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Pelagic C:N:P Stoichiometry in a Eutrophied Lake: Responses to a Whole-Lake Food-Web Manipulation

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Abstract

Changes in the ecological stoichiometry of C, N, and P in the pelagic zone are reported from a whole-lake manipulation of the food web of Lake 227, an experimentally eutrophied lake at the Experimental Lakes Area, Canada. Addition of northern pike eliminated populations of planktivorous minnows by the third year (1995) after pike introduction, and in the fourth year after pike addition (1996), a massive increase in the abundance of the large-bodied cladoceran *Daphnia pulicaria* occurred. Accompanying this increase in *Daphnia* abundance, zooplankton community N:P declined, seston concentration and C:P ratio decreased, and dissolved N and P pools increased. During peak abundance, zooplankton biomass comprised a significant proportion of total epilimnetic phosphorus (greater than 30%). During the period of increased *Daphnia* abundance, concentrations of dissolved inorganic nitrogen (TIN) increased more strongly than dissolved phosphorus (TDP), and thus TIN:TDP ratios were elevated. Sedimentation data indicated that increased grazing led to greatly reduced residence times of C, N, and especially P in the water column during 1996. Finally, previously dominant N-fixing cyanobacteria were absent during 1996. Our results show that strong effects of food-web structure can occur in eutrophic lakes and that stoichiometric mechanisms play a potentially important role in generating these effects.

Key words: ecological stoichiometry; cascading trophic interactions; carbon; nitrogen; phosphorus; plankton; nutrient cycling; food webs; ecosystem experimentation; cyanobacteria.

Introduction

Nutrient inputs and food-web structure are arguably two of the most important forces governing the structure and function of lake ecosystems. Many researchers have documented major effects of increasing inputs of limiting nutrients to lake ecosystems (Edmondson 1970; Dillon and Rigler 1974; Vollenweider 1976; Schindler 1977, 1978). These studies are classics of the limnological literature and remain relevant to understanding the effects of both point and nonpoint sources of nutrients to lakes from an increasingly human-dominated landscape. Similarly, it is now well established that trophic interactions, especially the effects of size-selec-

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tive predation as mediated by the nature of a lake's fish community, also have major effects on the abundance, dynamics, and composition of zooplankton, phytoplankton, and microbial components of lakes (Hrbácek and others 1961; Brooks and Dodson 1965; Shapiro and Wright 1984; Carpenter and others 1985).

More recently, limnologists have sought to understand how nutrient dynamics and food-web structure interact to affect the dynamics, composition, and productivity of planktonic communities. For example, much discussion surrounds whether the effects of higher trophic levels on lower levels (that is, the strength of the "trophic cascade") vary with lake trophic status (McQueen and Post 1988; Persson and others 1988; Elser and Goldman 1991). Considerable research also has examined how changes in food-web structure affect the internal cycling and retention of nutrients within pelagic ecosystems (Mazumder and others 1989; Sarnelle 1992; Schindler and others 1993). Changes in zooplankton abundance resulting from altered intensities of planktivory can alter the cycling of limiting nutrients within the mixed layer (Carpenter and others 1992a; Sterner and others 1992). Furthermore, changes in zooplankton biomass and community composition can modify the vectors of nutrient loss from the water column (Mazumder and others 1989; Elser and Foster 1998; Sarnelle 1999). This can occur either directly (by sedimentation of nutrients contained in fecal pellets or zooplankton remains) or indirectly (by alteration of the size structure of suspended particles). Such studies contribute to ongoing efforts to unify trophic ecology and biogeochemistry into a common, synthetic framework (Carpenter and Kitchell 1993; Sterner and others 1996). In this study, we use the perspective of ecological stoichiometry to examine how trophic dynamics and biogeochemistry interact in regulating lake ecosystem dynamics during a whole-lake food-web manipulation of a eutrophied lake.

Ecological stoichiometry is the study of the balance of energy and multiple chemical elements in ecological interactions (Reiners 1986; Sterner 1995; Elser and others 1996; Hessen 1997). Ecological stoichiometry already has proven to be valuable in understanding various connections between trophic interactions and nutrient cycling (Elser and Urabe 1999). For example, Elser and others (1988) showed that changes in food-web structure (that is, introduction or removal of the top predator) caused shifts in the primary limiting nutrient (N vs P) in two temperate lakes. Phytoplankton were P limited when zooplankton were dominated by the cladoceran *Daphnia* but N limited when zooplankton were copepod dominated. Using the stoichiometric perspective, Sterner and others (1992) described how such changes in relative nutrient availability were likely due to changes in the N:P stoichiometry of consumer-driven nutrient cycling as the zooplankton communities shifted from P-rich *Daphnia* to low-P copepods. Thus, changes in food-web structure appear to differentially alter the storage, turnover, and fate of key limiting nutrients due to the contrasting demands for these nutrients by different consumer taxa. By expressing trophic interactions in biogeochemical terms, a stoichiometric perspective potentially can improve our ability to understand and interpret the effects of changes in nutrient inputs on food-web dynamics and, reciprocally, the effects of changes in food-web structure on internal nutrient cycling.

We already know that nutrient stoichiometry affects how lake ecosystems respond to nutrient loading (Schindler 1977; Smith 1983). For example, Schindler (1977) argued that, relative to N and inorganic C, P is the key limiting element in most lakes because lake biota can draw on alternative nutrient supplies (atmospheric N_2 and CO_2) when P is present in excess, thus returning the ecosystem to P limitation. This tendency has been strongly supported by subsequent observation and experimentation. For example, consider the experimental fertilization of Lake 227 (L227) at the Experimental Lakes Area, Canada (Schindler and others 1973). Initially (1970–74), the lake was fertilized with N and P at a molar ratio of 29:1. This generated increased biomass of a diverse phytoplankton community with chlorophytes, dinoflagellates, nonnitrogen fixing cyanobacteria, and chrysophytes (Schindler 1977; Findlay and others 1994; Hendzel and others 1994). During 1975–89, the fertilization N:P was lowered to 11:1 whereas the P-loading rate remained constant. This greatly increased the late summer dominance of N-fixing *Aphanizomenon schindleri*. However, interannual variability in *Aphanizomenon* dominance was relatively high (Findlay and others 1994; Hendzel and others 1994). N fertilization was terminated in 1990 whereas again the P-loading rate was held constant (fertilization N:P now 0). After this, the duration and predictability of monospecific *Aphanizomenon* blooms increased (Findlay and others 1994; Hendzel and others 1994). Clearly, the N:P ratio of available nutrients has played a key role in determining the species composition of the L227 phytoplankton and thus the contribution of N fixation to the lake's N budget (Findlay and others 1994).

