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1 · *Cascading trophic interactions*

James F. Kitchell and Stephen R. Carpenter

Introduction

The extent to which physical–chemical or biotic factors influence community structure and ecosystem function continues as one of the fundamental issues of ecology. The action and interaction of abiotic and biotic factors was recognized in early concepts of plant succession (McIntosh, 1985) and continues in the most contemporary reviews of plant–animal interaction (Strong, 1992). In animal community ecology, there have been several recent syntheses of the effects of multiple controlling factors (Menge & Sutherland, 1976, 1987; Fretwell, 1977; Oksanen *et al.*, 1981; Power, 1992; Strong, 1983, 1992). Vigorous debate has surrounded the relative roles of predation and competition (Hairston, Smith & Slobodkin, 1960; Murdoch, 1966). Predation has been viewed from the standpoints of predator control of prey communities (Oksanen, 1983, 1990) and of prey constraints on predator communities (Price *et al.*, 1980; Kareiva & Sahakian, 1990; Hunter & Price, 1992).

Like the other branches of ecology, limnology has evolved through debates about the roles of abiotic and biotic factors (Edmondson, 1991). In some respects, lakes are ideal systems for the study of multifactor interactions at the ecosystem scale (Carpenter, 1988*a*, pp. 4–5). Boundaries are clear and the difficulties of system definition that plague some areas of ecology (McIntosh, 1985) are lessened. Lakes are amenable to experimentation on a variety of scales, including whole-lake manipulations (Frost *et al.*, 1988). At a global scale, insolation and climate have dominant effects on lake ecosystems (Brylinsky & Mann, 1973). At scales ranging from lake districts to individual lakes, nutrient input rate, water renewal rate and lake morphometry are prominent abiotic factors (Schindler, 1978; Fee, 1979; Carpenter, 1983). At these scales, biotic effects are also evident and may contribute to the substantial variability observed in basic ecosystem processes such as primary production.

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Over the past several decades, two general lines of inquiry have emerged in the efforts of aquatic scientists. The seminal observations of Hrbacek *et al.* (1961) and the pioneering work of Brooks & Dodson (1965) set the stage for an immense diversity of studies designed to clarify the unknowns of grazing, competition and predation as interactions of primary importance in regulating aquatic populations and community structure (Kerfoot & Sih, 1987). A second pursuit emerged from general interest in water quality, flourished during the limiting nutrient debate, and remains fully established as the first order of consideration in limnological textbooks (e.g. Wetzel & Likens, 1991).

Each of the topics identified in the preceding paragraphs is complex; a contemporary synthesis would be a book-length monograph in itself. Our goals are more modest and specific: to present the results of a large-scale experimental test of the trophic cascade hypothesis which coupled abiotic and biotic effects and was proposed to explain the unaccounted for variability of primary production rates in lakes (Carpenter, Kitchell & Hodgson, 1985).

The trophic cascade hypothesis states that nutrient input sets the potential productivity of lakes and that deviations from the potential are due to food web effects (Carpenter *et al.*, 1985). Nutrient and food web effects are complementary, not contradictory, but they act at different time scales (Carpenter, *et al.*, 1985; Carpenter, 1988*a*). Food web effects stem from variability in predator–prey interactions and their effects on community structure (Carpenter & Kitchell, 1987). Acting through selective predation, variability at the top of the food web cascades through zooplankton and phytoplankton to influence ecosystem processes (Carpenter *et al.*, 1985). This is the definition of trophic cascades used throughout this book. Our usage derives from Paine (1980). It is distinct from the cascade model used by theorists to describe the statistical distribution of links and other static properties of food webs (Cohen, 1989).

In this chapter, we first summarize the roots of the trophic cascade idea for lakes. We consider the major kinds of studies that have been used to learn about lake ecosystems: comparisons, long-term studies, simulation models, mesocosms and ecosystem experiments. We then explain our approach, in which ecosystem experiments are central but all five methods of study are represented. Finally, we explain the goals and structure of the remainder of the book.

