

Nutrients and zooplankton as multiple stressors of phytoplankton communities: Evidence from size structure

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Abstract

Anthropogenic alterations of nutrient inputs and food-web structure are two of the primary stressors affecting lake phytoplankton. This paper explores the independent and interactive effects of nutrients and food-web structure (as indexed by zooplankton size) on phytoplankton size structure by fitting time-series models to data from three lakes where both factors have been manipulated. I assessed phytoplankton size structure using three different approaches: small and large size classes, normalized size spectra, and average phytoplankton size. Increased phosphorus loading and increased zooplankton size had positive effects on large phytoplankton, slope of size spectra, and mean phytoplankton size, but negative effects on the relative abundance of small phytoplankton. The absolute abundance of small phytoplankton was increased by increased nutrients and decreased by increased zooplankton size. There was some evidence for nutrient \times zooplankton interactions, particularly from interlake comparisons which revealed that phytoplankton size structure responded to enrichment in qualitatively similar but quantitatively different ways in lakes with different food webs. Specifically, small phytoplankton increased more strongly with enrichment in lakes with many planktivores and few large zooplankton, while large phytoplankton increased more in lakes with few planktivores and many large zooplankton. Thus, food-web structure may influence the extent to which small vs. large phytoplankton respond to nutrient enrichment. Overall, size structure was an excellent descriptor of shifts in phytoplankton communities following manipulation of nutrient inputs and food-web structure. Size spectra and size classes were highly effective approaches for summarizing size structure; average phytoplankton size was somewhat less effective.

Predicting the effects of anthropogenic stressors on phytoplankton biomass and community structure is fundamental to the effective management and restoration of lake water quality. However, predicting phytoplankton dynamics is no easy task. Phytoplankton community composition is notoriously difficult to anticipate, particularly at the species level (Reynolds 1984). As a result, many researchers are exploring alternative community metrics, including higher taxonomic categories, guilds, and size-based variates.

Size-based variates are a leading candidate for a predict-

able index of phytoplankton community structure. Allometric scaling explains much of the variation among individual phytoplankton in growth and respiration rates, nutrient uptake kinetics, sinking rates, and susceptibility to grazing. Smaller cells tend to grow more quickly, obtain nutrients more efficiently at low nutrient levels, sink more slowly, and be grazed more than larger cells (Malone 1980; Reynolds 1984). These properties have been used to predict patterns in seasonal succession (Reynolds 1984) and transmission of energy and contaminants from phytoplankton to higher trophic levels (Malone 1980). This paper evaluates whether size structure is a predictable metric of phytoplankton community response to two common anthropogenic stressors which have the potential to strongly influence phytoplankton: increases in nutrients and alterations of food-web structure.

Nutrient availability, particularly of phosphorus (Schindler 1977), determines potential phytoplankton biomass, while grazing by zooplankton determines how much of this potential is realized (Carpenter et al. 1985). Zooplankton grazing is in turn influenced by the abundance of zooplanktivorous fish (Hrbáček et al. 1961; Brooks and Dodson 1965), such that phytoplankton can be affected by trophic interactions that cascade from fish to phytoplankton (e.g., Carpenter et al. 1985, 1987; Gulati et al. 1990; Kitchell 1992; Carpenter and Kitchell 1993; Findlay et al. 1994).

Nutrient availability and food-web structure (as indexed by zooplankton) also affect phytoplankton size structure. Allometric scaling predicts that small phytoplankton should outcompete large phytoplankton when nutrients are scarce, while larger phytoplankton should outcompete small phytoplankton when grazing pressure is high (Malone 1980). Comparative studies generally support these expectations.

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Table 1. Expected changes in phytoplankton size structure due to increases in nutrient loading or mean length of crustacean zooplankton, derived from comparative studies, mesocosm experiments, models, and single-factor whole-lake experiments (including Kalff and Knoechel 1978; Gliwicz 1975; Nilssen 1978; Spodniewska 1978, 1979; Harris 1980; Malone 1980; Watson and Kalff 1981; Sprules and Knoechel 1984; Sprules and Munawar 1986; McQueen 1990; Watson et al. 1992; Mazumder 1994; Reynolds 1994; Bendorff 1995). Symbols: + indicates an increase, - indicates a decrease, and nc indicates no change.

Variate	Increased nutrients	Increased mean crustacean length
Small phytoplankton biomass	+/nc	-
Large phytoplankton biomass	+	+
Percent small phytoplankton	-	-
Mean phytoplankton size	+	+

Although small phytoplankton dominate under low nutrient conditions, large phytoplankton become dominant as lakes become more eutrophic (Kalff and Knoechel 1978; Spodniewska 1978, 1979; Watson and Kalff 1981; Sprules and Knoechel 1984; Watson et al. 1992). Heavy grazing by *Daphnia* and other large zooplankton on small, readily edible phytoplankton promotes growth of large, less edible phytoplankton (Nilssen 1978; Leibold 1989; Watson et al. 1992; Mazumder 1994). As a result of these changes, increased nutrients and increased large zooplankton tend to decrease the relative abundance of small phytoplankton and increase average phytoplankton size (Gliwicz 1975; Harris 1980). These and other patterns from the literature provide expectations for the independent effects of nutrients and zooplankton on phytoplankton size structure (Table 1).

In many lakes, anthropogenic perturbations of nutrients and food-web structure occur concurrently, yet relatively little is known about how these factors interact. Does nutrient loading affect how zooplankton graze phytoplankton? Do zooplankton influence how phytoplankton respond to increased nutrients? Several recent studies indicate that nutrients and zooplankton have additive and independent effects on total chlorophyll (Vanni 1987; Mazumder et al. 1988; Drenner et al. 1990; Elser and Goldman 1991; Carpenter et al. 1991, 1996; Cottingham et al. 1997). However, effects may not be independent for less aggregated variates such as size structure or functional groups. For example, Mazumder (1994) used data from mesocosm experiments to show that enrichment of mesoeutrophic systems leads to increased small phytoplankton when grazing pressure is low, but increased large phytoplankton when grazing pressure is high. Thus, the presence of large zooplankton may control the extent to which small vs. large phytoplankton respond to nutrient enrichment. To date, the dynamic consequences of this prediction have not been tested at the scale of whole lakes.

This paper explores the independent and interactive effects of nutrients and food-web structure (as indexed by zooplankton size) using time-series data from lakes where both factors have been manipulated. I quantify the effects of nutrients and zooplankton size on three aspects of phytoplank-

ton size structure (size classes, size spectra, and mean size), then compare these effects to expectations from the literature. I also assess whether there are statistical and(or) biological interactions between nutrient loading and zooplankton grazing. Results suggest that increases in nutrients and(or) zooplankton size can have substantial effects on phytoplankton size structure and that zooplankton size may have some effect on how phytoplankton size structure responds to increased nutrients.

Methods

Whole-lake experiments—Paul, Peter, and Long Lakes (Gogebic County, Michigan: 89°32'W, 46°13'N) are small, seepage systems that were studied intensively from 1991 to 1994 as part of an experiment to evaluate whether lakes with different food webs respond differently to increased nutrient loading. Lake characteristics, experimental design and execution, and responses to manipulation are described fully elsewhere (Carpenter et al. 1996; Christensen et al. 1996). Here, I include only information relevant to the quantification of the effects of the manipulations on phytoplankton size structure.

Both food-web structure and nutrient loading were manipulated during the experiment. In May 1991, Long Lake was divided into three separate basins (east, west, and central) by plastic curtains (Christensen et al. 1996). Piscivorous fishes were then removed from East Long and Peter Lakes and replaced with zooplanktivorous golden shiners (*Notemigonus crysoleucas*) (Schindler et al. 1993; Carpenter et al. 1996). This manipulation resulted in zooplankton communities dominated by rotifers and cyclopoid copepods. In East Long Lake, the stocked planktivores did not survive their first summer, and beginning in mid-1992, the zooplankton community was dominated by large *Daphnia* (Christensen et al. 1996). However, in Peter Lake, the high-planktivory food web was maintained until mid-1994, when *Daphnia* invaded following a midsummer fishkill (Carpenter et al. 1996; Schindler et al. 1997). Thus, East Long Lake had both small and large zooplankton during 1991–1994, while Peter Lake had small zooplankton for most of this period.

In contrast, the food webs of Paul and West Long Lakes were maintained as low-planktivory systems dominated by piscivorous bass (*Micropterus salmoides* in both lakes and *Micropterus dolomieu* in West Long Lake only). In Paul Lake, the zooplankton community was dominated by carnivorous larvae of *Chaoborus* spp. and a mixed herbivore assemblage of large cladocerans and intermediate sizes of copepods. In West Long Lake, large cladocerans dominated the zooplankton. Paul and West Long Lakes therefore represent systems with moderately large and large zooplankton, respectively.

