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Cascading Trophic Interactions and Lake Productivity

Fish predation and herbivory can regulate lake ecosystems

Stephen R. Carpenter, James F. Kitchell, and James R. Hodgson

Limnologists have been studying patterns in lake primary productivity for more than 60 years (Elster 1974). More recently, concern about eutrophication has focused attention on nutrient supply as a regulator of lake productivity. However, nutrient supply cannot explain all the variation in the primary productivity of the world's lakes. Schindler (1978) analyzed a sample of 66 lakes that were likely to be limited in productivity by phosphorus because their nitrogen/phosphorus ratios exceeded five. Phosphorus supply, corrected for hydrologic residence time, explained only 48% of the variance in primary production, and lakes with similar phosphorus supply rates differed nearly a thousandfold in productivity. Phosphorus loading explains 79–95% of the variance in chlorophyll *a* concentration (Dillon and Rigler 1974, Oglesby 1977, Schindler 1978), but chlorophyll *a* concentration is a poor predictor of primary production (Brylinsky and Mann 1973, Oglesby 1977).

> **Altering food webs by altering consumer populations may be a promising management tool**

The concept of cascading trophic interactions, on the other hand, explains differences in productivity among lakes with similar nutrient supplies but contrasting food webs. The concept reflects an elaboration of long-standing principles of fishery management based on logistic models (Larkin 1978). Simply put, a rise in piscivore biomass brings decreased planktivore biomass, increased herbivore biomass, and decreased phytoplankton biomass (Figure 1). Specific growth rates at each trophic level show the opposite responses. Productivity at a given trophic level is maximized at an intermediate biomass of its predators. Productivity at all trophic levels, and energy flow through the food web, are highest where intensities of predation are intermediate at all trophic levels (Kitchell 1980). Although this simple conceptual model is heuristically useful, real ecosystems exhibit nonequilibrium dynamics that result from different life histories and variable interactions among the major species.

Cascading trophic interactions and nutrient loading models are complementary, not contradictory. Potential productivity at all trophic levels is set by nutrient supply. Actual productivity depends on the recycling of nutrients and their allocation among populations with different growth rates. The phosphorus availability to phytoplankton, for example, is determined by processes that operate over a wide range of temporal and spatial scales (Harris 1980, Kitchell et al. 1979). Nutrient excretion by zooplankton is a major recycling process (Lehman 1980) that is strongly influenced by

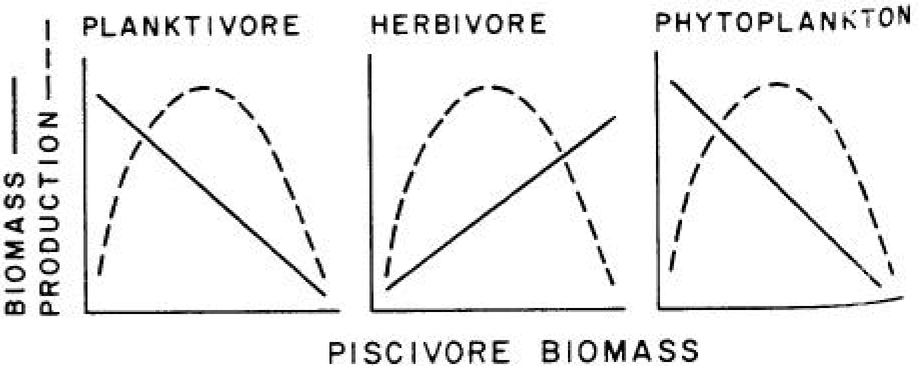

Figure 1. Piscivore biomass in relation to biomass (solid line) and production (dashed line) of vertebrate zooplanktivores, large herbivores, and phytoplankton.

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selective predation on zooplankton by fishes (Bartell and Kitchell 1978). Thus, by regulating recycling rates, consumers regulate primary production.

