

**Population, Community, and Ecosystem Variates as Ecological Indicators:
Phytoplankton Responses to Whole-Lake Enrichment**



Kathryn L. Cottingham; Stephen R. Carpenter

Ecological Applications, Vol. 8, No. 2 (May, 1998), 508-530.

Stable URL:

<http://links.jstor.org/sici?sici=1051-0761%28199805%298%3A2%3C508%3APCAEVA%3E2.0.CO%3B2-T>

Ecological Applications is currently published by The Ecological Society of America.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/esa.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is an independent not-for-profit organization dedicated to creating and preserving a digital archive of scholarly journals. For more information regarding JSTOR, please contact support@jstor.org.

POPULATION, COMMUNITY, AND ECOSYSTEM VARIATES AS ECOLOGICAL INDICATORS: PHYTOPLANKTON RESPONSES TO WHOLE-LAKE ENRICHMENT

KATHRYN L. COTTINGHAM¹ AND STEPHEN R. CARPENTER

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

Abstract. We quantified the reliability of phytoplankton population, community, and ecosystem variates as indicators of whole-lake enrichment. Variates with high sensitivity to perturbation and low background variability were assumed to be more reliable indicators than variates with low sensitivity or high variability. Our data set included weekly data in four lakes (three manipulated and one reference) during two pretreatment summers and two summers of enrichment. We determined background variability by evaluating change in each variate from year to year in the reference lake throughout the experiment and in each manipulated lake during the pretreatment period. We evaluated sensitivity to enrichment using the frequency of departure from expected conditions for each variate during the period of experimental enrichment. Using this information, we then (1) tested the expectation that species populations are more reliable indicators of perturbation than ecosystem variates (biomass, chlorophyll, and primary productivity), and (2) evaluated whether community variates (genera, taxonomic divisions, allometric variates, and community diversity) were reliable indicators of enrichment.

Contrary to expectations from other perturbations, phytoplankton species populations were less reliable indicators of enrichment than community and ecosystem variates. Chlorophyll, species diversity, and species evenness were the most reliable indicators of enrichment: each changed significantly only during the first year of enrichment and only in the three enriched lakes. Simultaneous changes in multiple taxonomic divisions also signaled enrichment very reliably. In contrast, the frequency of significant changes in species populations differed little between the reference lake and the enriched lakes, even after experimental enrichment. Changes in species were difficult to detect reliably due to high background variability in all four lakes: most taxa were not present often enough during a single year to assess reliably whether they had increased or decreased compared to the previous years. Genera and allometric variates were also unreliable indicators due to high variability and moderate sensitivity, respectively. Reliable indicators of phytoplankton responses to enrichment were very different from reliable indicators of animal responses to toxic stressors, suggesting that it may be difficult to make generalizations regarding the use of population, community, and ecosystem variates as indicators of a wide array of perturbations.

Key words: diversity; dynamic linear model; ecological indicators; natural variability; nutrient enrichment; perturbation; phytoplankton; taxonomy; whole-lake experiments.

INTRODUCTION

Natural ecosystems are increasingly impacted by anthropogenic perturbations, including habitat loss and degradation, chemical and organic pollution, exotic species, and overharvesting. To assess the consequences of these perturbations, ecologists and ecosystem managers are attempting to develop effective programs for the rapid detection of ecosystem change following perturbation. Unfortunately, we lack the resources to monitor all possible ecological parameters in all ecosystems of concern. Therefore, we need ways

to decide what to measure. One approach to selective monitoring is to focus on a subset of variates (usually called “ecological indicators”) that describe ecosystem conditions, allow detection of change in those conditions, and point to the possible causes of observed change (Thornton et al. 1993). This paper describes a method for systematic evaluation of a large number of candidate indicators, then applies this method to a case study: responses of freshwater phytoplankton to nutrient enrichment.

Reliable ecological indicators will share a number of common properties (e.g., Noss 1990, Bernstein 1992, McCormick and Cairns 1994). For example, indicators should minimize both false positives (signaling a response when in fact there has not been a perturbation) and false negatives (failing to signal a response when a perturbation has occurred) (Cairns et al.

Manuscript received 12 November 1996; revised 23 June 1997; accepted 25 August 1997.

¹ Present address: National Center for Ecological Analysis and Synthesis, 735 State Street, Suite 300, Santa Barbara, California 93101-3351 USA.

1993, McCormick and Cairns 1994). Indicators also need to balance sensitivity to perturbation with low natural variability (Kelly and Harwell 1990). Sensitivity ensures that the effects of perturbation are detected quickly and at low levels of perturbation, while low variability ensures that there is a suitable baseline against which the effects of perturbation can be evaluated; these two properties could be mutually exclusive (Frost et al. 1992). Finally, indicators should be measurable consistently across time and space (Noss 1990). Suppositions about the kinds of variates that might fit these descriptions abound (see e.g., McKenzie et al. 1992), but few have been tested experimentally.

In aquatic ecosystems, species populations tend to be more sensitive to perturbation than aggregate properties such as total biomass, productivity, and nutrient cycling (Odum 1985, Schindler 1990, 1996, Howarth 1991). Evidence to support this generalization comes primarily from studies of acidification and toxic contaminants. For example, zooplankton biomass changes little with acidification, despite large changes in community composition (Schindler et al. 1985, Frost et al. 1995). Howarth (1991) found no studies in which changes in ecosystem function were observed without changes in population and community structure, although he did identify a number of studies in which community composition changed without an accompanying shift in function. Because of this apparently greater sensitivity, species populations are generally expected to be more reliable ecological indicators than ecosystem variates (Noss 1990, Rapport 1990, Schindler 1990, Vitousek 1990).

The lower sensitivity of biomass and functional variates is often attributed to complementarity among functionally similar species within a trophic level (Schindler 1990, Frost et al. 1995). When sensitive species are lost, others with similar functional roles may increase, thereby buffering aggregated variates from change (Frost et al. 1995). Changes in species composition therefore tend to be more readily apparent than changes in more aggregated variables. For the purposes of this paper, we refer to these aggregated properties as "ecosystem" variates; examples include the total biomass of organisms at a particular trophic level as well as functional variates such as primary and secondary productivity or nutrient cycling (e.g., nutrient turnover rates, nitrogen fixation, and sulfate reduction).

Unfortunately, high sensitivity to perturbation does not necessarily imply that a particular variate is a reliable ecological indicator. For example, although species populations may be more sensitive to perturbation than ecosystem variates, they also can be quite variable (Frost et al. 1992). In fact, population variates are noted for high statistical variance as well as variability in presence and/or absence across time and space (Bernstein and Zalinski 1986, McCormick and Cairns 1994). Furthermore, if only a subset of populations can be

monitored, how does one choose from among the candidates? It is difficult, if not impossible, to predict which species are going to be ecologically important after perturbation (e.g., Schindler et al. 1985, Soranno et al. 1993, Schindler 1996), particularly if the type of perturbation is not known in advance. Therefore, a subset of species chosen now is unlikely to give adequate information about response to an unknown future perturbation.

If populations are too variable and ecosystem variates are too insensitive to be reliable ecological indicators, then we need to identify alternative indicators that better balance sensitivity and variability. Community variates that incorporate information from multiple populations, yet retain some information about population identity, could be more reliable indicators than either species populations or ecosystem variates (Bernstein and Smith 1986, Frost et al. 1992, Cairns et al. 1993, McCormick and Cairns 1994). For example, taxonomic categories at levels higher than species (Sullivan and Carpenter 1982, Herman and Heip 1988, Warwick 1988, Keough and Quinn 1991), allometric or size-based groupings (Sprules 1984), guilds (Cranston 1990, Smith and Simpson 1992), and diversity properties such as species diversity, richness, and evenness (Odum 1985, Rapport et al. 1985, Caswell and Weinberg 1986) have all been proposed as possible indicators of ecosystem perturbation. However, few of these community-level candidates have been compared to population or ecosystem variates within a single data set using a rigorous quantitative approach.

In this study, we determine whether population (species), community (genera, divisions; size classes, size spectra, average size; diversity, richness, evenness) and ecosystem (primary productivity, total chlorophyll, total biomass) variates are reliable indicators of phytoplankton responses to deliberate experimental enrichment. Our data set includes weekly data from four lakes (three enriched and one reference system) during two summers of pretreatment sampling and two summers of enrichment. We used dynamic linear models (West and Harrison 1989, Pole et al. 1994) to evaluate the background variability and sensitivity to enrichment of each variate at the time scale of a summer. We determined background variability by evaluating change in each variate from year to year in the unmanipulated reference lake throughout the experiment, and in each manipulated lake during the pretreatment period. We determined sensitivity from the frequency of departure from expected conditions for each variate during the period of experimental enrichment. Using this information, we (1) tested the expectation that species populations are more reliable indicators of perturbation than ecosystem variates, and (2) evaluated which community variates are reliable indicators of enrichment. Our results demonstrate that reliable indicators of phytoplankton responses to enrichment are very different from reliable indicators of animal responses to toxic

TABLE 1. Qualitative assessment of zooplanktivory and dominant zooplankton and phytoplankton taxa in each lake in each year of the experiment, extracted from Carpenter et al. (1996), Cottingham (1996), and Carpenter et al. (unpublished data).

Lake	Year	Planktivory	Dominant zooplankton	Dominant phytoplankton
Paul	1991	low	<i>Holopedium gibberum</i> , <i>Skistodiatomus oregonensis</i> , <i>Daphnia pulex</i>	chrysophytes, chlorophytes
	1992	low	nauplii, <i>S. oregonensis</i> , <i>H. gibberum</i> , <i>Cyclops varicans rubellus</i> , <i>Orthocyclops modestus</i>	chrysophytes, chlorophytes
	1993	moderate†	nauplii, <i>S. oregonensis</i> , <i>H. gibberum</i> , <i>Basmina longirostris</i>	chrysophytes, cyanobacteria
	1994	low	nauplii, <i>D. pulex</i> , <i>O. modestus</i> , <i>H. gibberum</i>	chrysophytes, chlorophytes
Peter	1991	high	<i>Asplanchna</i>	chrysophytes, chlorophytes, dinoflagellates
	1992	high	<i>Asplanchna</i> , <i>C. varicans rubellus</i> , nauplii	chrysophytes, dinoflagellates
	1993	high	<i>Asplanchna</i>	cyanobacteria, chlorophytes
	1994	high until midsummer; then low‡	<i>Daphnia rosea</i> , <i>Diacyclops thomasi</i> , <i>B. longirostris</i> , <i>Asplanchna</i>	chlorophytes, cyanobacteria
West Long	1991	low	<i>D. pulex</i> , <i>Asplanchna</i> , <i>D. rosea</i>	chrysophytes, chlorophytes, cryptophytes
	1992	low	<i>D. pulex</i> , <i>Asplanchna</i> , <i>O. modestus</i>	chrysophytes, dinoflagellates
	1993	low	<i>D. rosea</i> , <i>D. pulex</i>	cyanobacteria, cryptophytes, chlorophytes
	1994	low	<i>D. rosea</i> , <i>D. pulex</i>	cyanobacteria
East Long	1991	high	<i>Asplanchna</i>	chrysophytes, dinoflagellates
	1992	moderate through midsummer; then low§	<i>Asplanchna</i> , <i>D. pulex</i>	chrysophytes, dinoflagellates
	1993	low	<i>D. rosea</i> , <i>Asplanchna</i> , <i>D. pulex</i>	cryptophytes, chrysophytes, dinoflagellates
	1994	low	<i>D. rosea</i> , <i>D. pulex</i>	chlorophytes, cryptophytes

† Due to a large cohort of young-of-year largemouth bass; see Post et al. (1997) for details.

‡ There was a midsummer fish kill of the dominant planktivores; see Schindler et al. (1997) for more information.

§ Golden shiners stocked into this lake in May 1991 to increase zooplanktivory did not survive into their second year, probably due to low pH. This lake was essentially fishless beginning in late 1992 (Christensen et al. 1996).

stressors. This suggests that it may be difficult to make general statements regarding the use of population, community, and ecosystem variates as indicators of a wide array of perturbations.

METHODS

Whole-lake experiments

Paul, Peter, West Long, and East Long lakes (Gogebic County, Michigan, USA: 89°32' W, 46°13' N) are small, stratified, seepage systems that were studied intensively from 1991–1994 as part of an experiment evaluating the role of food web structure in lake response to increased nutrient loading. Lake characteristics, experimental design and execution, and responses to manipulation are described in detail elsewhere (e.g., Carpenter et al. 1996, Christensen et al. 1996, Cottingham 1996); a brief summary of the food web structure for each lake in each year appears in Table 1. This paper focuses on epilimnetic phytoplankton as indicators of nutrient enrichment.

During 1991 and 1992, each lake was monitored under baseline nutrient conditions (P loading rates of ~0.1–0.2 µg per liter of epilimnion per day). In 1993 and 1994, Peter, West Long, and East Long lakes were enriched with liquid fertilizer from late May through early September. The fertilizer, which contained PO₄,

NH₄, and NO₃ at an N:P ratio of 25:1 by atoms (Carpenter et al. 1996), was added at identical target loading rates for each lake. Realized loading rates were, however, slightly different among lakes. In 1993, the average daily loading rates of phosphorus were 1.2 µg·L⁻¹·d⁻¹ in Peter Lake, 1.4 µg·L⁻¹·d⁻¹ in West Long Lake, and 1.3 µg·L⁻¹·d⁻¹ in East Long Lake. In 1994, rates were slightly lower, averaging 0.7 µg·L⁻¹·d⁻¹ in Peter Lake and 0.9 µg·L⁻¹·d⁻¹ in West and East Long lakes (Carpenter et al. 1996).

Limnological analyses

Sampling methods for Paul, Peter, and Long lakes have been thoroughly described elsewhere (Carpenter and Kitchell 1993, Voichick and LeBouton 1994) and are recounted only briefly here. Each year during the period of summer stratification (approximately mid-May to mid-September), we sampled each lake weekly at a central station. In the field, we recorded temperature, oxygen, and light profiles, and took epilimnetic water samples at 100%, 50%, and 25% of surface irradiance using a van Dorn sampler. We then analyzed water samples for chlorophyll and primary productivity, as well as phytoplankton species composition. All variates were measured weekly except for primary productivity, which was measured monthly in 1991 and

1992 and biweekly (once every two weeks) in 1993 and 1994.