In 1991 and 1992, each lake was monitored under baseline nutrient conditions (P loading rates of about 0.1–0.2 $\mu\text{g liter}^{-1} \text{d}^{-1}$). Beginning in May 1993, Peter, West Long, and East Long Lakes were enriched daily during the summer season using liquid fertilizer containing phosphate, nitrate, and ammonium at the ambient N:P ratio of 25:1 by atoms (Carpenter et al. 1996). Time-courses for nutrient loading

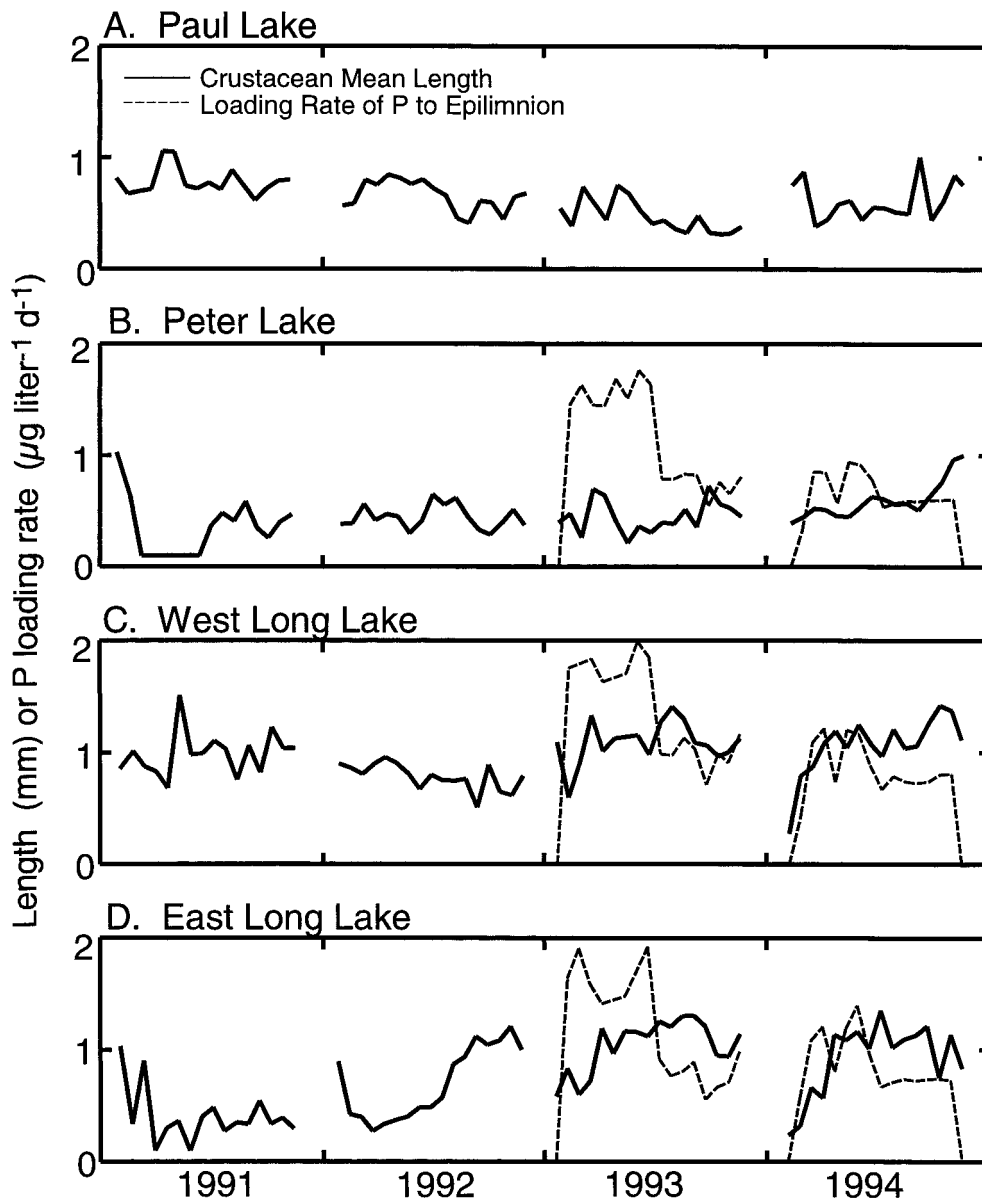


Fig. 1. Mean crustacean zooplankton length (mm) and experimental nutrient addition rate ($\mu\text{g P liter}^{-1} \text{d}^{-1}$) during the summer stratified period, 1991–1994. A. Paul Lake, the reference system, was not enriched and was dominated by moderately large zooplankton. B. Peter Lake was fertilized and dominated by small crustaceans for nearly all of the monitoring period. C. West Long Lake was fertilized and had large crustaceans throughout the experiment. D. East Long Lake was fertilized and had small crustaceans in 1991 and early 1992 and large crustaceans from late 1992 through 1994.

rates (as P) and food-web effects (as biomass-weighted mean crustacean length) are summarized in Fig. 1; many previous studies support the use of mean crustacean length as an indicator of top-down food-web effects (Brooks and Dodson 1965; Pace 1984; Gulati et al. 1990; Carpenter et al. 1991; Soranno et al. 1993).

Limnological analyses—During summer stratification (approximately mid-May to mid-September), each lake was sampled weekly at a central station (Carpenter and Kitchell

1993; Voichick and LeBouton 1994). Temperature, oxygen, and light profiles were measured; phytoplankton were sampled with van Dorn casts at 25, 50, and 100% of surface irradiance; and zooplankton were sampled with two vertical hauls of the entire water column with a calibrated 80- μm mesh net.

Phytoplankton samples from the three van Dorn casts were pooled, preserved in glutaraldehyde, mounted in methacrylic resin, and enumerated and measured by species (St. Amand 1990; Cottingham 1996). For each sample, the mean

greatest axial linear dimension (GALD), mean individual biovolume (protoplasm exclusive of loricae and sheaths, determined by geometric formulae), and density of each taxon were determined (Elser et al. 1986; St. Amand 1990). Biovolume ($\mu\text{m}^3 \text{ ml}^{-1}$) was converted to fresh biomass (mg liter^{-1}) assuming that $1 \mu\text{m}^3 = 1 \times 10^{-6} \mu\text{g}$ (Elser and Carpenter 1988).

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). Mean crustacean length was weighted by biomass (Elser et al. 1987).

Quantification of phytoplankton size structure—Methods for evaluating the size structure of field assemblages of phytoplankton vary widely among researchers (Munawar and Munawar 1975). The simplest and most commonly used approach divides phytoplankton biomass into small and large size classes using a specific size criterion (e.g., Munawar and Munawar 1981; Mazumder et al. 1992; Carpenter et al. 1996). Normalized size spectra (Sprules et al. 1983; Mazumder et al. 1988; Ahrens and Peters 1991) and mean phytoplankton size (Lewis 1976; Carpenter et al. 1993) are two alternative approaches that assess size structure using more detailed information on size variation among individuals. To date, these three alternative measures of size structure have not been systematically compared for field assemblages of phytoplankton.

Size classes: I divided phytoplankton into small vs. large size classes using a threshold GALD (μm) that approximates the maximum size above which phytoplankton are not readily consumed by filter-feeding zooplankton (Gelin and Ripl 1978). Estimates of the actual threshold for edibility range from 5 to 10 μm (Gliwicz 1975; McCauley and Downing 1985) to as much as 64 μm (Munawar et al. 1988; Munawar and Munawar 1981). Most studies that consider two phytoplankton size fractions choose one threshold and assume that it is a functionally valid separation of small vs. large taxa. Preliminary analyses with this dataset indicated that all thresholds at or below 30 μm yielded consistent qualitative results both within and among lakes; however, results began to diverge when phytoplankton in the 30–40- μm size range were included in the small, edible size class (Cottingham 1996). I used a threshold of 30 μm for this paper.

Using this threshold and the data from microscopic enumeration, I created time series for the biomass of phytoplankton in the small and large size classes, as well as the percent of biomass due to small phytoplankton, for each of the four lakes for the period from 1991 to 1994. I then analyzed the effects of P input rate and mean crustacean length on each time series using the statistical procedures described below.

Normalized size spectra: I used normalized size spectra (e.g., Sprules et al. 1983; Sprules and Munawar 1986; Ahrens and Peters 1991) to examine and quantify the distribution of phytoplankton biomass among multiple size classes. This method fits a linear model to the relationship between the logarithm of normalized abundance (or bio-

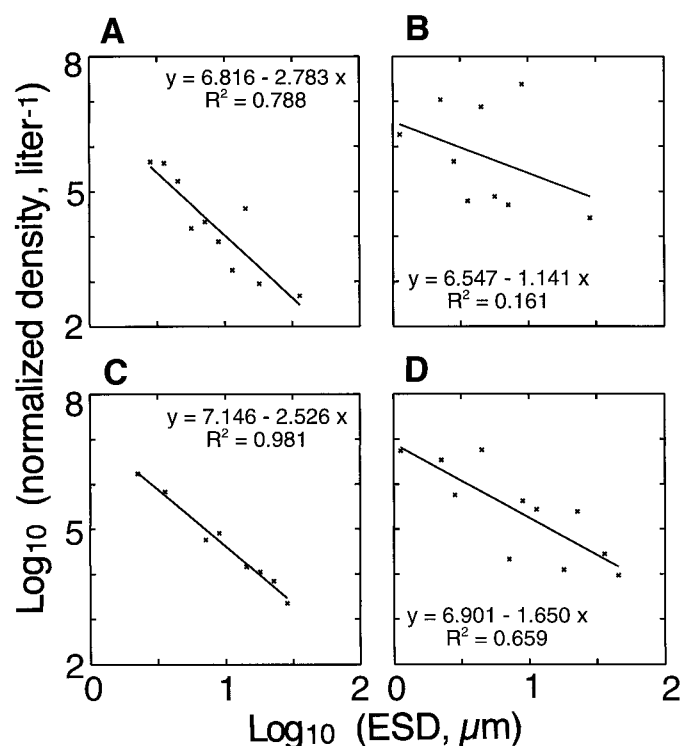


Fig. 2. Example of normalized size spectra for four sampling dates in late August. These panels exemplify the contrasts between food webs with small vs. large crustacean zooplankton and without vs. with experimental nutrient enrichment. A. Small zooplankton and low nutrient loading, Peter Lake on 27 August 1991. B. Small zooplankton and high nutrient loading, Peter Lake on 25 August 1993. C. Large zooplankton and low nutrient loading, West Long Lake on 22 August 1991. D. Large zooplankton and high nutrient loading, West Long Lake on 24 August 1993.

mass) within each size class and the logarithm of average cell size within the class (Fig. 2). Sheldon et al. (1972) hypothesized that at equilibrium, total abundance will be distributed uniformly among logarithmic size classes; normalized size spectra provide a quantitative test of this hypothesis. Specifically, if the hypothesis is true, then the slope of the linear model should be -1 , with little unexplained variance (mean square error, or MSE) (Sprules and Munawar 1986). Steeper slopes indicate that there are more small organisms than predicted, while shallower slopes indicate that there are more large organisms than predicted; high residual variation indicates that size structure cannot be described by a simple linear model.

