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EFFECTS OF GRAZER COMMUNITY STRUCTURE ON PHYTOPLANKTON RESPONSE TO NUTRIENT PULSES

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Abstract. Sensitivity, the magnitude of change following perturbation, and return rate, the rate of recovery, are two key components of ecological stability. We quantified these properties for phytoplankton in lakes using pulsed nutrient loading as the perturbation. Theory predicts that grazer community structure should influence how phytoplankton respond to pulsed nutrient loading. In particular, phytoplankton in lakes with large, effective grazers such as *Daphnia* are expected to be less sensitive to, but recover more slowly from, nutrient perturbations than phytoplankton in lakes with smaller grazers. We tested these predictions by adding standardized small and large pulses of nutrients (~10 and ~100 μg P/L of epilimnion; with N at an N : P ratio of ~25:1 by mass) to two natural ponds with contrasting grazer communities that resulted from the deliberate addition of planktivorous fishes to one pond. Site-specific responses were examined by conducting the experiment in the same ponds over two consecutive summers (1994 and 1995), but switching the fish treatments between years.

In both years, phytoplankton in the pond with large-bodied zooplankton grazers were less sensitive to small pulses of nutrients than were phytoplankton in the pond with small grazers, confirming the expectation that large zooplankton can buffer lakes against nutrient perturbations. However, responses to the large nutrient pulse were less consistent: phytoplankton in the pond with large zooplankton were less sensitive to the large perturbation only in 1995. This unexpected result appears to be due mainly to a 2.6 times greater total zooplankton biomass in the pond with small grazers on the day of the large pulse in 1994. Thus, although the presence of large-bodied zooplankton appears to reduce phytoplankton sensitivity to small nutrient pulses, other factors, including zooplankton biomass, need to be incorporated into predictions for phytoplankton responses to large perturbations.

Consistent with expectations, larger zooplankton appeared to slow recovery from nutrient perturbations, since the pond with fish and small grazers had faster return rates following the large nutrient pulse in both years of the experiment. Differences in life history traits between small and large species of zooplankton appear to account for these differences in recovery rates. Our results thus provide some support for theoretical expectations that management activities which alter grazer community structure may also affect the stability of phytoplankton communities to nutrient perturbations; additional experiments are needed to confirm the generality of this result.

Key words: Bayesian time series analysis; Daphnia; *grazing; nitrogen; phosphorus; phytoplankton; pulse perturbation; resilience; resistance; stability; zooplankton.*

INTRODUCTION

Understanding how ecosystems respond to perturbation is a fundamental goal of ecology. Two key characteristics of response to perturbation are sensitivity (the magnitude of response to perturbation) and return rate (the rate at which the system recovers toward its pre-perturbation state). By these definitions, sensitivity is the inverse of what many authors have called resistance or inertia, while return rate is akin to resilience or elasticity (Webster et al. 1975, Grimm and Wissel 1997).

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There is a rich body of theoretical expectations regarding stability, sensitivity, and return rate. For example, return rate is expected to increase with increased nutrient loading rate (DeAngelis et al. 1989) and to decrease with increasing food chain length (Pimm and Lawton 1977, Carpenter et al. 1992). Return rate has also been linked to nutrient processing rates, particularly the relative magnitudes of internal vs. external sources of nutrients (DeAngelis 1980, 1992). Ecosystems with rapid nutrient turnover are expected to have faster return rates than systems that depend on internal nutrient recycling (Jordan et al. 1972, DeAngelis 1980, 1992, O'Neill and Reichle 1980, Webster et al. 1983). Sensitivity, on the other hand, is thought to be related to nutrient storage, particularly the total nutrient standing stock within the system and the amount of nutrients

tied up in community components that turn over slowly (e.g., trees in terrestrial systems; fish in aquatic systems) (Jordan et al. 1972, O'Neill et al. 1975). Systems with more stored nutrients are expected to be better buffered from perturbation than systems with less stored nutrients (Webster et al. 1983).

Few of these expectations about sensitivity and return rate have been tested empirically. Imprecise and inconsistent terminology (Grimm et al. 1992, Grimm and Wissel 1997) and difficulties in translating theoretical definitions to parameters that can be measured empirically have been two major stumbling blocks to tests of ideas about these properties (Holling 1973, Santos and Bloom 1980, Grimm et al. 1992). For example, defining the baseline conditions against which responses to perturbation can be compared can be quite challenging due to the intrinsic variability of most natural ecosystems.

Lakes are ideal systems in which to test ideas about stability, sensitivity, and return rate (Holling 1973, Schindler 1988, Carpenter et al. 1992). There is a clear boundary between ''lake'' and ''not lake,'' and nutrient cycling patterns are relatively well understood (Carpenter and Kitchell 1988, Kerfoot and DeAngelis 1989). Lakes are perturbed by a variety of human activities, including overfishing, introduction of exotic species, changes in land use, habitat degradation, and chemical and organic pollution (Schindler and Bayley 1989, National Research Council 1992). These perturbations create ample opportunity to study responses to anthropogenic perturbations. At present, the most common and serious anthropogenic perturbation of lakes is eutrophication due to increased nutrient availability (National Research Council 1992). Pulses of limiting nutrients into temperate lakes are associated with mixing events and rainstorms (Harris 1980, 1987, William et al. 1994), as well as seasonal changes in hydrology such as spring snowmelt. Extreme nutrient pulses are generally associated with the combination of these natural events with anthropogenic activities, particularly changes in land use (Soranno et al. 1996). Nutrient pulses can induce blooms of nuisance phytoplankton, especially in lakes that have been heavily impacted by humans.

Phytoplankton responses to changes in nutrients appear to be strongly influenced by food web structure, particularly grazer size structure. A typical pelagic food web for north temperate lakes consists of piscivorous fishes; planktivorous predators, both vertebrates (fish) and invertebrates (*Chaoborus*, notonectids); herbivores (zooplankton); and primary producers (phytoplankton). Changes in top predators, particularly the relative importance of invertebrate vs. fish zooplanktivory, can alter primary producers through a series of cascading trophic interactions (Carpenter et al. 1985, Crowder et al. 1988, Gulati et al. 1990, Kitchell 1992, Reynolds 1994, Benndorf 1995). For example, the relative importance of invertebrate vs. fish predation on zooplankton generally determines the size structure of zooplankton communities (Brooks and Dodson 1965, Hall et al. 1976). Zooplankton size structure in turn determines the grazing pressure on phytoplankton, because larger grazers, especially *Daphnia* spp., tend to be more effective at suppressing phytoplankton biomass and productivity than smaller grazers (Levitan et al. 1985, Carpenter et al. 1991, Hansson 1992, Sarnelle 1992). This suggests that phytoplankton embedded in food webs that promote the presence of large, effective zooplankton should be better buffered from changes in nutrients than phytoplankton in food webs that lack such strong grazer control of algal growth. In fact, several empirical studies indicate that large zooplankton can mediate phytoplankton responses to sustained increases in the external supply of limiting nutrients (Lynch and Shapiro 1981, Mazumder et al. 1992, Carpenter et al. 1996, Schindler et al. 1997, Cottingham et al. 1997, but see Brett and Goldman 1996).

Simulations of nutrient pulses in model ecosystems suggest that phytoplankton in food webs that promote large zooplankton also tend to be less sensitive to pulses of nutrients than phytoplankton in food webs that lack large zooplankton (Fig. 1; Cottingham and Carpenter 1994). However, once perturbed, phytoplankton in food webs with large zooplankton tend to have slower return rates than phytoplankton in food webs with smaller zooplankton. To date, however, there have been few field studies of pulsed nutrient perturbations in lakes (Seager et al. 1992). In particular, we know of no direct empirical tests of the effects of grazer community structure on the sensitivity and return rates of natural phytoplankton communities to pulsed nutrient additions.

We performed a field experiment to evaluate phytoplankton sensitivity and return rate by contrasting the response of ponds with different grazer community structure to standard pulses of limiting nutrients. We manipulated grazer communities by altering the relative importance of fish vs. invertebrate predation on zooplankton. Specifically, we tested the predictions that (1) phytoplankton in fishless ponds with large, effective zooplankton grazers are less sensitive to nutrient pulses than phytoplankton in ponds with fish and small grazers, and (2) phytoplankton in ponds with large zooplankton recover more slowly from nutrient pulses than phytoplankton in ponds without large zooplankton.

