

Trophic Cascades in Lakes: Lessons and Prospects

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Around 1980, three lines of thinking that were influential in aquatic sciences came together in the concept of trophic cascades. (1) By the mid-1970s phosphorus (P) was established as the currency of lake ecosystem functioning, and control of P inputs was shown to be effective in mitigating cultural eutrophication (Schindler 2006). Although P inputs explained patterns of phytoplankton biomass and production, a substantial amount of variance remained unexplained (Carpenter et al. 1991). As early as 1965, Brooks and Dodson (1965) suggested that size-selective predation could affect lake productivity. (2) Biomanipulation of food webs was proposed to increase grazing rates and thereby control nuisance algae in lakes (Shapiro et al. 1975). The mechanisms through which biomanipulation improved water quality proved to be far more complex than grazing alone. Nonetheless, biomanipulation became an important management tool and a fertile research area (Scheffer 1998, Jeppesen et al. 1998). (3) Synthesis of food web concepts integrated strong interactions (trophic linkages capable of completely reorganizing a food web) with flow of organic carbon and nutrients through networks (Paine 1980). In addition to introducing the term “trophic cascade”, Paine’s paper suggested that massive changes in community structure could have implications for ecosystem processes such as biogeochemical flows.

Following the introduction of the trophic cascade concept to limnology (Carpenter et al. 1985), a number of whole-lake experiments, cross-lake comparisons, and long-term studies showed that manipulation of top predators caused big changes in lake communities and ecosystem processes. In its simplest form, the trophic cascade addresses changes in a four-level food chain of piscivorous fishes, planktivorous fishes, zooplankton and phytoplankton: a large increase (decrease) in piscivores causes a decrease (increase) in planktivores, an increase (decrease) in zooplankton, and a decrease (increase) in phytoplankton. This simple skeleton rapidly proved insufficient. Cascades depended on complex processes such as ontogenetic changes in diet and habitat use of fishes (Werner and Gilliam 1984), behavioral shifts related to foraging opportunity and predation risk (Werner et al. 1983), size-selective predation (Brooks and Dodson 1965), body size shifts among zooplankton (Pace 1984), nutrient recycling by zooplankton (Bergquist and Carpenter 1986), stoichiometry of zooplankton (Elser et al. 1988), and others. Nonetheless, whole-lake data from diverse studies established that big shifts of top predator biomass caused substantial changes in prey communities and ecosystem processes in lakes (Carpenter et al. 1987, 1991, Carpenter and Kitchell 1993, Carpenter et al. 2001, Jeppesen et al. 1998, Hansson et al. 1998, Schindler et al. 1997). Some important ecosystem changes included shifts in phytoplankton biomass, benthic plant biomass, N:P ratio of nutrient flow to phytoplankton, primary production, bacterial production, total ecosystem respiration, and direction and magnitude of net CO₂ exchange between the lake and the atmosphere.

Research in terrestrial, marine and flowing-water ecosystems has also demonstrated effects of cascades on plant biomass and production (Pace et al. 1999). Lakes, streams and marine ecosystems provide many striking examples of trophic cascades (as represented in this volume in chapters by Paine, Estes et al., Sandin et al. and Essington) Although our chapter focuses on freshwater lakes, all of the research themes that we highlight below are well-developed in stream ecology: nonconsumptive effects of predators (Peckarsky et al. 2008), food web interactions with abiotic resources such as light (Wootton and Power 1993) and nutrients (Biggs et al. 2000), subsidies of organic matter and prey across ecosystem boundaries (Wallace et al. 1997, Nakano et al. 1999, Polis et al. 2004), and the importance of spatially extensive long-term study for

understanding ecosystem dynamics (Power et al. 2005, 2008). An additional chapter on trophic cascades could easily be written based upon the literature of stream ecology.

In this short chapter, we present four important findings that emerged from studies of trophic cascades in lakes but were not expected when this research was initiated almost 30 years ago. (1) Animal behavior – habitat choices and migrations of fishes and zooplankton – amplifies the rate and impact of trophic cascades. (2) Nutrient enrichment intensifies effects of trophic cascades on primary producers, contradicting early expectations. (3) Flow of terrestrial organic matter into lakes subsidizes consumers and thereby stabilizes alternative food webs established by trophic cascades. (4) Whole-lake studies – comparisons, experiments, and long-term observations – spanning many years were crucial for measuring and understanding effects of trophic cascades, and often contradicted inferences from small enclosures studied for short periods of time. These four findings are serendipitous discoveries that emerged as unintended benefits of trophic cascade studies, yet have implications for a range of ecological research topics as well as ecosystem management. Below, we review these four discoveries. We close with a brief synthesis of current and future frontiers for research on trophic cascades.