Primary productivity (PPR) and chlorophyll *a* were measured for each of the three water samples. PPR was measured using replicate estimates of in situ ^{14}C fixation (Vollenweider 1974). Two 125 mL light bottles and a DCMU (dichlorophenol dimethylurea) control bottle were incubated with 185 kBq of $\text{NaH}^{14}\text{CO}_3$ at each depth from 1000 to 1600 h. After incubation, phytoplankton were collected on glass-fiber filters, rinsed with 1 mol/L HCl, and dried overnight before liquid scintillation counting. Total chlorophyll *a* was measured fluorometrically after filtering water through glass-fiber filters, freezing the filters in the dark, and extraction in methanol (Marker et al. 1980). Means of the three water samples were used for all chlorophyll and PPR analyses included in this paper.

Samples for microscopic analysis of epilimnetic phytoplankton were pooled from the three van Dorn casts, preserved in glutaraldehyde, mounted in methacrylic resin, and enumerated and measured (St. Amand 1990, Cottingham 1996). Organisms were identified to species as much as possible. For each sample, the mean greatest axial linear dimension (GALD), mean individual biovolume (protoplasm exclusive of loricae and sheaths, determined by geometric formulae), and total concentration of each taxon were determined (St. Amand 1990). Biovolume (cubic micrometers per milliliter) was converted to biomass (milligrams per liter) assuming a specific gravity of 1.0. Information on mean GALD and total biomass of each phytoplankton taxon was then used to estimate other variates describing phytoplankton community structure.

Assembly of data sets for analysis

Prior to analysis with dynamic linear models (DLM), time series for each variate in each lake were compiled into a master database of standard length and format. All time series were truncated to a maximum of 16 samples per year at 1-wk intervals from 15 May to 7 September (64 total observations). For variates sampled at biweekly or monthly intervals (i.e., PPR), a certain number of weeks were missing, but this was easily handled by the DLM (see *Methods: Dynamic linear models*).

Species-level information was then aggregated in different ways to determine the other community and ecosystem variates; only chlorophyll and PPR were not determined from the cell counts (Table 2). For example, to obtain data on higher taxonomic categories, we aggregated species into genera and divisions (cyanobacteria, chlorophytes, cryptomonads, dinoflagellates, and chrysophytes; diatoms and euglenoids were rare throughout this study and were not analyzed at this level of taxonomic resolution). We quantified size structure by (1) aggregating species by size into small (<30 μm) vs. large ($\geq 30 \mu\text{m}$) size classes, (2) calculating the biomass-weighted average GALD (Elser

TABLE 2. List of variates by category.

Category	No. variates	List of variates
Population		
Species†	145	includes 81–107 species per lake
Community		
1) Taxonomic		
Genera‡	107	includes 67–81 genera per lake
Divisions	5	cyanobacteria chlorophytes cryptomonads chrysophytes dinoflagellates
2) Allometric	5	biomass <30 μm biomass $\geq 30 \mu\text{m}$ slope for size spectrum mean square error for size spectrum biomass-weighted average GALD
3) Diversity	3	species richness Shannon-Wiener species diversity Shannon-Wiener species evenness
Ecosystem	3	total biomass total chlorophyll primary productivity

† Only species that could be uniquely identified were included in this analysis; organisms identified only to genus or to a higher taxonomic category were not included.

‡ Only genera that could be uniquely identified were included; organisms classified to higher taxonomic categories were not included.

et al. 1986), and (3) fitting linear regressions to normalized biomass size spectra (e.g., Ahrens and Peters 1991, Cottingham 1996; we used the slope and residual mean square error of the regressions here). We also calculated three indices of community diversity: species richness (number of species present in each sample), Shannon-Wiener species diversity (H'), and evenness (Pielou 1977). Finally, we summed the biomass of all species as an estimate of total phytoplankton biomass based on microscopic cell counts.

Species, genera, divisions, size classes, and total biomass required logarithmic transformation to improve model fit. Because zeros cause problems during log transformation, we replaced all zeros with 10^{-6} , the lowest recorded biomass for any taxon, prior to taking the base 10 logarithm. Transformation enhanced our ability to detect decreases in particular variates following enrichment, but had little effect on the detection of increases. This substitution was rarely used for divisions, size classes, and total biomass. However, it was often used for species and genera, many of which were missing from >50% of the samples. Other variates (primary productivity, total chlorophyll, species diversity, richness, evenness, biomass-weighted average GALD, and the summary statistics for size spectra) were untransformed, and analyses were performed in the units in which the data were recorded.

Dynamic linear models

At present, there are many statistical methods for detecting changes following perturbation (Stow et al. 1998). Time series analysis works well when there are long-term records extending both before and after the perturbation. Although most ecological time series work has used autoregressive integrated moving-average (ARIMA) models (Box et al. 1994), ecological data may not meet the assumptions of these models. For example, ecological time series may be nonstationary, sampled at irregular intervals, contain missing values, or contain outliers and rare events that have great influence on model structure and parameter values. A less restrictive and more flexible approach is needed for broadscale, comparative analyses of the responses of many different variates in multiple ecosystems.

We assessed trends and events using dynamic linear models (DLM; West and Harrison 1989, Pole et al. 1994), which have recently been introduced as tools for studying phytoplankton ecology (Soudant et al. 1997). We used DLM fit to premanipulation data to estimate the probability distribution (mean, variance) expected in the absence of perturbation, then compared postmanipulation data to this expected distribution to check for manipulation effects. DLM easily handle missing values and unequally spaced data, and the influence of outliers and rare events can be minimized. Thus, DLM overcome some key difficulties of ARIMA models for ecological data.

DLM are distinct from the more familiar general linear models (GLM) in two ways (Ljung 1987, West and Harrison 1989, Pole et al. 1994). First, they explicitly account for structure contained within a time series due to the ordering of the data points: the observations are given and analyzed in a specific sequence Y_1, Y_2, \dots, Y_t . Second, parameters are dynamic and time ordered, changing through time as the system changes. There are two equations for each DLM: an observation equation relating observations to parameters, and a system equation describing the evolution of parameters through time. We used the simplest possible DLM, one parameter (μ) for the level of the series. Preliminary analyses showed that more sophisticated models were overparameterized and ill-fitting. The equations were as follows:

$$Y_t = \mu_t + v_t, \quad v_t \sim N[0, V_t] \quad (1)$$

$$\mu_t = \mu_{t-1} + \omega_t, \quad \omega_t \sim t_{n-1}[0, W_t]. \quad (2)$$

The observation Eq. 1 equates the observation at time t (Y_t) with the model state parameter (the level, μ_t) plus a stochastic error term v_t , called the observation variance. The observation variance is normally distributed with zero mean and variance V_t . The system evolution Eq. 2 describes the evolution of the state parameter or level through time; the evolution variance has a Student t distribution with mode 0 and scale matrix W_t . The

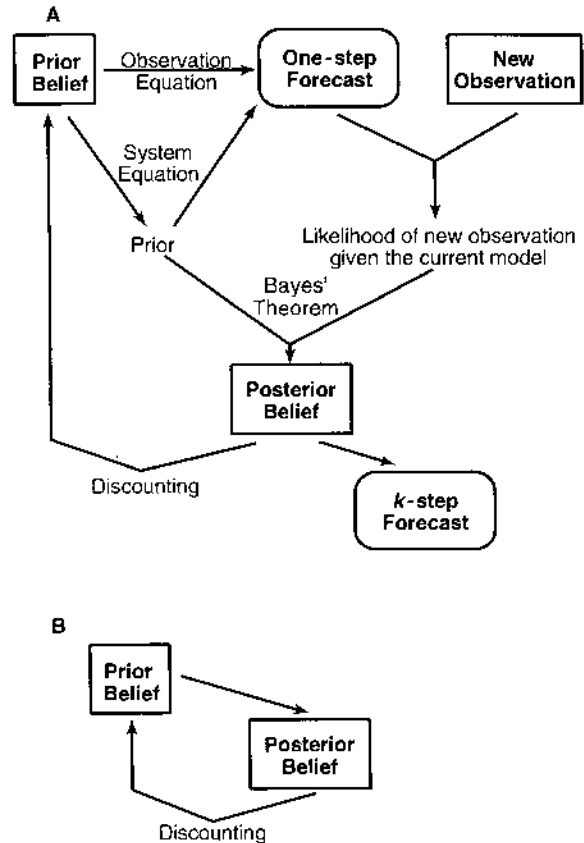


FIG. 1. Schematic showing how dynamic linear models (DLM) are estimated, with emphasis on how Bayesian learning is incorporated into the estimation procedure (modified from Lamon et al. [1998], with permission).

error terms v_t and ω_t are assumed to be temporally and mutually independent (Pole et al. 1994). We used Bayesian learning to estimate μ_t and V_t (West and Harrison 1989, Pole et al. 1994). W_t and some aspects of V_t were incorporated into the estimation process through discount factors, δ_{μ} and δ_v , which were determined separately for each time series (Pole et al. 1994, Appendix).

Model fitting consisted of an iterative cycle of steps for each time period (Fig. 1A; Pole et al. 1994). First, we calculated the prior probability for the parameters at time t using the system evolution equation and the posterior parameter distribution for time $t - 1$. Second, we made a one-step-ahead forecast for the observation Y_t using the observation equation and the prior for time t . Third, we compared the one-step-ahead forecast for time t to the observation for time t using a likelihood function. Finally, we used Bayes' theorem to determine the posterior parameter distribution from the prior and the likelihood. For each new observation, the cycle of posterior to prior to one-step-ahead forecast to likelihood to posterior was repeated. When desired, predictions for more than one step ahead (i.e., k steps ahead, where $k \geq 1$) were made just after the posterior dis-

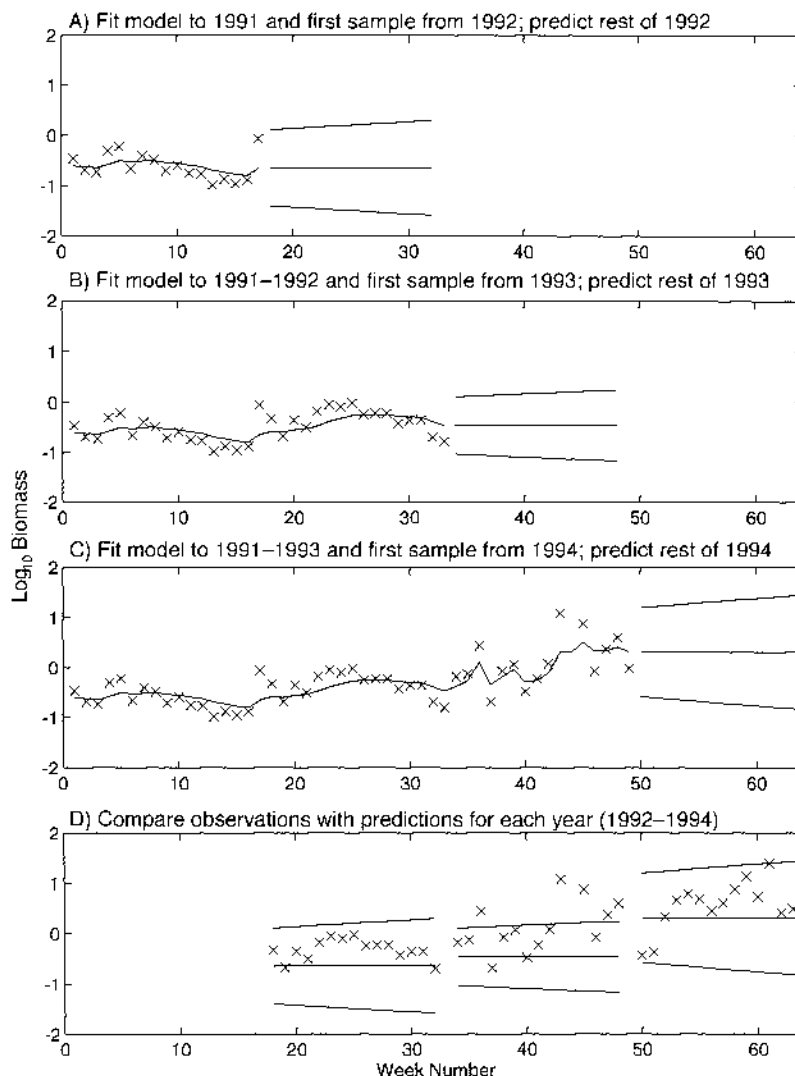


FIG. 2. Schematic showing how we used dynamic linear models (DLM) to evaluate the background variability and sensitivity to enrichment for each variate in each lake. The sample data are total phytoplankton biomass in West Long Lake; we compared observations (x) with DLM predictions (middle, straight line) and 90% high posterior density (HPD) intervals (outer, dashed lines).

tribution was determined. Missing values were handled by skipping steps 2 and 3, then setting the posterior mean (the level) equal to the prior mean and the posterior variance to the prior variance plus a small amount of additional uncertainty (discounting; Fig. 1B). Equations for each step of the analysis are described fully elsewhere (West and Harrison 1989, Pole et al. 1994). A summary appears in the Appendix.

All DLM were fit using original software developed within the Matlab programming environment (Ljung 1991) by KLC and cross calibrated to commercial software (BATS; Pole et al. 1994). This software allowed automated fits of the nearly 50 000 (4 lakes \times 45 discount factors \times 270 variates) DLM analyzed for this paper.