The trophic cascade concept in lakes

The ideas about a trophic cascade in lakes derive from two primary sources. First is the extension of thermodynamic principles to ecology, which yields the expectation that organic production in lakes should be a function of nutrient status. Strong correlations exist between nutrient loading or nutrient concentration and primary production (Schindler, 1978). Flow of energy and matter upward through food chains is a central paradigm of the ecosystem approach (Lindeman, 1942; LeCren & Lowe-McConnell, 1981; Odum, 1969). Although the correlations confirm a logical expectation, the log–log regressions used in these empirical analyses account for only part of the variance observed when primary production rates or their surrogates are considered as a function of nutrient loading rates (Carpenter *et al.*, 1991). At any given level of nutrient loading or concentration, algal concentration or production may differ among lakes by an order of magnitude or more. Measurement error may account for some of that variance, but a mechanistic alternative is also plausible.

The second major element of the cascade idea derives from the evolutionary principles widely employed in contemporary population biology and community ecology. Consumers are typically selective in the types and sizes of resources they consume (Hall *et al.*, 1976; Kerfoot & Sih, 1987). This tenable extension of natural selection theory is embodied in aquatic ecology as the principles of size-selective predation (Hrbacek *et al.*, 1961; Brooks & Dodson, 1965), the keystone predator concept (Paine, 1966) and theories of optimal foraging and habitat usage (Werner, 1986). In lake ecosystems, the result of selective predation plays a major role in community composition at each trophic level (de Bernardi, 1981). Piscivores determine the size and species composition of the planktivorous fish assemblage beneath them in a food web (Tonn & Magnuson, 1982). Selective planktivory by fishes and invertebrate predators profoundly influences the community of herbivorous zooplankton which, in turn, regulates the amount and kinds of phytoplankton that compete for nutrients (Brooks & Dodson, 1965; Sommer, 1989). Much of the available nutrient pool derives from recycling through excretion processes that are strongly size-dependent (Kitchell *et al.*, 1979; Peters, 1983). Thus, the rates of primary production can be substantially influenced by a trophic cascade of size-selective predation processes that start at the top of the food web.

The components of the cascade argument have a crucial nexus at the zooplankton (Fig. 1.1). Larger herbivores are consumed selectively by planktivorous fishes (Brooks & Dodson, 1965). Carnivorous zooplankton feed most heavily on smaller zooplankton (Hall *et al.*, 1976). Abundant planktivorous fishes shift the zooplankton composition toward dominance by smaller individuals. When planktivorous fishes are absent, predation by planktivorous invertebrates and competition among herbivores shift the zooplankton toward larger individuals (Brooks & Dodson, 1965; Hall *et al.*, 1976). Large herbivores such as *Daphnia* have a greater impact on phytoplankton because they consume a broad range of sizes and morphologies of algae (Burns, 1968; Gliwicz, 1980; Bergquist, Carpenter & Latino, 1985). Owing to their size, large zooplankton have lower mass-specific rates of nutrient excretion (Peters, 1983). In comparison with a small-bodied zooplankton assemblage of equal biomass, an assemblage dominated by large *Daphnia* should graze a broader spectrum of algae but recycle nutrients at lower rates. Thus, algal biomass and primary production should be less in *Daphnia*-dominated lakes than in lakes dominated by small zooplankton such as *Bosmina*, small calanoid copepods, or rotifers. Zooplankton biomass should be directly related to nutrient concentration but, for equivalent zooplankton biomass, algal biomass and production should be inversely related to mean zooplankton size (Carpenter & Kitchell, 1984).

Evidence for trophic cascades stems from a variety of sources as represented in recent reviews (Northcote, 1988; Power, 1992). Although each case has its idiosyncracies, the central idea about the effects of a top predator are documented through experimental studies in ponds (Hurlbert & Mulla, 1981; Spencer & King, 1984), lakes (Henrikson *et al.*, 1980; Shapiro & Wright, 1984; Carpenter *et al.*, 1987), rivers (Power, 1990) and intertidal (Paine, 1980) and subtidal marine communities (Estes & Palmisano, 1974; Mann & Breen, 1972). Important evidence has also come from studies of variability in lakes spanning gradients of nutrient richness and food web structure (Carpenter *et al.*, 1991; Persson *et al.*, 1992).