METHODS

Study site

Monday Bog and Wednesday Bog are small, fishless ponds located at the University of Notre Dame Environmental Research Center near Land O'Lakes, Wisconsin, USA (46°13′ N, 89°32′ W). Both ponds are dystrophic, surrounded by extensive mats of *Sphagnum*, and stratified in summer with anoxic hypolimnia (Herwig and Schindler 1996). These ponds have annual

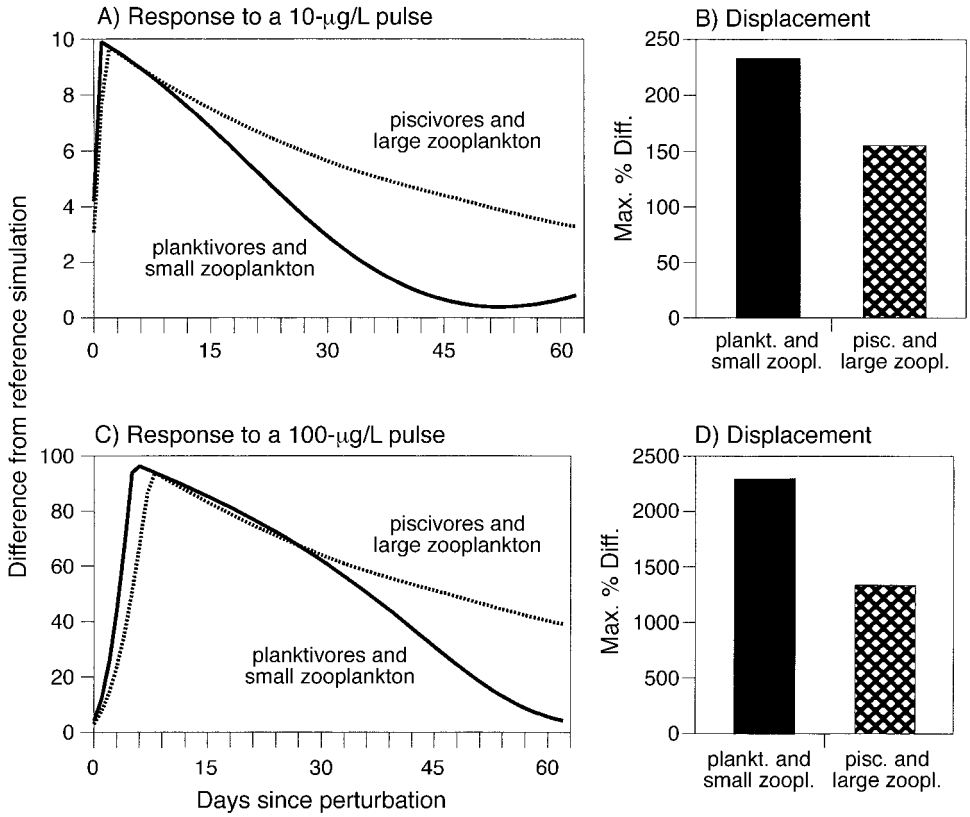

FIG. 1. Effects of food web structure on phytoplankton sensitivity to, and return rate from, pulses of nutrients as simulated using the model described by Cottingham and Carpenter (1994). Responses are contrasted for a model lake dominated by planktivorous fishes and small zooplankton vs. a model lake dominated by piscivorous fishes and large zooplankton. Both models have a baseline nutrient loading rate of 0.1 μg $P \cdot L^{-1} \cdot d^{-1}$, so the perturbations of 10 and 100 μg P/L are 100 and 1000 times the background loading rate. (A) Difference in phytoplankton biomass between reference and perturbed simulations for a 60-d period following a 10-μg/L nutrient pulse. (B) Maximum percentage difference in phytoplankton biomass between the reference and perturbed simulations. (C, D) These panels are analogous to (A) and (B), respectively, but for a 100-μg/L nutrient pulse. In these simulations, phytoplankton in the model with piscivores and large zooplankton were less sensitive to nutrient pulses, but they also recovered more slowly than phytoplankton in the model with planktivores and small zooplankton.

winter fish kills, such that both ponds are usually fishless. In the absence of fish, a diverse community of invertebrate predators that includes notonectids, dytics, and large *Chaoborus americanus* co-occurs with zooplankton communities dominated by large-bodied zooplankton grazers, especially *Daphnia pulex* (Herwig and Schindler 1996).

Experimental design

We used planktivorous fish to establish contrasting zooplankton communities in the two ponds. Because large zooplankton, especially *Daphnia*, usually dominate both Monday and Wednesday bogs, we added planktivorous fish to one pond to establish a treatment in which the zooplankton community was dominated by smaller grazers; the size-selective effects of planktivorous fish on larger zooplankton are well established (Brooks and Dodson 1965, Nilssen 1978, Gulati et al. 1990, Kitchell 1992, Carpenter and Kitchell 1993). We refer to these treatments as ''the pond with fish'' and ''the pond without fish'' throughout the rest of this paper. This design provides the most realistic evaluation of the effects of food web structure, as manifested by grazer size, on phytoplankton stability, even though it is more indirect than alternative approaches to manipulating grazer community structure (e.g., sieving, adding organisms from stock cultures).

The experiment was conducted in these two ponds over a 2-yr period, with the fish treatments switched between years. During 1994, we maintained Wednesday Bog in its fish-free state and established Monday Bog as the fish treatment. To ensure the removal of fish during the winter, we added liquid rotenone to both ponds in late September 1994. Then, during 1995, the treatments were reversed: we maintained Monday Bog as a fish-free system and Wednesday Bog as the fish treatment. In both years, we created the fish treatment by transferring planktivorous fish trapped from nearby Tuesday Lake (<100 m from both ponds) to the treatment pond; all species added are common to plankti-

vore-dominated fish communities in the area (He and Wright 1992). On 25 May 1994, we trapped 410 fish from Tuesday Lake and added them to Monday Bog: 363 redbelly dace (*Phoxinus eos*), 5 golden shiners (*Notemigonus crysoleucas*), 6 brook sticklebacks (*Culaea inconstans*), 19 fathead minnows (*Pimephalus promelas*), 13 fine-scale dace (*Phoxinus neogaeus*), and 4 central mudminnows (*Umbra limi*). This stocking was enhanced by successful spawning of fathead minnows; young-of-year fatheads were first noted on 21 June and sightings continued throughout the summer. In 1995, we trapped 300 fish on 30 May and added them to Wednesday Bog: 200 brook sticklebacks and 100 fathead minnows.

Two additional manipulations were necessary in 1994 only. Five days prior to the fish addition, we added quicklime ($CaCO_3$) to Monday Bog (2.01 kg) and Wednesday Bog (2.00 kg) to raise pH above baseline levels (4.6–4.8: Herwig and Schindler 1996) and ensure fish survival. Two days later, pH had increased to ~7.0 in both ponds; pH declined slowly through the rest of the summer, but remained >5.4 at all times. To compensate for the anticipated negative effects of this rapid pH change on zooplankton (Yan et al. 1995), we pooled six horizontal net tows from Ed's Bog (a similar dystrophic, fishless pond <2 km from Tuesday Lake [Arnott and Vanni 1993]), then added half of the collected zooplankton to each pond on 31 May. There was no evidence for a persistent negative effect of liming on zooplankton once pH stabilized. Liming effects on pH persisted through the winter of 1994–1995, so we did not need to artificially raise the pH to ensure fish survival in 1995.

We monitored both ponds for a 3–6 wk reference period after fish manipulation to quantify plankton community dynamics in the absence of nutrient perturbations. At the end of this period of acclimation, we perturbed each pond with two pulses of nutrients. Pulse sizes were comparable between ponds in order to explicitly contrast the responses of the two food web structures, as recommended in the literature (Harrison and Fekete 1980, Vitousek et al. 1981). We monitored water chemistry, phytoplankton, and zooplankton following these standardized nutrient pulses, then evaluated sensitivity and return rate by comparing responses with the reference period.

Pulse perturbations

We added one small pulse and one large pulse of nutrients to each pond in each year. The small pulse was roughly comparable to an extreme precipitation event in an oligotrophic to mesotrophic lake (McTigue 1992), and to a typical precipitation event in a eutrophic lake (Lake Mendota, Madison, Wisconsin, USA; T. Reed-Andersen and R. C. Lathrop, *unpublished data*). The large pulse was comparable to an extreme nutrient loading event in a eutrophic lake (T. Reed-Andersen and R. C. Lathrop, *unpublished data*). To ensure that pulses were approximately the same magnitude in each pond, we estimated the volume of the epilimnion just prior to the first nutrient pulse in each year using table salt (NaCl) as a hydrologic tracer. This was accomplished by adding 600 g of salt dissolved in several gallons of water to each pond, then estimating epilimnetic volume by comparing the conductivity of the ponds one day after the salt addition to a standard conductivity–salt concentration curve for each system. On 6 July 1994, the estimated volumes were 119.7 m^3 for Monday Bog and 105.8 m^3 for Wednesday Bog; on 7 June 1995, estimated volumes were 169.0 m^3 in Monday Bog and 154.7 m^3 in Wednesday Bog.