Animal Behavior and Cascades

Beyond the direct impacts of predator-prey interactions, trophic cascades can be either weakened or intensified by behavioral responses of both prey and predators. Animals at intermediate trophic levels may avoid top predators with consequences for lower trophic levels and ecosystem processes. Behaviors of top predators that affect choice of foraging sites or prey preferences may also alter trophic cascades.

Non-consumptive effects of predators (e.g. intimidation) can have strong effects on ecological communities (Peckarsky et al. 2008, Ripple et al. this volume, Berger this volume) Predator avoidance behaviors are well known and are the focus of recent reviews (Lima and Dill 1990, Lima 2002) including one specifically focused on trophic cascades (Schmitz et al. 2004). Analogous development in the field of animal ecology is based on the ratio of benefit (growth) to cost (predation risk) at the individual, population, guild or community scales and has also evoked a series of recent reviews (Werner and Peacor 2003, Pressier et al. 2005, Luttberg and Kerby 2005). Theoretical work develops similar themes and a rich complexity of possible responses based around food chain or food web interactions (Abrams 1995). In a pioneering test of these ideas at the whole lake scale, limnologists used acoustic sampling to demonstrate that behavioral responses accelerate the trophic cascade from piscivores to zooplankton (Romare and Hansson 2003). Thus the presence of a refuge changes interaction strengths and trophic cascades (Fig. 1).

The importance of predator avoidance also emerged in fisheries science through development of a theory for “foraging arena” effects (Walters and Juanes 1993) that modify the basic functional response of a predator-prey interaction. Non-linear and threshold-like responses emerge in ways that influence fisheries yields (Walters and Kitchell 2001, Walters and Martell 2004). Schmitz et al. (2004) summarize their review by calling for a new conceptual view of ecological systems as “landscapes of fear”. Wirsing et al. (2008) refer to “seascapes of fear”. The titles of Pressier et al. (2005) and Luttberg and Kerby (2005) express much the same view.

Taken together, these reviews indicate that behavioral effects are more rapid and intense than predicted by simple predator-prey models. The consequences of behavior for trophic cascades are well-expressed in aquatic ecosystems. Moreover, they have important implications for ecosystem consequences of trophic cascades, and for applications of cascades in conservation, restoration and biological control.

Schmitz et al. (2004) used some of our early work (Carpenter et al. 1987) as an example of indirect effects owing to behavioral responses that altered the trophic cascade in Peter Lake. We assembled a list of 32 specific predictions written in our grant proposals for whole-lake experiments on trophic cascades (Carpenter and Kitchell 1993). Of the 32 predictions, 16 were confirmed, one was equivocal and 15 were not supported by the results. Some of the latter owed to behavioral responses. When 90% of the largemouth bass were removed from Peter Lake and 49,601 zooplanktivorous minnows added shortly thereafter, the minnows behaved as expected and immediately began exploiting the large zooplankton as prey. That lasted about two weeks. Perception of predation risk owing to the remaining bass population rose and by the end of the first month nearly all of the minnows were densely aggregated in refugia (beaver channels) where they gradually starved and many were eaten by piscivorous birds. That result was unexpected and our monitoring program represented it only sparingly.

He and Kitchell (1990) conducted a whole lake manipulation to measure the relative effects of behavioral responses vs. direct predation effects in a system that contained 13 species of potential prey fishes, but no piscivores. We expected that potential prey would aggregate in littoral refugia and/or leave the side where pike had been added (Fig. 2). The response was stronger than expected. Emigration began immediately after a few pike were added and was led by those prey species whose size and morphology made them most vulnerable. Fish not only left the side with pike, but many left the lake through an outlet stream at the pike-free side. Pike did prey on some fishes, but over the course of the summer, emigration accounted for 50-90% of the total change in biomass for individual species exceeding the direct effects of predation (He et al. 1993).

Nutrient Inputs and Cascades

Variation among lakes in many ecological properties including primary production is strongly related to loading of the limiting nutrients, nitrogen and phosphorus. For this reason limnologists often study nutrient enrichment gradients and a natural question concerns how trophic cascades vary in their potential to control of phytoplankton biomass and productivity in oligotrophic (low productivity) relative to eutrophic (high productivity) lakes. High nutrient inputs to lakes lead to eutrophic conditions with noxious algae that are often too large for grazing, limiting the potential for herbivore control. Low nutrient inputs lead to oligotrophic conditions and dominance by smaller, more easily grazed algae. Therefore, it is plausible that nutrient enrichment could weaken trophic cascades in lakes.

