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ECOSYSTEMS

Dynamics of a Boreal Lake Ecosystem during a Long-Term Manipulation of Top Predators

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Abstract

We assessed the long-term (16 years) effects of introducing piscivores (northern pike) into a small, boreal lake (Lake 221, Experimental Lakes Area) containing abundant populations of two planktivorous fish species. After the introduction, pearl dace were extirpated and yellow perch abundance was greatly reduced. *Daphnia* species shifted from *D. galeata mendota* to larger bodied *Daphnia catawba*, but the total zooplankton biomass did not increase, nor did the biomass of large grazers such as *Daphnia*. Phytoplankton biomass decreased after the northern pike introduction, but increased when northern pike were partially removed from the lake. Phosphorus (P) excretion by fish was ~0.18 mg P m^{-2} d^{-1} before pike addition, declined rapidly to approximately 0.03–0.10 as planktivorous perch and dace populations were reduced by pike, and increased back to premanipulation levels after the pike were partially removed and the perch population recovered. When perch were abundant, P excretion by fish supported about 30% of the P demand by primary producers, decreasing to 6–14% when pike were abundant. Changes in phytoplankton abundance in Lake 221 appear to be driven by changes in P cycling by yellow perch, whose abundance was controlled by the addition and removal of pike. These results confirm the role of nutrient cycling in mediating trophic cascades and are consistent with previous enclosure experiments conducted in the same lake.

Key words: food web; trophic cascade; bottom-up top-down; Experimental Lakes Area; nutrients; fish; phytoplankton; zooplankton; piscivores.

Introduction

Hairston and others (1960) hypothesized that, in food webs with 3-trophic-levels, herbivore populations are regulated by carnivores and that producers and carnivores are resource regulated. Several models relevant to the regulation of these food webs have further stimulated research, including ''biomanipulation'' (Shapiro and others 1975), ''trophic cascade'' (Carpenter and others 1985) and ''bottom-up top-down'' (McQueen and others 1989). For lakes, these models acknowledge that nutrient loading is of primary importance in determining maximum productivity, but that food web structure accounts for variance in primary production at a given nutrient loading rate (Carpenter and others 1985). What is less understood are the mechanisms accounting for changes during a food web manipulation and whether these changes can be sustained over the long-term. Biomanipulation often involves introduction (or

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restoration) of top predator populations in an attempt to reduce the abundance of small fish and hence phytoplankton. Abundant populations of small fish can enhance phytoplankton by suppressing herbivore populations that play an intricate role in nutrient recycling and/or by recycling and translocating nutrients to primary producers (Schindler and others 1993; Vanni 2002).

From a practical perspective, it has been proposed that food web manipulations can be used to improve water quality by reducing algal densities. Kasprzak and others (2002) stated that the biomanipulation technique ''is sufficiently advanced from both the scientific and management point of view to make sound predictions of water quality improvements in many cases''. However, results of whole-lake biomanipulation experiments in which fish were added or removed to control primary productivity are varied and estimated success rates are as low as 20% (DeMelo and others 1992). Long-term manipulations of piscivores at the whole-lake scale are surprisingly scarce (Reynolds 1994; Drenner and Hambright 1999; Jeppesen and others 2000) and the mechanisms for success or failure are often unclear.

The response of phytoplankton to manipulation of upper trophic levels may result from changes in direct grazing impacts by herbivorous zooplankton, and/or from changes in nutrient cycling that accompany alterations of consumer populations (Wright and Shapiro 1984; Benndorf 1987; Vanni and Findlay 1990; Schindler and others 1993; Vanni 2002). Dominance by large zooplankton may also result in decreased nutrient cycling per unit zooplankton biomass because large zooplankton excrete at lower mass-specific rates than small zooplankton (Wen and Peters 1994). In addition, large zooplankton may sequester relatively more phosphorus (P) than small zooplankton, and therefore excrete less P than small zooplankton, per unit mass (Sterner and Elser 2002). However, effects of food web structure on mass-specific excretion by zooplankton may be offset by increased zooplankton biomass, which often accompanies reduction in planktivorous fish abundance (Schindler and others 1993).

Both fish and zooplankton can be important sources of nutrients for phytoplankton, and the relative importance of these two consumer groups in nutrient cycling depends in part on food web structure. For example, when piscivores are abundant and planktivorous fish are scarce, zooplankton biomass may be high and dominated by large species, resulting in high grazing rates on phytoplankton. These conditions may also result in reduced nutrient cycling by fish, because both mass-specific nutrient excretion rates and population biomass are typically lower for large fish than for small fish (Schindler and others 1993; Vanni 2002). Both fish and zooplankton can be important sources of nutrients for phytoplankton, and the relative importance of these two consumer groups in nutrient cycling depends in part on food web structure. For example, Schindler and others (1993) showed that fish provided more P than zooplankton in a lake with abundant planktivores and no piscivores, while zooplankton were more important than fish in a lake with piscivores and few planktivores. Enclosure experiments have also shown that nutrient cycling by fish can increase phytoplankton biomass and alter phytoplankton species composition (Vanni and Findlay 1990; Vanni and Layne 1997; Attayde and Hansson 1999, 2001). In addition, because most fish (including most ''planktivores'') consume benthic prey and excrete nutrients into the water column, fish often translocate nutrients from littoral to pelagic habitats, while zooplankton usually recycle nutrients already in the pelagic zone (reviewed by Vanni 2002).

Carpenter and others (1985), Benndorf and others (1984), Elser and others (1988) and Findlay and others (1994) have documented changes in phytoplankton communities from short-term, whole-lake biomanipulation experiments (2–5 years). The responses differed considerably among these studies, as did the suspected mechanisms responsible for the observed changes. Elser and others (1988) hypothesized that alteration of the N:P ratio supplied to phytoplankton by zooplankton caused changes in the phytoplankton nutrient status. Findlay and others (1994) concluded that changes observed in phytoplankton, after piscivore additions, were due to bacterial competition for P and not grazing by zooplankton. In all studies, phytoplankton biomass was reduced after piscivore additions, but for varying lengths of time. In addition to biological parameters that potentially can affect food webs, the different responses observed from whole-lake predator manipulation experiments could be reliant on physical characteristics of a lake and trophic status, which can strongly affect biomanipulation responses (Benndorf and others 2002). The essential questions left unanswered are (1) whether a system manipulated with predators can reach a new steady state that can be maintained long-term (Benndorf 1995); and (2) what mechanisms are responsible for food web changes.

We present results of a long-term whole-lake manipulation in Lake 221, Experimental Lakes Area (ELA), in which piscivores were added and

most were later removed. Our study is unique for two reasons. First, it is longer (16 years) than most food web manipulations and involved the manipulation of a single variable, northern pike (*Esox lucius*) densities. Second, our results can be compared to earlier enclosure experiments in the same lake, in which fish and zooplankton were manipulated (Vanni 1988; Vanni and Findlay 1990). The use of enclosure manipulations allowed us to more effectively evaluate the mechanisms accounting for the whole-lake response.

