

## TROPHIC CASCADES, NUTRIENTS, AND LAKE PRODUCTIVITY: WHOLE-LAKE EXPERIMENTS

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**Abstract.** Responses of zooplankton, pelagic primary producers, planktonic bacteria, and CO<sub>2</sub> exchange with the atmosphere were measured in four lakes with contrasting food webs under a range of nutrient enrichments during a seven-year period. Prior to enrichment, food webs were manipulated to create contrasts between piscivore dominance and planktivore dominance. Nutrient enrichments of inorganic nitrogen and phosphorus exhibited ratios of N:P > 17:1, by atoms, to maintain P limitation. An unmanipulated reference lake, Paul Lake, revealed baseline variability but showed no trends that could confound the interpretation of changes in the nearby manipulated lakes. Herbivorous zooplankton of West Long Lake (piscivorous fishes) were large-bodied *Daphnia* spp., in contrast to the small-bodied grazers that predominated in Peter Lake (planktivorous fishes). At comparable levels of nutrient enrichment, Peter Lake's areal chlorophyll and areal primary production rates exceeded those of West Long Lake by factors of approximately three and six, respectively. Grazers suppressed pelagic primary producers in West Long Lake, relative to Peter Lake, even when nutrient input rates were so high that soluble reactive phosphorus accumulated in the epilimnions of both lakes during summer. Peter Lake also had higher bacterial production (but not biomass) than West Long Lake. Hydrologic changes that accompanied manipulation of East Long Lake caused concentrations of colored dissolved organic carbon to increase, leading to considerable variability in fish and zooplankton populations. Both trophic cascades and water color appeared to inhibit the response of primary producers to nutrients in East Long Lake. Carbon dioxide was discharged to the atmosphere by Paul Lake in all years and by the other lakes prior to nutrient addition. During nutrient addition, only Peter Lake consistently absorbed CO<sub>2</sub> from the atmosphere, due to high rates of carbon fixation by primary producers. In contrast, CO<sub>2</sub> concentrations of West Long Lake shifted to near-atmospheric levels, and net fluxes were near zero, while East Long Lake continued to discharge CO<sub>2</sub> to the atmosphere.

**Key words:** bacteria; carbon dioxide flux; chlorophyll; lake ecosystem; fish; food web; nutrient effects; Paul Lake, Peter Lake, East and West Long Lakes; phosphorus input; trophic cascades; zooplankton.

### INTRODUCTION

In the 20 years since Paine (1980) coined the term, trophic cascades have been the topic of a great diversity of research in community and ecosystem ecology. Trophic cascades have been defined in several ways (Persson 1999). We define them as reciprocal effects of predators on prey that alter the abundance, biomass, or productivity of a population, community, or trophic level across more than one link in the food web (Pace et al. 1999).

Cascades are but one of many factors that control plant biomass and production (Polis 1999). After

Strong (1992) asked whether trophic cascades were "all wet," reviewers have attempted to compare the prevalence of cascades in terrestrial and aquatic systems (Pace et al. 1999, Persson 1999). The question of the relative importance of trophic cascades across ecosystem types is still unresolved. It is apparent, however, that examples are known from many types of ecosystems, and that the importance of cascades (as compared to other processes that control biomass and production) is quite variable among ecosystem types and over time within a given ecosystem (Pace et al. 1999, Persson 1999, Polis 1999).

Lake ecosystems provide many well-documented examples of trophic cascades, stemming from the seminal work of Hrbáček et al. (1961), Brooks and Dodson (1965), and Hurlbert et al. (1972). Concepts of trophic cascades (Carpenter et al. 1985) and biomanipulation

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(Shapiro et al. 1975) have linked community structure to biogeochemical processes in pelagic ecosystems and prompted a diversity of comparative and experimental studies. In lakes, it is now accepted that cascades are reasonably common, and in some situations can be manipulated to manage plant biomass of lakes (Hansson et al. 1998, Jeppesen et al. 1998, Meijer et al. 1999, Persson 1999). The research frontier has shifted to work that attempts to define the conditions under which cascades are important, and the contexts in which biomaniipulation is likely to succeed.

Several important ideas now motivate research on the conditions conducive to cascades in lakes. Benndorf (1987, 1995) proposes that cascades are most likely to control phytoplankton biomass when nutrient inputs are low to moderate. Above a certain threshold of P inputs, Benndorf (1987, 1995) argues that biomaniipulation will be ineffective in controlling chlorophyll. Reynolds (1994) argues that cascades are most likely to control phytoplankton in small, shallow, unstratified lakes capable of supporting extensive macrophytes. Other physicochemical variables that may affect the potential for trophic cascades include flushing rate (Reynolds 1994) and quality of food for zooplankton (Gulati and DeMott 1997), for example the carbon:phosphorus ratio (Elser et al. 1998). A number of biological factors influence the capacity of the food web to regulate phytoplankton, including refuges for the keystone grazer *Daphnia* spp. (Shapiro 1990) and the capacity of piscivorous fishes to regulate the planktivores (Hambright 1994).

At present, it is difficult to predict the conditions under which food web structure will control pelagic primary producers. Many proposed generalizations have counterexamples. While small lakes may be most conducive to trophic cascades (Reynolds 1994), for example, cascades have altered phytoplankton biomass in large, deep lakes (Hansson et al. 1998) and the north central Pacific Ocean (Shiomoto et al. 1997). Factors such as nutrient input, flushing, basin morphometry, and fish species composition may interact, and are not well separated by the limited number of case studies in the literature. Thus, there is need for experimental tests of the impact of trophic cascades under a range of conditions. Our experiments were conducted on entire lakes to challenge directly the capacity of food web structure to regulate lower trophic levels under enriched conditions. Experiments spanned the summer stratified season, during which most of the productivity and crucial biotic interactions occur in these lakes. This time scale allowed for predator-prey interactions within the entire food web to encompass both functional and numerical responses, while avoiding the disruption of food web linkages that can occur in enclosure experiments (Lodge et al. 1998, Schindler 1998, Carpenter 1999, Pace 2001). The whole-lake spatial scale encompassed cross-habitat interactions (e.g., littoral-pelagic) that are critical for movements of organisms, life

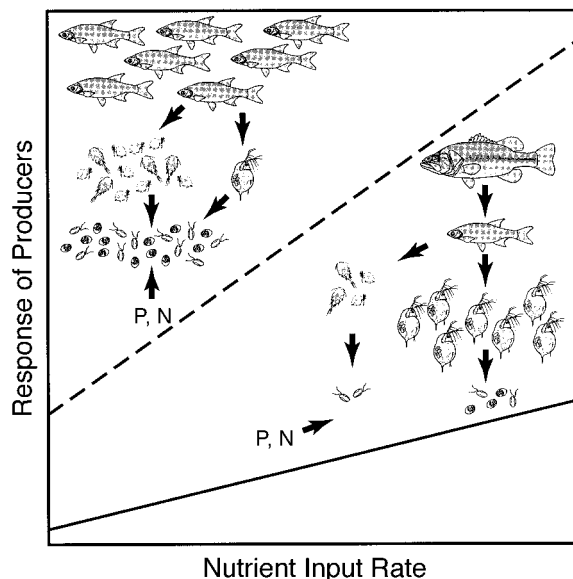


FIG. 1. Hypothesized relationship of primary producers (biomass or primary production rate) vs. nutrient input rate in lakes with three and four trophic levels.

cycles of some species, and population responses that can inhibit as well as stabilize trophic cascades (Kitchell et al. 1994, Reynolds 1994, Scheffer 1997, Jeppesen et al. 1998). Another benefit of the whole-lake experimental scale is that nominal physical conditions (i.e., mixing, thermal structure, light fields) were maintained. These conditions affect growth, nutrient cycling and succession within the plankton over the seasonal cycle, and are difficult to mimic in smaller scale experiments (Schindler 1998).

This paper is an integrated summary of whole-ecosystem experiments designed to measure the responses to nutrient enrichment of four lakes with contrasting food webs for seven years. We summarize year-to-year changes, providing a test of nutrient and food web effects on annual ecosystem responses, including integrative measures of pelagic ecosystem response such as production and biomass of producers, consumers, and decomposers. By focusing on annual responses of ecosystem processes, this paper complements earlier papers that addressed weekly temporal dynamics or community changes in these lakes (Pace and Cole 1996, Carpenter et al. 1998a, b, Cottingham and Carpenter 1998, Cottingham et al. 1998, Pace et al. 1998, Cottingham 1999).

We hypothesize that primary producers will respond more strongly to nutrient enrichment in lakes with three trophic levels (planktivorous fishes, small zooplanktonic herbivores, and phytoplankton) than in lakes with a fourth trophic level, piscivorous fishes (Fig. 1). Nutrient enrichment should increase pelagic chlorophyll and primary production, as well as increase the lake's uptake of  $\text{CO}_2$  from the atmosphere. In lakes with piscivorous fishes, large-bodied zooplankton are pre-

TABLE 1. Characteristics of the experimental lakes prior to initial nutrient enrichment in 1993.

Characteristic	East Long Lake	Paul Lake	Peter Lake	West Long Lake
Area (ha)	2.31	1.74	2.67	3.39
Mean depth (m)	4.9	3.9	6.0	4.4
Max. depth (m)	14.4	12.8	19.9	17.7
Color†	9.5	1.6	1.5	3.9
Thermocline depth (m)	2.8	4.1	4.2	4.2
Photic depth (m)	2.6	5.7	6.3	5.1
Depth to anoxia (m)	4.5	6.5	7.9	5.1

Notes: Photic depth is depth of 1% surface irradiance. East and West Long Lakes are separate basins of the same lake.

† Absorbance at 440 nm; units are per meter.

dicted to dominate and to suppress the response of phytoplankton to nutrients. At equivalent levels of nutrient enrichment, lakes with piscivorous fishes and large-bodied zooplankton should have lower pelagic chlorophyll and primary production, accompanied by lower uptake of CO<sub>2</sub> from the atmosphere, than would be expected in lakes with planktivorous fishes and small-bodied zooplankton. This experiment directly addresses the hypothesis that consumers can impede the effects of nutrient enrichment on primary producers. Because we conducted our experiments in stratified lakes, our findings are also relevant to the hypothesis that cascades are more likely in shallow lakes (Reynolds 1994). Unexpectedly, we found that we needed to consider the effects of changes in colored dissolved organic carbon (DOC) on trophic cascades. Consideration of the role of DOC expanded our focus from primary production to include microbial production, as well as CO<sub>2</sub> exchange between the lake and the atmosphere as an integrative measure of ecosystem response.

## METHODS

### Study sites and experimental plan

Paul Lake, Peter Lake, and Long Lakes lie within a 1-km radius at the University of Notre Dame Environmental Research Center near Land O' Lakes, Wisconsin, USA (89°32' W, 46°13' N). The lakes and watersheds are privately owned and are not accessible to the public. Fish populations are not exploited. Prior to manipulation, all lakes supported similar food webs dominated by largemouth bass (*Micropterus salmoides*) and, in Long Lake only, smallmouth bass (*Micropterus dolomieu*) and yellow perch (*Perca flavescens*). In May 1991, Long Lake was divided into three basins with a plastic curtain (Christensen et al. 1996). The western-most curtain was removed in September 1996 to assess whether the barrier affected overwinter fish survival. We assume this change did not affect comparison of observations in 1997 to earlier years. Morphometric characteristics of the four lakes were similar (Table 1). East Long Lake's thermocline lies at a shallower depth

than those of the other lakes because of high concentrations of colored DOC that stain the water (Christensen et al. 1996).

The experimental design involved reconfiguration of the fish communities in 1991, followed by nutrient enrichment in 1993–1997 (Fig. 2). Throughout the experiment, Paul Lake was left unmanipulated as a reference ecosystem.

Peter Lake was manipulated to enhance planktivory, culminating in removal of remaining piscivores by electroshocking, angling, and finally rotenone in May 1991. The lake was restocked with planktivorous golden shiners (*Notemigonus chrysroleucas*) and other planktivorous fishes (fathead minnow, *Pimephales promelas*; redbelly dace, *Phoxinus eos*). Planktivores were the dominant trophic level in the fish biomass throughout the study. On 15 July 1996, 80 largemouth bass (mean mass 211 g) were introduced into Peter Lake in an attempt to change the food web configuration. However, these bass did not survive the next winter, and Peter Lake remained a planktivore-dominated system.

West Long Lake's fish community remained dominated by piscivorous bass throughout the experiment. During 1992 and 1993, perch populations died out in West Long Lake for reasons we do not understand, but which may have been related to overwinter survival. In any case, this change enhanced piscivore dominance and effectively diminished planktivory in West Long Lake.

We had originally planned to convert East Long Lake's fish assemblage to one dominated by planktivores. Unexpected hydrologic changes following curtain installation thwarted this plan as the lake water became dark and acidic, while the depth of the oxygenated layer diminished (Christensen et al. 1996). Throughout the experiment, fish populations of East Long Lake were low, variable, and difficult to quantify due to low catch per effort and negligible recapture rates. Frequently encountered fish species were largemouth bass, yellow perch, bluegill (*Lepomis macrochirus*), and brook stickleback (*Culaea inconstans*).

Starting in May 1993, Peter Lake and Long Lakes were enriched with commercial liquid fertilizer (NH<sub>4</sub>NO<sub>3</sub> plus urea), to which we added concentrated H<sub>3</sub>PO<sub>4</sub> to achieve a N:P ratio >16:1, by atoms. Inorganic N:P ratios (by atoms) of added nutrients in each year of enrichment were 17.0 (1993), 30.4 (1994), 29.8 (1995), 34.4 (1996), and 31.5 (1997). In 1993, our goal was to match the natural N:P ratios of the lakes. In later years, our goal was to maintain P limitation of primary producers. Phosphorus enrichment levels were selected to span a range from natural loading rates to rates high enough to cause inorganic P accumulation in the epilimnion. Maximum P input rates used in this experiment are ~20 times the natural rates for these lakes, yet below the highest rates known from the world's lakes (Carpenter et al. 1996).

Enrichment occurred during the summer stratified

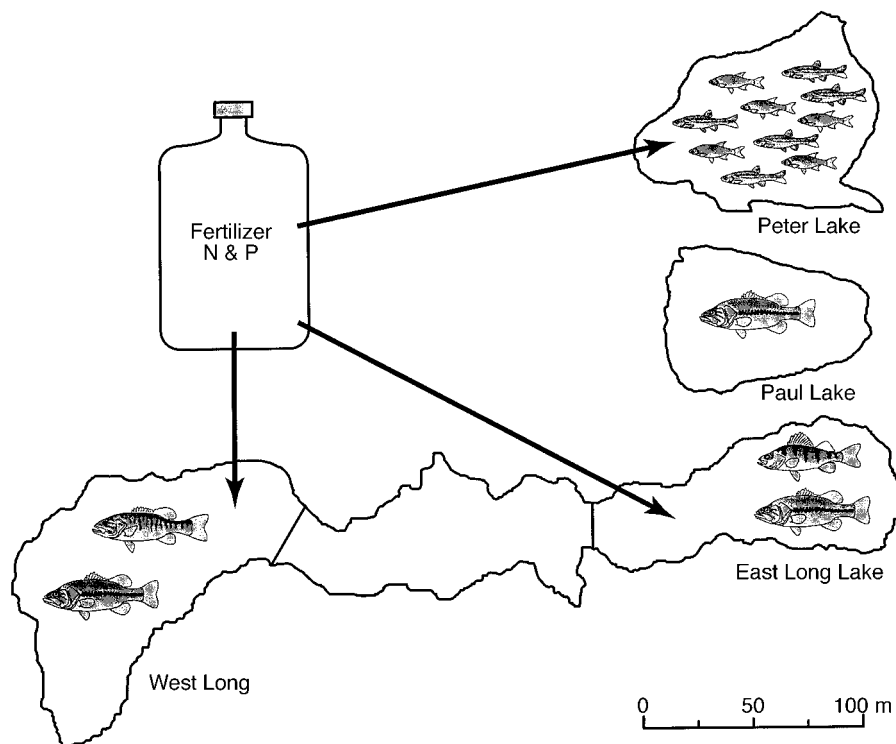


FIG. 2. Experimental plan, showing fish and nutrient treatments with outlines of the lakes. Fishes: redbelly dace and golden shiners in Peter Lake; largemouth bass in Paul Lake; largemouth and smallmouth bass in West Long Lake; largemouth bass and yellow perch in East Long Lake.

season, approximately June, July, and August each year. Nutrients were added from a central station daily in 1993–1994 and weekly in 1995–1997. Dye and chemical tracer (LiBr) studies showed that nutrients mixed throughout each lake's epilimnion within 24 h. LiBr additions, changes in concentration over time, and potential effects on aquatic organisms are presented by Cole and Pace (1998).