We used commercial liquid fertilizer containing nitrogen (N, as ammonia and nitrate) and phosphorus (P, as phosphate) at an N:P ratio of ~25:1 by mass to create our nutrient perturbations. In 1994, we added fertilizer that represented ~10 μg P/L of epilimnion to each pond on 6 July. On 12 June 1995, we added the same absolute amount of nutrients as in 1994 (i.e., we did not correct for the difference in epilimnetic volume between years); because the epilimnia were somewhat larger, absolute pulse concentrations were somewhat smaller (~7 μg/L). In 1994, large pulses were not equal in the two ponds due to a calculation error: we added ~155 μg/L of P to Monday Bog, and ~179 μg/L in Wednesday Bog on 25 July. As for the small pulse, the same absolute amount of nutrients was added in the second year of the experiment (18 July 1995). The resulting large pulse sizes in 1995 were somewhat lower, and more comparable between ponds: ~110 μg/L to Monday Bog, and ~120 μg/L in Wednesday Bog.

Limnological sampling

We sampled each pond at 3–4 d intervals during the reference (pretreatment) period, at 1–2 d intervals immediately following each pulse perturbation, and at 3–4 d intervals during recovery from each pulse. The higher sampling frequency following nutrient perturbations was designed to capture short-term dynamics following nutrient addition. At each pond, we took two replicate water samples from the epilimnion using an integrated depth sampler; we took samples from the surface to 1.25 m in Monday Bog and to 1.75 m in Wednesday Bog. We sampled for zooplankton by taking two vertical hauls of a conical net (30 cm diameter, 80-μm mesh) from 2.5 m to the surface in Monday Bog and from 4.0 m in Wednesday Bog. We also took surface water samples for pH; estimated the Secchi depth; and, approximately weekly, we determined temperature and dissolved oxygen profiles.

In the laboratory, we subsampled the replicate samples of epilimnetic water for nutrients, chlorophyll, and phytoplankton community composition. Subsamples for total Kjeldahl nitrogen and total phosphorus were frozen, then analyzed with a Lachat autoanalyzer (Zellweger Analytics, Inc., Milwaukee, Wisconsin) (Voichick and LeBouton 1994). Subsamples for total chlorophyll *a* were vacuum filtered onto Whatman GF/F filters (Whatman Inc., Clifton, New Jersey), while sub-

samples for chlorophyll *a* <35 μm were prefiltered through 35-μm mesh prior to vacuum filtration. All filters were frozen for at least 24 h prior to extraction in methanol and fluorometric determination of chlorophyll concentrations (Marker et al. 1980).

On selected dates during the reference, perturbation, and recovery periods, we also saved one subsample of epilimnetic water from each pond for determination of phytoplankton community composition. These samples were preserved in glutaraldehyde, then identified and enumerated in 25-mL Utermohl chambers (>22 h settling period) using phase contrast on a Nikon Diaphot inverted microscope. We first counted all natural units in 50 fields at 400× magnification, rotating the slide once after the first 25 fields were counted. Fields were spread evenly throughout the chamber, except that we did not count fields at the edge of the chamber in order to avoid bias. Natural units that were partially in a field were only counted if they lay along the top or right edges of the field. If we encountered either <50 natural units of the dominant organism or <200 total natural units in the first Utermohl chamber, we prepared a second chamber from the same water sample and counted until one of those criteria was met. We identified organisms to genus as much as possible; however, small flagellated taxa and small (<5 μm diameter) round nonmotile taxa were enumerated as aggregated groups. We determined densities for 42 unique taxa, then estimated the total biomass of each taxon using estimates of individual biomass from the same or similar genera from nearby lakes (K. L. Cottingham and S. R. Carpenter, *unpublished data*). Finally, we estimated the biomass of major phytoplankton groups by aggregating related taxa: cyanobacteria, chlorophytes, chrysophytes, dinoflagellates, cryptophytes, and also ''others'' (diatoms, unidentified flagellates, *Gonyostomum*, etc.).

Zooplankton samples were stored in Lugol's preservative in the dark prior to enumeration. In 1994, the two zooplankton hauls from each pond were preserved and enumerated separately; in 1995, they were pooled and enumerated together. We report all 1994 results as the average counts from the two hauls. We enumerated zooplankton samples from a clear plastic counting dish marked with 1.3 × 1.3 cm grid cells using a binocular dissecting microscope (Carpenter and Kitchell 1993, Voichick and LeBouton 1994). Samples were split into equal fractions with a Folsom plankton splitter when they were too dense to count effectively. In each dish, we identified the large-bodied species (*Chaoborus*, large copepods, *Daphnia*, and other relatively large cladocerans) to genus and counted the number of individuals found in the entire dish. We counted smaller taxa in at least three successive grids from the counting dish; counting of grids continued until the standard error of the number of animals per grid cell was <10% of the mean. These smaller taxa were identified to genus (e.g., small cladocerans like *Bosmina*) or lumped into aggregate categories (e.g., nauplii, copepodites, rotifers). We measured the lengths of up to 50 individuals of the dominant zooplankton taxa in each sample (*Bosmina*, *Daphnia*, nauplii, some copepods) during enumeration. For the subdominant taxa, we assumed that the lengths were similar to those observed in 3–10 yr of data on five nearby lakes (S. R. Carpenter et al., University of Wisconsin, Madison, *unpublished data*). We then estimated the biomass of each taxon using published length vs. dry mass regressions (Downing and Rigler 1984).

We also sampled epilimnetic chlorophyll concentrations in nearby unmanipulated Tuesday and Paul lakes at biweekly and weekly intervals, respectively, as reference systems to monitor regional environmental conditions. Both lakes were sampled throughout the summers of 1994 and 1995 from a central location near the deepest part of the lake (Voichick and LeBouton 1994). Water samples from 100, 50, and 25% of surface irradiance were collected using a van Dorn bottle and processed as described for total chlorophyll *a*, above; concentrations from the three depths were then averaged to provide a single estimate for epilimnetic chlorophyll.

Determining sensitivity and return rate from field data

We assessed sensitivity and return rate using dynamic linear models, or DLMs (West and Harrison 1989, Pole et al. 1994), which have recently been introduced as tools for analysis of ecological time series (Soudant et al. 1997, Lamon et al. 1998, Cottingham and Carpenter 1998). Traditionally, sensitivity and return rate have been estimated in experiments either by contrasting treatments vs. controls (e.g., MacGillivray et al. 1995), or by comparing before vs. after conditions (e.g., Kaufman 1982, Tilman and Downing 1994). Regardless of whether control or pre-perturbation data are selected, defining the reference state is difficult, particularly in highly variable systems (Grimm et al. 1992). Here we focus on before vs. after comparisons. ''Before'' conditions are often quantified as a function of the pre-perturbation mean and some variation around that mean, often estimated as a confidence interval (Bloom 1980, Santos and Bloom 1980, Kilgour et al. 1998). However, one difficulty with the arithmetic mean is dealing with variability, autocorrelation, and nonstationarity (trends) in time series. DLMs provide a way to deal with variability and temporal trends explicitly. In addition, DLMs easily handle missing values and unequally spaced data (Pole et al. 1994).

DLMs are distinct from the more familiar general linear models (GLM) in two ways (Ljung 1987, West and Harrison 1989, Pole et al. 1994). First, DLMs explicitly account for structure contained within a time series due to the ordering of the data points. Second, parameters are dynamic and time ordered, changing through time as the system changes. There are two equations for each DLM: an observation equation re-

lating 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:

$$Y_t = \mu_t + \nu_t \qquad \nu_t \sim N[0, V_t] \tag{1}$$

$$\mu_t = \mu_{t-1} + \omega_t \qquad \omega_t \sim t_{n_{t-1}}[0, W_t] \tag{2}$$

The observation equation (Eq. 1) equates the observation at time t (Y_t) with the model state parameter (the level, μ_t) plus a stochastic error term ν_t called the observation variance. The observation variance is normally distributed with zero mean and variance V_t. The system evolution equation (Eq. 2) describes the evolution of the state parameter or level through time; the evolution variance ω_t has a Student t distribution with mode 0 and scale matrix W_t. The observation and evolution variances 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, which were determined separately for each time series. Discount factors control the relative weighting of recent observations as compared to past observations (West and Harrison 1989, Pole et al. 1994). With lower discount factors, very recent observations are weighted more heavily than past observations. This weighting leads to more flexibility in fitting the model to fluctuations in the data, but also creates more uncertainty around model predictions. In contrast, higher discount factors weight past observations more heavily, making the model less sensitive to short-term fluctuations in the data. In this paper, we focused on DLMs with the optimal discount factors for each dataset; the optimal discount factors were found by fitting each model with 45 different combinations of discount factors, then selecting the combination that gave the best fit to the data (see Cottingham and Carpenter 1998: Appendix for more details).

