

Trophic cascades revealed in diverse ecosystems

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‘Since then I have lived to see state after state extirpate its wolves. I have watched the face of many a new wolfless mountain, and seen the south-facing slopes wrinkle with a maze of new deer trails. I have seen every edible bush and seedling browsed, first to anemic desuetude, and then to death. I have seen every edible tree defoliated to the height of a saddle horn.’
Aldo Leopold 1949 (Ref. 1)

This wolf–deer–plant interaction described 50 years ago would today be called a trophic cascade. Cascades are defined as reciprocal predator–prey effects that alter the abundance, biomass or productivity of a population community or trophic level across more than one link in a food web (Box 1). Trophic cascades often originate from top predators, such as wolves, but are not necessarily restricted to starting only in the upper reaches of the food web.

Despite Leopold’s observations of trophic interactions in terrestrial systems, the predatory effects arising from cascading trophic interactions have been described most often in lakes, streams and intertidal zones. The preponderance of aquatic cases led Strong² to assert that trophic cascades were ‘all wet’ – prominent only in certain simple ecosystems in which dominant herbivores exert ‘runaway consumption’. In more diverse ecosystems with highly speciated trophic groups and extensive spatial heterogeneity, trophic cascades were hypothesized to be less evident because they are blocked by complex interactions^{2,3}.

However, new findings illustrate that trophic cascades are not categorized so simply. Here, we review recent evidence that suggests that trophic cascades are not restricted by ecosystem type or trophic complexity. We consider how experimental studies are altering the static view of cascades revealing variable and context-dependent aspects. We also appraise the wider implications of recent cascade research for resource management and conservation.

Widespread trophic cascades

Cascades are turning up in interesting places, ranging from the insides of insects⁴ to the open ocean⁵. There are continuing observations of trophic cascades in streams, lakes and the marine intertidal zone, but new examples are emerging from studies of terrestrial and marine ecosystems including fields, soils, forests and the open ocean (Table 1). Thus, contrary to previous assertions^{2,3}, cascades do not appear to be restricted by ecosystem type, diversity, habitat

New studies are documenting trophic cascades in theoretically unlikely systems such as tropical forests and the open ocean. Together with increasing evidence of cascades, there is a deepening understanding of the conditions that promote and inhibit the transmission of predatory effects. These conditions include the relative productivity of ecosystems, presence of refuges and the potential for compensation. However, trophic cascades are also altered by humans. Analyses of the extirpation of large animals reveal loss of cascades, and the potential of conservation to restore not only predator populations but also the ecosystem-level effects that ramify from their presence.

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complexity, types of top predators or the trophic mode of consumers. It is possible that trophic cascades are less likely under conditions of high diversity or extensive omnivory in food webs, but data are insufficient to test these possibilities rigorously. Furthermore, the appearance of trophic cascades in high diversity marine and terrestrial systems including tropical forests (Table 1) implies that more will be found as the search expands to new environments. However, the general importance of trophic cascades in terrestrial systems remains uncertain⁶. Experiments in aquatic systems suggest that trophic cascades hinge on strong interactions promoted by particular species and are best revealed by powerful, large-scale manipulations⁷. Terrestrial ecologists might well want to consider this experience in evaluating the significance of land-bound cascades.

Trophic cascades have powerful impacts on ecosystems. For example, the presence of brown trout (*Salmo trutta*) in a New Zealand stream results in a sixfold difference in annual primary production compared with an adjacent stream with very similar nutrient concentrations but with a different top predator, the common river galaxias (*Galaxias vulgaris*), and no trout (Table 1). The basis for this trophic cascade is well documented. Trout predation lowers the density of grazing invertebrates leading to a higher biomass of attached algae⁸. In the presence of trout, herbivorous mayflies (e.g. *Delatidium* spp.) spend more time secluded under rocks and less time foraging on upper, exposed surfaces⁹. Thus, grazing declines and algal biomass accumulates, even in the absence of changes in mayfly abundance⁹. At the ecosystem level, these interactions amount to huge differences in primary and invertebrate secondary production, simply on the basis of different top predators¹⁰.