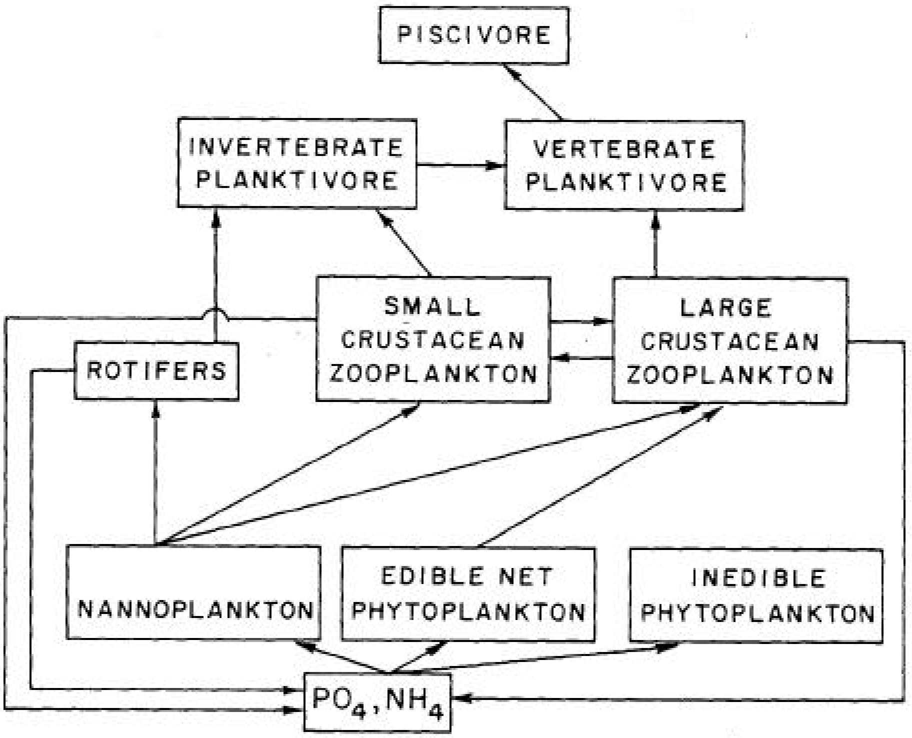

Figure 2. Conceptual model of trophic structure in a typical lake. See text for further details.

The trophic cascade

To explain the details of cascading trophic interactions, we consider a lake food web that includes limiting nutrients and four trophic levels: piscivores such as bass, pike, or salmon, zooplanktivores, herbivorous zooplankton, and phytoplankton (Figure 2). Invertebrate planktivores like insect larvae and predaceous copepods take smaller prey than vertebrate planktivores like minnows. (Even though the rotifers include herbivores and predators, we will treat them collectively as a size class of zooplankton that includes grazers and is preyed on most heavily by invertebrates.) Small crustacean zooplankton include grazers, such as *Bosmina*, which remain small throughout their life cycle, and the young of large crustacean grazers, such as *Daphnia pulex*, and invertebrate planktivores. We divide the phytoplankton into three functional groups: nannoplankters subject to grazing by all herbivores, edible net phytoplankters like *Scenedesmus* that are grazed only by larger zooplankton, and inedible algae.

Examples of consumers controlling species composition, biomass, and productivity are available for each trophic level. Changes in the density of large piscivorous fishes result in changes in density, species composition, and behavior of zooplanktivorous fishes. In Wisconsin lakes containing bass or pike, spiny-rayed planktivorous fishes replace soft-rayed minnows, which are common in the absence of piscivores (Tonn and Magnuson 1982). The depletion of prey fishes by salmonids stocked in Lake Michigan (Stewart et al. 1981) and in European reservoirs (Benndorf et al. 1984) shows how piscivores can regulate zooplanktivorous fishes. Prey fish biomass declines as their predators increase in density; in contrast, prey fish productivity reaches a maximum at intermediate predator densities (Larkin 1978).

High planktivory by vertebrates is associated with low planktivory by invertebrates as well as high densities of rotifers and small crustaceans. Where planktivorous fishes are absent, invertebrate planktivores and large crustacean zooplankton predominate. Planktivorous fishes select the largest available prey and can rapidly reduce the density of zooplankters larger than about 1 mm (Hall et al. 1976). In contrast, planktivorous invertebrates select and deplete herbivores smaller than 0.5–1 mm. Lynch (1980) concludes that contrasting planktivore pressures have led to two distinct types of life history in cladoceran herbivores. Heavy planktivory by invertebrates favors large cladocerans that grow rapidly until they cannot be taken by the planktivores. At this size, these cladocerans shift energy allocation from growth to producing many. small offspring. Planktivorous fishes, which consume large zooplankton (including invertebrate planktivores), promote dominance of small cladocerans that grow continually, reproduce at an early age, and have small clutches of large offspring.

