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Stephen R. Carpenter; James F. Kitchell; Kathryn L. Cottingham; Daniel E. Schindler;
David L. Christense; David M. Post; Nicholas Voichick

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CHLOROPHYLL VARIABILITY, NUTRIENT INPUT, AND GRAZING: EVIDENCE FROM WHOLE-LAKE EXPERIMENTS¹

STEPHEN R. CARPENTER, JAMES F. KITCHELL, KATHRYN L. COTTINGHAM,
DANIEL E. SCHINDLER, DAVID L. CHRISTENSEN, DAVID M. POST, AND
NICHOLAS VOICHICK

Center for Limnology, University of Wisconsin, Madison, Wisconsin 53706 USA

Abstract. A Planktivore Lake with small herbivorous zooplankton and a Piscivore Lake with large grazers were monitored for 2 yr and then enriched for 2 yr with inorganic phosphorus and nitrogen. An unenriched lake with an undisturbed fish community served as a reference ecosystem. Added nutrients increased biomass of both phytoplankton and zooplankton. In the Planktivore Lake, phytoplankton were stimulated more than zooplankton. This situation was reversed in the Piscivore Lake. Time series models predicting chlorophyll from P input rate and crustacean length fit well for total chlorophyll and the edible fraction ($<35 \mu\text{m}$), but were less successful for the large fraction ($>35 \mu\text{m}$). A 1-mm change in mean crustacean length had about the same effect on chlorophyll as a decrease in P input rate of $1 \text{ mg}\cdot\text{m}^{-3}\cdot\text{d}^{-1}$. There was no evidence of interaction between grazer and P input effects. Although effects of grazers and P input are equal and additive, the range of mean crustacean lengths among lakes is $\approx 1 \text{ mm}$, while the range of P input rates is substantially $>1 \text{ mg}\cdot\text{m}^{-3}\cdot\text{d}^{-1}$. Therefore, the potential for increasing eutrophication by P input exceeds the potential for controlling eutrophication by food web manipulation. Nevertheless, biomanipulation can reduce chlorophyll concentration at P input rates of $1.5 \text{ mg}\cdot\text{m}^{-3}\cdot\text{d}^{-1}$ or more; these rates characterize a large fraction of the world's stratified lakes.

Key words: Bayesian analysis; biomanipulation; cascading trophic interactions; chlorophyll; ecosystem; grazing; lake; phosphorus; time series analysis.

INTRODUCTION

Ecologists have adopted both deterministic and stochastic views of trophic cascades. Most analyses have emphasized deterministic, reciprocal responses of alternating trophic levels (e.g., increased predation decreases herbivory and leads to increased producer biomass) (Hairton et al. 1960, Fretwell 1977, Carpenter et al. 1985, McQueen et al. 1986, Gulati et al. 1990, Power 1990, Matson and Hunter 1992, Persson et al. 1992, Reynolds 1994). The deterministic view of trophic cascades is heuristically clear and testable, but treats the variability of ecosystems as error to be overcome by massive manipulations, minimized by large samples, or ignored. In contrast, the stochastic view of trophic cascades emphasizes variability derived from strong interactions in ecosystems (Carpenter and Kitchell 1987, Carpenter 1988). Variable outcomes of whole-lake food web manipulations (Benndorf 1990, Reynolds 1994) suggest that a stochastic view may be useful.

Simulation models of lakes support the hypothesis that variation in phytoplankton biomass attributable to food web effects is equivalent to the variability that cannot be explained by nutrient supply (Carpenter and Kitchell 1987). This idea has been tested in numerous enclosure studies (Vanni 1987, Mazumder et al. 1988, Drenner et al. 1990, Elser and Goldman 1991, Hansson

1992), but extrapolation from enclosure data to lakes is uncertain. Comparative studies using data from whole lakes show significant effects of both nutrients and grazing (Pace 1984, Quiros 1990, Carpenter et al. 1991, Sarnelle 1992, Cyr and Pace 1993, Mazumder 1994a). In comparative studies, grazing and phosphorus inputs may not be orthogonal, and consequently estimates of their effects may not be independent. Also, comparative studies may not predict responses of individual lakes to perturbations of nutrient input or grazing. This question is addressed by whole-lake manipulations. However, outcomes of whole-lake food web experiments have been highly variable and suggest that alkalinity, lake morphometry, and refuges from predation complicate the joint effects of nutrients and grazing (Benndorf 1990, Jeppesen et al. 1990a, Shapiro 1990, Moss et al. 1994, Reynolds 1994). Independent manipulations of nutrients and grazing in whole lakes are needed to resolve their effects.

In this paper, we estimate effects of grazing and P input on phytoplankton biomass from whole-lake experiments in which food web structure and nutrient input were manipulated independently. This approach overcomes many of the problems noted above. We estimate and compare the probability distributions for effects of zooplankton grazing and P input, and consider their interactions. These distributions suggest that, with respect to chlorophyll responses, a 1-mm increase in mean grazer length is approximately equivalent to a $1 \text{ mg}\cdot\text{m}^{-3}\cdot\text{d}^{-1}$ reduction in P input.

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METHODS

Lakes and experimental manipulations

Paul, Peter, and Long lakes (89°32' W, 46°13' N) are part of the University of Notre Dame Environmental Research Center near Land O' Lakes, Wisconsin, USA. Paul and Peter lakes have been studied intensively since 1951 and are well described in the literature (Carpenter and Kitchell 1993). Long Lake lies ≈1 km from Paul and Peter lakes in a similar catchment. Morphometrics and physical characteristics of the lakes are similar (Table 1). The lakes were remapped in 1993. Hypsometric data reported here update our previous publications on these lakes. Prior to experimental enrichment, P input rates to all three lakes were 0.1–0.2 mg·m⁻³·d⁻¹ (Carpenter et al. 1995).

