Journal of Plankton Research Vol.20 no.10 pp.1889–1914, 1998

Responses of epilimnetic phytoplankton to experimental nutrient enrichment in three small seepage lakes

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Abstract. This paper describes the responses of three epilimnetic phytoplankton communities to experimental nitrogen and phosphorus enrichment as compared to the phytoplankton community in a fourth, unmanipulated, lake. Increased nutrient inputs increased total phytoplankton biomass, primary productivity, chlorophytes, cryptomonads and species turnover rates in all three enriched lakes; cyanobacteria increased in two of the three enriched lakes. However, nutrient addition also led to declines in previously dominant dinoflagellates and chrysophytes, and in species diversity. At the species level, there were large changes in community composition from year to year in both enriched and reference lakes, suggesting that phytoplankton community composition is highly dynamic even in the absence of enrichment. Overall, changes in total biomass, productivity and species diversity were consistent among the enriched lakes, while changes in species composition differed due to variation in the physical, chemical and biotic environment of each lake. This suggests that aggregated variates are more useful for quantitative prediction of nutrient effects, while species responses can be used to signal qualitative differences in environmental conditions among lakes.

Introduction

Eutrophication of lake ecosystems is of great concern, in part because humans rely heavily on clean water for fish, drinking, irrigation and industry. Research on eutrophication is extensive and ranges from comparative studies (Vollenweider, 1976) to deliberate whole-lake experiments to assess the impacts on lake physics, chemistry and biology (Schindler, 1977; Stockner, 1981; Holmgren, 1984; Johannessen *et al.*, 1984; Perrin *et al.*, 1984; Welch *et al.*, 1989).

Phytoplankton are the focal point for biological studies of eutrophication for several reasons. First, growth of primary producers is tied directly to nutrients, making phytoplankton the most likely group of organisms to respond to increased nutrient availability. Second, phytoplankton community composition can have strong influences on water quality. For example, toxin-producing cyanobacteria can make water unsafe for drinking (Repavich *et al.*, 1990). Furthermore, the transfer of primary production to higher trophic levels depends on the effective utilization of the phytoplankton community as a food source. When zooplankton cannot effectively graze phytoplankton, the energy and nutrients contained within phytoplankton are lost from the pelagic food web. A predictive understanding of the effects of increased nutrients on phytoplankton biomass, productivity and community composition is therefore important.

In this paper, we describe the responses of epilimnetic phytoplankton communities to identical and simultaneous nutrient additions in three experimental lakes. We describe changes in total biomass, primary productivity, major

taxonomic groups (divisions), species diversity, species turnover rates and dominant species, and compare these patterns to those observed in an unmanipulated reference lake during the same period. We also evaluate the extent to which changes in different phytoplankton variates vary among lakes subjected to the same nutrient treatment.

Method

Study lakes and experimental manipulations

This paper focuses on epilimnetic phytoplankton communities in one reference (Paul) and three experimental (Peter, West Long and East Long) lake basins. All four basins are small (<4 ha), deep (maximum depths of 9–19 m), steep-sided, meromictic seepage lakes located within 5 km of one another at the University of Notre Dame Environmental Research Center near Land O'Lakes, WI, USA. The lakes are located within infertile glacial outwash soils and are surrounded by extensive *Sphagnum* mats; as a result, all four lakes have high dissolved organic carbon concentrations and relatively low pH (Carpenter and Kitchell, 1993). Paul and Peter lakes were divided by an earthen dike in 1951; since then, Peter has been the focus of both liming and food web manipulations, while Paul has been the unmanipulated reference basin (Carpenter and Kitchell, 1993). Long Lake was first manipulated in May 1991, when it was divided into three separate basins (East, West and Central) by plastic curtains (Christensen *et al.*, 1996). For simplicity, we refer to the separated lake basins of the formerly contiguous Paul–Peter and Long lakes as 'lakes', rather than 'lake basins', throughout this paper.

Each lake was monitored from mid-May to mid-September in each year. During 1991 and 1992, lakes were monitored under baseline nutrient conditions (phosphorus loading rates of ~0.1–0.2 μg l^{-1} epilimnion day^{-1}). From late May through early September 1993 and 1994, nitrogen (N) and phosphorus (P) (as phosphate) were added daily to Peter, West Long and East Long lakes at a 25:1 ratio by atoms (Carpenter *et al.*, 1996). Nitrogen was added as both ammonia and nitrate at a ratio of ~2.5:1 by weight. All nutrient additions occurred from a central floating station within each lake; experiments with dye tracers confirmed that all nutrients added in the center of the lake would be mixed throughout the epilimnion within 24 h (Schindler, 1995). In each year, approximately two-thirds of the nutrients were added in the first half of the summer, which may mimic spring run-off events (Carpenter *et al.*, 1996). The average daily P loading rates in 1993 were 1.2 μg l^{-1} epilimnion day^{-1} in Peter Lake, 1.4 μg l^{-1} day^{-1} in West Long Lake and 1.3 μg l^{-1} day^{-1} in East Long Lake. In 1994, P loading rates were slightly lower, averaging 0.7 μg l^{-1} day^{-1} in Peter Lake and 0.9 μg l^{-1} day^{-1} in West and East Long lakes (Carpenter *et al.*, 1996, unpublished data).

Paul Lake was maintained as an unmanipulated reference system throughout 1991–94. The fish community was dominated by adult largemouth bass (*Micropterus salmoides*), while the zooplankton were dominated by zooplanktivorous larvae of *Chaoborus* spp. and a mixed herbivore assemblage of large cladocerans (especially *Daphnia* spp. and *Holopedium gibberum* Zaddach) and

moderately sized copepods (especially *Cyclops varicans rubellus*, *Orthocyclops modestus* Herrick and *Skistodiaptomus* sp.). In 1993, there was a brief natural perturbation in the form of a large cohort of young-of-year largemouth bass (Post *et al.*, 1997). Planktivory by these fish eliminated the large cladocerans in late July, and small cladocerans (especially *Bosmina longirostris* Muller) dominated the zooplankton in August and September. Large cladoceran grazers recovered by May 1994.

Peter Lake had high zooplanktivory for most of this study (Schindler *et al.*, 1997; Carpenter *et al.*, 1996). Stocked golden shiners (*Notemigonus crysoleucas*) dominated the fish community from 1991 through mid-summer 1994, when fish abundance declined precipitously (Carpenter *et al.*, 1996; Schindler *et al.*, 1997). The zooplankton community was dominated by rotifers and cyclopoid copepods (mostly *C.varicans rubellus*) until the planktivory decline, when *Daphnia* spp. increased greatly.

Communities in West and East Long lakes were set up to mimic those in Paul and Peter, respectively. In West Long Lake, largemouth and smallmouth bass (*M.salmoides* and *Micropterus dolomieu*) dominated the fish community, while large cladocerans (especially *Daphnia pulex* Leydig and *Daphnia rosea* Sars) dominated the zooplankton. Like Peter Lake, East Long Lake was stocked with zooplanktivorous golden shiners (*N.crysoleucas*) in May 1991, creating a zooplankton community dominated by rotifers in 1991 and early 1992. However, the stocked fish did not survive (presumably due to pH: Christensen *et al.*, 1996). Beginning in mid-1992, the zooplankton community was dominated by large *Daphnia*.

Limnological analyses

During summer stratification (approximately mid-May to mid-September), we sampled each lake weekly at a central station (Carpenter and Kitchell, 1993; Voichick and LeBouton, 1994). We recorded temperature, oxygen and light profiles; sampled for zooplankton by taking two vertical hauls of the entire water column with a calibrated 80-μm-mesh net; and took van Dorn samples at 25, 50 and 100% of surface irradiance for analysis of epilimnetic nutrient concentrations, primary productivity and phytoplankton community composition.

Zooplankton samples were chilled, preserved with cold sugared formalin, and enumerated and measured by species. Dry masses were calculated from lengths using taxon-specific regressions (Downing and Rigler, 1984). Soluble (orthophosphate, ammonia and nitrate/nitrate) and total (phosphorus, nitrogen) nutrient concentrations were determined with a Lachat autoanalyzer (Voichick and LeBouton, 1994) for each of the van Dorn samples, then averaged. Total phosphorus was determined after persulfate digestion, and total Kjeldahl nitrogen was determined after mercuric sulfate digestion.

Primary productivity (PPR) was measured monthly in 1991–92 and biweekly in 1993–94 using *in situ* measurements of ^{14}C fixation (Vollenweider, 1974) for each van Dorn sample. Two 125 ml light bottles and a dichlorophenol dimethylurea (DCMU) control bottle were incubated with 185 kBq of $NaH^{14}CO_3$ at each

depth from approximately 09:30 to 15:30 h. After incubation, phytoplankton were collected on glass-fiber filters, rinsed with 1 N HCl and dried overnight before liquid scintillation counting (Voichick and LeBouton, 1994).