Model fitting consisted of an iterative cycle of steps for each time period (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.

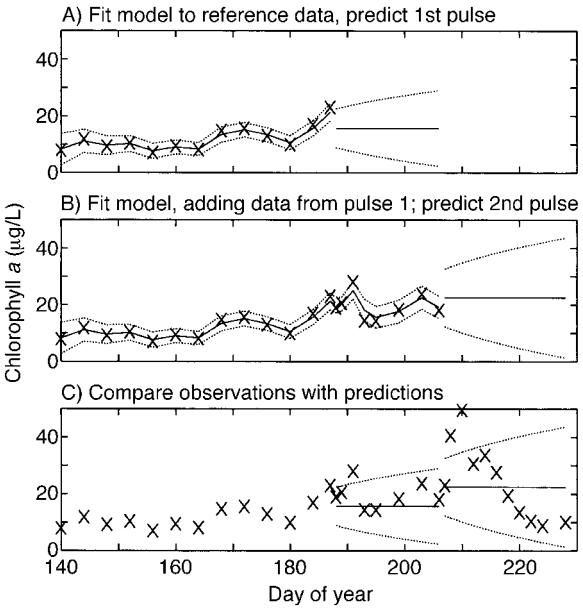

FIG. 2. Demonstration of how we fit the dynamic linear models (DLMs) to the data from each lake-year. (A) We fit a model to the data from the reference period, then used this model to predict dynamics during the period after the first pulse. (B) We then continued fitting the model using data from the period after the first pulse, then used this model to predict dynamics during the period after the second pulse. (C) Finally, we compared observations after each pulse with the predictions made for dynamics in the absence of these pulses.

A detailed description of the DLM methodology appears in Pole et al. (1994). Cottingham and Carpenter (1998) detail specific adaptations to this type of ecological time series. All DLMs were fit using software developed by K. L. Cottingham to run within the Matlab programming environment (Ljung 1991).

Use of DLMs to estimate sensitivity and return rate

We assessed changes in total chlorophyll *a* in each pond in each year by a sequential process of fitting a DLM to some of the data, making predictions for the next part of the series, and then continuing to fit the model. After the full DLM was fit, observations were compared to predictions for each part of the time series (Fig. 2).

Specifically, we first fit a DLM to the data to estimate the mean and variance of the response variable during the pre-perturbation time period. We then forecast the future level and 90% highest posterior density (HPD) intervals for the response if no perturbation had occurred. This gave us an expected probability distribution for the future state of the ecosystem based on our reference data. HPD intervals represent the range of values in which 90% of the distribution lies (Box and Tiao 1973). Because of discounting, HPD intervals grow through time as forecasts are made further into the future.

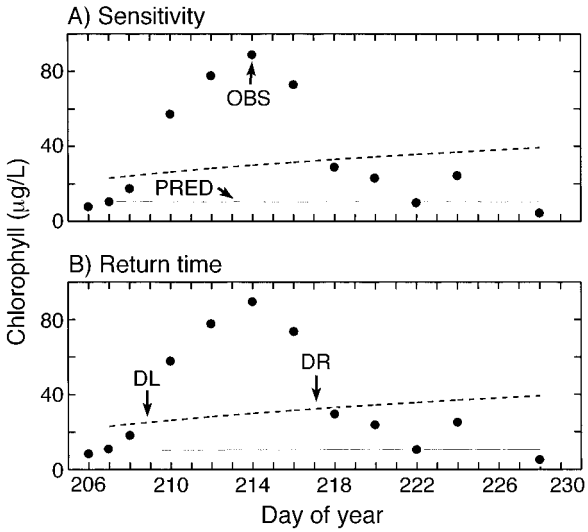

FIG. 3. Demonstration of how we compared observations and predictions in order to estimate sensitivity and return rate. (A) We calculated sensitivity from the maximum difference between observed values (OBS) and predicted values (PRED). (B) We calculated return rate as the inverse of return time, where return time was the number of days the system was outside the prediction limits [the date of reentry (DR) − date left (DL) + 1].

After making a prediction for the period after the small nutrient pulse, we continued fitting the DLM, adding the data from the time period between the small and large nutrient pulses. We then forecast the level and 90% HPD intervals for the period after the large nutrient pulse in order to estimate the expected probability distribution in the absence of that manipulation.

Finally, we compared the observed responses to each nutrient perturbation with the probability distribution expected in the absence of the perturbation (predicted values), and estimated sensitivity and return rate following each pulse based on how much and for how long the observed data differed from expectations (Fig. 3). We determined sensitivity from the maximum difference between the observed data and the predicted level; the greater this difference, the greater the sensitivity to that perturbation. Similarly, we used the number of days the observed samples were outside the 90% HPD interval to estimate return time; return rate was the inverse of return time. The greater the number of days the response was outside the HPD interval, the more slowly the system recovered.

RESULTS

Nutrients

During the reference period, total Kjeldahl nitrogen (TKN) and total phosphorus (TP) concentrations were similar between the two ponds, as indicated by a high degree of overlap of their standard errors (Fig. 4). There

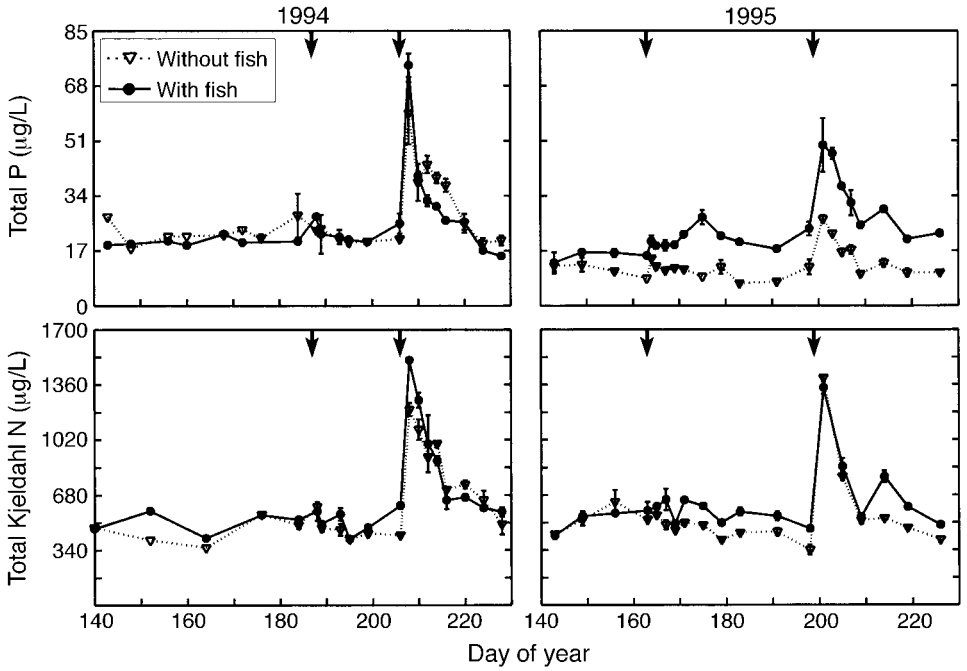

FIG. 4. Total phosphorus and total Kjeldahl nitrogen in each pond during the summers of 1994 and 1995. Mean and standard deviation are indicated for dates on which replicate field samples were available. The pond without fish is indicated by triangles and dotted lines, while the pond with fish is indicated by circles and solid lines. Timing of the pulse perturbations is indicated by the arrows at the top of each panel.