Paul Lake (henceforth the Reference Lake) served as an unmanipulated reference ecosystem for this study, as it has since the pioneering experiments of Hasler and colleagues. The food web of the Reference Lake is dominated by piscivorous largemouth bass (*Micropterus salmoides*), zooplanktivorous larvae of *Chaoborus* spp., relatively large cladoceran herbivores (especially *Daphnia pulex*, *D. rosea*, and *Holopedium gibberum*), and phytoplankton dominated by small gelatinous colonies, colonial chrysophytes, and unicells <20 μm in length (Carpenter and Kitchell 1993).

Peter Lake (henceforth the Planktivore Lake) underwent manipulations that enhanced planktivory in 1988–1991 (Carpenter and Kitchell 1993), culminating in removal of piscivores by electroshocking, angling, and finally rotenone in May 1991. The lake was restocked with zooplanktivorous golden shiners (*Notemigonus crysoleucas*) which were maintained as the top predator throughout this experiment.

Long Lake was divided into three basins with plastic curtains in May 1991. The West Basin (henceforth the Piscivore Lake) was used for the experiment described here. The food web of the Piscivore Lake was dominated by piscivorous bass (*Micropterus salmoides* and *M. dolomieu*). Some benthivorous and planktivorous perch (*Perca flavescens*) occurred in 1991 (Schindler et al. 1993). Premanipulation zooplankton were predominantly large cladocerans, especially *Daphnia pulex*. Premanipulation phytoplankton were dominated by colonial chrysophytes, chlorophytes, cyanophytes, and unicells <20 μm in diameter.

Starting in May 1993, the Planktivore and Piscivore lakes were enriched with liquid fertilizer containing PO₄, NH₄, and NO₃ at an N:P ratio of 25 by atoms. Nutrients were added at a central station daily during summer stratification. Dye studies showed that added nutrients mixed throughout each lake's epilimnion within 24 h. P addition rates changed from week to week with movement of the thermoclines. On each day, each lake received the same mass of P per unit epilimnion volume. Summer mean enrichment targets were selected to seek a threshold for grazer control of chlo-

TABLE 1. Limnological characteristics of the study lakes prior to enrichment (August 1992 except as noted).

Characteristics	Reference Lake	Planktivore Lake	Piscivore Lake
Area (ha)	1.7	2.7	3.4
Mean depth (m)	3.7	5.7	4.7
Thermocline depth (m)	4.1	4.2	4.2
Photic depth (m)	5.7	6.3	5.1
Dilution rate (in 1993, d ⁻¹)	0.0029	0.0050	0.0025
Color (m ⁻¹ at 440 nm)	0.70	0.45	0.65

rophyll (Carpenter et al. 1995, Cottingham and Knight 1995). In each summer, we added the majority of the nutrients in the first half of the summer, which may mimic spring runoff and accelerate algal response.

Limnological analyses

Our methods have been thoroughly described elsewhere (Carpenter and Kitchell 1993, Voichick and LeBouton 1994). Relevant methods will be recounted briefly here. During summer stratification (approximately mid-May to mid-September) each lake was sampled weekly at a central station. Profiles of temperature, oxygen, and light were recorded. Samples at six depths (1, 5, 10, 25, 50, and 100% of surface irradiance) were taken for chemistry and phytoplankton analyses. Two vertical hauls of the entire water column with a calibrated net (80-μm mesh) were taken for zooplankton.

Chlorophyll *a* corrected for pheopigments was determined by fluorometry (Marker et al. 1980) for unfiltered samples (total chlorophyll) and samples screened through a 35-μm mesh. The smaller fraction is an index of edible algal biomass (Bergquist and Carpenter 1986). We refer to the difference between total and edible chlorophyll as large chlorophyll, which represents algal cells or colonies retained by a 35-μm mesh. Here we report mean chlorophyll concentrations integrated upward from the depth of 5% of surface irradiance (approximately mid-metalimnion). Phytoplankton samples were pooled from the three upper samples, preserved in glutaraldehyde, mounted in methacrylic resin, and enumerated (St. Amand 1990). Dissolved inorganic P, NO₃, NH₄, Kjeldahl N, and total P were determined using an autoanalyzer (Voichick and LeBouton 1994).

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). Here we report total crustacean biomass and mean crustacean lengths. These are calculated over all copepod and cladoceran individuals.

Statistical analyses

This study employs two before–after control–impact designs (Stewart-Oaten et al. 1986), one for the Planktivore Lake and one for the Piscivore Lake. The Reference Lake serves as a control for any regional trends

or inadvertent changes in methodology that may confound the effects of manipulation. The manipulated lakes provide the four treatment combinations needed to measure effects of nutrient input, food web structure, and their interaction: a planktivore-dominated food web at low (1991–1992) and high (1993–1994) nutrient input, and a piscivore-dominated food web at low (1991–1992) and high (1993–1994) nutrient input.

Statistical perspectives on ecosystem experiments emphasize the ecological significance of effect sizes (Hurlbert 1984, Stewart-Oaten et al. 1986, 1992, Carpenter et al. 1989, Carpenter and Kitchell 1993). In this vein, our goal is to estimate and compare probability distributions for the effects of grazing and P input on chlorophyll in the manipulated lakes. Time series analyses are required to correct for serial correlation in the data (Box et al. 1994). These analyses may be interpreted from either a Bayesian or classical perspective (Box and Tiao 1975). We will adopt the Bayesian interpretation, which treats effects of grazing and nutrients as stochastic parameters represented by random variables (Box and Tiao 1973).