Use of DLM to detect changes in phytoplankton time series

Changes in each phytoplankton variate were assessed by a sequential process of fitting a DLM to some of the data, making predictions for the next year of the series, and then continuing to fit the model (Fig. 2). After the full DLM was fit, observations were compared to the predictions for each year. This procedure is outlined below:

1) We fit a DLM to the data from 1991 and the first sample from 1992 (Fig. 2A) using the mean and variance of data from 1991 as the initial prior probabilities for the level and variance. We then forecast the level and 90% highest posterior density (HPD) intervals for the rest of 1992 in order to compare the actual

results in 1992 with our expectations based on prior information. This analysis indicated potential background rates of change in all four lakes prior to enrichment. Bayesian HPD intervals correspond to many people's intuitive (but incorrect) interpretation of confidence intervals in frequentist statistics (Box and Tiao 1992). That is, HPD intervals represent the range of values in which 90% of the distribution lies. Because of discounting, the HPD intervals grow through time as forecasts are made further and further into the future. In the results, we refer to these intervals as the "prediction limits."

2) We continued fitting the DLM to the data from step 1, adding all data from 1992, plus the first sample from May 1993, which was taken prior to the beginning of experimental fertilization (Fig. 2B). We then forecast the level and 90% highest posterior density (HPD) intervals for the rest of 1993. For Peter, West Long, and East Long lakes, this generated a nominal state for what might have happened had we not added nutrients to these systems; differences from this state could indicate responses to the onset of experimental enrichment. For Paul Lake, this was another opportunity to evaluate background variability.

3) We continued fitting the DLM from step 2, adding all data from 1993 plus the first sample from May 1994, which was taken prior to the beginning of enrichment (Fig. 2C). We then forecast the level and 90% HPD interval for the rest of 1994. This allowed us to determine which variates showed delayed or continuing responses to experimental enrichment in Peter, West Long, and East Long lakes.

4) We finished fitting the DLM by adding data from 1994 to the model from step 3. We then evaluated model fit using the cumulative predictive density (CPD, described in the Appendix), plus standard methods for analyzing residuals: normal probability plots, mean absolute deviation, mean square error, and correlations between one-step-ahead predictions and observations.

Analysis of DLM output

After all dynamic linear models were fit, we compared the predictions for each variate to the observations from 1992, 1993, and 1994, and determined whether that variate had changed significantly in each year (Fig. 2D). To do this, we calculated the percent of observations that fell either above or below the 90% HPD interval around the predictions made at the beginning of each year. The more observations outside the 90% HPD intervals (prediction limits), the more evidence that a particular variate changed in a particular year.

There were four basic patterns of response: (1) no observations outside the prediction limits, and thus no change in that variate in that year (Fig. 3A); (2) a few observations outside the prediction limits, but probably not enough to infer that there was significant change from expectations (Fig. 3B); (3) many observations

above the prediction limits, suggesting an increase during that year (Fig. 3C); and (4) many observations below the prediction limits, suggesting a decrease during that year (Fig. 3D). To separate case 2 from cases 3 and 4, we defined an ecologically significant change as one for which $\geq 20\%$ of the observations were outside of the prediction limits. We would expect 10% of the observations to differ from the prediction limits by chance (because they are 90% HPD intervals), so this cutoff balances the need to minimize both false positive and false negative results. Qualitative results were robust to $\pm 10\%$ changes in this cutoff.

In evaluating whether a particular variate was a reliable indicator of nutrient enrichment, we tested for two conditions. First, that the variate changed significantly in all three enriched lakes in 1993; this would show that the variate was consistently sensitive to the onset of experimental enrichment and reduce the likelihood of "false negative" results. Second, that the variate did not change significantly in Paul Lake at any time or in Peter, West Long, or East Long lakes in 1992; this would show that background rates of change were low and reduce the likelihood of "false positive" results. Variates which were sensitive to enrichment in only one or two of the enriched lakes or which changed significantly in 1994 were considered less reliable indicators because of their lack of consistency or tardiness in responding to the experimental perturbation.

RESULTS

Model fit and choice of discount factors

A one-parameter DLM was a suitable description of seasonal and interannual dynamics for most variates. Depending on the discount factors for the evolution and observation variance, the level parameter tracked the dynamics of each series either slowly (δ_w and δ_v nearer 1) or quickly (δ_w and δ_v nearer 0.8 or 0.9, respectively) (Fig. 4A). The discount factors δ_w and δ_v for each variate in each lake were selected based on the cumulative predictive density (CPD) of the one-step-ahead forecasts. The shape of the surface tracing CPD vs. δ_w and δ_v , and hence the optimal value for these parameters, varied considerably among lakes (Fig. 4B-E) and types of variates (not shown). The optimal δ_w was 0.99 for 54% of the variates, between 0.825 and 0.975 for 14%, and 0.8 for the remaining 32%. The optimal δ_v was 0.99 for 15% of the variates, between 0.925 and 0.975 for 2%, and 0.9 for the remaining 83%. All further results are based on the optimal δ_w and δ_v for each time series.

Given the optimal δ_w and δ_v , observations during unmanipulated lake-years generally fell within the 90% HPD intervals around the level. One-step-ahead predictions were positively correlated with observations for all variates (Table 3); correlations tended to be higher for community and ecosystem variates than for population variates. Residuals from these one-step-ahead

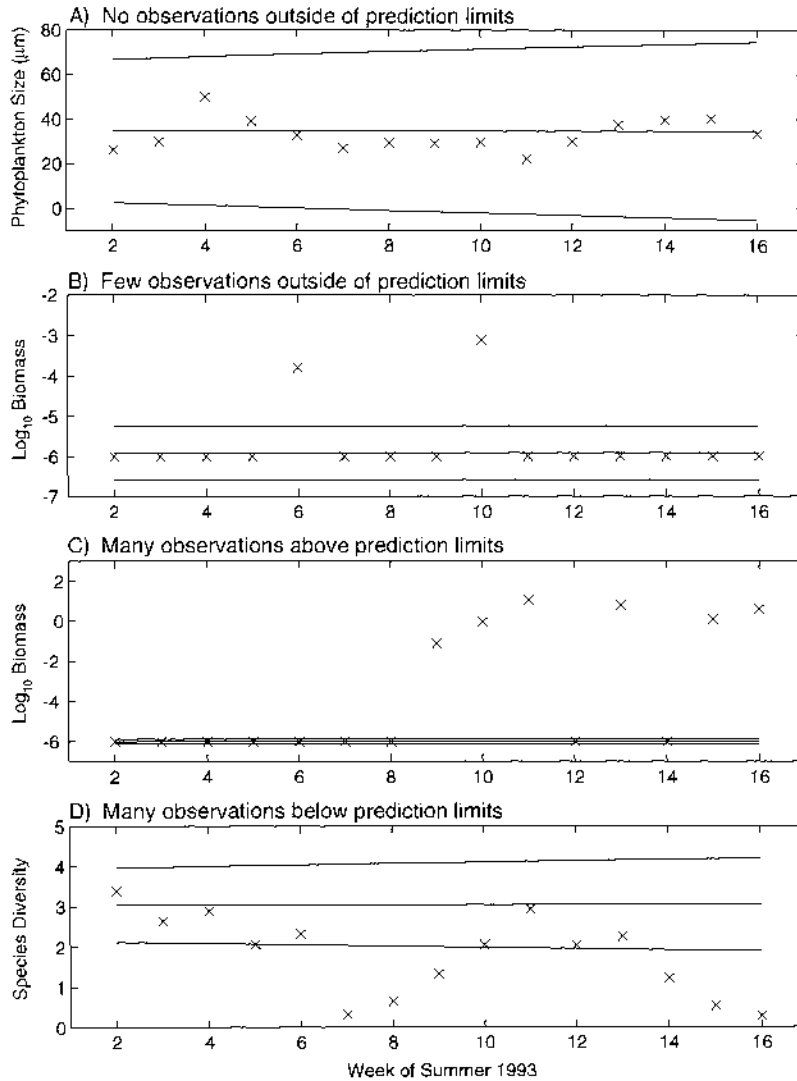


FIG. 3. Typical patterns of change from one year to the next; symbols are as in Fig. 2 and all data are from 1993. (A) Biomass-weighted average phytoplankton size, East Long Lake; (B) *Achnanthes*, Paul Lake; (C) *Anabaena*, West Long Lake; (D) Shannon-Wiener species diversity, Peter Lake.

predictions were normally distributed for many, but not all, variates. Skewed residuals occurred for variates that were mostly within one narrow range of values, but had occasional outbreaks or bloom-type behavior; this pattern was most common for rare species and genera.

Background variability and sensitivity to enrichment of population, community, and ecosystem variates

Most species had high background variability and did not change significantly with enrichment (Fig. 5A, Table 4). On average, only one-third of the species were present in a sufficient number of samples (>20%) to register as having changed significantly from one year to the next. As a result, few species changed significantly within any particular year of the experiment.

Neither the number nor the proportion of species that showed significant change from one year to the next increased after enrichment in the enriched lakes. In fact, there was little difference between the enriched and reference lakes in the number of taxa which changed significantly from year to year.

Nevertheless, several species did change significantly following experimental enrichment (Fig. 5A, Table 4). Some increased considerably in only one of the enriched lakes (e.g., *Anabaena flos-aquae* and *A. macrospora* in West Long, *Monoraphidium capricornutum* and four species of *Staurastrum* in Peter, and *Schizochlamys compacta* and *Cystomonas starri* in East Long), while others changed in two of the three enriched lakes, including *Dictyosphaerium pulchellum*, *Gymnodinium* sp. 1, *Selenastrum minutum*, *Sphaero-*

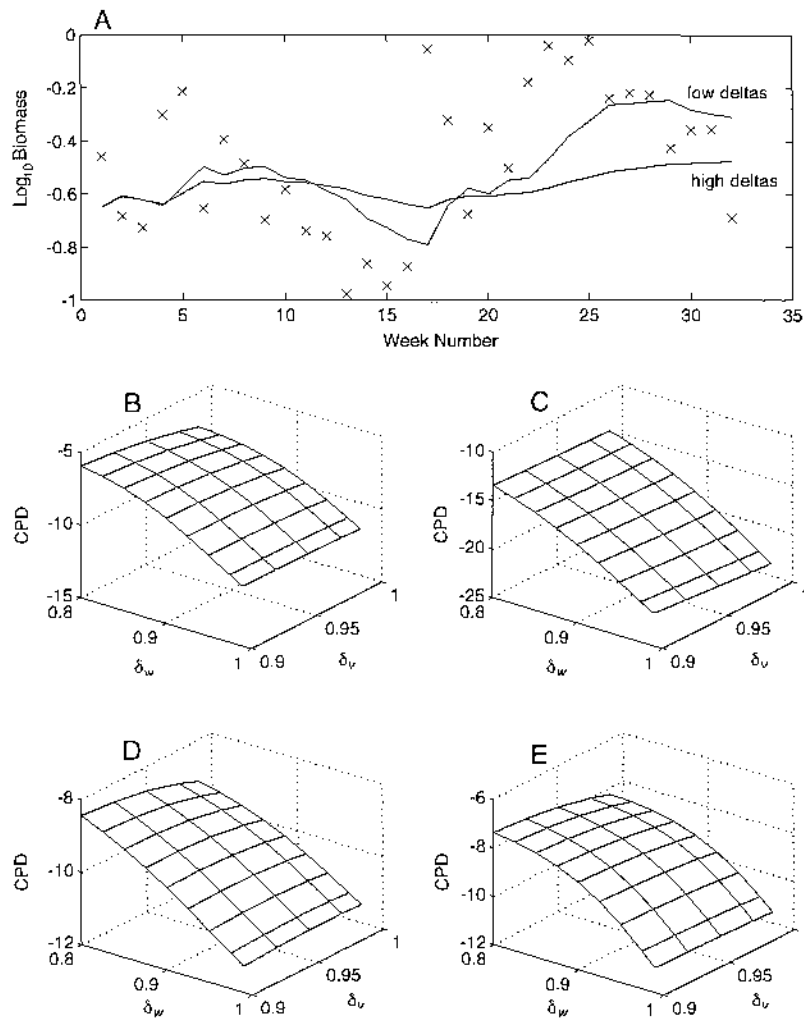


FIG. 4. Comparing and selecting discount factors for total biomass using data from 1991–1992. (A) Effects of different discount factors on model responsiveness to change: the model with $\delta_u = 0.9$ and $\delta_w = 0.8$ is more responsive to fluctuations than the model with $\delta_u = \delta_w = 0.99$ (for West Long Lake only). (B–E) Cumulative predictive density (CPD) at each value of δ_w and δ_v in each lake: (B) Paul Lake, (C) Peter Lake, (D) West Long Lake, (E) East Long Lake.

TABLE 3. Pearson product-moment correlations between observed values and one-step-ahead model predictions for each type of variate. The data are for all four lakes pooled; differences among lakes were small.

Variate type	Mean \pm 1 SE	n
Population		
Species	0.212 \pm 0.015	292
Community		
Taxonomic		
Genera	0.231 \pm 0.019	182
Divisions	0.454 \pm 0.055	20
Allometric	0.361 \pm 0.046	20
Diversity	0.529 \pm 0.043	12
Ecosystem		
Total biomass/chlorophyll	0.473 \pm 0.106	8
Primary productivity	0.508 \pm 0.055	4

cystis schroeteri, and *Teilingia granulata*. However, only one species, *Scenedesmus denticulatus*, changed significantly in all three enriched lakes but not in the unenriched control lake. Overall, there were few consistently responsive species, and the presence or absence of a particular species did not appear to be a particularly reliable indicator of enrichment in these lakes.

