Human Involvement in Food Webs*

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Annu. Rev. Environ. Resour. 2010. 35:1–23

The *Annual Review of Environment and Resources* is online at environ.annualreviews.org

This article's doi:
10.1146/annurev-environ-031809-133103

1543-5938/10/1121-0001$20.00

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Key Words

bottom-up, fisheries, intraguild predation, mesopredator, top-down, trophic cascade

Abstract

Human involvement in food webs has been profound, bringing about enormous and disproportionate losses of large apex predators on land and in water. The losses have modified or even eliminated concatenations of indirect interactions propagating from predators to herbivores to plants, *inter alia*. Food webs are a synthesis of bottom-up energy and nutrient flow from plant producers to consumers and top-down regulation of producers by consumers. The trophic cascade is the simplest top-down interaction and accounts for a great deal of what is known about food webs. In three-link cascades, predators suppress herbivores, releasing plants. In longer cascades, predators can suppress smaller mesopredators, releasing their prey animals. Hunting, fishing, and whaling have brought parallel losses of large apex predators to food webs. Without apex predators, smaller mesopredators have often become superabundant, sometimes with unprecedented suppression of their prey, extinctions, and endangerment. Flourishing mesopredators also can reverse the web regulation and suppress apex predators that have become rare owing to hunting and fishing. This can prevent fisheries recovery and lead to persistent alternative ecosystem states. Although food-web modules of large animals are increasingly well understood, the parts of webs consisting of small inconspicuous organisms, such as mutualists and parasites, and webs in obscure places, such as in the soil, are much of the challenge of future research.

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INTRODUCTION

As the consummate omnivores, humans are predisposed to deep involvement in food webs. Humans prey upon animals at all trophic levels, use almost half of the terrestrial earth to raise livestock (1), consume a large fraction of the sea's plants and animals (2), and appropriate more than a quarter of terrestrial net primary productivity for food (3). Although we set our ideas in general food-web theory, our examples place somewhat greater emphasis on aquatic systems. This largely reflects our interests, the huge ecosystem services from food webs of large marine systems (4), and the tendencies in the literature (5). At the same time, diverse, powerful food webs continue to be discovered in terrestrial systems (6–8), and the commonalities among biomes indicate the scientific power of food-web ecology and its application (9). Beyond this review are some emerging, exciting topics, for example, those of tiny organisms that play large roles in food webs in the soil (10) and among parasites and mutualists (11). We need these food webs, but they do not need us (12), and future work should think small as well as large.

Food webs are the synthesis of bottom-up energy and nutrient flow from plant producers to consumers and top-down regulation of producers by consumers. The former has no feedback, and all negative feedback in food webs comes from the top down. The trophic cascade is the simplest top-down interaction: (*a*) predators suppress herbivores and allow plants to thrive, and (*b*) apex predators suppress smaller mesopredators, releasing herbivores to suppress plants. Trophic cascades account for a great deal of what is known about the functioning of food webs on land and in the sea (13).

Humans persecute large species of animals in the gamut of ecosystems, with huge food-web effects. At mid- and high latitudes, carnivore decrease can lead to irruption of large herbivores, such as ungulates. The resulting heavy grazing can cascade into apparent competition among plants that are differentially preferred, resistant, and tolerant of grazing.[1] This string of indirect interactions has shifted the constitution of vegetation over large areas. Absent apex predators, such as wolves, big cats, or piscivorous fish, the numbers of smaller mesopredators, such as coyote, skunks, and planktivorous fish, become abnormally abundant. The prey of these, such as rare, endangered, and sensitive animals, are then depressed.

Many of the changes brought to food webs by humans will never be reversed. Extinct key species cannot be replaced, and people do not desire to live closely with large fierce animals. Fisheries recovery by definition requires reestablishment of the food web on which the target species depend. In some cases, remediation is conceivable. In others, biological or social impediments augur for pessimism.

HUMANS ON THE SCENE

Human influence in food webs accelerated with each technological advancement and increase in population. Warmly clad hunters with division of labor, new weapons, and symbioses with dogs penetrated deeper into prey food webs than earlier people without these devices (14). Megafaunal extinctions followed humans region by region (15). Large animals went first. Bronze age agriculturalists of China vanquished elephants, rhinoceros, big cats, and others by hunting and forest clearing (16). Fire, deforestation, advanced fishing methods (17), animal domestication, and early agriculture undoubtedly carried humans profoundly into food webs (18). In Roman Europe, protopastoralist hunters coexisted with tarpan horses, aurochs, bison, and elk. The suppression of nondefended, slow growing trees by these large herbivores, in food-web theory, cascaded through the vegetation by apparent competition. The result was likely open parklands, thorny shrubs, and grasses with basal meristems that resisted browsing (19). In recent centuries, large terrestrial predators, such as the American alligator (20), wolves, large cats, and large bears (21), were virtually or actually exterminated from areas where humans or agriculture were dense.

In America, pre-Colombian early agriculture simplified the flora and subsidized garden hunting (animals were attracted to and were hunted in cultivated fields and gardens), and sophisticated fishing endeavors depleted fauna around population centers (22). Dense populations of shore dwellers reduced valued species, such as the sea otter, and thrust human influence multiple trophic levels into food webs (23). Seafaring colonists and explorers from Europe caused the famous rapid, global extinctions of species, such as Steller sea cow and the great auk (24). With fossil-fueled vessels, fishermen captured a more diverse fauna at far higher rates than the early wind-powered craft (25). The magnitude of twentieth century harvest would have made the jaws drop of eighteenth century Nantucket whalers and nineteenth century Gloucester cod fishermen, who themselves depleted stocks. Industrial fishing in the twentieth century diminished ocean food chains (26), flattened trophic pyramids (27), and shifted trophic control of large oceanic food webs on a massive scale (28). On land, deforestation drove animal

Trophic cascade: the apex predator suppresses its prey and allows the prey of the prey to increase

Top-down interactions: negative feedback upon producers from consumers, as in carnivores diminishing populations of herbivores, which they require for food

Mesopredators: animals that are smaller than apex predators and are suppressed by them; without apex predators, mesopredators threaten smaller animals

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[1] Apparent competition is a shift in abundance of species or guilds driven by a consumer. The species most vulnerable to the consumer declines, allowing species that are resistant or tolerant of the consumption to increase. Plants that are preferred by herbivores and that do not tolerate the herbivory decrease. Those that are shunned by the herbivores or that tolerate herbivory are thereby able to increase at the expense of the preferred species.

loss (29–30). Persecution of large predators released mesopredators (21) and large herbivores (9) and continued lopping tops off of food webs that had begun 12,000 years earlier.