The response variates we wished to predict with time series models were chlorophyll (edible, large, and total) and crustacean biomass. Predictor variates were indices of P input and grazing. Daily P input rate per unit epilimnion volume was used as a predictor for chlorophyll and crustacean biomass. By standardizing the P input rate to the epilimnion volume, we adjusted for mixing events that diluted the nutrients we added. As an index of food web effects, crustacean mean length was used as a predictor for chlorophyll. Previous studies have shown that mean length of crustacean zooplankton is a good predictor of food web effects, especially when increases in crustacean length are caused by increased densities of large *Daphnia* (Brooks and Dodson 1965, Pace 1984, Gulati et al. 1990, Carpenter et al. 1991, Carpenter and Kitchell 1993). Crustacean biomass is not a satisfactory index of food web effects because it could also be altered by changes in food caused by changes in P input.

The analysis has two steps. The first is an exploratory analysis to find the best model to predict the response from past values of predictors. The second is to estimate and interpret the parameters and their probability distributions for the selected models. For exploratory analyses, we fit the very general time series intervention model (Ljung 1987)

$$\alpha(B)f_C(C_t) = [\omega_P(B)/\delta_P(B)]f_P(P_{t-kP}) + [\omega_Z(B)/\delta_Z(B)]f_Z(Z_{t-kZ}) + [\theta(B)/\phi(B)]\epsilon_t \quad (1)$$

In this model B is the backshift operator such that $B^i x_t = x_{t-i}$ where x is a given time series. $\alpha(B)$, $\omega(B)$, $\delta(B)$, $\theta(B)$, and $\phi(B)$ are polynomials in the backshift operator (Wei 1990, Box et al. 1994). C_t is the time series of the response variable (a chlorophyll size fraction or crustacean biomass), P_t is the time series of P input

per unit epilimnion volume, Z_t is the crustacean length time series, and ϵ_t is a series of independent normally distributed errors. The functions f_C , f_P , and f_Z are transformations to meet assumptions of normally distributed residuals and stationarity (Wei 1990, Box et al. 1994). Lags in the P input and crustacean length effects are kP and kZ , respectively.

For each response series, the optimal form of Eq. 1 was determined using the identification procedures of Ljung (1987), Wei (1990), and Box et al. (1994). Criteria used to compare models were prediction error, magnitude of parameters relative to their standard deviations, autocorrelation functions of residuals, normal probability plots of residuals, and cross-correlation functions of residual and predictor series. Models were identified, fit, and evaluated using the System Identification Toolbox of Matlab (Ljung 1987, 1991).

The optimal models had straightforward interpretations. Both chlorophyll and crustacean biomass series were log transformed to normalize residuals. Predictors were in the original units. Trends in the time series (see *Results*) suggested that both response and manipulation variables be differenced (Wei 1990). Models for differenced series fit better than models for the original series. The optimal model for chlorophyll was

$$R_t = \omega_P \Delta P_{t-kP} + \omega_Z \Delta Z_{t-kZ} + [(1 + \theta B)/(1 + \phi B)]\epsilon_t \quad (2)$$

In Eq. 2, R_t is the chlorophyll growth rate:

$$R_t = \Delta \log(C_t) = \log(C_t) - \log(C_{t-1}) = \log(C_t/C_{t-1}) \quad (3)$$

The predictors are the weekly changes in P input rate per unit epilimnion volume and crustacean length:

$$\Delta P_{t-kP} = P_{t-kP} - P_{t-kP-1} \quad (4)$$

$$\Delta Z_{t-kZ} = Z_{t-kZ} - Z_{t-kZ-1} \quad (5)$$

Values of kP and kZ were selected using the diagnostics discussed by Ljung (1987) and Wei (1990). Parameters estimated by minimizing prediction errors (Ljung 1987) are ω_P , ω_Z , θ , and ϕ .

Differencing is a common data transformation for modeling time series with trends (Wei 1990, Box et al. 1994). The statistical reason for differencing is to simplify parameter estimation. In applications, the original series (or predictions) can always be recovered from the differenced series (or predictions) if one knows any point on the original series. The ecological interpretation of a model for differenced series is that large perturbations (indicated by large first differences) of the predictor variables are followed by large changes (i.e., large first differences) in response variables.

Effects of P input rate alone were fit by the analogue of Eq. 2 with no intervention term for crustacean length:

$$R_t = \omega_P \Delta P_{t-kP} + [(1 + \theta B)/(1 + \phi B)]\epsilon_t \quad (6)$$

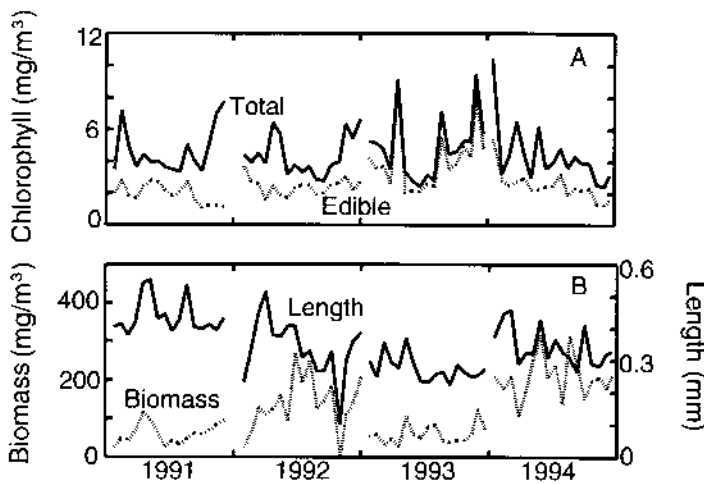


FIG. 1. Time series for the Reference Lake during summer stratification in 1991–1994. (A) Total chlorophyll (solid line) and edible chlorophyll ($<35 \mu\text{m}$, dotted line). The difference between the two lines is large chlorophyll. (B) Crustacean mean length (solid line) and dry biomass (dotted line).

In Eq. 6, R_t was either the weekly growth rate of chlorophyll or crustacean biomass (Eq. 3).