Researchers proposed several alternative models to describe the variation of trophic cascades with enrichment. McQueen et al. (1986) argued from enclosure experiments and lake comparative data that trophic cascades were attenuated in eutrophic systems limiting zooplankton control of phytoplankton, while in oligotrophic lakes trophic cascades facilitated

zooplankton control of phytoplankton. This ‘nutrient attenuation’ model in graphical form represents a wedge of potential lake conditions with the greatest scope for trophic cascades at the low end of nutrient loading gradients (Fig. 3A). Sarnelle (1992) used a simple predator-prey model and derived an alternative prediction that phytoplankton are strongly suppressed across nutrient enrichment gradients. His ‘nutrient facilitation’ model was consistent with data on phytoplankton responses to large-bodied grazers, the cladoceran *Daphnia*, in enclosures and whole lake manipulation studies. Graphically, this model also describes a wedge of lake conditions where the greatest scope for the effects of trophic cascades increases with nutrient enrichment (Fig. 3B). Elser and Goldman (1991) studied the variation of phytoplankton-zooplankton interactions in lakes of contrasting nutrient levels using enclosures. Nutrients strongly limited zooplankton control of phytoplankton at low inputs suggesting little scope for trophic cascades in oligotrophic lakes, while in more eutrophic systems phytoplankton size, palatability, and rapid growth rates limited grazer control. Lakes with intermediate nutrient loading (mesotrophic lakes) had the greatest scope for trophic cascades. This ‘mesotrophic maximum’ model describes a set of lake conditions resembling a banana where the potential for trophic cascade impacts is narrow at either end of the nutrient loading gradient and wider in the middle (Fig. 3C).

These models were based on evidence from small-scale and short term enclosure studies, lake observational studies, and a few whole lake manipulations. The evidence, however, from these studies was insufficient to provide a strong test of the interaction of trophic cascades and nutrients that would distinguish among the three models (Carpenter and Kitchell 1993). We conducted a series of food web and nutrient manipulations in lakes with contrasting fish communities that could then be enriched over a range of nutrient loads. We reasoned consistent with the views of some other researchers (e.g. Benndorf 1990) that the ‘banana’ model was most likely especially because grazer control would be limited at high nutrient loads through destabilized predator-prey dynamics (Carpenter 1992). Over several years, we established Peter Lake as a planktivore dominated system by removal of piscivores and stocking of minnows. We contrasted Peter Lake with the western basin of Long Lake where the dominant fish was piscivorous largemouth bass. We enriched both Peter and West Long lakes with nitrogen and phosphorus for five years. Similar loadings were used for the two lakes within each year, but loads varied among years. These nutrient loads ranged from the low, natural rates of the study lakes to highly eutrophic systems encompassing much of the global variation in lakes (Carpenter et al. 2001). Corresponding to the expected differences resulting from size-selective planktivore predation, zooplankton in West Long were large-bodied grazers, primarily the cladoceran, *Daphnia* while the zooplankton of Peter Lake were a mixture of small-bodied grazers.

Phytoplankton primary production and biomass were strongly suppressed in West Long Lake at all nutrient loads while phytoplankton biomass and productivity increased substantially across the same nutrient loading gradient in Peter Lake. The outcome clearly supported the “nutrient facilitation” model (Fig. 3D). Manipulations in eutrophic Lake Mendota (Lathrop et al. 2002) and fish manipulation studies from a variety of eutrophic lakes (Hansson et al. 1998) support the result that trophic cascades can lead to strong limitation of phytoplankton through grazer control even in enriched systems, although control of algae in highly enriched lakes can easily be destabilized by fishing or massive runoff events. Through these studies, lake researchers have established that trophic cascades are evident across a range of lake conditions and largely

independent of nutrient loading and primary production. The key food web features of lakes that promote cascades are relatively stable and abundant populations of piscivores and large-bodied zooplankton grazers especially large species of *Daphnia*.

Lakes in the Landscape

Cross-ecosystem subsidies are well documented in numerous landscapes (Polis et al. 2004). Lakes typically receive a significant amount of organic carbon from their surrounding watersheds. In fact, the loading of terrestrial organic carbon to these systems is typically as large, or larger than that from aquatic primary production (Caraco and Cole 2004). How and if these terrestrial inputs influence trophic cascades depends on the magnitude of the input relative to local primary production; the mode of transport and physical form of the input; and the organisms in the receiving ecosystem.

There are three pathways by which terrestrial organic carbon can enter a lake ecosystem: (1) as terrestrial dissolved organic carbon in inflowing ground or surface waters; (2) as terrestrial particulate organic carbon in flowing surface waters or by aeolian deposition; (3) as terrestrial organisms that enter lakes, often accidentally from land. By far the largest input of terrestrial organic carbon to lakes is dissolved organic carbon which is only available to microorganisms. Clearly, some bacterial respiration is fueled by terrestrial dissolved organic carbon. However, for terrestrial dissolved organic carbon to become a subsidy to the lake food web requires that bacteria assimilate it and pass this organic matter up the food web. Thus, bacterivorous consumers (flagellates, ciliates, some cladocerans) and higher consumers that feed on these ultimately utilize terrestrial dissolved organic carbon. Jansson et al. (2007) term this pathway, heterotrophic energy metabolism and suggest that it is a subsidy especially to cladoceran zooplankton and possibly to the small fish that consume them, potentially setting up a subsidized cascade.