The story of cod and other groundfish in the North Atlantic perhaps best sums up the past century of human involvement in oceanic food webs. Groundfish collapse profoundly changed the food web of hundreds of species over which it once dominated. In the North Atlantic, these species were the foundation for one of the world's richest fisheries, supporting multinational fleets (operated by Basque, Dutch, French, and English fishermen in the continental shelf areas of the Barents Sea, North Sea, Icelandic waters, Grand Banks, Scotian Shelf, and Georges Bank) since the fifteenth and sixteenth centuries.

> At the great cod-fishery of the Lofoden Islands, the fish approach the shore in the form of what the natives call "cod mountains"—vast shoals of densely-packed fish, 120 to 180 feet in vertical thickness. . . . And these shoals keep coming in one after another for two months, all along the coast (31, p. 30).

The cod fishery expanded from hooks and lines cast from open boats to large, powerful trawlers that allowed fishermen to fish longer and deeper, over a much expanded geographic area. Landings increased rapidly, went through series of booms and busts, then collapsed in the early 1990s. "Of all the stories about the world's fisheries, this is the saddest" (32, p. 113).

Equally sad stories are told on land. That of the passenger pigeon is instructive about food-web circuitry and ecological engineering. The first Europeans discovered in North America three to five billion pigeons, close to the current number of birds of all species that overwinter in the United States (30). The passenger pigeon became extinct in the early twentieth century following massive harvesting and deforestation (33).

> A great number of persons, with horses and wagons, guns and ammunition, had already established encampments on the borders. Two farmers from the vicinity of Russelsville, distant more than a hundred miles, had driven upwards of three hundred hogs to be fattened on the pigeons which were to be slaughtered. Here and there, the people employed in plucking and salting what had already been procured, were seen sitting in the midst of large piles of these birds. The dung lay several inches deep, covering the whole extent of the roosting-place (34).

Passenger pigeons ate massive quantities of tree seeds and produced prodigious amounts of feces. Nesting and roosting broke limbs, thinned crowns, and even toppled trees over large geographic scales. Influences of this bird were so great as to shape the landscape, plant community composition, fire frequency and extent, and ecosystem properties of large sections of the eastern United States (30). Apparent competition was probably in play in the vegetation, with the understory determined by the increased light and high nutrient inputs; the extinction of these birds would have cancelled this food-web dynamic.

THE STRUCTURE OF FOOD WEBS

Nature is based upon species or similar groups of species, guilds, joined in circuits of consumption called food webs. Matter and energy flow from the bottom up, from autotrophs to heterotrophs. Negative feedback in food webs comes from the top down, from consumers who can regulate the rate of resources issuing from producers.

Direct Interactions

Direct interactions occur between species or between an abiotic influence and an organism. Predators eat prey, parasites infect hosts, herbivores eat plants, competitors compete, mutualists confer benefit upon each other, and the abiotic influence of nutrients promotes the growth of plants, and so on.

Aggregations of Functionally Similar Species

Food webs have vast numbers of linkages because each consumer species eats and each resource species is eaten by many other species (35). The operational simplification of aggregating species into groups, guilds, or trophospecies with similar functions is a common and valid approach to food-web research. Thus, similar-sized species of fish that eat the same set of zooplankton species are planktivores in the same way larger fish that eat planktivorous fish are piscivores. Likewise, ungulates, deer, elk, caribou, and moose are herbivores. Aggregation serves different purposes in different applications. An aggregation of many fish species into two guilds, predators and prey, across 26 fished ecosystems of the North Atlantic has provided the insight that latitude, temperature, and species diversity factor into the resilience of a fishery to exploitation (13). Some apparently reasonable aggregations comprise species that are not functionally homogeneous (36). Many communities of predators are functionally heterogeneous, apex predators eat smaller mesopredators that also compete with them to set up a dynamic more complex than a simpler chain. This is intraguild predation. Humans play large roles in the gamut of trophic interactions.

Indirect Interactions

Indirect interactions propagate beyond direct interactions to concatenations of species in chains and webs of biotic and abiotic cause and effect. Most food-web science deals with subsets of particular indirect interactions, called community modules (37). A fuller spectrum of interactions radiates away from the subset (35). The subset of wolves, ungulates, and plants has great practical and theoretical interest (9). Decimation of ungulate predators, especially wolves, by hunting over the past century has contributed to dramatic increases in the populations of these herbivores, which have indirectly changed vegetation. At the same time, this, and every, food web involves a huge number of allied indirect interactions and additional species. For example, mice supported by acorns disperse mutualistic mycorrhizae of oaks (38). The mice can thereby promote oak recolonization where ungulate overgrazing, in the absence of wolves, has eliminated these desirable trees (39). Indirect interactions fall into two main categories, bottom-up and top-down.

Intraguild predation: omnivorous predator species compete with each other for a range of prey species; some species even eat each other

Bottom-up interactions: the transfer of matter and energy without negative feedback up the food web from producing green plants to consuming animals

Trophic guild: a group of species with similar diets, e.g., predators with similar prey species

Bottom-Up Indirect Interactions

Bottom-up interactions are the *sine qua non* of food webs. They transfer energy and nutrients harvested by autotrophs from the sun to heterotrophic consumer species. Every organism is built of energy and nutrients passed to it from the bottom up, and every food web relies on bottom-up interactions (**Figure 1**, see color insert). An early clear statement of bottom-up interactions concerned decomposition, in Hamlet Act 4, Scene 3: "A man may fish with the worm that hath eat of a king, and eat of the fish that hath fed of that worm." The matter and energy of the decomposing king flows to the worm then to the fish. This illustrates the lack of feedback from strictly bottom-up interactions; neither worms nor fish affects the availability of carrion, the food of Hamlet's worms. Bottom-up interactions were the first paradigm of food-web science and dominated the first half of the twentieth century (40). The most common evidence adduced for bottom-up forcing is a positive correlation in space or time among biomasses of trophic guilds. Examples are average fisheries yields positively correlated with primary production (38, 41, 42).

Top-Down Indirect Interactions

The Green World Hypothesis of Hairston et al. (43) was the antithesis of bottom-up food webs. Predators suppress herbivores and thereby allow vegetation to flourish and determine the ecosystem character (lots of green plants) of the terrestrial earth (**Figure 1**). Biomass of predators and herbivores, and herbivores and plants, are negatively correlated. This was among the most-cited papers in ecology in the second half of the twentieth century (44). The synthesis of top-down and bottom-up interactions has had substantial theoretical reinforcement (45–47). As we discuss below, the nature of food webs in the sea and allied areas continues to be debated (48).