Methods

Study Sites

Lake 221 is a 9 ha, oligotrophic lake situated in the ELA in northwestern Ontario, Canada (49°38′ 40″N, 93°43′45″ W). The lake thermally stratifies shortly after ice-off and remains stratified until late September. It has a maximum depth of 5.7 m, a single intermittent inflow stream and outlet. Precipitation is the major external nutrient source. Lake 221 has chemical characteristics of other oligotrophic systems in the region with total P concentrations averaging 11 $\mu g\ L^{-1}$ (Findlay and others 1994). The lake is well sheltered, situated in a boreal forest comprised of jack pine (*Pinus banksiana* Lamb) and black spruce (*Picea mariana* Mill). Resuspension of sediment and internal nutrient loading are negligible in these small sheltered lakes (Schindler and others 1987). Prior to 1987, Lake 221 was dominated by yellow perch (*Perca flavescens*) with a small population of pearl dace (*Margariscus margarita*). In 1987, 124 northern pike (total wet weight mass of 62 kg) were added to Lake 221 representing a stocking density of 6.9 $kg\ ha^{-1}$, a moderate biomass for ELA lakes (Findlay and others 1994). From 1987–1995, there was successful reproduction of northern pike in Lake 221. In 1994–1995, 85% of the northern pike present in the lake were removed. Findlay and others (1994) examined the responses of the phytoplankton and nutrients for the first 5 years of the Lake 221 manipulation.

We sampled Lake 221 for 2 years prior to northern pike additions. During these 2 years, enclosure experiments were conducted in which yellow perch and zooplankton densities were manipulated to assess their impacts on phytoplankton. We hoped these experiments would facilitate interpretation of mechanisms accounting for the whole-lake response to northern pike additions. Vanni (1988) added large herbivorous zooplankton (*Daphnia catawba*) and an invertebrate predator (*Chaoborus americanus*) to enclosures in Lake 221 and found that both taxa reduced the abundance of resident zooplankton, although *Chaoborus* had stronger impacts than *D. catawba*. Vanni and Findlay (1990) further examined how phytoplankton assemblages responded to manipulations of yellow perch and *Chaoborus* in Lake 221. Both predators reduced the abundance of zooplankton and caused similar changes in estimated grazing rates. However, phytoplankton biomass increased (that is, showed a typical trophic cascade response) only when fish were present, and not when *Chaoborus* were present. Vanni and Findlay (1990) attributed the differential response of phytoplankton to differences in P cycling by yellow perch and *Chaoborus*. Yellow perch excreted considerably more P than *Chaoborus* and phytoplankton biomass was significantly correlated with P excretion by yellow perch.

Lake 239 was chosen as the reference lake because similar chemical, biological and physical parameters were measured over the same time period as Lake 221. Lake 239 has a surface area of 51 ha and a maximum depth of 30 m, and so is larger and deeper than Lake 221. However, in several comparative studies, including Lake 239 and ELA lakes much smaller in surface area and shallower in depth than Lake 221, it was shown that there was synchrony amongst phytoplankton, zooplankton and water chemistry in unmanipulated lakes (Findlay and others 2001; Rusak and others 2002). Therefore we feel that temporal dynamics in Lake 239 are indicative of unmanipulated ELA lakes in general. The lake has resident populations of lake trout, northern pike, yellow perch and cyprinids (Beamish and others 1976). Lakes 221 and 239 are 4 km apart and are subjected to the same climate regime.

Fish Sampling, Abundance Estimates, and Excretion Modeling

Northern pike were captured from 1987 to 2000 using techniques described in Mills and others (1987). No sampling occurred in 1993, 1996 and 1998. Using trap nets we captured, tagged (White and Beamish 1972) and recorded the fork length (mm) and weight (g) of each individual that moved from Lake 222 to Lake 221 in the spring of 1987, and conducted a mark-recapture study in Lake 221 using the Jolly-Seber closed population model (Seber 1982) from this time to fall 1994. As Lake 221 does not have a discrete inflow the lake was treated as a closed system and therefore immigration and emigration did not occur. We used the Leslie-DeLury removal method (Seber 1982) to

estimate the abundance in 1994 and 1995 when northern pike were removed from the lake by gillnetting during two week periods each fall. We used standardized over-night sets of four multi-mesh gill nets in 1997, 1999 and 2000 to sample Lake 221 fishes. We converted the catches of pike from these nets to abundance using the relationship between abundance and gill net catch established in 1994 and 1995. Although we did not sample the northern pike population in 1996, we assumed the abundance in 1996 was the difference between the estimate for 1995 and the number of individuals that we removed from the lake. We extrapolated estimates for 1993 and 1998 from estimates for adjacent years using the length frequency distributions from following years. Average condition (k) indices (Bagenal and Tesch 1978) were calculated for all northern pike captured in each year.

Yellow perch were extremely abundant in Lake 221 prior to northern pike introduction and there was a small resident population of pearl dace (Beamish and others 1976). We used trap nets to capture these species in 1986, the year prior to northern pike introduction. We calculated mark-recapture estimates of yellow perch abundance for the spring and fall of that year using the Schnabel and Peterson methods (Seber 1982). These studies were conducted over short time periods, so mortality of individuals was not an issue. We also initiated the catch-per-unit-effort (CPUE) sampling using 3.2 cm (1¼ inch) gill nets in fall 1986. We continued this method for the remainder of the study, with the exceptions of 1993, 1996 and 1998 when no sampling occurred. We used the ratio of abundance to CPUE from 1986 to calculate abundance from CPUE data for other years of the study. The confidence intervals for the 1986 abundance estimates were moderate, and we recognize that this introduces uncertainty in our extrapolated abundance estimates for other years, but we believe these estimates are realistic based on other data collected for yellow perch populations in other lakes at the ELA (Ken Mills, unpublished data; Eddy 2000). For years of no sampling (1993, 1996 and 1998), we extrapolated the CPUE data from adjacent years to estimate the abundance. We used the length frequency distribution of perch from adjacent years to indicate whether these estimates were likely similar or very different from one of the adjacent years. For example, for the 1996 estimate we saw evidence of an extremely large 1996 year class in the 1997 length frequency distribution. Therefore, yellow perch abundance in 1996 must have been higher than 1995, so we assigned a much higher abundance to 1996 than 1995.

P cycling via excretion by fish was estimated using data on fish population abundance, size structure and size-specific excretion rates. For each species of fish (yellow perch, pearl dace and northern pike), the number of fish in each size class (10 mm intervals) was multiplied by the per capita fish excretion rate to obtain excretion by that size class. These size class rates were then summed to obtain an excretion rate for the entire population. Per capita fish excretion rates for each size class were estimated with the multiple regression of Schindler and Eby (1997, their Table 3), in which P excretion rate (X, in g P d^{-1}) is obtained as a function of fish body mass (B, in g wet mass), temperature (T, in °C) and prey P concentration (F, the proportion of wet mass comprised of P):

$$\text{Log } X = -4.776 + (0.902 \times \log B) + (96.801 \times F) + (0.008 \times T)$$

The temperature was set to 20°C as this represents the approximate mean epilimnetic temperature for Lake 221 in summer. F was set to 0.001 for perch and dace, reflecting that their diet consists mainly of benthic invertebrates and zooplankton, and to 0.005 for pike, reflecting a piscivorous diet (Schindler and Eby 1997, their Table 2). Because we do not know how fish abundance and size structure varied within the years, we obtained a single estimate for P excretion for each year, which is indicative of average summer conditions.

We also estimated the proportion of primary production supported by P excretion by the fish in Lake 221. To do so, we first estimated the P demand by primary producers (mg P m^{-2} d^{-1}) by multiplying the mean daily primary production for a given year (mg C m^{-2} d^{-1}) with the P:C ratio of seston (mg P mg C^{-1}). P excretion by the fish assemblage (combined excretion rates of the three species) was then divided by P demand to estimate the proportion of primary production supported by excretion of P by fish. We estimated this proportion only through 1994 because primary production measurements ceased after 1994. The estimation of P demand in this manner assumes that the C:P ratio of seston (which includes phytoplankton, bacteria and detritus) is not significantly influenced by allochthonous matter, which may have a much different C:P ratio. However, Hecky (1993) showed that this is not a problem in ELA lakes with water residence times longer than a few months, and Lake 221 has a residence time of 2 – 4 years.