The natural P input rates for all four lakes were calculated using Vollenweider's (1976) P loading equation:

$$L_p = [P]q_s(1 + (q_s/z)^{0.5})$$

where  $L_p$ , the quantity to be estimated, is the P input to the lake (measured in no. milligrams P per square meter per year),  $[P]$  is the volume-weighted mean lake P concentration (no. milligrams P per cubic meter),  $q_s$  is the hydraulic load (no. meters per year), and  $z$  is the mean depth (no. meters). Phosphorus concentration was measured weekly. Hydraulic loads to the lakes were measured using a tracer, LiBr (Cole and Pace 1998). This approach produced estimates of baseline P input that agree well with estimates based on sediment cores taken from Peter Lake, West Long Lake, and Paul Lake (Houser et al. 2000). Estimates of natural P input from Vollenweider's equation were adopted for the years in which fertilizer was not added. In years in which we enriched the lakes, total P input rate was

equal to the natural rate (mean of estimates for the unenriched years) plus the rate of enrichment.

#### *Field and laboratory methods*

Piscivore populations were measured by Schnabel mark-recapture methods using electroshocking in May and August of each year (Hodgson et al. 1997). Planktivore populations were measured every other week using purse seines and beach seines (Schindler et al. 1993). In spring and fall, Schnabel mark-recapture methods were used to estimate population sizes of the dominant planktivores.

Limnological samples were taken weekly during summer stratification (approximately mid-May to mid-September) in each lake at a central station (Bade et al. 1998). Profiles of temperature, oxygen, and light were measured. Samples at six depths (1, 5, 10, 25, 50 and 100% of surface irradiance) were collected for measurement of chemical, phytoplankton, and bacterial variates. Two vertical hauls of the entire water column (80- $\mu$ m mesh net) were taken for zooplankton. Efficiencies of net capture were determined for each species at least once each year by comparing net hauls to vertical profiles measured with Schindler-Patalas traps. Surface irradiance was measured continuously with a pyroheliometer.

Soluble reactive phosphorus,  $\text{NO}_2 + \text{NO}_3$ , and  $\text{NH}_4$  were determined using an autoanalyzer on glass fiber



filtered (GF/F) samples (Bade et al. 1998). Total P was determined after persulfate digestion. Kjeldahl N was measured so that total N could be calculated. Dissolved inorganic carbon was measured by gas chromatography (Stainton 1973). Dissolved organic carbon (DOC) was measured using either an Astro 2001 total organic carbon (TOC) analyzer with persulfate and UV oxidation (1991–1993) or a Shimadzu model 5050 high-temperature TOC analyzer (1994–1997). Samples for particulate organic carbon (POC) were concentrated by filtration through precombusted GF/F and analyzed by catalyst-assisted oxidation to  $\text{CO}_2$  on a Carlo-Erba Model NA 1500 carbon–nitrogen analyzer.

Chlorophyll *a* was determined by fluorometry, and corrected for pheopigments (Marker et al. 1980). Total chlorophyll was measured on GF/F filters. Chlorophyll in particles  $>35 \mu\text{m}$  was calculated by difference, after measuring chlorophyll concentration in samples passed through a  $35\text{-}\mu\text{m}$  mesh screen (Carpenter et al. 1996). We report areal chlorophyll densities and chlorophyll concentrations integrated from depths of 5–100% of surface irradiance. Below the 5% layer, chlorophyll concentrations were highly variable due to thin layers of algae, photosynthetic bacteria, and detrital chlorophyll that characterize the interface of the aerobic and anaerobic layers in these lakes. This zone accounts for a low percentage of total productivity and was therefore excluded from this analysis.

Primary production was measured on a one-to-four-week basis by in situ incubations using  $\text{NaH}^{14}\text{CO}_3$ . Two light bottles and a dichlorophenol dimethylurea (DCMU) control were incubated at each of the six sampling depths for six hours. After incubation, samples were collected on GF/F filters, rinsed with 0.1 mol/L HCl, and dried prior to liquid scintillation counting. Rates of primary production at each depth were calculated, accounting for activity in the labeled algae, total activity and volume of the bottle, dissolved inorganic carbon concentration, efficiency of scintillation counting, duration of the incubation, and carbon fixation in the DCMU control (Bade et al. 1998). Daily rates of primary production were calculated by the method of Carpenter and Kitchell (1993), which uses lake-specific regressions to interpolate primary production from continuous measurements of surface irradiance, as well as weekly measurements of water temperature, transparency, dissolved inorganic carbon, and chlorophyll. Here, we report areal and volumetric rates of primary production, integrated from the surface to the depth of 5% of surface irradiance.

Zooplankton samples were chilled, preserved with cold sugared formalin or Lugol's solution, and enumerated and measured by species. Dry masses were calculated from lengths using species-specific regressions (Downing and Rigler 1984). Here we report total crustacean biomass, mean crustacean length, and biomass of all *Daphnia* species. Crustacean values were

calculated over all copepod and cladoceran individuals, including juveniles.

Bacterial abundance and production were determined in a pooled sample from the epilimnion. Bacterial concentration was determined by epifluorescence microscopy using the acridine-orange direct-count method (Hobbie et al. 1977). Duplicate filters were prepared within one to two hours of sampling and stored in a freezer until counting.

Bacterial production was measured as the uptake of  $^3\text{H}$ -leucine into protein as described by Pace and Cole (1996).  $^3\text{H}$ -leucine incorporation was measured every other week in 1991–1992, and weekly in 1993–1994 and 1996–1997, in six replicate samples at each depth. Previous studies showed that 17 nmol/L leucine was sufficient to maximize uptake rates in these lakes (Pace and Cole 1994). Extraction and isolation of labeled protein followed standard procedures (Pace and Cole 1994, Bade et al. 1998). Radioactivity was measured by liquid scintillation counting. Conversions of counts per minute to incorporation rates accounted for radioactivity and concentration of the added isotope, volume of the sample, duration of the incubation, and scintillation counting efficiency.

Carbon dioxide flux between the lakes and the atmosphere was calculated as  $\alpha K(C_w - C_s)$  where  $\alpha$  is the chemical enhancement factor,  $K$  is the gas exchange coefficient expressed as a piston velocity,  $C_w$  is the  $\text{CO}_2$  concentration in the water, and  $C_s$  is the  $\text{CO}_2$  concentration the water would have were it in equilibrium with the atmosphere (Schindler et al. 1997a). Data to calculate  $\text{CO}_2$  flux were measured in 1992–1997. According to the formulation of Hoover and Berkshire (1969),  $\alpha$  was significantly different from 1.0 only in Peter Lake (undersaturated, high pH), where its mean value was 3.0. In these small sheltered lakes, we assumed a constant value for  $K$  of 2 cm/h based on  $\text{SF}_6$  additions to other low-wind lakes (Cole and Caraco 1998). The partial pressure of  $\text{CO}_2$  was measured in surface water by a headspace-equilibration technique (Cole et al. 1994). At the same time, samples were taken for  $\text{CO}_2$  in the overlying atmosphere. Gas chromatography was used to measure the  $\text{CO}_2$  concentrations.  $C_w$  was then calculated from the partial pressure of  $\text{CO}_2$  using water temperature and temperature-corrected values of Henry's constant (Weiss 1974).

#### Statistical calculations

Means of chemical, microbial, phytoplankton, and zooplankton variates were calculated for each lake during each year over the time interval 15 June–31 August. This interval was selected because it occurs within the summer stratified season each year, does not include transient changes at the beginning or end of fertilization, and embraces consistent time series for all response variates in each year. Chlorophyll and primary production were  $\log_{10}$ -transformed to reduce heteroscedasticity and normalize residuals. Other response

variates (chemical concentrations, zooplankton biomasses and body sizes, proportion of chlorophyll in large particles, bacterial biomass and production, and gas flux) were analyzed in the natural units.

Standard errors of annual means were calculated so that variability among years could be compared with variability among samples within each year. Standard errors were corrected for the serial correlation among samples (Box et al. 1978). For these variates in these lakes, lag-1 autoregressive processes with positive autoregressive coefficients fit the time series (Pace and Cole 1996, Carpenter et al. 1998a, b, Pace et al. 1998). This type of serial correlation causes the usual estimator of the variance to underestimate the true variance of the annual means (Box et al. 1978). We corrected for this bias by adjusting variances upwards using the method of Box et al. (1978).

To evaluate the effects of our manipulations on ecosystem responses, we calculated regressions predicting the annual mean of each ecosystem response variate in each lake from annual measures of nutrient input, food web structure, and DOC. Although DOC was not a part of our experimental design, variability in DOC had important effects on the results and must be accounted for to determine the effects of nutrients and food web structure. These regressions assume that there is no significant autocorrelation in the response (dependent) variates from year to year in each lake. Autocorrelations of all zooplankton, primary producer, and microbial variates presented here were nonsignificant at lags longer than two weeks, and terms for autocorrelations among annual cycles were not significant. In several previous papers, we have shown that ecosystem responses of these lakes usually fit lag-1 week autoregressive models with no indication of autocorrelation among annual cycles (Carpenter and Kitchell 1993, Carpenter et al. 1996, 1998, Pace and Cole 1996, Pace et al. 1998). In addition, we found that carryover of P in the epilimnion from year to year was not detectable. Low carryover of added P is known from other whole-lake eutrophication experiments, at least during the first several years of enrichment (Schindler et al. 1978). In the enrichment years, chlorophyll concentrations in late May and early June (prior to addition of nutrients) were similar to those of pre-enrichment years. Thus, each year's manipulation began from a similar baseline state.

Regressions were calculated to examine the relationship of zooplankton variates (crustacean biomass, *Daphnia* biomass, crustacean mean length) to P input rate, planktivore biomass, and their interaction (P input rate  $\times$  planktivore biomass). To test for interactions, data were centered prior to analysis (Aiken and West 1991). East Long Lake was omitted from these regressions, because reliable estimates of planktivore biomass were not available for East Long Lake.

Regressions were calculated to predict annual means of chlorophyll (concentrations and areally integrated), primary production (per unit area and per unit volume),

bacterial biomass, leucine incorporation, and POC from annual means of P input rate, grazer variates, and DOC using all four lakes. Two sets of regressions were calculated, each using a fixed model structure: (1) P input rate, crustacean mean length, and DOC as predictors; and (2) P input rate and crustacean mean length as predictors. As an alternative approach to coping with collinearity of predictors in these regressions, stepwise multiple regressions were calculated. Candidate predictors were P input rate, crustacean mean length, crustacean biomass, *Daphnia* biomass, the ratio of *Daphnia* to crustacean biomass, and DOC. Stepwise regressions were fit using *P* values of 0.15 to enter or remove predictors.

To assess the relationship between fishes and ecosystem responses, regressions were calculated to predict annual means of chlorophyll (concentrations and areally integrated), primary production (per unit area and per unit volume), bacterial biomass, leucine incorporation, and POC from annual means of P input rate, grazer variates, and planktivore or piscivore biomass using data from Paul Lake, Peter Lake, and West Long Lake. Two sets of regressions were calculated, each using a fixed model structure: (1) P input rate, DOC, and planktivore biomass as predictors and (2) P input rate, DOC, and piscivore biomass as predictors.

For all regressions, we examined normal probability plots of residuals, plots of residuals against predictors, and plots of residuals against interaction terms of predictors. Plots of residuals against P input rate showed curvature that could be removed by fitting either a quadratic model in P input rate or a linear model in  $\log(P$  input rate). The latter approach was chosen, because it required fitting of fewer parameters. When necessary, response variates were transformed to normalize residuals.

## RESULTS

In this experiment, the independent variates are nutrient input rate and fish community structure. Dissolved organic carbon (DOC) concentration was not intentionally manipulated, but changes in DOC must be considered to interpret the responses of East Long Lake. Thus we consider first the nutrient manipulations and DOC changes, then the fish communities, before turning to the dependent variates: zooplankton, primary producers, bacteria, and gas exchange between lakes and the atmosphere.

### Nutrients

During the summer stratified seasons of 1993–1997, nutrients were added to East Long, West Long, and Peter lakes (Table 2). Phosphorus input rates reported here are means for each summer's period of enrichment. These input rates include natural inputs calculated using sediment cores and the Vollenweider model (Houser et al. 2000).

Dilution rates were measured using LiBr as a tracer

TABLE 2. Annual input rates of phosphorus ( $\text{mg} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ ) to the basins during the summer enrichment periods of 1991–1997.

Year	P input rate			
	East Long Lake	Paul Lake	Peter Lake	West Long Lake
1991	0.33	0.27	0.25	0.2
1992	0.44	0.29	0.30	0.62
1993	2.9	0.31	3.1	4.1
1994	2.2	0.41	2.1	2.7
1995	3.8	0.40	1.2	1.4
1996	6.2	0.35	6.1	6.3
1997	3.4	0.28	3.2	3.4

Notes: Natural P loads were estimated by Houser et al. (2000). Natural P inputs are presented for 1991 and 1992, and natural plus artificial P inputs are presented for 1993–1997.

(Cole and Pace 1998). Because dilution rates could not be measured in every lake every year, we did not attempt to correct P input rates for dilution. Peter Lake flushes slightly more rapidly than West Long Lake (Table 3). This difference would diminish Peter Lake's chlorophyll response relative to West Long Lake for an equivalent P input rate (Vollenweider 1976). Such an effect would cause an underestimation of any grazing impact in West Long Lake.

Total P concentrations in the epilimnion were closely related to P input rates (Fig. 3A). There are two outliers, East Long Lake in 1996 and 1997. East Long Lake has a shallow epilimnion and anoxic hypolimnion (Christensen et al. 1996). The hypolimnion became more P-rich over the course of the experiment (Houser et al. 2000). Entrainment as the mixed layer deepens over the summer may explain the high P concentrations in East Long Lake in 1996–1997. Alternatively, the staining of East Long Lake may cause its producers to become limited by light at lower P loads, leading to accumulation of inorganic P in the epilimnion. Total P concentrations in the reference lake, Paul Lake, ranged  $8.8\text{--}11.6 \text{ mg/m}^3$ .

Total N concentrations in the epilimnion tended to increase with enrichment rates (Fig. 3B). The total N concentration of East Long Lake was comparable to that of the other lakes, for a given level of enrichment. Total N concentrations in the reference lake, Paul Lake, ranged  $273\text{--}424 \text{ mg/m}^3$ .

Soluble reactive P concentrations were generally near or below the detection limit ( $\sim 2 \text{ mg/m}^3$ ), as expected for P-limited lakes (Fig. 4A). Notable exceptions were all the enriched lakes at the highest enrichment rate (in 1996) and East Long Lake in 1997. Soluble reactive P concentrations in the reference lake, Paul Lake, ranged from less than the detection limit to  $5 \text{ mg/m}^3$ .

Dissolved inorganic N ( $\text{NH}_4 + \text{NO}_3 + \text{NO}_2$ ) concentrations were generally above detection limits ( $\sim 1 \text{ mg/m}^3$ ) in all lakes, all years. Concentrations reached high levels under enrichment in East and West Long

TABLE 3. Residence time estimated as volume/outflow for the experimentally enriched lakes, with standard deviation among years for each lake.