Like the species populations, phytoplankton genera tended to be highly variable and only somewhat sensitive to enrichment (Fig. 5B). On average, <50% of the genera were present in >20% of samples, meaning that less than one-half of the genera could signal a significant change from one year to the next. Few genera changed significantly within any particular year of the experiment, and the number of genera that changed significantly from one year to the next did not increase after enrichment (Fig. 5B). Some genera, however, did

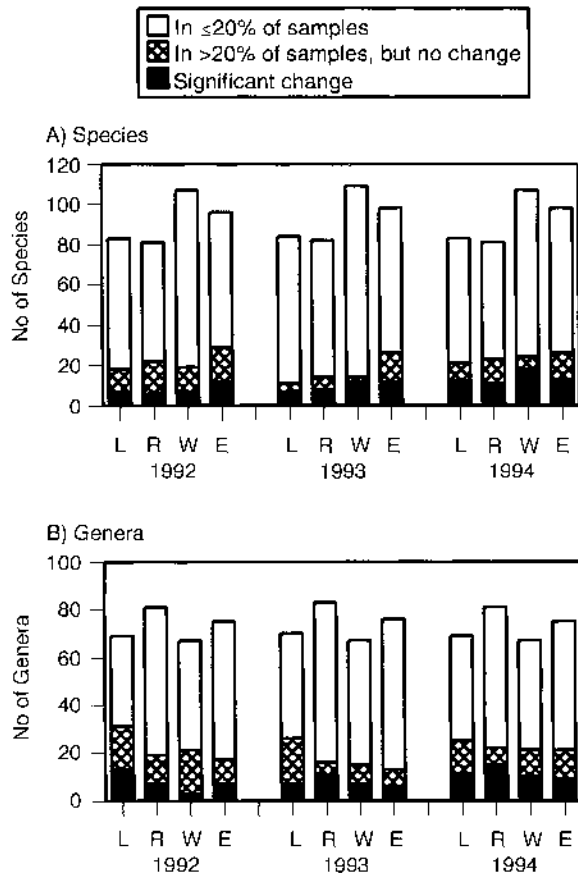


FIG. 5. Numbers of (A) species and (B) genera in each response category in each lake in each year: each histogram bar is subdivided to show taxa present in $\leq 20\%$ of the samples and therefore not able to register a significant response; taxa present in $> 20\%$ of the samples, but with $\leq 20\%$ of the samples outside the prediction limits; and taxa that showed significant change (were present in $> 20\%$ of the samples and with $> 20\%$ of the total number of samples outside the prediction limits). Abbreviations: L = Paul Lake, R = Peter Lake, W = West Long Lake, and E = East Long Lake.

change significantly following the onset of experimental enrichment, and the identities of these genera conveyed some information about enrichment (Table 5). For example, *Dictyosphaerium* and *Gymnodinium* changed significantly in all three enriched lakes. *Chroomonas*, *Cryptomonas*, *Scenedesmus*, *Schroederia*, *Sphaerocystis*, and *Teilingia* increased in two of the three enriched lakes, while *Dinobryon* and *Ochromonas* decreased in two of the three lakes. Thus, although the number of genera changing significantly from year to year was not particularly sensitive to enrichment, there were a few individual taxa that were consistently sensitive to our experimental perturbation.

Unlike species and genera, taxonomic divisions were highly sensitive to experimental enrichment (Fig. 6). All five divisions changed significantly in Peter and West Long lakes in 1993, and four of the five changed in East Long Lake. Cryptomonads increased and chry-

sophytes and dinoflagellates declined in all three enriched lakes; chlorophytes and cyanobacteria increased in West Long and Peter lakes; and chlorophytes declined in East Long Lake. However, this high sensitivity was offset somewhat by high background variability, including significant "false positive" changes in non-enriched lake-years, as well as delayed responses to enrichment in one or two taxa in each enriched lake (Fig. 6). Change in three or more divisions was therefore a more reliable signal of enrichment than change in a single division.

Although background variability was lower for the size-based variates than for taxonomic divisions, allometric variates were also much less sensitive to enrichment (Fig. 7). None of the five variates changed significantly in all three enriched lakes during the first year of enrichment, suggesting that size-based variates could give "false negative" results. The large size class ($> 30 \mu\text{m}$), slope of the normalized size spectrum, and average GALD increased in two of the three enriched lakes, while the small size class ($\leq 30 \mu\text{m}$) and the mean square error of the normalized size spectrum changed in only one lake. Delayed responses were observed for large phytoplankton in Peter Lake, slope of the normalized size spectrum in West Long Lake, and mean square error in East Long Lake. Furthermore, average GALD increased in 1994 in the reference lake. Clearly, none of the five allometric variates met the reliability criteria of high sensitivity and low background variability in these lakes and at this temporal scale.

In contrast, all three community diversity variates were very sensitive to experimental enrichment, and two of the three had low background variability (Fig. 8). Species diversity, evenness, and richness decreased significantly in all three enriched lakes in 1993. However, species richness also declined significantly in Peter Lake in 1992 and increased in Peter and East Long lakes in 1994, suggesting that background variability was higher for species richness than for species diversity and evenness.

The ecosystem variates were also highly sensitive to enrichment (Fig. 8). Chlorophyll and primary productivity increased in all three enriched lakes in 1993, while total biomass increased in Peter and West Long lakes. However, primary productivity also increased significantly in the unenriched control lake in 1994, suggesting that changes in factors other than nutrient loading can cause changes in productivity. Therefore, of the three ecosystem variates, only chlorophyll showed both high sensitivity and low background variability.

DISCUSSION

Dynamic linear models

Dynamic linear models could be fit to all of our time series, whereas other time series approaches were in-

TABLE 4. Significant changes in each species; "+" indicates a significant increase in that lake in that year (>20% of the samples were above the prediction limits), "-" indicates a significant decrease, and "x" indicates that the species was present but did not change significantly. Abbreviations: L = Paul Lake, R = Peter Lake, W = West Long Lake, and E = East Long Lake.

Division	Species name	1992				1993				1994			
		L	R	W	E	L	R	W	E	L	R	W	E
Cyanobacteria	<i>Anabaena affinis</i>		x										x
	<i>Anabaena aphanizomenoides</i>										x		
	<i>Anabaena circinalis</i>									x			
	<i>Anabaena flos-aquae</i>							+		x		x	x
	<i>Anabaena laponica</i>											x	
	<i>Anabaena macrospora</i>					x	x	x			x	+	x
	<i>Anabaena subcylindrica</i>												
	<i>Anabaena variabilis</i>												
	<i>Aphanizomenon flos-aquae</i>												
	<i>Aphanocapsa elachista</i>	+	x									x	
	<i>Chroococcus dispersus</i>												
	<i>Chroococcus limneticus</i>		x										x
	<i>Dactylococcopsis smithii</i>	+			x								
	<i>Gomphosphaeria aponina</i>												
	<i>Gomphosphaeria lacustris</i>						x	x			x		
	<i>Lynghya contorta</i>										x		
	<i>Merismopedia tenuissima</i>	x	x	x	x	x		-			x	x	-
	<i>Microcystis aeruginosa</i>	x											
	<i>Microcystis incerta</i>												
	<i>Oscillatoria limnetica</i>	x	x	x	x	x	+	x	x	x	x	-	x
<i>Oscillatoria</i> sp. 2	x	x		x	x								
Chlorophytes	<i>Actinastrum hantzschii</i>												x
	<i>Ankistrodesmus falcatus</i>					x	+		x	x	x	x	x
	<i>Ankistrodesmus falcatus</i> v. <i>mirabilis</i>	x	x	+	-			-	x				
	<i>Arthrodesmus incus</i>			x									
	<i>Arthrodesmus</i> sp. 3												
	<i>Arthrodesmus subulatus</i>	x	x			x						+	x
	<i>Botryococcus braunii</i>	+	x		x	x					x	x	x
	<i>Carteria platyrhyncha</i>										x		x
	<i>Characium limneticum</i>		x	x									
	<i>Chlamydomonas dinobryoni</i>												
	<i>Chlamydomonas globosa</i>										x		x
	<i>Chlamydomondopsis curvata</i>										+		+
	<i>Closteriopsis longissima</i>				x								
	<i>Closterium moniliferum</i>												
	<i>Cosmarium tenue</i>							x				+	
	<i>Crucigenia fenestrata</i>											x	
	<i>Crucigenia quadrata</i>						x						
	<i>Crucigenia rectangularis</i>	x					x				x		
	<i>Cystomonas starrii</i>										+	+	+
	<i>Dictyosphaerium pulchellum</i>	x			x	x	+	x			x	+	+
	<i>Elakatothrix gelatinosa</i>	x		x		x	x	+			x	x	x
	<i>Eurastrum abruptum</i>	x					x						
	<i>Franceia droescheri</i>											x	
	<i>Gloeocystis ampla</i>	x											
	<i>Gloeocystis</i> sp. 1							x			x	x	x
	<i>Golenkinia radiata</i>							x					
	<i>Gonatozygon aculeatum</i>										x		
	<i>Kirchneriella contorta</i>	+	x				x	x					
	<i>Micractinium pusillum</i>											+	x
	<i>Monomastix astigmata</i>	x	+	x	x	-	x	x	x	x	x	+	x
	<i>Monoraphidium capricornutum</i>										+	+	x
	<i>Oocystis borgei</i>	x							x		x		
	<i>Oocystis parva</i>						+	x	+	x	+	+	+
	<i>Oocystis</i> sp. 1	x	x	x	x								x
	<i>Oocystis</i> sp. 2	x	x	x			x						
	<i>Paulschulzia tenera</i>							x				x	
	<i>Pediastrum duplex</i>							x					
	<i>Pediastrum tetras</i>	x			+								x
	<i>Quadrigula chodatti</i>	+									x		
	<i>Quadrigula lacustris</i>										+	x	x
	<i>Scenedesmus denticulatus</i>										x	+	+
	<i>Scenedesmus quadricauda</i>												
<i>Scenedesmus</i> sp. 1											x		
<i>Schizochlamys compacta</i>										x		+	
<i>Schroederia judayi</i>		x	x					+	+	+	x	x	

TABLE 4. Continued.

Division	Species name	1992				1993				1994			
		L	R	W	E	L	R	W	E	L	R	W	E
Diatoms (continued)	<i>Cymbella microcephala</i>												
	<i>Fragilaria construens</i>												x
	<i>Fragilaria crotonensis</i>										x		
	<i>Navicula cryptocephala</i>												
	<i>Navicula</i> sp. 1							x		x			x
	<i>Nitzschia acicularis</i>	x	x		x		x			x	+	x	x
	<i>Nitzschia gracilis</i>												
	<i>Nitzschia perminuta</i>	x					+	x					
<i>Tabellaria fenestrata</i>	x		x	x	x		x	x				x	
Others	<i>Euglena acus</i>												
	<i>Gonyostomum semen</i>												x

appropriate for some of our data. DLM overcame many of the problems with ARIMA models, including missing values, unequally spaced data, and the undue influence of outliers and rare events. DLM allowed us to incorporate history, estimate nominal states for each variate, and quantify uncertainty in these predictions. Fits to phytoplankton variates above the level of genus were quite good and correspondence between one-step-ahead predictions and observations was excellent. Like ARIMA models, however, DLM could not describe the extreme seasonal variations of many species and genera.

Discount factors, δ_{ω} , and δ_{ν} , differed widely among

these time series. For >80% of the variates examined, the lowest discount factor for the evolution variance ($\delta_{\omega} = 0.90$) yielded the best model. For one-third of the variates, the lowest discount factor for the observation variance ($\delta_{\nu} = 0.80$) was selected. With these low discount factors, the information value of each data point is relatively low, such that information from the last two to five samples dominates model estimation (Pole et al. 1994). This suggests that there was little continuity in the phytoplankton community from week to week, especially for species or genera. Continual fluctuations in light, nutrients, and mixing rates make the epilimnion a very volatile environment, and week-

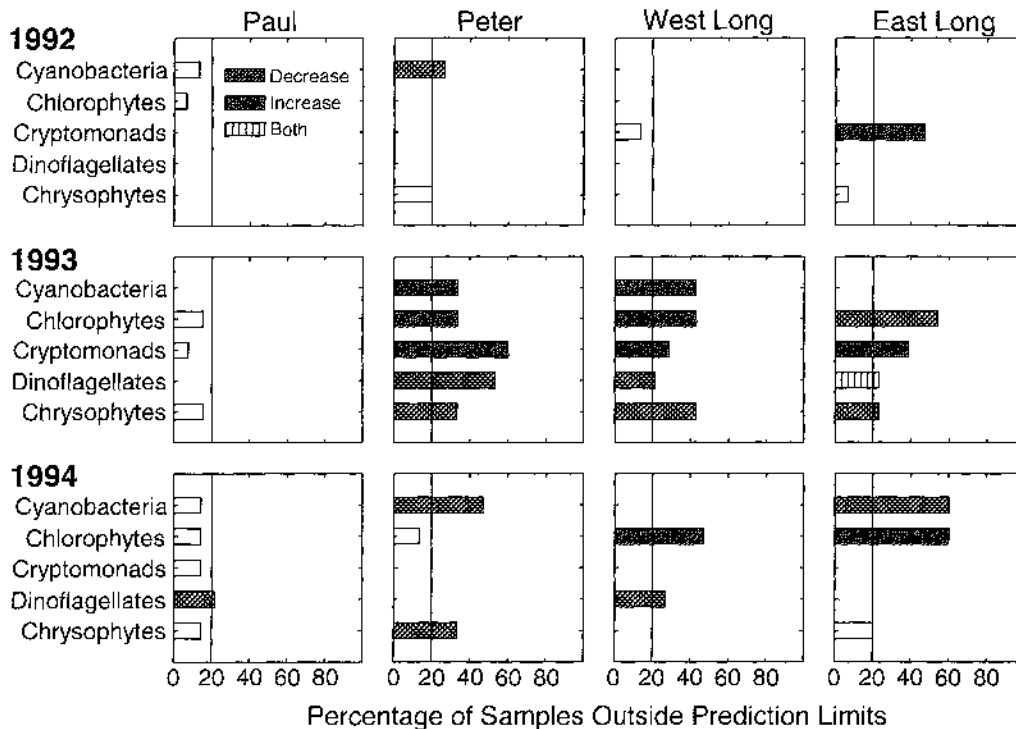


FIG. 6. Percentage of samples outside the prediction limits for each taxonomic division in each lake during 1992, 1993, and 1994. Filled bars indicate significant increases (>20% of samples above the prediction limits), cross-hatched bars indicate significant decreases (>20% of samples below the prediction limits), vertically lined bars indicate >20% of samples above prediction limits and >20% of samples below prediction limits, and open bars indicate nonsignificant changes.

