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Consumer Control of Lake Productivity

Large-scale experimental manipulations reveal complex interactions among lake organisms

Stephen R. Carpenter and James F. Kitchell

There is no common currency for ecological interactions. For example, the consumption of a small fish by a larger one entails all the following characteristics: behavioral interplay during pursuit and capture, an instantaneous reduction of the prey population, greater reproductive potential for the predator, a flux of organic energy, and a transfer of mineral nutrients such as phosphorus and nitrogen. Thus the same event is viewed differently by behavioral, population, evolutionary, physiological, community, and ecosystem ecologists. Many ecological problems involve complexes of interactions that transcend the boundaries among traditional subdisciplines. Complex interactions arise when system components are linked by multiple types of pathways (e.g., predation, behavioral cues, and transfers of energy and nutrients) (Carpenter 1988a). Consequently, new combinations of approaches are often necessary.

This article summarizes the evidence that a set of complex interactions regulates lake ecosystem pro-

Whole-lake fishery experiments can reveal fundamental mechanisms that regulate ecosystems

ductivity. The major components involve species interactions such as predation and competition, traditionally studied by population and community ecologists, plus physicochemical processes traditionally studied by limnologists and ecosystem ecologists. Nutrient input, water-turnover time, and vertical mixing are the major physicochemical factors. These have demonstrable effects on lake productivity (measured as total annual carbon fixation by the phytoplankton), but they explain only about half of the observed variability in productivity (Carpenter and Kitchell 1987, Schindler 1988, Schindler et al. 1978).

A few years ago, we offered the hypothesis that much of the unexplained variance in lake productivity is due to food web dynamics (Carpenter et al. 1985). Changes in top carnivores are transmitted to lower trophic levels through a trophic cascade. For example, an increase in biomass of large piscivorous fishes should cause a decrease in biomass of small planktivorous fishes, causing increased biomass of herbivorous zooplankton and decreased biomass of

phytoplankton (Carpenter et al. 1985, 1987).

The hierarchy of controls

Because the importance of physicochemical factors has been unequivocally demonstrated in lakes (Schindler 1988, Schindler et al. 1978), this article emphasizes the role of the trophic cascade and reviews recent tests of that hypothesis. Trophic cascades were originally described in marine intertidal communities (Paine 1980) and are now evident in many community types (Carpenter 1988a, McNaughton 1984, Power et al. 1985, Riemann and Sondergaard 1986). Trophic cascades and physicochemical factors act at different time scales to determine the productivity of lakes. Nutrient loading and water retention time set the long-term potential productivity of a lake, while interannual variability around that potential derives from species interactions and food web effects on nutrient cycling (Carpenter et al. 1985).

Aquatic community ecologists have long known of the powerful effects of predators on the structure of prey assemblages (Brooks and Dodson 1965). The evolutionary and behavioral consequences of predation have been extensively analyzed in lake communities (Kerfoot and Sih 1987, Zaret 1980). In an ecosystem context, Shapiro et al. (1975) argued that biomass and productivity of entire trophic levels could be regulated by the trophic level above. Shapiro's arguments sparked the top-down-versus-bottom-up controversy (Mc-

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Queen et al. 1986): Are lake ecosystems regulated by predation (from the top down) or by physico-chemical factors such as nutrient supply (from the bottom up)? Clearly, both top-down and bottom-up forces are important (Bartell et al. 1988). Posing the question as a dichotomy is inappropriate. Questions about controls of variability are better asked as "How much and when?"

Thermodynamics dictates that resource supply must constrain biomass at each trophic level. Abundant experimental data show that prey populations are structured by predation (Carpenter 1988a, Kerfoot and Sih 1987, Zaret 1980), and they are often inhibited or eliminated by predators (Murdoch and Bence 1987). Debate has shifted to the conditions and time scales at which particular processes (e.g., mixing, trophic cascades, and nutrient loading) have major effects on ecosystem function and can be altered to meet management objectives.