Bayesian analysis of models 2 or 6 (Eq. 2 or Eq. 6) follows standard normal theory (Box and Tiao 1973). Given a noninformative prior, the posterior distribution of the parameters is a multivariate t (Box and Tiao 1975). This distribution is a joint distribution of all the parameters. For our purposes, the distributions of the intervention parameters ω are of greatest interest, while the other parameters (θ , ϕ , and the variance of ϵ) are nuisance parameters that complicate interpretation. A common method for eliminating nuisance parameters while accounting for their effects is to integrate the joint parameter distribution over the nuisance parameters, yielding a marginal distribution of the parameter(s) of interest (Box and Tiao 1973). Marginal distributions of ω were obtained by integrating over the probability distributions of the other parameters as shown by Box and Tiao (1973: 116–118).

Model predictions

To evaluate the ecological implications of the models, we examined chlorophyll distributions predicted to result from various scenarios of P input and grazing. The probability distribution of chlorophyll concentrations resulting from a given scenario was calculated from a specified initial chlorophyll concentration, P input perturbation, and crustacean length perturbation. From Eqs. 2 and 3, the mean log total chlorophyll concentration following a perturbation of P input and crustacean length is

$$\log(C_t) = \log(C_{t-1}) + I_t + N_t \quad (7)$$

In Eq. 7, terms from the right-hand side of Eq. 2 have been separated into an intervention model I and a noise model N (Box and Tiao 1975):

$$I_t = \omega_p \Delta P_{t-kp} + \omega_z \Delta Z_{t-kz} \quad (8)$$

$$N_t = [(1 + \theta B)/(1 + \phi B)]\epsilon_t \quad (9)$$

The variance of N_t is estimated as the variance of the residuals of the model $R_t = I_t$, where R_t is defined in Eq. 3. If Q is the covariance matrix of the intervention parameters and p is the perturbation vector $[\Delta P \ \Delta Z]'$, then

$$\text{var}[\log(C_t)] = p'qp + \text{var}(N_t) \quad (10)$$

Eq. 10 does not include terms for the covariances of parameters of I_t with those of N_t , which were negligible for our data. $\log(C_t)$ is a normally distributed random variable with mean given by Eq. 7 and variance given by Eq. 10. Consequently C_t is a lognormally distributed random variable with mean

$$C_t = \exp[\log(C_t)] \exp\{\text{var}[\log(C_t)]/2\} \quad (11)$$

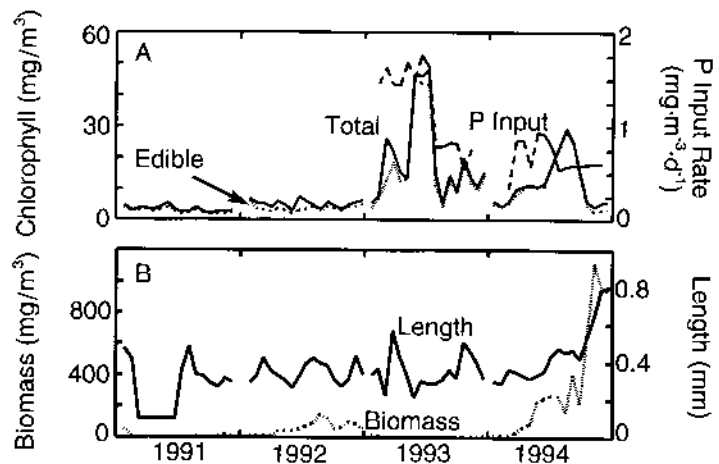
(Miller 1984).

RESULTS

Limnological responses

The variability seen in the Reference Lake (Fig. 1) is typical of that observed in the past decade (Carpenter and Kitchell 1993). Chlorophyll fluctuated between 2 and 10 mg/m^3 and was dominated by the edible fraction (Fig. 1A). The phytoplankton was dominated by colonial chrysophytes, gelatinous green algae, and unicells $<20 \mu\text{m}$ in length. Crustacean zooplankton dry biomass fluctuated between 50 and 400 mg/m^3 (Fig. 1B). Crustacean mean length was generally between 0.3 and 0.5 mm. Each year large cladocerans were a significant component of the zooplankton community, which remained very similar to that described in Carpenter and Kitchell (1993). There were no significant cross-correlations between crustacean length and chlorophyll in the Reference Lake. This result is consistent with the lack of detectable signals in the same lake during 1984–1990 (Carpenter and Kitchell 1993). The Reference Lake exhibits no detectable trends or shifts that suggest changes near the time we began enrichment of the other lakes.

FIG. 2. Time series for the Planktivore Lake during summer stratification in 1991–1994. (A) P input rate (dashed line). Total chlorophyll (solid line) and edible chlorophyll ($<35 \mu\text{m}$, dotted line). The difference between the two lines is large chlorophyll. (B) Crustacean mean length (solid line) and dry biomass (dotted line).



In the Planktivore Lake, significant shifts in chlorophyll and crustacean biomass accompanied nutrient enrichment and perturbations of the fish community (Fig. 2). During 1991 and 1992, chlorophyll concentrations were comparable to the Reference Lake's, and dominated by edible-sized particles as in the Reference Lake (Fig. 2A). The rotenone used to remove piscivores in 1991 severely reduced crustacean biomass and mean length for a few weeks (Fig. 2B). In 1992, the crustacean biomass was dominated by small copepods, especially juveniles.