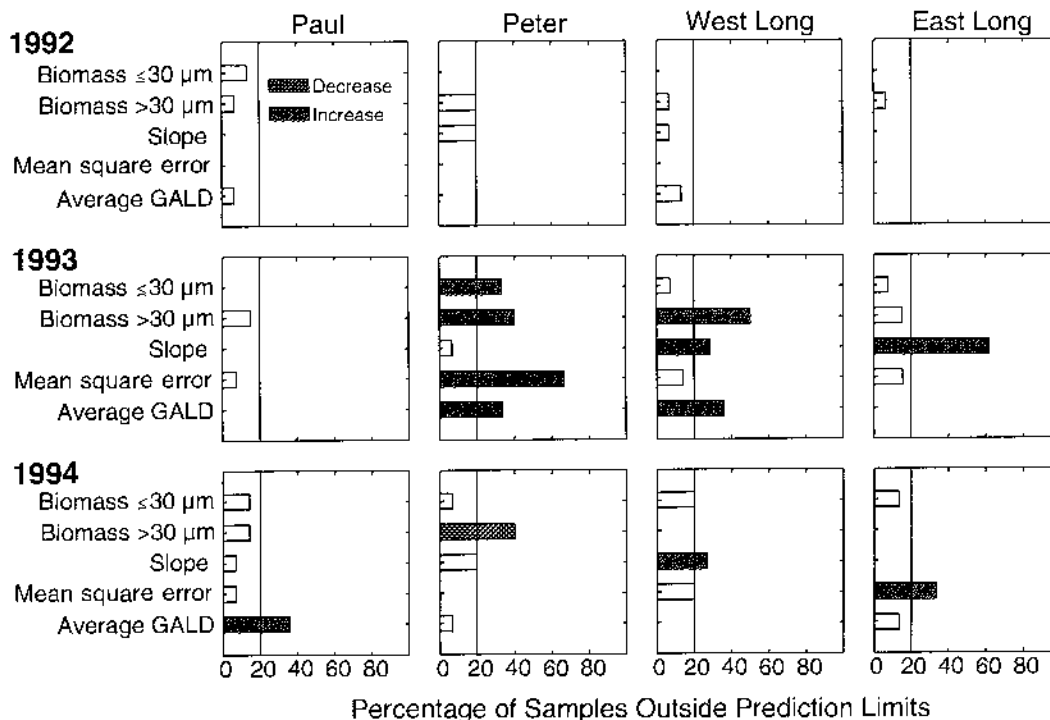


FIG. 7. Percentage of samples outside the prediction limits for each allometric variate. Presentation is as in Fig. 6.

to-week variability in the phytoplankton community reflects this. Over longer time scales, though, there is an extensive ecological memory in the algal community due to a sediment "seed bank" of resting spores and cysts (e.g., Sandgren 1988b, Padisak 1992, Hansson 1993). Emergence from this seed bank contributes to the rapid and variable appearance of species in the epilimnion, but also ensures that a pool of species is available for colonization should epilimnetic conditions change dramatically within a relatively short time period.

Population vs. ecosystem variates as ecological indicators

One of the goals of this study was to test the expectation that species populations are more reliable indicators of perturbation than ecosystem variates because functional complementarity buffers aggregated variates from change (Odum 1985, Schindler 1990, Howarth 1991, Frost et al. 1995). This expectation hinges on two assumptions: (1) population variates are more sensitive to perturbation than ecosystem variates, and (2) population variates have sufficiently low background variability to ensure that changes due to perturbation can be detected. Our results do not support either of these assumptions.

Contrary to expectations from the perturbation literature (e.g., Odum 1985), but consistent with limnological understanding, phytoplankton ecosystem variates were very sensitive to enrichment. Chlorophyll, total biomass, and primary productivity increased con-

siderably following the onset of experimental enrichment in Peter, West Long, and East Long lakes: mean chlorophyll concentrations increased by a factor of 2.8–4.7, total biomass by a factor of 3.7–8.2, and primary productivity by a factor of 3.1–7.1. This result is very similar to other whole-lake enrichments (e.g., Schindler et al. 1971, 1973, Schindler 1974, Holmgren 1984) as well as patterns observed following cultural eutrophication of lakes around the world (Harper 1992, Thompson and Rhee 1994). It is well established that phytoplankton chlorophyll, biomass, and productivity scale to phosphorus loading; Schindler (1988) showed that these variates are proportional to P loading regardless of other stressors, including acidification. In fact, relationships between phytoplankton ecosystem variates and P loading (e.g., Dillon and Rigler 1974, Vollenweider 1976, Schindler et al. 1978) have been a vital component of lake management strategies for >2 decades (Cooke et al. 1993).

Several other studies also belie the complete generality of the relative insensitivity of ecosystem variates. For example, although phytoplankton productivity is relatively resistant to acidification, benthic algal production and production:respiration ratios were very sensitive to experimental acidification at the Experimental Lakes Area (Turner et al. 1995, Schindler 1996). In mesocosm experiments, low concentrations of atrazine, mercury, and other chemical stressors promoted change in primary productivity, nutrient cycling, and daily patterns of production and respiration (Pratt and

TABLE 5. Significant changes in each genus; “+” indicates a significant increase in that lake in that year (>20% of the samples were above the prediction limits), “-” indicates a significant decrease, and “x” indicates that the genus was present but did not change significantly. Abbreviations: L = Paul Lake, R = Peter Lake, W = West Long Lake, and E = East Long Lake.

Division	Genus name	1992				1993				1994			
		L	R	W	E	L	R	W	E	L	R	W	E
Cyanobacteria	<i>Anabaena</i>		x			+	+	+		x	x	x	x
	<i>Anabaenopsis</i>									x			
	<i>Aphanizomenon</i>												
	<i>Aphanocapsa</i>	+	x								x		
	<i>Chroococcus</i>		x								x		
	<i>Dactylococcopsis</i>	+			x								
	<i>Gomphosphaeria</i>	x	x	x		x	x			+			
	<i>Lyngbya</i>		x		x					x			
	<i>Merismopedia</i>	x	x	x	x	x		-		x	x	-	x
	<i>Microcystis</i>	x											
	<i>Nostoc</i>	+		x									
	<i>Oscillatoria</i>	x	x	x	x	x	+	x	x	x	-	x	x
Chlorophytes	<i>Actinastrum</i>											x	x
	<i>Ankistrodesmus</i>	x	+	+	-	x	x	x	x	x	x	x	x
	<i>Arthrodesmus</i>	x	x	x		x				x		+	x
	<i>Bambusina</i>											x	
	<i>Botryococcus</i>	+	x		x	x				x	x	x	
	<i>Carteria</i>									x			x
	<i>Characium</i>		x	x									
	<i>Chlamydomonas</i>	+	x	x	x		x	x	x	x	+	x	x
	<i>Chlamydomondopsis</i>									+			
	<i>Clasteriopsis</i>				x								
	<i>Closterium</i>												x
	<i>Coelastrum</i>												x
	<i>Cosmarium</i>						x				+		
	<i>Crucigenia</i>	x			x	x				x	x		
	<i>Cystomonas</i>									+	+	+	+
	<i>Dictyosphaerium</i>	x			x	x	+	x			x	+	+
	<i>Elakatothrix</i>	x		x		x	x	+		x	x	x	x
	<i>Eudorina</i>									x			
	<i>Eurastrum</i>	x				x							
	<i>Franceia</i>						x			x			
	<i>Gloeocystis</i>	x			x		x	x		x	x		x
	<i>Golenkinia</i>						x						
	<i>Gonatozygon</i>									x			
	<i>Kirchneriella</i>	+	x			x	x						
	<i>Lobomonas</i>	x	x	x	x	x		x	x	x	x	x	x
	<i>Micractinium</i>										+	x	x
	<i>Monomastix</i>	x	+	x	x	-	x	x	x	x	+	x	x
	<i>Monoraphidium</i>									+	+	x	x
	<i>Mougeotia</i>	x											
	<i>Nephrocytium</i>										x		
	<i>Oedogonium</i>												x
	<i>Oocystis</i>	x	x	x	x	x	x	x	x	+	+	+	x
	<i>Pandorina</i>											x	
	<i>Paulschulzia</i>						x				x	x	
	<i>Pediastrum</i>	x			+		x						x
	<i>Quadrigula</i>	+								+	x	x	x
	<i>Scenedesmus</i>	x	+	x	x	x	x	x		x	x	+	+
	<i>Schizochlamys</i>									x		x	+
	<i>Schroederia</i>	x	x	x				+	+	+	x	x	x
	<i>Selenastrum</i>	x		x	x	x	x			x	+		+
<i>Sphaerocystis</i>	x	x	x	+	x		x	x	x	+	+	x	
<i>Staurastrum</i>	x		x	x					x	+	x		
<i>Sticheococcus</i>													
<i>Stigeoclonium</i>							x		x				
<i>Teilingia</i>		x	x		x					+	+		
<i>Tetracystis</i>	-		x		-				+				
<i>Tetraedron</i>	x	x		x	x				x		x		
<i>Tetrastrum</i>												x	
<i>Ulothrix</i>		x											
<i>Volvox</i>							x		x		x	x	
<i>Xanthidium</i>	x	x	x		x						x	x	
Cryptophytes	<i>Chroomonas</i>	x		x							x	+	+
	<i>Cryptomonas</i>	x	x	x	+	x	+	+	+	x	x	x	x
	<i>Rhodomonas</i>					+	+			x	x	x	x

TABLE 5. Continued.

Division	Genus name	1992				1993				1994			
		L	R	W	E	L	R	W	E	L	R	W	E
Dinoflagellates	<i>Ceratium</i>	x								x			
	<i>Glenodinium</i>			x	x			x	x				x
	<i>Gymnodinium</i>	x	x	x	+	x	-	-	+	-	x	-	-
	<i>Peridinium</i>	+	x	x	x	x	-	x	x	x	+	x	x
Chrysophytes	<i>Chlorocloster</i>		x	x	+								
	<i>Chrysocapsa</i>												x
	<i>Chrysochromulina</i>			x	x								
	<i>Chrysococcus</i>					x			+	x		x	x
	<i>Chrysolykos</i>		+				x				x		
	<i>Chrysosphaerella</i>	+	+	+	x					+			
	<i>Diceras</i>	+	x	x	x	x	x	x		x	x	x	x
	<i>Dinobryon</i>	x	x	x	x	x	-	-	x	x	x	x	x
	<i>Ellipsoidion</i>							x					
	<i>Erkenia</i>							x			x		x
	<i>Kephyrion</i>	x	x	x	x	x	x	-		x	x		x
	<i>Mallomonas</i>	x	x	x	+	x	x	x	-	x	+	x	x
	<i>Ochromonas</i>	x	x	x	x	x	-	x	-	x	x	x	+
	<i>Pseudotetraedron</i>				x								
	<i>Stichogloea</i>	x	x	+		-	+			+	x		
	<i>Syncrypta</i>		+										
<i>Synura</i>	-	x	x	x	x	+	x	x	x	x	x	x	
<i>Uroglena</i>	+	x	x	x	x	x	x	x	x	x	x	x	
Diatoms	<i>Achnanthes</i>	x				x	x		x			x	
	<i>Amphipleura</i>												
	<i>Asterionella</i>				x							+	
	<i>Cocconeis</i>												
	<i>Cyclotella</i>		x							x		x	
	<i>Cymbella</i>				x								
	<i>Fragilaria</i>	x			x						x	x	
	<i>Frustulia</i>		x										
	<i>Gomphonema</i>							x					
	<i>Melosira</i>												
	<i>Navicula</i>	x	x		x	x	x	x		+	x	x	x
	<i>Nitzschia</i>	x	x		x	x	x			x	+	x	x
	<i>Pinnularia</i>			x									
	<i>Rhizolenia</i>				x						x		x
	<i>Stauroneis</i>			x									
<i>Tabellaria</i>	x		x	x	x		x	x				x	
Others	<i>Euglena</i>												
	<i>Trachelomonas</i>			x	x		x			x	x	x	
	<i>Gonyostomum</i>	x	+	x	x	x				x		x	

Cairns 1996). Clearly, not all ecosystem variates are robust to all perturbations.

In contrast to the high sensitivity to enrichment of phytoplankton ecosystem variates, significant changes were detected in few phytoplankton species. This can be traced to high background variability: two-thirds of the species were not present in enough samples to determine whether they were significantly different from expectations, and wide fluctuations in biomass from week to week led to high forecast uncertainty and wide prediction limits for the remaining one-third. Consequently, only a handful of species changed significantly in two or more enriched lakes. This suggests that signals at the population level were not particularly consistent among lakes—and therefore, that in these lakes and at this temporal scale, phytoplankton species were not reliable indicators of enrichment. McCormick and Cairns (1994) expressed similar reservations about the

use of phytoplankton population variates as ecological indicators.

There are many possible explanations for why we did not detect widespread changes in phytoplankton species, including the particular kind of perturbation examined, the organism chosen, and the time scale at which our study was conducted. For example, we focused on an enrichment perturbation that maintained N:P ratios at high, pre-manipulation levels. This is a less severe perturbation than enrichment at low N:P ratios, since phytoplankton communities respond to both total nutrient supply and ratios of nutrients (e.g., Tilman et al. 1982). Low N:P ratios swing the competitive advantage from eukaryotic algae with efficient P uptake mechanisms to heterocystous cyanobacterial species with the ability to fix atmospheric nitrogen (Smith 1983). Judging from the results of whole-lake enrichments at low N:P ratios (e.g., Persson et al. 1975,

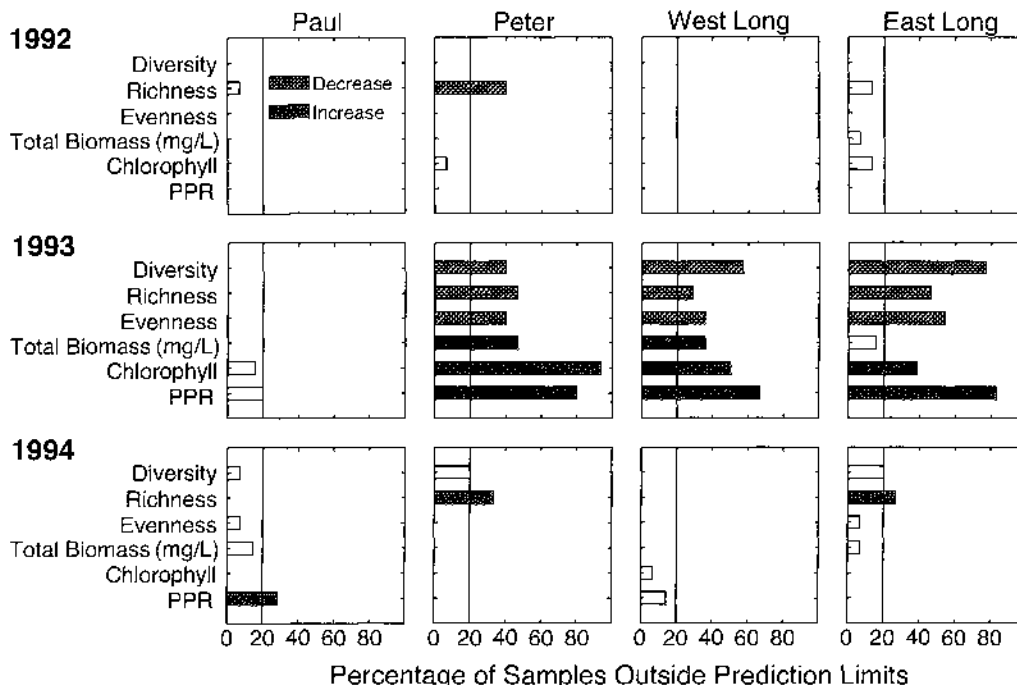


FIG. 8. Percentage of samples outside the prediction limits for community diversity and ecosystem variates. Presentation is as in Fig. 6.