Zooplankton Sampling and Enumerating

Zooplankton from Lakes 221 and 239 were sampled weekly to monthly during the ice-free season at a fixed station over the deepest part of each lake. Vertical hauls were taken with an apparatus consisting of two Plexiglas barrels 13 cm in diameter, each fitted with a 2 m long plankton net with 53 μm mesh (Vanni and Findlay 1990). Each sample consisted of two vertical hauls of the entire water column pooled into a composite sample. Samples were preserved in 3% sucrose-formalin.

The biomass of each species (μg dry mass L^{-1}) was estimated by multiplying population density (individuals L^{-1}) by mean individual biomass (μg dry mass individual^{-1}). Individual species biomasses were estimated from length measurements and length–weight regression equations for cladocerans and copepods (Malley and others 1989; Lawrence and others 1987), and published individual masses for rotifers (Schindler and Noven 1971).

Chaoborus were enumerated and separated into two size categories from zooplankton samples taken during the day from Lake 221. We recognize that these will be underestimates compared to samples taken at night. *Chaoborus* biomass was estimated by multiplying abundance by the mean individual dry weight determined from measurements and weights of 100 individual animals varying in size.

Phytoplankton and Bacteria Sampling and Enumeration

Lakes 221 and 239 were sampled for phytoplankton and bacteria bi-weekly or monthly during the ice-free seasons. Euphotic zone samples were obtained from a deep station on each lake using an integrating sampler (Shearer 1978).

A 125 mL aliquot of lake water was fixed in Lugol's solution for identification and enumeration of phytoplankton and a 25 mL aliquot was preserved in 2% formalin for bacteria enumeration. Phytoplankton were identified and enumerated using the Utermöhl technique (Nauwerck 1963). Cell counts were converted to biomass (wet weight) by estimating cell volumes and assuming a specific gravity of 1. Estimates of cell volume for each species were obtained by measurements of up to 50 cells of an individual species and applying the geometric formula best fitted to the shape of the cell (Vollenweider 1968; Rott 1981). The algal assemblage was separated into three size categories based on maximum linear dimension: nanoplankton (< 10 μm), netplankton (10–30 μm) and microplankton (>30 μm).

Primary production was measured on the same samples obtained for phytoplankton analysis using the ^{14}C incubation technique (Shearer and others 1985).

For bacterial enumeration, 2 ml aliquots were stained using the DAPI technique (Porter and Feig 1980) with a final stain concentration of 1.0 μg ml^{-1}. Samples were filtered onto a prestained 0.2 μm polycarbonate membrane filter and examined using epifluorescence microscopy. Cell counts were converted to biomass by measuring 50 individual bacteria cells and applying the geometric formula best fitted to the shape of the cell. Measurements were performed using a micro-metered eyepiece. Measurements carried out with the eyepiece were randomly checked with measurements performed on the electron microscope.

Chemical Sampling and Analysis

Euphotic zone dissolved and suspended fractions of carbon (C), nitrogen (N) and P were routinely measured in Lakes 221 and 239 from the same samples as the phytoplankton. Totals of C, N and P were obtained by summing the fractions. Chlorophyll was measured fluorometrically. Analytical methods are described by Stainton and others (1977).

Statistical Analysis of the Response to Piscivore Manipulations

The before:after – control:impact (BACI) design proposed by Stewart-Oaten and others (1986, 1992) was used to test whether the manipulation resulted in statistically significant changes in biomass of the individual taxonomic phytoplankton and zooplankton groupings. The BACI design uses the difference between a control site (C = Lake 239) and an impacted site (I = Lake 221) as the parameter of interest, and uses samples taken repeatedly through time as replicates. The mean difference during the ''before'' period (B = 1985–1986) was compared to the mean difference during the period when pike were abundant (A_p = 1987–1994) and the period following pike removal (A_r = 1995–2000). Stewart-Oaten and others (1986) demonstrated that, as long as other assumptions of the BACI design were met, ''pseudoreplication'' in time was not a concern. The Lake 221 data satisfied these requirements (Findlay and others 1994).

A standard t-test (or Satterwaithe's modification for unequal variances) was used to test for a

significant change before and after differences. All statistical tests were done using SAS (SAS Institute Inc. 1990).

Phytoplankton and zooplankton community changes at a species level were assessed by correspondence analysis (CA) (SAS Institute Inc., 1990). Mean annual biomasses, for the ice-free seasons from 1985 to 2000, were calculated for each phytoplankton and zooplankton species in Lakes 221 and 239 resulting in a phytoplankton matrix of 32 lake-years by 243 species and a zooplankton matrix of 32 lake-years and 28 species. Very rare species are problematic because they result in a large number of zeroes in the matrix. Therefore, only 147 phytoplankton species and 15 zooplankton species that contributed more than 1% to the total biomass in at least one lake-year were retained for analysis. Phytoplankton and zooplankton biomass values were transformed by log (100 biomass+1). Preliminary analysis showed that the results were still highly influenced by rare species.

Final CA included a further down-weighting of rare species according to Hill (1979). In brief, if Amax is the frequency of the commonest species, then the abundance of species rarer than Amax/5 is reduced in proportion to their frequency. Frequency of species j is:

$$f_j = (\sum a_{ij})^2 / \sum a_{ij}^2$$

where a_{ij} = abundance of species j in sample i. If f_j for species j is greater than Amax/5 then its weighting factor is 1, otherwise it is f_j/(Amax/5).

Results

Fish

There was very high survival of northern pike introduced into Lake 221. Essentially 100% of the pike moved from Lake 222 to Lake 221 in the spring of 1987 survived to fall 1987, and there was very high survival in 1988 (93%) and 1989 (90%) (Figure 1a). The pike doubled their weight within the 1st year (from 400–500 g to 1 kg) with weight loss occurring in subsequent years. Annual survival dropped to 54% by 1990 as pike abundance decreased from 194 fish in 1989 to 80 fish in 1990. The drop in annual survival (Figure 1a) was matched by a drop in condition as prey populations collapsed. Pike abundance increased in 1992 due to recruitment of new fish. The population size distribution was relatively stable from 1992–1994 with the pike population represented by relatively few large pike, larger numbers of intermediate-sized pike plus a few small pike. This distribution was observed during the pike removal in 1994–1995.

In the fall of 1994, 118 of the estimated 238 northern pike were netted and removed from Lake 221. Very few young-of-the-year were caught, but all the very large pike (the bulk of the spawning population and of population biomass) were removed. In 1995 an additional 106 northern pike were netted and removed, leaving an estimated population of 42 pike (larger in size than young-of-the-year). As the bulk of the sexually mature spawning population was removed in 1994, reproduction in 1995 and in particular 1996 was extremely low. Pike condition remained high as abundances increased from 1997 to 2000 (Figure 1a).

Prior to introduction of northern pike, Lake 221 was dominated by yellow perch with a small population of pearl dace estimated at 400 individuals. No pearl dace were caught after 1988 and we believe they were extirpated from the lake. The yellow perch population was also dramatically reduced following the introduction of pike (Figure 1b). Yellow perch population was represented by two distinct size classes, and based on stomach content analysis the smaller individuals ate zooplankton and the larger class was omnivorous (unpublished data, K. Mills, Freshwater Institute, Winnipeg). The larger size class of yellow perch disappeared by the fall of 1988, followed by a drastic reduction of the smaller size class by 1989. From 1991 to 1995 yellow perch abundance remained low, but following the pike removal in 1996 perch abundance increased to levels observed in the fall of 1987 (Figure 1b).

