto islands. Islands typically support few large predators and grazers, and apex predators such as mammalian carnivores are often absent. Consequently, insular endemic species regularly evolve in the absence of predation and thus lack adequate antipredator defenses. For example, many insular animals exhibit tame or fearless behavior that increases their vulnerability to introduced predators, and some island birds are flightless ground nesters. Similarly, many island plants do not produce the same noxious chemicals or physical defenses found in their closest mainland relatives—features that discourage herbivory.

Consequently, the introduction of nonnative predators can be catastrophic for sensitive island communities, to the point of driving insular prey species to extinction. The examples are numerous. Worldwide, of all the species that have gone extinct since 1600, 90% of the 30 species of reptiles and amphibians, 81% of the 65 mammal species, and 93% of the 176 species and subspecies of birds have been insular forms. Predation by introduced animals has been a primary cause for about 40% of the extinctions of birds on islands, and alien predators are endangering about 40% of currently threatened insular bird species. Introduced rats and domestic cats are notorious killers. Introduced rats have successfully invaded at least 80% of the world's 123 major island groups and are known to prey on a variety of insular vertebrates, including amphibians, reptiles, mammals, and birds. Indeed, predation by Pacific rats (*Rattus exulans*), black rats (*Rattus rattus*), and Norwegian rats (*Rattus norvegicus*) has been documented on

at least 15, 39, and 53 insular bird species, respectively, and introduced rats are thought to be responsible for 54% of insular bird extinctions caused by predators. For example, the introduction of black rats on Big South Cape Island, New Zealand, in 1964 resulted in the rapid extinction of 5 species of land bird, 1 species of bat, and an unknown number of invertebrates, including a species of large flightless weevil. On the Galapagos Islands, introduced black rats have reduced populations of the giant tortoise and the dark-rumped petrel by preying on eggs.

Mongoose and domestic cats have also been introduced to islands, at times deliberately to control nonnative rodents. Unfortunately, they instead often eradicate native prey species. On Hawaii, introduced mongoose had little impact on rodents but decimated flightless rail populations. Domestic cats have been accidentally or deliberately introduced to at least 65 island groups and are thought to be responsible for 26% of insular bird extinctions caused by predators. Incredibly, 375 cats on Macquarie Island near Australia killed an estimated 56,000 rabbits and 58,000 ground-nesting seabirds each year. On subantarctic Marion Island, 5 cats were introduced as pets in 1949 and by 1975 about 2000 cats were killing 450,000 burrowing petrels annually and were suspected in driving another petrel species to local extinction. In the mid-1900s about 5 cats were introduced to Kerguelen Island in the sub-Antarctic and their descendants have killed more than 3 million petrels per year and are responsible for the extinction of several bird populations. In the most infamous and perhaps most extreme example known, the lighthousekeeper's pet cat on Stephen Island, a tiny island off New Zealand, arrived in 1894 and within a single year this one cat exterminated the flightless Stephen Island wren. The indirect effects of these changes, although likely important in some cases, are largely unstudied.

The effects of introduced predators extend far beyond their prey species and can include modification of ecosystem-level processes. For example, the New Zealand flatworm (*Artioposthia triangulata*) was accidentally introduced to the British Isles in the early 1960s and, with no natural predators, has spread rapidly. The flatworm is a voracious predator of native earthworm species. Earthworms, through their burrow excavation and casting activity, provide an invaluable ecosystem service by shaping the structure and hydrological patterns of soils. Flatworm infestations and the consequent depletion of earthworms alter both soil structure and hydrology. The ramifications are far-reaching and directly impact human welfare. By depleting native earthworms, the introduced New Zealand flatworm increases

the risk of surface runoff and therefore the potential of soil erosion, agrochemical pollution, and flooding.

Threatened prey species often recover, sometimes rapidly, when alien predators are controlled or eradicated on islands. However, the removal of alien predators can also yield unexpected results. For instance, a recent eradication of introduced black rats on Bird Island in the Seychelles has resulted in a population explosion of exotic crazy ants (*Anoplolepis longipes*). Ironically, these ants are now threatening those bird colonies that the rat eradication was intended to protect. Furthermore, simulation models predict that on islands colonized by both cats and rats, elimination of cats may release rat populations, and that increased numbers of rats may actually increase predation pressures on island birds. In essence, this cascade represents another example of the mesopredator release phenomenon, with cats on islands as top predators and rats as the mesopredators. On a variation of the theme, controlling cats on islands that also support exotic rabbits may result in more rabbits, excessive grazing by these prolific herbivores, and severe impacts to insular vegetation and associated animal species; this example, therefore, directly follows the predictions from the models of HSS and Fretwell. Clearly, alien predators on islands represent a complex, unpredictable, and occasionally dramatic example of the relationship between predators and biodiversity.