Holmgren 1984, Findlay et al. 1994), phytoplankton may respond very differently to additions of nutrients at low vs. high N:P ratios. In Lake 227, for example, responses to high N:P enrichment were very similar to those documented for Peter, West Long, and East Long lakes. However, when N:P ratios were reduced, there was a pronounced shift towards nitrogen-fixing cyanobacteria with little change in biomass or productivity (Findlay et al. 1994, Hendzel et al. 1994). Applying the quantitative approach introduced here to comparable data from a low N:P enrichment experiment would be one way to quantify whether species populations are more sensitive to enrichment at low N:P ratios than at high N:P ratios.

A second explanation for the insensitivity of species population is our focus on phytoplankton rather than zooplankton or benthos. Much of the evidence for species sensitivity to perturbation comes from animal populations like zooplankton, benthos, or fish (Schindler et al. 1985, Howarth 1991, Frost et al. 1995, Pratt and Cairns 1996). Species of zooplankton or benthos could therefore be more reliable indicators of enrichment than species of phytoplankton; we plan to test this possibility in a future analysis.

Interestingly, fossils of siliceous phytoplankton species are reliable indicators of environmental change at paleoecological time scales (e.g., Dixit et al. 1992, Smol 1992, Anderson 1993). For example, indicator species and suites of species have been identified for a number of large-scale anthropogenic disturbances, including acidification (e.g., Charles et al. 1990), eu-

trophication (Anderson et al. 1990), changes in food web structure (Leavitt et al. 1989), and climate shifts (Smol et al. 1991). The difference between our findings and those of paleolimnological studies could be due to our focus on dynamics within and among summers; this is a very short temporal scale as compared to paleolimnological investigations that look at changes in samples that cover ~2- to 3-yr intervals over decades to centuries (Smol 1992). The week-to-week oscillations in phytoplankton abundance that predominate in our study are smoothed out in the sediment record. In addition, summer taxa are supplemented by those that occur in the fall, winter, and spring, providing a more balanced perspective across an annual cycle. Thus, temporal scale may have an important effect on whether phytoplankton species are considered to be reliable indicators.

Despite these caveats, it is clear that species populations are not necessarily more reliable indicators than ecosystem variates in every ecosystem and for every stress. This suggests that we need to be very careful in making generalizations about indicators of ecosystem responses to perturbation (Schindler 1996). Rather than asking which are better, population or ecosystem variates, we should focus on determining what kinds of variates work best under particular conditions, and seek general patterns among systems and among stressors.

Community variates as ecological indicators

Community variates, including higher taxonomic entities, allometric variates, and diversity properties, have

been suggested as possible ecological indicators by a number of researchers. There is published evidence to support the use of each of the variates considered in this paper as an ecological indicator. However, never before have all of these different variates been compared for the same data using the same quantitative approach. Thus, this study is a unique attempt to evaluate a wide variety of candidate indicators using a quantitative approach. Our results show that shifts in multiple taxonomic divisions and declines in species richness and evenness were reliable community-level indicators of nutrient enrichment.

Phytoplankton genera were only slightly more reliable indicators of enrichment than species populations. Patterns in the proportions of taxa that were sensitive to enrichment were quite similar for species and genera, although increases and decreases in several indicator taxa were detected somewhat more readily at the genus level. This suggests that little additional information is gained when phytoplankton are identified to species rather than genera.

In contrast, changes in phytoplankton taxonomic divisions, particularly concurrent changes in several divisions, were highly reliable indicators of enrichment in these lakes. Changes at this level of taxonomic aggregation have a long history as diagnostics of nutrient enrichment (e.g., Pearsall 1932, Nygaard 1949). We therefore expected to detect changes in several taxonomic divisions with enrichment, including increases in cyanobacteria and chlorophytes at the expense of the pre-enrichment dominants, chrysophytes and dinoflagellates (Reynolds 1984, Harper 1992). Our results supported this expectation: all five taxonomic divisions were sensitive to enrichment. However, background variability was also relatively high, so that changes in any one division were not particularly reliable signals of enrichment. In contrast, changes in three or more divisions were a very consistent signal of enrichment in these lakes. The direction of change also carried information about enrichment—for example, declines in chrysophytes and dinoflagellates occurred in all three enriched lakes (as well as in many lakes in the literature; e.g., Pollinger 1988, Sandgren 1988a).

Because species identification is time-consuming and requires specially trained taxonomists, it is worthwhile to know whether we even need to evaluate samples at the species level (Sullivan and Carpenter 1982, Herman and Heip 1988, Warwick 1988). We do need to identify organisms to a level where there is reliable sensitivity to perturbation, but more aggregated taxonomic categories may work equally well or better than species. Warwick (1988) suggested that changes due to anthropogenic perturbations were easier to detect for taxonomic categories like genera, families, and orders, because these taxa respond less to environmental variability than species. Our data support this pattern, particularly when phytoplankton are aggregated into divisions. Phytoplankton genera, though, gave similar re-

sults as species. Therefore, identification to genus or even to division could improve efficiency of phytoplankton monitoring without large sacrifices in the amount of information obtained.

Size-based phytoplankton variates were less reliable indicators of enrichment than taxonomic divisions. Odum (1985) and Rapport et al. (1985) predicted that perturbations should favor smaller organisms, but enrichment tends to have the opposite effect, in that large phytoplankton usually increase with enrichment (Mallone 1980, Schindler 1990, 1996). We observed increases in average phytoplankton size and the biomass of large phytoplankton in Peter and West Long lakes, as well as increases in the slope of the normalized size spectrum in West Long and East Long lakes. All of these changes indicate that large phytoplankton were consistently more abundant after enrichment. Persistent increases in small phytoplankton were detected only in Peter Lake, supporting results of comparative studies that on average, biomass of small phytoplankton may not show sustained increases with enrichment (Watson et al. 1992). Overall, though, no allometric variate was sensitive to enrichment in all three enriched lakes, suggesting that changes in size structure may be difficult to detect with a single measure, particularly at a summer time scale. Approaches which focus on shorter term patterns or evaluating the source of shifts in size structure (e.g., changes in community composition) may therefore be more reliable diagnostics of enrichment.

The utility of community diversity indices as ecological indicators has been widely criticized (e.g., Sullivan and Carpenter 1982, Keough and Quinn 1991, Ignatiades et al. 1992), but our results demonstrate that some diversity indices can be reliable indicators of phytoplankton responses to experimental enrichment. Odum (1985) and Rapport et al. (1985) predicted that species diversity declines, while dominance increases, after perturbation. Because phytoplankton species richness declines with increased productivity (Schindler 1987), we also expected richness to decline with nutrient enrichment. We observed significant declines in species diversity, richness, and evenness in Peter, West Long, and East Long lakes in 1993. Like chlorophyll, species diversity and evenness changed significantly only in the enriched lakes and only in the first year of enrichment, suggesting that these variates are very reliable indicators of enrichment. This result supports Caswell and Weinberg (1986), who argued that community indices, especially species evenness and diversity, have more power to detect changes than individual populations. Species richness, though, had higher background variability, and in particular, showed evidence of rapid adjustment to enriched conditions by increasing in 1994 in Peter and East Long lakes. These increases were due in part to several new species not previously noted in these lakes, suggesting that immigration can be an important factor in stabilizing com-

munity responses to perturbation. Species richness, then, was not as reliable as an indicator as species diversity and evenness.

One negative aspect of phytoplankton diversity indices is the labor required to estimate them, particularly in contrast to ecosystem variables such as chlorophyll (Sullivan and Carpenter 1982). Determining diversity and evenness requires the identification and enumeration of all species in a particular sample. Community diversity variables are therefore less viable candidates for high intensity monitoring programs (e.g., daily or subdaily time scales and/or multiple lakes), but the information gathered in the process of calculating these indices may be valuable for other reasons.

Recommendations for monitoring programs

Our results demonstrate that chlorophyll indicates deliberate nutrient enrichment very reliably. Chlorophyll should therefore be a dependable indicator of cultural eutrophication, the most widespread water quality problem in lakes of the United States (National Research Council 1992). Human fixation of nitrogen and nitrogen runoff will also make eutrophication a widespread problem of estuaries and coastal oceans for the foreseeable future (Vitousek 1994). Chlorophyll can be assayed rapidly and cheaply. Surface chlorophyll can be quantified by remote sensing (e.g., Lillesand and Kiefer 1994, Richardson 1996). If a monitoring or assessment program is intended solely to detect eutrophication, then chlorophyll is probably the optimal indicator. However, programs with broader objectives should consider a broader range of indicators.

For example, certain species-level data are indicative of serious correlates of eutrophication—blooms of potentially toxic blue-green algae in freshwater and dinoflagellates in marine systems (Paerl 1988). Sampling focused on these taxa is necessary to document these problems.

Species-level data appear to be reliable indicators of toxic chemical stress (Schindler 1990, Howarth 1991, Frost et al. 1995). Acid deposition, toxic metals, and organic toxins are common stressors of aquatic systems (National Research Council 1992). Monitoring programs intended to detect toxic stress should therefore consider taxon-specific indicators, probably zooplankton, benthos, or fish, rather than phytoplankton.

Community properties such as species diversity and richness may be related to ecosystem recovery from stress (Tilman and Downing 1994, Tilman 1996) or the capacity to recover from repeated stresses (Mooney et al. 1995). Our data demonstrate the utility of species diversity and evenness, but not species richness, as indicators. All species must be enumerated to calculate these indices. However, our data do not show that diversity indices provide information about eutrophication beyond that provided by simpler measurements such as chlorophyll. The observation that ecosystem function may depend on biodiversity (Johnson et al.

1996) does not mean that diversity is necessarily a useful indicator of ecosystem perturbation.

Like other researchers, we conclude that no single indicator of ecosystem status is sufficient (Cairns and van der Schalie 1980, Kelly and Harwell 1990, Noss 1990, Rapport 1990). The choice of indicators for lake monitoring programs will depend on the stresses one wants to detect. However, it seems unlikely that comprehensive, species-level data on phytoplankton would be needed for effective monitoring of lakes. Taxon-specific studies can be targeted on species that are especially problematic (such as potentially toxic algae) or are especially sensitive to toxins or food web change (such as certain zooplankton species). An important generality that emerges from this study, and many others, is that ecosystem stresses of lakes are usually not subtle. Consequently, ecosystem stress can be documented effectively using relatively few selected indicators.

ACKNOWLEDGMENTS

We thank Andy Pole for updated versions of his BATS software and advice on how to program the DLM, Conrad Lamon for allowing us to adapt Fig. 1, and Craig Stow for productive discussions on how to use DLMs to assess potential indicators. Shelley Arnott, Lamon, Tony Ives, Jim Kitchell, Tim Allen, Dave Armstrong, Jack Stanford and two anonymous reviewers provided valuable reviews on earlier drafts of the manuscript. Our research was funded by the National Science Foundation. KLC was also supported by a postdoctoral fellowship at the National Center for Ecological Analysis and Synthesis (a center funded by NSF, the University of California at Santa Barbara, and the State of California). This manuscript is a contribution from the University of Notre Dame Environmental Research Center.