P excretion by fish was approximately 0.18 mg P m^{-2} d^{-1} before pike addition (1986) and declined rapidly as yellow perch and pearl dace populations were reduced by pike (Figure 1c). P excretion rates ranged from around 0.03 to 0.10 from 1987 to 1995, and then increased rapidly after pike were removed and the perch population recovered. During the time pike were present, excretion by pike represented a large proportion (40–80%) of P excretion by fish. Prior to the pike addition and after their removal, excretion by yellow perch represented the largest fraction of P excretion by fish (Figure 1c); excretion by pearl dace was generally negligible.

Zooplankton Dynamics

Prior to the introduction of pike, the Lake 221 zooplankton community was dominated by cladocerans (*Holopedium gibberum*, *Daphnia galeata*

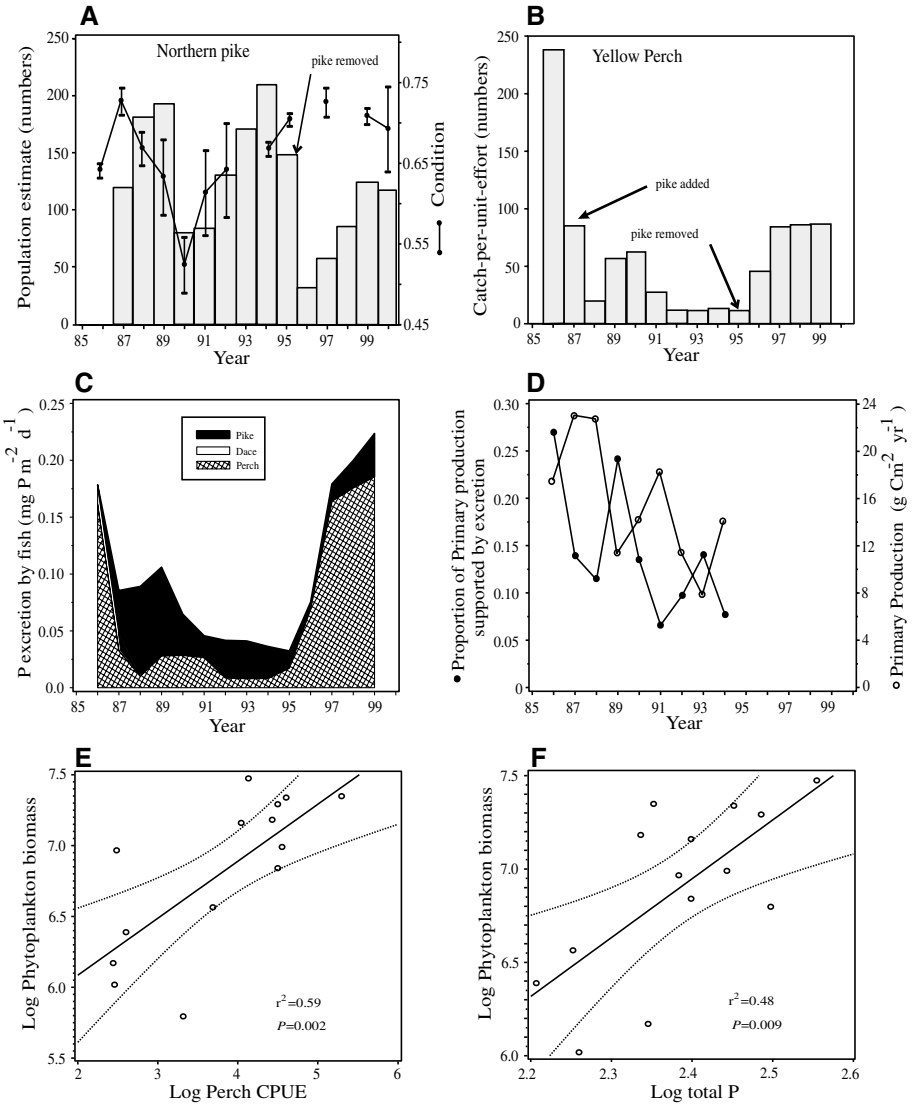

Figure 1. (**A**) Northern pike abundance (bar graph) and condition estimates (means on 95% confidence limits), (**B**) catch-per-unit-effort estimates for yellow perch, (**C**) estimates of P excretion by fish, (**D**) proportion of primary production supported by P recycled by fish and annual estimates of primary production, (**E**) linear regression of the log phytoplankton biomass and log catch-per-unit-effort of yellow perch, (**F**) linear regression of the log phytoplankton biomass and log total P for Lake 221 from 1985 to 2000.

mendota), calanoid copepods and cyclopoid copepods similar to the assemblage observed in reference Lake 239 (Figure 2). Rotifers represented 5–10% of zooplankton biomass (Figure 2) with a similar rotifer assemblage persisting in reference Lake 239 from 1985 to 2000 representing 5–20% of the zooplankton biomass.

Two years following the introduction of pike, zooplankton biomass in Lake 221 decreased by 75% (Figure 2). The zooplankton contained more than 10% of the total P in Lake 221 and zooplankton P decreased similarly to biomass. *D. catawba*, a large bodied cladoceran, increased in abundance replacing the former dominant, *D. galeata mendota* (Figure 2, Table 1). Although average individual body size increased slightly due to the species shift to *D. catawba*, the number of cladoceran individuals decreased: so there was no notable increase in the total cladoceran biomass (Fig. 2). By 1991, *D. catawba* abundance declined, and *Daphnia* spp. were rarely encountered in Lake 221 until 1998 (Figure 2). Other cladocerans that were less prominent prior to the northern pike addition had sporadic periods of greater biomass throughout the remainder of the study (Table 1).

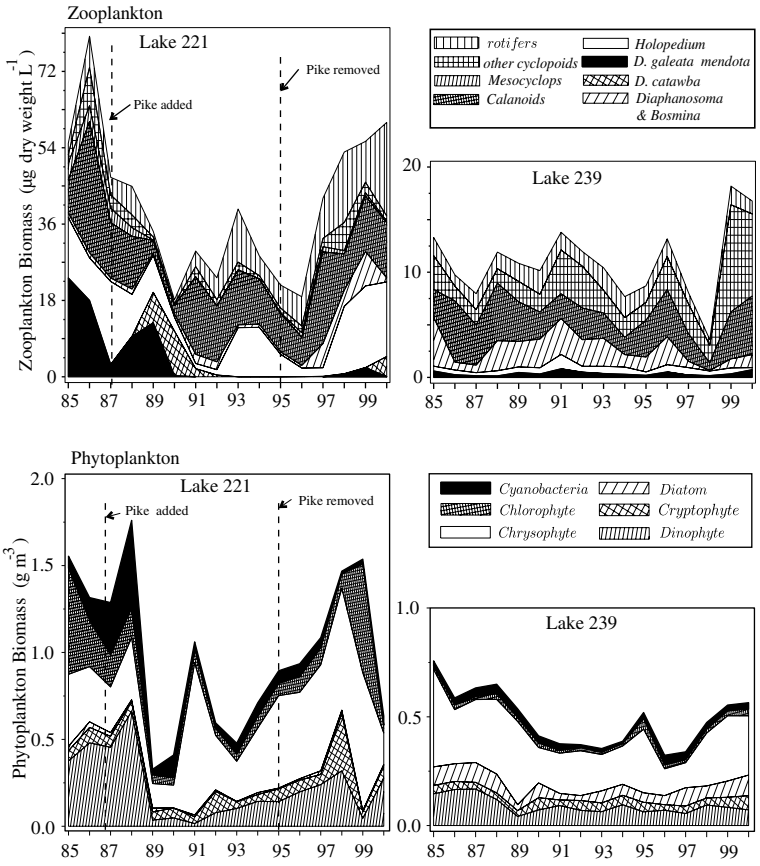

Figure 2. Ice-free mean total zooplankton and total phytoplankton represented by major taxonomic groupings for reference Lake 239 and Lake 221 from 1985 to 2000.