Lake	Years	Residence time (d)	1 SD
East Long Lake	1992–1996	1914	1319
Peter Lake	1993–1996	1285	813
West Long Lake	1992–1996	1611	1293

Note: Data are taken from the detailed water budgets by Cole and Pace (1998).

lakes (Fig. 4B). In Peter Lake, dissolved inorganic N concentrations were highest at the highest enrichment rate. Dissolved inorganic N concentrations in Paul Lake ranged  $11\text{--}18 \text{ mg/m}^3$ .

### Organic carbon

Following the isolation of East Long Lake by the curtain in 1991, DOC concentrations increased  $\sim 4 \text{ mg/L}$ , color (absorbance at  $440 \text{ nm}$ ) increased  $\sim 0.8 \text{ m}^{-1}$ , the thermocline rose  $\sim 0.6 \text{ m}$ , and the thickness of the surface layer of oxygenated water decreased  $\sim 1.7 \text{ m}$  (Christensen et al. 1996). Shifts in DOC were correlated with changes in chlorophyll and primary production in East Long Lake (Carpenter et al. 1998a, b). In

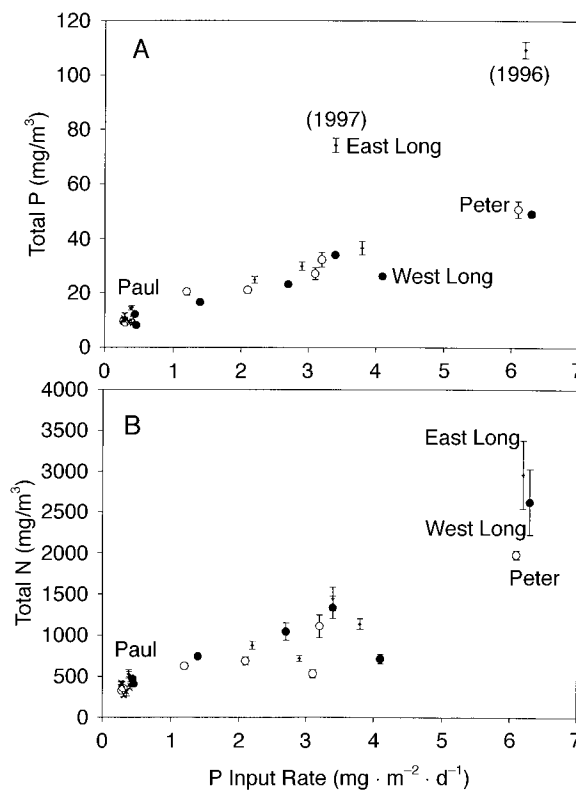


FIG. 3. (A) Total P concentration ( $\text{mg/m}^3$ ) and (B) total N concentration ( $\text{mg/m}^3$ ) vs. P input rate ( $\text{mg} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ ) in the epilimnia of four experimental lakes, 1991–1997. Symbols: Paul Lake, x; East Long Lake, +; Peter Lake, o; West Long Lake, ●. Error bars show  $\pm 1 \text{ SE}$ .

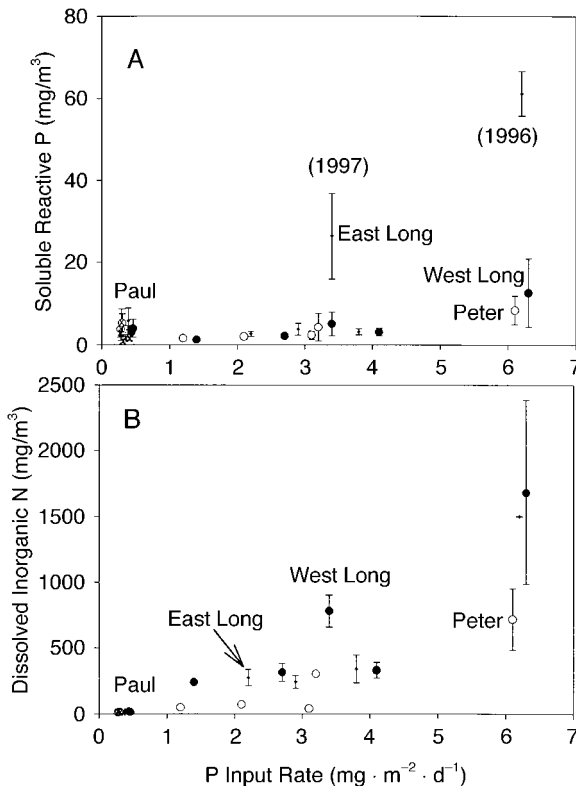


FIG. 4. (A) Soluble reactive P concentration ( $\text{mg}/\text{m}^3$ ) and (B) dissolved inorganic N concentration ( $\text{mg}/\text{m}^3$ ) vs. P input rate ( $\text{mg} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ ) in the epilimnia of four experimental lakes, 1991–1997. Symbols: Paul Lake,  $\times$ ; East Long Lake,  $+$ ; Peter Lake,  $\circ$ ; West Long Lake,  $\bullet$ . Error bars show  $\pm 1$  SE.

these lakes, DOC and water color correlate strongly ( $r = 0.91$ ; Carpenter et al. 1998b). Thus, DOC levels are inversely related to light penetration and primary production per unit lake area (Carpenter et al. 1998b).

Seasonal mean concentrations of DOC show consistent differences among lakes, but little trend with P input rate (Fig. 5A). Paul Lake and Peter Lake had DOC concentrations of 4–6 mg/L with generally low intra-annual variation. West Long Lake had DOC concentrations of 7–9 mg/L with generally low variation within each year. East Long Lake had the highest DOC concentrations (11–16 mg/L) and the highest variability both within and among years. Because the increase in DOC concentrations occurred between the times of curtain installation and the initial fertilization (Christensen et al. 1996), DOC and P input rate are correlated over time in East Long Lake (Carpenter et al. 1998b).

Particulate organic carbon (POC) concentration increased with nutrient enrichment in East Long Lake and Peter Lake (Fig. 5B). Summer mean POC concentrations were consistently higher in Peter Lake than in West Long Lake.

#### *Piscivorous and planktivorous fishes*

Paul Lake was dominated by piscivorous largemouth bass throughout the experiment (Fig. 6). Largemouth

bass consumed smaller individuals of their own species as well as benthic invertebrates, littoral zooplankton, and a diversity of minor prey (Hodgson and Hodgson 2001). During 1993 and 1994, recruitment events caused planktivory to increase as abundant year classes of bass fed on zooplankton (Post et al. 1997). These intervals of planktivory were relatively brief and resembled a similar episode of planktivory by a large year class of largemouth bass in Peter Lake in 1985 (Carpenter et al. 1987).

West Long Lake, like Paul Lake, was dominated by piscivores (Fig. 6). Both largemouth and smallmouth bass were piscivorous in West Long Lake (He et al. 1994). Unlike Paul Lake, planktivory by fishes in West Long Lake was significant in most years of the experiment (Hodgson et al. 1997). In 1991 and 1992, yellow perch accounted for most of the planktivore biomass. In 1996, the planktivore biomass consisted of young-of-the-year (YOY) largemouth bass. In 1997, the planktivore biomass consisted primarily of YOY largemouth bass (72%) and YOY yellow perch (28%).

Peter Lake was dominated by planktivorous minnows throughout the experiment (Fig. 6). Minnow populations were highly variable over time, in both abun-

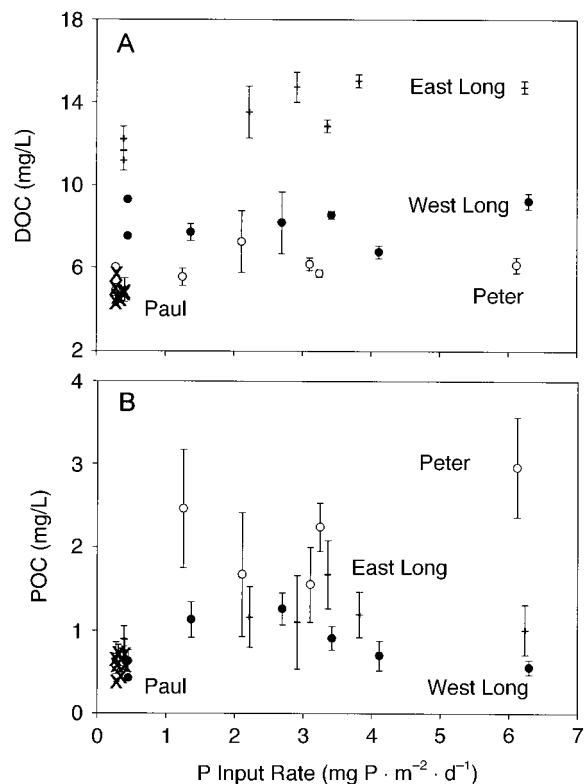


FIG. 5. (A) Dissolved organic carbon (DOC) concentration ( $\text{mg}/\text{L}$ ) and (B) particulate organic carbon (POC) concentration ( $\text{mg}/\text{L}$ ) vs. P input rate ( $\text{mg} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ ) in the epilimnia of four experimental lakes, 1991–1997. Symbols: Paul Lake,  $\times$ ; East Long Lake,  $+$ ; Peter Lake,  $\circ$ ; West Long Lake,  $\bullet$ . Error bars show  $\pm 1$  SE.



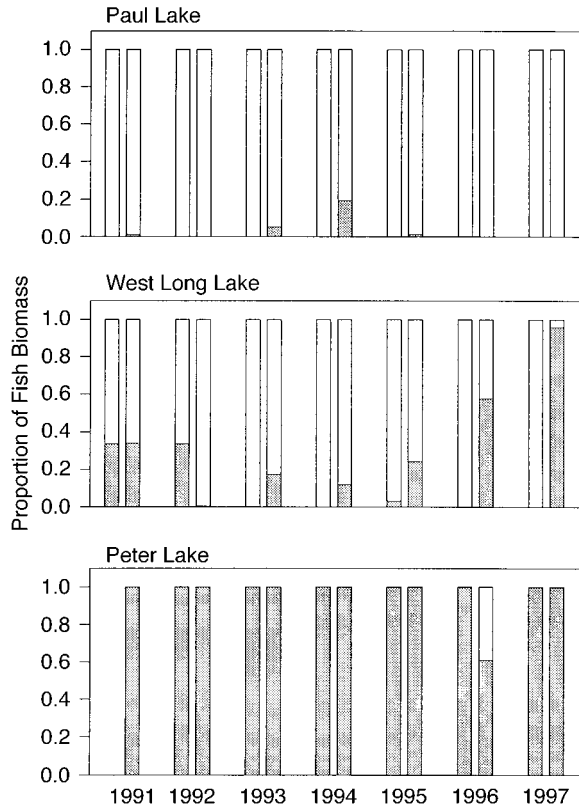


FIG. 6. Relative biomass of planktivores (shaded bars) and piscivores (open bars) in Paul Lake, West Long Lake, and Peter Lake, during 1991–1997. In each year, results of May and August population surveys are shown.

dance and community structure (Schindler et al. 1993, 1997a). For example, a midsummer die-off of minnows in 1994 caused a short-lived trophic cascade (Carpenter et al. 1996). Some piscivorous largemouth bass were present early in 1991, prior to bass removal. During summer 1996, piscivorous bass were introduced to Pe-

ter Lake, but this introduction failed to produce a persistent population or notable reductions in planktivory. In 1997, no bass were captured during two nights of intensive electroshocking.

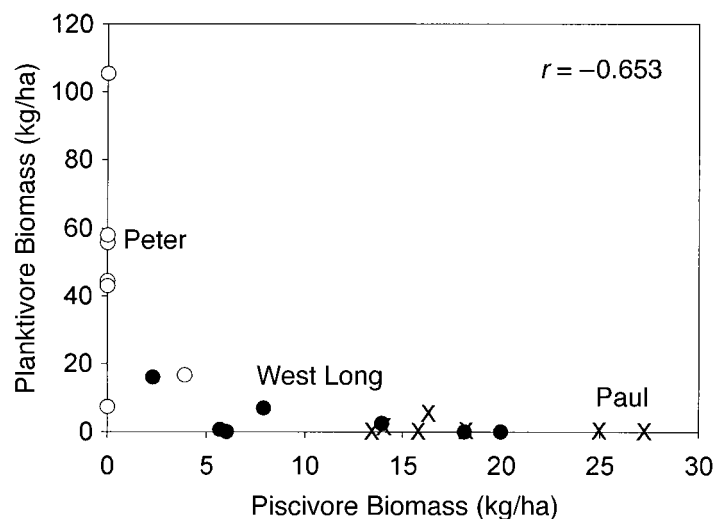
Planktivore biomass was inversely related to piscivore biomass (Fig. 7). In Peter Lake, where piscivory was consistently low, planktivore biomass was highly variable. In Paul Lake and West Long Lake, piscivore biomass was variable. However, piscivore biomass was apparently sufficient to maintain consistently low biomass of planktivores.

We interpret East Long Lake's fish treatment as one of variable, but generally low, planktivory (Carpenter et al. 1998b, Pace et al. 1998). Fish communities were impacted by declining pH, increasing DOC, and oxygen depletion following installation of the curtain (Christensen et al. 1996). Fish abundance was low and could not be measured reliably. During 1991–1992, the fish community of East Long Lake was dominated by bluegills, yellow perch, sticklebacks, and minnow species. In later years, yellow perch disappeared, while bluegills persisted at low densities. Sticklebacks were abundant in nearshore areas. Largemouth bass often entered East Long Lake by moving over or around the curtain during periods of high water. However, largemouth bass populations were too small to measure. It is unlikely that bass established a persistent, overwintering population in East Long Lake. Abundance of large *Daphnia* corroborate the low fish abundances, suggesting that planktivory was low throughout the experiment.

#### Zooplankton

Zooplankton species composition showed some variability over time in each lake. In Paul Lake, the dominant zooplankton were large cladoceran grazers (*Daphnia pulex*, *D. rosea*, and *Holopedium gibberum*) and copepods (*Cyclops varicans rubellus*, *Orthocy-*

FIG. 7. Planktivore biomass (kg/ha) vs. piscivore biomass (kg/ha) in Paul Lake (×), Peter Lake (○), and West Long Lake (●).



*clops modestus*, *Skistodiaptomus* species) (Post et al. 1997). *Bosmina longirostris* was abundant during brief periods of high planktivory by YOY bass (Post et al. 1997).

In Peter Lake, large-bodied zooplankters were excluded by planktivory most of the time, leaving rotifers, *Cyclops varicans rubellus* and *Bosmina longirostris*, to dominate the zooplankton. During episodes of low planktivory in 1994, 1996 and 1997, *Daphnia rosea* became abundant in Peter Lake.

The zooplankton of West Long Lake were consistently dominated by large-bodied grazers, *Daphnia pulex* and *D. rosea*, throughout this study. *Mesocyclops edax*, *Bosmina longirostris*, and *Asplanchna* spp. were common subdominant zooplankton.

In East Long Lake, rotifers and small-bodied crustaceans predominated in 1991 and 1992, corresponding with relatively high planktivory (Carpenter et al. 1998a, Pace et al. 1998). By mid-1993, the large grazers *Daphnia pulex* and *D. rosea* dominated the zooplankton of East Long Lake, and maintained this dominance through 1996 (Carpenter et al. 1998a, Pace et al. 1998). During 1994–1996, the most common subdominant zooplankton species were *Mesocyclops edax*, *Bosmina longirostris*, and *Asplanchna* spp. In 1997, however, *Daphnia* species were subdominant to the predaceous copepod *Mesocyclops edax* and a smaller bodied cladoceran herbivore, *Bosmina longirostris*.

Crustacean mean length provides an index of both size-selective predation and grazing intensity (Brooks and Dodson 1965, Pace 1984, Peters and Downing 1984, Carpenter and Kitchell 1993). Crustacean zooplankton of West Long Lake were consistently larger than those of Peter Lake (Fig. 8A). Crustaceans of East Long Lake were more variable in length than those of any other lake. In most years, crustaceans of East Long Lake were larger than those of Peter Lake. Crustacean length in Paul Lake ranged 0.33–0.51 mm, representing the variability of an unmanipulated reference system. The lower crustacean sizes occurred in 1993 and 1994. These shifts resulted from the bass recruitment events discussed by Post et al. (1997).