LITERATURE CITED

- Ahrens, M. A., and R. H. Peters. 1991. Patterns and limitations in limnoplankton size spectra. *Canadian Journal of Fisheries and Aquatic Sciences* 48:1967-1978.
- Anderson, N. J. 1993. Natural versus anthropogenic change in lakes: the role of the sediment record. *Trends in Ecology and Evolution* 8:356-361.
- Anderson, N. J., B. Rippey, and A. C. Stevenson. 1990. Change to diatom assemblage in a eutrophic lake following point source nutrient re-direction: a paleolimnological approach. *Freshwater Biology* 23:205-217.
- Bernstein, B. B. 1992. A framework for trend detection: coupling ecological and managerial perspectives. Pages 1101-1114 in D. H. McKenzie, D. E. Hyatt, and V. J. McDonald, editors. *Ecological indicators*. Elsevier Applied Science, New York, New York, USA.
- Bernstein, B. B., and R. W. Smith. 1986. Community approaches to monitoring. Pages 934-939 in *IEEE Oceans '86 Conference Proceedings, Volume 3*. Marine Technology Society/Institute of Electrical and Electronics Engineers, Washington, D. C., USA.
- Bernstein, B. B., and J. Zalinski. 1986. A philosophy for effective monitoring. Pages 1024-1029 in *IEEE Oceans '86 Conference Proceedings, Volume 3*. Marine Technology Society/Institute of Electrical and Electronics Engineers, Washington, D. C., USA.
- Box, G. E. P., G. M. Jenkins, and G. C. Reinsel. 1994. *Time series analysis: forecasting and control*. Prentice-Hall, Englewood Cliffs, New Jersey, USA.
- Box, G. E. P., and G. C. Tiao. 1992. Bayesian inference in

- statistical analysis. John Wiley and Sons, New York, New York, USA.
- Cairns, J., Jr., P. V. McCormick, and B. R. Niederlehner. 1993. A proposed framework for developing indicators of ecosystem health. *Hydrobiologia* **263**:1–44.
- Cairns, J., Jr., and W. H. van der Schalie. 1980. Biological monitoring. Part I—Early warning systems. *Water Research* **14**:1179–1196.
- Carpenter, S. R., and J. F. Kitchell, editors. 1993. *The trophic cascade in lakes*. Cambridge University Press, New York, New York, USA.
- Carpenter, S. R., J. F. Kitchell, K. L. Cottingham, D. E. Schindler, D. L. Christensen, D. M. Post, and N. Voichick. 1996. Chlorophyll variability, nutrient input, and grazing: evidence from whole-lake experiments. *Ecology* **77**:725–35.
- Caswell, H., and J. R. Weinberg. 1986. Sample size and sensitivity in the detection of environmental impact. Pages 1040–1045 in *IEEE Oceans '86 Conference Proceedings, Volume 3*. Marine Technology Society/Institute of Electrical and Electronic Engineers, Washington, D. C., USA.
- Charles, D. F., M. W. Binford, E. T. Furlong, R. A. Hites, M. J. Mitchell, S. A. Norton, F. Oldfield, M. J. Paterson, J. P. Smol, A. J. Uutala, J. R. White, D. R. Whitehead, and R. J. Wise. 1990. Paleoecological investigation of recent lake acidification in the Adirondack mountains, N. Y. *Journal of Paleolimnology* **3**:195–241.
- Christensen, D. L., S. R. Carpenter, J. J. Cole, K. L. Cottingham, S. E. Knight, J. P. LeBouton, M. L. Pace, D. E. Schindler, and N. Voichick. 1996. Pelagic responses to changes in dissolved organic carbon following diversion of a seepage lake. *Limnology and Oceanography* **41**:553–559.
- Cooke, G. D., E. B. Welch, S. A. Peterson, and P. R. Newroth. 1993. *Restoration and management of lakes and reservoirs*. Lewis, Boca Raton, Florida, USA.
- Cottingham, K. L. 1996. *Phytoplankton responses to whole-lake manipulations of nutrients and food webs*. Dissertation. University of Wisconsin, Madison, Wisconsin, USA.
- Cranston, P. S. 1990. *Biomonitoring and invertebrate taxonomy*. *Environmental Monitoring and Assessment* **14**:265–273.
- Dillon, P. J., and R. H. Rigler. 1974. The phosphorus–chlorophyll relationship in lakes. *Limnology and Oceanography* **19**:767–773.
- Dixit, S. S., J. P. Smol, J. C. Kingston, and D. F. Charles. 1992. Diatoms: powerful indicators of environmental change. *Environmental Science and Technology* **26**:23–33.
- Elser, J. J., M. M. Elser, and S. R. Carpenter. 1986. Size fractionation of algal chlorophyll, carbon fixation, and phosphatase activity: relationships with species-specific size distributions and zooplankton community structure. *Journal of Plankton Research* **8**:365–83.
- Findlay, D. L., R. E. Hecky, L. L. Hendzel, M. P. Stainton, and G. W. Regehr. 1994. Relationship between N-2-fixation and heterocyst abundance and its relevance to the nitrogen budget of Lake 227. *Canadian Journal of Fisheries and Aquatic Sciences* **51**:2254–2266.
- Frost, T. M., S. R. Carpenter, A. R. Ives, and T. K. Kratz. 1995. Species compensation and complementarity in ecosystem function. Pages 224–239 in C. Jones and J. Lawton, editors. *Linking Species and Ecosystems*. Chapman and Hall, New York, New York, USA.
- Frost, T. M., S. R. Carpenter, and T. K. Kratz. 1992. Choosing ecological indicators: effects of taxonomic aggregation on sensitivity to stress and natural variability. Pages 215–227 in D. H. McKenzie, D. E. Hyatt, and V. J. McDonald, editors. *Ecological indicators*. Elsevier Applied Science, New York, New York, USA.
- Hansson, L. A. 1993. Factors initiating algal life-form shift from sediment to water. *Oecologia* **94**:286–94.
- Harper, D. 1992. *Eutrophication of freshwaters*. Chapman and Hall, New York, New York, USA.
- Hendzel, L. L., R. E. Hecky, and D. L. Findlay. 1994. Recent changes of N-2-fixation in Lake 227 response to reduction of the N:P loading ratio. *Canadian Journal of Fisheries and Aquatic Sciences* **51**:2247–2253.
- Herman, P. M., and C. Heip. 1988. On the use of meiofauna in ecological monitoring: who needs taxonomy? *Marine Pollution Bulletin* **19**:665–668.
- Holmgren, S. K. 1984. Experimental lake fertilization in the Kuokkel area, northern Sweden. *Phytoplankton biomass and algal composition in natural and fertilized subarctic lakes*. *Internationale Revue der Gesamten Hydrobiologie* **69**:781–817.
- Howarth, R. W. 1991. Comparative responses of aquatic ecosystems to toxic chemical stress. Pages 169–195 in J. J. Cole, G. Lovett, and S. Findlay, editors. *Comparative analyses of ecosystems: patterns, mechanisms, and theories*. Springer-Verlag, New York, New York, USA.
- Ignatiades, L., K. Pagou, and V. Gialamas. 1992. Multivariate analysis of phytoplanktonic parameters: a sample study. *Journal of Experimental Marine Biology and Ecology* **160**:103–114.
- Johnson, K. H., K. A. Vogt, H. J. Clark, O. J. Schmitz, and D. J. Vogt. 1996. Biodiversity and the productivity and stability of ecosystems. *Trends in Ecology and Evolution* **11**:372–377.
- Kelly, J. R., and M. A. Harwell. 1990. Indicators of ecosystem recovery. *Environmental Management* **14**:524–545.
- Keough, M. J., and G. P. Quinn. 1991. Causality and the choice of measurements for detecting human impacts in marine environments. *Australian Journal of Marine and Freshwater Research* **42**:539–554.
- Lamon, E. C., III, S. R. Carpenter, and C. A. Stow. 1998. Forecasting PCB concentrations in five species of Lake Michigan salmonids: a dynamic linear model approach. *Ecological Applications*, in press.
- Leavitt, P. R., S. R. Carpenter, and J. F. Kitchell. 1989. Whole-lake experiments: the annual record of fossil pigments and zooplankton. *Limnology and Oceanography* **34**:700–717.
- Lillesand, T. M., and R. W. Kiefer. 1994. *Remote sensing and image interpretation*. John Wiley and Sons, New York, New York, USA.
- Ljung, L. 1987. *System identification: theory for the user*. Prentice-Hall, Englewood Cliffs, New Jersey, USA.
- Ljung, L. 1991. *System identification toolbox user's guide*. MathWorks, Natick, Massachusetts, USA.
- Malone, T. C. 1980. Algal size. Pages 433–463 in I. Morris, editor. *The physiological ecology of phytoplankton*. Blackwell Scientific, Boston, Massachusetts, USA.
- Marker, A. F. H., C. A. Crowther, and R. J. M. Gunn. 1980. Methanol and acetone as solvents for estimation of chlorophyll a and phaeopigments by spectrophotometry. *Archiv fuer Hydrobiologie Beihaendlungen Ergebnisse der Limnologie* **14**:52–69.
- McCormick, P. V., and J. Cairns, Jr. 1994. Algae as indicators of environmental change. *Journal of Applied Phycology* **6**:509–526.
- McKenzie, D. H., D. E. Hyatt, and V. J. McDonald, editors. 1992. *Ecological indicators*. Elsevier Applied Science, New York, New York, USA.
- Mooney, H. A., J. Lubchenco, R. Dirzo, and O. E. Sala, coordinators. 1995. *Biodiversity and ecosystem functioning: basic principles*. Pages 275–326 in V. H. Heywood, executive editor. *Global Biodiversity Assessment*. Cambridge University Press, London, UK.
- National Research Council. 1992. *Restoration of aquatic ecosystems*. National Academy Press, Washington, D.C., USA.

- Noss, R. F. 1990. Indicators for monitoring biodiversity: a hierarchical approach. *Conservation Biology* 4:355-364.
- Nygaard, G. 1949. Hydrobiological studies of some Danish ponds and lakes. *Biologiske Skrifter* 7:1-293.
- Odum, E. P. 1985. Trends expected in stressed ecosystems. *Bioscience* 35:419-22.
- Padisak, J. 1992. Seasonal succession of phytoplankton in a large shallow lake (Balaton, Hungary)—a dynamic approach to ecological memory, its possible role and mechanisms. *Journal of Ecology* 80:217-30.
- Paerl, H. W. 1988. Nuisance phytoplankton blooms in coastal, estuarine, and inland waters. *Limnology and Oceanography* 33:823-847.
- Pearsall, W. H. 1932. Phytoplankton in the English lakes. II. The composition of the phytoplankton in relation to dissolved substances. *Journal of Ecology* 20:241-262.
- Persson, G., S. K. Holmgren, M. Jansson, A. Lundgren, B. Nyman, D. Solander, and C. Anell. 1975. Phosphorus and nitrogen and the regulation of lake ecosystems: experimental approaches in subarctic Sweden. Pages III-3-III-19 in *Proceedings of the Circumpolar Conference on Northern Ecology*, 15-18 September 1975, Ottawa, Canada, National Research Council of Canada, Ottawa, Canada.
- Pielou, E. C. 1977. *Mathematical ecology*. John Wiley and Sons, New York, New York, USA.
- Pole, A., M. West, and J. Harrison. 1994. *Applied Bayesian forecasting and time series analysis*. Chapman and Hall, New York, New York, USA.
- Pollinger, U. 1988. Freshwater armored dinoflagellates: growth, reproduction strategies, and population dynamics. Pages 134-174 in C. D. Sandgren, editor. *Growth and reproductive strategies of freshwater phytoplankton*. Cambridge University Press, New York, New York, USA.
- Post, D. M., S. R. Carpenter, D. L. Christensen, K. L. Cottingham, J. R. Hodgson, J. F. Kitchell, and D. E. Schindler. 1997. Seasonal effects of variable recruitment of a dominant piscivore on pelagic food web structure. *Limnology and Oceanography* 42:722-729.
- Pratt, J. R., and J. Cairns, Jr. 1996. Ecotoxicology and the redundancy problem: understanding effects on community structure and function. Pages 347-370 in M. C. Newman and C. H. Jørgensen, editors. *Ecotoxicology: A hierarchical approach*. CRC Lewis, New York, New York, USA.
- Rapport, D. J. 1990. Challenges in the detection and diagnosis of pathological change in aquatic ecosystems. *Journal of Great Lakes Research* 16:609-618.
- Rapport, D. J., H. A. Regier, and T. C. Hutchinson. 1985. Ecosystem behavior under stress. *American Naturalist* 125:617-40.
- Reynolds, C. S. 1984. *The ecology of freshwater phytoplankton*. Cambridge University Press, New York, New York, USA.
- Richardson, L. L. 1996. Remote sensing of algal bloom dynamics. *BioScience* 7:492-501.
- Sandgren, C. D. 1988a. The ecology of chrysophyte flagellates: their growth and perennation strategies as freshwater phytoplankton. Pages 9-104 in C. D. Sandgren, editor. *Growth and reproductive strategies of freshwater phytoplankton*. Cambridge University Press, New York, New York, USA.
- , editor. 1988b. *Growth and reproductive strategies of freshwater phytoplankton*. Cambridge University Press, New York, New York, USA.
- Schindler, D. E., S. R. Carpenter, J. J. Cole, J. F. Kitchell, and M. L. Pace. 1997. Influence of food web structure on carbon exchange between lakes and the atmosphere. *Science* 277:248-251.
- Schindler, D. W. 1974. Eutrophication and recovery in experimental lakes: implications for lake management. *Science* 184:897-899.
- Schindler, D. W. 1987. Detecting ecosystem responses to anthropogenic stress. *Canadian Journal of Fisheries and Aquatic Sciences* 44 (Supplement 1):6-25.
- Schindler, D. W. 1988. Experimental studies of chemical stressors on whole lake ecosystems. *Internationale Vereinigung für theoretische und angewandte Limnologie, Verhandlungen* 23:11-41.
- Schindler, D. W. 1990. Experimental perturbations of whole lakes as tests of hypotheses concerning ecosystem structure and function. *Oikos* 57:25-41.
- Schindler, D. W. 1996. Ecosystems and ecotoxicology: a personal perspective. Pages 371-398 in M. C. Newman and C. H. Jørgensen, editors. *Ecotoxicology: a hierarchical treatment*. CRC Lewis, New York, New York, USA.
- Schindler, D. W., F. A. J. Armstrong, S. K. Holmgren, and G. J. Brunskill. 1971. Eutrophication of Lake 227, Experimental Lakes Area, Northwestern Ontario, by addition of phosphate and nitrate. *Journal of the Fisheries Research Board of Canada* 28:1763-1782.
- Schindler, D. W., E. J. Fee, and T. Ruzyczynski. 1978. Phosphorus input and its consequences for phytoplankton standing crop and production in the Experimental Lakes Area and in similar lakes. *Journal of the Fisheries Research Board of Canada* 35:190-196.
- Schindler, D. W., H. Kling, R. V. Schmidt, J. Prokopowich, V. E. Frost, R. A. Reid, and M. Capel. 1973. Eutrophication of Lake 227 by addition of phosphate and nitrate: the second, third, and fourth years of enrichment, 1970, 1971, and 1972. *Journal of the Fisheries Research Board of Canada* 30:1415-1440.
- Schindler, D. W., K. H. Mills, D. F. Malley, D. L. Findlay, J. A. Shearer, I. J. Davies, M. A. Turner, G. A. Linsey, and D. R. Cruikshank. 1985. Long-term ecosystem stress: the effects of years of experimental acidification on a small lake. *Science* 228:1395-1401.
- Smith, S. D. A., and R. D. Simpson. 1992. Monitoring the shallow sublittoral using the fauna of kelp (*Ecklonia radiata*) holdfasts. *Marine Pollution Bulletin* 24:46-52.
- Smith, V. H. 1983. Low nitrogen to phosphorus ratios favor dominance by blue-green algae in lake phytoplankton. *Science* 221:669-671.
- Smol, J. P. 1992. Paleolimnology: an important tool for effective ecosystem management. *Journal of Aquatic Ecosystem Health* 1:49-58.
- Smol, J. P., I. R. Walker, and P. R. Leavitt. 1991. Paleolimnology and hincasting climatic trends. *Internationale Vereinigung für theoretische und angewandte Limnologie, Verhandlungen* 24:1240-1246.
- Soranno, P. A., S. R. Carpenter, and M. M. Elser. 1993. Zooplankton community dynamics. Pages 116-152 in S. R. Carpenter and J. F. Kitchell, editors. *The trophic cascade in lakes*. Cambridge University Press, New York, New York, USA.
- Soudant, D., B. Beliaeff, and G. Thomas. 1997. Dynamic linear Bayesian models in phytoplankton ecology. *Ecological Modelling* 99:161-169.
- Sprules, W. G. 1984. Towards an optimal classification of zooplankton for lake ecosystem studies. *Internationale Vereinigung für theoretische und angewandte Limnologie, Verhandlungen* 22:320-325.
- St. Amand, A. L. 1990. Mechanisms controlling metalimnetic communities and the importance of metalimnetic phytoplankton to whole lake primary productivity. Dissertation. University of Notre Dame, Notre Dame, Indiana, USA.
- Stow, C. A., S. R. Carpenter, K. E. Webster, and T. M. Frost. 1998. Long-term environmental monitoring: some perspectives from lakes. *Ecological Applications* 8:269-276.
- Sullivan, P. F., and S. R. Carpenter. 1982. Evaluation of fourteen trophic state indices for phytoplankton of Indiana

lakes and reservoirs. *Environmental Pollution (Series A)* **27**:143-153.