# IV. SUMMARY AND SYNTHESIS OF CASE STUDIES

It is abundantly clear from the preceding examples that the manifestations of predation in nature are dramatic and diverse, occurring at organizational levels ranging from the behavior of individuals to the dynamics of ecosystems and on timescales ranging from ecological to evolutionary. Numerous studies show or suggest that predators influence the abundance, distribution, and population structure of their prey. Indirect effects of predation are less appreciated by scientists and the public, despite the fact that they occur broadly in nature, are important to ecosystem function, and often result in processes that benefit human welfare. Trophic cascades are the most common of known indirect effects. These may be nearly as ubiquitous in nature as the transfer of material and energy upward through food webs. In any case, ecologists should be more surprised by the absence of such top-down effects than by discoveries of new ones.

Despite extensive evidence for trophic cascades from many of the planet's major ecosystems, we know little else about their influences on overall food webs. The lake studies provide an important exception because here a relationship between the top-down effects of predation and the bottom-up effects of production has been shown. These findings indicate that predators may fuel production in odd-numbered food chains, and that maximum production across all trophic levels should be realized at intermediate intensities of predation. A corollary to this hypothesis is that the length of food chains under top-down control is necessarily limited not by production and the efficiency of energy transfer but by the population constrictions that occur at consumer-regulated trophic levels. Such constrictions may be common in nature because intermediate intensities of predation probably occur rarely, except in highly managed ecosystems.

The theory of trophic cascades also provides guidance on where in a food web one might expect to find strong competitive interactions. Competition should be most strongly manifested within trophic levels in which populations are resource rather than consumer limited. These occur at the odd trophic levels in odd-numbered systems and even trophic levels in even-numbered systems. Although this prediction requires further analysis, it provides hope for an integrated theory of what previously has been viewed and treated as the largely unrelated processes of top-down, lateral, and bottom-up species interactions.

What humans perceive as "dysfunctional ecosystems" are often consequences of the recently altered roles of predators (e.g., losses of native species or introductions of exotics). Local extinctions and invasions are increasingly common, but unless these changes are observed or known from historical records, their significance to extant ecosystems may be difficult to understand. This point is illustrated by the following example. In a recent essay, Paine argued that the HSS model is generally correct for herbivorous insects but incorrect for herbivorous mammals—a contention supported by numerous examples of plant damage by mammalian grazers. The purported difference between insects and mammals as agents of herbivory has at least three possible explanations: that vegetation is intrinsically more vulnerable to mammalian than insect herbivores, that mammalian herbivores are less vulnerable to predation than their insect counterparts, or that the predators of mammals have been lost in disproportionately large numbers. The known reductions of large carnivores in North America make the latter mechanism a strong possibility.

Extinct interactions are difficult to infer from historical records; therefore, how might these alternatives be

assessed? As seen in some of the preceding examples, predation often leaves a mark on species-level characters, especially behavior, life history, and morphology. Vermeij's analysis of shell damage and morphological change (ostensibly from crushing predators) in Mesozoic marine gastropods provides a good example of one such record. The sudden increase in crushing predators was responsible for what Vermeij termed the "Mesozoic marine revolution." Using this perspective, Richard Palmer confirmed that shell structures indeed reduce the incidence of attack from crushing predators by experimentally removing spires from gastropod shells. Behavioral patterns also provide clues about the role of predators, as described in the case studies for sea urchins, pagophillic pinnipeds, and North American pronghorn. Other examples could be cited, but those listed are sufficient to make the point that morphology and behavior, when thoughtfully and cautiously interpreted, frequently reflect evolutionary response to predation.

Although these examples provide insight into species-level responses to predation on historical timescales, they afford little insight into the food web effects of predators. For this purpose, one might profitably examine the characteristics of producers. Plants can deter herbivores by modifying their morphology, demography, and chemistry. The degree to which these defensive characters exist among plant species and populations sometimes indicates the intensity of herbivory on historical timescales. Examples of this approach are provided by studies of differences in meristem location in steppe vegetation between the eastern and western slopes of the northern Rocky Mountains, variation in the resistance of birch trees to insect herbivores in boreal forests, the susceptibility to grazing damage in marine algae across coral reef habitats, and the evolution of reduced chemical and physical defenses in insular plants in the absence of herbivory. Mismatches in extant communities between the intensity of herbivory and the degree of plant resistance sometimes can be taken as evidence for recent changes in top-down regulation, as suggested from the previously described contrast between Northern and Southern Hemisphere kelp forests. Similar approaches might be taken to discern the evolutionary importance of apex predators in other ecosystems.