I created size spectra following the method of Ahrens and Peters (1991). Using the average biovolume (μm^3) for individuals within a taxon, I assigned each taxon to one of 19 size classes of successively doubled biovolume. Because I included only phytoplankton in these analyses, my smallest and largest size classes differed somewhat from those of Ahrens and Peters (1991). My smallest size class had equivalent spherical diameters (ESD) of 1.0–1.3 μm , while the largest size class ranged from 64 to 81.3 μm . Total biomass within each size class was calculated by summing across taxa, and any size class with zero biomass was not included,

leaving an average of nine size classes for each sampling date.

I calculated the normalized density (liter^{-1}) of each size class by dividing the total biovolume in that class ($\mu\text{m}^3 \text{ liter}^{-1}$) by the change in biovolume across the size class (μm^3). The size spectrum for each sampling date consisted of a $\log_{10}\text{-}\log_{10}$ plot of normalized density in each size class vs. the geometric mean equivalent spherical diameter (ESD). Choice of the abscissa does not affect the results, since all of the possible choices (ESD, biovolume, and biomass) are functions of one another (Sprules 1988). Linear regression models [$\log_{10}(\text{normalized density}) = b_0 + b_1 (\log_{10}\text{ESD})$] were fit to each size spectrum using the least-squares criterion (Fig. 2).

Patterns in the intercept (b_0), slope (b_1), and residual MSE through time were explored by plotting the time series for each variate in each experimental lake during the period from 1991 to 1994. I then quantified the effects of P input rate and mean crustacean length on slope and MSE using the statistical procedures described below.

Mean phytoplankton size: On each sampling date, mean phytoplankton size was estimated using a biomass-weighted average of the greatest axial linear dimension (GALD; Carpenter et al. 1993):

$$\overline{\text{GALD}} = \frac{\sum_{i=1}^N (B_i \times \text{GALD}_i)}{\sum_{i=1}^N B_i} \quad (1)$$

B_i indicates the biomass of species i , GALD_i is the average individual GALD for species i , and N is the number of species present. Time series for mean GALD were then compiled and analyzed as described below.

Statistical analyses—Effects of P input and zooplankton size on various measures of phytoplankton size structure were quantified using ARIMA transfer functions (Box et al. 1994) of the form described by Carpenter et al. (1996). The response variates I wanted to predict were biomass of phytoplankton in small and large size classes, the percent of total biomass in the small size class, the slope and MSE of linear regressions fit to normalized size spectra, and mean GALD. The primary predictor variates were daily P input rate per unit epilimnion volume ($\mu\text{g liter}^{-1} \text{ d}^{-1}$) and mean crustacean length (mm); these series were not correlated with one another and hence can be used to represent the independent manipulations (Carpenter et al. 1996). I also evaluated the effects of a third predictor, the product of the nutrient and zooplankton time series, in order to determine whether there was a statistical interaction between nutrient and zooplankton effects.

Time-series analysis of each variate proceeded in two steps. I performed exploratory analyses to identify the best predictive model using the identification procedures of Ljung (1991), Wei (1990), and Box et al. (1994). Models were compared using prediction error, magnitude of parameters relative to their standard deviations, autocorrelations and normal probability plots of residuals, cross-correlation func-

tions of residual and predictor series, and Akaike's final prediction error. After identifying the best model, I calculated joint and marginal parameter distributions as Bayesian posterior distributions assuming a noninformative prior distribution (Box and Tiao 1973; Carpenter et al. 1996). Results are presented using the marginal probability distributions (MPD) for the effects. MPD can be interpreted directly as probabilities: the height of the curve (ordinate) at a particular effect size (abscissa) gives the relative probability of observing an effect of that size, and the area to the right (left) of the abscissa indicates the relative probability of observing a larger (smaller) effect. In addition, the P -value for the usual null hypothesis that a parameter is equal to 0 can be determined from the relative height of the MPD curve where the effect size is 0.

I adjusted the raw time series for P loading rate, mean crustacean length, and phytoplankton size structure to meet the assumptions of ARIMA models. First, I created a dataset that ran through the 4 yr of the experiment by ignoring data gaps during fall, winter, and spring, and stacking data from subsequent summers. This approach assumes that the covariance among observations is consistent across years. Second, I ensured that all time series were the same length (60 samples) and that there were the same number of samples in each year (15) by dropping early May and late September samples from years with too many samples and creating data points for missing samples in 1993 (21 June; 2, 3, and 5 August) by averaging the values for the samples before and after the missing date. Finally, I transformed variates to ensure normally distributed residuals for a stationary series (Wei 1990; Box et al. 1994). Biomasses of small and large phytoplankton and mean GALD were transformed using natural logarithms [$\ln(x + 1)$]. All time series were differenced to remove trend (Wei 1990; Box et al. 1994).

The primary model for each response variate assumed additive and independent effects of nutrients and zooplankton:

$$R_t = \omega_p \Delta P_{t-kP} + \omega_z \Delta Z_{t-kZ} + \left(\frac{1 + \Theta B}{1 + \Phi B} \right) \epsilon_t \quad (2)$$

In equation 2, R_t is the growth rate in the response variate V from time $t - 1$ to time t (Carpenter et al. 1996). For the variates that were log-transformed prior to analysis (mean GALD, small and large size classes), $R_t = \log(V_t/V_{t-1})$. For the untransformed variates (percent of biomass in the small size class, slope, MSE), $R_t = V_t - V_{t-1}$. The parameters of primary interest were the estimated effect sizes, ω_p and ω_z . The predictors were the weekly changes in P input rate ($\mu\text{g liter}^{-1} \text{ d}^{-1}$) and mean crustacean length (mm):

$$\Delta P_{t-kP} = P_{t-kP} - P_{t-kP-1}; \quad (3)$$

$$\Delta Z_{t-kZ} = Z_{t-kZ} - Z_{t-kZ-1}. \quad (4)$$

Values for the lags in the effects of P input (kP) and crustacean length (kZ) were selected using diagnostic procedures described by Ljung (1987) and Wei (1990). Autoregressive (Θ) and moving average (Φ) parameters at a backshift of B were used to correct for autocorrelations in the series. ω_p , ω_z , Θ , and Φ and their joint error distribution were estimated by minimizing prediction errors (Ljung 1987). All models

were identified, fit, and evaluated using the System Identification Toolbox of Matlab (Ljung 1987, 1991).

In addition to the additive model for independent effects, I also used a second, more complicated model to test for statistical interaction (ω_1) of the nutrient and zooplankton time series:

$$R_t = \omega_P \Delta P_{t-kP} + \omega_Z \Delta Z_{t-kZ} + \omega_1 \Delta I_{t-kI} + \left(\frac{1 + \Theta B}{1 + \Phi B} \right) \epsilon_t. \quad (5)$$

All terms in Eq. 5 were the same as in Eq. 2, with the addition of kI (the lag in the product of P input and crustacean length) and ΔI_{t-kI} :

$$\Delta I_{t-kI} = \Delta P_{t-kI} \times \Delta Z_{t-kI}. \quad (6)$$

Because I was interested in effects of the experimental manipulations in Peter, West Long, and East Long Lakes, I first fit models to data from each manipulated lake. I then grouped the manipulated lakes together and analyzed the joint dataset in order to better estimate zooplankton effects because the largest difference in mean crustacean length was found between Peter Lake and the two basins of Long Lake. No models were fit to data from Paul Lake due to lack of contrast in both the nutrient and zooplankton time series (Carpenter et al. 1996; Fig. 1).

Results

Size classes—In Paul Lake, the unenriched lake with moderately large zooplankton, total phytoplankton biomass fluctuated from 1991 to 1994, but showed no persistent changes (Fig. 3A). There was an unusual bloom of large *Volvox* colonies on one sampling date in June 1994; otherwise, biomass remained <2 mg liter⁻¹, consistent with trends from 1984 to 1990 (Carpenter et al. 1993). Biomass in each size class also varied from year to year, but there were no persistent changes.

Phytoplankton dynamics were less consistent in Peter Lake, the enriched lake with small zooplankton (Fig. 3B). Total biomass increased from 1991 to 1993, but decreased somewhat in 1994. From 1991 to 1992, biomass in each size category increased approximately in proportion to its 1991 abundance. In contrast, increases following experimental enrichment were due first to intermediate-sized phytoplankton (20–30 μ m) and later to phytoplankton >40 μ m. In 1994, phytoplankton >40 μ m dominated only in May and early June; phytoplankton <30 μ m dominated for the rest of summer (Fig. 3B).

In West Long Lake, an enriched lake with large zooplankton, average total biomass increased every year, including a 10-fold increase during the period of experimental enrichment (Fig. 3C). As in Peter Lake, phytoplankton in the 20–30- μ m size range dominated in the first few weeks of enrichment. However, phytoplankton >40 μ m dominated throughout the rest of 1993, and this shift to very large taxa persisted throughout 1994.

In East Long Lake, an enriched lake with large zooplankton, total biomass increased from 1991 to 1993, then stabilized in 1994 (Fig. 3D). Total biomass was much lower than in Peter or West Long Lakes. Size structure shifted from

dominance by phytoplankton >40 μ m in 1991 to dominance by phytoplankton <40 μ m in 1992 (Fig. 3D). As in the other enriched lakes, intermediate size classes (especially those taxa between 30 and 40 μ m) responded strongly to the early stages of enrichment, but phytoplankton >40 μ m dominated in late summer. Unlike West Long Lake, however, phytoplankton <20 μ m were dominant in midsummer 1994, with strong contributions from taxa in the 30–40- μ m size range in late summer.