Differences in size structure among herbivorous zooplankton communities lead to pronounced differences in grazing and nutrient recycling rates. Effects of zooplankton on phytoplankton biomass and productivity are not intuitively clear because they result from countervailing processes (grazing vs. nutrient recycling) and potentially compensatory allometric relationships. Larger zooplankters can ingest larger algae (Burns 1968). Absolute grazing rate (cells · animal^{-1} · t^{-1}) increases with grazer size, but mass-specific grazing rate (cells · mg animal^{-1} · t^{-1}) declines with grazer size (Peters and Downing 1984). Similarly, absolute excretion rate increases with grazer size, and mass-specific excretion rate decreases with grazer size (Ejsmont-Karabin 1983, Peters and Rigler 1973). Herbivorous zooplankton alter phytoplankton species composition and size structure directly by selective grazing and indirectly through nutrient recycling (Bergquist 1985, Carpenter and Kitchell 1984, Lehman and Sandgren 1985). Changes in phytoplankton size structure imply substantial changes in chlorophyll concentration and productivity because of several allometric relationships. Increasing algal cell size is accompanied by decreases in maximum growth rate, susceptibility to grazing, cell quotas for N and P, and intracellular chlorophyll concentrations and by increases in sinking rate and half-saturation constants for nutrient uptake (Reynolds 1984).

We investigated the complex interactions among zooplankton and phytoplankton using simulation models that yielded response surfaces of algal biomass and productivity as functions of zooplankton biomass and zooplankter body size (Carpenter and Kitchell 1984). Chlorophyll *a* concentrations were highest at low biomasses of small herbivores, declining smoothly as both biomass and grazer mass increased. The response of primary production to zooplankton biomass was unimodal, with maximum production at intermediate zooplankton biomass. The zooplankton biomass that maximized primary production declined as herbivore mass increased. At low herbivore biomass, productivity was limited by recycling; it increased as grazer biomass increased. When herbivore biomass was high, productivity was restrained by grazing and declined as grazer biomass rose. Although the model was far more complex than the familiar logistic equation of population biology, the phytoplankton as a whole behaved logistically in two respects: Productivity was related parabolically to chlorophyll *a*, with maximum productivity at intermediate chlorophyll *a*, and specific productivity decreased as chlorophyll *a* increased.

An increase in piscivore density cascades through the food web in the following way. Vertebrate zooplanktivores are reduced while planktivory by invertebrates increases, shifting the herbivorous zooplankton community toward larger zooplankters and higher biomass. Chlorophyll *a* concentration declines.

A decrease in piscivore density has the reverse effects. Vertebrate zooplanktivory rises at the expense of invertebrate zooplanktivores, and small zooplankters dominate the herbivore assemblage. Chlorophyll *a* concentration rises. A change in piscivore density can increase or decrease primary production, which is a unimodal function of zooplankton biomass.

Rates of cascading responses

In natural systems, sequences of cascading trophic interactions will propagate from stochastic fluctuations in piscivore year-class strength and mortality. Fish stocks, reproduction rates, and mortality rates in turn exhibit enormous variance (Peterson and Wroblewski 1984, Steele and Henderson 1984).

Fluctuations in piscivore reproduction do not cascade instantaneously through lake food webs. Rather, lags in ecosystem response occur because generation times differ among trophic levels. In temperate lakes, piscivores and many invertebrate and vertebrate planktivores reproduce annually. Crustacean herbivores and rotifers, which go through a generation in several days, pass through many generations in a summer. Phytoplankton generation times are shorter still, ranging from hours to a few days. Inorganic nutrients turn over in only a few minutes to a few hours. Because of this hierarchy of generation and turnover times, ecosystem components respond at different rates to changes in piscivore abundance.

The longest lags in the trophic cascade result from predatory ontogeny and predatory inertia. Predatory ontogeny occurs when a piscivore cohort develops, and the fish act first as zooplanktivores and then as piscivores (Figure 3, solid lines). As zooplanktivores, the fish drive the ecosystem toward small zooplankton and higher chlorophyll concentrations. These trends reverse as the fish grow and increase the proportion of planktivorous fish in their diet. Predatory inertia refers to the persisting effect of older age classes despite reproductive failure in any one year (Stewart et al. 1981). It takes several consecutive year-class failures to reduce piscivory enough for vertebrate planktivores to increase, with associated shifts in zooplankton and phytoplankton.

Cascading trophic interactions can be reversed by increasing or decreasing the intensity of piscivory. Because of lags, however, responses to increased piscivory involve transitions among food web configurations that do not occur during responses to decreased piscivory. Hysteresis will therefore occur when a change in piscivory is reversed: The sequence of ecosystem states and the rate of transition among states in the reverse pathway will differ from those of the forward pathway. The hysteresis effect is illustrated by two contrasting disturbances (Figure 3). Solid lines show the results of an unusually strong piscivore year class, which could occur naturally or through stocking young fish. Dashed lines show the results of a reduction in piscivores, such as those caused by winter kill or human exploitation. In each case, the system returns to the same state, but the pathways are very different.