Terrestrial insects and other terrestrial prey items are a very minor component of organic carbon flow from land to lake ecosystems, generally less than 0.1% of the total supply of organic carbon to aquatic consumers from both terrestrial and aquatic sources. However, terrestrial prey are available to top and mid-level predators and can therefore have a large effect on trophic cascades. In small lakes, fish consume significant quantities of terrestrial prey (Hodgson and Kitchell 1987, Hodgson and Hansen 2005). Young of year fish are often planktivorous and terrestrial prey are not significant for them. However even for relatively small (age 1+) fish, terrestrial prey averages about 20% of their total consumption. For adults, terrestrial prey averages nearly 40% (Fig. 4A).

Particulate organic matter of terrestrial origin can enter lakes via stream flow and by aeolian deposition. This direct input of terrestrial particles is also a relatively small component of the total organic carbon budget, on the order of a few percent. Particulate organic carbon can also be formed by flocculation of terrestrial dissolved organic carbon within the lake. Either way, these particles represent another pathway of a terrestrial subsidy to the lake ecosystem. In the water column terrestrial particulate organic carbon can be consumed by zooplankton. The terrestrial particulate organic carbon that reaches sediments can be consumed by a host of benthic invertebrates. Using Paul Lake as an example, Cole et al. (2006) found that terrestrial particulate

organic carbon was a major diet item for both zooplankton (about 30% of consumption) and benthos (about 60% of consumption). The fish that feed on zooplankton and benthos are also subsidized, indirectly, by terrestrial particulate organic carbon. The terrestrial particulate organic carbon subsidy to fish averages about 30% consumption across age classes but the pathway differs. Young of year fish consume terrestrial particulate organic carbon via zooplankton, while adult fish consume terrestrial particulate organic carbon via benthos, and fish that consumed either zooplankton or benthos (Fig. 4A).

In these small lakes, the terrestrial subsidy to fish, combining all pathways is quite large ranging from about 40 to 90% in lakes that were not eutrophied (Fig. 4B). Even after artificial eutrophication of Peter Lake in 2002 (by the addition of N and P fertilizer over the course of 12 weeks) about 30% of fish biomass was made from terrestrially-derived organic carbon. In Paul Lake the average adult large mouth bass is formed from about 70% terrestrial organic carbon. Thus these piscivores can quickly reduce the population of a planktivores to very low levels without suffering the consequence of losing their main source of organic carbon. In Peter Lake, prior to fertilization, the populations of fat head minnows and pumpkinseed sunfish, which are about 40% terrestrial, can exert strong influence on the size of zooplankton and still be somewhat independent on the amount of zooplankton prey available to them.

While these studies demonstrate the potential for predator biomass to be stabilized by cross-system subsidies of terrestrial organic carbon inputs. Vander Zanden et al. (2005) used literature data and a model to show that benthic resources (subsidized by terrestrial organic matter) augmented piscivore biomass and intensified trophic cascades. A few studies which have directly examined the intersection of cross-system subsidies and trophic cascades (Nakano et al. 1999, Polis et al. 2004). Knight et al. (2005) studied an intriguing case of a cascade that involved fish, dragonflies (a preferred prey of fish), bee-flies (a favorite prey item for adult dragon flies) and the pollination of *Hypericum* by bee flies. In a series of nearly identical small ponds, Knight et al. (2005) selected four ponds with fish and four ponds without fish. Fishless ponds had a greater abundance of the aquatic larval stage of dragonflies, more adult dragonflies and significantly fewer pollinator visits to pond-side *Hypericum* than did ponds with fish.

Trees that fall into lakes represent a cross-system subsidy of a different type with different implications for cascades. The logs create habitat for periphyton and invertebrates which in turn are preyed upon by fish. In addition they provide refuge for fishes of a range of sizes, as well as foraging sites for sit-and-wait predators (see preceding section on “Animal Behaviors and Cascades”). Sass et al. (2006) examined the food web of two basins of an experimentally-divided lakes, before and after the removal of fallen trees and logs from one basin. Prior to removal of the woody habitat, the food webs of both basins were essentially identical and fish consumed mostly aquatic prey. In the basin from which coarse wood was removed, the major predator, large-mouthed bass, consumed fewer fish, and relatively more terrestrial insects and grew more slowly than their counterparts in the reference basin.

In summary, terrestrial subsidies to aquatic foodwebs can help support high populations of top predators and thereby stabilize or even intensify trophic cascades. Fallen trees may also affect trophic cascades by providing food for benthic invertebrates that feed on periphyton as well as habitat and refuge for invertebrates and fishes of a range of body sizes. These findings show that

trophic cascades cannot be fully understood by studying ecosystems in isolation from their surroundings. Landscape connections have important implications for trophic cascades.