Taking a stoichiometric perspective, how should

food-web changes alter how pelagic ecosystems respond to their external N and P loading? If food-web components (such as zooplankton) came to be important in the overall nutrient supply regime via consumer-driven nutrient recycling (sensu Elser and Urabe 1999), and if those internal components have a contrasting N:P stoichiometry relative to the external supply, then major changes in lake ecosystem dynamics should ensue. For example, consider Smith's (1983) multilake survey of the relationship between cyanobacteria dominance and lake TN:TP. His compilation showed that at high TN:TP (P likely limiting), cyanobacteria never achieved appreciable dominance but at low TN:TP (N potentially limiting), cyanobacteria dominance was high but variable. His more detailed consideration of the dynamics of cyanobacteria and TN:TP in Lake Trummen (Sweden) suggests a connection to food-web structure: in a summer after a winterkill that eliminated planktivorous fish and resulted in increased *Daphnia* biomass, cyanobacteria were greatly reduced despite low TN:TP. Such a response suggests that increased dominance of low N:P *Daphnia* in the food web can interfere with ecosystem compensation (sensu Schindler 1977) for an N deficiency in the external loading by inhibiting the proliferation of N-fixing cyanobacteria (MacKay and Elser 1998; Elser 1999). This interference might involve stoichiometric mechanisms of differential nutrient storage, loss, and recycling of N and P as argued by Sterner and others (1992) and recently reviewed by Elser and Urabe (1999). Thus, in addition to the direct effects of ingestion that are normally considered as part of the trophic cascade concept (Carpenter and others 1985), changes in zooplankton biomass and community structure might affect phytoplankton communities via major alterations in the internal nutrient regime. Unfortunately, the stoichiometric perspective on trophic interactions is relatively new, and thus there are few data on the C:N:P composition of major pelagic ecosystem components before and after a major food-web alteration. Such data are especially lacking for highly eutrophic environments.

In this article, we report the outcome of a whole-lake manipulation of the food web of L227. We hypothesized that changes in the C:N:P stoichiometry of the planktonic food web are important mechanisms involved in altered ecosystem dynamics after changes in food-web structure. If stoichiometric mechanisms play an important role in determining the response of eutrophic lakes to altered trophic structure, we expected several responses after enhancement of piscivores in L227: (a) the C:P and N:P ratios of zooplankton biomass would decrease; (b) the zooplankton P pool would become an important internal component of the total water column; (c) sedimentation losses of P would increase disproportionately (for example, sedimentation C:P and N:P ratios would decline); (d) the relative availability of N compared with P for phytoplankton, as gauged by concentrations of inorganic N and P in the surface layers, would increase; (e) the dominance of cyanobacteria in the phytoplankton community would decrease; and (f) the contribution of N fixation to the lake's N budget would be diminished. Although somewhat delayed and temporary (lasting 1 year), the response of L227 to addition of piscivores was spectacular. Most of the observed changes are consistent with the above predictions, indicating that there is a major stoichiometric aspect underlying the influence of food-web structure on eutrophied lakes.

Methods

Study Site

L227 is a small (5 ha, 10-m maximum depth) headwater lake located at the Experimental Lakes Area (ELA) in northwestern Ontario, Canada. The lake generally has strong thermal stratification each year from May until September. L227 has been continuously fertilized since 1969 (Schindler and Holmgren 1971). Throughout this period P has been added at an annual rate of 0.56 g P m^{-2}. As described above, since 1990, no inorganic N has accompanied the P enrichment. Details of this fertilization regime are presented in Schindler and Holmgren (1971, 1973), Findlay and others (1994), and Hendzel and others (1994). Before 1993, the fish community of L227 was composed entirely of dense populations of cyprinid minnows (particularly, fathead minnows, *Pimephales promelas*) and dace (*Semotilis margarita*, *Phoxinus eos*, *Phoxinus neogaeus*; Beamish and others 1976; George 1994) and lacked piscivores. We have no direct estimates of minnow populations size in L227. However, a quantitative survey of cyprinid densities in lakes lacking piscivorous fishes in northwestern Ontario indicated that densities are commonly in the range of 10–15 kg ha^{-1} (Kelso 1985, 1988). We would expect densities to be higher in L227 given its eutrophic status. Indeed, catch per unit effort (CPUE) values for L227 cyprinids before pike introduction were generally seven times higher than in unfertilized L110 (Elser and others 1998). Thus, George (1994) roughly estimated that cyprinid densities in L227 in 1992, before pike introduction, were 105 kg ha^{-1}. Historically, the biomass of L227 zooplankton generally

has been low and dominated by copepods, small cladocera, and rotifers (Malley and others 1988)

Food-Web Manipulation

During early to mid-May of 1993 and 1994, northern pike were collected by angling from nearby lakes (L222, L663) and held for 1–3 days in fish pens. They were measured, weighed, sexed, and tagged and then transported to L227 in water-tight poly vinyl chloride (PVC) tubes. Little handling mortality (less than 5%) was observed during transfer. In 1993, 60 pike were introduced to L227; in 1994, an additional 140 fish were added. Pike had an average individual weight of approximately 0.67 kg fresh weight (George 1994). Thus, we added a total of 143 kg of pike to L227, an areal density of 26 kg ha^{-1}. This density of pike biomass is likely six times higher than pike densities in pike-dominated lakes in the ELA region (Elser and others 1998). No formal monitoring of pike population dynamics was made during the postintroduction period although visual observation, occasional angling, and netting indicated that pike survived in L227 during 1993–95. In fall 1995 and spring 1996, the lake was intensively fished with gill and trap nets to extirpate pike and prevent their potential downstream migration into other ELA lakes. Netting efforts during the rest of 1996 and in spring 1997 verified the absence of pike from the lake in 1996.

Sampling Schedule and Data Analysis

During 1992–96, the lake was monitored for most stoichiometric variables at 7- or 10-day intervals from mid-May (1992–95) or early June (1996) until late August or early September. Unfortunately, sampling during early summer in 1996 was somewhat limited. Zooplankton were sampled for stoichiometric analysis only during July and August in 1996, and thus we focus on zooplankton data primarily for those months here. Seston samples for stoichiometric analysis were taken for only one date in mid-June in 1996 but more frequently in July and August.

To have comparable data intensity for all years, we broke the data series into two data "bins" per month, and all observations within each half-month interval were averaged. Data for each year are presented as summertime means of those approximately biweekly observations with variability summarized as standard errors for each year's four to six observations. Strategies for statistical analysis of whole-lake experiments are diverse and subject to considerable discussion (Hurlbert 1984; Carpenter and others 1989). Because no valid reference lake for comparison to L227 exists at the ELA (due to the 25-year fertilization regime and its hypereutrophic status), we do not perform analyses used previously in whole-lake experiments, such as randomized intervention analysis (Carpenter and others 1989), repeated measures analysis of variance (ANOVA; Elser and others 1995c), or Before-After Control-Inversion (BACI) analysis (Stewart-Oaten and others 1986). Intervention analyses using a reference system have debatable validity in this case. Instead, we primarily take the strategy advocated by Hurlbert (1984) and present for interpretation the growing season averages and standard estimates of variability because the magnitudes of most of the responses we document for L227 in 1996 are massive, making statistical analysis superfluous. To provide some measure of the magnitude of interannual changes relative to data variability associated with sampling, analysis, and seasonality, we performed simple ANOVA for primary response variables (seston abundance and C:N:P, zooplankton biomass and N:P, bacteria abundance, nutrient concentrations and ratios) combined with Scheffe's comparison tests ($P = 0.05$) to gauge whether parameters in 1996 were significantly different from preceding years. To add a level of conservatism to these comparisons, we used only data from the biweekly "bins." Thus, approximately four to six data values were associated with each study year in the ANOVA analysis.