Samples for phytoplankton identification were pooled from the three van Dorn samples, preserved in glutaraldehyde, filtered onto mixer ester nitrocellulose filters (0.45 μm), and mounted in methacrylic resin (St. Amand, 1990). Three slides were prepared and enumerated to species for each sample, with the volume filtered for each slide scaled to cell density; volumes ranged from 5 to 30 ml per slide. Each slide was then examined using an Olympus BHT compound microscope equipped with Nomarski optics (×100, ×200, ×400 and ×1000), phase optics (×400) and epifluorescence. Because phytoplankton in these lakes can vary in size by several orders of magnitude, counts were peformed at multiple magnifications for all samples. Two different protocols were used, depending on the size and type of the dominant taxa. Protocol A was used when samples were dominated by soft phytoplankton >10–20 μm greatest axial linear dimension (GALD), and protocol B was used when samples were dominated by soft phytoplankton that were fragile, difficult to identify, or <10–20 μm in size. In both cases, we counted based on 'natural units', or the form in which each taxon appears. Specifically, when a taxon is a filament with multiple cells, the natural unit is the filament; when a taxon appears as a spherical colony, the natural unit is the colony and we measured cells per colony; and when a taxon appears as a single cell, the natural unit is a cell. In protocol A, a minimum of 300 natural units and 15 fields were counted at ×200 (maximum of 100 fields), then fragile, difficult to identify, and taxa <10 μm GALD were counted at ×400 (minimum of 100 natural units and 10 fields). In protocol B, a minimum of 400 natural units and 15 fields were counted at ×400 (maximum of 100 fields), then taxa above 20–30 μm GALD were counted at ×200 (minimum of 15 fields). In both protocols, the number of fields counted at ×200 and ×400 was distributed evenly among the three slides made for each sample, except for very large taxa (>200 μm), which were counted at ×100 on one entire slide only. In all cases, a minimum of 400 natural units per sample were identified. Counting for each sample was completed when the standard error of the mean of the total number of natural units per field was <10%.

During identification and enumeration, the GALD, width and depth were determined for up to 30 individuals of each taxon. We then estimated average individual biovolume (the protoplasm exclusive of loricae and sheaths) for each taxon using these measurements and standard geometric formulae (St. Amand, 1990). Biovolume (μm^3 ml^{-1}) was converted to fresh biomass (mg l^{-1}) assuming 1 $\mu m^3 = 1 \times 10^{-6}$ μg (Elser and Carpenter, 1988).

Evaluation of community responses

Phytoplankton community structure was evaluated at both weekly and seasonal time scales. Total biomass, species diversity and the distribution of biomass among taxonomic groups were examined weekly. Total phytoplankton biomass was determined by summing the biomass of all taxa present in each lake on each

sampling date. Species diversity was calculated using Shannon–Wiener's index (Pielou, 1977). To assess shifts among different kinds of taxa, we aggregated all species into one of six major taxonomic groups (cyanobacteria, chlorophytes, cryptomonads, dinoflagellates, chrysophytes and others). In this study, 'others' includes diatoms and euglenoids (both of which were rare in all four lakes) as well as cysts and unidentified taxa. We refer to these taxonomic groups as 'divisions' throughout this paper, as most of the groups correspond to strict taxonomic divisions or phyla. The exception is the chrysophytes, for which the taxonomic placement (class versus division) is still under debate.

Because the species richness was high (up to 180 species per year in each lake), species information was examined at a seasonal scale using species turnover rates (number of species 'exchanged' per year), community similarity (percent overlap) and species ranks. Species turnover from year to year was assessed with the index used by Magnuson *et al.* (1994):

$$T_{jk} = \frac{N_{\text{gained}} + N_{\text{lost}}}{N_j + N_k} \tag{1}$$

In equation (1), T_{jk} is the turnover rate from year j to year k, N_{gained} is the number of species present in year k but not in year j, N_{lost} is the number of species present in year j but not in year k, N_j is the total number of species in year j and N_k is the total number of species in year k. Year-to-year similarity in each lake was assessed using the seasonally averaged relative biomass from each year and the Bray–Curtis similarity coefficient (Bray and Curtis, 1957). Seasonally averaged relative biomass (b_{ik}) was calculated for each species i in year k as:

$$b_{ik} = \left(\frac{1}{m}\right) \sum_{j=1}^{m} \left(\frac{B_{i,j}}{\sum_{i=1}^{p} B_{i,j}} \right) \tag{2}$$

where m is the number of samples in year k, $B_{i,j}$ is the biomass of species i in sample j and p is the number of species present in that year. Finally, species rankings (where one is the most dominant species) were determined separately for seasonal averages of total and relative biomass (including zeros when a species was absent), then averaged as described by Elser and Carpenter (1988). In this paper, all species with an average ranking ≤10 were considered community dominants; the top five species in each year, including ties, are included in Table I.

Results

Paul Lake

In unmanipulated Paul Lake, total phytoplankton biomass fluctuated slightly from 1991 to 1994, but showed no sustained trend (Figure 1A). On average, total biomass was somewhat higher in 1992 and 1994 than in 1991 and 1993 (Figure

Table I. Top five species in each lake in each year as determined from the average rank based on abundance and biomass

Lake	Rel. rank	1991	1992	1993	1994
Paul Lake	1	*Synura uvella/sphagnicola*	*Tetracystis pulchra*	*Ochromonas* spp.	*Tetracystis pulchra*; *Stichogloea olivacea*
	2	*Tetracystis pulchra*	*Synura uvella/sphagnicola*	*Stichogloea olivacea*; unknown chlorophyte microflagellate	*Volvox* spp.; *Cryptomonas caudata*
	3	*Merismopedia tenuissima*	*Mallomonas* sp. 3	*Merismopedia tenuissima*	*Oocystis parva*; unknown chlorophyte microflagellate
	4	*Dinobryon divergens*	*Cryptomonas caudata*	*Peridinium umbonatum*	*Sphaerocystis schroeteri*
	5	*Stichogloea olivacea* *Cryptomonas* sp. 2	unknown chlorophyte microflagellate	*Synura uvella/sphagnicola*	*Cryptomonas erosa*
Peter Lake	1	*Peridinium umbonatum*	*Peridinium umbonatum*	*Oscillatoria limnetica*	*Monoraphidium capricornutum*
	2	unknown chlorophyte microflagellate	*Chrysosphaerella longispina*	*Dictyosphaerium pulchellum*	*Oscillatoria limnetica*
	3	*Uroglena* spp.	*Kephyrion* sp. 3	*Cryptomonas ovata*	*Staurastrum tryssos*
	4	*Peridinium wisconsinense*	*Dinobryon sertularia*	*Peridinium umbonatum*	*Staurastrum iotanum*; *Cryptomonas erosa*; *Cryptomonas ovata*
	5	unknown chrysophyte microflagellate	*Dinobryon divergens*	*Erkenia subaequiciliata*	*Sphaerocystis schroeteri*
West Long Lake	1	*Cryptomonas* sp. 2	*Gymnodinium* sp. 1	*Anabaena flos-aquae*	*Anabaena flos-aquae*; *Anabaena macrospora*
	2	*Synura uvella/sphagnicola*	*Cryptomonas* sp. 2	*Anabaena macrospora*	*Cystomonas starii*
	3	*Uroglena* spp.	*Mallomonas* sp. 3	*Cryptomonas ovata*	*Cryptomonas caudata* *Cryptomonas erosa*
	4	*Gymnodinium* spp.	*Cryptomonas ovata*	*Gymnodinium* sp. 1	*Cryptomonas ovata*
	5	*Cryptomonas ovata*	*Merismopedia tenuissima*	unknown chlorococcales	*Arthrodesmus subulatus*
East Long Lake	1	*Peridinium umbonatum*; *Peridinium wisconsinense*	*Gymnodinium* spp.	*Cryptomonas ovata*	*Cystomonas starii*
	2	*Chrysosphaerella longispina*	*Peridinium umbonatum*	*Gymnodinium* sp. 1	*Schizochlamys compacta*; *Cryptomonas ovata*
	3	*Dinobryon sertularia*	*Peridinium wisconsinense*	*Synura uvella/sphagnicola*	*Cryptomonas erosa*
	4	*Gymnodinium* spp.; *Ankistrodesmus falcatus* v. *mirabilis*	*Mallomonas* sp. 3	*Uroglena* spp.	*Chroomonas* spp.
	5	*Cryptomonas* sp. 2	*Cryptomonas ovata*	*Cryptomonas erosa*	*Monomastix astigmata*