# V. THEORETICAL STUDIES OF PREDATION AND BIODIVERSITY

The topic of predation and biodiversity involves interactions among multiple species at different trophic levels that interact in nonlinear, complex ways. A full understanding of this topic requires the analysis of mathematical and computer models, which permit one to keep track of multiple forces influencing the dynamics of interacting populations. A rich theoretical literature exists exploring impacts of predation on the dynamics and structure of ecological communities. Here, we summarize highlights of this work, emphasizing conceptual insights rather than mathematical details.

A predator can influence whether or not a particular species is present in a community either by facilitating its persistence (i.e., predators can enrich species composition) or by preventing it from invading (i.e., predators can constrain species composition). If removing an apex predator greatly increases the abundance of a particular prey, and this prey is a predator on species at lower trophic levels, predator removal could indirectly lead to shifts in competitive interactions and thus persistence of species several trophic levels removed (as in a trophic cascade). Even if a predator does not dramatically affect composition, it may strongly influence relative abundances of resident community members. Finally, predators can influence the existence and magnitude of temporal fluctuations in abundance. Mathematical models help one understand all these effects.

To analyze mechanisms influencing species composition, we consider the growth of species when rare. If each species in a community increases when rare, diversity is maintained in the face of perturbations. In theoretical studies, one writes equations describing the dynamics of each species and then analyzes this set of equations (e.g., with and without a top predator). To illustrate the basic approach, we discuss a simple model in detail and then briefly discuss results from other models. Theoretical studies suggest that there is no single relationship between predation and biodiversity but instead many relationships, depending on numerous contingent details of systems.

## A. Predation as a Density-Independent Mortality Factor: Effects on Biodiversity

As discussed previously, predator removal can unleash competition among prey and induce a wave of additional extinctions. To understand this effect, we express the growth rate of each species as a function of three factors: $dN/dt = $ [inherent growth] $-$ [effect of resident competitor] $-$ [mortality from resident predator], where $N$ is abundance. Predation may both facilitate coexistence (e.g., by reducing the abundance and impact of competitors) and hamper coexistence (e.g., by direct mortality).

The most basic effect of predation is increased prey mortality. The simplest form of predation is that described by a fixed, density-independent mortality term. Generalist predators can occasionally act in this manner. Assume that two species experience strong, direct competition, described by the classic Lotka–Volterra competition model, with added mortality due to predation:

$$\frac{dN_1}{dt} = N_1 r_2 (K_1 - N_1 - \alpha_{12} N_2)/K_1 - m_1 N_1, \quad (1)$$

where $N_1$ is the density of species 1, $N_2$ is that of species $j$, $r_1$ and $K_1$ respectively are the intrinsic growth rate and carrying capacity of species 1, and the competition coefficient $\alpha_{12}$ is the effect of an individual of species 2 on species 1 (compared to the effect of 1 on itself). The second term expresses predation as density-independent mortality at a constant per capita rate $m_1$. (A comparable equation for species 2 completes the model.)

Using the criteria that each species should increase when rare, after some algebra the following condition for species coexistence emerges:

$$\frac{1}{\alpha_{21}} > \frac{K_1(1 - m_1/r_1)}{K_2(1 - m_2/r_2)} > \alpha_{12}, \quad (2)$$

where the term $K_1(1 - m_1/r_1)$ is the effective carrying capacity of species 1 in the face of predation. This inequality implies several interesting conclusions. If $\alpha_{12}\alpha_{21} > 1$, no pattern of imposed, density-independent mortality leads to coexistence. (This in effect says that interspecific competition is stronger than intraspecific competition.) Likewise, if competition coefficients are unity, one will not observe coexistence, regardless of the pattern of mortality. If the two competitors have the same intrinsic growth rate, and predation is uniform (or more generally, $r_1/m_1 = r_2/m_2$), mortality drops out, so there is no effect of predation on coexistence.

However, if $\alpha_{12}\alpha_{21} < 1$ and the two competitors differ in the ratio $m/r$, predation can occasionally facilitate coexistence. Consider a case of a competitive hierarchy, such that $\alpha_{12} = 0$, but $\alpha_{21} > 0$ and species 2 is competitively excluded. In the absence of the predator, species 2 is excluded if $K_2 < K_1\alpha_{21}$; with the predator, coexistence is permitted if $K_2(1 - m_2/r_2) > K_1(1 - m_1/r_1)\alpha_{21}$. Comparing these two inequalities, it can be seen that the predator facilitates coexistence only if $m_2/r_2 < m_1/r_1$. In other words, the dominant competitor must either experience higher mortality or have a lower intrinsic

growth rate. However, if predation is too low (low $m$ for both species), there will still be competitive exclusion. Moreover, if predation is too intense, there will not be coexistence because one (or both) species is directly eliminated by predation.