Monitoring (1992–96)

Minnow abundance was assessed as the CPUE of cyprinids by using standardized deployments of 12–15 baited minnow traps and a single winged fyke net at monthly intervals (George 1994). Each monthly sampling consisted of 3 or 4 nights of collecting. After each night's sampling, traps and nets were emptied, and minnow biomass was estimated by pouring fish into a calibrated cylinder and expressing the catch in terms of volume. The mean of catch volume for all sampling nights in a monthly set was calculated and used as the estimate for that month's minnow abundance. Subsamples were frozen for later examination and determination of the species composition of the minnow assemblage (George 1994).

The lake was monitored for major pools of C, N, and P by using methods described in detail in Elser and others (1995a, 1998). Functional pools of C, N, and P were largely defined on the basis of the filter sizes used in water processing. Functional pools were dissolved N and P [NO_3^-, NO_2^-, NH_4^+, as well as total dissolved N and P (TDN and TDP), measured in water passing a 0.2-μm polycarbonate filter], seston C, N, and P (particulate C, N, and P passing

an 85-μm Nitex mesh net and collected on a GF/F glass-fiber filter), and zooplankton C, N, and P (materials on an 85-μm mesh Nitex net). We focused on TDP and not soluble reactive phosphorus (SRP) as a measure of P availability because SRP is an unreliable estimate of PO_4^{3-} at low concentration (Stainton 1980). Previous studies (Elser and others 1995a) and concurrent information on small particles (less than 1 μm) indicate that bacteria generally contributed approximately 15% or less to total seston biomass in L227 during this period. Sampling focused on dynamics in the epilimnion and generally involved replicate (two or three) composite samples generated by mixing water collected from three depths in the mixed layer. The lake was sampled at weekly (1992–94) or 10-day (1995–96) intervals. Samples for water chemistry, seston analyses, and bacterial enumeration were collected using a Van Dorn sampler. Zooplankton samples were collected with a 15-L clear Schindler-Patalas trap fitted with an 85-μm Nitex net. Zooplankton were collected both during the day and at night to assess epilimnetic densities of vertically migrating zooplankton.

Samples for chemical analysis were analyzed for NO_3^-, NO_2^-, NH_4^+, TDN, and TDP according to the methods of Stainton and others (1977). Samples for bacterial enumeration were preserved with 2% filtered formaldehyde and kept chilled until enumeration. Samples were counted by epifluorescent direct count by using 4′,6-diamidino-2-phenylindole staining after filtration onto darkened 0.2-μm polycarbonate filters (Porter and Feig 1980). Zooplankton samples were split into three parts by using a plankton splitter. One subsample was preserved with Lugol's solution (Pennak 1989) for later enumeration and measurement of zooplankton by taxon; one subsample was placed onto a preweighed GF/C filter for later reweighing and determination of C and N; the third subsample was placed onto a preweighed GF/C filter for later reweighing and determination of P. Samples of seston and zooplankton for C and N determination were analyzed using a Perkin-Elmer (Wellesley, MA, USA) model 2400 elemental analyzer whereas seston and zooplankton P were analyzed using the acid molybdate technique after high temperature digestion with persulfate (APHA 1992; Elser and others 1995a). Preserved zooplankton samples were enumerated under a microscope, and biomass of various taxa was determined by microscopic measurement of body lengths of animals in taxonomic categories showing considerable variation in body size during the sampling season (for example, most cladoceran taxa, copepodids). Mean individual biomass (μg dry weight animal^{-1}) was calculated for these taxa by using the approach described in Downing and Rigler (1986) and specific equations found in Downing and Rigler (1986) and Malley and others (1989). Less variable taxonomic categories were assigned fixed individual biomass values according to Malley and others (1989).

Sedimentation rates of C, N, and P were determined using replicate (two or three) sediment traps suspended at the top of the hypolimnion (6 m). Methods are described in more detail in Elser and others (1995b) and Elser and Foster (1998). Each trap consisted of an array of three, 5-cm-diameter, 60-cm-long PVC tubes. Traps were deployed for 1-week intervals during 1992–94 and for 8–10-d intervals during 1995–96. Material collected from each array of three tubes was combined into a single sample. Particulate matter in the pooled samples then was filtered onto precombusted GF/F filters that were dried and kept in a desiccator until later analysis for C, N, and P content as previously described. We also collected a water sample from the trap depth on each occasion for analysis of seston C, N, and P. These values were used to correct the determinations of sedimented material for the contribution of ambient seston to the sample; this was always a minor component.

Long-Term Data

Selected long-term data from the ELA records were combined with similar data for the 1992–96 period. In particular, we focused on dissolved nutrient concentrations (TIN and TDP) during spring and early summer (May and June) and phytoplankton biomass and species composition during the subsequent summer (June, July, and August). In the routine monitoring program for L227, phytoplankton samples generally were collected every second week by using an integrating sampler that collected water from throughout the epilimnion. Biomass was estimated based on microscopic enumeration of samples coupled with cell volume estimates. Details on these can be found in Findlay and others (1994). In particular, we concentrated on the biomass of N-fixing cyanobacteria taxa (that is, members of the Nostocales; Findlay and others 1994). Following the contribution of this group provides information about whether lake N fixation responded to the food-web manipulation.

Results

Fish Dynamics

In fall 1995, netting to remove pike from the lake yielded 315 fish, 25% of which were recaptured