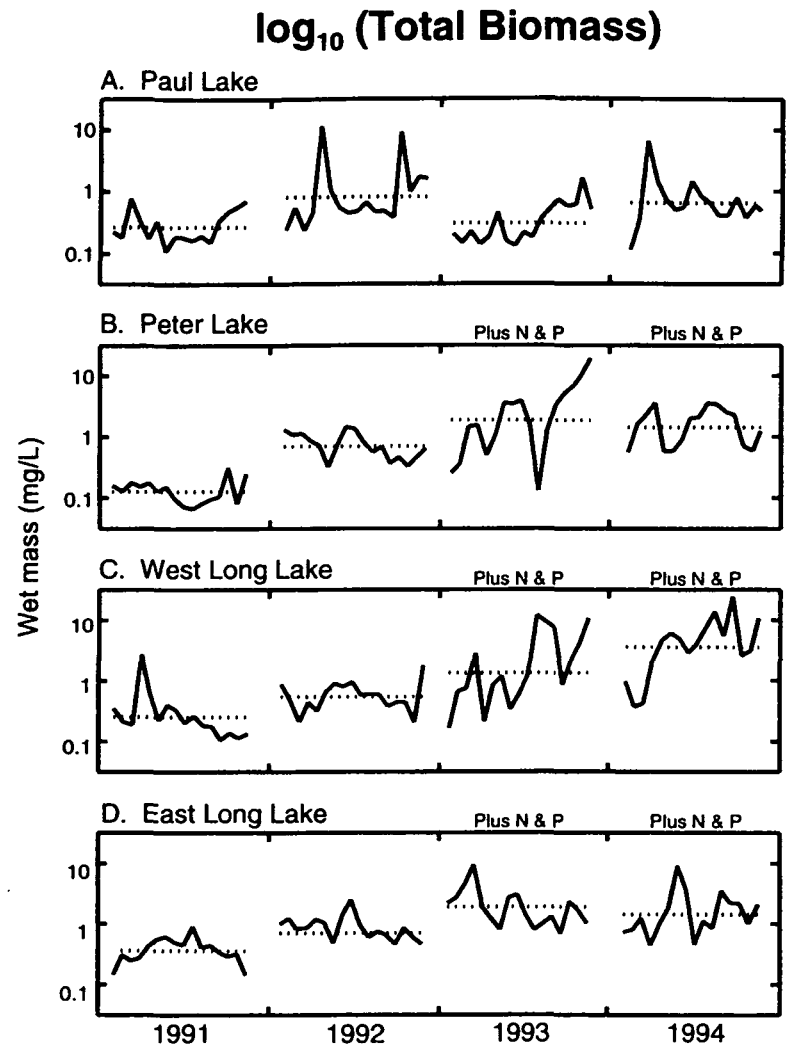

Fig. 1. Total phytoplankton biomass (wet mass, mg l^{-1}, on a $\log_{10}$ scale) in each lake from 1991 to 1994. Dotted lines indicate the mean of all observations taken during that year in that lake.

1A). Primary productivity averaged 2–6 mg carbon (C) fixed m^{-3} h^{-1} with little intra- or inter-annual variability (Figure 2A).

In 1991, Paul Lake was dominated by spring and fall blooms of chrysophytes (especially *Synura uvella/sphagnicola* Ehrenberg) with midsummer blooms of chlorophytes (mainly *Tetracystis pulchra* Brown et Bold) and cryptomonads (Figure 3A). Dinoflagellates and cyanobacteria were at low levels throughout the summer and never contributed >20% to the total biomass.

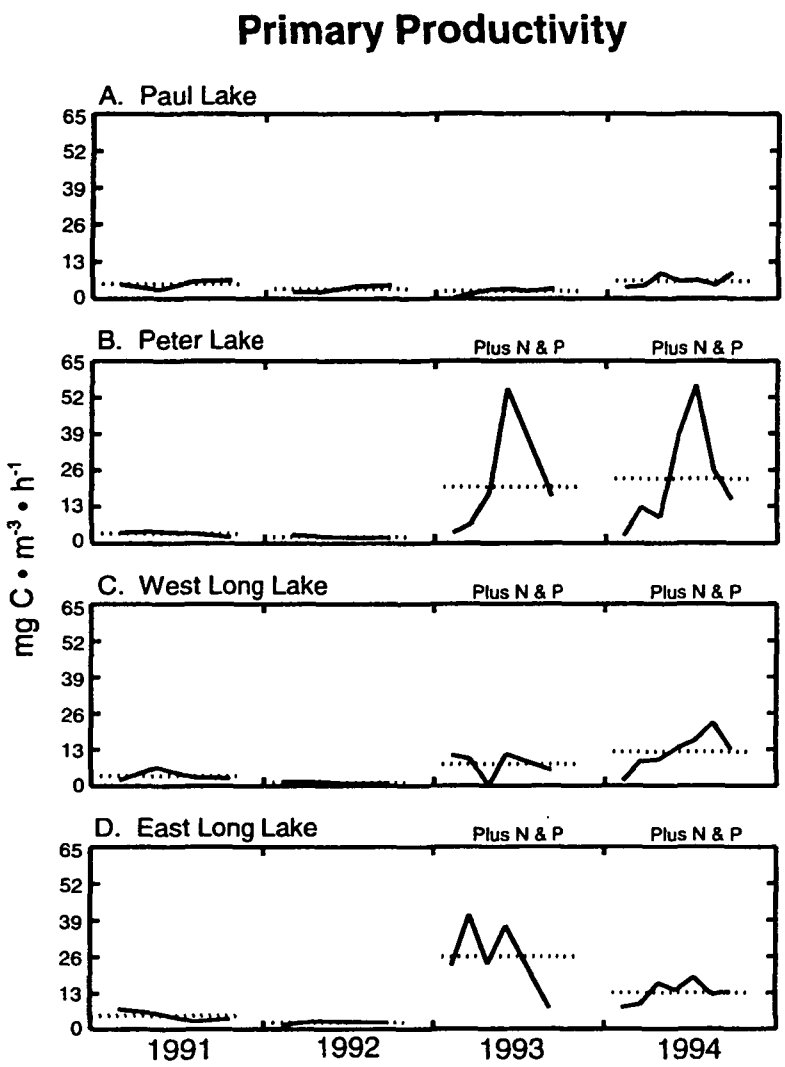

Fig. 2. Primary productivity (mg C m^{-3} h^{-1}) in each lake from 1991 to 1994. Dotted lines indicate the mean of all observations taken during that year in that lake.

Similar patterns were observed in 1992, except that the fall bloom was composed of both chrysophytes and chlorophytes, not just chrysophytes. Dominant taxa again included *T.pulchra* and *S.uvella/sphagnicola*, as well as *Mallomonas* sp. 3. [The numbering of species is used to indicate unique taxa that were seen repeatedly but could not be positively classified to a particular species; species were numbered chronologically as encountered by A.S.A.] Cryptomonads (especially *C.caudata* Schiller and *C.ovata* Ehrenberg) and cyanobacteria

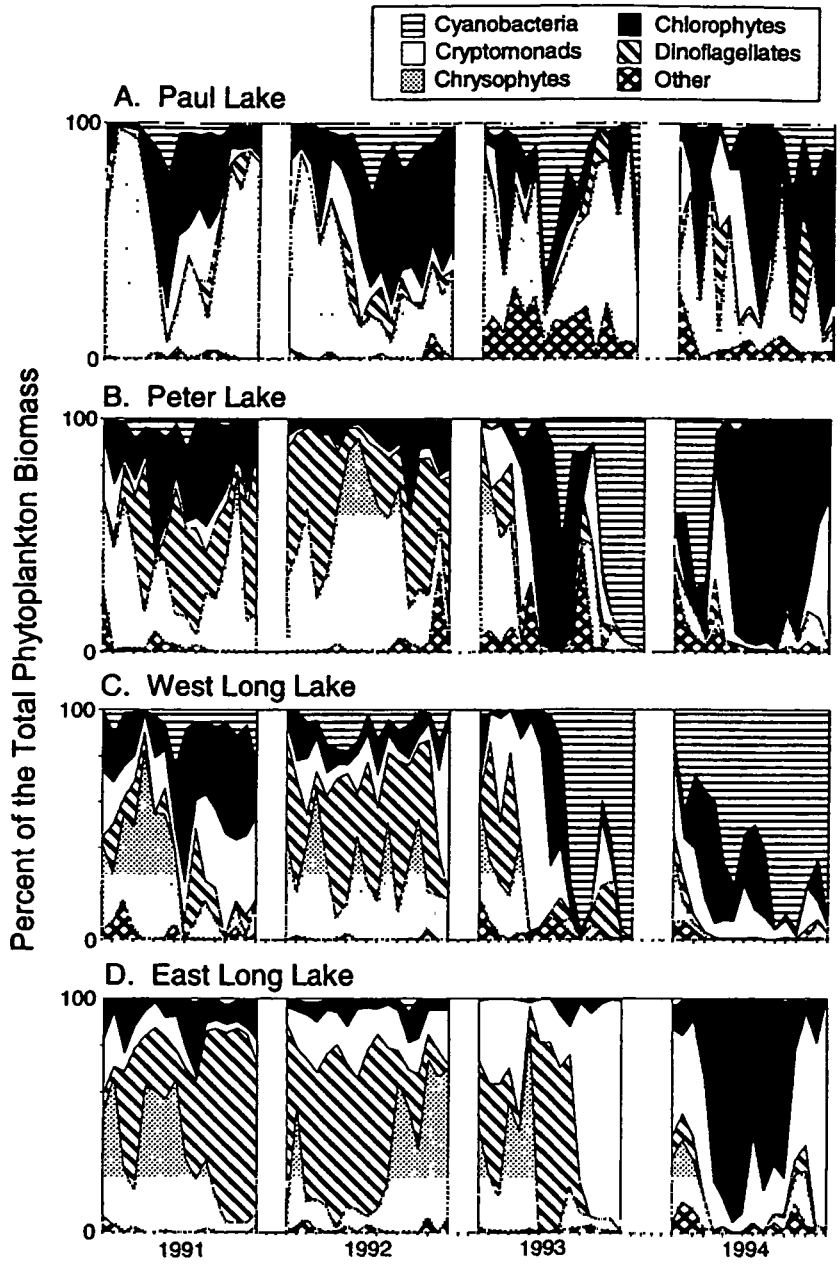

Fig. 3. Community composition (as a percent of total biomass) for phytoplankton divisions (cyanobacteria, chlorophytes, cryptomonads, dinoflagellates, chrysophytes, others) present in these lakes from 1991 to 1994.

were somewhat more abundant than in 1991, but were still <30% of the total biomass at all times.