A comparative analysis of these state variables in 25 lakes sampled from 2 to 6 years each revealed both nutrient and predation effects (Fig. 1.2) (Carpenter *et al.*, 1991). Total phosphorus concentration during spring (a surrogate for nutrient input) was positively correlated with summer mean chlorophyll ($r^2 = 0.40$, $p < 0.001$). Zooplankton mean length, an indicator of size-selective predation and the intensity of grazing, was negatively correlated with summer mean chlorophyll ($r^2 = 0.45$, $p < 0.001$). A multiple regression combining food web and

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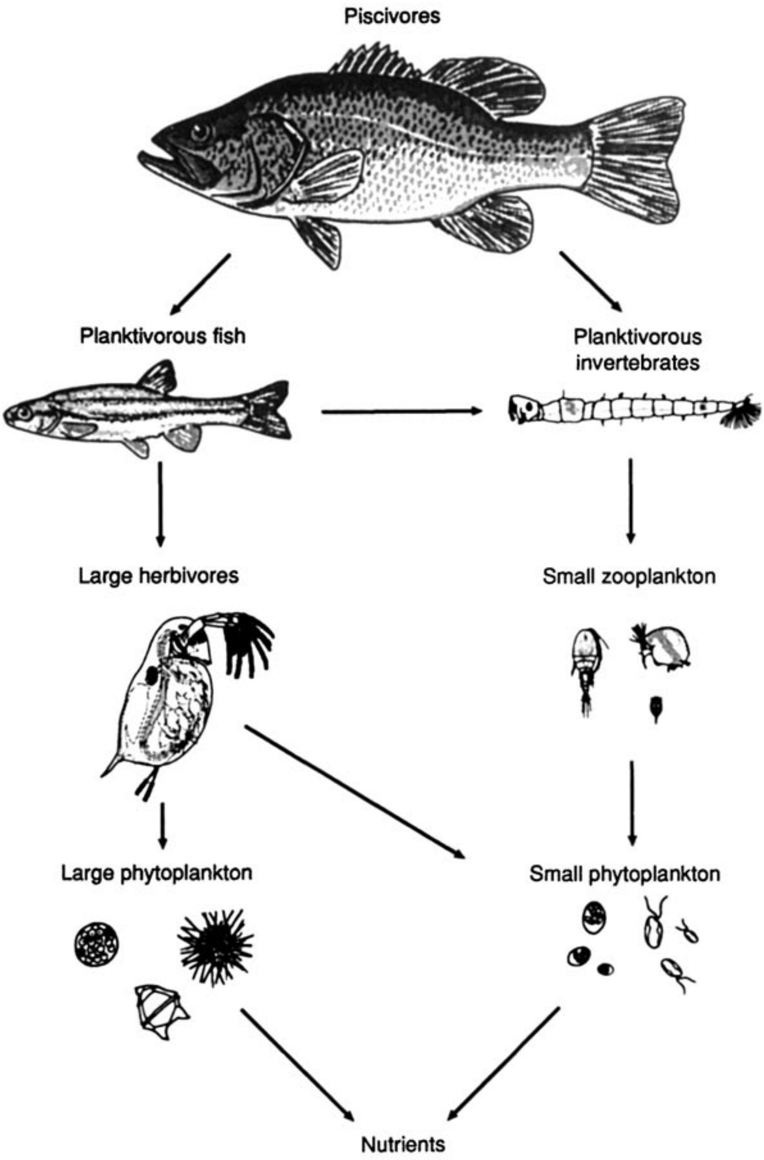

Fig. 1.1. Major interactions of the trophic cascade illustrated with selected organisms from our experimental lakes. Nutrients (mainly inorganic phosphorus and nitrogen) are provided by inputs from the watershed and recycling by animals. The relationship of this food web to the microbial food web is detailed in Fig. 14.1. Organisms are not to scale; for scale drawings see Figs. 4.1, 8.1, 11.1, and 14.2.