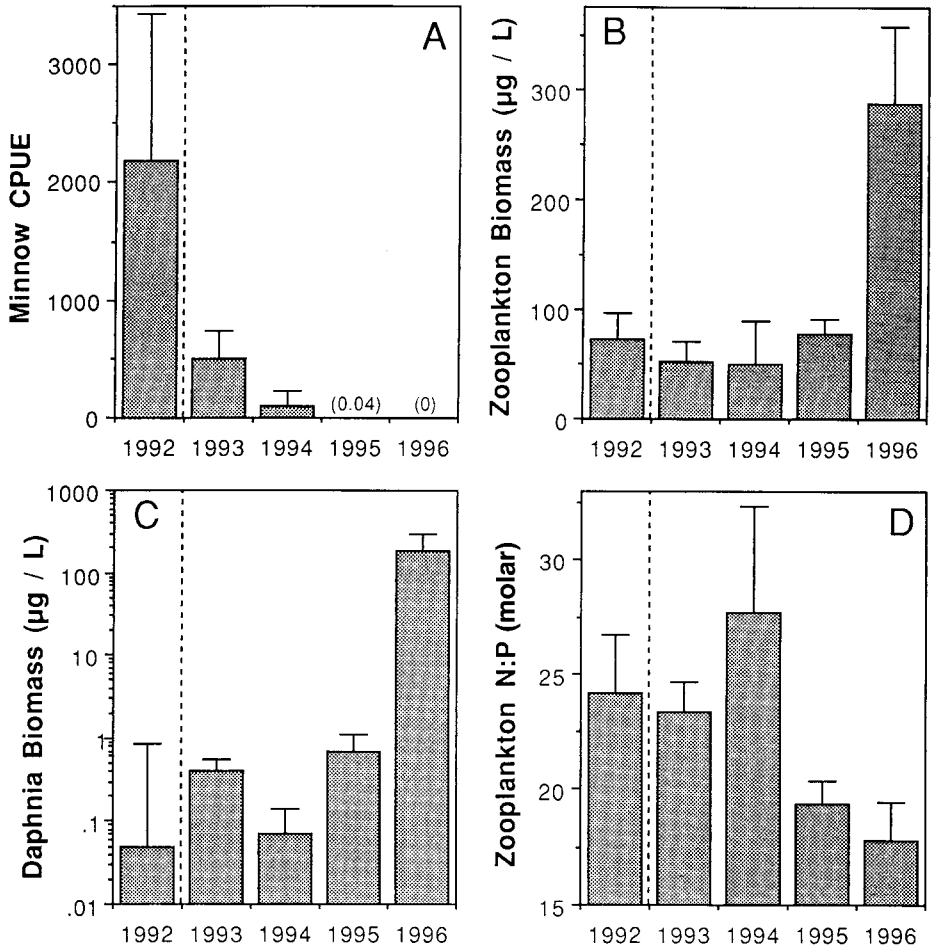

Figure 1. Dynamics of planktivorous fish and zooplankton during the study period. The vertical dashed lines indicate the timing of pike additions in spring 1993 (pike also added in 1994). (**A**) Mean summer (June–August) CPUE of minnows by volume (mL). Error bars indicate ±1 standard error (SE). (**B**) Summer mean epilimnetic zooplankton biomass (based on direct determinations of dry weight in zooplankton samples). Data for zooplankton reflect average values of samples collected during day and night. (**C**) Summer mean epilimnetic *Daphnia* biomass. During 1992–95, the *Daphnia* species was predominantly *D. galeata*. In 1996, greater than 98% of the *Daphnia* biomass was *D. pulicaria*. Note the logarithmic scale of the y axis. (**D**) Summer mean epilimnetic zooplankton community N:P ratio (molar).

fish of the original 200 added in 1992 and 1993; the remaining fish were spawned in the lake during the preceding years. The 25% survival rate of the introduced pike after 3 years is surprisingly high, given that the fish were required to over-winter (some twice) in this eutrophic lake in which oxygen under the ice is severely depleted. The recaptured fish had grown considerably during their time in the lake, increasing from a mean weight of 0.7 kg each to 1.2 kg when removed. Recruited fish had a mean body size of 0.12 kg. Pike netting during spring 1996 yielded an additional 70 fish (mean size 0.15 kg). Netting efforts in 1997 and 1998 produced no further pike. Thus, in 1996 L227 was essentially a fishless lake.

Addition of pike decimated minnow populations in L227 within 2 years of introduction (Figure 1A). Examination of preserved minnow collections during the initial phase of the experiment (1993) indicated that fathead minnows were eliminated before redbelly and finescale dace (George 1994). During summer 1994, total minnow catches were less than 5% of their levels in 1992. By 1995, minnow catches had been reduced by four orders of magnitude; juvenile pike exceeded minnows in trap collections during 1995. During 1996, no minnows were captured. Thus, we can consider both 1995 and 1996 to be years in which the zooplankton community of L227 experienced minimal vertebrate planktivory whereas levels of planktivory in 1994 were also greatly reduced. The contention that minnows were exterminated in L227 by 1996 is supported by our observations of gut contents of pike removed during 1995 and 1996. Pike stomachs contained no minnows and instead were dominated by various benthic invertebrates and corixids.

Zooplankton Dynamics

Summertime average zooplankton biomass in the epilimnion changed little during the 1992–95 period but increased more than fourfold in 1996 [Figure 1B; ANOVA for effect of year: $P < 0.001$ for 1992–96. Similarly, changes in the abundance of *Daphnia* were subtle during the first years of the study; very few *Daphnia* were found in any samples in 1992, but limited numbers appeared during

1993–95 (Figure 1C). During this period, all *Daphnia* observed in our routine enumerations were predominantly a relatively small-bodied daphnid, *D. mendotae*. However, the large-bodied *D. pulicaria* increased dramatically in 1996 (Figure 1C; ANOVA: $P < 0.05$; however, no pairwise comparisons of years were significant due to extreme variance in *Daphnia* biomass during 1996) and had summertime average biomass exceeding 100 $\mu g\ l^{-1}$. The N:P ratio of zooplankton biomass declined during the overall observation period, reaching its lowest levels in 1996 when summertime average N:P was around 17:1 (Figure 1D; ANOVA: $P < 0.05$; however, no pairwise comparisons of years were significant). *Chaoborus* can be an important component of pelagic communities, especially in the absence of fish predation. However, our zooplankton sampling approach was generally insufficient to adequately characterize *Chaoborus* dynamics, although zooplankton samples were occasionally dominated by small *Chaoborus* individuals. Sampling methods by Freshwater Institute personnel were better suited for assessing *Chaoborus* dynamics. Their samples do not indicate any major changes in *Chaoborus* abundance during the study period (M. Paterson, personal communication).

A more detailed examination of zooplankton data for L227 during July and August 1996 indicates the highly dynamic nature of the zooplankton response during this unusual year. By the time the first samples were available in early July, *Daphnia pulicaria* were already dominant (98% of the biomass), and total zooplankton biomass (620 $\mu g\ L^{-1}$) was higher than ever previously observed in the lake. Visual observations from earlier in the year (K. Mills, personal communication) indicated the presence of large-bodied zooplankton under the ice as well as immediately after ice-out in late April, coincident with elevated NH_4 levels in the epilimnion mentioned below. Zooplankton biomass fluctuated somewhat during the remaining July sampling dates but remained dominated by *Daphnia*. By 24 July, zooplankton N:P was low (14:1) and similar to published values of *Daphnia* N:P (Andersen and Hessen 1991).

The dense *Daphnia* population did not last. *Daphnia* biomass crashed from 375 $\mu g\ L^{-1}$ on 24 July to 2.1 $\mu g\ L^{-1}$ on 4 August. This decline was associated with high densities of various invertebrate predators (notonectids, diving beetles) in the pelagic area, a phenomenon we have not observed previously in L227. Indeed, zooplankton samples during this period contained considerable numbers of broken zooplankton carapaces and other remains, indicating a degree of "sloppy feeding" of the invertebrate planktivores. However, our zooplankton sampling approach did not capture these highly mobile invertebrate planktivores effectively. Total zooplankton biomass also declined, though not as greatly as *Daphnia*. During the rest of August, total zooplankton biomass was relatively low (compared with earlier in the year, but still higher than in previous years) and was dominated by an omnivorous calanoid copepod, *Epischura lacustris*.

Microplankton Dynamics, Sedimentation, and Nutrient Availability

Seston mass (as indicated by seston C concentration) was high and relatively constant from 1992 through 1995 (Figure 2A). During these years, seston C:P and N:P ratios were relatively high, indicative of P-limited algal growth (Figure 2B). This indication of P limitation seems paradoxical, given that the external nutrient load is deficient in N. However, low external N:P ratios favor the proliferation of cyanobacteria that are able to meet their N requirements by N_2 fixation and thus eventually deplete available P supplies (Hendzel and others 1994). Seston mass and elemental composition changed radically in 1996.