Phytoplankton community composition shifted in 1993 and 1994 (Figure 3A) following a fish recruitment event which temporarily reduced the abundance of large zooplankton in late summer 1993 (Post *et al.*, 1997). Chrysophytes dominated through the summer (*S.uvella/sphagnicola* and *Ochromonas* spp. Wyssotzki). Midsummer increases in chrysophytes (mainly *Ochromonas*) and cyanobacteria (mainly *Oscillatoria limnetica* Lemmermann) were much larger in 1993 than in 1991 or 1992 (Figure 3A). Chrysophyte biomass was unusually high in May 1994 due to a bloom of *Stichogloea olivacea* Chodat. During this chrysophyte bloom, there was a 1 week bloom of the green alga *Volvox* spp. Linneaus.

In contrast to previous years, 1994 was characterized by high week-to-week variability (Figure 3A) and continuing shifts in dominance among chrysophytes, cryptomonads, dinoflagellates and chlorophytes. Even after the collapse of the *Volvox* bloom, chlorophytes continued to be a dominant feature in the phytoplankton community (Table I). Key taxa included *Botryococcus braunii* Kutzing, *Oocystis parva* West and West, *Sphaerocystis schroeteri* Chodat, *T.pulchra* and unidentified microflagellates. Previously, only *T.pulchra* and the microflagellates had been among the dominant species.

Overall, there were few sustained trends in community composition at the division level in Paul Lake during the study period (Figure 3A). All divisions were present in all years, and no one division dominated to the exclusion of the others. Chrysophytes and chlorophytes tended to be the key components of the community, while cyanobacteria, cryptomonads and dinoflagellates were at relatively low levels throughout 1991–1994. The only major trend was in variability: relative community composition appeared to be more seasonally dynamic in 1993 and 1994 (Figure 3A).

At the species level, there were clear shifts in community composition from year to year even in this unmanipulated system. Different species dominated in different years, and few of the identified taxa were consistently dominant (Table I). Community similarity in successive years tended to be quite low (20–43%; Figure 4A), which is consistent with annual turnover rates of 25–45% of the species changing from one year to the next (Figure 4B). Despite the high rates of community change, species diversity remained relatively constant over time (Figure 5A).

Peter Lake

There were definite shifts in the Peter Lake phytoplankton community from 1991 to 1994, especially following the onset of experimental enrichment in late May 1993 (panel B in Figures 1–5). Total phytoplankton biomass increased by a factor of five from 1991 to 1992 and again from 1992 to 1993 (Figure 1B), peaking at 20 mg l^{-1} in early September 1993. In 1994, biomass was higher than in 1991–92, but considerably lower than in 1993 (Figure 1B), probably due to a combination of slightly reduced nutrient loading and increased grazing by zooplankton

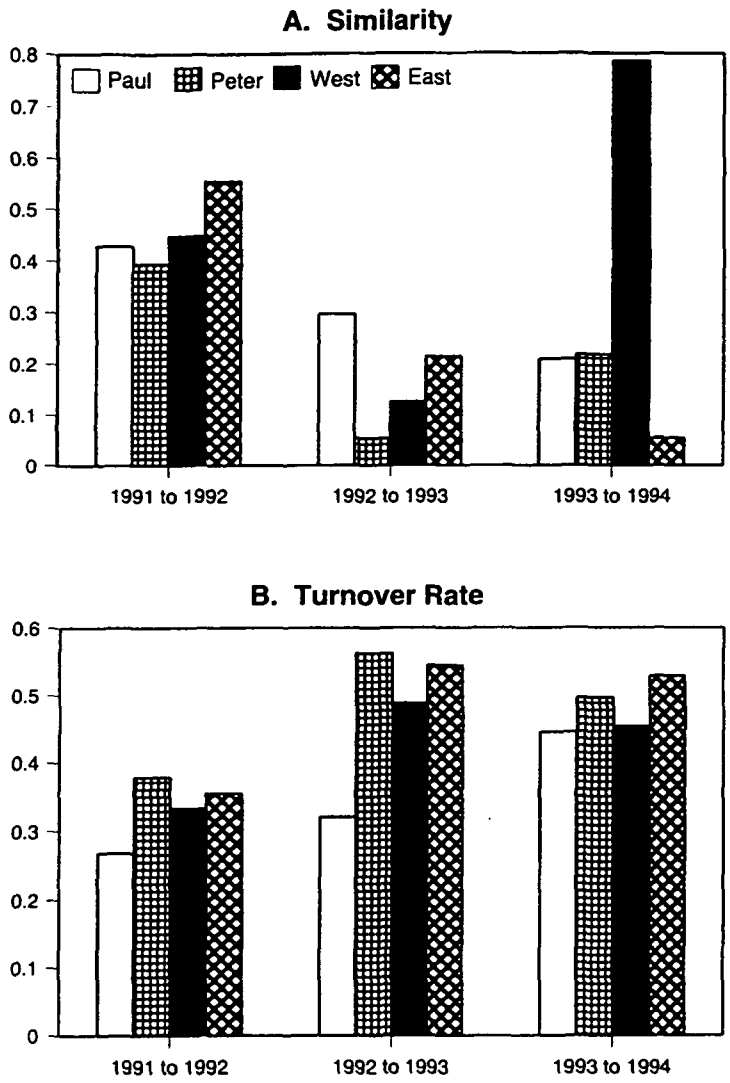

Fig. 4. Community similarity (%) and turnover (no. of species per year) in each of the four lakes. (**A**) Similarity between years for the phytoplankton of each lake, based on the Bray–Curtis similarity coefficient and seasonal mean biomass of each species. (**B**) Phytoplankton species turnover from one year to the next within each lake.

(Cottingham, 1996). Like total biomass, primary productivity increased 10-fold in 1993; however, unlike biomass, these increases persisted in 1994 (Figure 2B).

In 1991, the phytoplankton community was dominated by chrysophytes (*Dinobryon bavaricum* Imhof and *Uroglena* spp. Ehrenberg), dinoflagellates (*Peridinium umbonatum* and *P.wisconsinense* Eddy) and chlorophytes (unidentified microflagellates) (Figure 3B). In the fall, chrysophytes and dinoflagellates

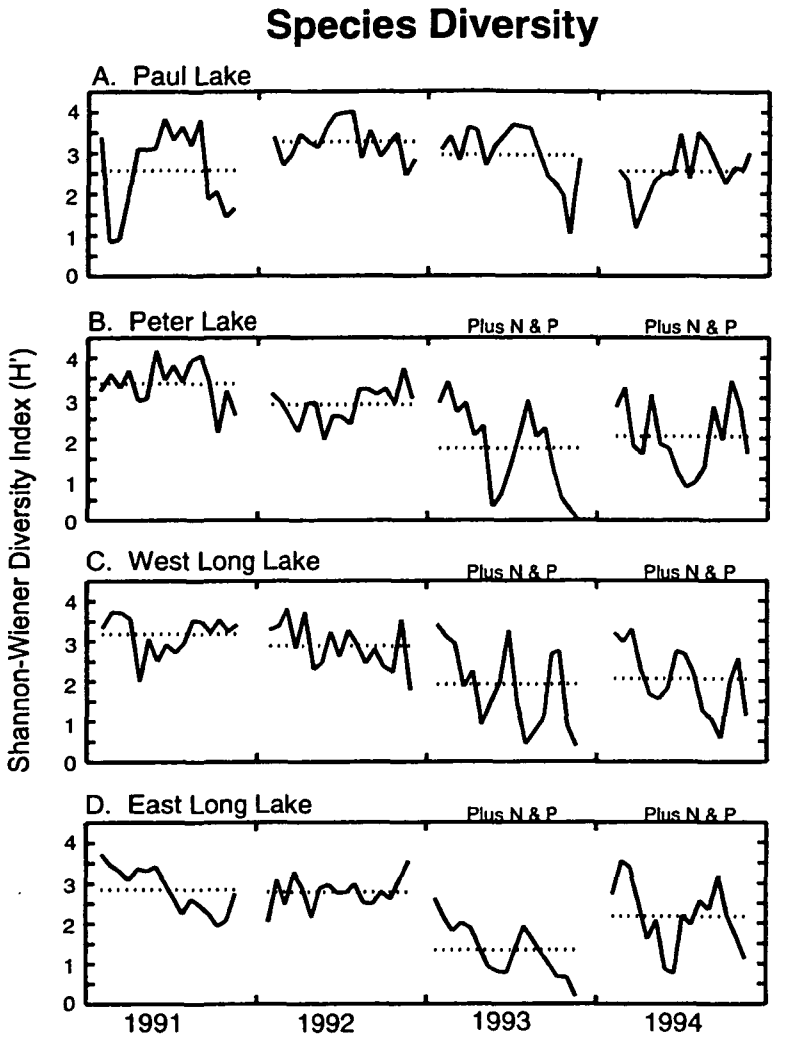

Fig. 5. Phytoplankton species diversity (Shannon–Wiener's *H'*) in each lake from 1991 to 1994. Dotted lines indicate the mean of all observations taken during that year in that lake.

continued to dominate. Cyanobacteria and cryptomonads were at extremely low levels through the summer, rarely contributing >5% of the total biomass.