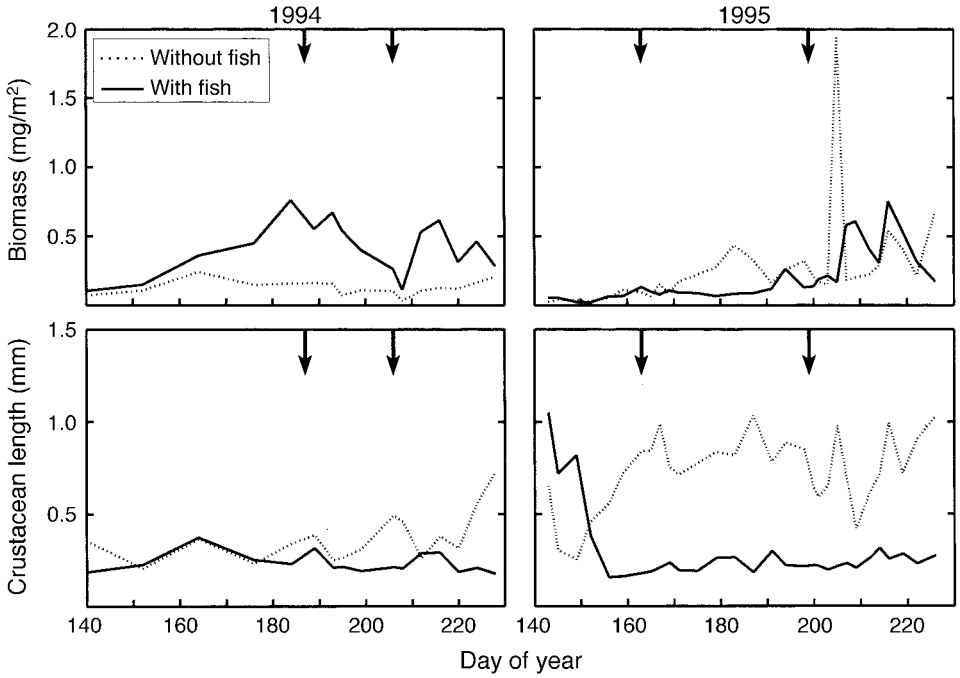

FIG. 5. Zooplankton biomass and crustacean mean length in each pond during the summers of 1994 and 1995. Symbols are as described in Fig. 4.

was little response of TP or TKN to the small nutrient pulse in either year. However, there were large increases in both nutrients following the large nutrient pulse, particularly in 1994 (Fig. 4). In both years, the increase in TP following the large pulse was slightly larger in the pond with fish than in the pond without fish, suggesting that nutrients were incorporated into the zooplankton more quickly in the pond without fish.

Zooplankton

In 1994, zooplankton body size (as mean crustacean length) was somewhat similar in the two ponds, while total zooplankton biomass was very different (Fig. 5, Table 1). In 1995, the opposite was true: mean crustacean size was very different, while total biomass remained comparable between ponds. This suggests that the contrast in grazer size structure was much greater in 1995 than in 1994.

Throughout 1994, zooplankton biomass was higher in the pond with fish than in the pond without fish, with maximal differences near the time of the small nutrient pulse (Fig. 5, Table 1). In 1995, zooplankton biomass was more similar between ponds, especially during the pre-perturbation period. After the small perturbation, there was more biomass in the pond without fish than in the pond with fish, but by 2 wk after the large pulse, biomass was again comparable in the two ponds.

Unlike biomass, there was little difference between ponds in crustacean mean length during 1994, but a

TABLE 1. Means (± SE) in the fish treatments during the reference (premanipulation) period in 1994 and 1995.

Response variate	1994		1995	
	No fish	With fish	No fish	With fish
pH	6.0 ± 0.1	5.9 ± 0.1	5.0 ± 0.0	5.4 ± 0.1
Secchi depth (m)	1.7 ± 0.0	1.4 ± 0.0	2.2 ± 0.0	1.9 ± 0.0
Total P (μg/L)	22.8 ± 1.2	19.8 ± 0.4	11.0 ± 1.0	15.4 ± 0.8
Total Kjeldahl N (μg/L)	459.7 ± 36.0	511.8 ± 30.3	532.8 ± 40.8	532.7 ± 34.8
Total zooplankton biomass (mg/m²)	0.146 ± 0.028	0.365 ± 0.118	0.056 ± 0.013	0.060 ± 0.014
Daphnia biomass (mg/m²)	0.019 ± 0.011	0.002 ± 0.001	0.027 ± 0.010	0.009 ± 0.004
Small cladoceran biomass (mg/m²)	0.002 ± 0.001	0.017 ± 0.012	0.001 ± 0.000	0.000 ± 0.000
Adult copepod biomass (mg/m²)	0.012 ± 0.005	0.055 ± 0.021	0.000 ± 0.000	0.007 ± 0.003
Nauplii biomass (mg/m²)	0.092 ± 0.019	0.249 ± 0.087	0.020 ± 0.003	0.038 ± 0.014
Rotifer biomass (mg/m²)	0.021 ± 0.011	0.042 ± 0.019	0.009 ± 0.002	0.006 ± 0.002
Crustacean mean length (mm)	0.300 ± 0.034	0.254 ± 0.032	0.542 ± 0.082	0.496 ± 0.138
Total chlorophyll *a* (μg/L)	9.6 ± 1.3	12.1 ± 1.3	7.0 ± 0.7	9.1 ± 1.2
Chlorophyll *a* <35 μm (μg/L)	7.4 ± 1.1	7.9 ± 0.7	4.3 ± 0.3	6.7 ± 1.2

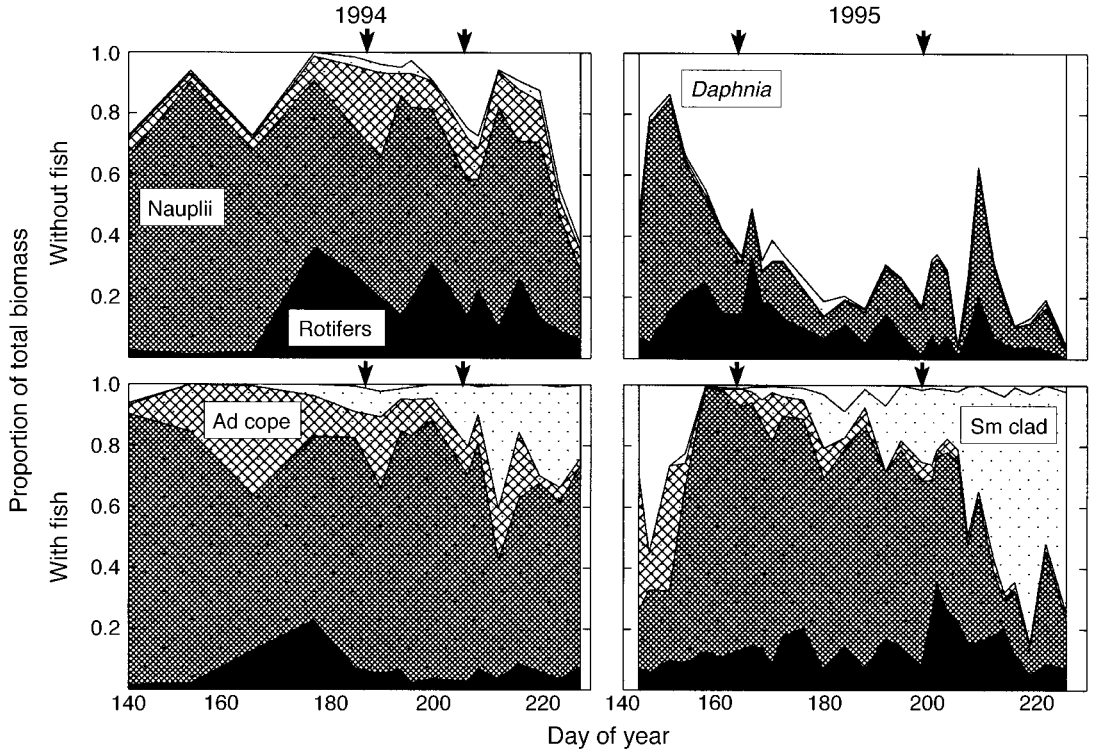

FIG. 6. Zooplankton community composition as a proportion of total biomass in each of five taxonomic categories: *Daphnia,* small cladocerans (''Sm clad''; *Alona, Bosmina, Ceriodaphnia, Chydorus, Diaphanosoma, Holopedium, Moina, Polyphemus, Scapholeberis,* and *Sida*), adult copepods (''Ad cope''; *Diaptomus leptopus,* miscellaneous cyclopoid copepods), nauplii, and rotifers. Copepodites were also present, but in proportions too low to be visible in this figure. Arrows above each panel indicate the timing of the pulse perturbations.

large difference was evident during 1995 (Fig. 5, Table 1). Crustacean mean length remained relatively constant throughout 1994, but diverged strongly between ponds in 1995. In 1994, mean size increased in the pond without fish following both the small and large nutrient pulses, but the maximum difference between ponds was <0.5 mm. In contrast, during 1995, effects of the fish manipulation were observed within 2 wk, and differences >0.7 mm were maintained throughout the summer.