Trophic cascades (linear chains of alternating suppression and release between successive pairs of consumer and consumed species) are the quintessential example of top-down interactions. The basic module is three guilds: predators suppress prey, and the prey of the suppressed prey increases. Humans play prominent roles in trophic cascades, suppressing predator populations by hunting and fishing and introducing predators to new places. When human changes increase grazing pressure, the effects cascade to the plant community and alter biogeochemical cycling (49). Many ecosystems have four guilds, involving the suppression of mesopredators by apex predators. Often, when humans remove the controlling influence of the apex predators, mesopredators increase (21).

EVOLVING HUMAN PERCEPTIONS ON FOOD-WEB STRUCTURE

The strictly bottom-up paradigm culminated in studies of energy flow and biotic productivity in Silver Springs, Florida (50), on coral reefs of Eniwetok Atoll (51), and salt marshes (52). This view addressed how producers and efficiency of trophic transfer structured ecosystems; consumers had no influence on the producers. The rate of input of the sun's energy to the green plant autotrophs at the bottom and the attenuation rates at each step up through the succession of heterotrophs were the sole determinants of the productivity and biomass of each trophic group. Consumers did not factor in to determination of rates of transfer, and as a result, they did not affect biomasses among the aggregated trophospecies. However, this view was influenced by an underappreciation of how humans had modified food webs.

The American Alligator

We suspect that by virtually eliminating the dominant apex predator, the American alligator (**Figure 2**), humans shifted the food webs in ecosystems such as Silver Springs to dynamics that encourage a strictly bottom-up perspective. Odum's study (50) makes only the briefest mention of the American alligator, among "Other Species" in an addendum to a table of secondary carnivores. However, as late as the mid-nineteenth century, the American subtropical freshwater ecosystems were dense with very large individuals (20). "The alligators were in such incredible numbers, and so close together from shore to shore, that it would have been easy to have walked across on their heads, had the animals been harmless" (53, p. 123).

This beast was decimated by hunting in the mid-nineteenth century (54–55) and probably doubly so in Silver Springs, a tourist attraction with famous water-skiing beauties. Large alligators with the greatest food-web influence were rare by mid-twentieth century. Coral reefs, the focus of another of the studies of this era done from a bottom-up point of view (51), are now known to be structured by top-down influences (56). Heavy fishing has eliminated herbivorous fish, which together with eutrophication, contributed to overgrowth of reefs by algae.

The basics of top-down thinking were in play by the beginning of the twentieth century in such applied fields as deer management (57) and the biological control of insects (58). Only recently have top-down forces been discovered in salt marshes (20, 59). Models of strictly bottom-up food webs have had enduring influence in fisheries (13, 48). In strictly bottom-up models, there is little theoretical justification for concern that excessive harvesting of larger fish can affect the populations of resource species upon which the harvest of larger fish is based.

Large Marine Ecosystems

> "I believe, then, that the cod fishery, the herring fishery, the pilchard fishery, the mackerel

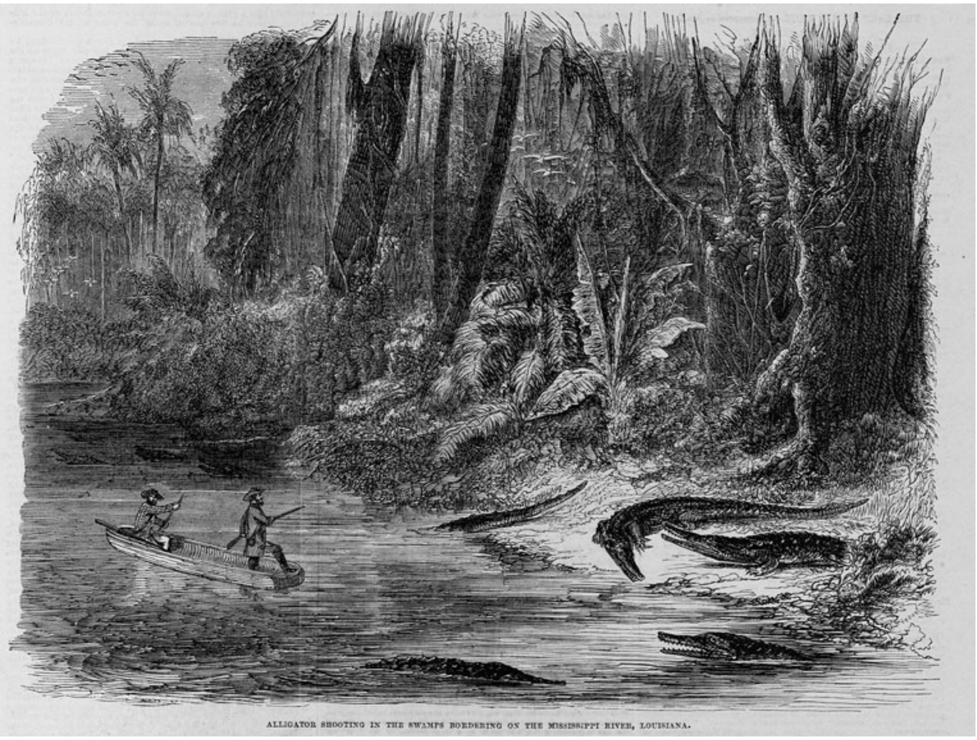

Figure 2

Alligators being shot by humans in the swamps bordering the Mississippi River, Louisiana. Excessive hunting between 1850 and 1960 resulted in dramatic reductions in alligator abundance. Reproduced with permission from Corbis, New York; name of figure is Bettmann BK003214.

> fishery, and probably all the great sea fisheries, are inexhaustible; that is to say, that nothing we do seriously affects the number of the fish. And any attempt to regulate these fisheries seems consequently, from the nature of the case, to be useless" (31, p. 30).

Fast forward to the present, and here are some observations. It has been estimated that the large predatory fish biomass in the global oceans today is only about 10% of preindustrial levels (60). Worm et al. (61) projected that by 2048 all commercially exploited fish stocks would collapse. Modeling studies in the North Atlantic revealed that, during the last half of the twentieth century, the biomass of high trophic-level fish declined by two-thirds (62). Among 21 populations of the once ecologically dominant cod, all have declined by more than 70% relative to historical levels, with 18 of the populations declining by more than 90% (63). Off the east coast of Atlantic Canada during the early 1990s, biomass levels of eight of ten cod stocks reached such low levels that they were placed under moratoria for directed fishing with only limited recovery to date. The declines of cod reached such an extreme state in some areas, such as in the southern Gulf of St. Lawrence, that Swain & Chouinard (64) predicted extirpation in less than 40 years, even in the absence of any fishery.