In 1992, the community shifted somewhat as the relative biomass of dinoflagellates (*P.umbonatum*) and chrysophytes (*Chrysosphaerella longispina* Lauterborn, *Kephyrion* sp. 6 and *Dinobryon sertularia* Ehrenberg) increased, while cryptomonads, cyanobacteria and chlorophytes remained at levels at or below those of 1991 (Figure 3B). The relative biomasses of both dinoflagellates and chrysophytes reached their 1991–94 maxima during 1992.

Responses to enrichment were evident quite early in 1993 (Figure 3B). As in

1992, dinoflagellates (mostly *P.umbonatum*) and chrysophytes (mostly *Erkenia subaequiciliata* Skuja) increased in late May and early June; however, in 1993, cryptomonads (especially *Rhodomonas minuta* Skuja) also increased during this period. Additional blooms followed: chlorophytes (*Dictyosphaerium pulchellum* Wood and an unidentified chlorococcalean alga), then cyanobacteria (*Oscillatoria limnetica* and *Anabaena macrospora* Klebahn), then a synchronous outbreak of dinoflagellates, cryptomonads and chrysophytes. From mid-August through mid-September, the phytoplankton community was dominated by a near monoculture of *O.limnetica*. The first year of enrichment therefore produced a major increase in cyanobacteria, together with modest increases in cryptomonads and chlorophytes, at the expense of chrysophytes and dinoflagellates.

Responses to the second year of enrichment (1994) were somewhat different (Figure 3B). As in 1993, dinoflagellates, cryptomonads and chrysophytes were most abundant in late spring and early fall. However, absolute biomasses of both dinoflagellates and chrysophytes were more comparable to 1991 than to 1993, and relative biomasses declined dramatically compared to the pre-enrichment period. Only cryptomonads (mainly *Cryptomonas erosa* Ehrenberg and *C.ovata*) continued to show a positive response to enrichment. *Oscillatoria limnetica* and several chlorophytes [especially *Monoraphidium capricornum* (Printz) Nygaard] were abundant earlier in the season than in 1993, occurring nearly simultaneously with the spring cryptomonad bloom. *Oscillatoria limnetica*, which was ~60% of the total biomass in late May, collapsed in mid-June and remained at or below pre-enrichment levels throughout the rest of 1994. Unicellular chlorophytes (especially *M.capricornum*, *Staurastrum iotanum* Wolle, *Staurastrum tryssos* Scott & Groenblad) were the most abundant group through the rest of the summer, representing nearly 100% of the total phytoplankton biomass in July and early August. Thus, the second year of enrichment produced increases in chlorophytes, cryptomonads and cyanobacteria, but not chrysophytes or dinoflagellates (Figure 3B).

There were clear shifts in community composition from year to year at the species level in Peter Lake. Average species diversity declined slightly from 1991 to 1992, then decreased by nearly 50% in 1993 and 1994 (Figure 5B). Diversity was lowest during bloom events, with minima reaching 0.1–0.5 during 1993 and 1994. Species shifts accompanied the reductions in diversity: for example, in 1991 and 1992, most dominant species were either chrysophytes or dinoflagellates, while in 1993 and 1994, most dominant species were either cyanobacteria or chlorophytes (Table I). Community similarity in successive years was generally lower than in Paul Lake, with a 56% turnover rate contributing to a 5% similarity index for 1992 versus 1993 (Figure 4B).

In summary, Peter Lake showed striking responses to enrichment in both 1993 and 1994, with substantial differences between years. Cyanobacteria (*Anabaena macrospora* and *O.limnetica*) increased from <5% to nearly 100% of the total biomass for much of August 1993 (Figure 3B). However, cyanobacterial dominance did not persist in 1994. Chlorophytes increased dramatically with enrichment in both 1993 and 1994 (Figure 3B), but with different taxa in each year (Table I). Cryptomonads also increased with enrichment, primarily during spring and fall

blooms. The relative biomass of dinoflagellates and chrysophytes, the pre-enrichment dominants, decreased with enrichment, and former dominants *Peridinium wisconsinense* and *P.umbonatum* both declined during 1993 and 1994. By 1994, not one chrysophyte or dinoflagellate taxon was listed as a community dominant.

West Long Lake

Changes in West Long Lake from 1991 to 1994 were comparable in magnitude to those in Peter Lake. Mean total biomass increased each year, but particularly after the onset of enrichment in 1993 (Figure 1C). Peak biomass was even higher than in Peter Lake, reaching 25 mg l^{-1} in late August 1994. However, increases in primary productivity in West Long Lake were much smaller than those observed in Peter Lake (Figure 2B and C). These changes were accompanied by substantial and sustained changes in community composition (Figure 3C).

In 1991, the phytoplankton community was dominated by colonial chrysophytes (*S.uvella/sphagnicola*, *Uroglena* spp.) in early summer and chlorophytes (*Sphaerocystis schroeteri*, *T.pulchra*) and cryptomonads (*Cryptomonas* spp.) during midsummer. Cyanobacteria and dinoflagellates rarely accounted for >20% of the total biomass.

Community composition shifted somewhat in 1992 as dinoflagellates replaced chlorophytes and cryptomonads as the co-dominant with chrysophytes (Figure 3C). Dinoflagellates averaged 40% of the total biomass, up from ~10% in 1991, primarily due to increases in *Gymnodinium* spp. Stein (Figure 3C). As in 1991, chrysophytes, dominated by *Mallomonas caudata* Iwanoff and *Mallomonas* sp. 3, represented 30% of the total biomass. Chrysophytes and dinoflagellates were co-dominant throughout the season, with no trends in seasonality; this was different from 1991 where the chrysophytes dominated only during the early part of the summer. Relative biomasses of cryptomonads, chlorophytes and cyanobacteria were similar to those in 1991, although cryptomonads showed a pronounced peak in early September.

Dramatic shifts in community composition were evident immediately following experimental enrichment in 1993. As in Peter Lake, chrysophytes (*Uroglena*), cryptomonads (*Cryptomonas*) and dinoflagellates (*Gymnodinium*) peaked in the spring, at times exceeding previous maxima. The responses of chrysophytes and dinoflagellates were relatively short lived: both returned with fall blooms in 1993, but were at or below 1991 levels throughout 1994. Cryptomonads fared better, sustaining spring and fall blooms in 1993, and maintaining a consistent presence throughout summer 1994. Chlorophytes increased only somewhat following the collapse of these spring blooms.

The primary responders to enrichment in West Long Lake were two heterocystous (nitrogen-fixing) species of cyanobacteria of the genus *Anabaena* [*A.macrospora* and *A.flos-aquae* (Lyngbye) de Brebisson], which took over the phytoplankton community in mid-July and continued to dominate through the rest of the summer. Although neither had previously been documented in the lake, their combined biomass quickly reached 15 mg l^{-1}, >10 times the pre-enrichment total biomass.

Responses to enrichment were quite similar in 1994 (Figure 3C). The dominant phytoplankton genus continued to be *Anabaena*, which had nearly 10 times the biomass of the next most abundant taxon (Table I). Although chlorophytes [primarily *Cystomonas starii* (Trainor et Verses) Ettl et Gartner, but also *Arthrodesmus subulatus* Kutzing, *Scenedesmus denticulatus* Lagerheim and *Dictyosphaerium pulchellum*] increased during the latter part of June, *Anabaena* again represented >60% of total biomass by late July. Total biomass of cyanobacteria was even higher than in 1993 (Figure 3C), despite the decrease in nutrient loading rate.

Chrysophytes and dinoflagellates were strongly affected by enrichment and subsequent dominance of *Anabaena*. Dinoflagellates declined from dominance in 1992 to a very minor part of the community by 1994 (Figure 3C). Individual taxa also declined, including previous dominants *Gymnodinium* sp. 1 Stein and *Gymnodinium* spp. Similarly, chrysophyte contributions to total biomass fell to <10% in June 1993 and never recovered (Figure 3C). As in Peter Lake, few chrysophyte taxa were dominant during enrichment (Table I).