Time scales of ecosystem regulation

Lake ecosystems are especially challenging to study because of their enormous temporal variability (Carpenter 1988a). The cascading-trophic-interactions hypothesis emphasizes the dynamic nature of lake food webs and the difficult combination of scales, which range from small size and rapid response of phytoplankton to decadal population dynamics of large fishes (Carpenter 1988b, Carpenter and Kitchell 1987, Carpenter et al. 1985). Because of the differences in response scales, we expect considerable variability in relationships among different trophic levels (Figure 1). We also expect the variance found in any given study to depend upon duration and frequency of data collection (Carpenter and Kitchell 1987).

The major processes that govern lake productivity have distinct time scales. Nutrient and hydrologic fluxes from watersheds usually vary on time scales of decades to centuries, commensurate with the scales of forest succession and soil development (Likens 1985). Trophic cascade effects vary at time scales of years to decades, commensurate with the life-spans of piscivorous fishes at the top

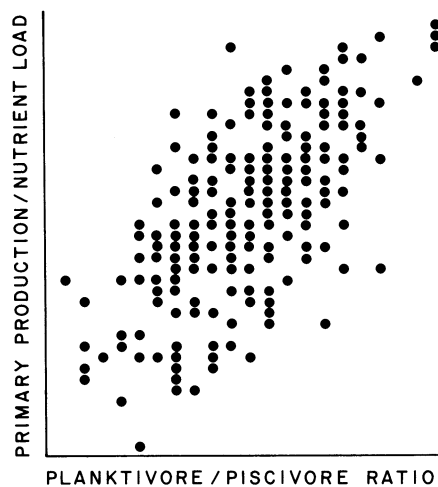


Figure 1. Relationship between the planktivore/piscivore ratio and lake primary productivity at constant nutrient supply. Each point represents the annual mean for a lake.

of the food web (Carpenter 1988b, Carpenter et al. 1985). The direct effects of weather on phytoplankton vary at subannual time scales, often days or weeks, commensurate with the rapid generation times of the algae (Harris 1980). This hierarchy of time scales must be considered in the design of studies intended to quantify and compare the effects of different processes on lake ecosystems.

As an example of the importance of time scale, we consider a hypothetical predator-prey system analyzed by regression of data from studies that employ different sampling frequencies and last for different periods of time. This example has many analogues in the ecological literature. For example, limnologists have been urged to derive theory from regression models (Peters 1986). Effects of predation from top carnivore to phytoplankton have been computed by regressing biomasses of adjacent trophic levels (McQueen et al. 1986). Such regression analyses are subject to a pitfall described below.

Dynamic oscillations that complicate regression analyses are common in food web data. Predator-prey systems are prone to oscillations (Figure 2), which have been described from models (May 1976) and observations of plankton (Murdoch and McCauley 1985) and fisheries (May 1984, Mills and Forney 1988, Walters 1986). Certain lacustrine records of food

web oscillations (e.g., Mills and Forney 1988) rival the famed small-mammal cycles (May 1976) as convincing, dramatic examples of the cyclic interactions between predator and prey.

When data from dynamic, non-equilibrium systems are analyzed by regression, results depend on the frequency of sampling and duration of the study (Box et al. 1978). One cycle of a predator-prey oscillation serves as an example. A sampling regime that is too short (relative to the period of the cycle) could produce positive or negative correlations of predator and prey densities (solid trajectories in Figure 2). A sampling regime that includes the whole cycle will produce a negative correlation, but the negative correlation does not demonstrate that predator effects are more important than resource effects. In fact, both effects are in balance at the time

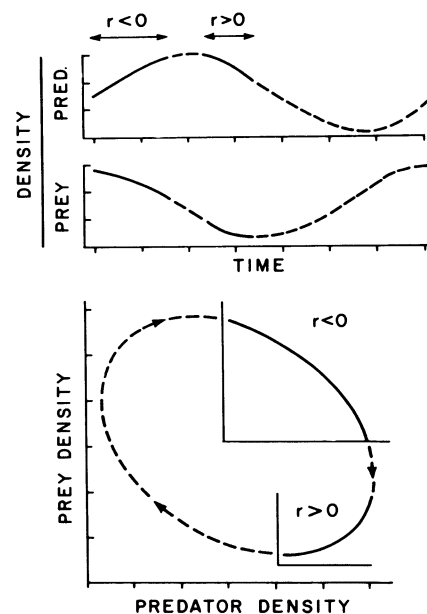


Figure 2. An oscillation of a predator-prey system illustrating the effects of the sampling period on the correlation between predator and prey density. The population densities as functions of time (top) correspond to an elliptical relationship (bottom) between predator and prey. The shape and tilt of the ellipse depend on the coefficients of the predator-prey interaction, and the period of oscillation is proportional to the life-cycle length of the longer-lived species. The correlation coefficient (r) between predator and prey depends on the time period of observation. Two periods of observation, one with negative r and one with positive r , appear as solid lines in the diagrams.

scale of one cycle, while the tilt of the ellipse arises from the coefficients that govern the predator-prey interaction and/or the initial conditions.