Following the northern pike introduction in 1987, calanoid copepods primarily decreased (Table 1). By 1991 through to 2000, abundances were again similar to those in 1987. Several cyclopoid species also became rare following the northern pike introduction (Table 1).

Rotifer biomass increased to 19% of the zooplankton biomass in 1988 following the northern pike addition, but decreased significantly from 1989 to 1990. Rotifer biomass was relatively unchanged from 1990 to 1996 except for 1993 (Figure 2). Following northern pike removal, rotifer biomass in Lake 221 increased 300% compared to premanipulation estimates (Figure 2).

The zooplankton community in reference Lake 239, which contained similar species as Lake 221, remained relatively unchanged from 1985 to 2000 (Figure 2).

Daytime collections also suggest that *Chaoborus* biomass changed (Figure 3, and Table 1). Prior to the manipulation, the population was represented by both large and small individuals of *C. punctipennis* (Figure 3). From 1988 to 1991, a larger species of *Chaoborus*, *C. flavicans*, became more abundant and the proportion of large individuals increased substantially (50–80%). From 1992 to 2000, *Chaoborus* abundance fluctuated somewhat, but was generally similar to that prior to the manipulation and was comprised mostly of small specimens (Figure 3).

The results of the initial *t*-test (1985–1986 vs. 1987–1994) using the BACI design indicated that cladocerans and cyclopoids showed significant changes in biomass from before to after the addition of pike (Table 2). However, cyclopoid and rotifer biomass were the only taxonomic zooplankton groupings that significantly differed from before (1985–1986) to after the pike were removed (1996–2000) (Table 2).

The power of BACI to detect changes is considerably decreased if the after differences are not constant. The annual mean ratios indicate differences that vary by discrete time periods (Figure 4a). One-way ANOVAs, with the after years treated separately, were used instead of *t*-tests on before vs. after to examine the response in greater detail. Duncan's Multiple Range test on mean annual differences revealed that 1998, because of an extremely high annual mean ratio, was distinctly different from all the other years (Figure 4b). 1990, 1995, 1992 and 1996 (years with low annual mean differences) were grouped together and separated

Table 1. Ice-free Seasonal Mean Zooplankton, Phytoplankton and Bacteria Biomass Estimates for Lakes 221 and 239

	1985–1986		1987–1994		1995–2000	
	L221	L239	L221	L239	L221	L239
Diaptomus spp.	12.77	4.32	7.31	3.55	10.17	3.40
Daphnia catawba	0.00	0.00	2.24	0.00	1.04	0.00
Daphnia galeata mendota	20.66	0.57	2.83	0.49	0.54	0.50
Diaphanosoma birgei	0.49	1.10	0.57	0.61	1.14	0.48
Bosmina longirostris	0.20	0.49	0.29	0.45	2.22	0.14
Holopedium gibberum	12.15	0.93	8.06	1.37	11.34	0.67
Diacyclops thomasi	4.16	0.84	0.21	0.76	0.01	1.23
Mesocyclops edax	3.82	0.12	0.65	0.29	0.85	0.13
Tropocyclops prasinus	0.21	0.08	0.10	0.07	0.84	0.08
Rotifers	5.01	1.40	4.94	1.76	12.93	1.26
Small *Chaoborus*	0.14	n/a	0.11	n/a	0.05	n/a
Large *Chaoborus*	0.08	n/a	0.13	n/a	0.02	n/a
Bacteria	0.28	0.07	0.43	0.13	0.15	0.15
Phytoplankton < 10 μm	0.23	0.20	0.31	0.19	0.54	0.20
Phytoplankton 10–30 μm	0.22	0.18	0.17	0.14	0.20	0.15
Phytoplankton >30 μm	0.96	0.28	0.33	0.17	0.35	0.12
Cyanobacteria	0.10	0.03	0.14	0.03	0.05	0.03
Chlorophytes	0.44	0.02	0.08	0.02	0.19	0.02
Euglenophytes	0.00	0.00	0.00	0.00	0.00	0.00
Chrysophytes	0.37	0.35	0.36	0.24	0.56	0.21
Diatoms	0.03	0.08	0.01	0.05	0.01	0.07
Cryptophytes	0.07	0.04	0.06	0.04	0.11	0.04
Dinoflagellates	0.43	0.16	0.19	0.09	0.22	0.08
Phytoplankton biomass	1.44	0.67	0.84	0.47	1.13	0.45

Zooplankton are in μg dry weight L^{-1}, phytoplankton are in g wet weight m^{-3} and bacteria are in μg wet weight ml^{-1}.

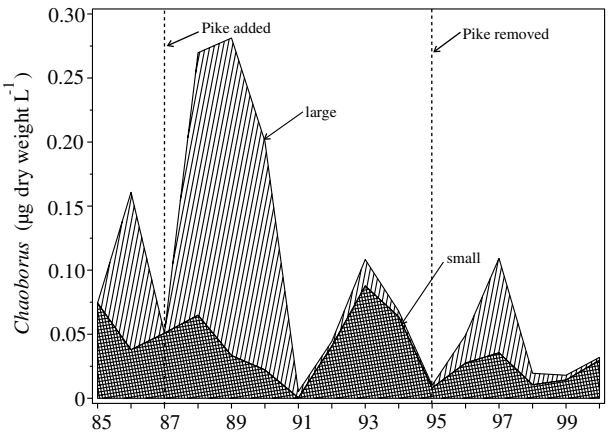

Figure 3. *Chaoborus* biomass for Lake 221 in 1985–2000.

from the remaining years. There was no obvious separation of years based on the addition or removal of pike (Figure 4b).

Axis 1 of the CA based on individual zooplankton species biomass accounted for 25% of the variance, with Axis 2 and Axis 3 accounting for an additional 20% and 11%, respectively (Figure 5a). Along Axis 1, species composition in 1986–1987 was similarly positioned to reference Lake 239 (Figure 5a). From 1988 to 1997 the community structure dramatically shifted from its original location indicating greatly increased dissimilarity to the reference lake. The zooplankton community structure in Lake 221 returned to its initial state from 1998 to 2000, after pike removal in 1995. Along Axis 2, Lake 221 was distinctly separated in three groups: 1985–1987 and 1998–2000 were positioned similar to Lake 239, and 1988-1991 were separated based on abundances of *Daphnia catawba* and *Asplanchna priodonta* and 1992–1997 were positioned based on *Holopedium gibberum* and several rotifers.

Phytoplankton and Bacteria Dynamics

Prior to manipulation, Lake 221 was dominated by dinoflagellates, chlorophytes and cyanobacteria. Phytoplankton biomass was 2–3 times higher than

Table 2. Probabilities from BACI *t*-test

	Before vs. pike abundant 1985–1986 vs. 1987–1994	Before vs. pike removed 1985–1986 vs. 1995–2000
Zooplankton		
Calanoid	0.54	0.34
Cladoceran	0.04*	0.31
Copepod	0.94	0.73
Crustacean	0.95	0.56
Cyclopoid	0.05*	0.01*
Rotifer	0.37	0.007*
Total biomass	0.91	0.67
Phytoplankton		
Cyanobacteria	0.23	0.24
Chlorophytes	0.004*	0.006*
Euglenophytes	0.50	0.18
Chrysophytes	0.86	0.10
Diatoms	0.59	0.02*
Cryptophytes	0.59	0.90
Dinoflagellates	0.21	0.95
Total biomass	0.53	0.37
Nutrients		
Total C	0.009*	0.10
Total N	0.008*	0.13
Total P	0.04*	0.36
C:P ratio	0.009*	0.10
N:P ratio	0.007*	0.09
C:N ratio	0.02 *	0.19
C:Chlorophyll ratio	0.007 *	0.08

**indicates a significant change (p = <0.05) between before and after.*

reference Lake 239 (Figure 2), which is indicative of the 2x difference in total P between the lakes (Figure 6). Algal species larger than 30 μm in a linear dimension dominated the assemblage (Table 1).