Changes in community composition were also prevalent at the species level. Diversity decreased from 1991 to 1993 before recovering slightly in 1994 (Figure 5C). Extremely low diversities (<0.5) were recorded during the *Anabaena* blooms in 1993 and 1994. Inter-year similarity declined in the first year of enrichment, but then increased to the highest recorded level, 79%, between 1993 and 1994 due to the continuing dominance of *Anabaena* (Figure 4A). In contrast, species turnover remained at rates comparable to those in Paul and Peter lakes due to ongoing changes in rare species (Figure 4B).

Summarizing community responses in West Long Lake, the relative biomass of cyanobacteria increased from <10% to nearly 100% for much of August in both 1993 and 1994 (Figure 3C). Chlorophytes increased somewhat with enrichment, although most of these increases occurred in 1994. Cryptomonads increased in 1993, but their contribution to total biomass changed little beyond the first month of enrichment due to the overwhelming dominance of cyanobacteria. As in Peter Lake, chrysophytes and dinoflagellates increased with enrichment only in the short term; by 1994, the relative abundance of both divisions had declined greatly.

East Long Lake

Responses to nutrient enrichment in East Long Lake were distinct from those observed in West Long and Peter lakes. Total biomass in East Long Lake followed the same pattern as in Peter Lake (increase from 1991 to 1993, followed by small declines in 1994), but peak biomasses were less than half those in West Long and Peter lakes (Figure 1). Primary productivity in East Long Lake was comparable to that of Peter Lake in 1993 and West Long Lake in 1994 (Figure 2). However, unlike West Long and Peter lakes, maximum biomass and primary productivity in East Long Lake occurred in early to mid-summer, rather than in September (Figures 1 and 2). These differences are coincident with one major difference in community composition: cyanobacteria did not increase in response to enrichment.

Table II. Summary statistics for selected environmental variables for each lake during each year of the experiment. The first line for each lake–year shows the mean ± 1 SE, and the second line indicates the range (minimum–maximum)

Lake	Year	Total P ($mg\ l^{-1}$) (n = 16–17)	Total N ($mg\ l^{-1}$) (n = 15–17)	N:P (n = 15–17)	Orthophosphate ($mg\ l^{-1}$) (n = 7–17)	Ammonia ($mg\ l^{-1}$) (n = 7–16)	Nitrite and nitrate ($mg\ l^{-1}$) (n = 7–16)	Epilimnetic pH (n = 3–4)	Thermocline depth (m) (n = 16–17)	Depth of 1% light (m) (n = 16–17)
Paul	1991	11.1 ± 0.6	422.5 ± 11.8	39.9 ± 2.3	3.8 ± 0.7	16.0 ± 1.5	4.3 ± 1.0	6.18 ± 0.04	3.1 ± 0.2	5.6 ± 0.1
		7.0–17.7	370.3–523.0	23.1–61.6	0.3–9.0	7.1–23.3	0.5–11.4	6.10–6.22	2.0–4.0	5.2–6.0
	1992	11.5 ± 1.0	373.9 ± 19.0	59.8 ± 27.7	4.5 ± 1.3	10.7 ± 1.0	4.2 ± 2.5	5.60 ± 0.09	3.9 ± 0.2	5.6 ± 0.0
		1.0–18.5	236.4–518.3	15.2–501.6	1.3–11.0	7.5–14.8	0.0–18.6	5.44–5.85	2.5–5.0	5.3–5.9
	1993	9.6 ± 0.5	272.4 ± 14.6	29.9 ± 2.8	1.0 ± 0.2	8.1 ± 2.2	2.2 ± 0.4	5.77 ± 0.10	3.6 ± 0.2	5.6 ± 0.0
		4.6–13.3	163.1–345.7	17.0–65.5	0.0–3.0	0.6–33.9	0.0–5.0	5.60–5.95	2.5–5.0	5.2–5.9
	1994	12.3 ± 0.9	425.3 ± 12.7	39.3 ± 4.3	1.5 ± 0.2	10.1 ± 1.4	2.9 ± 0.3	6.66 ± 0.09	3.6 ± 0.2	5.3 ± 0.1
		4.3–18.3	342.1–557.8	22.2–93.3	0.5–2.7	3.0–23.3	1.6–5.7	6.49–6.78	2.5–5.0	4.9–5.7
Peter	1991	10.1 ± 0.9	343.9 ± 14.2	38.0 ± 3.8	4.1 ± 0.7	12.8 ± 2.4	2.8 ± 0.6	6.58 ± 0.07	3.7 ± 0.2	7.4 ± 0.1
		5.7–18.0	282.7–467.7	19.9–77.9	1.0–8.3	4.8–33.8	0.2–7.1	6.44–6.67	2.5–5.0	6.5–8.4
	1992	9.0 ± 0.6	368.0 ± 19.7	46.1 ± 5.8	5.7 ± 0.9	12.0 ± 1.6	1.7 ± 0.6	6.16 ± 0.09	3.9 ± 0.2	6.4 ± 0.2
		2.8–13.5	235.0–544.0	26.2–111.8	1.0–8.3	7.2–19.6	0.0–5.1	6.04–6.43	3.0–5.0	3.6–7.1
	1993	25.9 ± 1.9	506.6 ± 29.3	20.3 ± 1.0	2.3 ± 0.4	15.0 ± 5.3	17.9 ± 5.2	6.56 ± 0.53	3.3 ± 0.1	5.2 ± 0.2
		15.0–48.0	346.2–770.6	14.0–27.5	0.3–6.0	0.1–75.3	1.6–73.7	5.95–8.15	2.5–4.5	4.1–6.2
	1994	18.9 ± 1.3	630.7 ± 36.3	34.2 ± 1.8	2.0 ± 0.3	41.3 ± 10.1	29.0 ± 8.1	7.22 ± 0.12	3.9 ± 0.2	5.9 ± 0.2
		11.7–28.9	354.9–833.7	26.8–55.0	0.5–5.5	3.1–112.7	0.9–98.7	7.00–7.41	2.0–5.0	4.4–6.7

Table II. Continued

Lake	Year	Total P (mg l^{-1}) (n = 16–17)	Total N (mg l^{-1}) (n = 15–17)	N:P (n = 15–17)	Orthophosphate (mg l^{-1}) (n = 7–17)	Ammonia (mg l^{-1}) (n = 7–16)	Nitrite and nitrate (mg l^{-1}) (n = 7–16)	Epilimnetic pH (n = 3–4)	Thermocline depth (m) (n = 16–17)	Depth of 1% light (m) (n = 16–17)
West	1991	11.9 ± 0.7 5.3–16.7	473.7 ± 8.3 426.7–528.7	43.0 ± 3.8 26.6 ± 86.3	4.7 ± 1.1 0.0–13.0	18.1 ± 2.6 5.3–41.3	3.2 ± 0.6 0.9–8.4	5.88 ± 0.10 5.75–6.07	2.8 ± 0.1 2.0–3.5	3.3 ± 0.1 2.9–4.0
	1992	8.5 ± 0.8 5.4–17.5	425.0 ± 15.1 279.8–524.3	53.8 ± 3.1 28.9 ± 71.6	4.9 ± 1.2 1.0–10.7	13.0 ± 2.0 4.5–20.6	1.9 ± 0.4 0.0–3.2	5.21 ± 0.10 5.05–5.50	3.9 ± 0.2 3.0–5.0	4.9 ± 0.1 4.2–5.3
	1993	24.2 ± 2.0 8.5–35.0	674.9 ± 47.7 350.8–1066.0	29.7 ± 2.1 18.9 ± 47.9	2.9 ± 0.3 0.7–6.3	129.2 ± 27.4 5.3–282.4	117.0 ± 23.3 1.5–244.0	5.12 ± 0.07 5.00–5.25	3.5 ± 0.1 2.5–4.5	4.8 ± 0.2 2.3–5.6
	1994	21.4 ± 1.5 13.2–38.3	904.3 ± 88.8 436.9–1500.0	44.3 ± 3.5 24.3 ± 63.6	2.0 ± 0.2 0.6–3.6	164.8 ± 39.1 11.2–447.5	102.3 ± 17.4 2.6–211.5	6.25 ± 0.09 6.05–6.41	3.6 ± 0.2 2.0–5.0	4.8 ± 0.1 3.7–6.0
East	1991	13.9 ± 0.7 9.7–18.3	526.2 ± 31.5 414.0–959.3	39.0 ± 2.4 25.9–54.3	4.6 ± 1.0 0.7–13.7	15.8 ± 2.0 6.4–32.3	3.3 ± 0.6 0.9–9.5	5.61 ± 0.07 5.53–5.74	2.5 ± 0.1 1.5–3.0	3.0 ± 0.1 2.5–3.8
	1992	15.5 ± 1.1 8.1–24.6	520.2 ± 25.7 325.2–690.1	36.3 ± 3.5 19.9–81.6	5.9 ± 1.1 1.0–10.0	16.0 ± 1.1 11.7–20.3	3.9 ± 0.3 2.9–4.7	4.99 ± 0.05 4.85–5.08	2.6 ± 0.1 2.0–3.5	2.6 ± 0.0 2.3–2.9
	1993	29.2 ± 1.9 19.0–46.7	716.1 ± 25.1 549.7–915.3	26.0 ± 1.8 15.7–41.2	4.2 ± 0.5 1.0–8.0	102.2 ± 23.9 3.2–255.3	68.6 ± 14.7 2.1–141.9	4.90 ± 0.15 4.65–5.17	2.3 ± 0.1 1.5–3.0	1.9 ± 0.1 1.5–2.4
	1994	23.7 ± 1.3 17.4–34.4	824.2 ± 43.4 556.2–1133.3	35.6 ± 2.0 21.5–49.1	2.8 ± 0.2 1.5–4.6	95.0 ± 18.1 12.9–253.7	137.7 ± 22.1 4.1–255.8	5.88 ± 0.10 5.73–6.16	2.5 ± 0.1 1.5–3.5	2.3 ± 0.0 1.9–2.6