If the system is sampled for many cycles (an even longer time scale), further complications arise. Environmental variance will produce scatter around the ellipse, causing nonsignificant correlations. Long-term trends (caused by dynamics of a higher-level predator or environmental changes) will displace successive cycles of the ellipse, tracing a spiral that could produce negative or positive correlations, depending upon the nature of the trends. In sum, a single predator-prey interaction can produce negative, zero, or positive correlations, depending on the frequency and duration of the sampling.

That correlations depend on the frequency and duration of sampling is a general property of time-varying systems like lakes. Indeed, plots of the correlation coefficient versus time scale are basic tools in the analysis of dynamic systems (Chatfield 1980). Lake ecosystem models demonstrate the relationships between time scale and the correlations of zooplankton biomass with primary production (Carpenter and Kitchell 1987) and piscivore density with primary production (Carpenter 1988b). Correlative analyses of food web components at a single time scale (e.g., data from multilake surveys or monitoring data at one sampling frequency) are therefore of dubious value if not downright misleading. Another investigator could obtain different results by sampling the same systems at a different time scale.

Experimental approaches

Experiments reveal both the powerful effects of predators on ecosystem processes and the dynamic variability of system response implied by Figure 1. Here we summarize four years of data from two whole-lake experiments that illustrate both the potential and the complexity of food web effects on lower trophic levels.

The two experiments involved three lakes near Land o' Lakes, Wisconsin. During 1984, Paul and Peter Lakes contained abundant piscivores (largemouth bass), few zooplanktivorous fishes, high biomasses of large