Biomass of crustacean zooplankton appeared to be larger under enrichment (Fig. 8B). Weekly fluctuations in crustacean biomass were directly related to enrichment (Carpenter et al. 1996). No consistent differences in crustacean biomass were evident among enriched lakes. In Paul Lake, crustacean biomass varied within 0.63–1.86 g/m<sup>2</sup>.

The allocation of crustacean biomass among *Daphnia* spp. and smaller grazers was different among lakes. Biomass of *Daphnia* spp. was consistently larger in West Long Lake than in Peter Lake (Fig. 8C). *Daphnia* of West Long Lake were dominated by *D. pulex* and *D. rosea*. Interannual variation in *Daphnia* biomass was large in East Long Lake, where *Daphnia* biomass exceeded that of Peter Lake in some years, but was less than that of Peter Lake in other years. Despite heavy

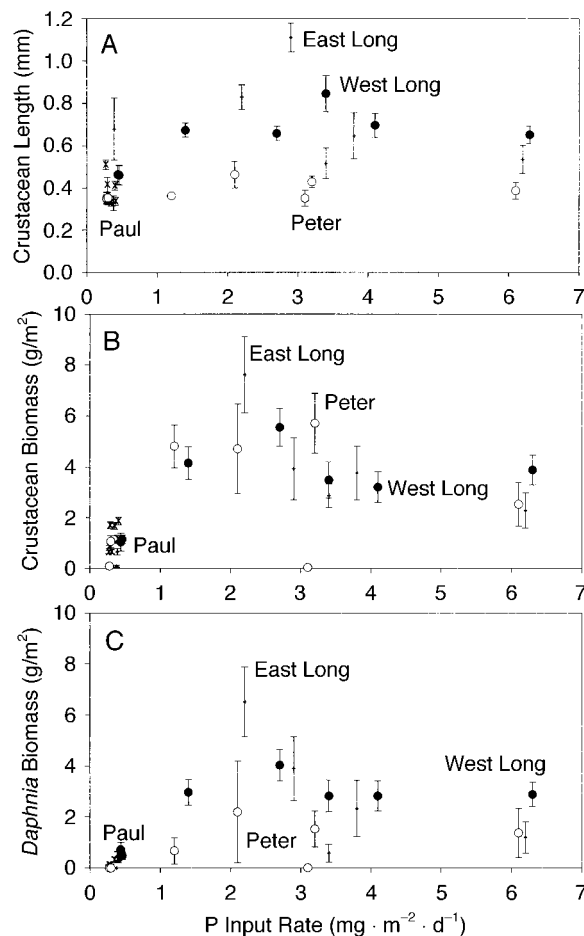


FIG. 8. (A) Crustacean mean length (mm), (B) crustacean biomass ( $\text{g}/\text{m}^2$ ), and (C) *Daphnia* biomass ( $\text{g}/\text{m}^2$ ) vs. P input rate ( $\text{mg} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ ) in the four experimental lakes, 1991–1997. Symbols: Paul Lake, ×; East Long Lake, +; Peter Lake, ○; West Long Lake, ●. Error bars show  $\pm 1$  SE.

fish planktivory, Peter Lake supported some *Daphnia* (including the smaller bodied species, *D. dubia* and *D. rosea*) in most years. The *Daphnia* resurgence following a fish die-off in Peter Lake in 1994 was described by Carpenter et al. (1996). *Daphnia* biomass in Peter Lake fluctuated around 2  $\text{g}/\text{m}^2$  in 1996 and 1997. Bass introduction in 1996 was followed by increased *Daphnia* biomass late in that summer. In 1997, no bass were caught in the lake and a large recruitment of minnows was observed. *Daphnia* biomass in the reference lake, Paul Lake, ranged 0.1–0.38  $\text{g}/\text{m}^2$ , with the lowest values occurring in 1993 and 1994 following bass recruitment events (Post et al. 1997).

Crustacean length was constrained to a narrow range of small-bodied animals when planktivore biomass was relatively high (Fig. 9A). At relatively low planktivore biomasses, crustacean length was variable and potentially large. Both *Daphnia* biomass (Fig. 9B) and total crustacean biomass (Fig. 9C) could be large at intermediate levels of planktivore biomass, but were low at

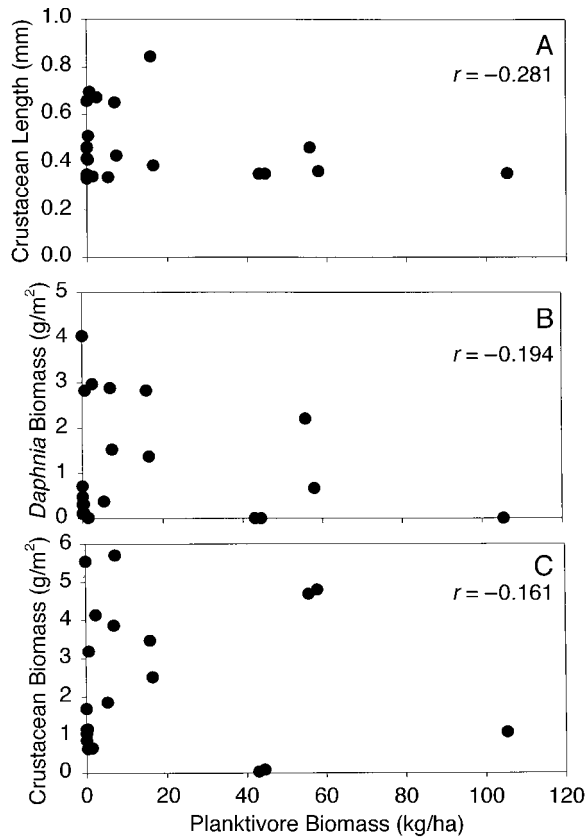


FIG. 9. (A) Crustacean length (mm), (B) *Daphnia* biomass ( $\text{g}/\text{m}^2$ ), and (C) total crustacean biomass ( $\text{g}/\text{m}^2$ ) vs. planktivore biomass ( $\text{kg}/\text{ha}$ ) in the three experimental lakes where planktivore biomass could be measured (Paul Lake, Peter Lake, and West Long Lake). Correlation coefficients are not significant ( $n = 21$ ,  $P > 0.05$ ).

the highest level of planktivore biomass. The ratio of *Daphnia* biomass to total crustacean biomass was directly correlated with mean crustacean length ( $r = 0.87$ ,  $n = 28$ ).

Regressions show significant positive effects of nutrient enrichment on all zooplankton variates (Table 4). Nutrient enrichment increased *Daphnia* biomass, which was an important factor in the positive response of mean crustacean length to enrichment. Total crus-

tacean biomass was not affected strongly by planktivore biomass, consistent with previously published time series analyses of these lakes (Carpenter and Kitchell 1993, Carpenter et al. 1996). Both *Daphnia* biomass and mean crustacean length have significant inverse relationships with planktivore biomass. For both *Daphnia* biomass and mean crustacean biomass, interaction terms improve the model fit. The interaction terms account for the fact that nutrient effects depend on the level of planktivory (Fig. 9B, C). When planktivore biomass is high, both *Daphnia* biomass and crustacean mean length are low, regardless of the level of nutrient enrichment. When planktivore biomass is low, the constraint of predation is removed, and both *Daphnia* biomass and crustacean mean length vary with nutrient enrichment.

#### Primary producers

Areal chlorophyll (integrated from the depth of 5% of surface irradiance) was moderately variable in the unenriched lakes (Fig. 10A). In the unenriched condition, differences in areal chlorophyll between Peter Lake and the basins of Long Lake were consistent with the differences in crustacean mean length: Peter Lake tended to have higher areal chlorophyll. After enrichment began, the differences among lakes were amplified. Areal chlorophyll in Peter Lake consistently exceeded that of West and East Long Lakes. The mean difference between Peter and West Long lakes was  $\sim 0.5$  log units during enrichment, indicating that areal chlorophyll of Peter Lake was about three-fold larger than that of West Long Lake under comparable P input rate ( $10^{0.5} \approx 3$ ). East Long Lake tended to have lower areal chlorophyll than West Long Lake. Analyses of weekly data indicated that low areal chlorophyll levels in East Long Lake can be explained statistically by the joint effects of grazing and colored DOC (Carpenter et al. 1998a, b). Areal chlorophyll in the reference lake, Paul, ranged within 1.16–1.26  $\log_{10}$ (areal chlorophyll), where chlorophyll data were in units of milligrams per square meter.

Chlorophyll concentrations (areal chlorophyll divided by the depth of 5% of surface irradiance) also differed between Peter Lake and West Long Lake during

TABLE 4. Regressions of zooplankton variates ( $\log_{10}$ -transformed) on P input rate, planktivore biomass ( $\text{kg}/\text{ha}$ ), and their interaction.

Dependent Variate	P input		Planktivore		Interaction		$R^2$	1 SE
	Coefficient	$t$	Coefficient	$t$	Coefficient	$t$		
Crustacean biomass	2.34	3.75	-0.00429	0.32	-0.0130	0.44	0.388	1.43
<i>Daphnia</i> biomass	1.83	5.39	-0.0169	2.32	-0.0321	2.01	0.639	0.771
Crustacean mean length	0.155	3.14	-0.00251	2.37	-0.00419	1.80	0.427	0.112

Notes: For each dependent variate, we present three parameters (coefficients for  $\log_{10}$ [P input rate], planktivore biomass, and interaction,  $\log_{10}$ [P input rate  $\times$  planktivore biomass]) and their  $t$  statistics (estimate/1 SE), coefficient of determination ( $R^2$ ), and standard error of residuals (1 SE). In all cases  $n = 21$  (planktivore biomasses were not available for East Long Lake). Significant values of  $t > 2.08$ .

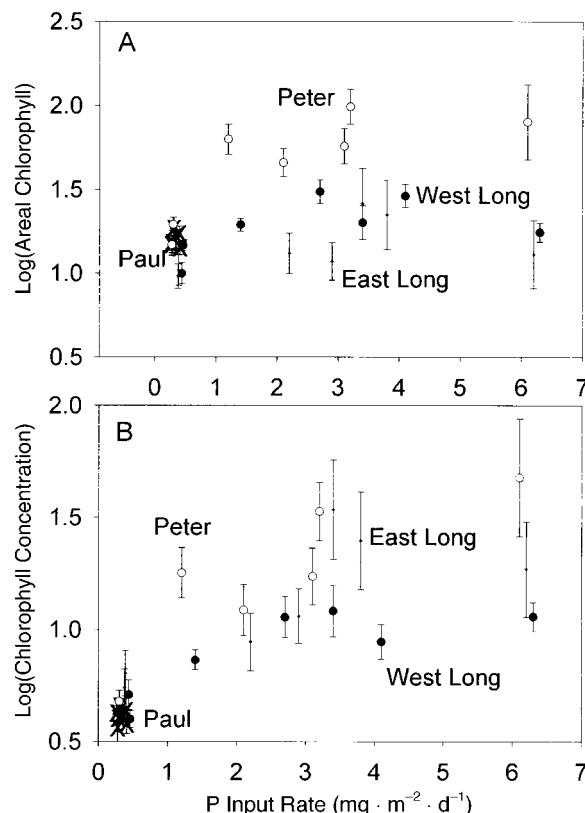


FIG. 10. The figure plots (A)  $\log_{10}$ (areal chlorophyll) and (B)  $\log_{10}$ (chlorophyll concentration) vs. P input rate ( $\text{mg} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ ) in the four experimental lakes, 1991–1997. Symbols: Paul Lake, ×; East Long Lake, +; Peter Lake, ○; West Long Lake, ●. Original data for areal chlorophyll were in units of milligrams per square meter; original data for chlorophyll concentration were in units of milligrams per cubic meter. Error bars show  $\pm 1$  SE.

enrichment. While the interpretation of areal chlorophyll vs. concentrations is debated (Carpenter et al. 1999, Nürnberg 1999), we found consistent results for these two measures of algal biomass. In Peter Lake, chlorophyll concentrations were somewhat more variable than areal chlorophyll. Nevertheless, the average difference between the two lakes was nearly 0.5 log units during enrichment, approaching a three-fold difference in chlorophyll concentrations. East Long Lake, however, had variable chlorophyll concentrations under enrichment, which could be as high as those of Peter Lake or as low as those of West Long Lake. Staining by colored DOC caused the photic zone of East Long Lake to be thin (Carpenter et al. 1998). Thus, the amount of chlorophyll per unit area is relatively low, though concentrations can be high. Effects of colored DOC on areal chlorophyll vs. chlorophyll concentrations are discussed in more detail by Nürnberg (1999) and Carpenter et al. (1999). Chlorophyll concentrations of Paul Lake ranged 0.56–0.63  $\log_{10}$ (chlorophyll concentration), where chlorophyll data were in units of milligrams per cubic meter.

The proportion of chlorophyll in large particles ( $>35 \mu\text{m}$ ) is reported as an index of blooms of large, potentially inedible phytoplankton (Cottingham et al. 1998, Cottingham 1999). In the reference ecosystem and in the other lakes prior to enrichment, this proportion ranged  $\sim 0.17$ – $0.52$  (Fig. 11). Throughout the experiment, the reference lake was dominated by a mixture of chrysophytes and chlorophytes, with a diverse assemblage of subdominant groups including cryptomonads, dinoflagellates and cyanobacteria (Cottingham et al. 1998). Prior to enrichment, Peter Lake tended to be dominated by chrysophytes, dinoflagellates, and chlorophytes (Cottingham et al. 1998). West Long Lake was dominated by chlorophytes and dinoflagellates prior to enrichment, while East Long Lake was dominated

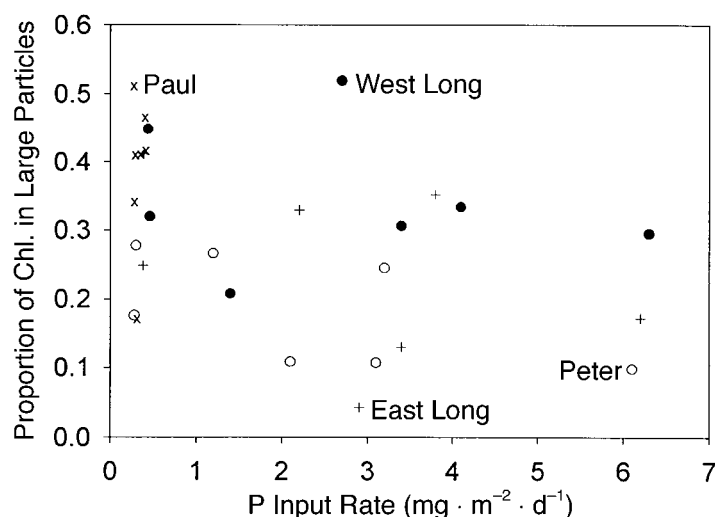


FIG. 11. Proportion of chlorophyll in large particles ( $>35 \mu\text{m}$ ) vs. P input rate ( $\text{mg} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ ) in the four experimental lakes, 1991–1997. Symbols: Paul Lake, ×; East Long Lake, +; Peter Lake, ○; West Long Lake, ●. In all cases, standard errors are smaller than the symbols.



by dinoflagellates and chrysophytes (Cottingham et al. 1998).

In Peter Lake and West Long Lake, the proportion of chlorophyll in large particles showed no strong trends related to P input rate (Fig. 11). In the years of enrichment, the proportion of chlorophyll in large particles tended to be greater in West Long Lake than in Peter Lake. These differences in size structure are correlated with differences in community structure (Cottingham et al. 1998, Cottingham 1999). Peter Lake exhibited high biomass of chlorophytes and cyanobacteria during enrichment (Cottingham et al. 1998). Biomass was consistently high, except during brief irruptions of *Daphnia*. West Long Lake, in contrast, exhibited blooms of cyanobacteria in August 1993 and throughout the summer of 1994 (Carpenter et al. 1995, Cottingham et al. 1998). The atomic N:P ratio of fertilizer was 17.0 in 1993 and 30.4 in 1994, and then remained ~30 through 1997. There is no evident relationship between the change in fertilizer N:P and the relative abundance of cyanobacteria in Peter Lake and West Long Lake (Cottingham et al. 1998). In later years of enrichment, blooms of cyanobacteria occurred occasionally each summer, while other groups were generally suppressed by grazers.