Summer mean enrichment rates for P were $1.16 \text{ mg}\cdot\text{m}^{-3}\cdot\text{d}^{-1}$ ($2.8 \text{ mg}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) in 1993 and $0.67 \text{ mg}\cdot\text{m}^{-3}\cdot\text{d}^{-1}$ ($1.8 \text{ mg}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) in 1994. Nutrient enrichment was followed by substantial increases in chlorophyll, dominated by the edible fraction (Fig. 2A). Colonial algae (chrysophytes, chlorophytes, and cyanophytes) and small unicells predominated. Crustacean length fluctuated between 0.2 and 0.4 mm from 1992 to mid-1994. During this period crustacean biomass was relatively low and dominated by small copepods. In mid-1994, planktivore density decreased precipitously and *Daphnia rosea* and *D. pulex* became

abundant. At this time, crustacean biomass and mean length increased and chlorophyll decreased substantially (Fig. 2A).

Plankton of the Piscivore Lake also responded strongly to nutrient inputs (Fig. 3). Prior to enrichment, chlorophyll concentrations were comparable to the other lakes but edible algae comprised a smaller proportion of the total (Fig. 3A). Colonial chrysophytes, chlorophytes, and cyanophytes made up the large fraction of chlorophyll, while small unicells dominated the edible fraction. Planktivory was negligible in the Piscivore Lake, and the crustacean biomass was dominated by large animals (mean lengths 0.4–1 mm), mainly *Daphnia pulex* and *D. rosea*, throughout the experiment (Fig. 3B).

Summer mean enrichment rates for P were $1.43 \text{ mg}\cdot\text{m}^{-3}\cdot\text{d}^{-1}$ ($3.7 \text{ mg}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) in 1993 and $0.86 \text{ mg}\cdot\text{m}^{-3}\cdot\text{d}^{-1}$ ($2.2 \text{ mg}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) in 1994. Nutrient enrichment was followed by increases in both chlorophyll and crustacean biomass. After mid-1993, blooms of large colonial phytoplankton dominated by *Anabaena* spp. were common.

Dissolved inorganic nitrogen accumulated after en-

FIG. 3. Time series for the Piscivore Lake during summer stratification in 1991–1994. (A) P input rate (dashed line). Total chlorophyll (solid line) and edible chlorophyll ($<35 \mu\text{m}$, dotted line). The difference between the two lines is large chlorophyll. (B) Crustacean mean length (solid line) and dry biomass (dotted line).

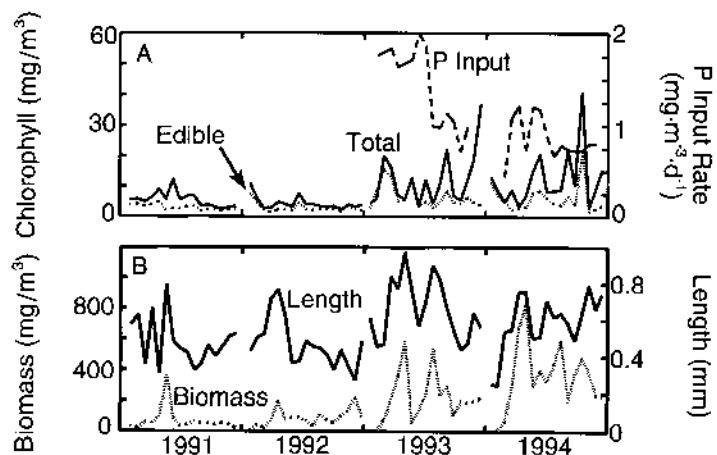


TABLE 2. Parameters of models fit to the time series. For each model the response variate, lake or lakes involved (PI = planktivore, Pi = piscivore), parameters with standard deviations, lags for intervention terms, and standard deviation of residuals are shown. Ellipses (...) denote parameters that could not be estimated due to lack of contrast (for ω s) or were not necessary (for θ or ϕ). For each lake, $n = 67$. All response variates were log transformed. "Chl" = chlorophyll.

Response variate	Lakes	ω_p	SD	Lag	ω_z	SD	Lag	θ	SD	ϕ	SD	s
Total Chl	PI	0.310	0.0948	1	0.190
Total Chl	Pi	0.0952	0.0667	0	-0.841	0.0678	0.256
Crustacean biomass	PI	0.160	0.155	3	0.305
Crustacean biomass	Pi	0.386	0.130	2	-0.743	0.0919	0.432
Edible Chl	PI and Pi	0.268	0.0533	0	-0.287	0.143	0	-0.842	0.0768	-0.391	0.121	0.204
Large Chl	PI and Pi	0.0266	0.0186	8	-0.00122	0.0613	4	-0.886	0.0512	-0.114	0.103	0.0892
Total Chl	PI and Pi	0.253	0.0548	0	-0.258	0.155	0	-0.867	0.0587	-0.310	0.107	0.225

richment in both Planktivore and Piscivore lakes during summers of 1993 and 1994. Concentrations of dissolved inorganic P were near detection limits. These trends, and the relatively high N:P ratio of the added nutrients, indicate that the manipulated lakes were P limited.

Time series models

Models were fit to time series that showed large contrasts between P input rate and crustacean length. The Reference Lake showed that our results were not confounded by any regional trends between years. However, the Reference Lake presented no contrasts in P input or crustacean length and was excluded from time series analyses for that reason. Both the Planktivore

and Piscivore lake time series contained contrasts in P input, and were fit separately to Eq. 6 to compare their responses to enrichment. The greatest contrast in crustacean length was that between the Planktivore and Piscivore lakes. To jointly estimate effects of grazing and P input, we fit Eq. 2 to series from both the Planktivore and Piscivore lakes.

Parameter estimates are collected in Table 2. We are primarily interested in the stochastic effects of P input and crustacean length in chlorophyll. We therefore focus on the probability distributions of these parameters.

P enrichment tended to stimulate phytoplankton in the Planktivore Lake, and crustaceans in the Piscivore Lake (Fig. 4). In the Planktivore Lake, the effect of P input on chlorophyll was clearly positive, while in the Piscivore Lake the effect of P input on chlorophyll tended to be positive (Fig. 4A). The situation was reversed for the effects of P input on crustacean biomass (Fig. 4B). P input had clearly positive effects on crustacean biomass in the Piscivore Lake, and largely positive effects on crustacean biomass in the Planktivore Lake. The variance of the P input effect was greater for crustacean biomass than for chlorophyll in both lakes (note different x axis scales in Fig. 4A and B and contrasting parameter standard deviations in Table 2).