Time-series models for the biomass of small and large phytoplankton and the percent of biomass in small phytoplankton fit reasonably well, particularly when datasets for all three enriched lakes were combined (Table 2). Agreement between model estimates and observations was quite good and residual standard deviations were relatively low. Residuals were normally distributed for most variates.

Qualitative effects of increased P input on phytoplankton size classes were consistent among lakes, although the magnitudes of effects differed (Fig. 4). Increases in P loading tended to be followed by increases in both the small and large size classes. Because increases were somewhat larger in the larger size class, the proportion of small phytoplankton decreased with increased nutrient loading. Increase in the small size class was largest in Peter Lake ($e^{0.4} \approx 1.5x$ vs. $1.1x$ in both West and East Long Lake), while increase in the large size class was largest in West Long Lake ($2.1x$ vs. $1.2x$ in Peter and $1.5x$ in East Long Lakes). Effects were statistically significant ($\alpha = 0.05$) for all three variates in the pooled dataset, but only for a subset of variates in each lake individually (Fig. 4).

Effects of mean crustacean length on phytoplankton size classes were also qualitatively consistent among lakes (Fig. 4). In each lake and in all lakes pooled, a 1-mm increase in mean crustacean length led to a 10–23% decrease in biomass of the small size class, a 22–78% increase in biomass of the large size class, and a 23–27% decrease in the percent of total biomass in the small size class. Although the magnitudes of zooplankton effects were roughly similar to those of P input, the variance was much higher, leading to more nonsignificant effects: only the positive effect of zooplankton on the large size class in West Long Lake and the negative effect on percent small biomass in the pooled dataset were significant at $\alpha = 0.05$.

Normalized size spectra—The linearity of normalized size spectra varied among lakes and years, but overall, these models adequately captured information about phytoplankton size structure and changes following experimental manipulations. I focused on two variables from the linear regressions fit to these spectra—the slope and residual MSE. In this dataset, the slope and intercept of the linear regressions for each sampling date were highly correlated ($r = -0.782$, $n = 240$). Because of this high redundancy, only the slope parameter was considered in further analyses.

Nearly all slopes were negative and less than -1 (Fig. 5), indicating that biomass was not uniformly distributed among size classes. However, slope fluctuated both seasonally and interannually in each lake. Increased (less negative; more shallow) slopes indicate an increase in larger phytoplankters, while decreased (more negative; steeper) slopes suggest an

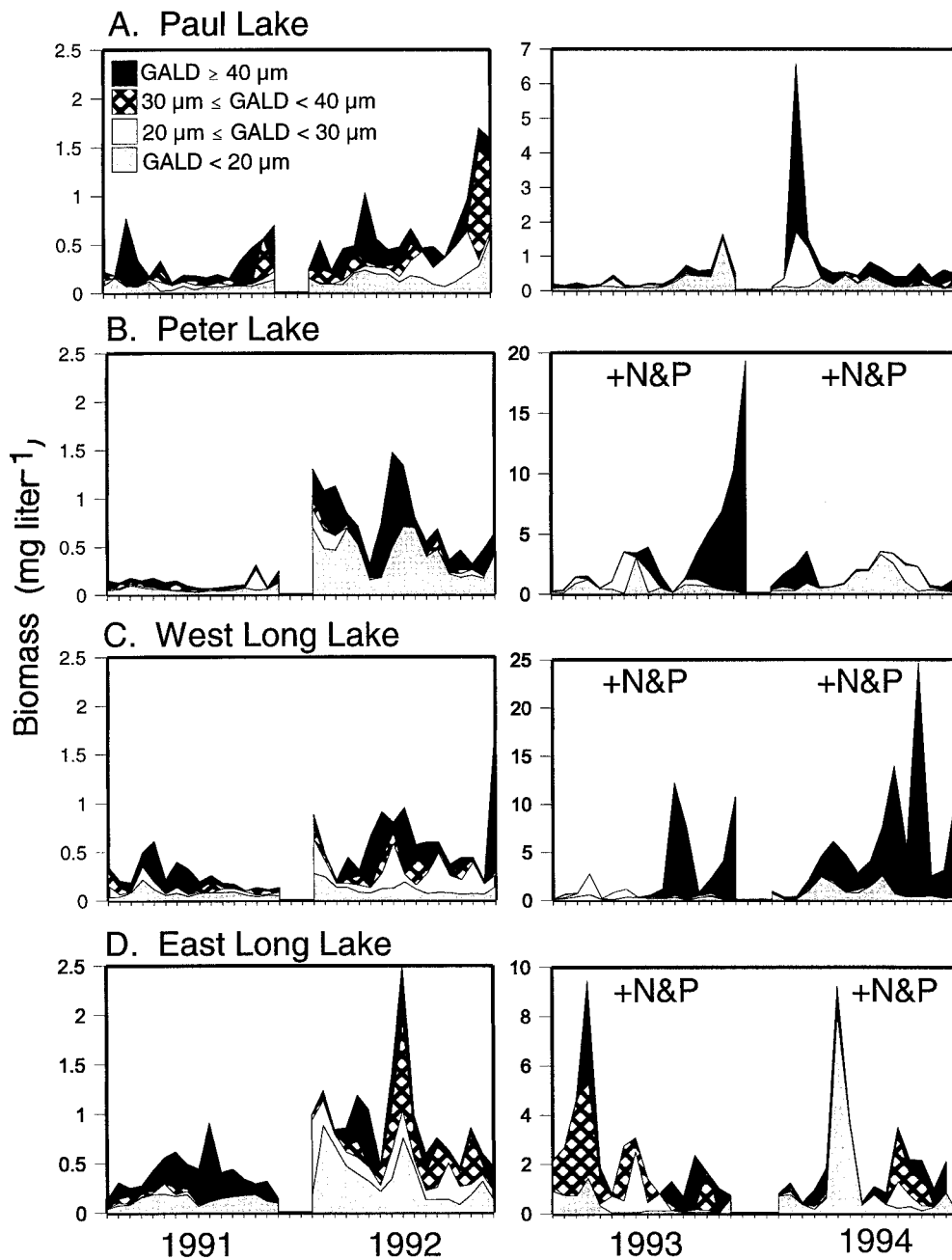


Fig. 3. Comparison of total phytoplankton biomass and community size structure in each lake prior to (1991–1992, left column) and during experimental enrichment (1993–1994, right column). Note the y-axis change between columns and among lakes in the right column.

increase in smaller phytoplankters. Peaks and troughs in the slope therefore correspond to blooms of large and small phytoplankton, respectively.

In Paul Lake, slope varied little except for early-summer blooms in 1991 and 1994 (Fig. 5A). In the other lakes, the slope was more variable, particularly during the years of experimental enrichment. On average, slope increased from 1991 to 1993 and decreased in 1994. In 1994, sustained increases in slope in West Long Lake (Fig. 5C) corresponded to continued domination by phytoplankton $>40 \mu\text{m}$, while declines in slope in East Long (Fig. 5D) and Peter (Fig. 5B)

Lakes corresponded to periods when phytoplankton $<20 \mu\text{m}$ were dominant.

Increases in MSE indicate deterioration in the fit of a linear model to the normalized size spectrum—and thus an increase in the complexity of phytoplankton size structure—while decreases signify improvement in model fit. In Paul Lake, MSE fluctuated little except for two 1-week increases (Fig. 6A). In Peter Lake, MSE increased in 1993 and remained relatively high during 1994 (Fig. 6B). In West Long Lake, MSE increased slightly in 1993 and stayed at that higher level in 1994, but changes were less pronounced than

Table 2. Best-fitting additive time-series models for each variate in each lake, including the parameter estimates, standard deviations (SD), and lags for the effects of nutrients (ω_p), zooplankton (ω_z), and their interaction (ω_1); moving-average parameters θ and their standard deviations, residual standard deviation (s), and the correlation between model estimates and observations (r). Ellipses indicate parameters that could not be reliably estimated (ω_1 in individual lakes) or did not improve model fit (θ).

Variate	ω_p	SD	Lag	ω_z	SD	Lag	ω_1	SD	Lag	$\theta \pm 1$ SD	s	r
Peter Lake												
Small	0.42	0.12	5	-0.27	0.23	0	0.245	0.891
Large	0.18	0.19	7	0.34	0.38	4	0.387	0.990
% Small	-0.20	0.11	7	-0.23	0.21	5	0.210	0.953
Slope	0.33	0.31	0	0.20	0.57	4	-0.20 \pm 0.13	0.634	0.925
										-0.28 \pm 0.13		
MSE	0.45	0.19	7	0.39	0.26	2	-0.99 \pm 0.11	0.362	0.706
GALD	0.60	0.24	7	0.81	0.43	5	0.04 \pm 0.13	0.471	0.873
										-0.37 \pm 0.13		
West Long Lake												
Small	0.10	0.08	2	-0.16	0.15	0	-0.49 \pm 0.13	0.239	0.846
										-0.39 \pm 0.13		
Large	0.72	0.09	7	0.26	0.11	0	-0.01 \pm 0.10	0.400	0.631
										0.01 \pm 0.10		
										-0.98 \pm 0.11		
% Small	-0.28	0.08	4	-0.27	0.14	0	-0.59 \pm 0.11	0.231	0.795
Slope	0.29	0.14	4	0.58	0.25	1	-0.55 \pm 0.12	0.403	0.845
MSE	0.08	0.04	2	0.23	0.10	0	-0.95 \pm 0.06	0.154	0.645
GALD	0.83	0.18	7	0.31	0.35	0	-0.52 \pm 0.12	0.497	0.757
East Long Lake												
Small	0.13	0.14	0	-0.10	0.20	6	0.371	0.991
Large	0.43	0.14	0	0.58	0.21	7	0.371	0.863
% Small	-0.20	0.10	6	-0.27	0.15	6	-0.47 \pm 0.13	0.260	0.828
Slope	0.63	0.13	0	0.58	0.21	3	-0.56 \pm 0.11	0.366	0.728
MSE	0.12	0.08	4	-0.38	0.14	6	-0.70 \pm 0.12	0.251	0.815
GALD	-0.19	0.12	5	0.35	0.21	0	0.336	0.968
All three manipulated lakes combined												
Small	0.17	0.06	1	-0.12	0.10	0	0.17	0.15	3	-0.28 \pm 0.08	0.277	0.918
										-0.27 \pm 0.08		
										-0.11 \pm 0.08		
Large	0.51	0.09	7	0.20	0.13	0	0.38	0.21	7	-0.23 \pm 0.07	0.400	0.850
										-0.12 \pm 0.07		
										-0.43 \pm 0.07		
% Small	-0.19	0.04	8	-0.25	0.07	0	-0.18	0.07	7	-0.47 \pm 0.07	0.228	0.783
										-0.46 \pm 0.07		
Slope	0.44	0.09	0	0.37	0.15	0	0.26	0.17	7	-0.45 \pm 0.07	0.463	0.815
										-0.22 \pm 0.08		
										-0.33 \pm 0.07		
MSE	0.17	0.04	1	-0.17	0.08	6	-0.92 \pm 0.03	0.278	0.707
GALD	0.38	0.11	7	0.29	0.17	6	0.40	0.30	4	-0.24 \pm 0.08	0.484	0.914
										-0.24 \pm 0.08		