Despite these reported massive changes to apex predators, Steele and colleagues (65–66) contended they knew of no cases where reductions in marine fish stocks had affected their food supply or that the major shifts in species composition induced by industrial-scale fishing resulted in a breakdown within the ecosystem, comparable to that observed in terrestrial systems. Similar opinions have been echoed in the Pacific, where substantial impacts of fisheries on major top-level predators, involving the removal of ∼50 million tonnes of tuna and other top-level predators since 1950, have been associated with only minor ecosystem-level impacts (67). Top-down control by predators is generally regarded as uncommon in the open ocean because of high species diversity, patchiness in productivity, and highly mobile and opportunistic predators. For instance, McCann et al. (68) showed that more spatially confined consumers, such as those occurring in lakes and ponds, exerted stronger top-down effects than wider ranging consumers in marine systems, which typically encounter multiple dispersed prey populations (5).

The concepts of top-down forces have come to the science of large marine ecosystems only recently and have yet to become the paradigm of structure and function of these food webs. Trophodynamics, strictly bottom-up function, has continued to maintain an audience that subscribes to the view that the supply of new recruits will inexorably generate biomass lost to fishing (69). As late as two decades ago, advocates of top-down forcing (70) were largely ignored or the approaches they suggested were ignored (71). At the same time, evidence for top-down forcing was mounting. Bax (72) showed that predation removes between 2 to 35 times more of the total fish production than fishing in a large number of systems. Detailed energetic studies on Georges Bank reinforced the contention that most of the production of fish is consumed by other species (73), shoring up the idea that consumers structure the food web and that prey populations respond when fishing reduced the abundance of their predators. In the past few years, fisheries studies with a top-down point of departure have become more frequent (74).

Resolving the Influence of Top-Down Control

Whether or not contemporary open-ocean food chains function as predicted by top-down interactions remains a crucial question, but many fisheries scientists contend that such a construct has uncertain relevance to marine systems given that the main body of observations and experiments illustrating top-down control were made within non-analagous systems (75, 76). Furthermore, many fisheries scientists believe that the perception of marine species and ecosystems as overexploited is exaggerated and "overly alarmist" (77) and that the quantitative basis for the conclusions drawn about the dire state of the global fisheries is technically flawed (78). Others contend that the if the ecosystem effects of fishing are difficult to evaluate, particularly because indicators of ecosystem states are still a matter of research and debate, concern about over exploitation may be unwarranted (79). A meta-analysis of 47 marine mesocosm experiments and of the time series of nutrients, plankton, and fish from 20 natural marine systems inferred that the effects of consumer-resource interactions do not cascade downward through marine pelagic food webs (80), leading to the view that biomanipulation (restoration of apex predators), as conducted in lake systems, would not be effective in controlling the response of marine primary producers to nutrient enrichment.

TROPHIC CASCADES: FROM WET TO DRY

There are several well-known classic examples of trophic cascades, particularly from aquatic systems, that have been extensively discussed and reviewed in the literature. These include the intertidal webs of Pacific invertebrates that gave early insights of top-down effects (81) and that have been a steady source of new information on more elaborate indirect interactions (82). Further to the north, the sea otter, sea urchin, kelp food chain was discovered as a result of an imbalance created by an intensive Russian fur trade that caused local extinctions of sea otters. The extinction released sea urchin herbivores to overgraze kelp, leading to the formation of so-called urchin barrens (83). Recently, killer whales have become a fourth link in the Pacific chain, eating sea otters and reversing the abundances of the species down the chain (84). Freshwater lakes (85) and rivers (86) provide additional observational and experimental evidence of cascading trophic interactions. Piscivores, such as bass and trout, are valued game fish, and heavy fishing reduces the pressure on planktivores and switches abundances of trophospecies down the chain. This allows algae to burgeon and waters to turn opaque green. One of our objectives is to draw attention to several other examples of trophic cascades, some more recent than others, in a diverse array of systems that as Pace et al. (87) suggested would emerge as the result of "purposeful management activities and the unwitting consequences of human-driven environmental change."

Shallow Benthic Marine Ecosystems

Top-down thinking challenges the widely held idea that dense phytoplankton and benthic algae on shallow reefs, in estuaries, and in sea grass meadows are a result of eutrophication (88). The apex predators are literally long gone, not unlike American alligators now severely reduced in freshwater habitats. Although the toll of heavy fishing is apparent, the top-down effects must be inferred. However, it would be illogical not to do so. A commonality is the historically low numbers of herbivores in these habitats (25). A meta-analysis of 54 experimental studies revealed that, even though both nutrient enrichment and absence of herbivores contributed to algal growth, the latter had greater influence than the former (56). This was especially true at lower latitudes and at lower nutrient levels. Importantly, suppressed herbivore populations make a larger contribution to the change in state from coral to algal-overgrown reefs, especially in the Caribbean Sea. Similar results were obtained in the cod-depleted Baltic Sea (89), where increased densities of small-bodied fish have reduced small gastropods that scrape algae from rocks and allowed increase of algae. In this relatively high-latitude case, eutrophication and the trophic cascade have roughly equal weight in the enhanced algal growth.

Continental Shelf and Inland Sea Ecosystems

Within the past decade, the science of large-marine ecosystems has increasingly adopted a top-down view cast in terms of trophic cascades quite similar to the view that guides terrestrial and freshwater research (74). The cornucopian, strictly bottom-up paradigm that prevailed for centuries, invoking vast geographic scale, great diversity, and extraordinary fecundity as capable of absorbing any level of exploitation, has given way to the view of trophic cascades. The modern perception is human-impacted global oceans are associated with intensive, industrial-scale fishing (trawling, purse seining, longlining) concentrated in relatively shallow (<200 m) continental shelves of the temperate and tropical seas (90). This huge fishing effort has caused widespread depletion, a disproportionate loss of the largest species, and a collapse of many local stocks. The magnitude of biomass removals, its spatial extent, and focused depletion on formerly dominant, large-bodied foundation species [sensu Soule et al. (91)] make fishing activity a strong candidate for effecting large-scale change to marine food webs and their contributions to ecosystem structure and function.

Cod, Seabirds, Forage Fish, and Plankton

Two examples highlight the dramatic restructuring of the entire food web of the eastern Scotian Shelf ecosystem in the Northwest Atlantic and the Baltic Sea that occurred during the early 1990s and that was associated with the collapse of cod and other large, formerly dominant predatory fishes (28). On the eastern Scotian Shelf, the cascading effects resulted in massive increases in the former prey of cod and other demersal species—small-bodied benthic and pelagic species, northern shrimp (*Pandalus borealis*), and snow crab (*Chionoecetes opilio*).