Seston C concentration decreased more than fivefold in 1996 relative to the 1992–95 period (Figure 2A; ANOVA: $P < 0.05$ for 1992–96). A similar decline in phytoplankton biovolume also occurred (D.L. Findlay, unpublished data). The decrease in seston P was not as great, so that seston C:P was substantially lower in 1996 (approximately 150:1) than in previous years (Figure 2B; ANOVA $P < 0.01$ for 1992–96). Seston N:P also was reduced in 1996 (Figure 2B; ANOVA $P < 0.01$ for 1992–96) These low C:P and N:P ratios indicate that the phytoplankton assemblage that remained in the presence of elevated zooplankton biomass was growing at relatively rapid rates with little nutrient limitation (Healey and Hendzel 1980). Accompanying the decline in total seston mass was a reduction in epilimnetic bacterial biomass (Figure 2C; ANOVA $P < 0.002$ for 1992–96), which in 1996 was approximately one-third of its value in earlier years (1992–94). Bacterial biomass in 1995 also was reduced somewhat relative to 1992–94.

Sedimentation rates of C, N, and P were somewhat variable during the study years and showed no strong evidence for major changes in 1996, although sedimentation rates of P appeared to increase during the 5 years of monitoring. This relative constancy of sedimentation occurred despite the fact that in 1996 the water column standing stock of particles available to settle was drastically reduced. Thus, it appears that changes in the zoo-

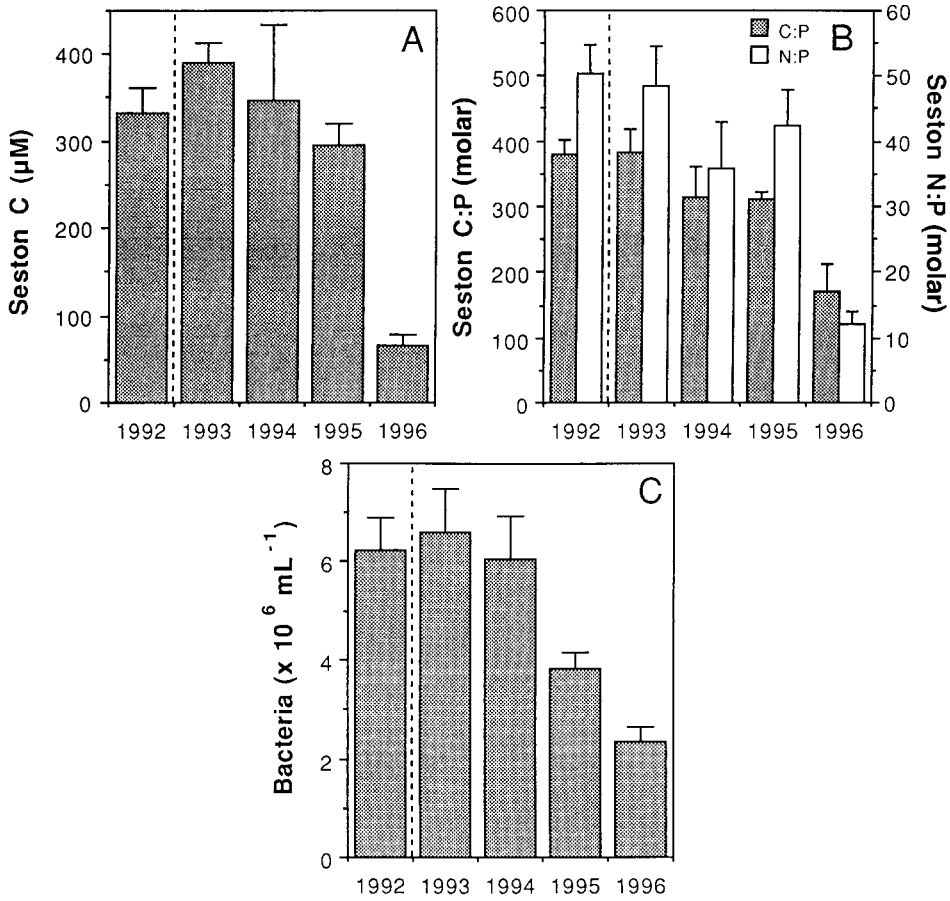

Figure 2. Dynamics of pelagic components at the base of the food web. (**A**) Mean summer epilimnetic seston carbon concentration. (**B**) Mean summer epilimnetic seston C:P and N:P (molar). (**C**) Mean summer epilimnetic bacterial abundance. Error bars indicate ±1 SE.

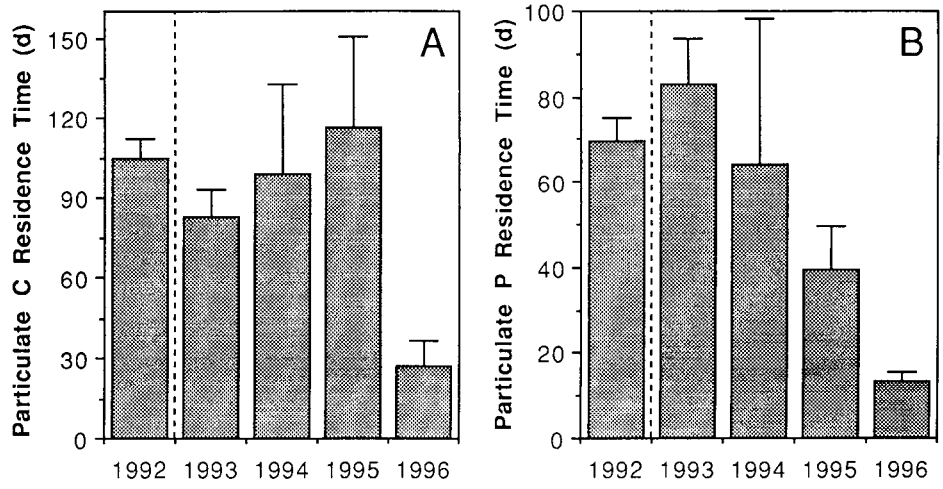

Figure 3. Dynamics of particulate sedimentation during the study period. (**A**) Carbon residence time. (**B**) Phosphorus residence time. Residence time was calculated for each element by dividing the areal seston concentration of that element above the sediment trap during an interval by the areal sedimentation rate of that element during the interval. Error bars indicate ±1 SE.

plankton community in 1996 increased the tendency of individual particles to sediment. To estimate these effects, we calculated particle residence times during each 7–10-day interval of sediment collection by dividing the areal particle density above the sediment traps at 6 m by the areal sedimentation rate (Figure 3). These values represent maximal residence times because they do not include the impacts of other particle loss processes. Residence times for particulate C before 1996 were long (80–120 days) relative to those for particulate P (40–85 days), reflecting the fact that sedimentation C:P ratio was generally lower than seston C:P. The same was true for nitrogen (sedimentation N:P was lower than seston N:P; data not shown). In 1996, residence times for particulate elements de-