in Peter Lake (Fig. 6C). In East Long Lake, there was little change in MSE in 1993, although there was a pronounced decrease in fit following the increase in phytoplankton $<20 \mu\text{m}$ in 1994 (Fig. 6D).

Time-series models for slope and MSE fit reasonably well for all four datasets (Table 2). The effects of increased P loading rate and increased mean crustacean length on the slope of the normalized size spectra were positive (Fig. 7), indicating that both nutrients and large zooplankton increased phytoplankton in larger size classes as compared to smaller size classes. The effect of P loading rate on MSE also tended to be positive, particularly in Peter Lake. However, the effect of zooplankton size on MSE differed among

lakes. In East Long Lake and in all enriched lakes combined, increased zooplankton size significantly decreased MSE, suggesting that a shift toward larger zooplankton improved the fit of a linear model to the normalized size spectrum (and thus made the distribution of biomass across size classes more uniform). However, in West Long and Peter Lakes, larger zooplankton led to a larger MSE and hence poorer model fits.

Mean phytoplankton size—Mean phytoplankton size, expressed as the biomass-weighted GALD, tended to be less variable (Fig. 8) than total biomass, biomass in particular size classes (Fig. 3), or size spectra (Figs. 5, 6). In Paul and

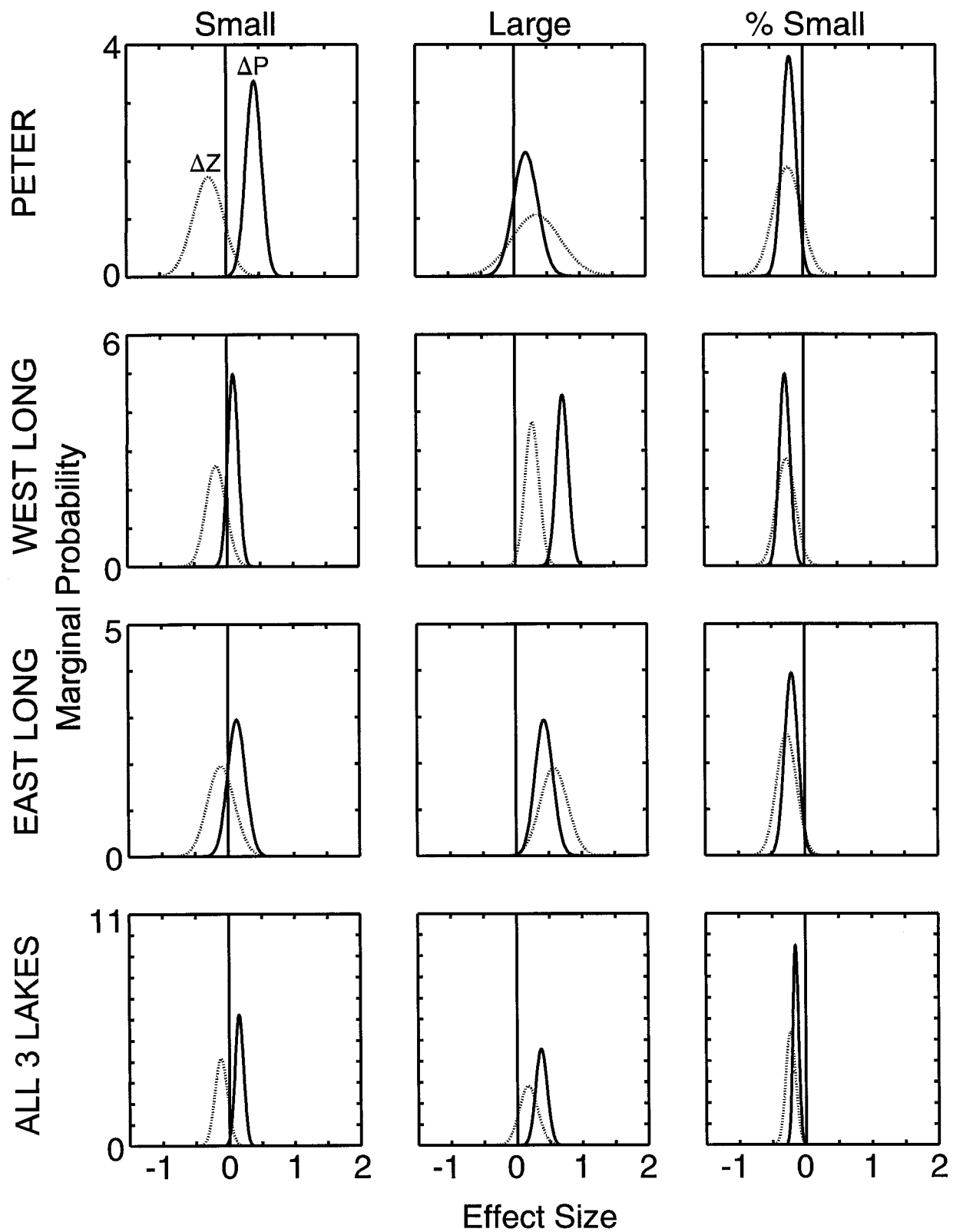


Fig. 4. Marginal probability distributions for the effects of P loading rate (ΔP) and mean crustacean length (ΔZ) on the small size class (left), large size class (center), and the percent of biomass in the small size class (right) for Peter Lake, West Long Lake, East Long Lake, and the pooled dataset for all three manipulated lakes.

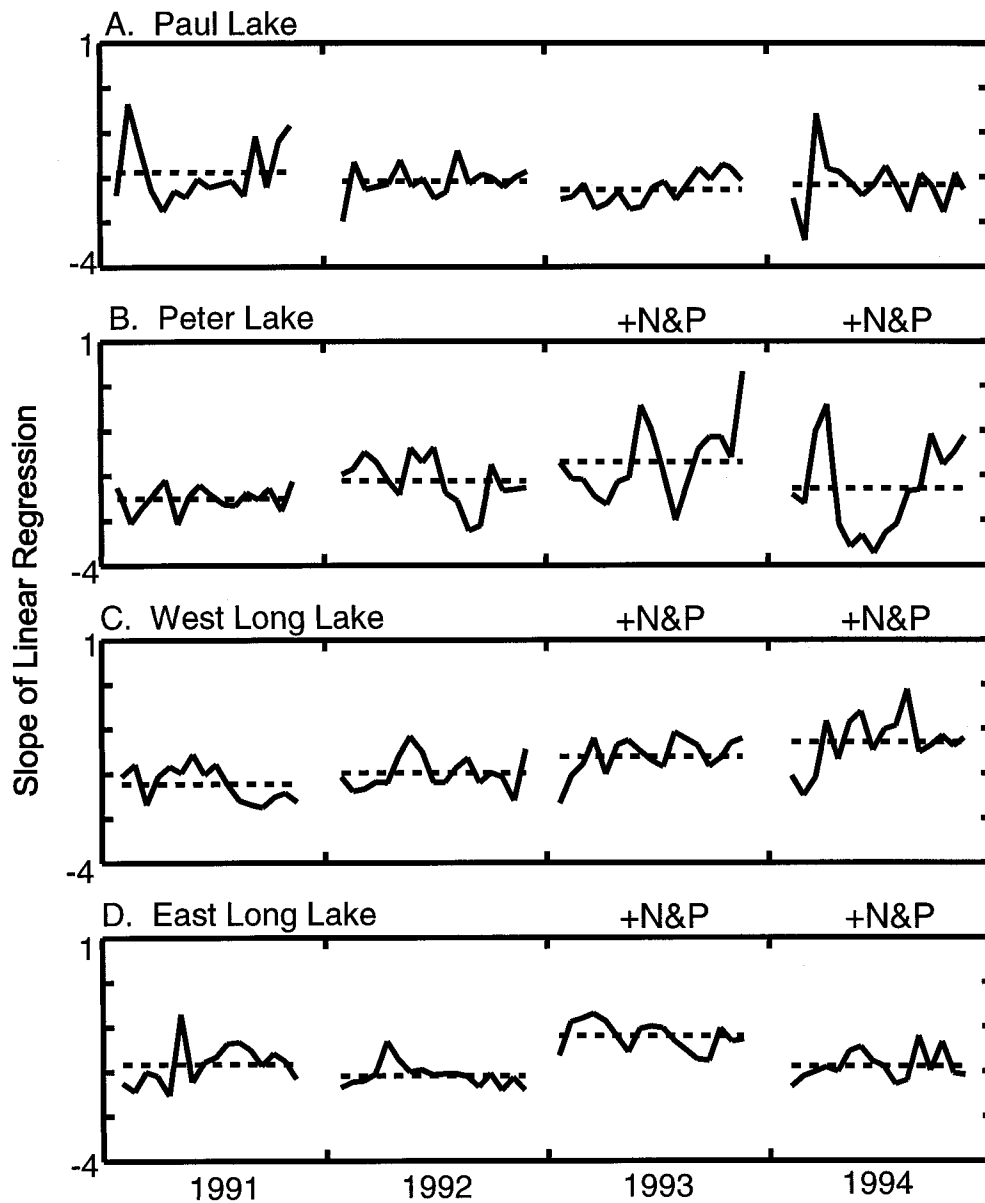


Fig. 5. Time-course for the slope of a linear regression fit to the normalized size spectrum for each sample in each lake from 1991 to 1994. Dashed lines indicate the mean of all observations taken during that year in that lake.

