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# Phosphorus in food webs: Compensatory responses in experimental lakes

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## Introduction

Evidence of the role of food web interactions in regulating lake productivity is growing rapidly and has been summarized in several recent reviews (Carpenter 1988, Northcote 1988, Mazumder et al. 1990, Carpenter et al. 1991, Power 1992). The magnitude of response to trophic cascades is also the focus of contemporary debate (Carpenter & Kitchell 1992, DeMelo et al. 1992, Strong 1992) and the basis for applied concerns where biomanipulation efforts have been pursued (Shapiro et al. 1975, Gulati et al. 1990, Kitchell 1992). Previous work on these questions identified two general and important mechanisms: 1) size selective predation processes as a primary cause of differences in plankton community structure (Hrbacek et al. 1961, Brooks & Dodson 1965) and 2) changes in nutrient cycling rates (phosphorus, in particular) which were due to the altered size distributions of the plankton (Kitchell et al. 1979, Carpenter & Kitchell 1984, Carpenter et al. 1985).

A second class of issues revolve around theoretical constructs that address the constraints of productivity on food web structure. Some ecologists argue that the fundamental basis for different types and intensity of feedback mechanisms derives from thermodynamic limitations to the number of trophic levels that can be supported at a fixed level of nutrient input (Power 1992). In simplified terms, a three-level food web can function at a lower productivity than that required to sustain four-level food webs. Addition or deletion of a trophic level results in non-linear ecosystem responses to changes in nutrient inputs. In odd-numbered food chains, levels one (primary producers) and three (predators on herbivores) increase with increased nutrient loading; level two (herbivores) does not due to control by its predator. In even-numbered food chains, levels two and four (piscivores) increase in response to increased nutrients while levels one and three do not; again, due to the regulatory capacity of their consumers. These simple concepts have some utility but are, of course, confounded by the widespread occurrence of omnivory, differences in the strength of species interactions, and the effects of trophic contogeny which combine to make chains into webs (Paine 1980, Persson et al. 1988, Polis 1991, Power 1992).

While the mechanisms of interaction remain fertile ground for continued work, the next generation of questions could also be profitably focused on the rates of response to changes in food web structure, the compensatory response potential of aquatic communities, the feedback mechanisms involved, and the ecosystem scale expression of those dynamics (Carpenter & Kitchell 1993). This report provides a brief summary of our accomplishments in attempting to address those questions. Seven years of experimental studies are used to offer evidence of responses in net phosphorus distribution among food web components and its consequences at the whole lake scale.

## Methods

Our central approach involved manipulation of fish populations to test the role of predation-competition interactions as they passed through food webs and were expressed in the nutrient cycling and plankton production processes. Description of the study lakes and limnological methods pursued in this large study were provided in detailed accounts of interim results (Carpenter et al. 1987). Briefly restated here, our general approach involved monitoring the biomass of each major food web component and the concentrations of major nutrients during the period of late-May through early September of 1984–90. We emphasize phosphorus in this analysis because it is generally regarded as the nutrient which regulates primary production processes for lakes in the Great Lakes region of North America.

Dissolved forms of P are consistently at or near detection levels in these waters. Accordingly, we combined the dissolved and particulate P results from samples screened to remove zooplankton. This trophic level would include all phytoplankton, microbes and small detritus. Based on phosphorus concentrations taken from the literature (Peters 1983), we calculated the amount of nutrient in zooplankton, the major invertebrate predator in these systems (*Chaoborus* spp.), and the fishes. Based on regular sampling of diets (Hodgson et al. 1991), fishes were differentiated as planktivores, which includes small minnows (*Chrosomus* spp. and *Umbra limi*), young-of-the-year largemouth bass (*Mi-*

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*cropterus salmoides*), and juvenile rainbow trout (*Oncorhynchus mykiss*). Piscivores included the sub-adult and adult groups of largemouth bass and rainbow trout. Including the animals present in this food web yields an operational definition of total phosphorus very different from that of represented in most traditional limnological texts.

## Food web manipulations

Manipulation of the food webs is only briefly recounted here as it is detailed elsewhere (Carpenter et al. 1987, Carpenter & Kitchell 1993). During the pre-manipulation years, the food webs of Paul and Peter lakes were dominated by piscivorous bass, large *Daphnia pulex*, low levels of phytoplankton biomass and productivity, and very little planktivory by small fishes. Tuesday Lake was dominated by planktivorous fishes, small zooplankton, much higher levels of chlorophyll and primary production rates that were 3–5 times greater than those in the bass dominated systems. Although the nutrient concentrations were similar in all three lakes, the food web of Tuesday lake had one less trophic level than that of Peter or Paul. Our experimental design was forged to test the importance of food web structure in establishing and maintaining these obvious differences in lakes that were otherwise similar in basic physical and chemical attributes (Carpenter et al. 1985, Carpenter & Kitchell 1988).