Three years after the northern pike introduction, phytoplankton biomass decreased 80% (Figure 2) with an associated 40% decrease in ^{14}C primary production (Figure 1d). Prior to the introduction, approximately 30% of the primary production was supported by P excreted by yellow perch and pearl dace (Figure 1c, d). During the manipulation, phytoplankton biomass was significantly correlated with perch abundance (Figure 1e), total P and P excreted by fish ($r^2 = 0.44$, $P = 0.009$). However, phytoplankton biomass was not significantly correlated with zooplankton biomass ($r^2 = 0.18$, $P = 0.18$). During this period, the size structure of the phytoplankton assemblage shifted and species less than10 μm in a linear dimension dominated (Table 1). Coincidental with the decrease in phytoplankton biomass, bacterial biomass increased in 1989–1990 (Table 1). Bacterial biomass was positively correlated with total N ($r^2 = 0.74$, $P = <0.002$) and *Chaoborus* abundance ($r^2 = 0.60$, $P = 0.014$) and negatively correlated with the suspended P:TDP ratio ($r^2- = 0.52$, $P = 0.04$) and rotifer biomass ($r^2 = -0.76$, $^2P = 0.0006$). In 1991, two mixotrophic phytoplankton species, *Chrysochromulina* and *Dinobryon*, dominated the algal community and phytoplankton biomass increased as bacterial biomass declined.

Beginning in 1995, following the removal of pike, and continuing through 1999, total phytoplankton biomass in Lake 221 increased from 0.6 to 1.5 g m^{-3} in contrast to the reference system that was remarkably unchanging (Figure 2). Chlorophytes and cryptophytes also increased but to a much lower degree (Figure 2). From 1996 to 2000 the abundance of species less than 10 μm and greater than 30 μm increased in Lake 221 (Table 1), whereas no similar increase was observed in reference Lake 239.

The results of the *t*-test from the BACI on the phytoplankton indicated that only chlorophytes significantly differed from before (1985–1986) to after the addition of pike (1987–1994) (Table 2). Chlorophytes and diatoms were the only taxonomic groups to significantly respond to the pike removal (1995–2000) (Table 2). Results of a one-way ANOVA using Duncan's Multiple Range test indicated that 1990, 2000 and 1989 were grouped separately from before (B) as well as all remaining years (Figure 4d). Years that followed the pike removal (1995–2000) tended to be grouped together along with 1988 and 1991, which were years with high annual mean ratios. During all phases of the experiment the ratio of difference between Lakes 221 and 239 phytoplankton fluctuated with no obvious trends apparent (Figure 4c)

Axis 1 of the CA based on individual phytoplankton species biomass accounted for 28.5% of the variance with Axis 2 and Axis 3 accounting for an addition of 16.3% and 15.7%, respectively (Figure 5b). Along Axis 1, species composition in 1985–1989 shifted to a community similar to that observed in reference Lake 239 in 1986–1990. From 1990 to 2000 reference Lake 239 shifted to a new quadrant (Figure 5b) due to increased abundances of chrysophytes coupled with decreased dinoflagellates. The Lake 221 phytoplankton assemblage remained similar with little movement along Axis 1, indicating that Lake 221 was again dissimilar to the reference lake.

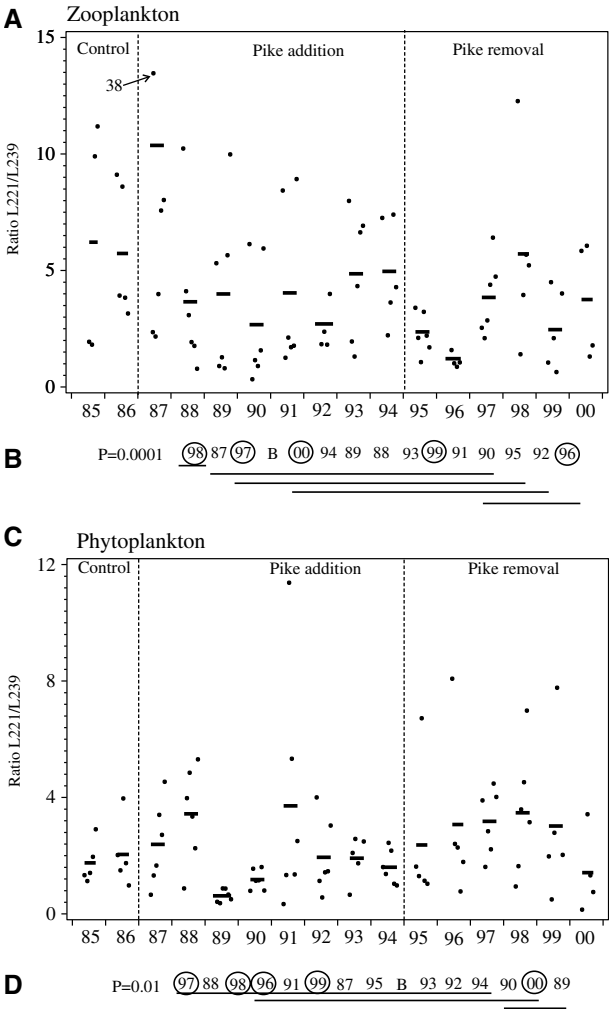

Figure 4. Ratios of Lake 221 to Lake 239 used for BACI analysis for: (**A**) total zooplankton biomass, (**C**) total phytoplankton biomass. Dots are the ratios on each sampling day through the open-water season; horizontal lines are the mean ratio of the year. Ratios are shown instead of differences of log (biomass +1) to maintain an arithmetic scale and because log(I) − log(C) = log(I/C) (C = control site, I = impacted site). ANOVA probabilities (P) indicating overall significant differences among years: (**B**) zooplankton (**D**) phytoplankton. B = mean of 1985–1988. Years joined by the same underline are not significantly different. Yearly mean ratios are ranked highest to lowest from left to right. Years incased in **O** indicate years following removal of 85% of the pike.

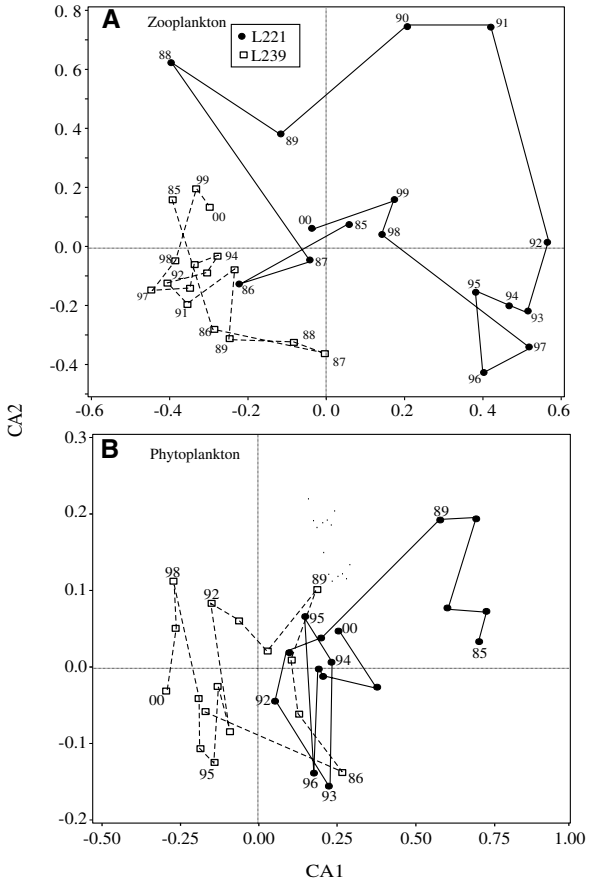

Figure 5. Results of a correspondence analysis for: (**A**) zooplankton communities, (**B**) phytoplankton communities for Lake 221 and reference Lake 239 from 1985 to 2000.