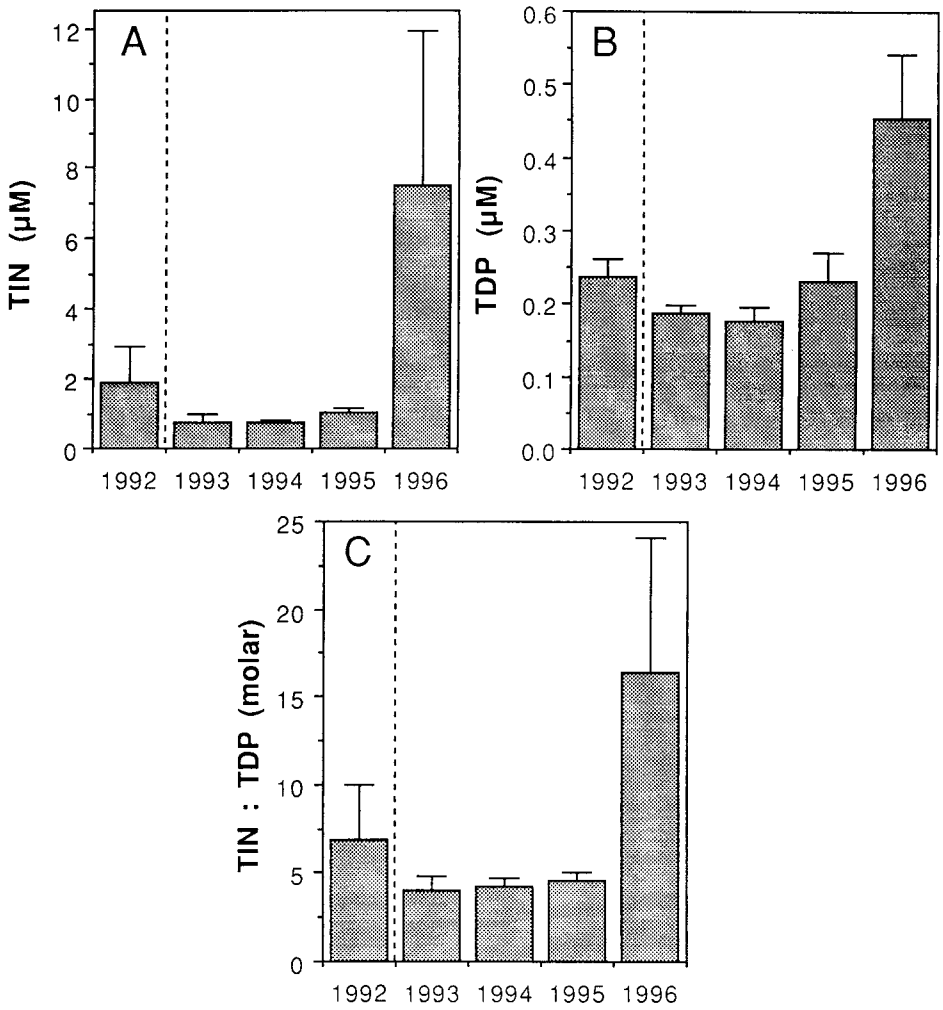

Figure 4. Dynamics of dissolved nutrient concentrations during the study period. (**A**) Mean summer epilimnetic TIN concentration. TIN is the sum of dissolved NO_3^- NO_2^-, and NH_4^+ concentrations. (**B**) Mean summer epilimnetic TDP concentration. (**C**) Mean summer epilimnetic TIN:TDP ratio (molar). Error bars indicate ±1 SE.

creased drastically (to 25 days for C and to 13 days for P). Thus, sedimentation became a more important loss process for particulate elements (and especially for P) after the change in the zooplankton community in 1996.

Summertime nutrient availability (in the form of dissolved N and P pools) was generally low and relatively constant during 1992–95 (Figure 4). Inorganic nitrogen was extremely low (generally less than 1 μM; Figure 4A), and concentrations of NH_4^+ exceeding 1 μM were rare during midsummer. TDP concentrations were low and changed little during 1992–95 (Figure 4B). The N:P ratio of dissolved nutrient pools (TIN:TDP) was quite low (5–12), and average values were less than 7 during 1992–95. In 1996, dissolved nutrient concentrations increased considerably (Figure 4). In 1996, TDP increased approximately twofold (ANOVA $P < 0.001$ for 1992–96) whereas TIN increased more than sevenfold (ANOVA marginally significant, $P = 0.06$, no pairwise comparisons of years were significant) relative to 1992–95. The increases were particularly pronounced in spring within the first few weeks after ice-out (data not shown) and were maintained during early summer (June). TIN concentrations declined during August 1996, after the decline in *Daphnia* and zooplankton biomass. Reflecting the disproportionate increases in inorganic N in 1996 relative to TDP, the TIN:TDP ratio increased in 1996 relative to 1992–95, reaching a mean value of 16:1 (Figure 4C; ANOVA marginally significant, $P = 0.06$, no pairwise comparisons of years were significant). These changes in nutrient ratios were particularly pronounced early in the 1996 growing season. During May-June 1996, the mean TIN:TDP ratio was 79:1, the second highest value in the 28-year data record (Figure 5A). Thus, especially strong changes in dissolved nutrient pools occurred during the early part of the 1996 growing season, when competitive events that lead to the establishment of phytoplankton community structure are proceeding.

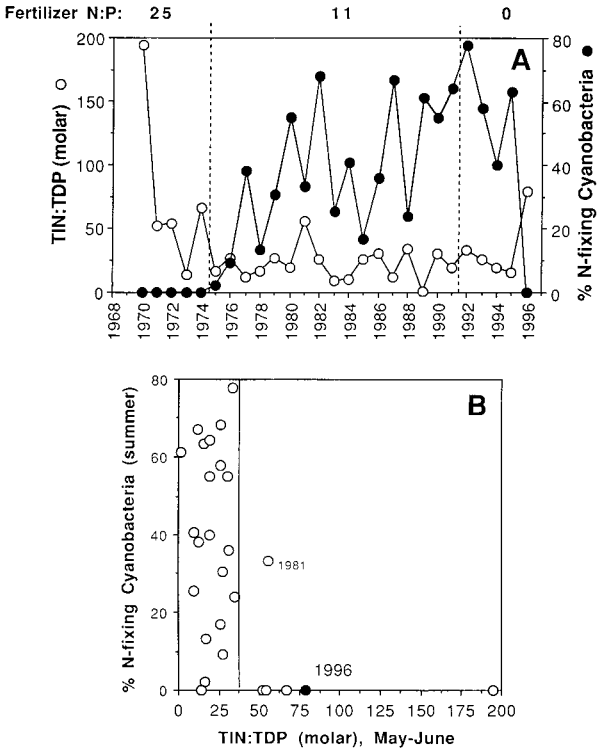

Figure 5. Long-term association of relative N and P availability and the dominance of N-fixing cyanobacteria in L227. (**A**) Dynamics of mean TIN:TDP ratio during spring and early summer (May and June) and the summertime (June–August) contribution of N-fixing cyanobacteria to total phytoplankton biomass from 1970 to 1996. Intervals when different fertilizer N:P ratios were applied to the lake are indicated. (**B**) Association of N-fixer dominance and early season TIN:TDP ratio in L227. A vertical line is placed that, with the exception of a datum from 1981, divides the data into regions with negligible contribution of N-fixers (TIN:TDP greater than 38) or with variable but generally high levels (TIN:TDP less than 38). Thus, similar to the study of Smith (1983), the data suggest the existence of a threshold N:P value above which N-fixer dominance is suppressed but below which N-fixers can dominate. The datum for 1996 is highlighted; note that other data values with 0% N fixers and high TIN:TDP ratios are from over 20 years ago during the period when fertilizer was added to the lake at N:P of 25. Error bars indicate ±1 SE.