Thompson, P., and G. Rhee. 1994. Phytoplankton responses to eutrophication. *Archiv für Hydrobiologie Beihandlungen Ergebnisse der Limnologie* **42**:125-166.

Thornton, K. W., D. E. Hyatt, and C. B. Chapman, editors. 1993. Environmental monitoring and assessment program guide. EPA/620/R-93/012. EMAP Research and Assessment Center, Environmental Monitoring and Assessment Program, Office of Research and Development, U.S. Environmental Protection Agency, Research Triangle Park, North Carolina, USA.

Tilman, D. 1996. Biodiversity: population versus ecosystem stability. *Ecology* **77**:350-363.

Tilman, D., and J. A. Downing. 1994. Biodiversity and stability in grasslands. *Nature* **367**:363-365.

Tilman, D., S. S. Kilham, and P. Kilham. 1982. Phytoplankton community ecology: the role of limiting nutrients. *Annual Review of Ecology and Systematics* **13**:349-372.

Turner, M. A., D. W. Schindler, D. L. Findlay, M. B. Jackson, and G. G. C. Robinson. 1995. Disruption of littoral algal associations by experimental lake acidification. *Canadian Journal of Fisheries and Aquatic Sciences* **52**:2238-2250.

Vitousek, P. M. 1990. Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. *Oikos* **57**:7-13.

———. 1994. Beyond global warming: ecology and global change. *Ecology* **75**:1861-1876.

Voichick, N., and J. P. LeBouton, editors. 1994. Methods of the Cascading Trophic Interactions Project, Fourth edition. Center for Limnology, Madison, Wisconsin, USA.

Vollenweider, R. A., editor. 1974. A manual on methods for measuring primary production in aquatic environments. Blackwell Scientific, London, UK.

Vollenweider, R. A. 1976. Advances in defining critical loading levels for phosphorus in lake eutrophication. *Memorie dell'istituto Italiano di Idrobiologia* **33**:55-83.

Warwick, R. M. 1988. The level of taxonomic discrimination required to detect pollution effects on marine benthic communities. *Marine Pollution Bulletin* **19**:259-268.

Watson, S., E. McCauley, and J. A. Downing. 1992. Sigmoid relationships between phosphorus, algal biomass, and algal community structure. *Canadian Journal of Fisheries and Aquatic Sciences* **49**:2605-2610.

West, M., and J. Harrison. 1989. Bayesian forecasting and dynamic models. Springer-Verlag, New York, New York, USA.

APPENDIX

The iterative analysis of the Dynamic Linear Model (Eqs. 1 and 2), variance estimation, and intervention algorithms is summarized here.

Iterative analysis

At each time step, the DLM uses current information to generate prior probabilities, then makes one-step-ahead forecasts and calculates posterior probabilities (Fig. 1). Forecasts for a longer time horizon of *k* steps can also be calculated. Equations for each of these calculations, presented below, were adapted from Table 3.2 of Pole et al. (1994) with modifications for how we handled information discounting and allowed the model to adapt to the onset of experimental enrichment.

At time *t* - 1, the current information (data *D*_{*t*-1}) can be summarized using the following two equations:

$$p(\mu_{t-1} | D_{t-1}) \sim t_{\delta_{\mu_{t-1}}}[m_{t-1}, C_{t-1}] \tag{A.1}$$

$$p(\phi_{t-1} | D_{t-1}) \sim G[n_{t-1}/2, d_{t-1}/2]. \tag{A.2}$$

In these equations, the notation *p*(*A*|*B*) indicates the probability of *A* given *B*. These probabilities take a number of different distributions, including normal (*N*), multivariate-*t* (*t*), and gamma (*G*). In Eq. A.1, the level parameter μ_{t-1} given the data *D*_{*t*-1} has a Student's *t* distribution with *n*_{*t*-1} degrees of freedom, mode *m*_{*t*-1} and scale matrix *C*_{*t*-1}. In Eq. A.2, ϕ_t is used to estimate the observation variance *V*_{*t*}, where $\phi_t = V_t^{-1}$. ϕ_t has a gamma distribution with parameters *n*_{*t*}/2 and *d*_{*t*}/2. The parameter *n* of the gamma distribution is also used to parameterize the *t* distribution for the level parameter. We learned about ϕ_t through information discounting (see *Estimating the variances*, below). Initial values for ϕ were set to 1 for all variates.

The prior probability for μ_t , the level at the next time interval *t*, is described by

$$p(\mu_t | D_{t-1}) \sim t_{\delta_{\mu_t}}[a_t, R_t] \tag{A.3}$$

and the prior probability for ϕ_t is:

$$p(\phi_t | D_{t-1}) \sim G[\delta n_t/2, \delta d_t/2]. \tag{A.4}$$

In Eq. A.3, the prior probability for μ_t is distributed as a student *t* distribution with $\delta_{\mu_t} n_{t-1}$ degrees of freedom, mode *a*_{*t*} = *m*_{*t*-1} and scale matrix *R*_{*t*} = *C*_{*t*-1}/ δ_{μ_t} ; δ_{μ_t} is the discount

factor for the observation variance. Therefore, the prior value for the mode of the level parameter at time *t* is the same as the posterior for time *t* - 1, with the variance increased by an amount 1/ δ_{μ_t} , where δ_{μ_t} is the discount factor for *W*_{*t*}. In Eq. A.4, the parameters of the gamma distribution for ϕ_{t-1} are decreased by δ_{ϕ_t} to create the prior distribution for time *t*.

One-step-ahead forecasts for time *t* are calculated using equation A.5:

$$p(Y_t | D_{t-1}) \sim t_{\delta_{Y_t}}[f_t, Q_t]. \tag{A.5}$$

In this equation, *f*_{*t*} = *a*_{*t*} and *Q*_{*t*} = *R*_{*t*} + *S*_{*t*-1}. Thus, step-ahead forecasts for the observation *Y*_{*t*} are determined from the priors for time *t* (*a*_{*t*}, *R*_{*t*}) and a measure of the observation variance, *S*_{*t*-1}, which is the ratio of the gamma distribution parameters (*d*_{*t*-1}/*n*_{*t*-1}).

K-step-ahead forecasts (e.g., those used to make predictions for more than one-step-ahead, as for a whole summer), are calculated as follows, assuming *k* ≥ 1:

$$p(a_{t+k} | D_t) \sim t_{\delta_{a_{t+k}}}[a_t(k), R_t(k)] \tag{A.6}$$

$$p(Y_{t+k} | D_t) \sim t_{\delta_{Y_{t+k}}}[f_t(k), Q_t(k)]. \tag{A.7}$$

In these equations,

$$a_t(k) = a_t(k - 1)$$

$$R_t(k) = R_t(k - 1) + (C_t(1 - \delta_{a_t})/\delta_{a_t})$$

$$f_t(k) = m_t(k)$$

$$Q_t(k) = R_t(k) + S_t$$

$$a_t(0) = m_t$$

$$R_t(0) = C_t$$

Finally, after calculating one-step-ahead and *k*-step-ahead predictions, posterior distributions for time *t* are calculated using equations A.8 and A.9:

$$p(\mu_t | D_t) \sim t_{\mu_t}[m_t, C_t] \tag{A.8}$$

$$p(\phi_t | D_t) \sim G[n_t/2, d_t/2]. \tag{A.9}$$

In these equations,

$$\begin{aligned}
 m_t &= m_{t-1} + A_t e_t \\
 C_t &= (S_t/S_{t-1})[R_t - A_t A_t' / Q_t] \\
 A_t &= R_t / Q_t \\
 e_t &= Y_t - f_t \\
 n_t &= \delta_n n_{t-1} + 1 \\
 d_t &= \delta_d d_{t-1} + S_{t-1} e_t^2 / Q_t \\
 S_t &= d_t / n_t
 \end{aligned}$$

If the time series continues, analysis resumes at Eq. A.1.

Estimating the variances

In practice, the error variances V_t and W_t are unknown and difficult to specify (West and Harrison 1989, Pole et al. 1994). Therefore, we used a process known as information discounting to estimate V_t and W_t . When making a forecast, information from two months ago is potentially less useful than information from last week; discounting is a formal means of describing this loss in the value of a particular data point with the passage of time (Pole et al. 1994). Discounting is incorporated into the DLM when calculating prior probabilities or making forecasts. If there is no additional information, the prior variance at time t is made larger than the posterior variance at time $t - 1$, simply due to the passage of time. For example, in calculating the prior probability of the level parameter μ_t at time t :

$$V[\mu_t | D_{t-1}] = V[\mu_{t-1} | D_{t-1}] + W_t \quad (\text{A.10})$$

In Eq. A.10, W_t represents the increment in variance over the time step t . Information discounting increases the variance by a proportion λ each time step:

$$V[\mu_t | D_{t-1}] = (1 + \lambda) V[\mu_{t-1} | D_{t-1}] \quad (\text{A.11})$$

More usually, Equation A.11 is written as:

$$V[\mu_t | D_{t-1}] = \delta_w^{-1} V[\mu_{t-1} | D_{t-1}] \quad (\text{A.12})$$

where $\delta_w = (1 + \lambda)^{-1}$.

A similar approach is used to increase the uncertainty in estimates that involve V_t . In this case, though, the discounting occurs in the degrees of freedom in the t distribution in the prior for μ_t (e.g., Eq. A.3) and in the gamma distribution parameters for ϕ_t (e.g., Eq. A.4).

The discount factors, δ_w and δ_{ν} , can take values from 0 to 1 (Pole et al. 1994: 21–23, West and Harrison 1989). Low discount factors allow rapid detection of changes in parameters but are sensitive to noise, while high discount factors reduce sensitivity to noise but may also slow a parameter's ability to adapt to change in the observations (Ljung 1987; see example in Fig. 2A). In practice, only discount factors

from ~0.8–1 are explored, since only information from the last few observations is incorporated into the model when $\delta < 0.8$.

Because discount factors represent a balance between resistance to noise and sensitivity to parameter change (Ljung 1987), they must be chosen carefully. Unlike the other parameters, discount factors generally do not change during the fitting process (but see *Variance intervention*, below). Instead, the usual practice is to fit models with several different δ_w 's and δ_{ν} 's, and then to compare the performance of one-step-ahead forecasts using the cumulative predictive density (CPD; West and Harrison 1989, Pole et al. 1994):

$$\text{CPD} = p(Y_n, Y_{n-1}, Y_{n-2}, \dots, Y_1 | D_0) = \prod_{t=1}^n p(Y_t | D_{t-1}) \quad (\text{A.13})$$

In Eq. A.13, Y_t is the observation at time t , n is the number of time periods, D_0 is the data available at the beginning of the time series, and $p(Y_t | D_{t-1})$ is the probability that the step-ahead forecast is correct, evaluated using the current mode and scale matrix for the Student's t distribution. Better fitting models have higher CPD. For analyses reported in this paper, we compared 45 alternative discount factors (δ_w , from 0.8 to 0.975 with a step of 0.025, plus 0.99; and δ_{ν} , from 0.9 to 0.975 with a step of 0.025, plus 0.99) for each variate, but report only the results for the discount factors which gave the maximum CPD for a model fit to all pre-enrichment data (1991–1992, see examples in Fig. 4B–E). Post-enrichment data were not included in the estimates of δ_w and δ_{ν} because of the large changes that occurred following enrichment.

Variance intervention

We used variance intervention to allow each DLM to respond quickly to any changes that might have occurred following experimental enrichment. These interventions involved deliberate increases in the variance around the level parameter μ_t and observation variance parameter ϕ_t during a 7-wk period immediately following the onset of experimental enrichment in 1993 and 1994. By increasing the variance, we increased the uncertainty in the parameter estimates during this period of time, and hence, increased the relative amount of information contained in new observations. This meant that the model was able to adapt to changes in the observations more readily.

Because there were too many variables and models to optimize the adjustments in all variances, we opted to increase variances by adopting lower discount factors during this period: δ_w was set to 0.9, and δ_{ν} was set to 0.4. These changes resulted in 2.5 and 1.1 times higher variances around μ_t and ϕ_t , respectively. Analyses with different adjustments to δ_w and δ_{ν} yielded similar results, and are not included here.