Nutrient Dynamics

Nutrient concentrations (C, N and P) in Lake 221 were higher than those observed in reference Lake 239 (Figure 6) prior to the introduction of northern pike. However, total N and P declined in the third year following pike introduction (1989), which coincides with the major decrease in phytoplankton biomass. The results of the *t*-test from the BACI indicate that total C, N and P significantly differed between ''before'' and after the addition of pike (Table 2). Total P was significantly correlated with phytoplankton biomass (Figure 1f) and chlorophyll ($r^2 = 0.47$, $p = 0.01$). With the pike removal in 1994, total P increased, a trend that was also observed in reference Lake 239 (Figure 6). Based on the results of the *t*-test from the BACI, nutrient levels during this period were not significantly different from premanipulation years (Table 2). The ratio of suspended P:total dissolved P also changed following pike introduction, due to higher concentrations of dissolved P. This trend also shifted back to premanipulation estimates over time. However, trends were similar in the reference lake. Nutrient status ratios, such as C:P and N:P, significantly differed between ''before'' and after the addition of pike (1987–1994) based on the *t*-test from the BACI (Table 2). However, Lake 221 re-

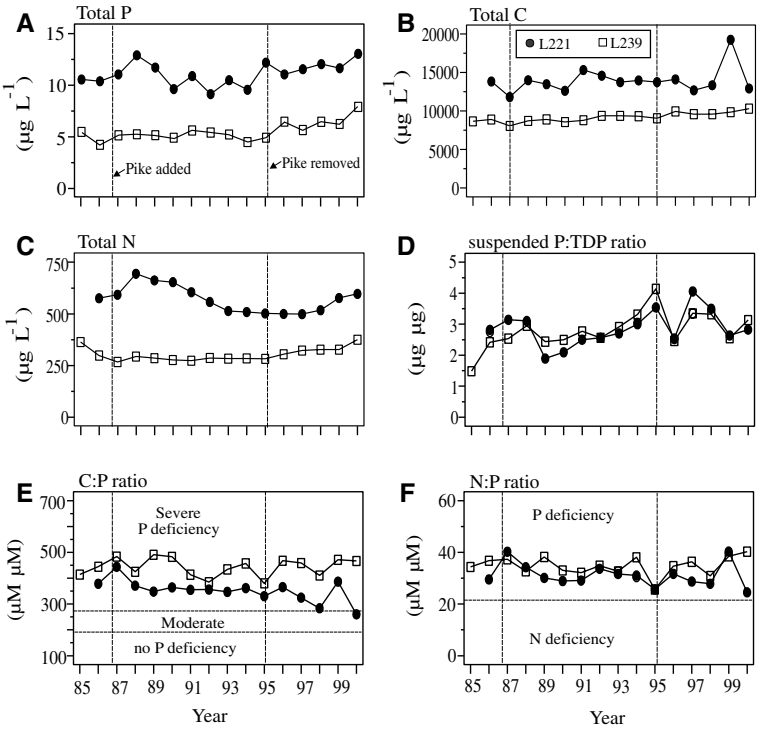

Figure 6. Mean ice-free concentrations of **A**) total phosphorus, **B**) total carbon, **C**) total nitrogen, **D**) ratio of suspended PL total dissolved phosphorus and algal nutrient status indicators **E**) carbon: phosphorus and **F**) nitrogen: phosphorus (ratios by weight) for Lakes 221 and 239 (1985–2000).

mained severely P deficient and moderately N deficient from 1985–2000, as did reference Lake 239 (Figure 6).

Discussion

The predicted response to a piscivore addition is a reduction in algal biomass. Although such reductions often occur, the mechanisms responsible for initiating change are not always clear (Reynolds 1994; Drenner and Hambright 1999; Jeppesen and others 2000). In general, three main mechanisms have been proposed as crucial to driving changes in phytoplankton productivity after biomanipulation. First, decreases in planktivory may allow large zooplankton to flourish, resulting in a greater grazing mortality of phytoplankton. In Lake 221 a shift to a large bodied *Daphnia* occurred but overall zooplankton biomass decreased. Therefore phytoplankton dynamics were not correlated with changes in zooplankton biomass or size. Second, food web alterations can result in changes in zooplankton composition, that favor species capable of altering supply rates of major nutrients (stoichiometry), and can enhance P sedimentation (Elser and others 1988). In Lake 221 the amount of P stored per liter in zooplankton biomass was a small proportion of the total P in the euphotic zone (always <10%). After the addition of pike to Lake 221, zooplankton biomass decreased, which resulted in lower amounts of P sequestered in zooplankton. Increases in the density of large, P-rich *Daphnia* were not sufficient to offset decreases in densities of other zooplankton taxa. Therefore the amount of P stored in zooplankton biomass decreased after the addition of pike to Lake 221. Presumably, P sedimentation by zooplankton also decreased with declines in zooplankton biomass. As a result, changes in zooplankton P cycling driven by stoichiometric considerations are highly unlikely to be responsible for the results we observed. Third, decreases in total fish biomass may decrease nutrient recycling and nutrient availability to phytoplankton. As has been found in previous biomanipulations (Carpenter and others 1985, 1992), piscivore additions to Lake 221 resulted in decreased algal biomass. For Lake 221, P excretion by fish mirrored the trends in phytoplankton biomass. Phytoplankton biomass declined as P excretion by fish declined (after northern pike addition), and when P excretion by fish increased (after northern pike removal) phytoplankton biomass increased. We postulate that recycling of P in Lake 221 by yellow perch increased with decreasing piscivory, which in turn stimulated algal biomass. Based on earlier enclosure experiments in Lake 221, Vanni and Findlay (1990) concluded that yellow perch render P more available to phytoplankton by directly excreting

and egesting P. Therefore, our whole-lake results are consistent with those of enclosure experiments conducted in 1985.

Several studies, focused on small shallow lakes, have found internal P recycling from sediments to be an important factor (Jeppesen and others 1999; Benndorf and others 2002). Jeppesen and others (1999) attributed higher chlorophyll *a* and TP concentrations, in small turbid lakes as compared to clearwater lakes, to differences in internal nutrient loading. One mechanism associated with the observed differences was the ability of submerged macrophytes to enhance water clarity by reducing sediment resuspension and suppress algal growth by competing for nutrient resources. Lake 221 is a highly stained lake (high DOC) with a steep rocky shore, and macrophytes are scarce. Furthermore, no difference in macrophyte abundance during years with and without pike was observed. Another possible mechanism is the P release from sediment, and its variation with fish biomass. When phytoplankton biomass is low (that is, during years when pike were abundant), decomposition rates of sedimented phytoplankton may have been low, resulting in high redox levels and hence low rates of P release from the sediment. Low P release rates may have then further accounted for low phytoplankton biomass. Thus, it is possible that low P cycling by fish during years of high pike abundance resulted in lower phytoplankton via a direct (excretion) effect and an indirect effect via effects on P release from sediments. Therefore it is possible that internal P loading from sediments may have accounted for some fraction of the changes in P (and phytoplankton) observed in Lake 221. However, previous studies on ELA lakes have documented internal nutrient loading to be negligible, even in experimentally eutrophied lakes (Schindler and others1987).