In East Long Lake, the proportion of chlorophyll in large particles was variable throughout the study. East Long Lake did not exhibit the cyanobacterial blooms seen in West Long Lake (Cottingham et al. 1998). Chlorophytes and cryptomonads were prevalent.

Responses of primary production are consistent with those of chlorophyll. Prior to enrichment, Peter Lake had higher areal primary production (integrated above the depth of 5% of surface irradiance) than either basin of Long Lake, consistent with the food web differences (Fig. 12A). During enrichment, differences in primary production among the lakes became larger. During enrichment, Peter Lake's areal primary production was more than six-fold ( $0.8 \log_{10}$  units) greater than that of West Long Lake. Areal primary production of East Long Lake was lower than that of West Long Lake, despite comparable P input rates and grazer assemblages. This difference is due to the higher colored DOC concentrations of East Long Lake (Carpenter et al. 1998a, b). Areal primary production of the reference lake, Paul Lake, varied between 2.4 and 2.7  $\log_{10}$ (areal primary production), where production data were in units of milligrams per square meter.

Volumetric primary production (areal production divided by the depth of 5% of surface irradiance) was consistently greater in Peter Lake than in West Long Lake, and differences were largest during enrichment (Fig. 12B). On average, Peter Lake's volumetric primary production during enrichment was approximately three-fold ( $0.5 \log_{10}$  units) greater than that of West Long Lake. Volumetric primary production of East Long Lake during enrichment ranged from rates similar to those of West Long Lake to rates almost as high as

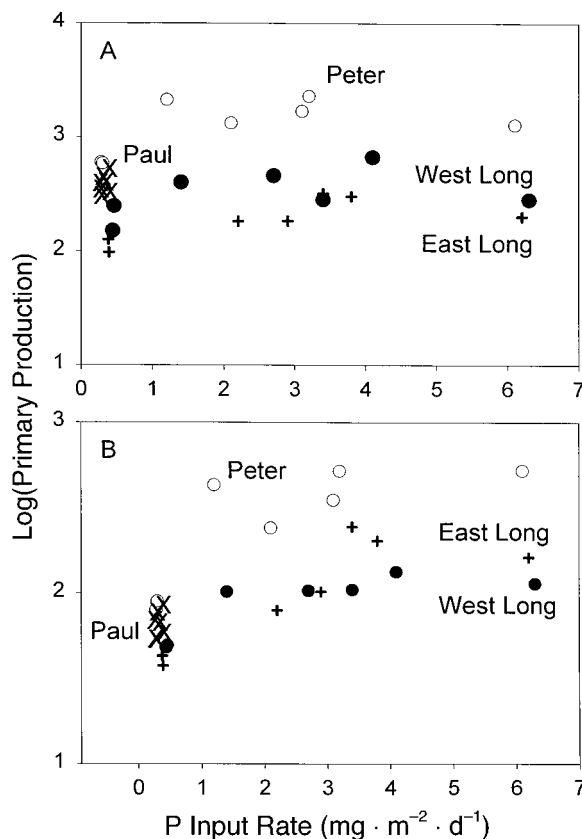


FIG. 12. The figure plots (A)  $\log_{10}$ (areal primary production rate) and (B)  $\log_{10}$ (volumetric primary production) vs. P input rate ( $\text{mg} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ ) in the four experimental lakes, 1991–1997. Symbols: Paul Lake,  $\times$ ; East Long Lake,  $+$ ; Peter Lake,  $\circ$ ; West Long Lake,  $\bullet$ . Original data for areal production were in units of milligrams per square meter per day; original data for volumetric production were in units of milligrams per cubic meter per day. In all cases, standard errors are smaller than the symbols.

those of Peter Lake. Although volumetric primary production rates were sometimes high in the thin photic zone of East Long Lake, vertically integrated primary production rates tended to be low. Volumetric primary production of Paul Lake ranged 1.7–2  $\log_{10}$ (primary production), where primary production data were in units of milligrams per cubic meter.

#### Bacteria

Concentrations of bacteria varied nearly 10-fold among lakes and years (Fig. 13A). Bacterial concentrations tended to be higher in Peter Lake than in the other enriched lakes, but this pattern was not consistent. Bacterial concentrations of Paul Lake were less variable than those of the enriched lakes, ranging within  $2\text{--}7 \times 10^9$  cells/L.

Bacterial production showed consistent differences among lakes during enrichment (Fig. 13B). Peter Lake generally had higher bacterial production than either basin of Long Lake. Bacterial production rates in the

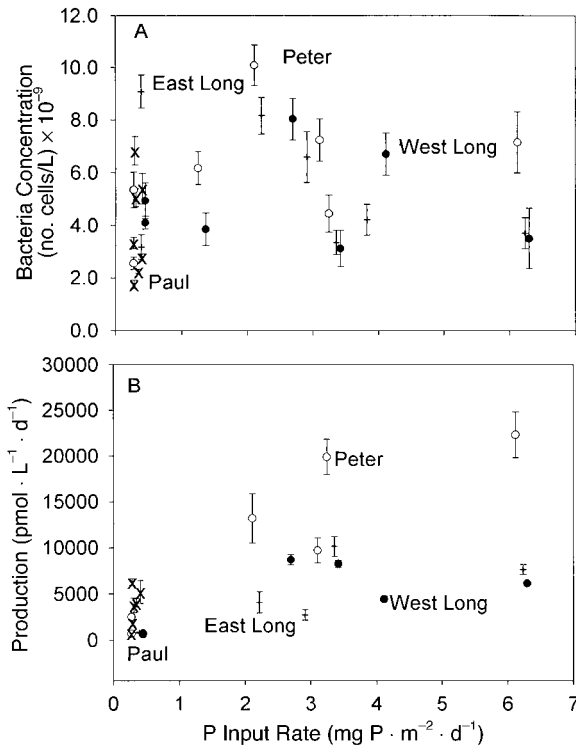


FIG. 13. (A) Bacterial concentration (no. cells/L) and (B) bacterial production (pmol leucine  $\cdot$  L $^{-1}$   $\cdot$  d $^{-1}$ ) vs. P input rate (mg  $\cdot$  m $^{-2}$   $\cdot$  d $^{-1}$ ) in the four experimental lakes, 1991–1997. Symbols: Paul Lake,  $\times$ ; East Long Lake, +; Peter Lake,  $\circ$ ; West Long Lake,  $\bullet$ . Error bars show  $\pm 1$  SE.

reference lake, Paul Lake, ranged 754–6276 pmol  $\cdot$  L $^{-1}$   $\cdot$  d $^{-1}$ . This range is approximately as large as the range seen in East and West Long Lakes.

#### CO $_2$ flux

Exchange of CO $_2$  between the lakes and the atmosphere is presented as an integrative index of ecosystem metabolism (Schindler et al. 1997a). Paul Lake dis-

charged CO $_2$  to the atmosphere (Fig. 14), consistent with a pattern known from a substantial majority of the world's lakes (Cole et al. 1994). East Long Lake, which had relatively low areal primary production, also discharged CO $_2$  to the atmosphere. Peter Lake, in contrast, had high primary production and was a net sink for atmospheric CO $_2$ . West Long Lake was an intermediate case. Under most conditions, it discharged CO $_2$  to the atmosphere. In the first two years of enrichment, however (1993 and 1994), West Long Lake absorbed CO $_2$  from the atmosphere at a small net rate.

#### Primary producer and microbe response to nutrients, grazers, and DOC

Regressions using a fixed model were used to compare the effects of nutrient input rate, grazers, and dissolved organic carbon (DOC) on primary producers and microbes (Table 5). All three predictors are significantly correlated (crustacean mean length  $\times$  P input rate,  $r = 0.380$ ; crustacean mean length  $\times$  DOC,  $r = 0.649$ ; P input rate  $\times$  DOC,  $r = 0.430$ ; for all correlations  $n = 28$ ,  $P < 0.05$ ). Because of this collinearity, a predictor having a large impact on a response variable may have a nonsignificant parameter, because the predictor is redundant with another predictor in the model. The ecosystem experiments were designed to create independent contrasts of food web structure and P input rate. The correlation of crustacean mean length and P input rate is relatively low, but significant at the 5% level. This correlation makes it less likely that effects of P input rate and crustacean length will both be significant in a given regression, i.e., it makes the experiment less likely to detect the effects it was intended to reveal. The experiment was not designed to investigate DOC effects, but unforeseen changes in DOC in the course of the experiment made it necessary to consider DOC effects. DOC is correlated with crustacean length and P input rate, potentially confounding the detection of effects by regression.

Despite collinear predictors, regressions indicated

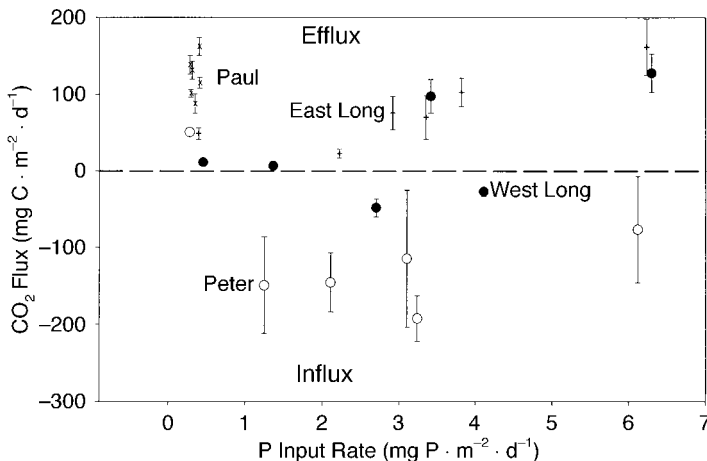


FIG. 14. Rate of CO $_2$  flux between the lake and the atmosphere (mg C  $\cdot$  m $^{-2}$   $\cdot$  d $^{-1}$ ) vs. P input rate (mg  $\cdot$  m $^{-2}$   $\cdot$  d $^{-1}$ ) in the four experimental lakes, 1991–1997. Symbols: Paul Lake,  $\times$ ; East Long Lake, +; Peter Lake,  $\circ$ ; West Long Lake,  $\bullet$ . Error bars show  $\pm 1$  SE.

TABLE 5. Regressions using  $\log_{10}$ (P input rate), mean crustacean length, and dissolved organic carbon (DOC) as independent variates.

Dependent variate	Intercept		P input		Crustacean length		DOC		$R^2$	1 SE
	Coefficient	<i>t</i>	Coefficient	<i>t</i>	Coefficient	<i>t</i>	Coefficient	<i>t</i>		
Areal chlorophyll	1.89	19	0.501	7.38	-0.448	2.18	-0.0443	3.91	0.725	0.152
Volumetric chlorophyll	1.09	11	0.634	9.19	-0.625	2.99	-0.0171	1.49	0.816	0.154
Areal production	3.47	27	0.534	6.01	-0.515	1.91	-0.0760	5.13	0.724	0.199
Volumetric production	2.53	22	0.669	8.39	-0.704	2.91	-0.206	1.55	0.747	0.178
Bacteria	4.21	2.92	0.807	0.812	2.26	0.749	-0.0392	0.236	0.090	2.22
Leucine	1.53	6.61	1.05	6.83	-1.09	2.26	-0.0503	1.79	0.704	0.339
POC	1.81	5.61	1.02	4.62	-1.30	1.94	-0.0159	0.430	0.477	0.494

Notes: For each dependent variate, parameter estimates and *t* values (parameter estimate/1 SE) for intercept, P input, crustacean length, and DOC are presented, as well as the overall coefficient of determination ( $R^2$ ) and standard error of residuals ( $n = 28$ ). Significant values of  $t > 2.05$ . Chlorophyll and primary production were  $\log_{10}$  transformed, and other dependent variates were analyzed in the natural units. To simplify presentation, bacterial biomass was divided by  $10^9$ , and leucine incorporation was divided by  $10^4$ .

many significant effects of P input rate and crustacean mean length. P input rate had a significant positive effect on every dependent variate except bacterial biomass. Crustacean mean length, an index of food web structure, had significant negative effects on chlorophyll (both areal and volumetric), primary production per unit volume, and leucine incorporation. Effects of crustacean mean length were negative and marginal ( $P \approx 0.06$ ) for areal primary production and POC. In the case of areal primary production, which may be influenced by either grazing or shading, effects of crustacean length may be confounded by the strong correlation of crustacean length and DOC. DOC had significant negative effects on chlorophyll and primary production per unit area. Our data do not provide a strong test of DOC effects because of the collinearity of DOC and the directly manipulated predictors.

We examined regressions that omitted DOC to assess the relationship of the response variates to P input rate and crustacean mean length alone (Table 6). Both predictors had significant and opposite effects on chlorophyll, primary production, leucine incorporation, and POC. For areal chlorophyll and primary production, the two-predictor models explained less variance than the three-predictor models. Dissolved organic carbon had its greatest effects on areal chlorophyll and primary production.

Stepwise multiple regressions were calculated to provide another perspective on the effects of collinear predictors. In addition, stepwise regressions gave the opportunity to compare other grazing indices: *Daphnia* biomass, crustacean biomass, and the ratio of *Daphnia* to crustacean biomass. These food web indicators are all correlated (Fig. 15).

For all response variates except bacterial concentration, stepwise regression produced models that explained most of the variance in the response variates. For chlorophyll and primary production, these regressions explain >80% of the variance among annual means. Phosphorus input had significant positive effects on chlorophyll, primary production, leucine incorporation, and POC (Table 7). Dissolved organic carbon had significant inverse effects on areal chlorophyll and primary production, as in the fixed-effect regressions. Dissolved organic carbon also had a significant inverse effect on leucine incorporation. This may be an indirect consequence of reduced primary production at high DOC, leading to reduced algal release of organic compounds consumed by bacteria.

Zooplankton had significant effects in every regression (Table 7), but these effects differed among response variates. For areal chlorophyll, volumetric primary production, leucine incorporation and POC, crustacean biomass had a significant positive coefficient.

TABLE 6. Regressions using  $\log_{10}$ (P input rate) and crustacean mean length as independent variates.

Dependent variate	Intercept		P input		Crustacean length		$R^2$	1 SE
	Coefficient	<i>t</i>	Coefficient	<i>t</i>	Coefficient	<i>t</i>		
Areal chlorophyll	1.75	15	0.438	5.30	-0.879	4.04	0.550	0.190
Volumetric chlorophyll	1.14	12	0.659	9.60	-0.458	2.53	0.799	0.158
Areal production	3.23	19	0.425	3.48	-1.26	3.89	0.422	0.282
Volumetric production	2.47	22	0.639	8.04	-0.904	4.31	0.721	0.183
Bacteria	4.099	3.08	0.750	0.79	1.87	0.75	0.088	2.18
Leucine	1.37	6.09	1.00	6.29	-1.58	3.74	0.657	0.357
POC	1.76	5.92	0.997	4.73	-1.45	2.61	0.473	0.485

Note: See Table 5 Notes, although DOC data are not presented here.