Ironically, the explosive increases in shrimp and crab led to the rapid proliferation of a lucrative commercial fishery, whose combined monetary value alone exceeded the benthic vertebrate fishery it replaced. Large-bodied herbivorous zooplankton declined while small-bodied zooplankton remained unchanged, consistent with size-selective predation by the small-bodied fishes and early life stages of shrimp that had increased with the collapse of cod. The decrease in large zooplankton with increased small, planktivorous fish was reminiscent of food-web restructuring in lakes (92). Both amplitude and duration of the spring phytoplankton blooms increased as the large zooplankton species declined (93), also reminiscent of changes in lakes driven by trophic cascades (85).

Overfishing of cod greatly impacted the Baltic Sea food web, resulting in explosive increases of its main prey, sprat (*Sprattus sprattus*), a zooplanktivorous clupeid fish. The cascade carried through, indirectly, to a decline in summer biomass of zooplankton followed by increases in phytoplankton (94). Sprat have a strong effect on the food web. They are the main prey of cod and other apex predators and a major regulator of large zooplankton. However, without the apex predators, sprat populations soar to unprecedented highs, the fish are stunted, and energy content of individuals plummets (95), a well-known outcome for trophic cascades in lakes (96). The cascade carried even further, to negatively affect reproduction of the piscivorous seabird *Uria aalge* (97). In the "junk food" hypothesis (98), overfishing of apex predators cascades through mesopredator, planktivorous fish to seabirds as well as to marine mammals in a variety of ecosystems.

Sharks, Rays, and Scallops

In the western Atlantic, intensive fishing greatly decreased 10 species of large sharks. Notable declines were from 87% for the sandbar shark and to 99% or more for bull, dusky, and smooth hammerhead sharks. The fishing virtually removed their predatory impact on a taxonomically diverse group of 14 ray, skate, and small shark species (99). The most conspicuous food-web response was seen in the cownose ray, *Rhinoptera bonasus*, which increased in numbers by more than 40 million individuals. This cascaded to heavy predation upon bivalves, such as bay scallops, soft-shell clams, hard clams, and oysters, all of which decreased greatly in numbers. Bay scallops were particularly hard hit, and by 2004, the predation by rays had terminated a century-old fishery.

Upwelling Ecosystems

At the eastern boundaries of oceans, winds pull nutrient-rich water from the depths to the surface and create some of the most productive fisheries in the world. Not surprisingly, these have been heavily fished (100) and show top-down food-web responses (101). For example, after the 1990s collapse of planktivorous sardines and anchovies in the northern Benguela food web off Namibia, jellyfish reached extraordinary high levels sufficient to foul fishing nets, spoil catches, and block power station coolant intakes (102). In this case, the indirect interaction was inferred to be omnivory and intraguild predation (discussed below) rather than a simple linear trophic cascade. Jellyfish eat fish eggs and larvae as well as zooplankton, which means competition with, and predation upon, sardines and anchovy. The hypothesis is that the shift from planktivorous fish to jellyfish in the Benguela is irreversible. Food web shifts from fish to jellyfish dominance, following heavy fishing, have also been observed in the Bering, Black, Caspian, and Japan Seas as well as in the Gulf of Mexico (103).

Geese, Blue Crabs, and Alligators in Salt Marshes

Salt marshes were long seen as strictly bottom-up food webs (52). However, a trio of top-down discoveries has been brought to science about these biomes in recent years. The first was in long-term studies of Arctic salt marshes in Hudson Bay (104). Until the late 1970s, snow geese populations had been low and grazed moderately, stimulating plants by aeration of the soil and fertilization with their dung; a bottom-up hypothesis was all that was necessary. Then, heavily fertilized food sources in large-scale agriculture and new wildlife refuges proliferated on the wintering grounds of the Gulf coast of the United States. Hunting pressure decreased on the wintering grounds. These changes resulted in more geese migrating back to Hudson Bay and heartier animals nesting upon arrival. Snow geese populations irrupted and changed from a passive receiver in a bottom-up chain to powerful top-down actor destroying vegetation that supports their reproduction on the summer breeding grounds in Hudson Bay.

The second and third examples apply to the salt marshes of the Atlantic and Gulf coasts of the United States, where the snow geese originally overwintered. Snails grazing on *Spartina alterniflora*, and on the fungi growing in leaf scars of previous grazing, can slow the growth and even kill the plant. Heavy fishing reduces blue crab, a major snail predator, and tips the balance against the plant (59). The third example is part and parcel of the decimation of the American alligator by hunting in the late nineteenth century, coupled with introduction of the nutria, a large herbivorous rodent, to Louisiana in the early 1900s (20). The theory is that widespread marsh damage owing to native muskrat and the introduced nutria would be slowed or prevented by dense populations of large alligators; more, larger alligators would eat many more of these herbivores. However, high densities of these ferocious creatures are precluded by people's fear of them and by the value to hunters of their skins and meat. Erosive losses of salt marsh on these coasts are serious, and the potential for contributions of top-down forces by alligators is substantial (20).

Big Predators, Big Herbivores, and Vegetation

Humans have long been deeply involved in the changing chains from wolves, big cats, wolverines, and bears to ungulate herbivores to vegetation (21). European and American explorers often found that Native Americans' hunting of bison, moose, elk, and deer was so heavy that these animals were sparse except where intertribal war reduced the take. Where hunting Native Americans were abundant, ungulates and other game were not (105). While suppression of the predators remained in place, deer populations rebounded from heavy hunting and, in the twentieth century, attained levels that are arguably as high as the European and North American landscapes have ever seen (39). Game laws, the growth of food subsidies for deer in expanded agriculture and landscaping, population-boosting management schemes, and severe reductions of predators—mainly wolves—contributed to the increases. Freed from predation, herbivores can explode in numbers and greatly impact plants, culminating in apparent competition that changes the vegetation (9).

Heavy deer browsing has changed the landscape over large areas in the upper midwestern United States. The native vegetation is forest glades of understory herbs and trees that are both preferred by deer and intolerant to grazing (39). Acorns, seedlings, and saplings of slow growing oaks, eastern hemlock, and northern white cedar are particularly vulnerable. Over the upper midwestern United States, deer find and eat most saplings of these species before they grow beyond 30 cm. Owing to large underground storage organs, palatable herbs and shrubs can endure longer, but clones shrink slowly with little sexual reproduction (106). Deer eat the flowering shoots. Dense deer populations can lead to decreasing plant species richness and cover as browse-tolerant plant species that are resistant to deer become abundant. The heavily grazed vegetation shifts into more open prairies of ferns and grasses that resist deer with chemical and physical defenses or tolerate their grazing with rapid growth and underground meristems. This interaction is labeled apparent because, in the absence of knowledge of the grazing, one could have inferred that plant competition drove the vegetation change. Yet other ecological changes follow indirectly from high deer populations. These include reduction in songbirds, pollinators, and invertebrates that depended upon the forest flora (9).