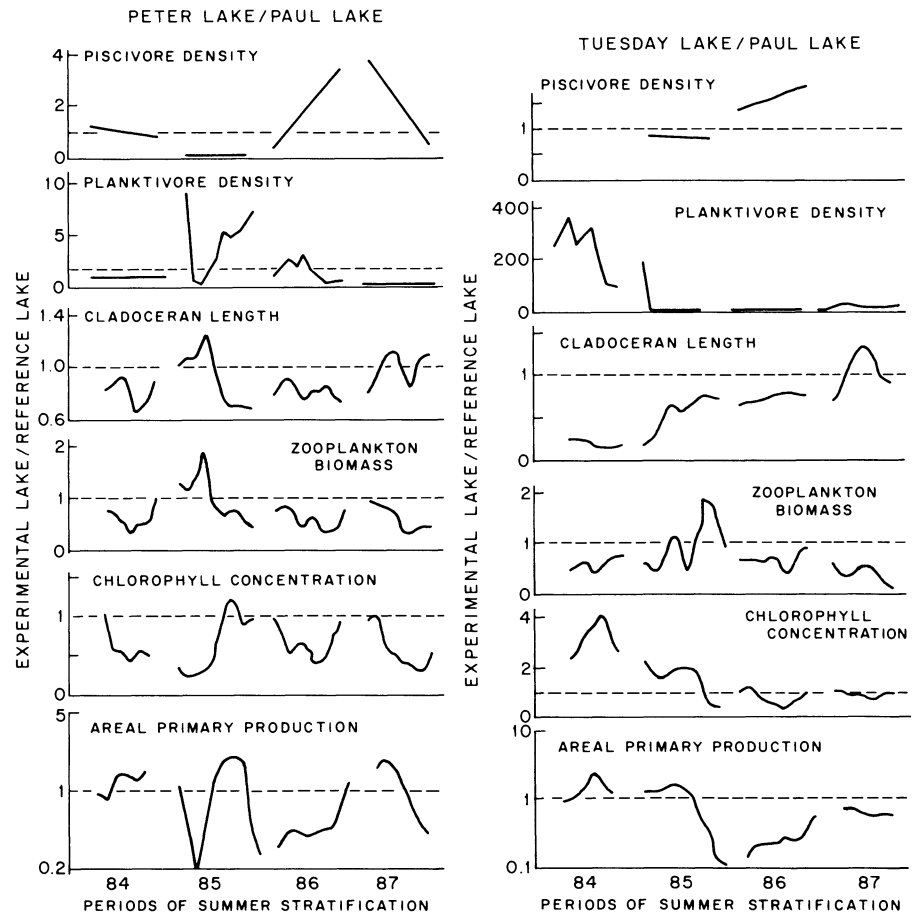


Figure 3. Whole-lake experiments. Piscivore density (fish/hectare), planktivore density (fish/trap-hours), cladoceran length (mm), zooplankton biomass (g dry mass/m²), chlorophyll concentration (mg/m³), and areal primary production (mg C · m⁻² · d⁻¹) versus time. To remove the effects of regional weather, we show the ratios of the experimental lake to an undisturbed reference system, Paul Lake. a. The summer seasons of 1984–1987 for the whole-lake experiment in Tuesday Lake. b. The summer stratified seasons of 1984–1987 for the whole-lake experiment in Peter Lake. Methods and detailed data appear elsewhere (Carpenter et al. 1987, Carpenter and Kitchell manuscript in preparation).

cladoceran herbivores, and relatively low algal densities (Carpenter et al. 1987). Tuesday Lake had no piscivores (as a result of occasional winterkills), but it harbored abundant zooplanktivores (minnows), low biomasses of small herbivores, and relatively high densities of phytoplankton. In May 1985, the experiment was initiated with a reciprocal fish manipulation that transferred 90% of the piscivore biomass from Peter Lake to Tuesday Lake and 90% of the planktivore biomass from Tuesday Lake to Peter Lake. Paul Lake remained undisturbed as a reference ecosystem. All trophic levels of all three lakes were monitored for three summers.

Bass addition and minnow removal from Tuesday Lake caused a massive,

sustained response in lower trophic levels (Figure 3a). The size of cladoceran herbivores increased through the study because planktivory (by fishes that feed selectively on larger herbivores) was reduced. In 1985, zooplankton biomass dynamics were bimodal. The first peak was composed of the small zooplankters present before the manipulation, while the second, higher peak was composed of large-bodied herbivores (*Holopedium* and *Daphnia*) that were new dominants in Tuesday Lake (Carpenter et al. 1987). Chlorophyll concentration and primary production decreased substantially as the large grazers assumed dominance. During 1986 and 1987, low densities of edible phytoplankton intensified competition among zooplankton.

Zooplankton biomass declined as the relative abundance of large-bodied animals increased.

In fall 1986, bass were removed from Tuesday Lake. In May 1987, minnows were reintroduced to the lake at two percent their premanipulation density. This low density did not affect lower trophic levels. We hypothesize that the lower trophic levels of Tuesday Lake will return to premanipulation conditions as the re-introduced minnow population grows by natural reproduction.

Bass removal and minnow addition to Peter Lake had effects on lower trophic levels that were as strong as, but more short-lived than, those observed in Tuesday Lake (Figure 3b). The ecosystem response was powerful but transient during the summer of 1985. Minnow densities in the open water of the lake crashed within a few weeks as small fish sought refuge near the lake margin and suffered heavy losses to predation by bass (Carpenter et al. 1987). While planktivore densities were low, the large cladocerans present in the lake grew explosively in size and biomass, sharply depressing chlorophyll concentrations and primary production. Recruitment of young of the year-bass increased 50-fold under the conditions of abundant food and low adult density. During the latter half of summer 1985, planktivory increased as young of the year-bass grew large enough to evade the cannibalistic adults, moved off-shore, and fed on zooplankton. Cladoceran length and zooplankton biomass declined sharply as chlorophyll concentration and primary production surged upward. During this period of high production, the phytoplankton was dominated by large, gelatinous colonies of *Sphaerocystis* (Carpenter et al. 1987).