This model illustrates several general points that are applicable to a wide range of models. First, predation will not always facilitate coexistence. Second, if a keystone predator effect is possible, the effect occurs only within a particular range of population parameter values. Typically, predator-mediated coexistence requires an intermediate level of predation. Very intense, generalized predation will almost always reduce species richness. This is particularly likely in systems in which prey species have not had a shared evolutionary history with predators (e.g., the brown rat snake as a predator on birds on Guam), the physical structure of the environment makes it easy for predators to encounter prey (e.g., no refuges, as in open lakes), or the species in question have low intrinsic growth rates. Third, predator-mediated coexistence requires a tradeoff: The species that is the superior competitor needs to be more vulnerable to predation. When this occurs, predator removal will endanger the persistence of inferior competitors (as in Paine's *Pisaster*). Finally, the appropriate measure of a species' vulnerability to predation combines mortality rates ($m$) and the ability to replenish losses ($r$). High, uniform rates of mortality tilt the balance of competitive interactions toward species with high intrinsic growth rates.

The previous model structure assumes that predation influences competition via changes in abundance. However, prey can also show behavioral shifts when faced with predators—for instance, spending more time in refuges and less on foraging. Such "higher order interactions" can either make coexistence more difficult or weaken competition, depending on the detailed nature of the behavioral changes.

The Lotka–Volterra model most literally applies to systems with strong, direct interference interactions, in which the only dynamical variables are each competing species density. In models of exploitative competition for a single limiting resource, predation that leads to density-independent mortality can influence which species wins, but it will not lead to coexistence. Predation is more likely to promote (or occasionally to destroy) coexistence when mortality rates are dynamical variables responding to prey abundance. We next explore several modifications of this model which illustrate the rich repertoire of dynamical behaviors made possible when predation varies dynamically in response to prey abundances.

## B. Numerical and Functional Responses

The rate of mortality imposed by a predator reflects both predator numbers and the attack rate per predator. The total rate of mortality is $mN = fP$, where $P$ is predator density and the parameter $f$ is the number of prey (of the focal species) captured per individual predator. Because predators consume prey, the rates of the demographic parameters (birth, death, and movement) of predators will often vary as a function of the abundance of prey. Thus, the number of predators should depend on prey numbers. This is the numerical response. The rate at which an individual predator captures prey of a given species should also depend on the number of prey that are available, typically (although not always) increasing with prey abundance but saturating at high prey numbers. This is the functional response. It is useful to express the functional response as $f = aN$, where $a$ is the attack rate per predator per prey—the risk of mortality an individual prey faces from an individual predator. Different predators have distinct numerical and functional responses and therefore will have different impacts on species coexistence.

## C. Specialist Predators and Biodiversity

Specialist predators (whose diets are restricted to single prey species) typically reduce abundance of their favored species, freeing up resources for nontarget species. This can facilitate coexistence if dominant competitors attract more specialist predators or parasites than do subordinates. This diversifying effect of specialized predation can be mimicked in Eq. (1) by letting the attack rate on each species be a function of the abundance of a specialist predator, $m_i N_i = a_i P_i N_i$, where $P_i$ is the abundance of predator species $i$, which is specialized in its foraging just to prey species $i$. To complete the model, we need an equation for the dynamics of each predator: $dP_i/dt = P_i[g_i(N_i, P_i)]$, where $g$ is a function which increases with $N_i$ (e.g., because predators convert prey consumption into births) but may decrease with $P_i$ (e.g., because predators interfere with each other). For any biologically reasonable system, at low numbers of their required prey specialist predators must decrease (i.e., $g_i < 0$). Hence, the growth rate of prey species $i$ when it is rare and other prey are resident will involve only the intrinsic growth of prey $i$, discounted by competition with the resident species. Because the residents continue to be attacked by their own specialist predators, their numbers will be depressed below carrying capacity, reducing competition imposed on the rare focal species. Thus, specialized predators are expected to facilitate prey coexistence.

An interesting twist is that specialist predator–prey interactions are often unstable when the predator is effective at limiting prey numbers because of time lags in the numerical response of predators to prey. This has two consequences for species coexistence. First, as shown by Peter Abrams and others, with saturating functional or numerical responses instability tends to depress average predator numbers and thereby increase average prey numbers. This increases competition, making coexistence more difficult. Second, with unstable dynamics between a resident specialist predator and its prey, there will be times when that prey is rare and an inferior competitor can invade and temporarily persist, only later to be competitively excluded when the predator is rare and the dominant competitor has rebounded in numbers. Thus, unstable specialist predator–prey dynamics induces instability in community composition as well.