SIZE MATTERS

Body size is a key trait in food webs, influencing abundance, distribution, species interactions, and physiological performance (107). Large animals, with larger food-web influences, have suffered greater losses to humans than smaller animals and plants, in a phenomenon known as trophic skew (108). On land, food webs are losing large apex predators and gaining smaller mesopredators (21). The consequences of such losses can be neatly illustrated by returning to our earlier example involving alligators. A large alligator kills ten times the number of nutria and muskrats as a small alligator (20). In coastal marine food webs, about 70% of extinctions, in recent human-dominated times, have been of large species at high trophic levels, among top and mesopredator species (27). The resultant webs are flatter with far more filter feeders and scavengers. However, the connections between body size and the influence of consumers in food webs are varied (109). Predators are proportionally larger than their prey in freshwater than in marine or terrestrial habitats, and vertebrate predators are proportionally larger than their prey than invertebrate predators. Although consumer size can translate into food-web influence, parasitoids (110) and other invertebrate predators, such as entomopathogenic nematodes, are smaller than their prey and can have powerful suppressive effects upon their hosts that transfer down trophic cascades.

Within the ocean, body size plays a fundamental role in structuring trophic interactions, and on a world scale, marine fisheries are largely size selective, targeting and/or incidentally removing the largest individuals and species. This has led to rapid temporal reductions in the body size of top predators. Thus, rates of phenotypic change in body size caused by commercial harvesting can be >300% higher than natural rates (111). Size reduction of target species is often the direct result of harvest management plans that set minimum size limits. This focuses fishing effort on larger individuals, yet the consequences of changes in predator size composition on large-scale trophic structure and function remain outstanding questions in ecology. However, newly emerging studies have begun to explore the consequences of losing individuals with specific traits within food webs. For example, Shackell et al. (112) documented an unexpected increase in prey biomass in an area where the aggregate biomass of piscivores remained unchanged owing to compensatory increases in abundance of unexploited species. Nonetheless, significant reductions in predator body size had occurred (**Figure 3**), suggesting predator body size was a major determinant of trophic control operating in an analogous manner to that reported for alligators in Louisiana marshes.

DIVERSITY AND TROPHIC STABILITY

Pertinent to human involvement, the stability of food webs is measured in terms of resilience and resistance to change. In theory, diversity increases when interaction strengths are on average weak between consumers and resource species (113). The lack of runaway consumption and instability in terrestrial food webs, such as in the grasslands of the Serengeti National Park, are part and parcel of trophic linkages between herbivores and their resources that are weakened by particular traits of species that make them more tolerant to grazing, such as underground storage organs and basal meristems (106) and more resistant to it, such as thorns and allelochemistry, which discourage the herbivores. Herbivore-plant interactions are also weakened by diverse and abundant apex predators that suppress herbivore populations, as with the wolf-ungulate-vegetation trophic cascade before human removal of apex predators. From this perspective, human removal of apex predators destabilizes both aquatic and terrestrial food webs by increasing the interaction

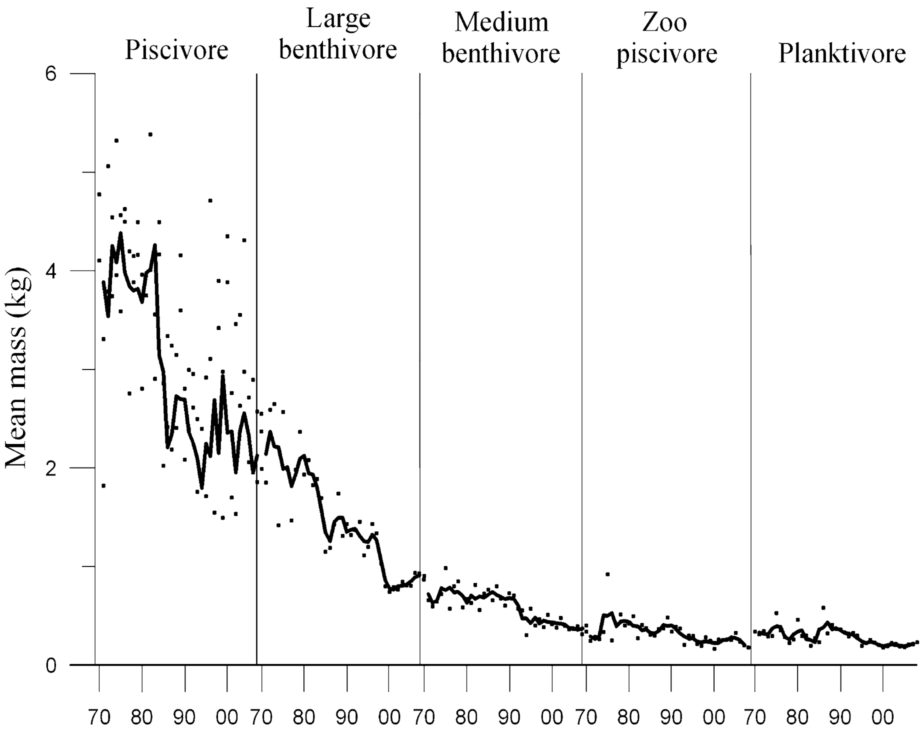

Figure 3

Changes in average body size associated with five functional groups of fish species from the western Scotian Shelf during the past 38 years (1970–2008). Note the large declines in body mass among the heavily exploited piscivore and large benthivore functional groups. Adapted from Reference 112.

strength between mesopredators, herbivores, and plants. The apex predators were the source of weakening to these lower-level interactions in the web.

In oceanic webs that are more resistant to disruption by fishing, productivity of apex predators is higher, and higher numbers of species fulfilling the apex role makes them more stable. For example, warmer water stocks are capable of recovering much faster from direct exploitation than populations residing in colder water systems (114), and the depletion of a dominant species can be compensated more readily in species-rich areas by increases in other functionally related species. Species compensation has been demonstrated in several exploited ecosystems [Georges Bank (73), North Sea (115), Scotian Shelf (116)], resulting in a dampening of variability in aggregate abundance with the depletion of target species. These processes preserve the trophic structure of warmer water systems by preventing the aggregate top predator biomass from declining, thereby maintaining a balanced state with their prey. The contextual dependency of the reaction of an ecosystem to exploitation effects explains why "the literature on top-down versus bottom-up community regulation is vast and varied" (117). Furthermore, Chalcraft & Resetarits (36) suggest that failure to consider turnover in species composition with trophic levels has produced conflicting results that support opposing models of trophic structure (i.e., bottom-up versus top-down effects).

OUT OF THE GUILDED CAGE

Some food webs are more complex than stepwise trophic cascades (118). Omnivores, which eat species from within their guild and from a range of trophic levels, are consumers that can compete with each other and even eat each other.