Models predicting chlorophyll from P input and crustacean length explained high proportions of variance in the combined data from the Planktivore and Piscivore lakes (Fig. 5). Edible chlorophyll was predicted most accurately, followed by total chlorophyll. The large chlorophyll fraction was the most difficult response to predict. For large chlorophyll, the range of concentrations that we observed was relatively limited, so the scope for calibration was small and a wider range of P input rates may have yielded a better fit. Models for all chlorophyll fractions have a tendency to underpredict the magnitude of high-chlorophyll events.

These data provided no evidence for a statistical interaction between P input and crustacean length for any chlorophyll fraction. Residuals had no significant cross correlations with ΔP , ΔZ , or $\Delta(PZ_i)$ and any time lag.

We achieved our goal of estimating independent ef-

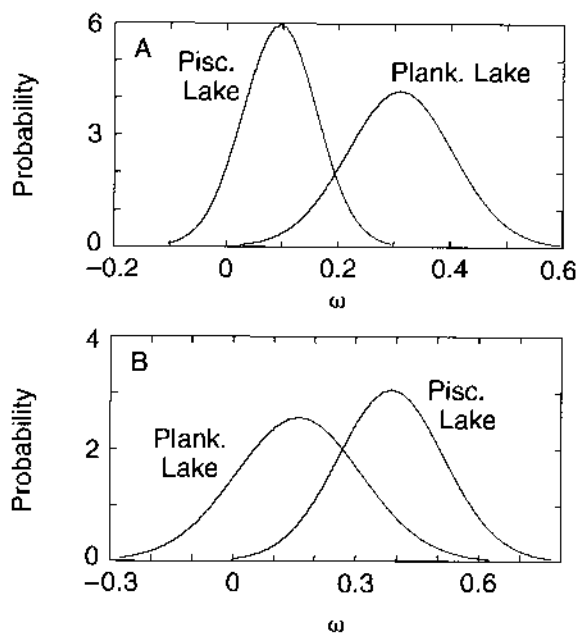


FIG. 4. Marginal probability distributions for P input rate effects (ω) on (A) total chlorophyll and (B) crustacean biomass in the Planktivore and Piscivore lakes. Time series for each lake were fit individually to Eq. 6, which does not include terms for zooplankton length effects.

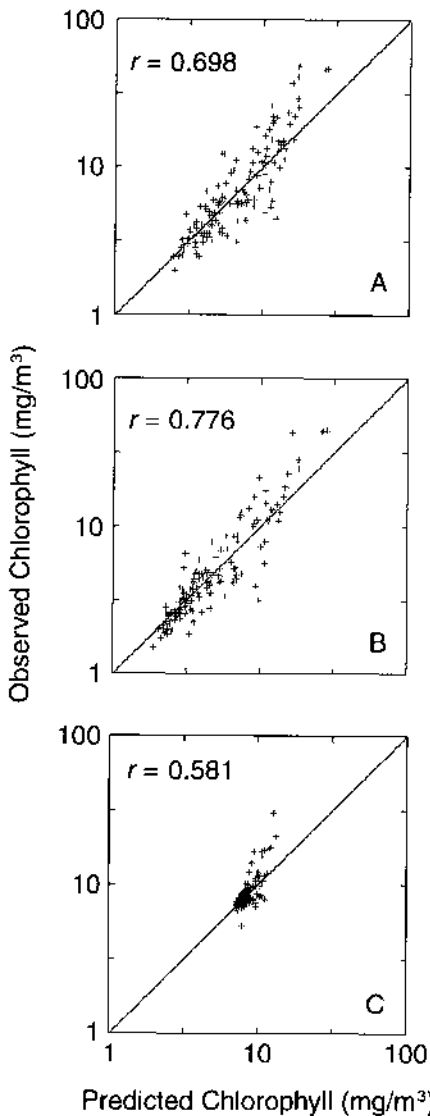


FIG. 5. Weekly observations vs. predictions from Eq. 7 for (A) total chlorophyll, (B) edible chlorophyll, and (C) large chlorophyll. The model was fit to time series from both the Planktivore and Piscivore lakes. Diagonal lines denote identical predictions and observations. Product-moment correlation coefficients are presented for each plot.

ffects of P input and grazing. Predictor series were not significantly correlated at any lag. Correlations between ω_p and ω_z were very small ($r = -0.104$ for total chlorophyll, $r = -0.064$ for edible chlorophyll, and $r = -0.049$ for large chlorophyll).

Responses of edible and total chlorophyll were stronger than those of the large chlorophyll fraction (Fig. 6). Edible chlorophyll responded to both P input and crustacean length. Effects of P input on total and edible chlorophyll were clearly positive, while effects of crustacean length on total and edible chlorophyll were clearly negative. Effects of P input on large phytoplankton were generally positive. Effects of crustacean

length on large phytoplankton were centered near zero; positive and negative responses were about equally likely.

Parameters for total and edible chlorophyll responses indicated that effects of P input and crustacean length were approximately equal and opposite (Table 2, Fig. 6). The parameter for effect of P input was centered near 0.3, indicating that the amount of chlorophyll doubles with a $1 \text{ mg}\cdot\text{m}^{-3}\cdot\text{d}^{-1}$ increase in P input ($10^{0.3} \approx 2$). The parameter for effect of crustacean length was centered near -0.3 , indicating that chlorophyll is halved with a 1-mm increase in crustacean length ($10^{-0.3} \approx 0.5$). The variance of grazer effects was greater than the variance of P effects (note different x axis scales in Fig. 6A and B, and contrasting parameter standard deviations in Table 2).