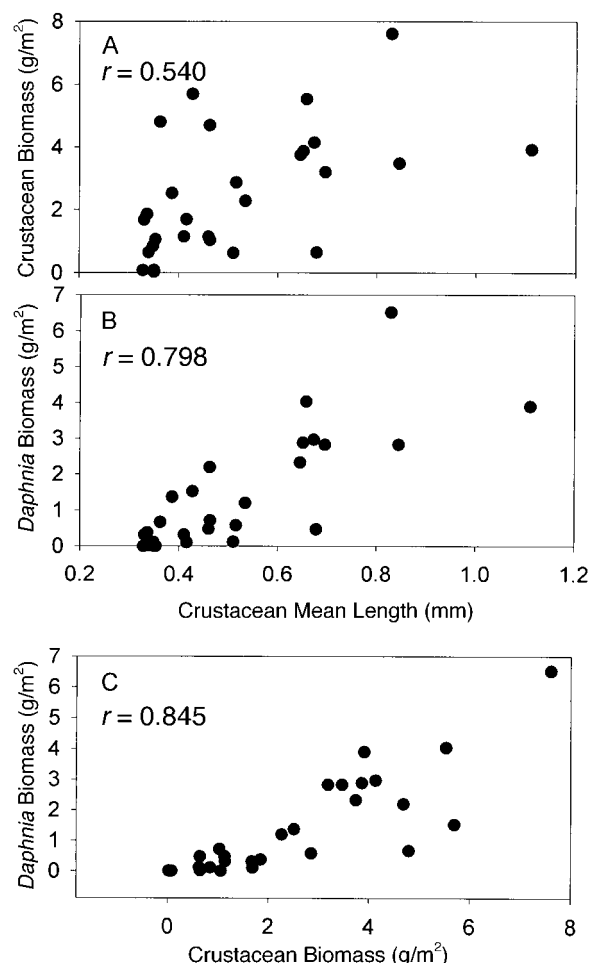


FIG. 15. Correlations of zooplankton variates used in regressions. (A) Crustacean biomass ( $\text{g}/\text{m}^2$ ) vs. crustacean mean length (mm), (B) *Daphnia* biomass ( $\text{g}/\text{m}^2$ ) vs. crustacean mean length (mm), and (C) *Daphnia* biomass ( $\text{g}/\text{m}^2$ ) vs. crustacean biomass ( $\text{g}/\text{m}^2$ ). All correlations are significant ( $P < 0.05$ ).

We interpret this as a bottom-up effect: more primary producers increase overall herbivore biomass. Time series analyses of weekly data have demonstrated this positive effect (Carpenter et al. 1996). In every regression with a positive effect of total crustacean biomass, there is a negative effect of a zooplankton variate related to *Daphnia*. For areal chlorophyll, leucine incorporation, and POC, there are negative effects of *Daphnia* biomass. For volumetric primary production, there are negative effects of *Daphnia* biomass and the ratio of *Daphnia* to crustacean biomass.

In the other regressions (Table 7), there are significant negative effects of the ratio of *Daphnia* to crustacean biomass (volumetric chlorophyll, areal primary production) or *Daphnia* biomass (bacterial concentration). These inverse effects of *Daphnia* are interpreted as grazing effects. *Daphnia* biomass is strongly correlated with crustacean mean length (Fig. 15B). Time

series analyses of weekly data have demonstrated significant negative effects of grazing as measured by *Daphnia* or zooplankton mean size in these lakes (Carpenter and Kitchell 1993, Carpenter et al. 1996, 1998a, b).

We have presented three different regression approaches (Tables 5, 6, and 7) to determine whether the general patterns are robust. Several important results emerge from all three regression approaches. Chlorophyll, whether areal or volumetric, had significant relationships with both P input rate and grazer variates in all regressions, in the expected directions. The same is true of primary production per unit volume. Areal primary production was significantly related to P input in all regressions, and to grazer variates in the two-predictor regressions (Table 6) and multiple regressions (Table 7). In the three-predictor regressions (Table 5), DOC had strong effects on areal production and the effect of crustacean length was marginal. However, the multiple regressions (Table 7) show strong effects on areal production of both DOC and *Daphnia* biomass/crustacean biomass. Thus, there is significant evidence of a grazer effect on areal production, even though the pattern is complex. Bacterial biomass was unrelated to P input rate and showed no inverse relationships with grazer variates. Leucine incorporation, in contrast, was related significantly to both P input rate and grazer variates. Thus our manipulations affected microbial production, but not biomass. Particulate organic carbon, a composite of bacteria, phytoplankton, and detritus, was directly related to P input rate and inversely related to crustacean mean length or *Daphnia* biomass.

#### *Primary producer and microbe response to nutrients, fishes, and DOC*

Regressions describing fish effects on primary producers and microbes can only be calculated using Paul Lake, Peter Lake, and West Long Lake, because fish biomass estimates could not be obtained for East Long Lake. Despite the lower degrees of freedom and loss of sensitivity caused by omission of East Long Lake, a number of significant responses occurred.

Planktivore biomass had significant positive coefficients for areal chlorophyll and on both areal and volumetric primary production (Table 8). All of these effects are in the direction forecast by the trophic cascade hypothesis. Planktivore biomass had no significant negative coefficients. In the planktivore regressions, P input rate had significant positive effects on all dependent variates except bacterial concentration. Dissolved organic carbon had significant negative effects on areal chlorophyll, both areal and volumetric primary production, leucine incorporation, and POC.

Piscivore biomass had significant negative coefficients for areal chlorophyll, and on both areal and volumetric primary production (Table 9). These effects match the expectations of the trophic cascade hypothesis. Piscivore biomass had no significant positive co-



TABLE 7. Best models found by stepwise multiple regressions. Candidate independent variates are  $\log_{10}$ (P input rate), mean crustacean length, crustacean biomass, *Daphnia* biomass, ratio of *Daphnia* biomass to total crustacean biomass, and dissolved organic carbon (DOC).

Dependent variate	Parameter	Estimate	<i>t</i>	<i>R</i> <sup>2</sup>	1 SE
Areal chlorophyll	Intercept	1.58	19	0.818	0.126
	P input	0.425	6.43		
	Crustacean biomass	0.0978	3.92		
	<i>Daphnia</i> biomass	-0.130	4.17		
	DOC	-0.0432	4.98		
Volumetric chlorophyll	Intercept	1.043	20	0.815	0.151
	P input	0.698	9.88		
	<i>Daphnia</i> /crustacean biomass	-0.341	3.02		
	DOC	-0.0736	6.25		
Areal primary production	Intercept	3.28	32	0.806	0.170
	P input	0.512	5.59		
	<i>Daphnia</i> /crustacean biomass	-0.543	3.70		
	DOC	-0.0736	6.25		
Volumetric primary production	Intercept	2.21	22	0.858	0.139
	P input	0.650	8.56		
	Crustacean biomass	0.0919	3.08		
	<i>Daphnia</i> biomass	-0.122	2.59		
	<i>Daphnia</i> /crustacean biomass	-0.302	1.84		
Bacteria concentration	Intercept	4.41	8.49	0.140	2.07
	<i>Daphnia</i> biomass	0.505	2.06		
	DOC	-0.179	1.83		
Leucine incorporation	Intercept	0.843	4.05	0.794	0.290
	P input	0.878	5.71		
	Crustacean biomass	0.250	3.61		
	<i>Daphnia</i> biomass	-0.322	3.83		
	DOC	-0.0533	2.44		
POC	Intercept	0.802	5.12	0.596	0.434
	P input	0.737	3.44		
	Crustacean biomass	0.293	3.57		
	<i>Daphnia</i> biomass	-0.376	3.83		

Note: See Table 5 Notes, although crustacean biomass, *Daphnia* biomass, and ratio of *Daphnia* biomass to total crustacean biomass are additionally presented here.

efficients. In the piscivore regressions, P input rate had significant positive effects on all dependent variates except bacterial concentration. Dissolved organic carbon had significant negative effects on areal chlorophyll, both areal and volumetric primary production, leucine incorporation, and POC.

## DISCUSSION

### Manipulations

Relatively high N:P ratios in added nutrients were intended to prevent nitrogen limitation. Prior to enrichment, bioassays and physiological studies showed

TABLE 8. Regressions using  $\log_{10}$ (P input rate), planktivore biomass (kg/ha), and dissolved organic carbon (DOC) as independent variates.

Dependent variate	Intercept		P input		Planktivore		DOC		<i>R</i> <sup>2</sup>	1 SE
	Coefficient	<i>t</i>	Coefficient	<i>t</i>	Coefficient	<i>t</i>	Coefficient	<i>t</i>		
Areal chlorophyll	1.98	12	0.545	7.17	0.00263	2.27	-0.101	4.08	0.775	0.145
Volumetric chlorophyll	1.21	6.69	0.662	7.93	0.00163	1.28	-0.0540	1.98	0.812	0.159
Areal production	3.59	20	0.547	6.47	0.00510	3.96	-0.149	5.38	0.796	0.161
Volumetric production	2.68	15	0.668	7.96	0.00403	3.16	-0.109	3.96	0.817	0.160
Bacteria	4.48	1.99	1.76	1.70	0.0236	1.49	0.0206	0.06	0.279	1.98
Leucine	1.68	3.23	1.10	4.57	-0.00002	0.01	-0.171	2.18	0.554	0.457
POC	2.22	3.70	1.19	4.29	0.00598	1.41	-0.198	2.19	0.553	0.527

Notes: For each dependent variate, parameter estimates and *t* values (parameter estimate/1 SE) for intercept, P input, planktivore biomass, and DOC are presented, as well as the overall coefficient of determination (*R*<sup>2</sup>) and standard error of residuals (*n* = 21). Significant values of *t* > 2.08. Chlorophyll and primary production were  $\log_{10}$  transformed, and other dependent variates were analyzed in the natural units. To simplify presentation, bacterial biomass was divided by 10<sup>9</sup> and leucine incorporation was divided by 10<sup>4</sup>.

TABLE 9. Regressions using  $\log_{10}$ (P input rate), piscivore biomass (kg/ha), and dissolved organic carbon (DOC) as independent variates.

Dependent variate	Intercept		P input		Piscivore		DOC		$R^2$	1 SE
	Coefficient	<i>t</i>	Coefficient	<i>t</i>	Coefficient	<i>t</i>	Coefficient	<i>t</i>		
Areal chlorophyll	2.10	13	0.434	4.68	-0.0102	2.26	-0.0963	3.82	0.774	0.145
Volumetric chlorophyll	1.27	7.14	0.597	5.83	-0.00594	1.20	-0.0512	1.84	0.810	0.160
Areal production	3.80	20	0.344	3.17	-0.0186	3.53	-0.140	4.75	0.774	0.170
Volumetric production	2.85	15	0.515	4.77	-0.0140	2.68	-0.102	3.49	0.797	0.169
Bacteria	5.51	2.50	0.698	0.55	-0.973	1.59	0.0718	0.21	0.290	1.97
Leucine	1.69	3.30	1.07	3.66	-0.00232	0.16	-0.169	2.13	0.554	0.457
POC	2.47	4.14	0.956	2.80	-0.0213	1.28	-0.188	2.04	0.545	0.533

Note: See Table 8 Notes, although piscivore, not planktivore, biomass data are presented here.

that the phytoplankton were either P-limited or co-limited by N and P (Carpenter and Kitchell 1993). Dissolved inorganic nitrogen accumulated in the epilimnia of enriched lakes during summer, while soluble reactive phosphorus did not. The only exception was 1996, when nutrient input rates were the highest, and both dissolved inorganic N and soluble reactive P accumulated in the epilimnia. Accumulation of excess inorganic N and P in 1996 suggests that other factors (e.g., light transmission or grazing) limited primary producers of enriched lakes. Thus we conclude that N was not the limiting nutrient for primary producers during these experiments.

Fish manipulations successfully maintained a food web with large-bodied cladoceran grazers in West Long Lake. In Peter Lake, fish manipulations generally maintained high planktivory and small-bodied grazers. However, minnow die-offs and bass introduction led to irruptions of *Daphnia* in 1994, 1996, and 1997. These events had short-term effects on chlorophyll and primary production (Carpenter et al. 1996, 1998), but did not have large effects on the annual averages reported here. In East Long Lake, food web structure and the zooplankton community varied considerably. Small-bodied grazers predominated in 1991, 1992, and 1997, and large-bodied *Daphnia* spp. predominated in 1993–1996.

The reference ecosystem, Paul Lake, was monitored to determine the background variability of an unmanipulated lake, and to detect any trends that might have affected all of the experimental lakes. Bass recruitment events in Paul Lake caused brief, transient food web responses in 1993 and 1994 (Post et al. 1997). However, there are no major trends in the reference lake to suggest patterns that should be considered when interpreting responses of the enriched lakes.

#### *Responses of the lakes to nutrients and herbivory*

The comparison of Peter and West Long lakes shows that food web structure has consistent effects on pelagic primary producers at a wide range of nutrient levels. The piscivore-dominated lake had substantially lower chlorophyll and primary production than the planktivore-dominated lake, at all levels of P enrichment that

we studied. These food web effects were evident in the unenriched condition, and at P input rates so high that inorganic P accumulated in the epilimnion.

Differences between Peter Lake and West Long Lake may underestimate the effects of food web structure on producers. Peter Lake flushes more rapidly, which should decrease chlorophyll for a given P input rate (Vollenweider 1976). Also, Peter Lake experienced several irruptions of *Daphnia*, which diminished the contrast in grazing between the two lakes. Thus the difference between Peter Lake and West Long Lake should be viewed as a minimal estimate of the potential impact of trophic cascades.

Food web structure also affected bacterial production. Among diverse lakes, bacterial production tends to track primary production (Cole et al. 1988, White et al. 1991), and this pattern was repeated in our experimental lakes (Pace and Cole 1996). In Peter Lake, where nutrients and small-bodied zooplankton produced the highest levels of chlorophyll and primary production, bacterial production was also highest. Bacterial abundance, on the other hand, did not show strong effects of either nutrient addition or food web structure. Bacterivory, which also tracked nutrients and food web changes, kept bacterial numbers within a relatively narrow range (Pace and Cole 1996, Pace et al. 1998). The much higher bacterial production in Peter Lake, without a concomitant increase in bacterial abundance, suggests that the trophic cascade caused bacteria to turn over more rapidly in Peter Lake vs. the other enriched lakes.

Responses of East Long Lake are difficult to interpret, because both grazing and colored dissolved organic carbon (DOC) can explain the reductions in chlorophyll and primary production. Time series analyses of weekly data suggest that both herbivory and colored DOC had substantial effects on chlorophyll and primary production in East Long Lake (Carpenter et al. 1998a, b).

Recently the use of areal vs. volumetric measures of chlorophyll and primary production for pelagic systems has been debated (Carpenter et al. 1999, Nürnberg 1999). Areal units place pelagic ecosystems on the same basis as terrestrial ecosystems, are appropriate

for interpretation of gas exchange between lakes and the atmosphere, and reflect the dynamics of buoyant cyanobacteria, which integrate the water column vertically. Volumetric units are appropriate for the mass action laws that govern interactions of chemicals and plankton in a three-dimensional environment, though this may be less pertinent for fishes that may experience the epilimnion as a two-dimensional environment (Essington and Kitchell 1999). For the present study, the distinction between areal and volumetric units is moot, because areal and volumetric chlorophyll and production responded in the same ways to nutrient and food web manipulation. The only exception is a minor one: in regressions against planktivore and piscivore biomass, areal and volumetric chlorophyll responded in the same direction, but the coefficients for fish effects on volumetric chlorophyll were not significant. Areal and volumetric production, however, responded significantly (and in the same direction) to fish variates. Also, areal and volumetric chlorophyll and primary production always responded significantly and in the same direction to grazer variates. The regressions involving fish variates had fewer degrees of freedom than those involving grazer variates, thereby displayed less power to detect effects.

#### *Trophic cascades*

Our results demonstrate numerous patterns consistent with the trophic cascade hypothesis: inverse relationship of piscivore and planktivore biomass; inverse relationship of planktivore biomass to biomass of *Daphnia* and crustacean mean size; and inverse relationship of crustacean mean size to chlorophyll and primary production. Other characteristics of the zooplankton community, such as *Daphnia* biomass or the ratio of *Daphnia* biomass to total crustacean biomass, were also inversely related to chlorophyll and primary production. Planktivore biomass was directly related to primary production and to chlorophyll per unit lake area. Piscivore biomass was inversely related to primary production and areal chlorophyll.

Fishes are likely to have threshold effects on trophic cascades. Piscivore biomass in these, and other, lakes is sustained by benthos (Carpenter and Kitchell 1993, Schindler et al. 1997b). The high piscivore biomass suppresses any planktivores that invade or recruit, even though the piscivores are supported largely by nonfish prey. Therefore, linear models may not represent the relationship between piscivore biomass and zooplankton or phytoplankton.