There is evidence from recent removal experiments of lizards (primarily *Anolis* spp.) that trophic cascades occur in highly speciated tropical food webs^{11,12}. Although greater leaf damage by insects is observed in the absence of lizards, it is uncertain whether these interactions strongly affect primary production or total plant biomass. A full trophic cascade, however, has been observed and documented experimentally in highly diverse lowland tropical forests in Costa Rica (Table 1) – a place where trophic cascades were presumed not to occur. Letourneau and Dyer¹³ found densities of *Piper* plants (*Piper* spp.), herbivores,

Box 1. Definitions, origins, terms and models associated with trophic cascades

Trophic cascades result in inverse patterns in abundance or biomass across more than one trophic link in a food web⁷. For a three-level food chain, abundant top predators result in lower abundances of mid-level consumers and higher abundance of basal producers. In this case, removing a top predator would result in a greater abundance of consumers and fewer producers. The trophic cascade concept arose from the observations and experiments of field ecologists who observed the powerful organizing force that alternative predatory regimes could instill in the marine intertidal zone¹⁵ and in lakes^{40,41}. The concept of trophic cascades has since radiated through ecology and become the focus of theoretical analyses, field studies and management application.

Particular terms are often used in association with trophic cascade. For example, 'top-down' control means regulation of lower food-web components by an upper-level predator. A contrasting term 'bottom-up control' describes regulation of food-web components by either primary producers or the input of limiting nutrients to an ecosystem. A well recognized problem with the concepts of 'top-down' and 'bottom-up' control is that they are difficult to separate in practice, and in many situations some form of resource ('bottom-up') and predatory (top-down) control is operative. These terms also tend to be used in the context of equilibrium conditions, yet most natural food-webs are probably rarely near equilibrium. Thus, although there is some descriptive value in the use of top-down or bottom-up control, this motif also creates a false dichotomy and is difficult to put into operation.

Trophic cascades also relate to early theoretical ideas in ecology about the relative importance of herbivory and predation⁴², as well as food-chain length in controlling primary productivity⁴³. Although these early models can represent the dynamics of some systems, nature is more commonly constructed of complex food-webs and not chains. In this context, trophic cascades are strong interactions within food webs that influence the properties of the system. The trophic cascade concept, however, is not necessarily meant to represent the predictions of equilibrium models based on food chain length. Rather, model predictions focus on variability and dynamics^{7,17}. Models of trophic cascades are also sufficiently flexible to reflect system responses to a pulse⁴⁴ as well as sustained perturbations²².

Although trophic cascades might be transitory, trophic interactions can also be strong and might stabilize systems in an 'alternate state'. An example is the otter-urchin-kelp interaction of coastal North America³⁷. Otters stabilize a system of abundant kelp forests by reducing urchin grazing. Removal of otters shifts the system to urchin dominance with substantial reductions in kelp coverage and productivity. Thus, trophic cascades can induce dramatic shifts in both the appearance and properties of ecosystems. The contrast of these states can be profound (e.g. slimy-green to clear-blue water, or a marine bottom dominated by a kelp forest versus an urchin-spined barren). These phenomena represent an important class of nonlinear ecological interactions. Understanding these interactions remains a challenge to the prediction of ecological dynamics and to the management of ecosystems.

ants and beetles that were consistent with a four-level trophic cascade (Fig. 1): beetles prey on ants that defend the *Piper* plants against herbivorous insects. In a comparison of four forests, *Piper* plants were at a low density in the forest with abundant beetles (Site 1, Fig. 1a), whereas *Piper* plants were abundant in forests with few beetles (e.g. Site 4, Fig. 1a). When beetles were added to enclosures¹⁴, ~15% of the *Piper* petioles harbored ants, whereas in controls 50% of the petioles had ants (Fig. 1b). Fewer ants resulted in greater herbivory and less leaf area remaining at the end of an 18-month experiment. This trophic cascade depends on two strong interactions: effective predation by the beetles on ants, and ant defense of *Piper* plants against herbivorous insects. Strong interactions of this type are the hallmark of cascades¹⁵.