Predictions of mean total chlorophyll and the probability of chlorophyll concentrations above $10 \text{ mg}/\text{m}^3$ demonstrated the approximate equivalence of P input and crustacean length effects, as the contours were at $\approx 45^\circ$ (Fig. 7). Chlorophyll concentrations $>10 \text{ mg}/\text{m}^3$ are commonly thought to indicate eutrophication (Voltenweider 1976). Increases of P input combined with decreases of crustacean length yield the highest probabilities of eutrophication, while decreases of P input combined with increases of crustacean length yield the lowest probabilities of eutrophication. To calculate these surfaces using Eqs. 7–11, C_{t-1} was set equal to the mean of both Planktivore and Piscivore lakes over

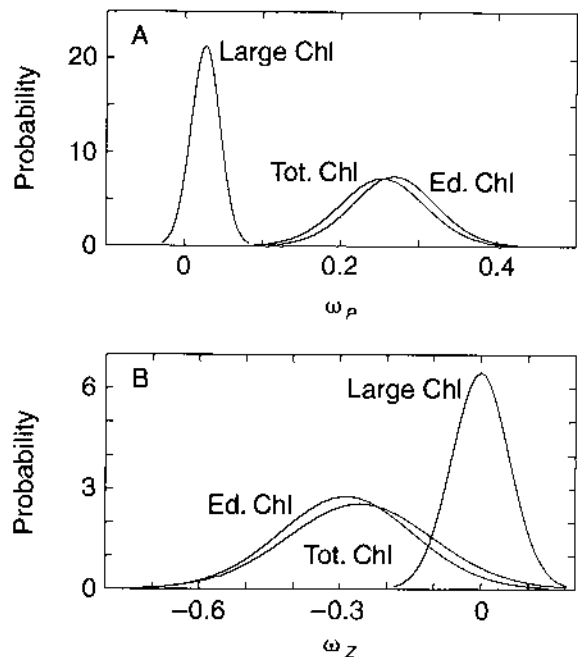


FIG. 6. Marginal probability distributions for effects on edible, large, and total chlorophyll for fits of Eq. 2 to time series from both the Planktivore and Piscivore lakes. (A) Effects of P input rate (ω_p); (B) Effects of crustacean length (ω_z).

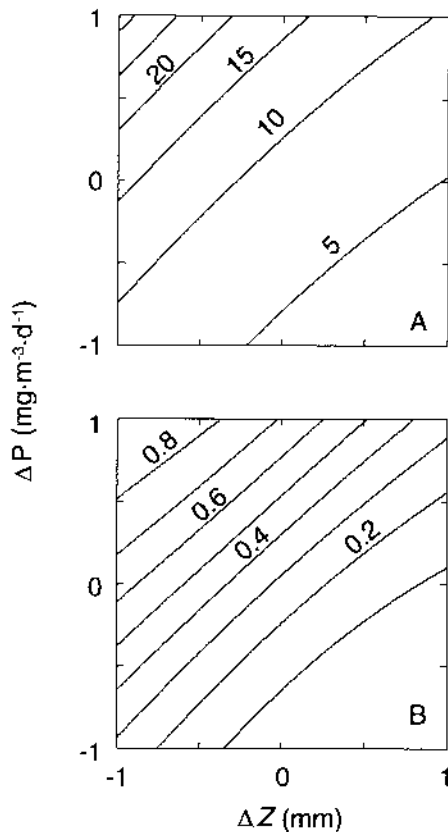


FIG. 7. (A) Predicted mean total chlorophyll concentrations (mg/m^3) from Eq. 11 vs. magnitude of perturbation for P input and crustacean length. (B) Probability of total chlorophyll concentrations $>10 \text{ mg}/\text{m}^3$ from Eqs. 7 and 10 vs. magnitude of perturbation for P input and crustacean length (Z).

all 4 yr ($9.5 \text{ mg}/\text{m}^3$). This arbitrary choice affects the particular values of the contours but not the shape of the surface.

DISCUSSION

Implications for whole-lake experiments

Our results underscore the importance of *changes* in P input rate and crustacean length for detection of ecosystem responses. The sensitivity of this experiment resulted from the great contrast in crustacean length between the manipulated lakes, the changes in P input rate during the course of the experiment, and the unplanned but instructive outbreak of large crustaceans in the Planktivore Lake late in 1994. These findings suggest that relatively frequent (e.g., monthly) perturbations may increase information gain from whole-lake experiments on nutrients and plankton. This finding is contrary to the generally accepted recommendation that whole-lake treatments should be sustained for years (Carpenter 1989, Benndorf 1990). However, these papers addressed experiments that considered responses of long-lived fishes as well as plankton. The most in-

formative manipulation frequency may scale with the turnover time of the ecosystem component of interest: relatively frequent but brief perturbations for plankton, less frequent but long-lasting perturbations for fish. Applications of biomanipulation to improve water quality require changes in fish communities that are sustained for many years (Shapiro 1990).

Our experiment did not reveal factors that regulate large phytoplankton as expressed in the large-chlorophyll fraction. Our analysis appears to be scaled inappropriately for dynamics of these algae in at least two respects. First, dynamics of large algae may need to be understood at time scales longer than weekly changes, because their growth rates are slower than those of some grazers and most other phytoplankton. Second, responses of large phytoplankton may be best understood at the division, genus, or species level. Lumping many taxa (e.g., cyanophytes and colonial chrysophytes) as "large chlorophyll" may obscure taxon-specific responses.