Lake ecosystems are buffeted at irregular intervals by variations in fish recruitment and mortality rates. The system responses are nonequilibrium, transient phenomena that are difficult to detect using long-term averages. Finer-grained time course data are needed.

Correlations vs. experiments

Ecologists have been urged to develop theories based on multiple regression analyses of data from the literature (Peters 1980). We doubt that this approach can be used successfully to analyze relationships between food web structure and productivity. Correlations among trophic levels reflect nutrient supply effects, which influence biomass at each trophic level in an essentially stoichiometric fashion (cf. McCauley and Kalff 1981). The effects of food web structure are independent of those due to nutrient supply. Therefore, the appropriate statistical procedure is to first remove nutrient effects by regression, and then seek food web effects in the residuals of the regressions. Such a study would be subject to the pitfalls of interpreting regressions pointed out by Box et al. (1978, pp. 487–498). Common statistical problems in data from the literature relevant to cascading trophic interactions are dependencies among predictor variables and lack of control or precise measurements of predictor variables.

Literature data have serious shortcomings, in addition to purely statistical problems, which make them unsuitable for regression analyses of cascading trophic interactions. Frequently, data on biomasses of trophic levels do not distinguish between edible and inedible items or reflect the breadth of predators' diets. Because predators' tastes are catholic, trophic levels are not distinct; they are only a statistical statement about organisms' most prevalent feeding relationships. Typically, researchers look at annual averages; this time scale may not reveal important but transient responses. Finally, the correlation approach does not account for time lags. It is not reasonable to expect today's algal production to correlate with today's biomasses of zooplankton, planktivores, and piscivores. Rather, algal production today may depend on yesterday's zooplankton, which depended on zooplanktivores during the past month, which depended on piscivore recruitment the previous year.

Because of these problems, clear cause-and-effect relationships do not emerge from multiple regression analyses of lake ecosystem data. Experimental manipulations of food webs are a more promising research strategy. The several published accounts of dramatic algal responses to increased grazing pressure in lakes where predation was altered suggest that such experiments will be fruitful.