Another unexpected place to find a trophic cascade is the open ocean. Here, physical forces and nutrient fluxes play a principal role in structuring ecosystems. However, there is evidence that a biennial population cycle in planktivorous pink salmon (*Oncorhynchus gorbuscha*) determines interannual variation in zooplankton and phytoplankton (Table 1). Annual salmon abundance is inversely related to zooplankton biomass, which in turn is inversely related to phytoplankton biomass⁵. These results, based on observations carried out over a decade, suggest that trophic cascades operate even in oceanic systems where productivity is relatively low. Such observations support the arguments of Verity and Smetacek¹⁶ for a shift in perspective among oceanographers towards assessing not just resource controls, but also predation and population dynamics as key features that structure marine ecosystems.

Cascades in context – enrichment and refuges

Research carried out in lakes, in which the specific ecological interactions promoting cascades are well described, is turning to context-dependent questions. What food-web structures promote rather than suppress trophic cascades? How does the trophic ontogeny of key predators alter the potential for strong cascades? What role do refuges and predator avoidance behavior play in trophic dynamics? These questions focus attention both on the dynamics of predator-prey interactions and on potential compensatory changes in food-web structure driven by predation.

Both variation in trophic cascades and the lack of expression of cascading effects are leading to a better appreciation of food webs as probabilistic and not static structures. Trophic cascades are by definition dynamic interactions and hence variation in their strength and duration is the norm⁷. Challenges remain for predicting rates of change, arriving at generalizations about food webs and determining the significance of trophic cascades in any specific case. Experimental data combined with new approaches to analysis are, however, providing a basis for assessing the overall significance of cascades (e.g. Ref. 17).

Enrichment

One lesson that is emerging from recent whole-lake experiments is that trophic cascades are enhanced by enrichment. For example, Fig. 2 presents two years of data from a series of whole-lake manipulations that we conducted¹⁸. Contrasting food webs were created by removing all fish from one lake and stocking it with planktivorous minnows [consisting principally of fathead minnows (*Pimephalus promelas*), redbelly dace (*Phoxinus eos*) and golden shiners (*Notemigonus crysoleucas*)]. A second lake was dominated by two species of piscivorous bass (*Micropterus dolomieu* and *Micropterus salmoides*). As a consequence of intense planktivory, zooplankton in the minnow lake were mainly small species of less effective grazers. In the bass lake, large-bodied species of the water flea, *Daphnia* spp., became strongly established; these zooplankton are highly effective grazers. In the year before nutrient addition, there was little difference in the average rates of primary and bacterial production in the two lakes, despite significant differences in the size structure and grazing activity of the zooplankton communities (Fig. 2). With nutrient additions, the differences in zooplankton community structure, and hence grazing, resulted in a greater than twofold difference in the average rates of primary production and bacterial secondary production^{17,19}. The bass lake had much lower productivity than the minnow lake despite similar nutrient loading (Fig. 2). A trophic cascade arising from top predators suppressed both autotrophic and heterotrophic microbial productivity in the bass lake. Phytoplankton biomass in the minnow lake conformed to predictions derived from standard eutrophication models that use nutrient loading to predict lake conditions. Phytoplankton biomass in the bass lake was far below these predictions¹⁸.