During 1986 and 1987, the plankton of Peter Lake resembled premanipulation conditions. The diets of the large cohort of juvenile bass switched to larger prey, including smaller members of their own cohort and bass spawned in 1986 and 1987. Low planktivore densities in 1987 may have accounted for modest elevations in zooplankton size and biomass and modest declines in chlorophyll and primary production.

These results illustrate both the power and complexity of fish effects

Table 1. Contrasting responses of phytoplankton species as a function of experimental time-scale. Species with increasing, decreasing, or unimodal responses to increased grazing in three- to five-day enclosure experiments are tabulated according to their response to whole-lake increases in grazer biomass lasting one to two years. Only those species with statistically unequivocal responses in both enclosure experiments and whole lake experiments are included (Bergquist 1985, Bergquist and Carpenter 1986, Carpenter et al. 1987, Elser et al. 1987, Elser and Carpenter 1988).

Whole-lake response	Response in enclosure		
	Increase	Decrease	Unimodal
Increase	2	20	16
Decrease	3	10	9

on lake ecosystems. Substantial and sustained suppression of planktivorous fishes maintain substantial reductions of chlorophyll and primary production (Figure 3a). On the other hand, even a residual piscivore population can rapidly eliminate the effects of introduced planktivores (Figure 3b). Variable reproductive rates and behaviorally mediated fluctuations of the fish population can lead to large, transient responses in ecosystem processes. Similar fluctuations have been observed in long-term studies of plankton communities affected by variable recruitment success of fishes (Mills and Forney 1988).

Scaling of experiments

Complex interactions often can be analyzed by experiments of relatively short duration using enclosures or other simplified systems smaller than whole lakes. However, results of such studies may not be applicable beyond the scales employed (Frost et al. 1988).

An example of scale-dependent experimental results arose during our studies of Paul, Peter, and Tuesday Lakes (Table 1). Experiments in small fishless enclosures were used to examine the responses of individual phytoplankton taxa to gradients of zooplankton biomass over periods of three to five days. Statistically significant species' responses were classified as increasing, decreasing, or unimodal across the zooplankton biomass gradient (Bergquist and Carpenter 1986). Unimodal responses have increasing growth rates at low zooplankton biomass, maximum growth rate at intermediate zooplankton biomass, and declining growth rate at high zooplankton biomass. Phytoplankton growth rates in enclosures were consistent with growth rates in

the lakes determined from weekly samples (Elser et al. 1987).

Each phytoplankton's response to whole-lake manipulation was compared with its response in enclosure experiments in the same lake. Phytoplankton responses in the three- to five-day-enclosure experiments were quite different from those in one- to two-year whole-lake experiments (Table 1). Overall, 23 of 60 species responded oppositely in whole-lake and enclosure experiments. Discounting unimodal responses, enclosure experiments correctly forecast whole-lake responses for only 34% of the taxa tested.

The differences in scale between the enclosure and whole-lake experiments cause them to measure different responses. Enclosure experiments reveal short-term regulation of the phytoplankton by fluctuations in biomass of the same zooplankton assemblage with which the algae coexist in the lake. In contrast, whole-lake experiments reveal processes that determine phytoplankton community structure over the long term under a broad range of food web structures, so the phytoplankton are exposed to zooplankton assemblages they have not encountered before. The distinction between enclosure and whole-lake responses is analogous to that between short-term processes that maintain community structure and long-term processes that establish community structure (Thorpe 1986).

Mobile predators such as fishes pose particular problems for enclosure experiments. For example, the responses of Peter Lake (Figure 3b) depended on recruitment and in-shore-offshore migrations of fishes and could not have occurred in an enclosure (Carpenter et al. 1987). In attempts to scale enclosure experiments properly, experimenters have

confined fish in cages (Elliot et al. 1983). Even experimental pond systems constrain large predators and eliminate vertical phenomena such as migration and stratification.

Extrapolation from short-term enclosure experiments to whole-lake dynamics can lead to major errors. On the other hand, certain small-scale experiments have revealed crucial information about regulatory processes and uncovered critical mechanisms that structure communities (reviewed in Carpenter 1988a, Kerfoot and Sih 1987, Riemann and Sondergaard 1986). For example, Vanni (1987) has used enclosure experiments to dissect the effects of food supply and fish predation on size structure, life history traits, and community composition of zooplankton. In general, such successful experiments are scaled properly to the phenomena of interest and extrapolated with appropriate caution to the whole-lake scale. A formalized approach to translating results from small-scale experiments to lake ecosystems would be extremely useful (Frost et al. 1988).