These effects are believed to be particularly important when considering impacts of insect herbivores on plant communities. However, most predators in the examples discussed in this article tend to have generalized diets.

## D. Generalist Predators and Biodiversity

### 1. Switching and "Enemy-Free Space"

The expectation that specialist predation helps competing species to coexist depends on the very general and reasonable assumption that specialist predators will have numerical responses to their prey. Generalist predators can have a wide range of effects on prey communities. A single, effective generalist can act like a whole suite of specialists in promoting prey coexistence if the predator ignores whichever prey species is temporarily the rarest, concentrating attacks on common prey—the mode of foraging behavior called switching. As shown by Roughgarden and Feldman, switching predators can readily prevent competitive exclusion. In our formulation for mortality due to predation, for example, on prey species 1, $m_1 N_1 = a_1 P_1 N_1$, we can represent switching with an attack rate $a_1 = a_1(N_1, N_2, \ldots)$, where $a_1$ declines toward zero as $N_1$ approaches zero but increases if the other $N_i$ decrease. In effect, a prey species may persist because of a refuge in relative rarity, as defined by the predator's behavioral responses. Because the predator is also reducing the abundance of potential competitive dominants, this is a potent mechanism for predator-mediated coexistence. If such a predator is removed, numerous prey species may risk extinction.

This idea is intuitively appealing, but there are surprisingly few demonstrations of it in natural systems. Those that do seem to involve prey species that are found in different habitats. A behavioral rule that predators leave patches with few prey, and aggregate in patches with numerous prey, leads to switching and will tend to foster prey coexistence. If prey species are spatially segregated, they are not likely to be strongly competing in any case. Other potential cases of switching seem to involve prey species with very different strategies for blending into the background, different activity times, or different behavioral tactics for escaping predation. John Lawton suggested that such species differences promoting coexistence be viewed as partitioning of enemy-free space, an aspect of niche differentiation.

In any case, several examples of species exclusion caused by predation discussed elsewhere in this article show that predators often do not tend to ignore rare prey species but rather continue attacking even to the point of extinction.

## 2. Saturating Functional Responses

All predators have a maximal capacity for attacking prey that is set by limited time or gut capacity. Time or effort expended in attacking one prey will be unavailable for attacking other prey. If predator numbers are fixed, an increase in abundance of one prey species may reduce attacks on another. As with switching, we can represent this as $a_i = a_i(N_1, N_2, \ldots)$, but now attacks decline with the abundance of each species. This inverse density dependence has two consequences. First, considering the effect of a prey species on itself, its mortality will decline with increasing abundance. This inverse density dependence can lead to alternative stable states for a given prey species—one at low and another at high densities. The low-density equilibrium may even be at zero density. Second, an increase in any prey species can reduce attacks on other prey species; this in effect makes alternative prey indirect mutualists. Such mutualism is most likely when considering predators that are constrained in their numerical responses (e.g., due to long generation lengths relative to those of their prey).

Unlike switching, saturating functional responses are universal. The existence of indirect mutualisms arising because predator functional responses can be swamped may explain many natural phenomena, such as herding, mixed-species flocks of birds and schools of fish, and synchronized mass emergences and migrations. One consequence of importance to biodiversity is that if some prey species are reduced in abundance, there is an immediate increase in predation on other, alternative prey, which thus risk extinction.

## 3. Numerical Responses and Apparent Competition

The potential for indirect mutualism via the functional response is often offset by a kind of indirect competition via the numerical response. Just as consumer species can reduce each other's abundance by depleting a shared limiting resource, alternative prey species can indirectly depress each other's abundance by increasing the abundance of a shared predator. This indirect interaction is known as apparent competition. It is particularly likely if predator population growth rates increase with the abundance of each prey type in the predator's diet and predator numbers are not strongly limited by other factors (e.g., territoriality or higher order predators). It is also more likely for predators with short generation lengths, not greatly exceeding those of their prey, or for predators which are highly mobile and can quickly aggregate into habitats with unusually high prey densities.

When any given prey species is rare, an increase in predator abundance will usually lead to an increase in its mortality. Predator abundance is expected to increase with the productivity and availability of alternative prey. The rate of predation on a focal prey is determined by the indirect, cumulative impact of alternative prey, sustaining the predator population at densities higher than allowed by the focal prey. Particularly when prey species are not strongly competing, the negative indirect interaction of apparent competition can limit prey species diversity.