Early in 1985, 90 % of the bass in Peter Lake and 90 % of the minnows in Tuesday Lake were captured and we conducted a reciprocal transplant of the tops of the food webs (equivalent biomass of fish and P) in these two systems. Bass remained in Tuesday Lake for the summers 1985 and 1986 after which they were removed through the use of rotenone. A modest minnow population was re-established in early 1987 and had recovered to premanipulation levels by 1989. During July of 1990 a cohort (4000) of YOY largemouth bass was introduced to Tuesday Lake as a test of competition-predation interactions among fishes (Carpenter & Kitchell 1993).

Addition of 49,601 planktivorous minnows to Peter Lake in early 1985 was followed by a rapid decline in their populations. The minnows sought refuge from the remaining adult bass and disappeared from the offshore habitats. Unlike previous years, cannibalism was diminished during 1985 and survival of YOY bass was exceptional. The 1985 bass cohort retained a dominant role in the Peter Lake food web as it ascended the trophic ladder for the next several years and suppressed subsequent cohorts through intense competition and predation. During 1988 and again in 1989 we attempted to impose higher levels of zooplanktivory on the Peter Lake system by stocking large numbers (3000) of juvenile rainbow trout. Those that did not fall victim to the resident bass grew quickly due to the abundant supply of large *Daphnia*, graduated to larger prey, and ultimately joined the ranks of piscivores. In 1990 a similar enhancement of zooplanktivory was performed by stocking large numbers (20,000) of juvenile golden shiners (*Notemigonus crysoleucas*).

No manipulation of Paul Lake was conducted during 1984–90. It was simply monitored as a basis for estimating variability in a limnologically similar reference system.

## Results and discussion

In our attempt to express the net effects of food web configuration on ecosystem function, we calculated total phosphorus represented in all trophic levels of the pelagic system. Those results are presented in Fig. 1. During the premanipulation year of 1984, total system phosphorus measured on an areal basis was similar in Peter and Paul lakes. The premanipulation food web of Tuesday Lake was very different from that of Peter or Paul in that it lacked a fourth trophic level, yet the total phosphorus levels were only slightly lower.

Over the seven-year period, average summer total phosphorus level in Paul Lake was 180 mg per square meter and ranged from 159 to 201 (Fig. 1). Thus, an unmanipulated system might be expected to vary within 20 % of its average state. Phosphorus at the bottom of the food web accounted for 36–53 % of the total (Table 1). The remainder was expressed in herbivorous zooplankton, their predator (*Chaoborus* spp.), and the dominant predator (bass). Although variable, each of those trophic levels contained a similar magnitude of total phosphorus. Peter Lake exhibited a similar distribution of total P during the premanipulation period of 1984 (Table 1).

Each level above the phytoplankton had captured roughly comparable amounts of nutrient. This could be due to the allometric consequence of declining P/B ratios with increased trophic lev-

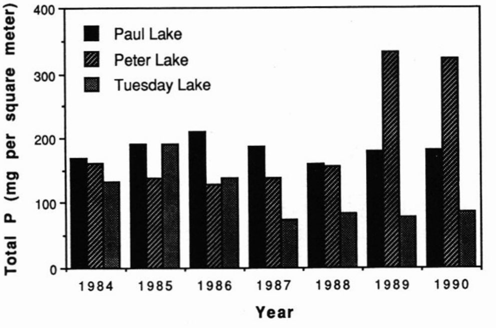

Fig. 1. Total phosphorus in all trophic levels over a seven year period in experimental lakes.

Table 1. Distribution of phosphorus among food web components in experimental lakes. Total phosphorus represented in each state variable is presented as averages for summer months (late May – early Sept.).

| Lake | Year | Dominant Predator | Total Phosphorus (mg per square meter) | | | | |
|---|---|---|---|---|---|---|---|
| | | | Dissolved and Particulate | Zooplankton | *Chaoborus* | Planktivorous Fishes | Piscivorous Fish |
| Paul | 1984–90 | Bass | 80 | 23 | 44 | 1 | 31 |
| Peter | 1984 | Bass | 80 | 35 | 19 | 1 | 27 |
| | 1988 | Bass/trout | 61 | 40 | 6 | 30 | 16 |
| | 1989 | Bass/trout | 72 | 167 | 5 | 18 | 71 |
| Tuesday | 1984 | Minnows | 50 | 24 | 46 | 12 | 0 |
| | 1985 | Bass | 51 | 19 | 82 | 8 | 31 |
| | 1989 | Minnows | 56 | 9 | 2 | 10 | 0 |

els (i.e., increased individual size), the fact that phosphorus concentrations tend to increase with size and trophic level (PETERS 1983), and/or the subsidy accrued to the pelagic system due to the omnivorous behavior of its apical predator. Adult bass in these unexploited lakes are classified as piscivores because of their functional role in limiting populations of other fishes. In fact, they eat large zooplankton, benthos, other bass, frogs, salamanders, birds, snakes, mice, i.e., virtually anything they can catch and ingest (HODGSON & KITCHELL 1987). The result is a substantial increase in allochthonous nutrient input which may be internally recycled through excretion and/or decomposition (CARPENTER et al. 1992).