East Long Lakes, mean GALD rarely exceeded $50 \mu\text{m}$ (Fig. 8A,D). In Peter Lake, there was a short-lived increase in mean GALD in late 1993 and early 1994, but this difference did not persist through 1994 (Fig. 8B). In West Long Lake, mean GALD increased considerably with enrichment, averaging $40\text{--}45 \mu\text{m}$ pre-enrichment vs. $100\text{--}400 \mu\text{m}$ post-enrichment (Fig. 8C).

Time-series models for these series fit reasonably well, with high correlations between model estimates and observations, low residual standard deviations, and normally distributed residuals (Table 2). Increased P loading had large, significant positive effects on mean GALD in Peter and West Long Lakes and in the pooled dataset; effects were largest in West Long Lake (Fig. 7). In contrast, nutrient loading had

a marginally significant negative effect on mean GALD in East Long Lake, although the raw time series shows that changes were relatively small compared to those observed in West Long and Peter Lakes (Fig. 8). The effect of increased mean crustacean length was positive in all manipulated lakes, but was not significant.

Statistical interaction of P loading rate and mean crustacean length—A second time-series model was also fit to each response variate to determine whether inclusion of a statistical interaction between the nutrient and zooplankton predictor series improved model fit and/or altered the estimates of the main effects. Based on residual standard deviations, addition of the third predictor improved model fit in

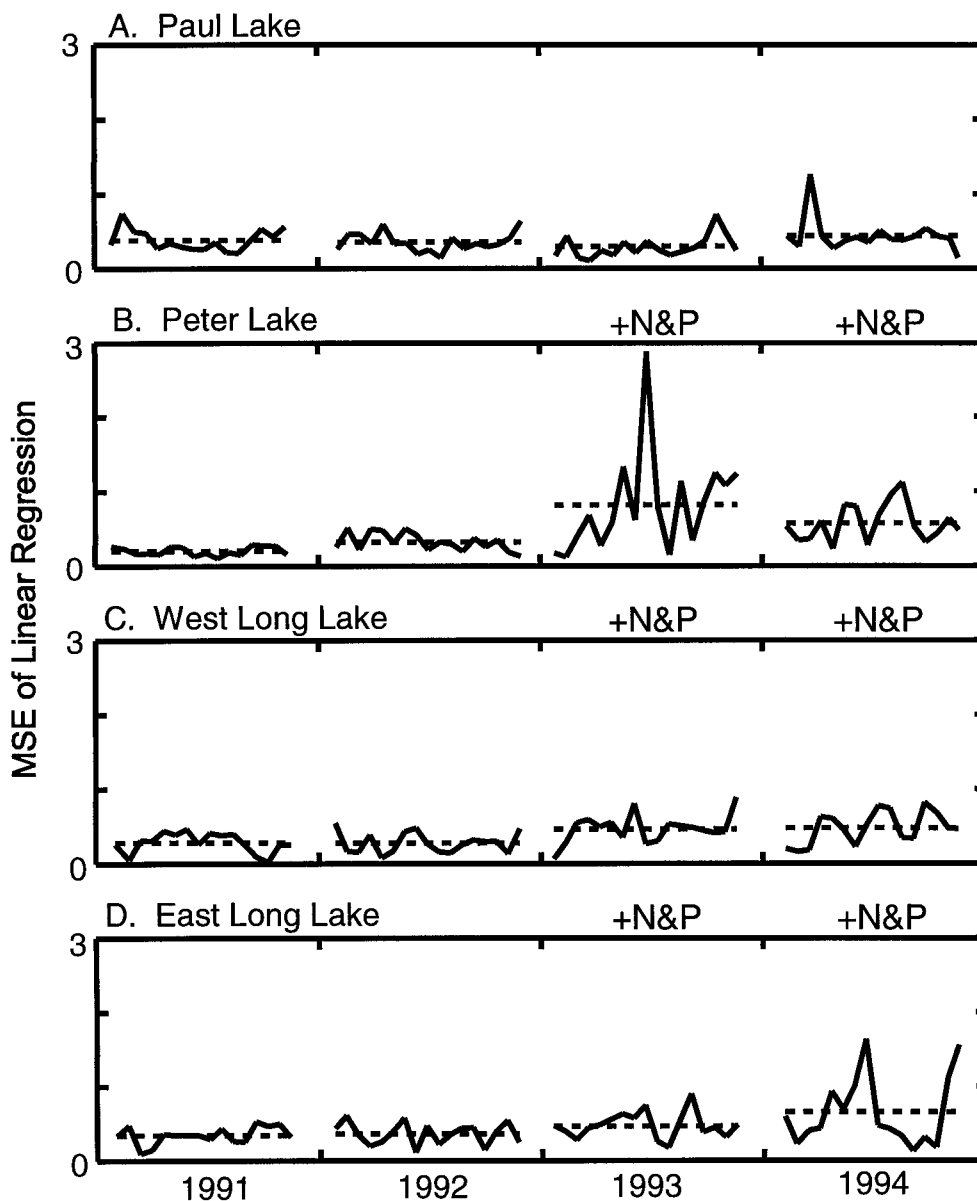


Fig. 6. As Fig. 5, but for the mean-square error (MSE) of the regression models.

all 24 time series (Fig. 9A). However, parameter estimates for the main effects of nutrients and zooplankton were not greatly altered by the inclusion of the interaction, and the qualitative interpretations of the main effects did not change for 23 of the 24 variates (Fig. 9B,C).

Discussion

Effects of nutrient enrichment and increased zooplankton size on phytoplankton size structure—ARIMA models provided an excellent description of time series for phytoplankton size classes, size spectra, and mean GALD. Models for additive, independent effects of nutrients and zooplankton fit the data well, explaining high proportions of the variance in the dataset. However, because residuals from this model were correlated to $\Delta P \Delta Z$ for many variates, I also fit a sec-

ond model that included a parameter for the nutrient–zooplankton interaction. Model fit improved with the addition of this parameter, suggesting that there was a statistical interaction of P input and crustacean length. However, improvements in model fit were relatively small for most variates (<15–20%). Estimates of the nutrient and zooplankton effects changed little, suggesting that biological interpretations of the main effects of nutrient and zooplankton should be the same regardless of which statistical model is examined. In addition, biological interpretation of the effect of $\Delta P \Delta Z$ is not straightforward—what does a change in P loading times a change in mean crustacean length at some point in the past mean to a phytoplankton? I therefore acknowledge the underlying statistical interaction and its subtle effects on parameters, but focus on the results from the additive model for simplicity and interpretability.