Since the introduction of the size efficiency hypothesis (Brooks and Dodson 1965), many experiments and case studies have demonstrated the size-selective impact of planktivores on zooplankton communities. Cross-lake comparisons of size effects are less common (Currie et al. 1999). Mills and Schiavone (1982) found a significant inverse correlation between biomass of fish planktivores and mean zooplankton length ( $r =$

$-0.80$ ,  $n = 18$ ,  $P < 0.01$ ). Currie et al. found a significant positive relationship between cladoceran body mass and the presence of piscivores. Our data suggest that the relationship of zooplankton size to planktivory may be wedge-shaped, i.e., the variability around the line changes with level of planktivory. When planktivory is high, large zooplankters are excluded from the community, but when planktivory is low large zooplankters can be abundant and mean zooplankton size is related to nutrient inputs.

While the effects of planktivorous fishes on zooplankton mean body size are consistent, relationships of planktivore biomass and zooplankton biomass among lakes are more variable. Previous whole-lake experiments showed that planktivory has variable effects on zooplankton biomass, even though impacts on body size and *Daphnia* are consistently inverse (Carpenter and Kitchell 1993). Relationships of zooplankton biomass and planktivorous fish biomass were non-significant in several studies (Mills and Schiavone 1982, Persson et al. 1992, Currie et al. 1999). Quiros (1990a) found a positive relationship between zooplankton biomass and planktivore biomass, suggestive of a resource-controlled effect. In a later study, he showed a positive relationship between the relative frequency of piscivorous fishes and macrozooplankton biomass, suggestive of a cascading effect (Quiros 1998). Our results show no significant relationship between planktivore biomass and total zooplankton biomass. This finding is consistent with the idea that planktivory affects zooplankton size structure and community composition more consistently than total biomass.

The effect of planktivorous fishes on phytoplankton biomass and production, however, is positive in some comparative studies (Mills and Schiavone 1982, Quiros 1990b, Persson et al. 1992). Such correlations may be explained by the impact of planktivores on zooplankton size structure, combined with the greater grazing capacity of large-bodied herbivores.

Several lines of evidence support an inverse relationship of large-bodied zooplankton to phytoplankton biomass, chlorophyll, or primary production. Larger-bodied zooplankters have greater per capita feeding rates and broader diets than smaller animals (Peters and Downing 1984). In particular, *Daphnia* seems to be an especially effective grazer owing to its broad diet, rapid numerical response, and ability to migrate (Shapiro 1990). Population interactions that stabilize the suppression of phytoplankton by *Daphnia* were described by Murdoch et al. (1998). In addition, *Daphnia* tends to sequester P rather than recycling it, exacerbating P limitation of phytoplankton (Elser et al. 1996). Many whole-lake experiments and biomanipulations show inverse relations of zooplankton body size to phytoplankton biomass or production (Carpenter and Kitchell 1993, Hansson et al. 1998, Jeppesen et al. 1998, Meijer et al. 1999). This pattern is consistent with several

comparative studies (Mills and Schiavone 1982, Pace 1984, Quiros 1990b, Carpenter et al. 1991). In contrast, Currie et al. (1999) failed to find a significant relationship between chlorophyll and zooplankton body mass. There are several reasons why our results are difficult to compare with those of Currie et al. (1999).

1) They tested for food web effects after correcting statistically for total phosphorus (TP) differences, whereas we used P input rates. In cross-lake data sets like those of Currie et al. (1999), the relationship of TP to P input rate may be noisy or inconsistent due to interlake differences in mean depth and flushing rate (Vollenweider 1976). Also, TP (unlike P input rate) is itself affected by the food web (Carpenter and Kitchell 1993, Schindler et al. 1993, Elser et al. 1996, Houser et al. 2000). Thus, statistical adjustments using TP may remove food web effects a priori, and thereby decrease the ability of subsequent statistical tests to detect food web effects.

2) The narrow range of grazer sizes considered by Currie et al. (1999) makes it unlikely that grazer effects would be detected. Currie et al. (1999) calculated zooplankton mass from measurements of body length using the regressions of Peters and Downing (1984). Based on this regression, the range of zooplankton mean lengths in Currie et al. (1999) is only 0.2 mm, compared with 0.6 mm in this study and ~1.1 mm among the world's lakes (Carpenter et al. 1996).

3) In addition, the length-mass regression adds substantial error variance that would tend to obscure any existing effects of zooplankton body size on producers. We used measurements of zooplankton length, which are relatively precise and more likely to reveal effects.

4) Our experiments were designed to produce contrasts in food web structure, whereas Currie et al. (1999) studied the existing variability among lakes in a region. There are many possible explanations for differences among comparative and experimental studies of trophic cascades (Carpenter and Kitchell 1988, Carpenter et al. 1991). Despite this, many comparative studies (Mills and Schiavone 1982, Pace 1984, Quiros 1990b, Carpenter et al. 1991) and whole-lake manipulations (Carpenter and Kitchell 1993, Hansson et al. 1998, Jeppesen et al. 1998, Meijer et al. 1999) indicate inverse effects of zooplankton body size or large daphnids on primary producers.

How stable are trophic cascades? In our study, food web effects were sustained through five years of experimental enrichment. This duration is sufficient to span tens of generations of zooplankton and hundreds of generations of phytoplankton. Thus, the trophic cascades were not brief, transient phenomena. They were sustained, long-term impacts of fishes on primary producers. Our findings are consistent with experiences in long-term biomanipulation of eutrophic lakes (Hansson et al. 1998, Meijer et al. 1999) and with comparative studies that correlate indices of size-selective predation with chlorophyll across broad cross-sections of lakes

(Mills and Schiavone 1982, Pace 1984, Carpenter et al. 1991, Persson et al. 1992, Sarnelle 1992, Mazumder 1994, Quiros 1998).

### *Implications for hypotheses*

Responses of Peter Lake and West Long Lake are relevant to several recent hypotheses about the conditions under which trophic cascades can control phytoplankton.

The data do not support the idea that P input rate must fall below a certain threshold for herbivory to control phytoplankton biomass (Benndorf 1987). On the contrary, herbivory reduced phytoplankton biomass and primary production across the full range of nutrient input rates that we considered. Phosphorus input rates in this study were sufficient to saturate inorganic P uptake, and exceeded the rates ( $1.4\text{--}5.5\text{ mg}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ ) proposed as an upper limit for food web control of chlorophyll (Benndorf 1995). Nevertheless, it is important to note that grazing was never able to eliminate cyanobacterial blooms in West Long Lake (Carpenter et al. 1995, Cottingham and Carpenter 1998, Cottingham et al. 1998). Many of the cyanobacteria were colonial, and contributed to the relatively high proportion of chlorophyll in large particles in West Long Lake. Although grazing consistently reduced chlorophyll and primary production, cyanobacteria were able to form visible blooms each year. In some summers blooms were almost continual, while in other summers blooms were episodic.

Colonial blue-green algae, which are resistant to grazing, are thought to inhibit the control of chlorophyll by trophic cascades (Benndorf 1987, Reynolds 1994). Despite blooms of blue-green algae in West Long Lake (Carpenter et al. 1995, Cottingham and Carpenter 1998, Cottingham et al. 1998), both chlorophyll and primary production were reduced by food web factors.

It has been proposed that rapid flushing (residence time  $<30\text{ d}$ ) aids biomanipulation by selecting against colonial cyanobacteria (Reynolds 1994). These lakes, however, have much longer residence times. Our experiments show that rapid flushing is not essential for the control of chlorophyll and primary production by grazing. However, our data do not contradict the idea that rapid flushing may aid the control of cyanobacteria in lakes.

The data contradict the proposition that trophic cascades are confined to shallow unstratified lakes capable of supporting abundant macrophytes (Reynolds 1994). Like Hansson et al. (1998), we find that grazing can effectively control phytoplankton in vertically stratified lakes. The experimental lakes offer limited habitat for macrophytes and were never colonized extensively by macrophytes during this study.

Large-bodied species of *Daphnia* are thought to be essential for trophic cascades from fish to phytoplankton (Pace 1984, Shapiro 1990, Carpenter and Kitchell



1993, Reynolds 1994). Our findings are consistent with this hypothesis.

The stability of food web configurations that reduce phytoplankton biomass has been considered by a number of authors (Shapiro 1990, Meijer et al. 1994, Reynolds 1994, Scheffer 1997). Data presented here show five years of food web control of phytoplankton in experimentally enriched lakes. It is important to note that fish communities of these lakes were not exploited. Nevertheless, this study shows that multiyear control of phytoplankton by grazing is possible where piscivore populations can be sustained and planktivores effectively suppressed. Dynamics of Peter Lake show that plankton communities respond rapidly to changes in planktivory (Carpenter et al. 1996). This reinforces the idea that fish community structure is a key to the stability of trophic structures that suppress phytoplankton. Rapid changes in fish communities may translate into rapid changes in plankton (Carpenter and Kitchell 1993, Mittelbach et al. 1995).

#### *Integrated ecosystem responses*

Lake metabolism integrates the responses of ecosystem production and respiration (Schindler et al. 1997a). In many lakes, high carbon inputs from the watershed lead to supersaturation of the water with CO<sub>2</sub> (Kling et al. 1991, Cole et al. 1994). Consequently, CO<sub>2</sub> diffuses out of the lake into the atmosphere. This situation occurs in the reference ecosystem, Paul Lake, and in all the lakes in the absence of nutrient enrichment. Nutrient enrichment should increase CO<sub>2</sub> fixation by primary producers, thereby drawing down CO<sub>2</sub> concentrations. In Peter Lake, we observed such a draw-down. Nutrient enrichment caused Peter Lake to become undersaturated with CO<sub>2</sub>, so that the net flux of CO<sub>2</sub> was into the lake. In West Long Lake, high herbivory tended to counter the stimulation of primary producers by nutrients. Although CO<sub>2</sub> concentrations were drawn down to some extent, the net flux was out of the lake in some years, and into the lake at a small rate in other years. East Long Lake, like Paul Lake, discharged CO<sub>2</sub> to the atmosphere throughout the experiment, despite considerable nutrient inputs. The high CO<sub>2</sub> discharge of East Long Lake probably results from a combination of high herbivory and high DOC levels.

Under a given nutrient regime, trophic cascades that decrease chlorophyll, and thereby decrease light extinction, may lead to increased production by light-limited benthic algae (Vadeboncoeur et al. 2001). In these whole-lake experiments, the responses of benthic algae to reductions in phytoplankton biomass were substantial, but did not completely compensate for decreases in pelagic primary production (Vadeboncoeur et al. 2001). Changes in CO<sub>2</sub> flux, which integrate responses of all producers and decomposers in the ecosystem, indicate that total ecosystem production and respiration were affected by food web structure.

We conclude that trophic cascades affected the responses of these lakes to nutrient inputs. Food webs that promote large-bodied herbivores had lower producer biomass, lower primary production, lower bacterial production, and higher rates of CO<sub>2</sub> discharge to the atmosphere. These impacts of trophic cascades occurred even when phosphorus input rates were so high that excess inorganic phosphorus accumulated in the epilimnion. These sustained trophic cascades appear to be linked to the stability of fish communities. Shifts in the balance of piscivory and planktivory are likely to lead to rapid responses in ecosystem processes.

#### *Nature of evidence for trophic cascades*

Demonstration of trophic cascades places relatively heavy demands on the data. In lakes, it is necessary to estimate biomass at every trophic level, to measure grazer body size, and to correct for possibly confounding effects of nutrient input rate and perhaps other factors, such as DOC. It is likely that comparably rich data sets will be needed to test for the prevalence of cascades in terrestrial and marine ecosystems. For lakes, ecologists have accumulated sufficiently rigorous data to show the widespread occurrence of cascades (Persson 1999). Nevertheless, a great deal of work is underway to determine the circumstances under which cascades are likely to be expressed or suppressed (Hansson et al. 1998, Jeppesen et al. 1998, Meijer et al. 1999, Persson 1999). In this study, we have shown the potential importance of cascades across a wide range of nutrient input rates, indicating that high nutrient inputs do not necessarily preclude trophic cascades. Our study also shows that DOC is an important covariate to consider, but our experiment was not designed to manipulate DOC, and many questions remain about the role of DOC in trophic cascades (Pace et al. 1999).

Cascades have been demonstrated in marine benthos, and a few examples are known for pelagic marine ecosystems (Paine 1980, Shiimoto et al. 1997, Micheli 1999, Pace et al. 1999, Persson 1999). In pelagic marine ecosystems, cascades have been investigated using multiyear time series that were not originally collected for the purpose of testing hypotheses about food web effects (Shiimoto et al. 1997, Micheli 1999). In such data sets, cascades may be difficult to detect because of time scale dependency of correlations (Carpenter and Kitchell 1988), lack of strong manipulations of food web structure (Carpenter 1988), management policies intended to stabilize fish stocks and thereby suppress variability that could reveal cascades (Walters 1986), or large observation errors. In addition, biotic mechanisms, such as interference competition, food quality, or migrations, may suppress cascades (Micheli 1999). While data sets demonstrating pelagic marine cascades are rare, we cannot determine whether the rarity is due to statistical problems or truly low prevalence of cascades.

The prevalence of cascades in terrestrial ecosystems is uncertain, although examples exist (Pace et al. 1999, Persson 1999, Polis 1999). Terrestrial ecosystems with large generalist mammalian grazers, keystone species subject to control by pathogen outbreaks, or the potential for massive insect outbreaks are among the more likely candidates for cascades. Experience with aquatic ecosystems suggests that serendipitous events, comparisons of extant data sets, and collections of case studies will be useful, but insufficient, to resolve questions about the frequency and control of terrestrial cascades. Carefully planned comparisons of contrasting ecosystems and deliberate ecosystem-scale experiments will probably be needed to determine the controlling factors of cascades in an unambiguous way.