Table 1. Examples of studies identifying trophic cascades^a

Ecosystem	Cascade	Evidence	Effect	Refs
Marine				
Open ocean	Salmon–zooplankton–phytoplankton	Ten-year time series	Twofold higher phytoplankton when salmon abundant	5
Coastal	Whales–otter–urchins–kelp	Long-term data and behavior	Increased predation by whales on otters leads to increased urchin grazing and up to ten times fewer kelp	38
Intertidal	Birds–urchins–macroalgae	Exclosure experiments to reduce bird predation on urchins; path analysis	Algal cover is 24-fold higher in the presence of birds	45
Freshwater				
Streams	Trout or galaxid–invertebrates–periphyton	Differential primary and secondary production in similar streams with trout versus galaxid as top predator	Annual primary production differed by sixfold	10
Shallow lake	Fish–zooplankton–phytoplankton	Long-term observations of lake under clear and turbid conditions	Dramatic changes in fish populations because of mortality from low oxygen or poor recruitment lead to shifts in zooplankton size structure and corresponding strong effects on phytoplankton	46
Pitcher plants	Mosquitoes–protozoa–bacteria	Experiments varying species combinations of protozoa and bacteria with the presence and absence of mosquitoes	Strong effects of mosquitoes on protozoan community composition, which in turn affect bacterial biomass and species composition	31
Terrestrial				
Meadow	Lizards–grasshopper–plants	Observations and experiments	Grasshopper density directly related to distance from lizard ‘sites’; plant biomass declined with distance from lizard ‘sites’	47
Soybean field	Spiders–insects–soybeans	Augmented and reduced spider densities in plots	Leaf damage related to manipulations of spider density	48
Oldfield	Mantids–insects–plants	Enclosures with and without mantids	Herbivore load reduced twofold with a corresponding increase in plant biomass	49
Tropical forest	Beetles–ants–insects– <i>Piper</i> plants	Observations and enclosure experiments with or without beetle additions	After ten months, the percentage of the leaf area eaten was ~40% in beetle addition plots and 10% in controls	13,14
Boreal forest	Wolves–moose–balsam fir	30-year time series; tree ring widths	Population cycles of wolves, moose and balsam fir growth on Isle Royale (USA)	50
Soil	Entopathogenic nematodes–caterpillars–bush lupine	Observations from a variety of sites with bush lupine	Presence of nematodes leads to low densities of caterpillars; high lupine mortality associated with abundant caterpillars	4

^aEntries are drawn from recent literature (1994–1998) and are a representative but not exhaustive list of systems where cascades have been observed.

Refuges

Although nutrient enrichment enhances the strength of trophic cascades, new studies of shallow lakes are also revealing that spatial heterogeneity and refuges can stabilize cascades. Shallow lakes are often intensely productive with extensive macrophyte beds and abundant open-water phytoplankton populations. Many shallow systems exhibit alternate states shifting from macrophytes to phytoplankton dominance²⁰. A clear-water, macrophyte-dominated state is promoted by a trophic cascade. When planktivorous fish populations in these shallow lakes are reduced, large-bodied zooplankton populations can take hold and, in the presence of rooted aquatic plants, build up large populations²¹. Zooplankton populations can stabilize under these conditions by using the rooted vegetation beds as a day-time refuge against visual predators. Zooplankton then migrate to the open water at night and graze heavily on phytoplankton, which sustains clear-water conditions. These interactions have been described extensively in shallow lakes in Europe and are now the basis for concerted management to rid shallow lakes of nuisance phytoplankton blooms^{22,23}. Key triggers are reducing planktivorous fish

stock and encouraging rooted plants. Understanding and exploiting trophic cascades now provides a successful basis for managing water quality in these systems.

Compensation and trophic cascades

Not all cascades propagate to lower trophic levels or have significant impacts on ecosystem processes. Numerous compensatory mechanisms dampen or eliminate cascades. Compensation in this case means that change in an upper trophic component does not propagate down the food web. For example, an increase in the number of predators can reduce herbivore number without a cascading increase in primary producers. Compensation at the level of either the consumers or primary producers truncates the cascade. Expression of compensation depends on the potential for individuals to respond to predation and on the trophic diversity and complexity of food webs³. Although the mechanisms suppressing cascades are too extensive to review fully here, recent studies have emphasized the importance of omnivores and have begun to investigate the potential for compensatory responses within complex microbial communities.