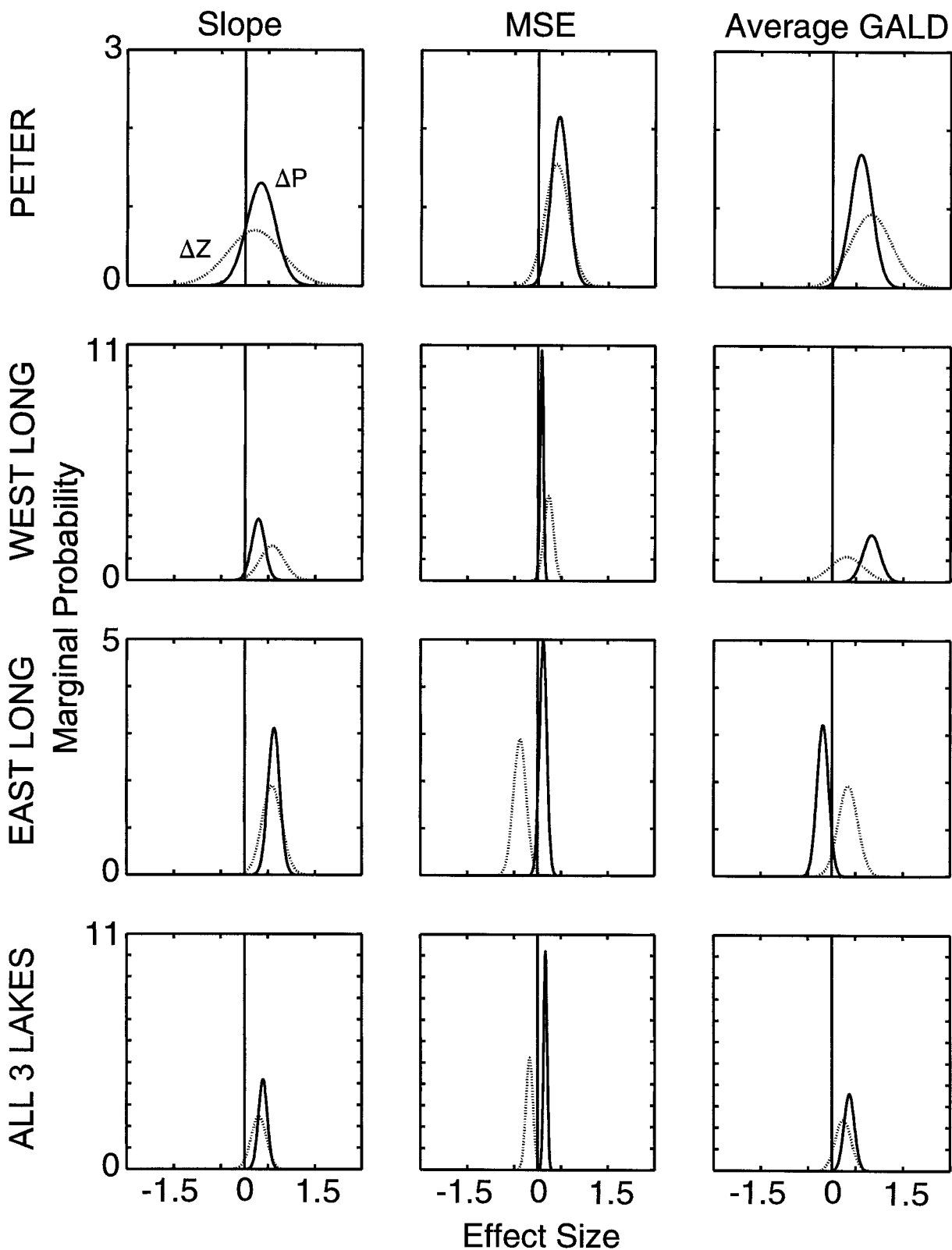


Fig. 7. As Fig. 4, but for the slope (left) and MSE (center) of the normalized size spectrum, and average phytoplankton size (GALD, right).

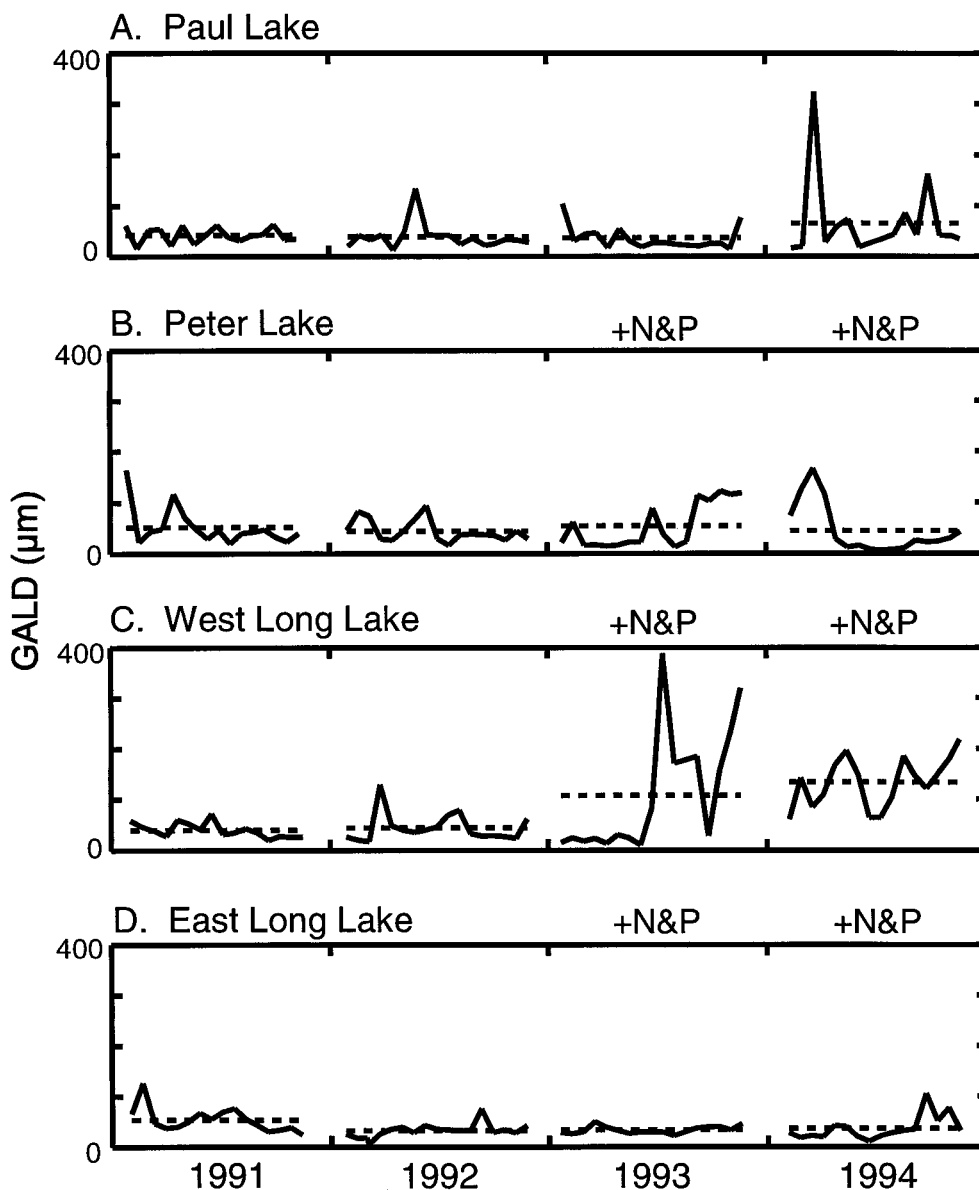


Fig. 8. Mean phytoplankton greatest axial linear dimension (GALD, μm) in each lake from 1991 to 1994.

Increases in either P loading rate or mean zooplankton size increased the biomass of large phytoplankton at the expense of small phytoplankton in Peter, West Long, and East Long Lakes, as indicated by declines in the relative abundance of the small size class in response to both factors. Specifically, increased P loading and increased mean crustacean length had positive effects on the biomass of large phytoplankton and mean phytoplankton size, but negative effects on the percent of total biomass due to small phytoplankton. Nutrients and zooplankton had opposite effects on the biomass of small phytoplankton: P loading rate had a positive effect on small phytoplankton, while mean crustacean length had a negative effect. These qualitative patterns were robust among the three methods of assessing size structure (small-large size classes, size spectra, and mean GALD)

and are generally consistent with expectations from the literature (Table 1).

With few exceptions, the direction of change in each size variate was consistent across all three manipulated lakes, suggesting that the effects of nutrient inputs and zooplankton grazing on size structure act in similar ways in different lakes. This implies that we should be able to predict the qualitative effects of these factors reasonably well.

However, quantitative parameter estimates differed considerably among lakes for some variates. These differences provide an indirect test of whether food-web effects altered the responses of phytoplankton size structure to increased nutrients and thus a way to look for biologically relevant nutrient-zooplankton interactions. Mazumder (1994) suggested that small phytoplankton increase with enrichment

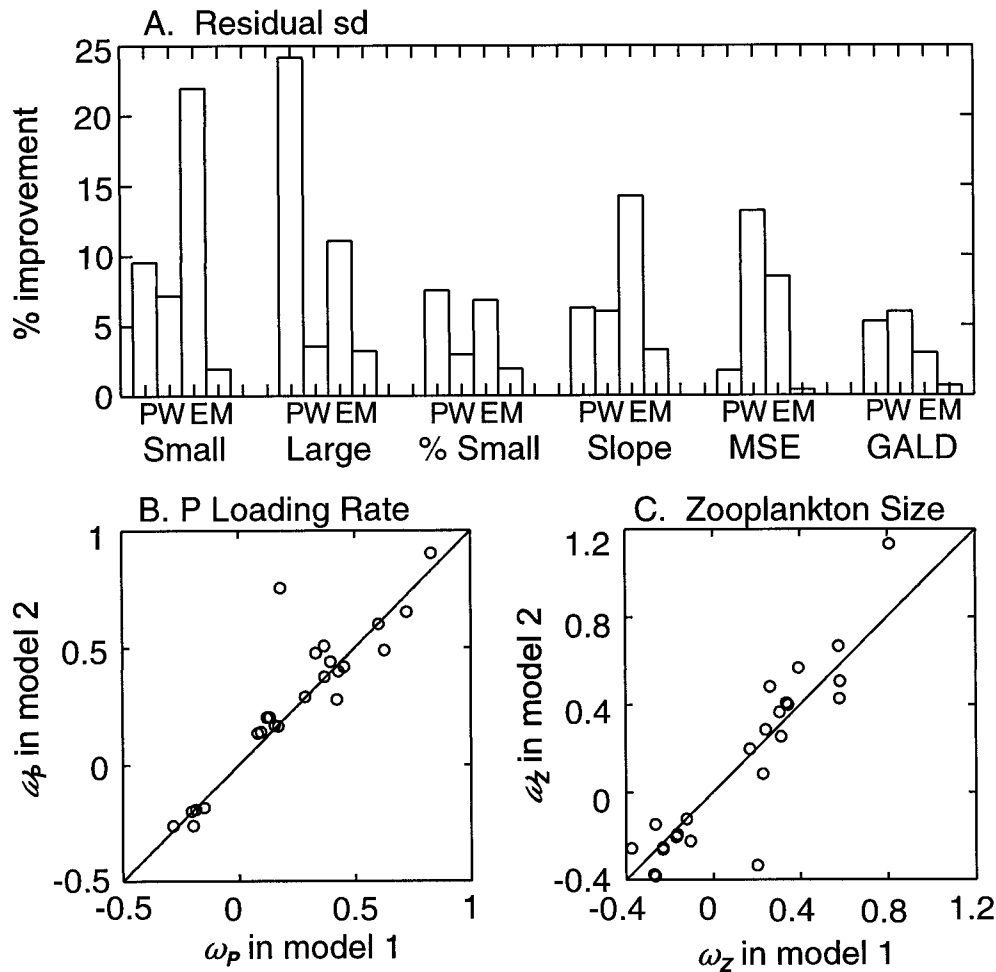


Fig. 9. Effect of adding a statistical interaction between P loading rate and mean crustacean length to the time-series models. A. Percent reduction in residual standard deviation for each variate. P indicates Peter Lake; W, West Long Lake; E, East Long Lake; and M, the pooled dataset with all three manipulated lakes. B. Estimates for the nutrient effect for all models, with vs. without the interaction term; the line represents a 1:1 relationship. C. As panel B, but for the zooplankton effect.

when large zooplankton are rare, while large phytoplankton increase when large zooplankton are abundant. Results from Peter, West Long, and East Long Lakes provide partial support for this suggestion. Parameter estimates for ω_p in the different lakes show that both small and large phytoplankton increased with enrichment, but the degree to which differently sized phytoplankton responded depended on food-web structure. Increased P loading tended to produce larger increases in small phytoplankton and smaller increases in large phytoplankton in the lake with many planktivorous fish and few large zooplankton (Peter Lake) than in the lakes with few planktivores and many large zooplankton (West and East Long Lake). This suggests that zooplankton size—and therefore food-web structure—may influence the extent to which small vs. large phytoplankton respond to nutrient enrichment.