Phytoplankton Community Composition and the Role of N Fixation

During 1992–95, phytoplankton biomass was high. During this period, the contribution of N-fixing cyanobacteria to the phytoplankton community was generally higher than throughout the previous 20 years of data, a continuation of a trend that began in 1990 when the fertilization N:P was reduced to 0 (Figure 5A).

In 1996, phytoplankton biomass plummeted as *Daphnia* invaded the planktonic community. Cyanobacteria were almost completely lacking from the phytoplankton community, and N fixers were absent (Figure 5A). Instead, the community was dominated by a diverse mixture of chlorophyte, chrysophyte, and cryptophyte taxa. This assemblage was similar to that observed in the lake during the early years of fertilization (Schindler and Holmgren 1971; Findlay and others 1994) when fertilizer N:P was 30:1. Because cyanobacteria were absent, we conclude that N fixation rates during 1996 were zero (Findlay and others 1994). Thus, nitrogen fixation was insignificant for the first time in over 2 decades, illustrating the ability of trophic cascades to affect nutrient biogeochemistry. To illustrate the coupling between the importance of N fixers in the phytoplankton assemblage and the relative availability of N and P, the long-term dynamics of early summer (May–June) epilimnetic TIN:TDP ratio and summertime dominance by N-fixing cyanobacteria are shown in Figure 5A; the relationship between percentage N fixers and TIN:TDP is shown in Figure 5B. These plots convey the unusual nature of 1996 in the long-term history of L227. Despite an extremely low N:P ratio of external loading, internal processes driven by food-web changes in 1996 appeared strong enough to raise the availability of N relative to P during the critical early season period when algal community composition was being established. This resulted in a phytoplankton assemblage similar to the one that dominated the lake 25 years earlier when external loading occurred at high N:P.

Discussion

Our whole-lake manipulation reinforces the conclusion from smaller-scale experiments and observational studies (Schindler and Comita 1972; Benndorf and others 1984; Reinertsen and others 1990; Vanni and others 1990; Sarnelle 1993; Urabe 1994; Horppila and others 1998) that strong effects of food-web structure can occur in eutrophic lakes. Indeed, L227 is one of the most eutrophic lakes subjected to a deliberate food-web manipulation. Whereas responses were somewhat delayed and potentially unstable (see discussion below), introduction of a fourth dominant trophic level (piscivorous pike) to L227 led to a spectacular increase in *Daphnia* and a major reduction in phytoplankton biomass (Figures 1 and 2). These responses are consistent with those predicted from biomanipulation (Shapiro and Wright 1984) or cascading trophic interaction (Carpenter and others 1985) theory. A major shift in phytoplankton species composition

also resulted (Figure 4). Thus, despite the fact that eutrophic lakes can be dominated by large algal taxa that are difficult to graze (Gliwicz 1990; Elser and Goldman 1991; Carpenter and others 1992b) or have increased nutrient levels capable of supporting high algal growth rates that might outstrip grazing (McQueen and Post 1988; Benndorf and Miersch 1991), alteration of food-web structure nevertheless can generate massive effects on pelagic community and ecosystem structure in eutrophic systems.

Our data on the C:N:P stoichiometry of major pelagic ecosystem components indicate that stoichiometric mechanisms contributed to ecosystem changes resulting from the food-web manipulation. Our a priori expectations were that elimination of planktivorous fishes would result in a pelagic food web in which P-rich zooplankton (for example, *Daphnia*) would have a greatly enhanced role in regulating internal nutrient availability and would differentially increase the availability of N relative to P. There are five main aspects of the stoichiometric impact of the L227 food-web manipulation:

- As predicted, zooplankton biomass became more P rich (lower C:P and N:P ratio) in 1996 (Figure 1D). This difference is consistent with dominance by *Daphnia*, which has a relatively low body N:P (Andersen and Hessen 1991). According to stoichiometric nutrient recycling theory (Sterner 1990), the shift in annual mean N:P from approximately 24:1 during 1992–94 to 18:1 in 1996 would be sufficient to generate major differences in the N:P ratio of animal-driven nutrient release. Furthermore, the mean value of 18:1 for all of 1996 does not indicate the situation during peak *Daphnia* dominance during midsummer 1996, when zooplankton community N:P was 14:1.
- The importance of the zooplankton as a nutrient pool in the water column increased greatly. Before the large increase of zooplankton (and especially *Daphnia*) in 1996 (Figure 1), zooplankton biomass contributed far less than 1% of total P in the mixed layer (Sterner and others 1996). In contrast, in 1996, zooplankton P represented more than 32% of total epilimnetic P. The contribution of zooplankton to epilimnetic N also increased but not to this extent (zooplankton contributed 16% of total N in 1996). Thus, in 1996 zooplankton became a major reservoir for P (a "sink", sensu Andersen 1997) in L227, leaving less P available for incorporation into phytoplankton biomass. Relatively high zooplankton contributions to epilimnetic N and P have been observed in previous surveys of pelagic nutrient pools (Hessen and others 1992; Hassett and others 1997). However, storage of limiting nutrient in grazer biomass generally has not been considered as a factor contributing to reduced algal standing stocks after planktivore reduction (but see Urabe 1994).
- Increased zooplankton biomass clearly increased overall dissolved nutrient availability, but these increases were larger for N than for P (Figure 4) as indicated by the increase in epilimnetic TIN:TDP ratio in 1996. Thus, inorganic nitrogen was unusually available in the mixed layer in 1996, unlike all years after reduction of L227's fertilizer N:P ratio. As predicted, changes in relative N and P availability caused the phytoplankton community to shift away from N-fixing cyanobacteria (Figure 5). The long-term association of N-fixer dominance and TIN:TDP ratio is remarkably similar to the plot of cyanobacteria dominance versus TN:TP of Smith (1983). The apparent threshold above which cyanobacteria were excluded in L227 (38) falls in the range of thresholds reported previously [31 in Smith and Bennett (1999), 49 in Smith and others (1995), 65 in Smith (1983)]. These differential changes in dissolved N and P and reductions in N-fixer dominance in response to the altered zooplankton community are consistent with the results of direct manipulations of *Daphnia* biomass in small enclosures in L227 (MacKay and Elser 1998). In those experiments, increased *Daphnia* abundance caused a twofold increase in NH_4^+ concentrations after 5 days, but TDP concentrations were unchanged. Rates of N fixation also were depressed in the presence of *Daphnia*. Thus, in this case, small-scale mesocosm experiments yielded accurate predictions about whole-ecosystem responses to zooplankton change.
- Seston C:P and N:P ratios were low in 1996 relative to prior years (Figure 2B), indicating relatively rapid growth rates of the remaining phytoplankton biomass (Healey and Hendzel 1980). Thus, decreased phytoplankton biomass (as measured by seston C, dry weight, or cell volume) in 1996 reflected the combined influence of less limiting nutrient (P) captured by the phytoplankton and alteration in the biomass produced per nutrient acquired. In this aspect, the whole-lake response to increased *Daphnia* differed from the mesocosm response reported by MacKay and Elser (1998), in which enhanced *Daphnia* resulted in increased seston C:P. On the

other hand, the reduction in seston C:P in L227 in response to increased *Daphnia* is similar to that seen during experimental studies in hypereutrophic Funada-ike Pond by Urabe (1994), in which enhanced *Daphnia* successfully cropped the algae, resulting in increased per capita P supply rate and lower seston C:P.