These patterns in zooplankton body size reflect contrasts in zooplankton community composition between treatments and years (Fig. 6, Table 1). As expected, *Daphnia* biomass was consistently higher in the pond without fish than in the pond with fish (Figs. 5 and 6, Table 1). However, in the pond without fish, the percent biomass due to *Daphnia* was much higher in 1995 than in 1994 (Fig. 6). In 1994, both ponds were dominated by nauplii and rotifers throughout the summer, with some *Daphnia* in the pond without fish and some adult copepods and small cladocerans in the pond with fish. In contrast, *Daphnia* dominated the pond without fish for most of 1995, while nauplii and small cladocerans dominated the pond with fish.

Phytoplankton

Biomass.—Phytoplankton biomass (measured as chlorophyll *a*) in the reference lakes (Tuesday, Paul) showed relatively low variability throughout 1994 and 1995, in marked contrast to the two experimental ponds (Fig. 7). Variability in the experimental ponds was generally within the range of variability of the reference systems during the premanipulation periods, but not following the nutrient pulses, particularly the large nutrient pulses. This suggests that the observed results in the experimental ponds were likely due to our manipulations, and not to a regional environmental shift.

Total chlorophyll *a* tended to be 5–10 μg/L lower in the pond without fish than in the pond with fish during the premanipulation period in each summer (Fig. 8, Table 1). Chlorophyll concentrations in both ponds were somewhat lower in 1995 than in 1994. Total chlorophyll *a* responded little to and recovered quickly from three of the four small nutrient pulses (Fig. 8). In 1994, total chlorophyll *a* increased slightly more in the pond with fish than in the pond without fish, but only for a single sample. In 1995, total chlorophyll again increased little in the pond without fish, but increased steadily in the pond with fish for 2 wk before leveling

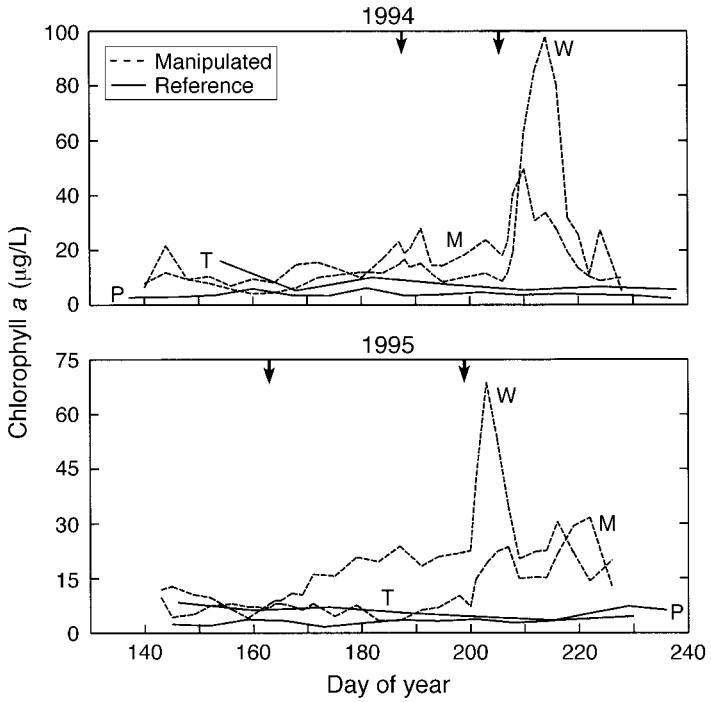

FIG. 7. Mean total chlorophyll *a* in the reference lakes (Paul [P] and Tuesday [T]; solid lines) and in the two experimental ponds (Monday [M] and Wednesday [W]; dashed lines) during the summers of 1994 and 1995. Timing of the pulse perturbations is indicated by the arrows at the top of each panel.

off at a concentration roughly twice that observed during the premanipulation period.

In contrast, total chlorophyll *a* responded a great deal to all four large pulses (Fig. 8). In 1994, the increase in total chlorophyll following the large nutrient pulse was twice as large in the pond without fish than in the pond with fish, while in 1995, increases were ~2.5 times larger in the pond with fish than in the pond without fish.

Size structure.—In both years, chlorophyll *a* in the <35-μm size class tended to be somewhat lower in the pond without fish than in the pond with fish (Fig. 8, Table 1). Overall, this ''edible'' chlorophyll tracked total chlorophyll relatively closely, except during the period immediately after the large nutrient pulse, when the large size fraction appeared to dominate responses (Fig. 8). This was particularly noticeable in the pond with fish in 1995.

Community composition.—Phytoplankton community composition differed among treatments and among years (Fig. 9, Table 2). In 1994, the pond without fish was dominated by chrysophytes (mainly *Dinobryon* and *Synura*) and dinoflagellates (*Peridinium*) until the large nutrient pulse, when chrysophytes declined and were replaced by *Gonyostomum*. During that same year, the pond with fish was dominated by dinoflagellates, chlorophytes, and chrysophytes during the reference period; dinoflagellates (mostly *Peridinium*) increased strongly after the small nutrient pulse, while chlorophytes (mainly *Spondylosium*) increased after the larger nutrient pulse.

In 1995, chlorophytes (mostly *Chlamydomonas*) dominated the pond without fish during the reference period, while dinoflagellates (*Peridinium*) and others (*Gonyostomum*) dominated after the small nutrient pulse (Fig. 9). As in 1994, *Gonyostomum* dominated after the large nutrient pulse, although unlike 1994, chrysophytes were rare in this treatment throughout the summer. The pond with fish had a more diverse community early in 1995: chlorophytes (mainly *Chlamydomonas*), chrysophytes (mostly *Dinobryon*), dinoflagellates (*Peridinium*) and others (dominated by *Gonyostomum*) were all represented. Although chrysophytes (*Mallomonas*, *Dinobryon*, and *Synura*) increased sharply after the small nutrient pulse, chrysophytes (*Synura*), dinoflagellates (*Peridinium*), and *Gonyostomum* were again codominant after the large nutrient pulse.

Sensitivity and return rate

We quantified phytoplankton responses to the nutrient pulses by fitting dynamic linear models (Fig. 10) to the data for total chlorophyll (Fig. 8). A one-parameter DLM was a suitable description of the dynamics for each of the total chlorophyll time series. Given the optimal discount factors, one-step-ahead forecasts were highly correlated to observations for all series (r between 0.64 and 0.76, $n = 31$ or 32, $P < 0.01$), and residuals from these forecasts were approximately normally distributed.

Given these DLMs, we calculated measures of sensitivity and return rate for each pulse in each year (Fig. 11). Both the relative sensitivity and the relative return rate depended on the size of the nutrient pulse. For

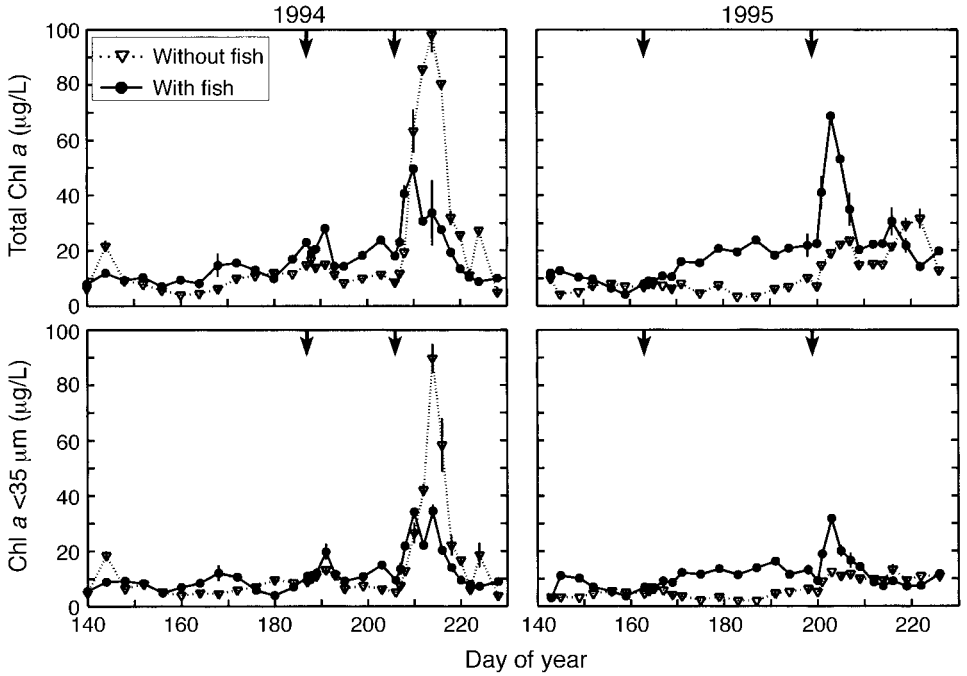

FIG. 8. Mean (±1 SD) total chlorophyll *a* and chlorophyll *a* <35 μm (''edible'' chlorophyll) in each pond during the summers of 1994 and 1995. The pond without fish is indicated by triangles and dotted lines, while the pond with fish is indicated by circles and solid lines. Timing of the pulse perturbations is indicated by the arrows at the top of each panel.