When a prey species is rare, its rate of population growth can be represented as $r - aP$. As noted previously, often the presence of alternative prey reduces the attack rate on a rare species. However, these same prey determine the magnitude of $P$. The net effect of prey on each other can only be determined by analyzing specific models. However, some general points are worth making. A given prey species is excluded by predation if $0 < r < aP$. Prey species with low $r$ are particularly vulnerable to exclusion by shared predation, as are species which have high attack rates. Another way of stating the exclusion criterion is that the maximal predator density which this prey can tolerate is $r/a$. All else being equal, prey with low values for $r/a$ are vulnerable to exclusion (note that a prey species with a high value for $r/a$ can sustain a high abundance of a generalist predator, which can then with impunity overexploit alternative prey with lower $r/a$). The upshot of these observations is that there is a tendency toward

the exclusion of prey species in the diet of polyphagous predators. The maintenance of high diversity requires mechanisms which offset this effect. Such mechanisms might include predator switching, constraints on the predator numerical response, or prey adaptations that reduce predation at low density (e.g., spatial refuges).

Often, apparent competition will be strongly asymmetrical. A productive prey, which can only be successfully attacked by predators when it is young, ill, or aged, may not be strongly limited by predation. However, this species can sustain a high population of the predator, which can then severely depress species more vulnerable through their life history.

If different prey species occupy different habitats, and predators have limited mobility, this too can prevent exclusion via shared predation. However, mobile predators can be sustained by productive prey in one habitat and with impunity can overexploit prey in low-productivity habitats. A serious effect of habitat fragmentation is that it exposes species in habitat remnants to predation from generalist predators sustained by alternative prey in the surrounding landscape. Most examples of dramatic prey limitation by predation seem to depend on the availability of alternative prey, which permit predator numbers to remain high. The brown rat snake on Guam can persist on a diet of rats and lizards, which permits it to eat out of existence every native bird species.

Previously, we discussed the cascading effects of top predator removal. Such removals shift the factors regulating intermediate mesopredators or herbivores, which will increase and become more regulated by food availability than they were in the past. This can unleash strong apparent competition effects at lower trophic levels. Prey species harmed by polyphagous predators via "mesopredator release" are victims of apparent competition.

## E. Generalist Predators and Community Stability

Generalist predators can have many different effects on the overall stability of communities. Here, we discuss a few interesting effects.

Richard Vance examined a Lotka–Volterra model akin to Eq. (1) but with a predator showing numerical responses to each prey species. Even if the pairwise interactions were all stable, the entire ensemble could show large-amplitude cycles, or even chaotic dynamics.

If generalist predators are mobile and seek out patches with high prey abundance, this can lead to switching. If these responses are rapid, then generalist predators help stabilize prey dynamics. However, there can be time lags in these responses, which in turn can be destabilizing. Recent theoretical explorations suggest that switching behavior in patchy environments leads to systems which persist but which have bounded oscillations. Moreover, in changing landscapes, mobile generalist predators can concentrate in habitat remnants, leading to transient spikes of high predation and extinction risk for prey species residing in these remnants.

Generalist predators usually have a mixture of a few strong interactions and many weak interactions with the species of prey in their diet. Theoretical studies have recently demonstrated that weak interactions can help reduce inherent instabilities in strong predator–prey interactions. However, the effect depends on detailed assumptions made about predator–prey feedbacks; for instance, if prey flow into a given habitat and contribute to the diet of a resident predator, this predation does not feed back to influence prey numbers in the source habitat. If the predator instead is highly mobile, its ability to feed in multiple habitats may permit severe overexploitation of prey in some habitats.

Given saturating functional responses, in unstable systems apparent competition can be reduced relative to that in stable systems because the nonlinearity in the functional response means that predators are harmed more by times of low prey abundance than benefited by times of high prey abundance. This reduces the number of predators which can be sustained, thereby weakening apparent competition effects. The dominant effect may then be competitive exclusion (if the prey are strong competitors) or indirect mutualism (with noncompeting prey and saturating functional responses).

The theoretical studies summarized here suggest that there is no universal effect on predation on biodiversity but rather many effects. More important, they help emphasize potential surprising effects of predator removal and highlight the range of information a conservationist needs to gauge the likely impacts of management alternatives. Most theoretical studies of predation have been limited to interactions across two trophic levels. More complex theoretical studies of trophic interactions are needed to investigate such phenomena as trophic cascades.

## VI. GENERALITY

There is much evidence for the influences of predators on species, populations, communities, and ecosystems. However, how predictable and widely occurring are

these effects? To what degree do predators regulate the structure and function of the planet's ecosystems relative to other biological interactions and physical forces?