- Sedimentation appears to have been altered by the food-web manipulation. Despite a large reduction in the standing stock of suspended C, N, and P in the water column, sedimentation rates did not decrease. The net result, then, was that positive effects (Bloesch and Burgi 1989) of zooplankton on sedimentation rates (due to repackaging from small, slowly sinking particles to larger, more rapidly sinking particles, such as large algae, fecal pellets, zooplankton carapaces, etc.) appeared to be largely counteracted by negative mechanisms (such as overall reduction in particle standing crops, as proposed by Sarnelle 1992). In fact, sedimentation rates of particulate P were highest in 1996 when particle densities were lowest, indicating that the food-web configuration in 1996 greatly decreased the potential residence time of particles in the surface waters (Figure 3). Some stoichiometric aspects of sedimentation also appeared to change after manipulation as C:P and N:P ratios of sedimenting particles were low in 1995 and 1996 relative to previous years. This reduction in sedimentation C:P and N:P concurrent with a reduction in zooplankton N:P is inconsistent with a previous multilake study showing a negative correlation between sedimentation N:P and zooplankton N:P in various ELA lakes (Elser and Foster 1998).

Clearly, food-web manipulation had major effects on ecosystem dynamics in L227. Although we cannot discount the importance of direct grazing by *Daphnia* on cyanobacteria (Sterner 1989 #1343) as a contributor to these effects, prior studies in L227 indicated weak grazing on established algal blooms in this system (MacKay and Elser 1998). Nevertheless, our data indicate that major alterations in the storage, fluxes, and relative availabilities of N and P in the pelagic waters of L227 are associated with increased zooplankton biomass and altered species composition in 1996. Consumer-driven nutrient cycling processes appeared to generate an increased N:P ratio in the available nutrient supply. According to resource ratio competition theory (Smith 1983), a higher N:P in the nutrient supply should result in decreased dominance of cyanobacteria in the phytoplankton community, as we observed (Figure 5). For the first time since the N:P ratio of external fertilizer was lowered from 29 to 11 (and then to 0), the phytoplankton community was dominated by a complex mixture of chlorophyte, chrysophyte, and cryptophyte taxa and not by N-fixing cyanobacteria. Thus, L227 in 1996 resembled the situations described by Schindler and Comita (1972) for Severson Lake and by Smith (1983) for Lake Trummen after winterkill of fish, in which the normal dominance of cyanobacteria in the phytoplankton community disappeared despite low TN:TP ratio. It is not surprising, then, that the food-web changes in L227 resulted in a disruption of N fixation, the mechanism by which lake ecosystems can compensate for deficiencies of N in the external nutrient load (Schindler 1977). In sum, it appears that introduction of piscivorous pike and elimination of planktivorous fish generated a significant low N:P internal sink in L227. This low N:P sink, the *Daphnia*-dominated zooplankton community, appeared to counteract the low N:P source of nutrients entering the lake, drastically altering the response of the lake ecosystem to its external nutrient load.

One surprise during this study was the sudden (and delayed) appearance, and subsequent disappearance (see below), of *Daphnia pulicaria*. Schindler and Comita (1972) observed an identical event after fishkill in Severson Lake in which the invading *Daphnia* increased rapidly to large numbers but had not been detected in the previous 10 years of intensive zooplankton sampling. Based on past sampling and paleolimnological analysis of zooplankton remains, *Daphnia* from the *pulex* species complex have not occurred previously in L227 (Malley and others 1988; Hann and others 1994). One possibility for a source of large *Daphnia* is that *Daphnia pulicaria* was introduced, by natural means or inadvertently by researchers, during the postmanipulation period and required a considerable time to build a population. Alternatively, the species may have recruited from low numbers of resting stages in the sediments that were undetected in the paleolimnological sampling. Close examination of 1995 zooplankton samples collected in vertical tows by Freshwater Institute personnel indicated that *D. pulicaria* was present at low levels during late summer and fall (approximately 0.1 animals L^{-1}). Furthermore, samples taken under the ice during winter 1995–96 contained *D. pulicaria*, suggesting that *D. pulicaria* slowly continued to build a population in the lake during the winter of 1995–96. This may have made it possible for *D. pulicaria* to be present at sufficiently high densities during spring 1996 to alter phytoplankton dynamics and nutrient availability. The possible role of external inoculation in

influencing the response of the L227 food web to pike introduction calls attention to the potential effects of historical contingency in community organization (Jenkins and Buikema 1998). Furthermore, delayed responses of food webs in the L227 experiment and in previous studies (for example, McNaught and others 1999) highlight the importance of sustained, multiyear investigations in whole-ecosystem experimentation, consistent with the general idea that relevant temporal scales covary with spatial scales of observation (Schindler 1998).

Considerable discussion regarding the effects of food-web structure on lower trophic levels has centered on the stability of those effects in eutrophic lakes (Gliwicz 1990; Shapiro 1990; Carpenter and others 1992b; Andersen 1997). Indeed, several sets of theoretical analyses have suggested that eutrophic lake communities are governed by alternative stable states characterized by major differences in algae–grazer interactions (Scheffer 1990; Andersen 1997; Gragnani and others 1999). The dynamics of L227 after pike introduction, and subsequent dynamics not analyzed here, fit this pattern. For example, in both 1995 and 1996, minnow predation on zooplankton was essentially absent, but in 1995 no major changes in the zooplankton community occurred, and the cyanobacteria-dominated algal bloom occurred as usual. In 1996, however, abundance of large-bodied *Daphnia* exploded and generated dramatically altered algal biomass and community composition. By late summer, *Daphnia* had disappeared nearly as rapidly as they had appeared. Subsequent events in L227 add to the appearance that alternative stable states underpin trophic interactions in this system: despite the continued lack of vertebrate planktivores in 1997 and 1998 (minnow CPUE was zero), zooplankton biomass was once again low, *Daphnia* were rare, and dense cyanobacteria blooms returned (J.J. Elser and Freshwater Institute, unpublished data). Such dynamics appear consistent with stoichiometric models of grazer–algae interactions. These models predict the existence of intrinsic high grazer and grazer-free stable states under eutrophic conditions (Andersen 1997), even without spatial heterogeneity or alternative autotroph components (for example, macrophytes; Scheffer 1990). Whereas nutrient loading, trophic cascade, and stoichiometric theories provide a fundamental understanding of eutrophic lake dynamics, our ability to make specific forecasts of the occurrence and intensity of cyanobacteria blooms in such systems may be inherently limited by the nonlinear mechanisms that underpin the nutrient-phytoplankton-zooplankton system (Sas 1989; Harris 1994; Andersen 1997; Elser 1999).

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