Zooplankton size alone cannot account for this result, since the time series models already include the effects of mean crustacean size as a co-predictor. It seems likely that zooplankton biomass, as well as size, was important to phy-

toplankton responses. Zooplankton in Peter Lake were smaller and showed smaller biomass responses with enrichment than in West and East Long Lake (Carpenter et al. 1996), suggesting that grazing pressure was substantially lower in Peter Lake than in the other lakes for most of the experiment. Unfortunately, I cannot test this explanation with time-series models because zooplankton biomass was highly correlated to P loading. Factorial experiments manipulating nutrients, zooplankton size, and zooplankton biomass would be a better test of zooplankton biomass as an explanation for why phytoplankton size structure responded to enrichment in qualitatively similar but quantitatively different ways in lakes with different food webs.

Nutrients and zooplankton as multiple stressors—Interestingly, there are two definitions of the word “stressor” within the ecological literature. On the one hand, a stressor is any factor that causes a system to go outside the range of normal variation (e.g., Auerbach 1981; Schindler 1990). According to this definition, stressors cause either an increase

or a decrease in a focal parameter; prefixes can be used to denote the direction of the effect (e.g., *distress* vs. *eustress*; Rapport et al. 1981). Alternatively (and perhaps more intuitively), a stressor is any factor that has a negative effect on an ecological system (e.g., Odum et al. 1979; Barrett 1981; Odum 1985; Howarth 1991); obvious examples include acidification (Schindler 1990; Frost et al. 1999; Leavitt et al. 1999) and disease (Lenihan et al. 1999). By this definition, factors which have positive effects are “subsidies,” not stressors.

Regardless of how stressors are defined, increases in nutrients (as seen with eutrophication) and increases in zooplankton size (as an indicator of increased grazing pressure) can be stressors of both phytoplankton communities and the human users of lake resources. Suppose that we adopt the first definition, in which stressors cause a system to go beyond its normal state. Judging from the evidence presented here, it is clear that phytoplankton size structure changed well beyond its usual state in response to changes in zooplankton size and to experimental eutrophication in Peter, West Long, and East Long Lakes. Thus, increased nutrient loading and changes in zooplankton size structure are stressors of phytoplankton.

If we adopt the alternative viewpoint and argue that stressors are implicitly negative factors, then increases in nutrient loading and in zooplankton grazing can be considered stressors of small phytoplankton, but subsidies of large phytoplankton. As grazing rates go up, small, relatively edible taxa are selectively removed from the community (a stressor), while large, relatively inedible taxa are not eaten and thereby benefit from reduced competition (a subsidy). As nutrient loading increases, the growth of all phytoplankton is stimulated (a subsidy). However, because higher nutrient availability tends to reduce the competitive advantage of small phytoplankters, smaller taxa may find it difficult to maintain dominance over larger taxa as nutrient levels increase (a stress).

Increased nutrients and increased grazing may also be stressors for the human users who rely on lakes for essential ecosystem services, since both factors have the potential to shift the phytoplankton community toward larger, relatively inedible taxa. Dominance of larger phytoplankton has negative impacts for two reasons. First, the efficiency with which primary production is passed to higher trophic levels such as zooplankton or fish may decline when the phytoplankton community is dominated by larger taxa (e.g., Lynch and Shapiro 1981). Second, cyanobacteria tend to be among the taxa favored by enrichment or overgrazing (Cottingham 1996; Watson et al. 1997); excessive growths of nuisance cyanobacteria may interfere with recreational and drinking water services (Repavich et al. 1990; Hall et al. 1999). Thus, increased nutrients and increased grazing are potential stressors of humans as well as phytoplankton.

Comparison of alternate methods of assessing size structure—The three alternative methods of assessing phytoplankton size structure generally led to similar conclusions regarding effects of nutrient and grazing. However, there were interesting differences within and among methods that warrant additional comment.

Size classes: Division of phytoplankton into small and large size classes is perhaps the simplest and most straightforward approach to assessing phytoplankton size structure. Although choosing a threshold for edibility is a deliberate simplification for how zooplankton actually select phytoplankton prey, small and large size classes appear to be very informative measures of phytoplankton community structure. Interestingly, analyses based on microscopic cell counts yielded somewhat more information about the effects of nutrients and zooplankton on small vs. large size classes than analyses of areal chlorophyll (Carpenter et al. 1996). Parameter estimates for the large size class in particular tended to be less uncertain and more significant for cell counts than for chlorophyll. This difference suggests that a systematic comparison of time series results for alternative strategies of dividing phytoplankton into size classes (e.g., chlorophyll, cell counts, nutrient concentrations) could yield some interesting results.

Normalized size spectra: This study is somewhat different from most analyses of planktonic size spectra because I evaluated size spectra of the phytoplankton assemblage only. More typically, size spectra include a wider range of planktonic organisms, including bacteria, protozoa, and zooplankton in addition to phytoplankton (*see e.g.*, Sprules et al. 1983; Sprules and Knoechel 1984; Sprules and Munawar 1986, 1991; Mazumder et al. 1988; Sprules 1988). I found that size spectra were as effective for exploring changes in phytoplankton as for exploring the whole plankton community.

My results support the suggestion that normalized size spectra are good indicators of disruption in plankton communities following experimental manipulation of nutrients and food webs (Sprules and Munawar 1986, 1991). The factors that influence phytoplankton size structure appear to have been heavily disrupted by sustained nutrient perturbations by changing zooplankton communities in Peter, West Long, and East Long Lakes. My results are consistent with previous studies which show that slopes increase with increased trophic state (Sprules and Munawar 1986, 1991; Mazumder et al. 1988; Ahrens and Peters 1991) and increased large zooplankton (Mazumder et al. 1988) and that residual MSE increases with increased P loading rate (Sprules et al. 1983; Sprules and Munawar 1986). Increased slopes indicate an increase in the relative abundance of larger taxa, while increased residual MSE indicates an uneven distribution of biomass across size classes. Both are similar to decreased species diversity (*see e.g.*, Odum 1985; Schindler 1988) in showing that the phytoplankton community has become dominated by relatively few taxa. I also found that residual MSE increased with increased zooplankton size in Peter and West Long Lakes, but not in East Long Lake. Since Peter and West Long Lakes were dominated by filamentous cyanobacteria after enrichment, while East Long Lake continued to be dominated by chrysophytes, dinoflagellates, and cryptophytes (Cottingham 1996), this difference suggests that increases in zooplankton size can be more destabilizing when cyanobacteria are abundant.

Mean phytoplankton size: Biomass-weighted mean GALD was a less useful descriptor of phytoplankton size structure than size classes or size spectra. Although analyses of size classes and size spectra suggested that large phytoplankton increased in East Long Lake with increased nutrients or zooplankton size, mean GALD appeared to decline. Visual inspection of the time series for mean GALD revealed little obvious change in East Long Lake following the onset of experimental enrichment, suggesting that mean GALD may not be sensitive to enrichment in all lakes. In addition, large changes in mean GALD in the reference lake suggest that natural variability may confound the interpretation of effects following nutrient or food-web perturbations. A further disadvantage is that many organisms need to be measured in order to calculate the index, yet much information is lost when these measurements are consolidated. If data on the sizes of individual phytoplankton or phytoplankton taxa are available, it may be more worthwhile to look at the size spectrum rather than mean GALD.

Synthesis: Size as a descriptor of phytoplankton communities—Overall, size structure offers a number of distinct advantages for studying phytoplankton communities. This study corroborates literature expectations that qualitative changes in size structure following perturbations of nutrient inputs and/or food-web structure are relatively consistent and predictable. The clear changes in size structure following these manipulations stand in marked contrast to highly variable changes in taxonomic structure, particularly species composition, after similar types of manipulations (Cottingham 1996; Watson and Kalff 1981).

In addition to increased predictability, size-based analyses offer a number of other benefits. For example, taxonomic expertise is not required, so analyses occur more rapidly (Sprules and Knoechel 1984; Mazumder et al. 1988) and are unbiased by differences in taxonomic judgment. Fractionation of water samples into two or more coarse size classes followed by analysis of chlorophyll or nutrients can provide a lot of information relatively quickly. Cell counts can be automated through the use of Coulter counters, flow cytometry, and image analysis (Chisholm 1992). For these reasons, phytoplankton size structure can be investigated in many lakes in a relatively short period of time, facilitating comparative studies of many lakes (Sprules and Knoechel 1984) or high-resolution temporal sampling. The robustness of the results across size classes, size spectra, and mean GALD suggests that all three methods can be used to assess size structure. However, size classes and size spectra may be somewhat more informative than mean GALD, given the amount of effort required to calculate each index.

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