The scale of ecosystem management

Substantial fish manipulations at the whole-lake scale have produced substantial responses in phytoplankton (Table 2). Where modified fish communities have been sustained for years, altered phytoplankton densities have also been sustained (Lakes Lillestockelidsvatten and Tuesday). Lesser fish manipulations have produced lesser or equivocal responses in the phytoplankton. These results support the implications of Figure 1: substantial, sustained fish manipulations reconfigure food webs and modify primary production independent of nutrient loading. Successful whole-lake investigations of nutrient and toxicant effects have also employed substantial (tenfold or greater) treatment manipulations sustained for many years (Schindler 1988, Schindler et al. 1978).

Most lakes contain fishes and support fisheries. A paradox of management emerges from the practice of maximizing fish yields by maintaining intermediate densities of adult fishes. These intermediate densities produce maximal variance in recruit-

Table 2. Results of whole-lake fish manipulations in which dynamics of all trophic levels were documented.

Lake	Fish manipulation	Phytoplankton response
Lillestockelidsvatten*	Planktivores removed	Primary production decreased to 8% of initial level
Michigan†	Piscivore stocking reduced planktivory to 10%–20% of initial level	Summer chlorophyll decreased to 20% of initial level
Tuesday‡	Piscivore stocking virtually eliminated planktivores	Chlorophyll and primary production decreased to 10%–20% of initial level
Peter‡	Planktivore stocking and piscivore recruitment caused 15-fold fluctuation in planktivory	Chlorophyll and primary production changed 10-fold
Round§	70% removal of planktivores	Chlorophyll decreased to 50% of initial level
St. George	50% removal of piscivores	No change detected

*Henrikson et al. 1980

†Kitchell and Crowder 1986, Scavia et al. 1986

‡This article

§Shapiro and Wright 1984

||D. J. McQueen, M. R. S. Johannes, J. R. Post, T. J. Stewart, and D. R. S. Lean, 1989, unpublished manuscript, York University, York, Ontario, Canada

ment success and maximal variance in biomasses of lower trophic levels (Carpenter and Kitchell 1987). Manipulations must overcome that variance to achieve sustained changes in lower trophic levels.

The magnitude of manipulation relative to the system's variance is no different from manipulations used in laboratory experiments. In both cases the experimenter applies treatments large enough to produce discernible changes relative to the intrinsic variability of the system. For real ecosystems, intrinsic variability is great, and manipulations must be substantial and sustained to be effective (Kitchell et al. 1988, Walters 1986).

Lake management operates at the spatial scale of whole ecosystems and the temporal scale of years to decades. On these scales, large manipulations of fish community structure can produce order-of-magnitude changes in water quality parameters such as algal biomass. A conflict of goals may occur because management to enhance water quality will typically require sustained high levels of piscivory. Maintenance of adequate piscivory may entail reduced or regulated exploitation of large fishes and lower total fishery yields. Decision

makers must understand the consequences of these alternatives (Figure 1 and Table 2). Compromise will yield a confusing result instead of an intermediate effect.

The observed variation in lakes includes variability induced by fisheries management and exploitation. Thus lake ecosystems are regulated by a combination of physicochemical and biotic interactions, which exhibit high variance at scales of years to decades through the dynamics of exploited fish populations. The temporal fluctuations of lake ecosystems indicate that no ecosystem state is maintained for long. Estimated means and variances of ecosystem variables are dependent upon the frequency and duration of sampling. To develop productive theories and informative experiments that reveal the context and contribution of controlling factors, we must accept the variability of ecosystems and the concern for scale that variance entails.

Whole-lake experiments are feasible and can reveal fundamental mechanisms that regulate ecosystems. Fisheries management agencies are ideally positioned to perform the necessary manipulations. Walters (1986) has argued that strong manipulations are

essential for effective analysis of fisheries dynamics. Our results show that basic ecological insights also derive from such experiments. An alliance of managers with researchers to perform powerful, large-scale manipulations would produce rapid progress in understanding the complex interactions that pervade both basic and applied aquatic ecology.

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