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nutrient variables to predict chlorophyll was highly significant ($R^2 = 0.68$, $p < 0.001$) and explained far more variance than regressions based on nutrient variables alone or food web variables alone (Carpenter *et al.*, 1991).

Analogous reasoning forms the basis for 'biomanipulation' as a management tool designed to improve water quality. Many of the ideas for that owe to Joseph Shapiro and his co-workers (Shapiro, Lamarra & Lynch, 1975) and have been widely adopted (Gulati *et al.*, 1990). As we have detailed elsewhere (Carpenter & Kitchell, 1992), biomanipulation and the trophic cascade hypothesis are similar but not the same. Biomanipulation draws from a diverse set of approaches designed to reduce the expression of an undesirable ecological attribute such as hypolimnetic oxygen depletion, bluegreen algae blooms or overly abundant littoral macrophytes. In contrast, the trophic cascade hypothesis seeks to explain the within- and among-lake variability in the basic primary production process.

Ecosystem epistemology

Ideas about ecosystem processes have been tested in five essentially different ways: mesocosms, interlake comparisons, long-term studies,

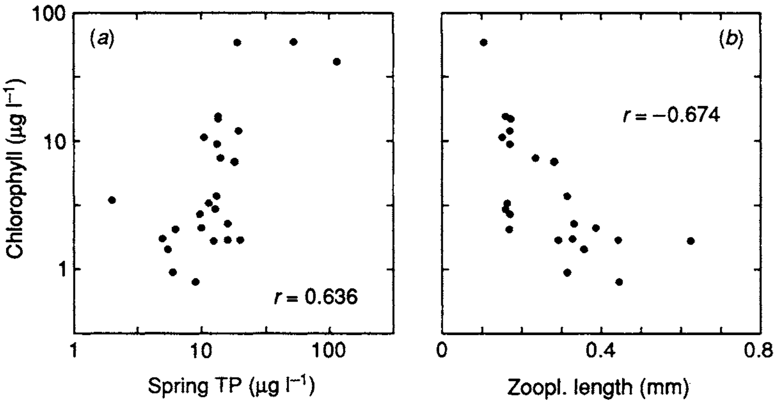

Fig. 1.2. Scatterplots relating photic zone chlorophyll concentration to (*a*) total phosphorus concentration during spring and (*b*) mean zooplankton length. Each data point is the mean of 2–6 summer stratified seasons for a lake in the Great Lakes region of North America (Carpenter *et al.*, 1991). Correlations are highly significant ($p < 0.001$). From Carpenter *et al.* 1991. Copyright © Springer-Verlag New York, Inc. Used by permission.

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simulation models, and ecosystem experiments. While these categories are somewhat arbitrary and have some obvious overlaps, all ecosystem studies could be assigned to at least one of them. Each approach has different strengths. All five approaches have been used in our research on the trophic cascade, although we view ecosystem experiments as the core of our work. We will review these before explaining why we think that ecosystem experimentation is central to understanding the trophic cascade.

Comparisons usually involve analysis of how some ecosystem property of interest (such as primary production or plankton community structure) changes along gradients of potential causal factors (such as nutrient supply or fish density). Comparative studies can easily be scaled to whole ecosystems, often at relatively low cost (Cole, Lovett & Findlay, 1991). They quickly reveal the range of possible system states and relationships among key variables. On the other hand, it can be very difficult to detect dynamics and infer responses to perturbation from comparisons of static properties of ecosystems (Carpenter & Kitchell, 1988; Carpenter *et al.*, 1991).