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## LITERATURE CITED

- Aiken, L. S., and S. G. West. 1991. Multiple regression: testing and interpreting interactions. Sage Publications, Newbury Park, California, USA.
- Bade, D., J. Houser, and S. Scanga. 1998. Methods of the Cascading Trophic Interactions Project. Fifth edition. Center for Limnology, University of Wisconsin-Madison, Wisconsin, USA.
- Benndorf, J. 1987. Food web manipulation without nutrient control: a useful strategy in lake restoration? *Schweizerische Zeitschrift für Hydrologie* **49**:237-248.
- Benndorf, J. 1995. Possibilities and limits for controlling eutrophication by biomanipulation. *Internationale Revue der gesamten Hydrobiologie* **80**:519-534.
- Box, G. E. P., W. G. Hunter, and J. S. Hunter. 1978. Statistics for experimenters. Wiley, New York, New York, USA.
- Brooks, J. L., and S. I. Dodson. 1965. Body size and composition of plankton. *Science* **150**:28-35.
- Carpenter, S. R. 1988. Transmission of variance through lake food webs. Pages 119-138 in S. R. Carpenter, editor. *Complex interactions in lake communities*. Springer-Verlag, New York, New York, USA.
- Carpenter, S. R. 1999. Role of microcosm experiments in aquatic ecology: reply. *Ecology* **80**:1085-1088.
- Carpenter, S. R., D. L. Christensen, J. J. Cole, K. L. Cottingham, X. He, J. R. Hodgson, J. F. Kitchell, S. E. Knight, M. L. Pace, D. M. Post, D. E. Schindler, and N. Voichick. 1995. Biological control of eutrophication in lakes. *Environmental Science and Technology* **29**:784-786.
- Carpenter, S. R., J. J. Cole, T. E. Essington, J. R. Hodgson, J. N. Houser, J. F. Kitchell, and M. L. Pace. 1998a. Evaluating alternative explanations in ecosystem experiments. *Ecosystems* **1**:335-344.
- Carpenter, S. R., J. J. Cole, J. F. Kitchell, and M. L. Pace. 1998b. Impact of dissolved organic carbon, phosphorus and grazing on phytoplankton biomass and production in experimental lakes. *Limnology and Oceanography* **43**:73-80.
- Carpenter, S. R., T. M. Frost, J. F. Kitchell, T. K. Kratz, D. W. Schindler, J. Shearer, W. G. Sprules, M. J. Vanni, and A. P. Zimmerman. 1991. Patterns of primary production and herbivory in 25 North American lake ecosystems. Pages 67-96 in J. Cole, G. Lovett, and S. Findlay, editors. *Comparative analyses of ecosystems*. Springer-Verlag, New York, New York, USA.
- Carpenter, S. R., and J. F. Kitchell. 1988. Consumer control of lake productivity. *BioScience* **38**:764-769.
- Carpenter, S. R., and J. F. Kitchell. 1993. The trophic cascade in lakes. Cambridge University Press, Cambridge, UK.
- Carpenter, S. R., J. F. Kitchell, J. J. Cole, and M. L. Pace. 1999. Predicting responses of chlorophyll and primary production to changes in phosphorus, grazing and dissolved organic carbon. *Limnology and Oceanography* **44**:1179-1182.
- Carpenter, S. R., J. F. Kitchell, K. L. Cottingham, D. E. Schindler, D. L. Christensen, D. M. Post, and N. Voichick. 1996. Chlorophyll variability, nutrient input and grazing: evidence from whole-lake experiments. *Ecology* **77**:725-735.
- Carpenter, S. R., J. F. Kitchell, J. R. Hodgson, P. A. Cochran, J. J. Elser, M. M. Elser, D. M. Lodge, D. Kretchmer, X. He, and C. N. von Ende. 1987. Regulation of lake primary productivity by food web structure. *Ecology* **68**:1863-1876.
- Christensen, D. L., S. R. Carpenter, K. L. Cottingham, S. E. Knight, J. P. LeBouton, D. E. Schindler, N. Voichick, J. J. Cole, and M. L. Pace. 1996. Pelagic responses to changes in dissolved organic carbon following division of a seepage lake. *Limnology and Oceanography* **41**:553-559.
- Cole, J. J., and N. F. Caraco. 1998. Atmospheric exchange of carbon dioxide in a low-wind oligotrophic lake measured by the addition of SF<sub>6</sub>. *Limnology and Oceanography* **43**:647-656.
- Cole, J. J., N. F. Caraco, G. W. Kling, and T. K. Kratz. 1994. Carbon dioxide supersaturation in the surface waters of lakes. *Science* **265**:1568-1570.
- Cole, J. J., S. Findlay, and M. L. Pace. 1988. Bacterial production in fresh and saltwater ecosystems: a cross-system overview. *Marine Ecology Progress Series* **43**:1-10.
- Cole, J. J., and M. L. Pace. 1998. Hydrologic variability of small, northern Michigan lakes measured by the addition of tracers. *Ecosystems* **1**:310-320.
- Cottingham, K. L. 1999. Nutrients and zooplankton as multiple stressors of phytoplankton communities: evidence from size structure. *Limnology and Oceanography* **44**:810-827.
- Cottingham, K. L., and S. R. Carpenter. 1998. Population, community, and ecosystem variates as ecological indicators: phytoplankton responses to whole-lake enrichment. *Ecological Applications* **8**:508-530.
- Cottingham, K. L., S. R. Carpenter, and A. L. St. Amand. 1998. Responses of epilimnetic phytoplankton to experimental nutrient enrichment in three small seepage lakes. *Journal of Plankton Research* **20**:1889-1914.
- Currie, D. J., P. Dilworth-Christie, and F. Chapleau. 1999. Assessing the strength of top-down influences on plankton abundance in unmanipulated lakes. *Canadian Journal of Fisheries and Aquatic Sciences* **56**:427-436.
- Downing, J., and F. H. Rigler. 1984. Secondary productivity in fresh waters. Blackwell, New York, New York, USA.
- Elser, J. J., T. H. Chrzanowski, R. W. Sterner, and K. H. Mills. 1998. Stoichiometric constraints on food-web dynamics: a whole-lake experiment on the Canadian shield. *Ecosystems* **1**:120-136.
- Elser, J. J., D. R. Dobberfuhl, N. A. MacKay, and J. H. Schampel. 1996. Organism size, life history, and N:P stoichiometry. *BioScience* **46**:674-684.

- Essington, T. E., and J. F. Kitchell. 1999. New perspectives in the analysis of fish distributions: a case study on the spatial distribution of largemouth bass. *Canadian Journal of Fisheries and Aquatic Sciences* **56**(Supplement 1):52–60.
- Gulati, R. D., and W. R. DeMott. 1997. The role of food quality for zooplankton: remarks on the state of the art, perspectives and priorities. *Freshwater Biology* **38**:753–768.
- Hambricht, K. D. 1994. Morphological constraints on the piscivore–planktivore interaction—implications for the trophic cascade hypothesis. *Limnology and Oceanography* **39**:897–912.
- Hansson, L. A., H. Annadotter, E. Bergman, S. F. Hamrin, E. Jeppesen, T. Kairesalo, E. Luokkanen, P. A. Nilsson, M. Søndergaard, and J. Strand. 1998. Biomanipulation as an application of food-chain theory: constraints, synthesis, and recommendations for temperate lakes. *Ecosystems* **1**:558–574.
- He, X., J. R. Hodgson, J. F. Kitchell, and R. A. Wright. 1994. Growth and diet composition of largemouth bass in four experimental lakes. *Internationale Vereinigung für Theoretische und Angewandte Limnologie* **25**:766–772.
- Hobbie, J. E., R. J. Daley, and S. Jasper. 1977. Use of nucleopore filters for counting bacteria by fluorescent microscopy. *Applied and Environmental Microbiology* **33**:1225–1228.
- Hodgson, J. R., X. He, D. E. Schindler, and J. F. Kitchell. 1997. Diet overlap in a piscivore community. *Ecology of Freshwater Fish* **6**:144–149.
- Hodgson, J. Y., and J. R. Hodgson. 2001. Exploring optimal foraging by largemouth bass (*Micropterus salmoides*) from three experimental lakes. *Internationale Vereinigung für Theoretische und Angewandte Limnologie*, *In press*.
- Hoover, T. E., and D. C. Berkshire. 1969. Effects of hydration on carbon dioxide exchange across an air–water interface. *Journal of Geophysical Research* **74**:456–464.
- Houser, J. N., S. R. Carpenter, and J. J. Cole. 2000. Food web structure and nutrient enrichment: effects on sediment phosphorus retention in whole-lake experiments. *Canadian Journal of Fisheries and Aquatic Sciences* **57**:1524–1533.
- Hrbáček, J. M., V. Dvoráková, V. Korinek, and L. Procházková. 1961. Demonstration of the effect of the fish stock on the species composition of zooplankton and the intensity of the metabolism of the whole plankton association. *Internationale Vereinigung für Theoretische und Angewandte Limnologie* **14**:192–195.
- Hurlbert, S. H., J. Zedler, and D. Fairbanks. 1972. Ecosystem alteration by mosquitofish (*Gambusia affinis*) predation. *Science* **175**:639–641.
- Jeppesen, E., M. Søndergaard, M. Søndergaard, and K. Christoffersen, editors. 1998. The structuring role of submerged macrophytes in lakes. Springer-Verlag, Berlin, Germany.
- Kitchell, J. F., E. A. Eby, X. He, D. E. Schindler, and R. A. Wright. 1994. Predator–prey dynamics in an ecosystem context. *Journal of Fish Biology* **45**:1–18.
- Kling, G. W., G. W. Kipphut, and M. C. Miller. 1991. Arctic lakes and streams as gas conduits to the atmosphere—implications for tundra carbon budgets. *Science* **251**:298–301.
- Lodge, D. M., S. C. Blumenshine, and Y. Vadeboncoeur. 1998. Insights and applications of large scale, long term ecological observations and experiments. Pages 202–235 in W. R. Setälä and J. Bernardo, editors. *Experimental ecology: issues and perspectives*. Oxford University Press, Cambridge, UK.
- Marker, A. F. H., C. A. Crowther, and R. J. M. Gunn. 1980. Methanol and acetone as solvents for estimating chlorophyll and pheopigments by spectrophotometry. *Ergebnisse der Limnologie* **14**:52–69.
- Mazumder, A. 1994. Phosphorus–chlorophyll relationships under contrasting herbivory and thermal stratification: predictions and patterns. *Canadian Journal of Fisheries and Aquatic Sciences* **51**:401–407.
- Meijer, M.-L., I. De Boos, M. Scheffer, R. Portielje, and H. Hosper. 1999. Biomanipulation in shallow lakes in the Netherlands: an evaluation of 18 case studies. *Hydrobiologia* **408/409**:13–30.
- Meijer, M.-L., E. Jeppesen, E. van Donk, B. Moss, M. Scheffer, E. Lammens, E. van Nes, J. A. van Berkum, G. J. de Jong, B. A. Faafeng, and J. P. Jensen. 1994. Long-term responses to fish-stock reduction in small shallow lakes: interpretation of five-year results of four biomanipulation cases in The Netherlands and Denmark. *Hydrobiologia* **275/276**:457–466.
- Micheli, F. 1999. Eutrophication, fisheries and consumer–resource dynamics in marine pelagic ecosystems. *Science* **285**:1396–1398.
- Mills, E. L., and A. Schiavone. 1982. Evaluation of fish communities through assessment of zooplankton populations and measures of lake productivities. *North American Journal of Fisheries Management* **2**:14–27.
- Mittelbach, G. G., A. M. Turner, D. J. Hall, J. E. Rettig, and C. W. Osenberg. 1995. Perturbation and resilience in an aquatic community: a long-term study of the extinction and reintroduction of a top predator. *Ecology* **76**:2347–2360.
- Murdoch, W. W., R. M. Nisbet, E. McCauley, A. M. de Roos, and W. S. C. Gurney. 1998. Plankton abundance and dynamics across nutrient levels: tests of hypotheses. *Ecology* **79**:1339–1356.
- Nürnberg, G. K. 1999. Determining trophic state in experimental lakes. *Limnology and Oceanography* **44**:1176–1179.
- Pace, M. L. 1984. Zooplankton community structure, but not biomass, influences the phosphorus–chlorophyll *a* relationship. *Canadian Journal of Fisheries and Aquatic Sciences* **41**:1089–1096.
- Pace, M. L. 2001. Getting it right and wrong: extrapolations across experimental scales. Pages 161–181 in R. Gardner, M. Kemp, V. Kennedy, and J. Peterson, editors. *Scaling relations in experimental ecology*. Columbia University Press, New York, New York, USA.
- Pace, M. L., and J. J. Cole. 1994. Primary and bacterial production: are they coupled over depth? *Journal of Plankton Research* **16**:661–672.
- Pace, M. L., and J. J. Cole. 1996. Regulation of bacterial by resources and predation tested in whole-lake experiments. *Limnology and Oceanography* **41**:1448–1460.
- Pace, M. L., J. J. Cole, and S. R. Carpenter. 1998. Trophic cascades and compensation: differential responses of microzooplankton in whole-lake experiments. *Ecology* **79**:138–152.
- Pace, M. L., J. J. Cole, S. R. Carpenter, and J. F. Kitchell. 1999. Trophic cascades revealed in diverse ecosystems. *Trends in Ecology and Evolution* **14**:483–488.
- Paine, R. T. 1980. Food webs: linkage, interaction strength and community infrastructure. *Journal of Animal Ecology* **49**:667–685.
- Persson, L. 1999. Trophic cascades: abiding heterogeneity and the trophic level concept at the end of the road. *Oikos* **85**:385–397.
- Persson, L., S. Diehl, L. Johansson, G. Andersson, and S. F. Hamrin. 1992. Trophic interactions in temperate lake ecosystems: a test of food chain theory. *The American Naturalist* **140**:59–84.
- Peters, R. H., and J. Downing. 1984. Empirical analysis of zooplankton filtering and feeding rates. *Limnology and Oceanography* **29**:763–784.
- Polis, G. A. 1999. Why are parts of the world green? Multiple

- factors control productivity and the distribution of biomass. *Oikos* **86**:3–15.
- Post, D. M., S. R. Carpenter, D. L. Christensen, K. L. Cottingham, J. R. Hodgson, J. F. Kitchell, and D. E. Schindler. 1997. Seasonal effects of variable recruitment of a dominant piscivore on pelagic food web structure. *Limnology and Oceanography* **42**:722–729.
- Quiros, R. 1990a. Empirical relationships between nutrients, phyto- and zooplankton and relative fish biomass in lakes and reservoirs of Argentina. *Internationale Vereinigung für theoretische und angewandte Limnologie* **24**:1198–1206.
- Quiros, R. 1990b. Factors related to variance of residuals in chlorophyll–total phosphorus regressions in lakes and reservoirs of Argentina. *Hydrobiologia* **200/201**:343–355.
- Quiros, R. 1998. Fish effects on trophic relationships in the pelagic zone of lakes. *Hydrobiologia* **361**:101–111.
- Reynolds, C. S. 1994. The ecological basis for the successful biomanipulation of aquatic communities. *Archiv für Hydrobiologie* **130**:1–33.
- Sarnelle, O. 1992. Nutrient enrichment and grazer effects on phytoplankton in lakes. *Ecology* **73**:551–560.
- Scheffer, M. 1997. *Ecology of shallow lakes*. Chapman and Hall, New York, New York, USA.
- Schindler, D. E., S. R. Carpenter, J. J. Cole, J. F. Kitchell, and M. L. Pace. 1997a. Food web structure alters carbon exchange between lakes and the atmosphere. *Science* **277**:248–251.
- Schindler, D. E., J. R. Hodgson, and J. F. Kitchell. 1997b. Density-dependent changes in individual foraging specialization of largemouth bass. *Oecologia* **110**:592–600.
- Schindler, D. E., J. F. Kitchell, X. He, S. R. Carpenter, J. R. Hodgson, and K. L. Cottingham. 1993. Food web structure and phosphorus cycling in lakes. *Transactions of the American Fisheries Society* **122**:756–772.
- Schindler, D. W. 1998. Replication versus realism: the necessity for ecosystem-scale experiments, replicated or not. *Ecosystems* **1**:323–334.
- Schindler, D. W., E. J. Fee, and T. Rusczyński. 1978. Phosphorus input and its consequences for phytoplankton standing crop and production in the Experimental Lakes Area and in similar lakes. *Journal of the Fisheries Research Board of Canada* **35**:190–196.
- Shapiro, J. 1990. Biomanipulation: the next phase—making it stable. *Hydrobiologia* **200/201**:13–27.
- Shapiro, J., V. Lamarra, and M. Lynch. 1975. Biomanipulation: an ecosystem approach to lake restoration. Pages 85–96 in P. L. Brezonik and J. L. Fox, editors. *Water quality management through biological control*. University of Florida, Gainesville, Florida, USA.
- Shiomoto, A., K. Tadokoro, K. Nagasawa, and Y. Ishida. 1997. Trophic relations in the subarctic North Pacific ecosystem: possible feeding effect from pink salmon. *Marine Ecology Progress Series* **150**:75–85.
- Stainton, M. P. 1973. A syringe gas-stripping procedure for gas-chromatographic determination of dissolved inorganic and organic carbon in freshwater and carbonates in sediments. *Journal of the Fisheries Research Board of Canada* **30**:1441–1445.
- Strong, D. R. 1992. Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. *Ecology* **73**:747–754.
- Vadeboncoeur Y., D. M. Lodge, and S. R. Carpenter. 2001. Whole-lake fertilization effects on distribution of primary production between benthic and pelagic habitats. *Ecology* **82**:1065–1077.
- Vollenweider, R. A. 1976. Advances in defining critical loading levels for P in lake eutrophication. *Memorie dell'Istituto Italiano di Idrobiologia* **33**:53–83.
- Walters, C. J. 1986. *Adaptive management of renewable resources*. MacMillan, New York, New York, USA.
- Weiss, R. F. 1974. Carbon dioxide in water and seawater: the solubility of a non-ideal gas. *Marine Chemistry* **2**:203–215.
- White, P. A., J. Kalff, J. B. Rasmussen, and J. M. Gasol. 1991. The effect of temperature and algal biomass on bacterial production and specific growth rate in freshwater and marine habitats. *Microbial Ecology* **21**:99–118.