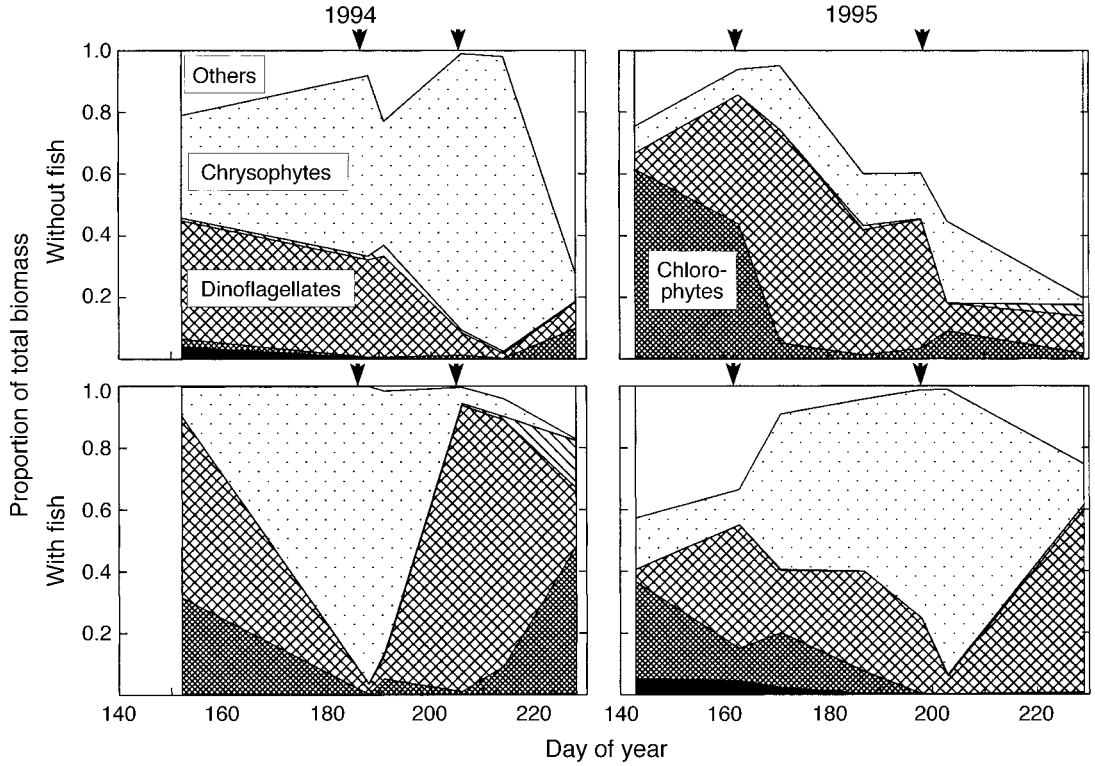

FIG. 9. Phytoplankton community composition as a proportion of total biomass in each of six taxonomic categories: cyanobacteria (solid), chlorophytes (fine cross-hatching), dinoflagellates (coarse cross-hatching), cryptophytes (diagonal hatching), chrysophytes (stippled), and ''others'' (diatoms, unidentified flagellates, unidentified small round nonmotile phytoplankton, and *Gonyostomum*) (open). Arrows above each panel indicate the timing of the pulse perturbations.

TABLE 2. Dominant phytoplankton genera in each pond on selected sampling dates.

Date	With fish		Without fish	
	Genus	Percentage of total biovolume	Genus	Percentage of total biovolume
A) 1994				
1 June	*Peridinium*	58.7	*Peridinium*	38.4
	Sphaerozosma	23.0	*Gonyostomum*	20.5
			Dinobryon	14.4
			Synura	10.9
7 July	*Synura*	92.1	*Synura*	53.3
			Peridinium	31.6
10 July	*Synura*	75.6	*Synura*	39.0
			Peridinium	32.7
			Gonyostomum	22.2
25 July	*Peridinium*	92.6	*Synura*	85.4
2 August	*Peridinium*	79.9	*Synura*	95.1
16 August	*Spondylosium*	45.2	*Gonyostomum*	71.6
	Peridinium	19.2		
	Gonyostomum	16.4		
	Cryptomonas	15.2		
B) 1995				
23 May	*Gonyostomum*	40.1	*Chlamydomonas*	58.6
	Chlamydomonas	30.9	*Gonyostomum*	24.5
	Dinobryon	15.8		
12 June	*Peridinium*	40.0	*Peridinium*	41.8
	Gonyostomum	20.1	*Bambusina*	39.8
	Tabellaria	12.8		
20 June	*Mallomonas*	28.1	*Peridinium*	69.1
	Peridinium	20.1	*Dinobryon*	16.9
	Dinobryon	11.4		
	Synura	10.7		
6 July	*Synura*	46.1	*Peridinium*	40.6
	Peridinium	32.5	*Gonyostomum*	38.7
17 July	*Synura*	71.8	*Peridinium*	41.8
	Peridinium	24.4	*Gonyostomum*	39.6
22 July	*Synura*	92.1	*Gonyostomum*	55.2
			Dinobryon	17.0
17 August	*Peridinium*	59.6	*Gonyostomum*	79.8
	Gonyostomum	23.4	*Peridinium*	12.1
	Synura	12.7		

sensitivity, phytoplankton increases in the pond without fish were consistently smaller than in the pond with fish following the small nutrient pulse. In fact, phytoplankton in the pond without fish were so insensitive to the small nutrient pulse that the return rate for this pond could not be calculated. Thus, we could not compare return rate between treatments for the small nutrient pulse. Following the large nutrient pulse, the relative sensitivity of phytoplankton in the different treatments differed among years: the pond with fish was less sensitive in 1994, while the pond without fish was less sensitive in 1995. In both years, though, phytoplankton in the pond with fish had a faster return rate following the large nutrient pulse than phytoplankton in the pond without fish.

DISCUSSION

Despite the importance of stability concepts for theoretical models of ecosystem dynamics and applied problems of resource management, our experiments are one of the few empirical tests of the effect of food web structure on the sensitivity and return rate of communities to perturbations (see also Steinman et al. 1990, 1991, 1992). We think that the difficulty of defining the baseline state of ecosystems that are dynamic and stochastic even in the absence of perturbation is one of the reasons why there are so few experimental tests of theoretical ideas about sensitivity and return rate. This paper demonstrates that dynamic linear models can be a powerful tool for the quantitative description of fluctuating baseline conditions in ecological