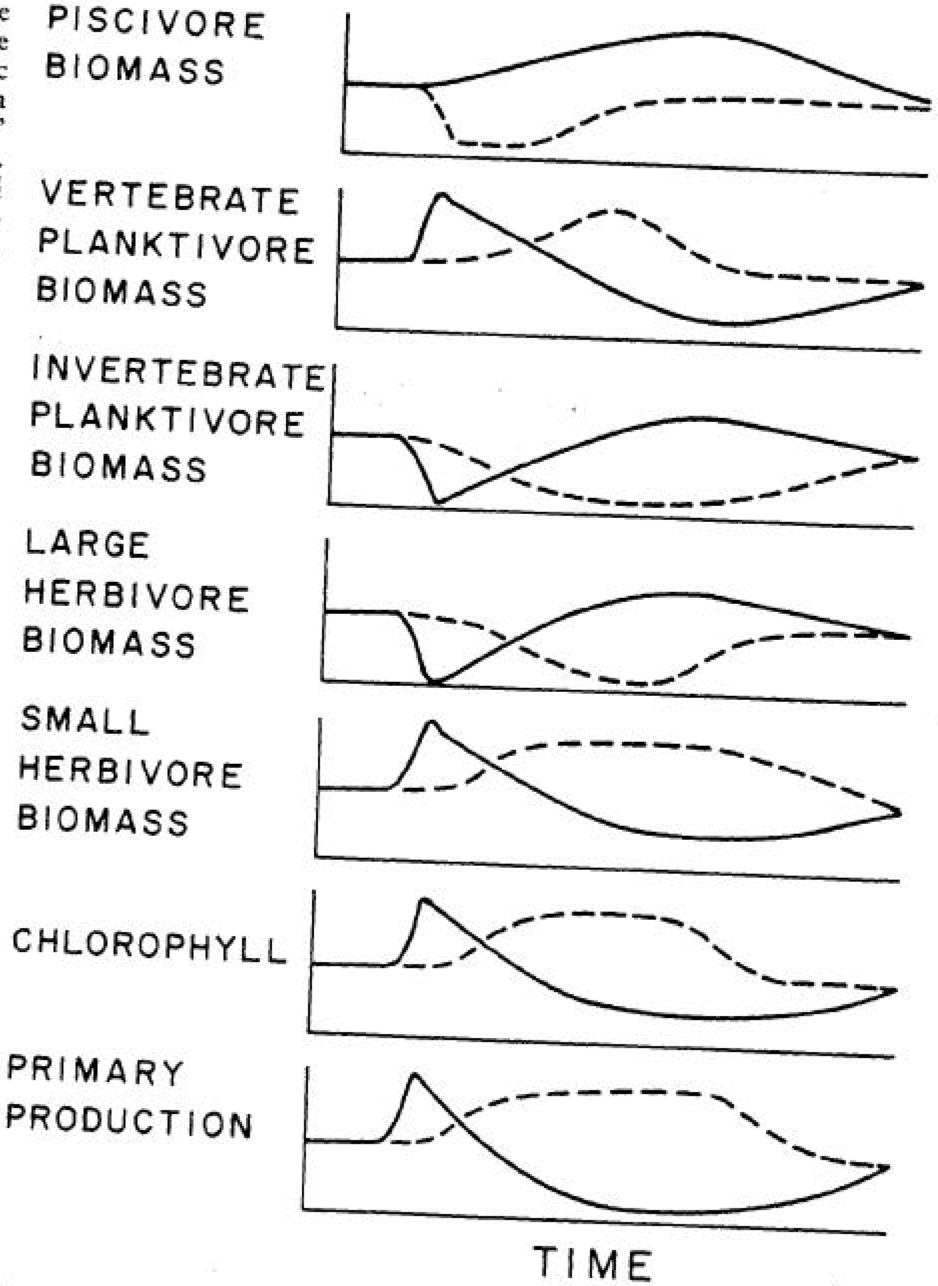

Figure 3. Time course of ecosystem response to a strong piscivore year class (solid line) and a partial winter kill of piscivores (dashed line).

Case studies

The idea that fishes can regulate lake ecosystem processes stemmed from the work of Hrbacek et al. (1961). Several experiments have been conducted in which zooplanktivorous fish were removed from lakes, usually with a poison such as rotenone. The consistent conclusions from these studies are that planktivore removal results in greater densities of larger zooplankton, which impose greater grazing pressure on the phytoplankton; increased frequency of grazing-resistant phytoplankters; reduced chlorophyll *a* concentrations and total algal densities; increased Secchi-disk transparency; and reduced total nutrient concentrations in the epilimnion (Benndorf et al. 1984, DiBernardi 1981, Henrikson et al. 1980, Kitchell et al. 1986, Shapiro 1980, Shapiro and Wright 1984). These experiments lack primary productivity data, with one exception. Henrikson et al. (1980) found that primary productivity decreased to 10–20% of baseline levels after zooplanktivorous fish were removed from a Swedish lake.

More extensive productivity data come from experiments using enclosures or microcosms. Korstad (1980) found that increased zooplankton biomass stimulated both productivity and specific productivity of phytoplankton. Bergquist (1985) found that grazed algae (< 22 μm) had maximum productivity at intermediate zooplankton biomass. Production of nongrazed algae was stimulated by increasing zooplankton biomass. Elliott et al. (1983) studied microcosms with no zooplanktivorous fish, those with caged fish that had limited access to the zooplankton, and those with unrestricted fish. Systems with caged fish had intermediate zooplankton biomass and maximum primary production. Studies of periphytic algae have found maximum productivity at intermediate densities of the following herbivores: crayfish (Flint and Goldman 1975), a herbivorous fish (Cooper 1973), tadpoles (Seale 1980), and snails (Gregory

1983). Similar unimodal curves of productivity versus grazer biomass occur in grasslands grazed by ungulates (McNaughton 1979).

Management implications

In sum, enhanced piscivory can decrease planktivore densities, increase grazer densities, and decrease chlorophyll concentrations. Stocking piscivores therefore has promise as a tool for rehabilitating eutrophic lakes. Shapiro was among the first to recognize the potential of food web alteration as a management tool and has termed the approach biomanipulation (Shapiro and Wright 1986). A recent review has advocated stocking piscivores and/or harvesting zooplanktivores as a practical approach toward enhanced fishery production and mitigation of water quality problems (Kitchell et al. 1986). The approach has been successfully used to control eutrophication in European reservoirs (Benndorf et al. 1984).

Limnology and fisheries biology have developed independently and remain largely separate professions (Larkin 1978, Rigler 1982). An analogous distinction persists between water quality management and fisheries management. The concept of cascading trophic interactions links the principles of limnology with those of fisheries biology and suggests a biological alternative to the engineering techniques that presently dominate lake management. Variation in primary productivity is mechanistically linked to variation in piscivore populations. Piscivore reproduction and mortality control the cascade of trophic interactions that regulate algal dynamics. Through programs of stocking and harvesting, fish populations can be managed to regulate algal biomass and productivity.

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