Whole-Ecosystem Approaches

According to the title of a famous paper, lakes are microcosms of broader ecological interactions (Forbes 1887). Microcosms can be useful representations of complex ecological interactions, exposing key processes through simplification, in the same way that mathematical models clarify complex processes (Scheffer and Beets 1994). However, in ecology the problem of extrapolating results from one scale to another is pervasive (Levin 1992). The most straightforward solution is to conduct studies at the appropriate scale. In the case of trophic cascades in lakes, theory has been evaluated using whole-ecosystem comparisons, experiments and long-term studies. Our current understanding of trophic cascades is synthesized from all three kinds of studies of whole ecosystems. These whole-ecosystem approaches have complementary strengths and weaknesses, so it seems reasonable to have more confidence in inferences that are consistent across all approaches (Carpenter 1998). Most importantly for this discussion, the whole-lake approaches sidestep many of the problems of extrapolation across scales that arise in microcosm experiments.

Extrapolations from microcosms to whole-lake results often fail. Pace (2001) evaluated microcosm and whole-lake responses of microbes and phytoplankton to nutrients and grazing, and found that the microcosms were about equally likely to get it right or wrong. Carpenter and Kitchell (1988) found that microcosms and lakes showed opposite responses for 38% of phytoplankton species studied, and consistent responses for only 34% of species. Schindler (1998) reviewed his experiences over about 30 years with microcosm and whole-lake experiments and found numerous cases where microcosms would have led to incorrect scientific conclusions and faulty management decisions in the absence of evidence from whole-ecosystem experiments. In view of the low reliability of microcosms, Carpenter (1996) suggested that overuse of microcosm experiments diverted human resources from useful research, and wasted resources by training graduate students in irrelevant approaches. Limnologists are aware of a number of microcosm artifacts, such as reduced mixing, enhanced sedimentation, fish mortality, excessive predation and overgrowth of periphyton (Pace 2001). These problems are sometimes downplayed in the literature, because they complicate inference and “everybody knows about it already”. Such a tendency to minimize artifacts only perpetuates a questionable body of research.

It is more constructive to view microcosm experiments as a form of modeling, subject to the same kinds of assumptions and limitations as mathematical or simulation models in ecology (Scheffer and Beets 1994). Like mathematical models, microcosms can be an inexpensive way to build intuition about more complex systems. Microcosm experiments across a gradient of scales could even reveal insights about the effect of scale itself. As with mathematical models, we should be very cautious about extrapolating results of microcosm studies to whole ecosystems. Fortunately, it has been possible to study trophic cascades in lakes using whole-lake comparisons, experiments and long-term data.

Frontiers

Nearly 30 years of research on trophic cascades in lakes has continued to expand our understanding of the phenomenon and our appreciation of its complexity. This short review has selected topics that have emerged in the course of ecosystem studies of trophic cascades in lakes, and seem likely to continue to motivate research in the foreseeable future. These are topics in basic science though they have implications for applied ecology. We close with some comments on additional research issues which are motivated by concerns of ecosystem management or conservation.

Trophic cascades are among the processes that cause large nonlinear changes in ecosystems, changes which may be difficult or even impossible to reverse (Scheffer, this volume). Such changes have been identified as a major concern for ecosystem management and sustainability (M.A. 2005). Cascades can create large changes in ecosystems including living resources and ecosystem services, with implications for human well-being. Thus it is important to understand the conditions that lead to trophic cascades – the subject of much of the research in this volume – as well as the indicators that a cascade may occur soon. Models demonstrate several kinds of statistical changes in time series that occur in advance of trophic cascades, and thereby can serve as leading indicators (Carpenter et al. 2008). Research is underway to evaluate these indicators using retrospective time series analyses as well as ecosystem experiments. Interesting insights are likely from this line of research in the future.

The massive and sometimes surprising changes we have seen in whole-lake experiments and real-world lake management were usually not forecast from models and small container experiments. Managing food webs is extraordinarily difficult, even in small experimental lakes where we completely control exploitation and inputs. In the case of food webs, the notion of "managing" implies a degree of predictability and control that is not consistent with the empirical record. Nonetheless, food webs provide a unique set of possibilities for manipulating ecosystems, and managers are likely to try these tools even if the outcome is a gamble. Also, people will continue to manipulate food webs by fishing as well as introductions of species. It is clear that introductions or deletions of species can have impacts on other species at distant positions in the food web, and on ecosystem processes (primary production, carbon sequestration, carbon exchange with the atmosphere, nutrient cycling, nutrient limitation).