''Planktivorous'' fish that forage in the littoral zone transfer nutrients via excretion of P and N into the pelagic zone (Schindler and others 1993; Attayde and Hansson 1999, 2001; Vanni 2002). Considering the combined excretion of P by zooplankton and fish Schindler and others (1993) estimated that 90% of the recycled P in Peter Lake (a lake with abundant ''planktivores'') was derived from excretion by fish, with zooplankton and *Chaoborus* accounting for the remainder. In contrast, they estimated that fish contributed 20% of the excreted P, in a lake containing piscivorous bass.

When yellow perch were abundant in Lake 221 (before pike addition), P excretion by fish supported about 30% of the P demand by primary producers. When pike were present, P excretion by fish supported between 6% and 14% of primary production (except in 1989 when the proportion was ~24%). The proportion of primary production supported by excretion by fish generally declined as the P excretion rate declined (Figure 1c, d). This suggests that other sources of P, besides P from fish, became relatively more important as yellow perch declined. In addition, the P availability to phytoplankton may have been further affected by competition with bacteria. Findlay and others (1994) concluded that, with reduced grazing pressure, bacteria out-competed phytoplankton for P thus constricting algal growth for a short period in Lake 221.

Our estimates of P excretion by fish, and therefore the proportion of phytoplankton P demand it sustained, are subject to a fair amount of uncertainty. Fish population estimates are often accompanied with substantial variance. However, it is quite possible that we underestimated P excretion by fish, because we made no attempt to sample larval fish, which would have higher mass-specific excretion rates than larger fish. In addition, by using the Schindler and Eby (1997) regression, we may have underestimated individual excretion rates. This is because their regression predicts lower rates than the few studies in which rates have been experimentally measured. For example, according to Schaus and others (1997) who quantified P excretion of gizzard shad (*Dorosoma cepedianum*) in a eutrophic reservoir, the excretion rate of a 10 g (wet mass) gizzard shad would be 2.1 μg P/g wet mass/h at 20°C, while the Schindler and Eby regression predicts a rate of 1.0 μg P/g wet mass/h. Using mass-P excretion relationships developed by Brabrand and others (1990) for roach (*Rutilus rutilus*), a 10-g sediment-feeding roach has a P excretion rate of 4.2 μg P/g wet mass/h at 17°. If we assume a Q_{10} of 2 (that is, that excretion rate doubles with a 10° increase in temperature), a 10-g roach is predicted to have a P excretion rate of 5.2 μg P/g wet mass/h at 20°, more than 5 × the rates we used for a 10-g fish. Brabrand and others (1990) also found that nonsediment feeding roach and carnivorous perch (*Perca fluviatilus*) had excretion rates that were only about 33% those of sediment feeding roach, i.e. that is, about 1.7 μg P/g wet mass/h at 20°, but this is still substantially higher than the rates predicted by Schindler and Eby (1997). Therefore, studies that have experimentally measured P excretion rates of fish in lakes have yielded rates that are higher than those predicted by Schindler and Eby (1997), that is, lower than the rates we used here. We used the Schindler

and Eby (1997) regression model because experimentally-derived data are not available for the fish species inhabiting Lake 221.

Grazing-induced changes in phytoplankton are almost always accompanied by changes in *Daphnia (*Drenner and Hambright 1999). Carpenter and others (2001) show that *Daphnia* biomass is equally good as zooplankton biomass in predicting phytoplankton response. In Lake the 221 *Daphnia* biomass declined even though body size increased. Based on our daytime samples, increased *Chaoborus* predation may have caused the initial decreases in *Daphnia* biomass, but cannot account for the sustained decreases in zooplankton after 1990. We believe these sustained decreases were maintained by low phytoplankton availability related to low nutrients in these later years. Vanni (1988) observed that *D. catawba* dominated predator-free enclosures while large *Chaoborus* hindered their colonization. Soranno and others (1993) also documented regulation of *D. pulex* and *D. rosea* in Peter and Paul lakes and the suppression of *D. pulex* by *C. flavicans* in mesocosm experiments. Zooplankton biomass in Lake 221 decreased similarly to the phytoplankton and *D. catawba* was present for only 2 years. We believe that increased zooplankton grazing was not a major factor in the changes we observed in the Lake 221 food web.

Lake trophic status is an important factor in determining the mechanisms for the success of a biomanipulation (Benndorf and others 2002). Most manipulations have been preformed in eutrophic systems where external P sources dominate nutrient inputs (Drenner and Hambright 1999). In these types of systems P excretion via fish would be overwhelmed by external inputs and grazing may appear more important. Lake 221 is oligo-mesotrophic and because external nutrient inputs are low, changes in the recycling of nutrients via fish excretion were detectable, leading to the conclusion that, phytoplankton biomass in Lake 221 was largely controlled by nutrient recycling by fish.

Long-term Response

The purpose of a whole-lake biomanipulation from a management perspective is to enhance water quality (Kasprzak and others 2002). If biomanipulation is to be effective, the ability to maintain a new steady state is essential. The Lake 221 manipulation lasted for 16 years and offers a unique long-term perspective, given that only the piscivore population was manipulated.

Other long-term studies have tried to address the issue of sustainability of water quality during biomanipulations. Noonan (1998), using a 12-year rotenone manipulation of Como Lake that was dominated by omnivorous fish, documented prolonged decreased algal biomass and increases in secchi depth. He concluded that increased light transparency stimulated macrophyte growth, which became an important mechanism in controlling P. However, small oligotrophic boreal lakes do not generally support large abundances of macrophytes and there was no associated increase in macrophyte growth in Lake 221 following the biomanipulation. In addition, light attenuation at ELA is driven primarily by changes in DOC, not phytoplankton (Fee and others 1996). Over the time of the study the secchi disc transparency only increased 1 m.

Wissel and Benndorf (1998), using data from a long-term biomanipulation (1979–1995) in a quarry lake, demonstrated the ability of *Chaoborus* to regulate zooplankton more effectively than planktivorous fish, causing an increase in algal biomass due to reduced grazing pressure. Benndorf (1995) concluded that sustained reduction of phytoplankton biomass by biomanipulation can be achieved only by P-limitation, which is an indirect bottom-up effect induced by top-down control of the food web.

The response of piscivore additions to Lake 221 did not invoke a true trophic cascade even though algal biomass decreased as hypothesized. Instead it appears that by reducing planktivorous fish the food web was controlled by bottom-up resources. The food web in Lake 221 shifted to a new four-level structure with a resident piscivore population that was reproducing. The lower trophic levels were relatively stable in the presence of piscivores suggesting a system that has the ability to achieve a new steady state and maintain it. However, the removal of pike caused dramatic shifts in community structure as planktivorous perch increased in abundance.

Conclusion

Yellow perch abundance, which was controlled by the addition and removal of pike, had an indirect effect on the phytoplankton by increasing nutrient recycling that in turn had bottom-up resource effects on higher trophic levels. Zooplankton were not a major factor in controlling phytoplankton biomass. In the absence of yellow perch, *Chaoborus* may have initially been a key species exerting predation pressure on lower trophic levels. The results of our long-term manipulation are also consistent with enclosure experiments (Vanni

1988; Vanni and Findlay 1990) conducted in this lake prior to the whole-lake manipulations. Based on these enclosure experiments, and assuming effective control of small fish by piscivory, we would have predicted that pike addition would cause increased abundances of *Chaoborus* and large *Daphnia*, but that phytoplankton would be more responsive to P cycling by fish than to increased herbivory by zooplankton. The results of the whole-lake experiment are in agreement with these predictions.

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