These important questions can be asked at two levels—within and between ecosystems. Within systems, the question of generality usually concerns the geographical extent of an effect that has been demonstrated at one or several sights. Michael Foster raised the issue for the influences of sea stars in mussel beds and sea otters in kelp forests, claiming that the interactions were less common than generally believed. Bruce Menge has begun to deal with the problem for sea stars and mussel beds by identifying some of the conditions along rocky shores under which sea star predation effectively limits or regulates mussel populations. Not surprisingly, sea star predation is important at many sites but not everywhere. For sea otters and kelp forests, Estes and Duggins approached the question by evaluating how consistently predictions of the otter–kelp forest paradigm played out at many sites with and without sea otters. In this case, the predictions held up (i.e., otter-dominated sites supported kelp forests and otter-free sites were deforested by sea urchin grazing) nearly everywhere they examined from southeast Alaska to the western Aleutian archipelago (Fig. 8), and similar results have been obtained from British Columbia. However, as mentioned previously, these patterns are less general in southern California kelp forests.

Across ecosystems, the question of generality for top-down influences of apex predators becomes one of both relative importance and variation in process. We know that trophic cascades are not limited to aquatic systems, as earlier suggested by Donald Strong. Nonetheless, understanding whether ecosystem function is controlled by trophic cascades involving a few key species (the HSS and keystone species models) or by a greater complexity of food web interactions within and across systems (a view espoused by Polis and Strong) remains one of ecology's most daunting challenges.
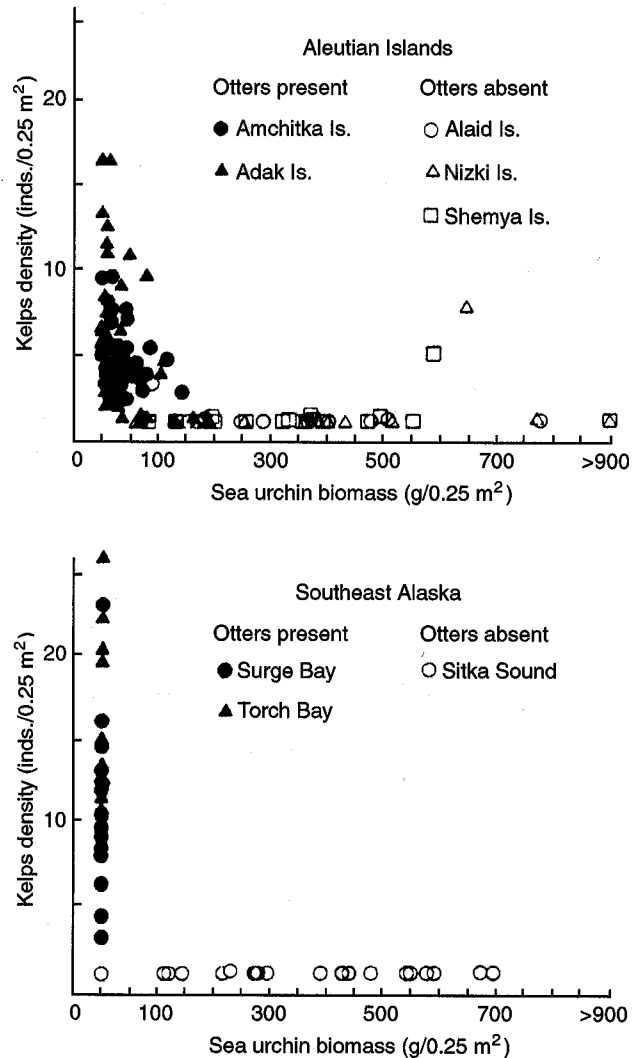


FIGURE 8  Epibenthic kelp density plotted against estimated sea urchin biomass from locations with and without sea otters in the Aleutian Islands and southeast Alaska. Points represent averages of 20 randomly selected plots from each location. These data show that kelp forest community structures vary predictably depending on the presence or absence of sea otters (reproduced with permission from Estes and Duggins, 1995).

## VII. THE FUTURE

Although predators have long concerned conservationists and resource managers, the future will bring heightened attention to this group. As a general rule, apex predators are more vulnerable to local extinctions than are lower trophic-level species. The rapid demise of predators has occurred in part because they have been (and in many areas still are) treated as competitors of humans for fish, wildlife, and agricultural resources; thus, they have been persecuted rather than conserved.

Habitat fragmentation has also hastened local extinction rates of large apex predators because their typically low densities and large home ranges render the smaller fragments incapable of maintaining viable populations. These facts, together with the increasing realization that predators are often essential for maintaining native ecosystems, is leading to a paradigm shift in conservation biology, especially in the area of reserve design. Earlier approaches to conservation planning focused on preserving representative habitats. Many ecologists now believe that this approach, although necessary, is not

sufficient. Large reserves, or a series of smaller connected reserves, are necessary to maintain viable populations of predators, which in turn are essential for maintaining the functional integrity of these systems. This view has important implications to restoration ecology, which until recently has focused mainly on the reintroduction of native plants and the elimination of exotic species.