Examples of manipulations of food webs to achieve societal goals include management of water quality and contaminant biomagnification. Eutrophication can be mitigated by restoration of top carnivores (Lathrop et al. 2002, Hansson et al. 1998). However, in lakes subject to enormous and variable loads of excess nutrients the food web may become unstable and the desired effects on water quality may break down. Food web manipulation can mitigate biomagnification of contaminants. Unfortunately, however, many real world cases have tradeoffs. For example, in the Laurentian Great Lakes the food webs that best mitigate biomagnification are dominated by fast-growing steelhead trout, an invasive in those systems (Stow et al. 1995). Yet some other species invasions may exacerbate contaminant biomagnification by increasing the length of food chains (Vander Zanden and Rasmussen 1996).

In lakes, as in oceans, fisheries management often focuses on one species at a time (Essington this volume). Such practices ignore trophic cascades (as well as other ecosystem phenomena)

and are therefore subject to surprising breakdowns when abrupt changes in food webs affect target species.

Over the past 50 years, ecosystems have changed more than at any previous time in the history of our species (M.A. 2005). The biota of both aquatic and terrestrial ecosystems has changed as a result of human activities including harvest and non-harvest mortality, land-use change, habitat loss and pollution. These changes often have disproportionately large effects on top predators, because top predators often have large body sizes, long maturation times, large range requirements, and complex life histories which may require multiple kinds of habitats or prey in the course of ontogeny. Thus it is reasonable to expect that trophic cascades played a role in the sweeping biotic changes of recent decades. Community and ecosystem structures that we see today may be legacies of lost cascades. Moreover, we expect that trophic cascades will be important in future changes as human action and natural processes continue to reorganize ecosystems. There is no foreseeable end to the need for research to understand and forecast the consequences of trophic cascades for ecosystems and their support of human well-being.

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Fig. 1. Romare and Hansson (2003) showed that in the presence of a refuge (shaded region) predator-prey dynamics are more rapid and complex than they are in the absence of a refuge.

Fig. 2. Ratio of prey fish in refuge versus prey fish in foraging arena during a year when northern pike were absent and a year when northern pike were present (He et al. 1993).

Fig. 3. Hypotheses and experimental evidence about the interaction of nutrient input and trophic cascades. Each panel shows primary producer response versus nutrient input rate for a lake with a planktivore-dominated food web (dashed line) and a lake with a piscivore-dominated food web (solid line). A. Decreasing difference hypothesis: the difference between the lakes is greatest at low nutrient conditions. B. Increasing difference hypothesis: the difference between the lakes is greatest at high nutrient conditions. C. Mesotrophic maximum or banana hypothesis: the difference between the lakes is greatest at intermediate nutrient conditions. D. Whole lake experimental results from planktivore- (Peter Lake) and piscivore- (West Long Lake) dominated lakes.

Fig. 4. Fish obtain a high but variable proportion of their organic carbon from terrestrial sources (Cole et al. 2006). (A) Proportion of organic carbon derived from four sources: terrestrial DOC (T-DOC), terrestrial POC (T-POC) or terrestrial prey (T-PREY), plus autotrophic production in the lake (AUTO) by three size classes of largemouth bass (young-of-year, 1+, and adult) in Paul Lake. (B) Proportion of terrestrially-derived organic carbon in fish species from several whole-lake experiments.

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Fig. 1. Romare and Hansson (2003) showed that in the presence of a refuge (shaded region) predator-prey dynamics are more rapid and complex than they are in the absence of a refuge.