Long-term studies involve analysis of ecosystem dynamics through direct observation or paleoecological surrogates (Strayer *et al.*, 1986; Likens, 1989). Despite their relative rarity, long-term records have made remarkable contributions by reducing the constraints of time scale that limit much ecological research (Strayer *et al.*, 1986; Likens, 1989; Magnuson & Bowser, 1990; Jassby, Powell & Goldman, 1990; Edmondson, 1991). Because the population dynamics of fishes play out over decades, long-term studies have been useful in studies of trophic cascades (Jassby *et al.*, 1990; Kitchell, 1992) (Chapter 15). The main disadvantage of long-term studies is the slow rate at which new insights develop (Walters, 1986; Carpenter, 1988*a*). One must wait for rare, unpredictable informative changes in order to learn about the system (Kitchell, 1992; Edmondson, 1991). Where good paleolimnological indicators exist, this difficulty may be circumvented. As detailed in Chapter 15, the documented history of manipulations in Peter, Paul and Tuesday Lakes, plus the calibration of neolimnological responses due to our experimental work, allow us to create a unique combination of paleolimnological observations that cover the entire range of trophic conditions in these lakes.

Simulation analyses are based on models designed to serve as a simplified surrogate for the complexities of natural systems. Models of ecosystem dynamics depend on the rationale that the major components

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and interactions have been included, and that forcing variables and parameters can be known rather precisely (e.g. Chapra & Reckhow, 1983). Simulation models have proven valuable for understanding the possible outcomes of postulated interactions in ecosystems (e.g. DeAngelis & Waterhouse, 1987). However, developing model structures that can cope with the variability of ecosystems remains a challenging problem (Beck, 1983; Walters, 1986). Simulation models are usually calibrated and tested using field data, and are therefore used with one or more of the other approaches. Models and their evaluation have played a central role in the design of our experimental work. As candidly detailed in Chapter 16, the mixture of successes and failures has been very informative.

Mesocosms are laboratory or field enclosures used for experimental studies of selected ecosystem components or interactions. Experimental ponds (Hall, Cooper & Werner, 1970; Hurlbert & Mulla, 1981) are mesocosms that are relatively large and complex but, due to their depth, offer environments that simulate only the littoral zone of lakes. Because mesocosm experiments can be controlled and replicated, they are a powerful experimental tool for studying ecological mechanisms (Hairston, 1989; Mazumder *et al.*, 1990; Soto & Hurlbert, 1991). Because of their typically small size, mesocosms necessarily exclude some processes that may be important for predicting ecosystem dynamics (Frost *et al.*, 1988; Carpenter & Kitchell, 1988). For example, inshore–offshore migrations of fishes and hydrodynamic fluxes of nutrients cannot easily be included in enclosure experiments. Therefore, mesocosm results may not be directly transferable to the ecosystem scale and can, in fact, yield erroneous extrapolations (Frost *et al.*, 1988). Recognizing these limitations, we have used mesocosm experiments to study selected interactions between zooplankton and their predators (Chapter 9) and between herbivorous zooplankton and the algae they graze (Chapter 12), and the complexities of interrelationships among microbes, protozoa and zooplankton (Chapter 14).

Experimentation at the ecosystem scale has made important contributions to ecology in general, and limnology in particular, over the past several decades (Likens, 1985; Schindler, 1988). Such experiments lack the scale problems of mesocosms and, unlike most comparative studies, can be designed to directly address ecosystem dynamics and responses to perturbation. Ecosystem manipulations can significantly increase learning rate, as measured by rate of reduction of error in model predictions (Walters, 1986; Carpenter, 1988*a*). Because ecosystem experiments simulate management actions at the appropriate scale, they have been a convincing means of resolving uncertainty in management controversies (Walters, 1986; Schindler, 1988; Kitchell, 1992). The main disadvantage of ecosystem experiments is that replication is difficult or impossible (Matson & Carpenter, 1990). Access to experimental sites often limits ecosystem experimentation. In fact, the University of Notre Dame Environmental Research Center, where we conducted our work, is among the few places on earth where controlled access to lakes allows for whole-lake experimental studies that are unaffected by perturbations of the watershed, anglers and/or a curious public. Despite these difficulties, deliberate or inadvertent perturbations of lake food webs have yielded valuable information about trophic cascades (Henrikson *et al.*, 1980; Shapiro & Wright, 1984; Carpenter *et al.*, 1987; McQueen *et al.*, 1989; Benndorf, 1990; Jeppeson *et al.*, 1990; Reinertsen *et al.*, 1990; Kitchell, 1992).