In 1991 and 1992, East Long Lake was dominated by dinoflagellates (*Peridinium umbonatum* and *P.wisconsinense*) and chrysophytes (mainly *Chrysosphaerella longispina* and *Dinobryon sertularia*) (Figure 3D). In 1991, chrysophytes dominated in the early part of the summer, while dinoflagellates dominated during midsummer (Figure 3D). In 1992, this order was reversed: dinoflagellates dominated early and chrysophytes later. In both years, cryptomonads and chlorophytes were present with low biomass throughout the season, while cyanobacteria were extremely rare.

Following the onset of enrichment in 1993, chrysophytes (*S.uvella/sphagnicola*), cryptomonads (*Cryptomonas ovata*) and dinoflagellates (*Gymnodinium* sp. 1) all showed a pronounced spring peak (as in Peter and West Long lakes; Figure 3). However, in East Long Lake, these peaks represented the maximal biomass for that year (Figure 1D). Following the collapse of this spring bloom, dinoflagellates [*Gymnodinium* sp. and *Glenodinium quadridens* (Stein) Schiller] dominated for several weeks, then cryptomonads (*C.ovata*) dominated into the fall. Neither cyanobacteria nor chlorophytes increased during the first year of enrichment in this lake (Figure 3D).

Community composition was very different in 1994 (Figure 3D, Table I). Spring abundance of dinoflagellates and chrysophytes was extremely low, more like 1991 than 1993. However, two chrysophyte taxa (*Synura* spp. Ehrenberg and *Ochromonas* spp.) were still listed among the dominant species (Table I). There were more cryptomonads than in 1991, but less than 1993. After several weeks of extremely low total biomass, chlorophytes began to increase, especially *Cystomonas starii* and *Schizochlamys compacta* Prescott, which combined for >80% of total biomass for much of the summer. This was the first year that chlorophytes dominated the phytoplankton community in East Long Lake (Table I). Cryptomonads (*Chroomonas* spp. Hansgirg, *Cryptomonas ovata*, *Cryptomonas erosa*) dominated at the end of August. Thus, in 1994, cryptomonads and chlorophytes increased with enrichment, while the relative biomasses of cyanobacteria, dinoflagellates and chrysophytes declined.

There were also clear shifts in species composition during this period. Average species diversity declined with enrichment (Figure 5D), particularly during bloom events. Community similarity was higher than in Paul Lake from 1991 to 1992, but much lower than in Paul Lake during subsequent years (Figure 4A). Similarity was lowest between the years of experimental enrichment, not at the beginning of enrichment as in Peter and West Long lakes (Figure 4A). Species turnover rates were comparable to those in the other enriched lakes (Figure 4B).

To summarize responses in East Long Lake, cyanobacteria were a minor component of the phytoplankton community in 1991–92 and remained that way in 1993–94, unlike West Long and Peter lakes (Figure 3). Chlorophytes increased strongly with enrichment in 1994, primarily due to two new taxa. Cryptomonads also increased strongly with enrichment, especially during the fall. Dinoflagellates and chrysophytes increased somewhat immediately following enrichment in 1993, but declined to a very low biomass in 1994.

Discussion

Nutrient enrichment had large and rapid effects on the epilimnetic phytoplankton communities of Peter, West Long and East Long lakes. Total biomass and primary productivity increased, while species diversity declined. There were enormous shifts in the relative abundance of major taxonomic groups: by the end of the second year of experimental enrichment, cyanobacteria, chlorophytes and cryptomonads had increased, while chrysophytes and dinoflagellates declined. Species turnover rates increased with enrichment, although turnover rates were also high in the unenriched reference system. Most of these changes were comparable in magnitude to those occurring over a much longer time period due to cultural eutrophication (Willen, 1972).

Our study is one of very few whole-lake experiments involving synchronous and identical nutrient additions to multiple lakes in the same area. As such, we are uniquely placed to evaluate the extent to which responses to the same nutrient treatment diverge in different systems, including systems with different food webs. Our results indicate that the consistency of responses to enrichment was relatively high for aggregate properties such as total biomass and primary productivity, somewhat lower for low-level taxonomic identifications (divisions), and very low for individual species. This pattern supports the hypothesis that the effects of perturbation on biotic communities may be more easily detected for higher taxa such as families or phyla, because the relative abundance of these groups shifts only in response to significant stressors; in contrast, species respond to fine-scale differences in environmental conditions, and thus may not reliably distinguish responses to a particular stressor (Warwick, 1988a,b). For phytoplankton, aggregate properties appear to be useful for quantitative prediction of nutrient effects, while species responses can be used to detect subtle differences in environmental conditions (e.g. light, nutrients, pH, zooplankton grazing) among lakes.

Total biomass, primary productivity and species diversity

Total phytoplankton biomass, primary productivity and phytoplankton species diversity responded to nutrient enrichment in similar ways in Peter, West Long and East Long lakes. Changes in each of these variates are consistent with expectations from the literature. For example, phytoplankton biomass and productivity nearly always increase when nutrient levels increase (Thompson and Rhee, 1994), while summer phytoplankton species diversity tends to be much lower in eutrophic lakes than in oligotrophic lakes (Schindler, 1988). The consistency of responses in these and other lakes suggests that the direction of enrichment-induced changes in total biomass, productivity and species diversity is fairly predictable across lakes. Many lake management strategies (Cooke *et al.*, 1993) exploit this predictability by using quantitative regression models that relate aggregate phytoplankton properties to nutrient loading (Dillon and Rigler, 1974; Vollenweider, 1976; Schindler *et al.*, 1978).

Divisions

Phytoplankton responses to enrichment in Peter, West Long and East Long lakes were also broadly similar for the major phytoplankton groups we called divisions. Our results generally support the expectation that as a lake becomes more eutrophic, cyanobacteria and chlorophytes replace chrysophytes and dinoflagellates as the dominants of the summer phytoplankton community (Reynolds, 1984; Harper, 1992). However, there was one exception.

Cyanobacteria are expected to increase when nutrients are added to oligotrophic or mesotrophic lakes, particularly when C:N:P ratios are favorable for their development (Thompson and Rhee, 1994). Cyanobacteria increased strongly with enrichment in Peter and West Long lakes, but not in East Long Lake. In West Long and Peter lakes, increases in cyanobacteria were due to *Anabaena* and *Oscillatoria*, both of which contribute to nuisance algal blooms worldwide. *Anabaena* is heterocystous and thus capable of nitrogen fixation, while *Oscillatoria* is not; interestingly, though, N:P ratios in both Peter and West Long lakes were relatively high (>20 by weight; Table II) throughout the entire experiment, suggesting that nitrogen-fixing cyanobacteria did not have a competitive advantage in these lakes.

The lack of increase in cyanobacteria in East Long Lake was unexpected, but not uncommon: cyanobacteria have not increased with deliberate enrichment in several other whole-lake experiments (Schindler, 1975; Stockner, 1981; Johannessen *et al.*, 1984; Perrin *et al.*, 1984; Welch *et al.*, 1989), particularly when nutrients were added at high N:P ratios (Holmgren, 1984). In our experiment, there are a number of plausible reasons why responses in East and West Long lakes, in particular, were so different—after all, these two basins should have shared the same pool of propagules for recruitment. Hypothesized factors favoring cyanobacteria over other taxa include high temperature (McQueen and Lean, 1987), high pH (Shapiro, 1973; Findlay *et al.*, 1994) and low N:P ratios (Smith, 1983; McQueen and Lean, 1987). However, epilimnetic temperature was similar in all four lakes (S.R.Carpenter *et al.*, unpublished data), and the average N:P ratio was lower in East Long than in West Long (Table II), suggesting that temperature or N:P ratios are unlikely to have prevented the growth of cyanobacteria in East Long as compared to West Long Lake. However, the lower pH and higher dissolved organic carbon (DOC) of East Long as compared to West Long during 1993 and 1994 suggest that pH and DOC could have been involved in the differential phytoplankton responses in these two basins (Christensen *et al.*, 1996). In particular, the higher loading of humic acids into East Long Lake may have suppressed cyanobacteria (Prakash, 1971), perhaps by reducing light availability. Although the depth of 1% of surface irradiance usually exceeds the thermocline depth in these lakes, the thermocline depth in East Long Lake generally exceeded the depth of 1% light during 1993 (Table II). This suggests that phytoplankton were regularly being mixed below the compensation depth in East Long Lake during enrichment; light limitation can be a stressor for cyanobacteria (Paerl, 1988). The non-response of cyanobacteria in East Long Lake therefore

appears to be due to changes in lake physics and chemistry following curtaining in 1991 (Christensen *et al.*, 1996).