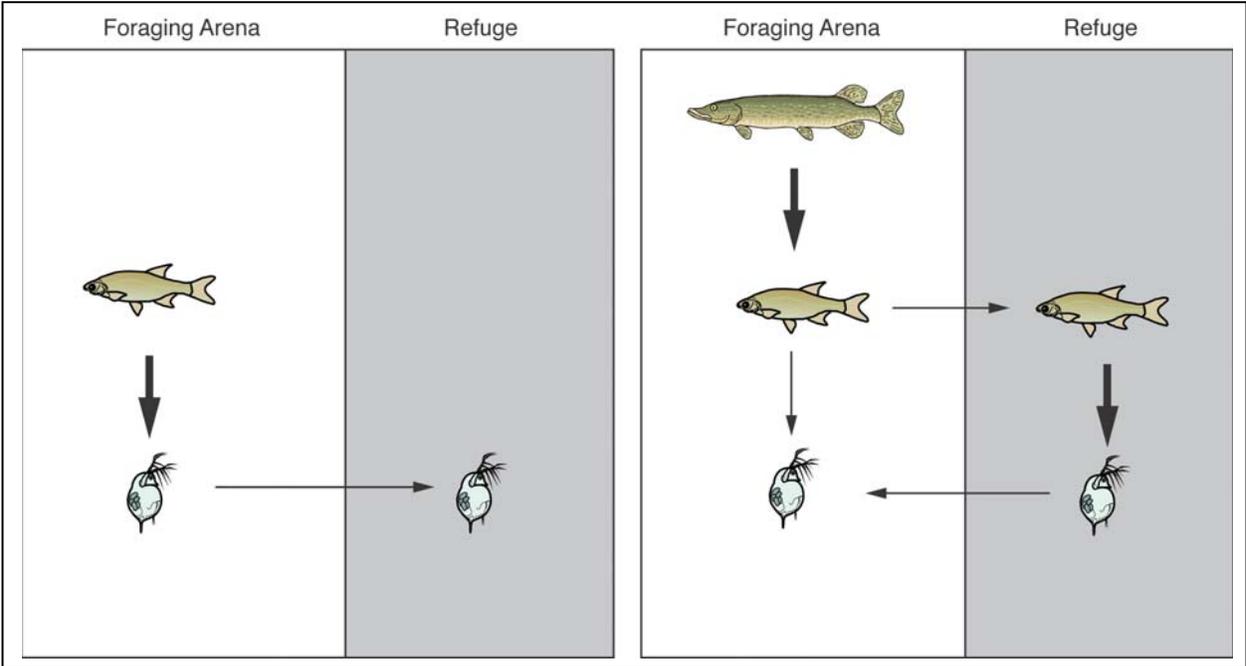


Fig. 2. Ratio of prey fish in refuge versus prey fish in foraging arena during a year when northern pike were absent and a year when northern pike were present (He et al. 1993).

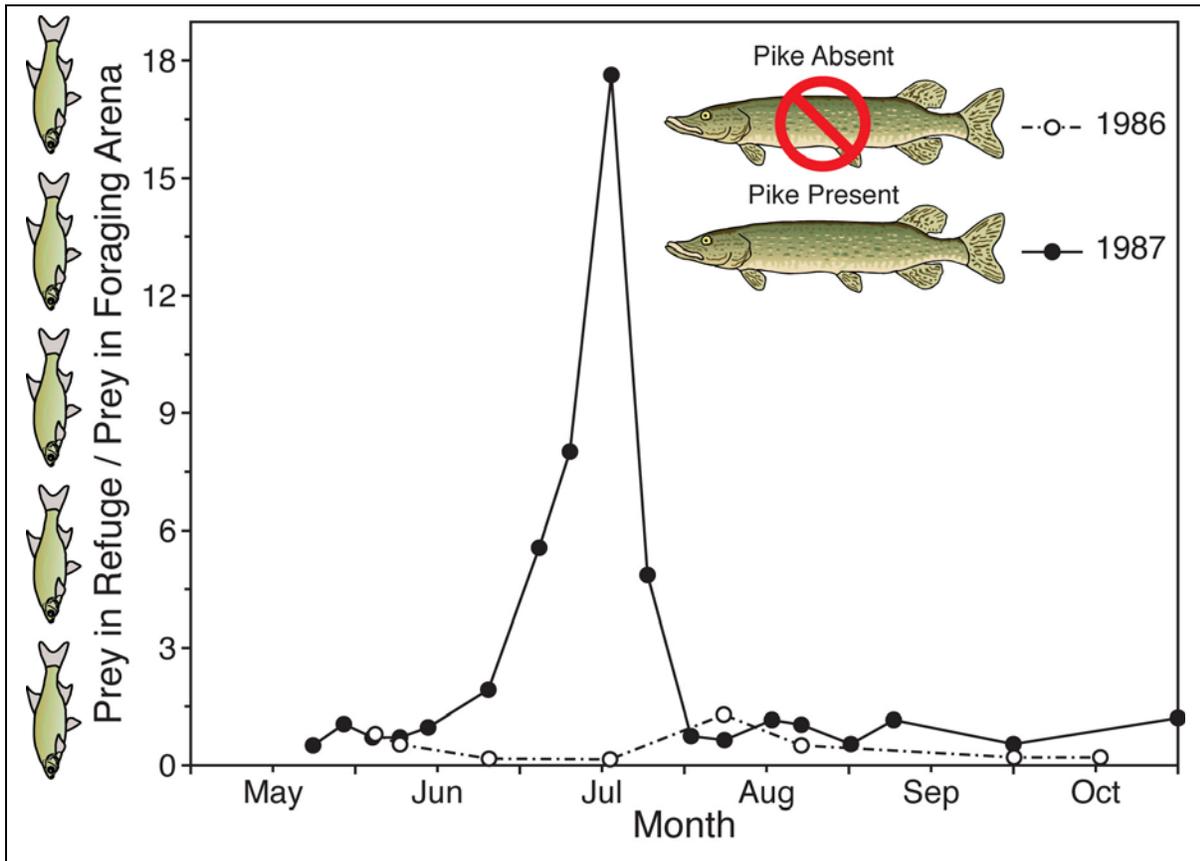


Fig. 3. Hypotheses and experimental evidence about the interaction of nutrient input and trophic cascades. Each panel shows primary producer response versus nutrient input rate for a lake with a planktivore-dominated food web (dashed line) and a lake with a piscivore-dominated food web (solid line). A. Decreasing difference hypothesis: the difference between the lakes is greatest at low nutrient conditions. B. Increasing difference hypothesis: the difference between the lakes is greatest at high nutrient conditions. C. Mesotrophic maximum or banana hypothesis: the difference between the lakes is greatest at intermediate nutrient conditions. D. Whole lake experimental results from planktivore- (Peter Lake) and piscivore- (West Long Lake) dominated lakes.