The Bayesian interpretation of time series parameters is a valuable addition to the statistical tools available for ecosystem experimentation. The approach focuses attention on effect sizes and distributions, rather than significance tests. Nuisance parameters (such as θ , ϕ , and the variance of ϵ), which must be estimated but interfere with understanding, can be integrated over their probability distributions. This integration allows marginal distributions of the interesting parameters (ω s) to be compared over all possible values of the nuisance parameters. The Bayesian interpretation does not require us to assume that parameters are fixed constants. The results translate directly into probabilities of future ecosystem states (e.g., Fig. 7B) which may be directly useful to managers (Walters 1986). If parameter distributions from several experiments were available, these could easily be combined (Walters 1986).

Grazing, phosphorus and eutrophication

The effect on chlorophyll of a 1-mm change in grazer length is about equal and opposite to a $1 \text{ mg}\cdot\text{m}^{-3}\cdot\text{d}^{-1}$ change in P input. The variance of grazer effects, however, is greater than that of P effects. There is no evidence for interaction between, or covariance of, P and grazer effects. Effects of grazers and P inputs are additive, opposite, and about equal, as suggested by simulation models of lake ecosystems (Carpenter and Kitchell 1987, Carpenter 1988), a comparative study of 25 lakes (Carpenter et al. 1991), and several enclosure experiments (Vanni 1987, Mazumder et al. 1988, Drenner et al. 1990, Elser and Goldman 1991).

While effects of grazing and P inputs are equivalent, their variability among lakes is not. Although the range of lengths for individual zooplankters can be several millimetres, the range of mean length for assemblages of planktonic crustacean grazers is only $\approx 1 \text{ mm}$ (Table 3). The lake-to-lake range of daily P input rates is larger

TABLE 3. Ranges of mean zooplankton lengths for cladoceran (CL) or crustacean (CR) assemblages and number of lakes sampled from selected publications. Zooplankton mean individual masses were converted to lengths using the equation of Peters and Downing (1984).

Range of zooplankton lengths (mm)	Number of lakes	Reference
0.548–0.860 (CL)	12	Pace 1984
0.302–1.27 (CR)	97	Quiros 1990
0.294–1.12 (CL)	24	Carpenter et al. 1991
0.490–1.18 (CR)	15	Carpenter et al. 1991
0.217–1.01 (CR)	28	Cyr and Pace 1993

than $1 \text{ mg} \cdot \text{m}^{-3} \cdot \text{d}^{-1}$ and different for deep vs. shallow lakes (Fig. 8). About 90% of lakes with mean depth $>3 \text{ m}$ have P input rates $< 1 \text{ mg} \cdot \text{m}^{-3} \cdot \text{d}^{-1}$. Even more of these relatively deep lakes have P input rates lower than those used in this experiment. Biomanipulation that increased mean crustacean length by $\approx 1 \text{ mm}$ could have substantial benefits in such lakes.

Shallow, unstratified lakes often have much higher P input rates than stratified lakes (Jeppesen et al. 1990b). Despite high P input rates, strong responses to fish community change are common in shallow, highly eutrophic lakes (Jeppesen et al. 1990a, b, Scheffer et al. 1993, Moss et al. 1994, Reynolds 1994, Mittelbach et al. 1995). Some successful biomanipulations of shallow eutrophic lakes have depended on restoration of macrophytes, which are a very minor component of our experimental ecosystems. The relative effects of grazing and P inputs on chlorophyll appear to differ between stratified and unstratified lakes (Mazumder 1994b). Our results may not apply to shallow, unstratified lakes.

We found substantial effects of food web manipulation on chlorophyll at P input rates up to $\approx 1.5 \text{ mg} \cdot \text{m}^{-3} \cdot \text{d}^{-1}$ (or $\approx 4 \text{ mg} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$) during two summers. We have not yet measured effects of food web manipulation at higher P input rates, or for longer periods of time, in these lakes. Results presented here show that lakes with small crustaceans are candidates for food web manipulations to reduce chlorophyll and improve water clarity, even if P input rates are relatively high. However, our study also shows substantial variability in response of chlorophyll to grazing. Like many other workers (Benndorf 1990, Reynolds 1994), we found that large, grazing-resistant phytoplankton (including nuisance blue-green algae) can attain high biomass as P inputs increase, even if large grazers are abundant. Other potential difficulties of biomanipulation were not addressed by our study. In highly eutrophic lakes, lack of a midwater oxygenated refuge may cause *Daphnia* to be eliminated (Shapiro 1990), or anoxia may eliminate piscivorous fish (Mittelbach et al. 1995). Harvest of piscivorous fish by anglers may also interfere with biomanipulation (Kitchell 1992). Both researchers and managers should expect variable responses to food web

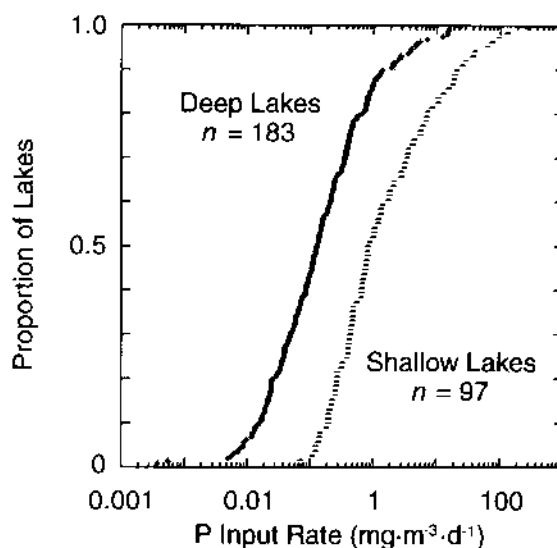


FIG. 8. Cumulative frequency distributions of P input rates to natural lakes (Canfield and Bachman 1981). Deep lakes have mean depth $>3 \text{ m}$; shallow lakes have mean depth $<3 \text{ m}$.

manipulations. As we gain experience with biomanipulations under a diversity of conditions, we will be better able to predict benefits. These predictions will always involve probabilities of success, rather than certainties.

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