Omnivory, Intraguild Predation, and Mesopredators

Intraguild predation can give quite different food-web dynamics from simple trophic cascades (44). Life-history omnivory can reverse the trophic polarity for apex predators, which have their smaller stages exposed to predation by species that are prey when they are adults. For example, young cod are prey to adult sprat, mesopredators that are a major prey of adult cod. Where adult cod have been fished to low levels, sprat can suppress the recovery of the cod population. Intraguild predation can shift trophic control and lead to a different outcome from a linear trophic cascade (118). Intraguild predation is common (119) and affects many food webs in which humans are involved.

Mesopredator Release, Suppression, and Species Introductions

Mesopredators eat species from a spectrum of trophic connections (21). Hunting and fishing that reduce apex predators, such as alligators, wolves, dingoes (120), and piscivorous fish also release smaller mesopredators, such as nutria, coyote, foxes, and planktivorous fish to create greater suppression of their prey, such as songbirds, endangered marsupials, and herbivorous zooplankton. In biological control, mesopredators can be the source of control of the target pest, and their suppression by other predators is undesirable (110). Mesopredators, such as snakes (121) mice, rats, and house cats, introduced to islands without apex predators threaten nesting seabirds, such as the albatross, with extinction (122). Introduced Arctic foxes, predator free on islands, so severely reduce nesting seabirds and the nutrients from dung as to lower plant productivity and transform vegetation from grasslands to shrublands (123). In a grisly story of unintended consequences, more than 50 species of terrestrial *Partula* snails have been driven extinct primarily by a predatory snail introduced in a failed attempt to control a previously introduced African herbivorous snail (124). Freshwater carp introduced to the Mississippi River system are archetypical intraguild predators, preying upon plankton, invertebrates, and small fish and competing with native fish. Without predators of their own, these carp species can reach massive size and numbers and are also a serious additional threat to the diverse mussel and snail fauna of the Mississippi River system and the Great Lakes (125).

Life-History Omnivory and Mesopredators in Large Marine Ecosystems

A great deal of the variation in changes to large marine fisheries caused by heavy fishing is consistent with a linear trophic cascade reminiscent of increases of planktivorous fish observed in lakes following heavy exploitation of piscivorous fish species. A meta-analysis within several discrete management areas across the North Atlantic revealed that reduced predation by cod, which had declined because of overfishing in the early 1990s, was the cause of sharply increased shrimp populations (126). The observation that increases in sand lance accompanied the declining biomass of cod, its main predator, on the eastern Shelf can also be accounted for as a simple trophic cascade, with another link from sand lance to gray seals, which appear to have benefited from cod collapse (127). However, this means that cod and gray seal compete. Cod are also prey of this marine mammal (28), raising the issue of intraguild predation and cod as a mesopredator; its recovery from depressed levels could be hindered by the apex predator, gray seal.

Also suggested by the data was life-history omnivory. In this same geographic area as the preceding examples, other benthic fish species co-occurring with cod either collapsed or were severely reduced in abundance. The dramatic increase in the biomass of small-bodied species, many of which were the former prey of the large-bodied demersal fish species, was the main contributor to the changing composition of the fish community.

Contributions to the changes from both mesopredator release and life-history omnivory are suggested in adjacent areas in the Northwest Atlantic, which had nearly identical compositional changes in the fish community, resulting from similar processes (128, 129). The persistence of small-bodied fish species in these systems was reinforced by their capacity to compete with and prey upon their former large-bodied benthic predators, particularly their early life stages, which has major consequences for recruitment (64). In this situation, the hunted has become the hunter. Such predator-prey role reversal has been observed in several different systems (130, 131). Walters & Kitchell (132) have argued that the reproductive success of large benthic fish in unexploited systems is partly due to high predation pressure exerted by adult stages on their prerecruits' competitors and predators. Such suppression of mesopredators is called cultivation in the fisheries literature.

Alternative Ecosystem States

The changing trophic role between mesopredators and apex predators provides an intrinsic mechanism that can maintain an alternate ecosystem state despite the cessation of fishing and other protective measures. Consistent with this viewpoint are the numerous examples of failures of collapsed marine fish species to recover (133). In the formerly cod-dominated systems still closed to fishing in the Northwest Atlantic, estimates of natural mortality are two to three times greater than historical, precollapse levels (134). In the case of eastern Scotian Shelf cod, a multivariate index of ecosystem state, derived from time series of biotic, abiotic, and human variables (135), revealed a transition to an alternative, persistent state and a lack of recovery of cod despite the cessation of directed fishing pressure for 17 years. Clearly a hysteresis has occurred in this ecosystem, and the common assumption that overfishing effects are reversible is indeed a tenuous one. This makes the prediction of the conditions required for recovery of apex predators and the associated timescales highly uncertain.

AVENUES TO RECOVERY?

Damaged food webs cause many different problems for humans. The absence of apex predators and unsuppressed mesopredators cause green opaque lakes (85), large conservation concerns, substantial economic losses, and poverty, as well as alterations in food-web structure and function that impact ecosystem services (136, 137). Visions of recovery range from fairly clear to obscure. Eradication campaigns are widely seen as a sensible management approach to introduced predators and herbivores on islands (138). At the same time, restoration schemes for continents, or "rewilding" to a prehistoric condition, are loaded with diverse, vague, and conflicting human values far from science; they are risky on social as well as biological grounds (139). In lakes where the original food web is often known, the culling of old stunted prey fish (96), reduced take of piscivores, and biomanipulation (140) can yield a restored food web. In large-scale ocean fisheries, the original state is often unknown (141). Even when some prior desirable food-web state is known or assumed, the tactics of culling undesirable fish (95), restocking depleted desirable top predators, and elimination of a new top predator are frequently considered but have not often been successful. For depleted cod fisheries, the culling of seals, fishing down small pelagics that are competing and preying upon cod, and other approaches have been vigorously debated (142). All proposed actions could bring unwanted consequences. Seals may be suppressing the biomass of small pelagics (143), but the introduction of seal control would run the risk of negative public reaction and the possibility of consumer action, such as boycotts of seafood products. Ocean food webs have many more species than lake food webs. Small pelagics could be suppressing jellyfish and other gelatinous predators, as has been suggested in the Benguela

Current. With cod, fishing capacity reduction and no-take zones have been implemented on Georges Bank and elsewhere. The message of trophic ecology is beginning to be heard and implemented with a focus upon aggregated guilds of species with similar prey rather than upon single species (144). Ocean food webs could profitably be viewed in a broader, more general perspective of ecosystem services (136), spatial scale, and time to recovery of other large-scale environmental losses (145).