If the maintenance or restoration of native predators is important to conservation biology, so is the elimination of exotic predators. Exotic predators have devastated many natural biotas, both because of their ability to reduce or exterminate native prey species and the many indirect effects of these prey throughout their food webs. As discussed previously, island biotas provide the most obvious and poignant examples of such effects. The removal of exotic species is usually expensive, time-consuming, and wrought with technical challenges. Nonetheless, exotic predators, because of their great mobility and low population density, are often easier to remove than other invasive species.

The conservation and management of predators requires more and better information than is currently available. As recently noted by George Schaller, field studies have been conducted on less than 15% of the species of mammalian carnivores. Although this is indeed a feeble record, there are even fewer successful efforts to understand the ecological importance of this group.

Are all or most of the predators important players in prey population regulation and ecosystem dynamics? Some clearly are important, but are these examples exceptions or a general rule? The fact that so many species already have been depleted or eliminated hampers the pursuit of answers. The depleted status of so many predators raises the additional question of how their influences vary with population density. Most apex predator populations probably were once regulated by competition for food, which in turn must have strengthened predator–prey interactions. However, humans have changed this, so we now must wonder how the strength of these interactions varies with distance below equilibrium density. The several possible functional relationships, shown in Fig. 9, have very different management implications. Conservationists might hope for a relationship like that depicted by B in Fig. 9 because this would mean that the maintenance or restoration of the ecological roles of predators requires only that they be present in low numbers. In contrast, fisheries and wildlife managers might hope for a relation more like that depicted by C, in which the influence of predators is of little consequence at population levels below carrying capacity.
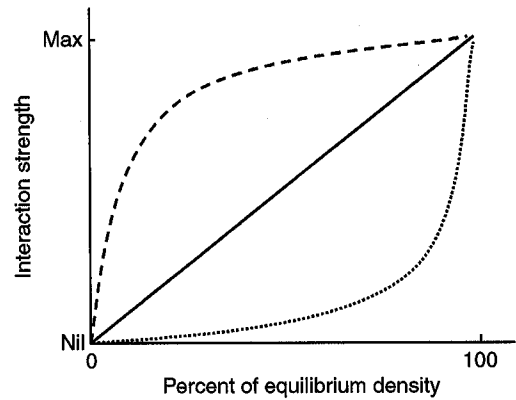


FIGURE 9 Several population relationships between predator-induced interaction strengths and predator population abundance relative to equilibrium density. In A (solid line), the relationship is linear. In B (dashed line), the main influences of predators occur at a wide range of population densities, whereas in C (dotted line) these influences occur only at high population densities.

A final need is for greater understanding of the full range of food web effects by predators. Most prior studies of predator effects focused on predator–prey interactions, thus creating the overly simplistic mind-set still held by many wildlife and fisheries managers. Most studies of indirect effects take this perspective only a step further by focusing on trophic cascades. However, as discussed previously, trophic cascades are expected to mediate competitive interactions and influence the strength of bottom-up forces by altering production levels at the base of the food web. Little is known about such interactions, although several examples of long and complex chain reactions among species show that they can be tremendously important to ecosystem function.

For the most part, food webs and ecosystem dynamics have been studied by one of two approaches. The oldest of these involves descriptions of food web structure and estimating the transfer of materials and energy through their various linkages, the critical assumption being that flux rate reflects interaction strength. The fallacy of this assumption is evident in the fact that strong top-down forces necessarily reduce prey abundance to such low levels that the interaction may no longer be apparent in a static food web. The second approach is to observe these dynamics directly by perturbing the system. Unfortunately, most experimental studies have been limited to processes acting on small spatial and temporal scales (for obvious logistical reasons) and to invertebrates and heterothermic fishes (for social and political reasons). Our general lack of understanding of the larger apex predators (especially large

mammals) is due in large part to the almost complete absence of experimental evidence.

Creative approaches are needed to put the ecological influences of large apex predators into a dynamical context. The use of historical information and opportunities provided by "natural experiments" holds promise in this regard. The historical record is a rich source of information that has barely been utilized. Assessments of the wolf/moose/boreal forest system from tree ring analysis and the sea otter–kelp forest system from faunal remains in Aleut kitchen middens illustrate the utility of this approach. Fortuitous change is another potential means of assessing the ecological roles of large apex predators. Studies by Terborgh on the recently formed islands of Lago Guri, by Crooks and Soulé on mesopredator release in urban habitat fragments, and by Estes and Palmisano on sea otters and kelp forests demonstrate the value of this approach. As these and other examples show, ecologists and resource managers must remain mindful of appropriate scales of time and space for both learning about predators and applying that knowledge to the conservation of biodiversity.

## Acknowledgment

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