Although dramatic changes in plankton community composition and ecosystem process rates followed the 1985 manipulation of Peter Lake (CARPENTER et al. 1987), average distribution of phosphorus among trophic levels showed little response. Additions of planktivorous fishes during 1988–90 and the increased predation on *Chaoborus* and large *Daphnia* that followed did result in dramatic responses. Whole system phosphorus approximately doubled (Fig. 1). Although some of the increase was due to the added fish biomass, most of the increment was associated with order of magnitude increases in populations of small Cladocera (e.g., *Daphnia dubia*, *Daphnia rosea*, and *Bosmina*) which prospered as a consequence of the size-selective mortality on their predators and competitors (Table 1).

Redistribution of total phosphorus among upper trophic levels was the immediate response to manipulation of Tuesday Lake in 1985. While the introduced bass focused on larger prey, *Chaoborus* and large *Daphnia* fluorished (Table 1). Both suffered in the following year as they became the largest prey available. Re-establishment of the minnows brought a growing predatory demand that eventually reduced total phosphorus to roughly half that of the premanipulation conditions. Changes in the plankton community yielded a 3–5 fold reduction in primary production rates during 1985–86 (CARPENTER & KITCHELL 1988); which occurred when total system phosphorus was at its highest (Fig. 1). The mechanisms for this reduction were increased grazing pressure on phytoplankton, as evidenced in decline in chlorophyll concentration, and reduced internal cycling of excreted phosphorus due to the increase in zooplankton size (CARPENTER & KITCHELL 1988).

Compensatory responses are evident in the 1984–87 behavior of Peter Lake and the 1987–90 behavior of Tuesday Lake. Dynamic and rapid changes in species composition followed the food web manipulations but did not appear in the conservative responses of total system phosphorus. Major changes did subsequently occur in Peter Lake, but their expression was through a complex response to increases in size-selective predation which, paradoxically, caused a dramatic increase in the cumulative nutrient pool of the biota.

The Tuesday Lake minnow populations recovered to former levels within three years after bass were removed, but the *Chaoborus* populations did not (Table 1). That failure was the primary component in the systematic decline of total system phosphorus (Fig. 1). Its explanation remains elusive. In addition, other populations such as those of the formerly abundant dinoflagellates (*Peridinium* spp.), have also failed to recover after the removal of bass, reestablishment of minnows and return to dominance by small zooplankton. We do not fully understand the causative components of this hysteresis in ecosystem state. We can speculate that it relates to exhaustion of the "seed bank" of resting stages (DESTASIO 1990) and its consequent depression of recolonization potential. It is clear, however, that the unique attributes and life history strategies of certain species can play an important role in the expression of processes expressed at the ecosystem scale.

As evidenced in the interannual responses of unmanipulated Paul Lake, no trend or event was apparent in nutrient loading to these lakes during the 1984–90 period. Experimental manipulation of the apical predators did, however, result in dramatic whole system responses. Peter Lake increased total system phosphorus by twofold as zooplankton biomass increased due to suppression of *Chaoborus* by predaceous fishes. Species not previously known from the lake came to dominate. Tuesday Lake was reduced to one half of its phosphorus content due primarily to loss of major phytoplankton species, depression of *Chaoborus* densities, and the failure of both to recover after the manipulation was reversed. In both experimental lakes, reallocation of critical nutrients and dramatic changes in both the sizes and species composition of the plankton communities derived from a cascade of food web interactions evoked by selective predation (KITCHELL et al. 1979).

The dynamics of primary production in these systems (CARPENTER et al. 1991) more closely followed those of the phosphorus pools represented among the consumers. Dissolved and sestonic P was very conservative (Table 1) and showed little response while chlorophyll concentrations and primary production rates changed 3–5X in response to the manipulation of predator populations and the consequent effects on plankton size distributions (CARPENTER & KITCHELL 1988). In addition to the effects of size selective predation, functional consideration of planktivory and piscivory must also be expanded to include the role of predators as direct sources of recycled phosphorus (REINERTSON et al. 1990, CARPENTER et al. 1992). Clearly, a complete view of limnological systems must account for the fishes as both the effect and the cause of trophic dynamics.

Our results demonstrate the magnitude and mechanisms of nutrient-mediated response to both differences and changes in food web structure in small, oligotrophic kettle lakes where nutrient loading rates remained similar throughout a seven year period of intensive study. These lakes are atypical in two major respects: 1) The fish populations are not exploited. The fishes of most lakes in most places are subject to exploitation which amplifies the interannual variability in limnological variables due to fishery-induced variability in fish populations and the consequent effects on food web interactions. 2) The drainage basins of these lakes are small and fully forested (LEAVITT et al. 1989). They are influenced by humans only to the extent that can be afforded to regular visits by researchers and an above-average adornment of limnological apparatus. Most lakes feel the effects of anthropogenic changes in both the amount and interannual variability in nutrient loading. Placing our experimental results in a more common and relevant context requires that we pursue the combined effects of food web dynamics and variable nutrient loading as they interact to regulate the behavior of lake ecosystems.

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