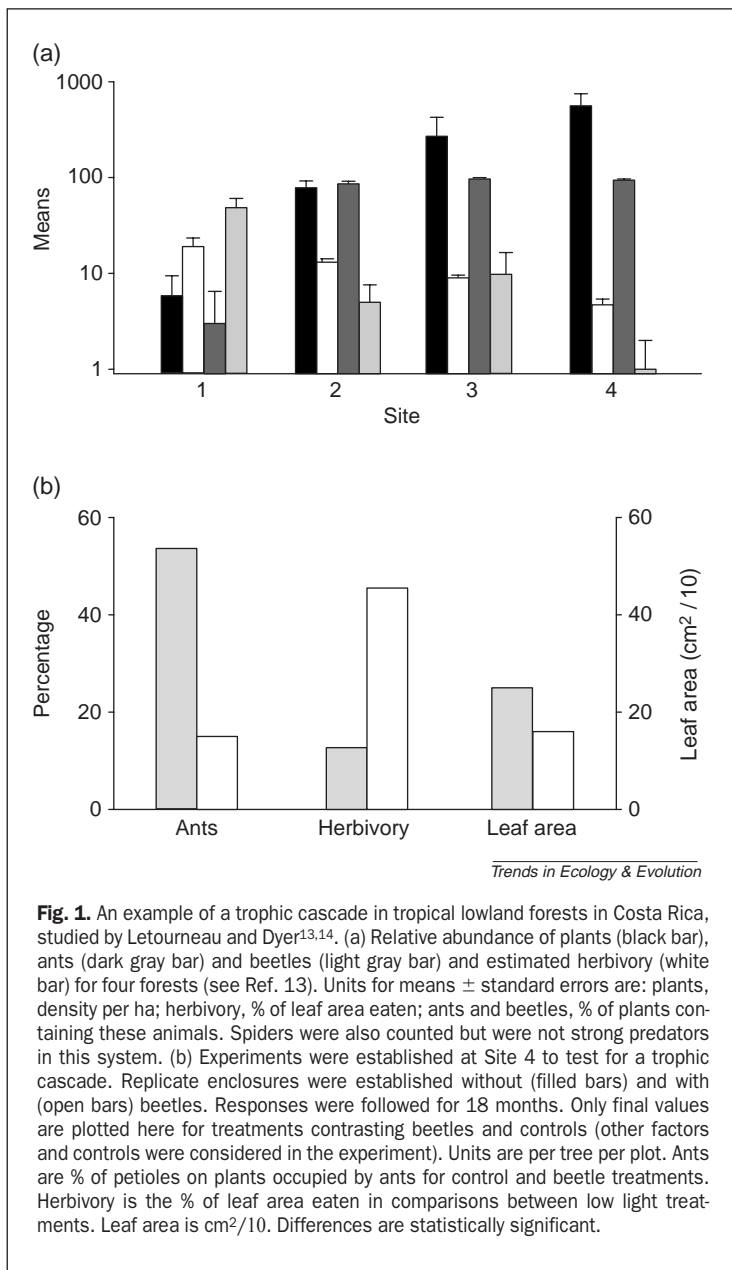


Fig. 1. An example of a trophic cascade in tropical lowland forests in Costa Rica, studied by Letourneau and Dyer^{13,14}. (a) Relative abundance of plants (black bar), ants (dark gray bar) and beetles (light gray bar) and estimated herbivory (white bar) for four forests (see Ref. 13). Units for means \pm standard errors are: plants, density per ha; herbivory, % of leaf area eaten; ants and beetles, % of plants containing these animals. Spiders were also counted but were not strong predators in this system. (b) Experiments were established at Site 4 to test for a trophic cascade. Replicate enclosures were established without (filled bars) and with (open bars) beetles. Responses were followed for 18 months. Only final values are plotted here for treatments contrasting beetles and controls (other factors and controls were considered in the experiment). Units are per tree per plot. Ants are % of petioles on plants occupied by ants for control and beetle treatments. Herbivory is the % of leaf area eaten in comparisons between low light treatments. Leaf area is $\text{cm}^2/10$. Differences are statistically significant.