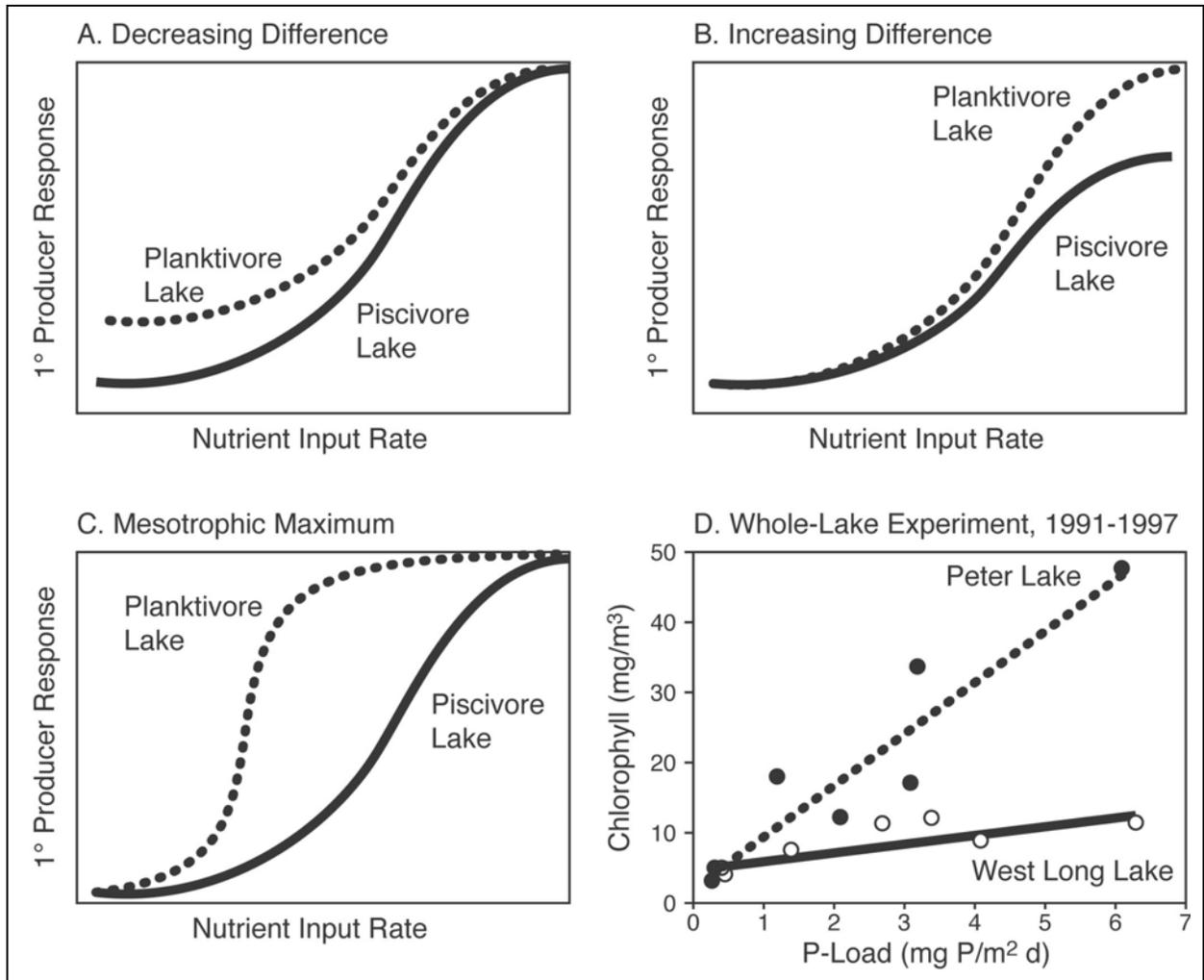


Fig. 4. Fish obtain a high but variable proportion of their organic carbon from terrestrial sources (Cole et al. 2006). (A) Proportion of organic carbon derived from four sources: terrestrial DOC (T-DOC), terrestrial POC (T-POC) or terrestrial prey (T-PREY), plus autotrophic production in the lake (AUTO) by three size classes of largemouth bass (young-of-year, 1+, and adult) in Paul Lake. (B) Proportion of allochthonous (terrestrially-derived) organic carbon in fish species from several whole-lake experiments.