Our approach

The central idea of this book – that effects derived from the fish community cascade through the food web to influence primary production processes – is obviously testable by whole-lake experimentation. More importantly, evidence from other approaches leaves gaps that can only be resolved by whole-lake experiments. Several comparative studies are consistent with the cascade hypothesis, but offer less direct insight about response capacity of perturbed lakes (Mills & Schiavone, 1982; Pace, 1984; Quiros, 1990; Carpenter *et al.*, 1991; Persson *et al.*, 1992). Mesocosm studies reveal a complex array of interactions that could dampen trophic cascades (Kerfoot & Sih, 1987; Frost *et al.*, 1988; Gulati *et al.*, 1990; DeMelo, France & McQueen, 1992). For example, compensatory shifts in species composition (Strong, 1992) (Chapter 8) or migrations of key predators or their prey (Chapters 5 and 9) could override cascade effects. Fishes and plankton, their functional and numerical responses to food resources, their habitat selection behaviors, their life history strategies and the integrated result in population and trophic dynamics all operate at the scale of entire lakes. Those variables function interactively with other large-scale processes such as mixing, diffusion and light extinction. Thus, the trophic cascade embodies a set of processes demanding the whole ecosystem as an experimental unit and the growing season as a minimum duration. As noted above, our ecosystem experiments were coordinated with comparative, long-term, simulation and mesocosm studies where these alternatives were appropriate and advantageous. Frost *et al.* (1988) and Tilman (1989) have discussed the utility of combining approaches at several scales for ecosystem studies.

When we initiated this project in the early 1980s, only two whole-lake food web experiments addressing fish, zooplankton, phytoplankton and nutrients were known to us (Henrikson *et al.*, 1980; Shapiro & Wright, 1984). Now, results are published from several more whole-lake experiments (Benndorf, 1990; Jeppeson *et al.*, 1990; Sanni & Waervagen, 1990; van Donk *et al.*, 1990; Giussani, de Bernardi & Ruffoni, 1990; Reinertsen *et al.*, 1990) and a large number of inadvertent perturbations of food webs in whole lakes. Like our work, most of these studies examined a comprehensive array of response variables ranging from fish to nutrients, and from population to ecosystem processes. We believe that our experiments are a unique and valuable addition to this literature for several reasons.

(1) Unlike several other whole-lake experiments, we employed a reference ecosystem (Likens, 1985) as a check for trends unrelated to our manipulations.
(2) Our experimental lakes lie in protected watersheds closed to the public. As a result, we were spared the confounding effects of unplanned or unknown human disturbance (Chapter 2).
(3) We employed statistical approaches that compensate for the lack of replicability inherent in large-scale experimentation (Chapter 3).
(4) We coordinated our experiments with paleolimnological studies to gain a long-term view (Chapter 15) and with simulation models to conduct specific tests of theory (Chapter 16).

It is clear from the literature that a wide range of responses can develop from perturbations of lake food webs (Carpenter & Kitchell, 1988). We do not yet know the conditions that cause one particular sequence of events to occur rather than the alternatives. Each ecosystem experiment is a valuable datum toward developing that understanding.

The seven intensive years of this program involved two major manipulations. The first (1984–6) was a reciprocal transplant of the tops of two contrasting food webs. Largemouth bass were removed from Peter Lake and planted in Tuesday Lake after its minnow population had been removed. Those minnows were then planted in Peter Lake. This experiment was designed to test maximum response capacity; i.e., to determine the greatest possible contrast of food web effects on commun-