Omnivory by top predators and mid-level consumers can exert strong regulation of other trophic levels in ways not predicted by cascading trophic interactions. In Costa Rican lowland streams, electric enclosures were used to limit or prohibit access by fish and shrimp to benthic communities. Increases in the number of insects in these enclosures did not lead to a significant reduction in algae, contrary to expectations based on cascading interactions²⁴. Similar results were observed when fish were excluded from areas of Venezuelan streams²⁵. In these cases, the top predators are omnivores; they consume both insects and algae thereby precluding the potential for cascades.

The presence of mid-level omnivores might also eliminate cascades. For example, in north temperate USA reservoirs, gizzard shad (*Dorosoma cepedianum*) grow rapidly to a large size and, therefore, have limited vulnerability to piscivores²⁶. Furthermore, whereas gizzard shad prefer to consume zooplankton, they can switch to feeding on phytoplankton and detritus when zooplankton populations decline. Via detritivory, these fish become important nutrient recyclers facilitating primary productivity while limit-

ing the potential for large-bodied zooplankton populations to develop²⁶. Gizzard shad also compete with the preferred prey of piscivores and thereby can limit the recruitment of both other planktivores and the major piscivore²⁷. In summary, gizzard shad block cascades in reservoirs and influence the biomass and size structure of both upper and lower trophic levels. Thus, it appears that complex interactions within food webs can limit trophic cascades and one model does not fit all cases.

Within communities, diversity and species replacement should provide a means for restricting or reducing predatory impact and hence trophic cascades. Microbial communities would appear to have significant potential to dampen cascades via rapid succession to predation-resistant forms depending on the potential diversity of the particular group. Recent experiments with soil microcosms by Mikola and Setälä²⁸ suggest that microbial biomass is not strongly affected by trophic cascades. The biomass of bacteria and fungi, as measured by phospholipid fatty acids, was either unaffected by the number of trophic levels or, in the case of fungi, increased in the two-level system in which predators were present. In a second set of experiments that varied both the number of trophic levels and the composition and number of microfauna species, there was little evidence for trophic cascades that affected ecosystem processes²⁹. These results support the possibility that microbial populations compensate for changes in predation by altering turnover rate³⁰. Although the mechanisms underlying these presumed compensations remain poorly understood, they might be related to a variety of processes in soils including enhanced microbial growth with increased consumer-driven nutrient recycling³⁰.

Other studies reveal that there are significant trophic cascades in the microbial world. For example, in microcosm experiments using aquatic communities derived from pitcher plants, mosquito predation had strong effects on protozoans that in turn affected bacterial biomass (Table 1). The trophic cascade in this case was not driven by a decline in protozoans in the presence of mosquitoes, but rather by an alteration in the protozoan community composition that shifted predation on bacteria and relative abundance of individual bacterial species³¹.

Trophic cascades mediated by microbial communities can also have significant impacts on ecosystem function. In our whole-lake experiments described in Fig. 2, we observed lower bacterial production and microbial community respiration in systems where *Daphnia* dominated the plankton¹⁹ (M.L. Pace and J.J. Cole, unpublished). The interactions between zooplankton grazers, phytoplankton producers and microbial decomposers were sufficient in the experimental lakes to create strong contrasts in the exchange of carbon dioxide (CO_2) with the atmosphere³². Food-web structure influenced whether the lakes were sources or sinks for atmospheric CO_2 . Even when phytoplankton productivity was increased with nutrient additions leading to a stronger demand for CO_2 to fuel photosynthesis, lakes that were dominated by large zooplankton grazers were net exporters of CO_2 to the atmosphere³² (S.R. Carpenter *et al.*, unpublished).