VALUES, FOOD WEBS, AND ECOSYSTEM SERVICES

Knowledge of how food webs function and are affected by humans rests on the values of basic science as well as on objectivity and rationality informed by empiricism in which humans are just another species, albeit a hugely powerful one. The future of food webs is in conservation, a social science that brings in additional values as much as in basic science. Utilitarian values include ecosystem services provided to humans. Economic services are easiest to understand. The largest predators on Earth, whales, have not done much in terms of direct contributions to the economy lately, but they did contribute mightily to it in earlier days (146). The contribution had a signal-response delay (137) in the enduring depression of sperm whale populations, which might indirectly contribute through the food web to richer oceanic fisheries in the present day (147). Fish have enduring economic value, and the loss of fisheries as part and parcel of food webs that support them is economic loss, apropos to the cod food web and its vigorous rearrangement by late twentieth century industrial fishing. The cod collapse and the cessation of fishing that occurred in the early 1990s in Atlantic Canada affected some 40,000 workers and hundreds of communities (148). Federal aid packages totaling more than $2 billion softened the short- to mid-term impact, but the fact that some of the eastern Canadian provinces have been losing human population, notably Newfoundland, speaks to the persistent economic effects that have cascaded, trophic style, to sad social and cultural ends. Other big players in food webs present more difficult problems in that they cost much more money to preserve than they could ever produce. Only small contributions to the larger human economy have ever been made by the most charismatic of terrestrial vertebrates, (e.g., big cats, elephants, rhinoceros), and the values upon which their future rests are more cultural, or intrinsic, than economic (136). The order Carnivora is in global trouble, and preservation will be very costly (149). Big predators do not live well together with humans (20, 150, 151). Hopes rest upon a combination of well-planned and -conducted ecotourism (137) with protected areas large enough to support the food web in its migrations upon which such species depend (152). An even more multifarious set of values affects the ecosystem services to the Louisiana coastline that might be supplied through the food web by large, dense populations of American alligators, which slow erosion losses caused by nutria grazing (20). Large, dense populations of American alligators terrify people, who support hunting them, which downshifts their density and size structure, provides income, and reduces their food-web influence.

SUMMARY POINTS

1. Food webs begin with direct interactions, such as between predators and prey. Indirect interactions occur among more than two species, such as the top-down force of the trophic cascade in predators suppressing herbivores with the result of increased plant growth.

2. Early humans had local influences upon food webs through the depletion of prey and fish, land clearing, burning, pastoralism, and agriculture, which subsidized garden hunting and fishing. Larger, later human populations with more sophisticated technology broadened and deepened penetration into many terrestrial and aquatic food webs.
3. Top-down forces complement the bottom-up forces of energy transfer from plants to herbivores and to higher consumers in food webs. In fisheries, top-down forces are the rationale for exhaustibility of stocks and have been controversial.
4. Release of herbivores has resulted from excessive hunting and fishing of apex predators. The decimation of wolves contributed to irruptions of ungulates, deer, elk, and moose, which transformed vegetation over large areas. Hunting of the American alligator probably released heavy herbivory by the introduced nutria, which has accelerated erosion loss of shoreline in Louisiana.
5. Mesopredators, such as coyotes, snakes, rats, house cats, foxes, and predacious snails, have been released to threaten sensitive prey species such as songbirds, seabirds, endangered mammals, and snails. Mesopredators are a negative factor for conservation but can be a positive one to biological control of insect pests.
6. Appreciation of food webs can contribute to understanding the collapse of cod and other apex predators in open-ocean systems and their unexpected lack of recovery despite cessation/reduction of fishing.
7. Restoration of food webs is a matter of values. The much desired recovery of fisheries and protection of the remainders of charismatic large animal webs engage some promising action and a great deal of hope. By contrast, large terrestrial predators do not coexist harmoniously with humans, and isolation in refuges is the only long-term hope for the most ferocious of them.
8. Humans have changed many food webs permanently.

FUTURE ISSUES

1. How can society restore large-bodied predators when the largest are most highly prized, most feared, and most persecuted?
2. Top-down food-web ecology thrives in theory and academic ecology. Its greatest value is in practice and application to management of resources.
3. Overlooking formerly abundant species' food webs can distort our interpretation of how nature works. At the same time, food webs of small organisms, parasites, mutualists, and soil organisms are poorly known. Who rules the world, the vertebrate king or the lowly worm?
4. Are historical baselines really relevant as objectives for recovery of degraded ecosystems? Or should we seek to maintain key ecosystem functions instead?
5. Should commercial-scale harvesting of natural resources occur at multiple trophic levels simultaneously to maintain ecosystem stability?

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

We thank William C. Leggett, Jonathan A.D. Fisher, and Nancy L. Shackell for reading an earlier draft of the manuscript and Nancy Shackell for help preparing **Figure 3**.

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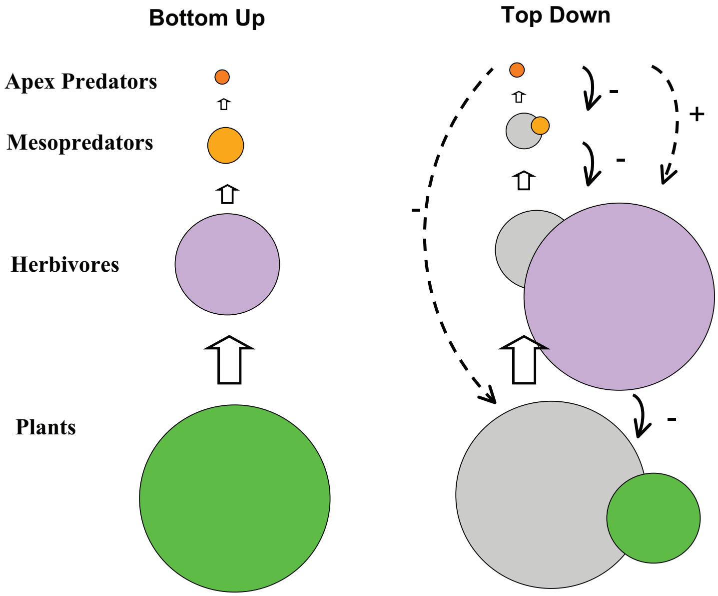

Figure 1

Alternative views of how food chains are structured. On the left, bottom-up controlled food webs, where productivity at the basal level determines the biomass at higher trophic levels. On the right, top-down control is shown whereby apex predators determine the abundances at lower levels through alternating strong and weak predation effects. The diameter of the circles represents the relative abundances of the corresponding trophic level, and indirect effects are indicated by dashed lines. The gray circles on the right image indicate the biomasses of the trophic guilds in the absence of top-down effects.

Annual Review of
Environment
and Resources

Volume 35, 2010

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