Unlike cyanobacteria, chlorophytes increased with increased P loading rate in all three enriched lakes, especially during the second year of enrichment. Increases were larger in East Long and Peter lakes than in West Long Lake, presumably because there was less competition with cyanobacteria. Although this increase corroborates literature suggesting that chlorophytes increase with enrichment (Schindler, 1975; Olrik, 1981; Holmgren, 1984), it is notable that chlorophytes also increased in the unenriched reference lake during 1994. However, different kinds of chlorophytes increased in enriched versus unenriched lakes. In the enriched lakes, increases were due primarily to unicellular taxa (*Monoraphidium capricornutum* in Peter and *Cystomonas starii* in West Long and East Long lakes), while in Paul Lake increases were due to gelatinous colonies (*T.pulchra*, *Sphaerocystis schroeteri*, *Botryococcus braunii*). This suggests that enrichment may have driven the chlorophyte increases in Peter, West Long and East Long lakes, while other factors may have caused the increase in Paul Lake. As with the cyanobacteria, species-specific responses to subtle environmental differences among systems were an important outcome of these whole-lake experiments.

Cryptomonads also increased with enrichment in all three enriched lakes. The literature suggests that cryptomonad responses to enrichment vary among systems, sometimes increasing (Holmgren, 1984) and sometimes decreasing (Schindler *et al.*, 1974; Skogheim and Rognerud, 1978). However, cryptomonads consistently increased with enrichment in our study. Because cryptomonads tend to have a relatively high demand for nutrients (Klaveness, 1988), the increases could be due to direct stimulation by increased nutrient availability. However, increases could also be due to upward migration from metalimnetic populations (Klaveness, 1988; St. Amand and Carpenter, 1993; Christensen *et al.*, 1995).

In contrast, increased P loading caused only short-lived increases in dinoflagellates. By the end of the first year of enrichment, dinoflagellates had declined in all three enriched lakes. Declines in dinoflagellates with enrichment have also been reported in other systems (Olrik, 1981; Holmgren, 1984; Pollingher, 1988), although increases have also been described (Schindler *et al.*, 1974; Spodniewska, 1978; Reinertsen, 1982; Reynolds, 1984). To compensate for their size (which might make it difficult to obtain nutrients at low nutrient concentrations), many dinoflagellate species have adaptations that allow them to be competitive at low nutrient concentrations, including lower sinking rates, fewer losses to grazing, facultative heterotrophy, and the ability to migrate vertically and obtain nutrients throughout the water column (Pollingher, 1988). Post-enrichment declines in dinoflagellates could therefore be due in part to the loss of the competitive advantage of these adaptations as high nutrient availability makes rapid growth more important than efficient nutrient acquisition (Pollingher, 1988).

In Peter, West Long and East Long lakes, chrysophytes increased strongly immediately after the beginning of enrichment, but then declined as enrichment continued. This pattern of short-term increase followed by longer-term decline has also been reported in a number of other studies (Schindler and Fee, 1974;

Persson, 1978; Skogheim and Rognerud, 1978; Trifonova, 1989). As with the dinoflagellates, declines in chrysophytes with enrichment could be due to the loss of a competitive advantage of the chrysophyte 'strategy', possibly through indirect effects of enrichment such as elevated pH, decreased free CO_2, increased grazing, or an inability to keep up with the high maximum growth rates of other taxa (Sandgren, 1988).

Species turnover, year-to-year similarity and dominant taxa

Changes in species composition were frequent in all four lakes throughout this experiment. Minimum rates of species turnover from year to year were 25%, even in the unmanipulated reference system. Although these rates are high compared to other pelagic organisms [annual turnover rates are ~10–20% for zooplankton (Arnott *et al.*, 1995) and 1–16% for fish (Magnuson *et al.*, 1994)], they are probably not unusual for phytoplankton communities. In 1993, species turnover rates increased sharply in the enriched lakes, such that more than half of the species were turning over from one year to the next. This suggests that the onset of experimental enrichment promoted major changes in the presence and absence of particular members of the phytoplankton community.

High species turnover rates contributed to large changes in species ranks between years and low similarity in average species composition from one year to the next. Year-to-year similarities ranged from 39 to 55% in the pre-enrichment period, and from 5 to 79% during enrichment. Pre-enrichment values were slightly lower than those previously reported for unmanipulated Paul Lake (Elser and Carpenter, 1988). The low similarities observed during the years of large shifts in community composition (Peter Lake from 1992 to 1993 and East Long from 1993 to 1994) are comparable to values reported during food web manipulations (Elser and Carpenter, 1988). However, the high similarity observed between the enriched years for West Long Lake is far greater than similarities reported for either manipulated or unmanipulated lakes by Elser and Carpenter (1988), apparently because of the persistent dominance of a few taxa, especially *Anabaena*.

Overall, phytoplankton community composition changed a great deal from year to year, regardless of experimental manipulation. These changes may be due to the fundamentally chaotic nature of phytoplankton dynamics at the level of individual species (Scheffer, 1991). However, there are a number of other explanations for the high variability in community composition in Paul, Peter, West Long and East Long lakes. For example, it may be that we considered a relatively short time period (4 years, with 2 years of enrichment). Had we enriched the lakes for longer periods, we might have observed more convergence in species responses, possibly in response to dispersal among adjacent lakes. Alternatively, since there are well-known examples of predictable sequences of phytoplankton succession in the literature (reviewed by Reynolds, 1984), there may be something unique about these lakes that may be related to their meromictic or dystrophic status. Therefore, the high variability in species composition within a lake may reflect true differences in environmental conditions from one year to the next.

Individual species and genera

High variability in species composition in all four lakes made it difficult to attribute changes in species composition in the enriched lakes to the manipulation. Evidence that enrichment caused the observed changes in Peter, West Long and East Long lakes is primarily correlative: several taxa which responded to our experiments have also responded to whole-lake nutrient additions in other lakes. However, none of these taxa increased in all three enriched lakes. For example, the cyanobacterium *Anabaena macrospora* increased with enrichment in West Long Lake and at the Experimental Lakes Area (ELA) (Schindler, 1975) and Lake Langvatn (Reinertsen, 1982). *Oscillatoria limnetica*, which responded in Peter Lake, also increased at ELA (Schindler, 1975). Similar patterns were observed for the colonial chlorophyte *Dictyosphaerium pulchellum* (Findlay, 1978; Reinertsen, 1982; Holmgren, 1984).

We also noted parallel responses between our lakes and others at the genus level: increases in the unicellular chlorophytes *Monoraphidium* (Schindler *et al.*, 1974; Findlay, 1978; Holmgren, 1984) and *Staurastrum* (Schindler and Fee, 1974; Reinertsen and Langeland, 1982) and the cryptomonads *Cryptomonas* (Findlay, 1978; Reinertsen, 1982; Holmgren, 1984) and *Rhodomonas* (Reinertsen, 1982; Holmgren, 1984), and decreases in the chrysophytes *Ochromonas* (Holmgren, 1984) and *Uroglena* (Findlay, 1978; Holmgren, 1984).

These similar responses of some species and genera to enrichment in lakes in very different geographical regions suggest that there may be some ubiquity in how phytoplankton taxa respond to enrichment. However, this optimism for generality must be tempered by the observation that, in this experiment, very few species responded to enrichment in the same way even in neighboring lakes such as Peter, West Long and East Long. Lake-specific factors appear to play a key role in species responses to enrichment. D.W.Schindler (1975) put it this way: 'While one can say with considerable certainty that a lake will respond to increased inputs of P and N by increased algal biomass and production, . . . there is no way of making reliable predictions of what species will respond' (p. 3228). Species data are valuable for distinguishing among lakes, but may be less likely to signal enrichment effects reliably than more aggregated properties, especially over short time scales.

Acknowledgements

We thank Dave Christensen, Susan Knight, Joe LeBouton, Nick Voichick, Geoff Steinhart, Mark Scheuerell, Amy Wagner and John Morrice for help with the field and laboratory work, and Jim Kitchell, Daniel Schindler, Brian Herwig, Jeremie Johnson, David Post, Xi He and Rusty Wright for performing the fish manipulations. Dave Findlay, Jim Kitchell, Tim Allen, Dave Armstrong, Tony Ives, David Post and Dick Lathrop provided feedback on previous drafts of this paper. Our research was funded through the National Science Foundation, including a graduate research fellowship to K.L.C. K.L.C. is also grateful for the financial and logistical support of the National Center for Ecological Analysis and Synthesis (a

center funded jointly by NSF, the State of California and the University of California at Santa Barbara) while preparing this manuscript for publication.

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Received on January 28, 1998; accepted on April 27, 1998