Human alterations of ecosystems and trophic cascades

Darwin's aphorism 'nature red in fang and claw' seems pallid in a world where humans have either eliminated or decimated populations of most large-bodied predators. This form of global change has been a long-term and

ongoing consequence of human population expansion. Recent studies in paleoecology provide ever stronger evidence that extinctions of large animals on land were closely associated with human migrations into new areas as opposed to climate change, disease and other possible causes³³. Marine ecologists have also documented local extinctions and extensive faunal declines, which related mainly to harvesting. Much of the sea is now viewed as impoverished with a principal symptom being the eradication of large animals^{34,35} and a shift towards harvesting lower on the food chain³⁶. The loss of large-bodied fauna on land and in sea suggests that many trophic cascades that formerly arose from top predators have disappeared.

For the remaining large predators of the modern world, conservation has the potential to re-establish cascades. We should expect new interactions to be revealed as protected populations increase towards former abundance. A classic example comes from studies of sea otters (*Enhydra lutris*) on the coast of western North America. As these populations have rebuilt from near extinction after decades of overhunting, a trophic cascade from otters to urchins to kelp has been re-established in many coastal waters. Otters control the size structure and biomass of urchin populations, which prohibit overgrazing and destruction of kelp forests³⁷. Expansion of the otter populations into previously unoccupied areas promotes kelp growth and limits urchins. This is consistent with the expectation of a strong trophic cascade³⁷.

However, conservation and population changes, as revealed by the otter example, do not occur in a vacuum. Large-scale human activities now appear to be interacting with another top predator to alter the otter–urchin–kelp cascade³⁸. In western Alaska, killer whales (*Orcinus orca*) have recently begun to prey on sea otters, driving a population decline with consequent effects on urchins and kelps (Table 1). The reason for this shift in killer whale behavior is unclear, but there are suggestions that a collapse of their preferred prey, seals and sea lions, might be related to overfishing³⁸. This example is one of many cases in which it appears that fisheries and fish management are altering trophic cascades with profound consequences for food webs in coastal ecosystems³⁹.

Prospects

The study of trophic cascades has matured. Cascades are no longer the sole province of lake and intertidal ecologists but clearly occur in a diversity of ecosystems on land and in the ocean. Early conceptual and theoretical analysis built around simple food chains of odd and even length are not applicable to most complex natural systems. Nevertheless, there are trophic interactions that generate strong effects. The growing number and diversity of reports of cascades suggest many remain to be discovered. Questions about trophic cascades have shifted from whether to when, where and how often. Exciting frontiers remain in discerning and modeling the variability generated by trophic cascades as well as in understanding ecological mechanisms that dampen or prevent cascades.

Trophic cascades are also finding their place in ecosystem management, restoration and conservation. Research in lakes provides dramatic examples of how cascades can be harnessed to improve water quality. The opportunity is open to manage food-web interactions more widely to serve societal needs in both wet and dry places. Trophic cascades are also becoming another signature of the vast and growing human impact on natural

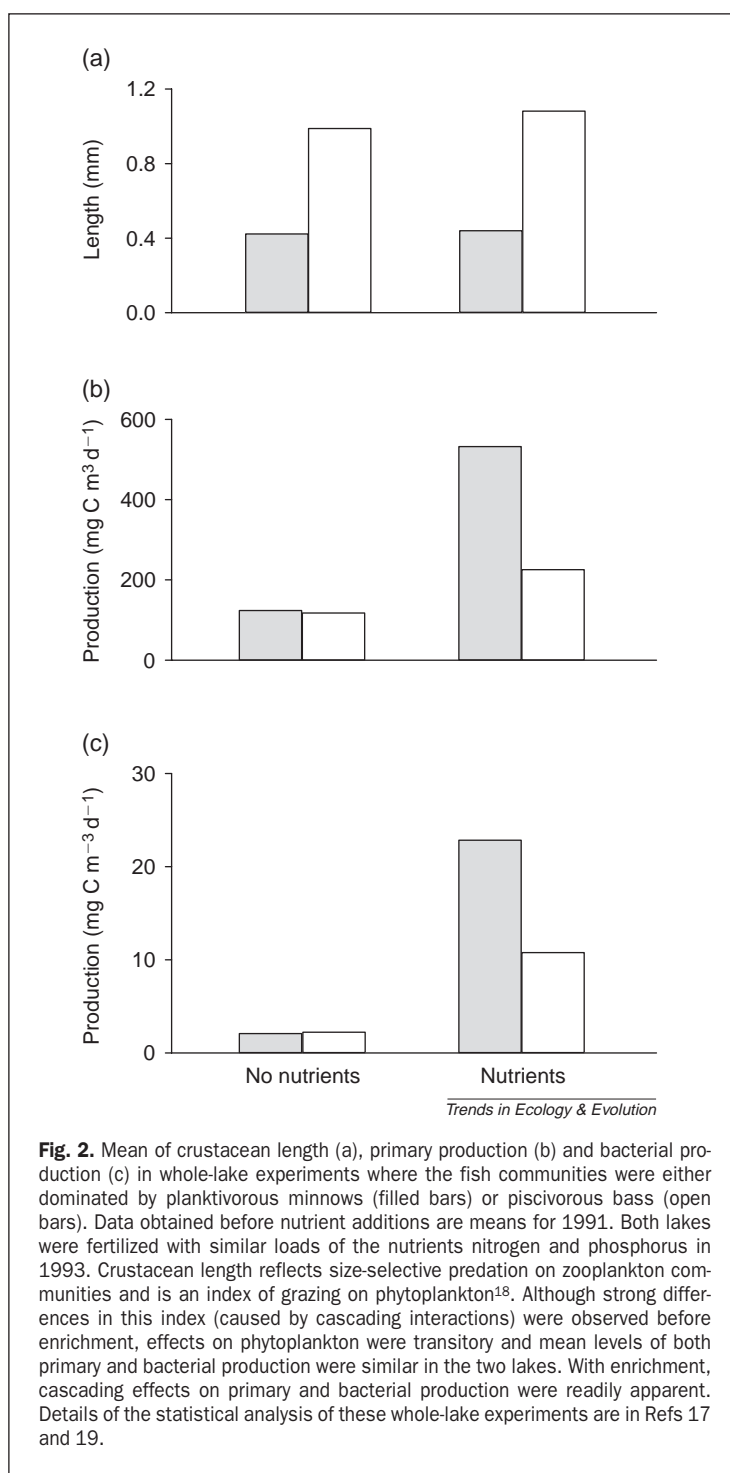


Fig. 2. Mean of crustacean length (a), primary production (b) and bacterial production (c) in whole-lake experiments where the fish communities were either dominated by planktivorous minnows (filled bars) or piscivorous bass (open bars). Data obtained before nutrient additions are means for 1991. Both lakes were fertilized with similar loads of the nutrients nitrogen and phosphorus in 1993. Crustacean length reflects size-selective predation on zooplankton communities and is an index of grazing on phytoplankton¹⁸. Although strong differences in this index (caused by cascading interactions) were observed before enrichment, effects on phytoplankton were transitory and mean levels of both primary and bacterial production were similar in the two lakes. With enrichment, cascading effects on primary and bacterial production were readily apparent. Details of the statistical analysis of these whole-lake experiments are in Refs 17 and 19.

systems. Cascades provide nonlinear and often surprising twists in ecosystem dynamics. The killer whale example suggests that in the future new cascades will emerge related to purposeful management activities and the unwitting consequences of human-driven environmental change. Research can help reduce the negative effects of such changes and offer the understanding required to provide management tools that can guide both restoration and sustainability goals.

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