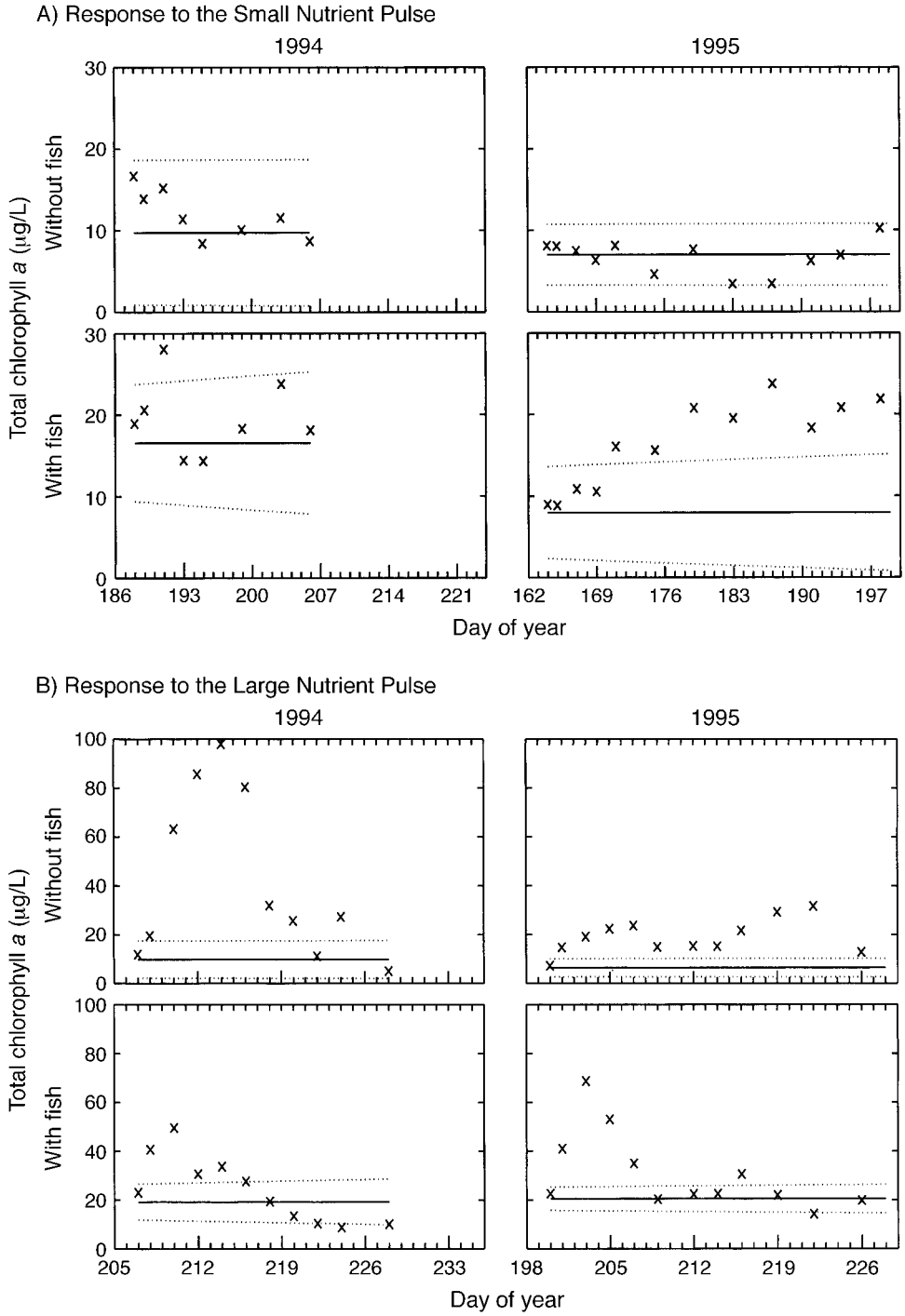

FIG. 10. Comparison of observed and predicted total chlorophyll *a* for the small (A) and large (B) nutrient pulses in each pond in each year. The × symbol denotes field observations; solid lines denote the predicted level from a dynamic linear model; dotted lines denote 90% HPD intervals around this prediction.

time series. We also provide evidence to support the idea that grazer size structure alters the response of phytoplankton to nutrient perturbations, although more experiments are needed to confirm the generality of this result.

Does grazer community structure affect phytoplankton sensitivity to nutrient pulses?

Our field experiment was designed to test the hypothesis that phytoplankton in lakes with zooplankton

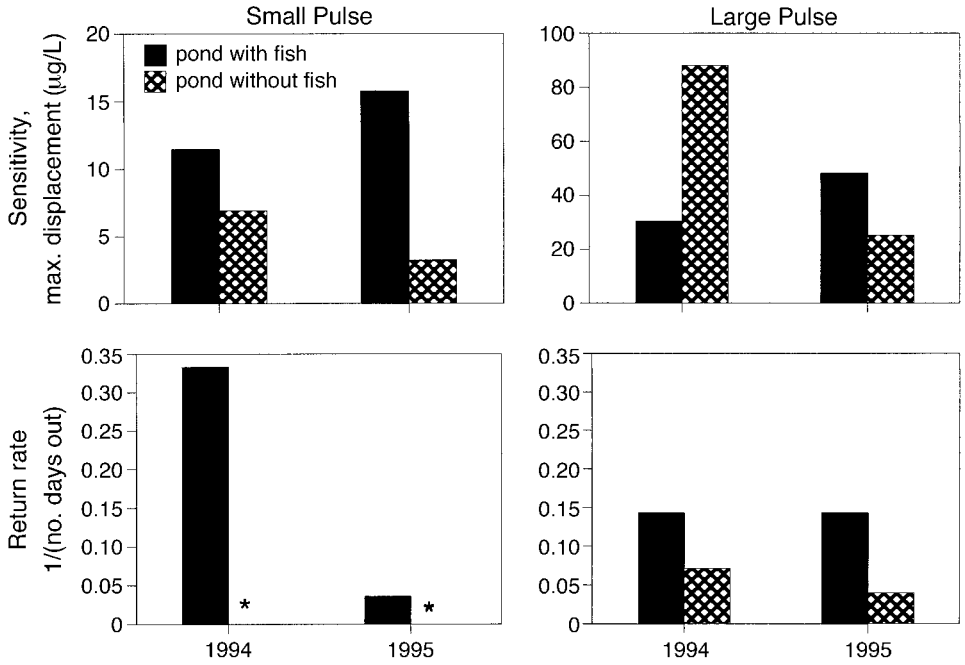

FIG. 11. Sensitivity and return rate following the small and large nutrient pulses in each year. The star symbols indicate that the return rate could not be calculated because the system never departed from the reference state.

communities dominated by large-bodied species are less sensitive to nutrient pulses than phytoplankton in lakes with small-bodied zooplankton (Nilssen 1978, Lynch and Shapiro 1981, Carpenter et al. 1992, Mazumder et al. 1992). Consistent with this hypothesis, we found that phytoplankton sensitivity to the small nutrient pulse was lower in the pond without fish in both years of the experiment. Reduced sensitivity to gradual increases in nutrients has been attributed to a difference in nutrient processing, since large zooplankton transfer nutrients from phytoplankton to higher trophic levels more efficiently than smaller zooplankton (Carpenter et al. 1992, Cottingham and Carpenter 1994, Schindler 1995, Romo et al. 1996). Our results suggest that a similar mechanism may also reduce phytoplankton sensitivity to sudden increases in nutrients. Larger grazers have higher clearance rates (Peters and Downing 1984), and can consume a larger range of algal sizes (Burns 1965). *Daphnia* also have high P concentrations in their bodies (Andersen and Hessen 1991, Hessen and Bjerkeng 1997). Therefore, it is not surprising that more of the P that we added ended up as *Daphnia* biomass rather than being retained within phytoplankton (Hessen and Nilssen 1986) or recycled back to phytoplankton (Sterner 1990).

Decreased sensitivity of primary producers to perturbation also has been observed in streams, where periphyton biomass declined less following elimination of light in highly grazed streams with snails than in little grazed streams without snails (Steinman et al. 1990). The link between sensitivity and nutrient processing rates has also been noted in terrestrial ecosystems (O'Neill et al. 1975, Vitousek et al. 1981, DeAngelis 1992). Both of these results suggest that there may be some ubiquity in features influencing sensitivity to perturbation.

The consistently lower sensitivity of the pond without fish to small nutrient pulses is particularly interesting because there were very different amounts of large zooplankton in this food web treatment in the different years. During 1994, *Daphnia* constituted ~20% of the total zooplankton biomass, while in 1995, *Daphnia* were 60–70% of the total biomass (Fig. 6). This suggests that relatively low abundances of large-bodied grazers may be sufficient to buffer phytoplankton in mesotrophic lakes from nutrient pulses typical of high-frequency events such as summer storms.

Unlike the small nutrient pulse, we observed large responses of phytoplankton to the large nutrient pulse in both 1994 and 1995. However, the relative magnitude of response in ponds with and without fish differed among years. In 1995, we observed the expected result: phytoplankton in the pond without fish were much less sensitive to the large nutrient pulse than phytoplankton in the pond with fish. However, in 1994, phytoplankton in the pond with fish were less sensitive to the large pulse than phytoplankton in the pond without fish. What might have caused this difference between years? In 1995, zooplankton biomass was nearly equal between ponds, and large zooplankton were abundant in the pond without fish. However, in 1994, there were 2–5 times more zooplankton biomass in the pond with fish than in the pond without fish. In addition to this biomass difference, *Daphnia* biomass was relatively

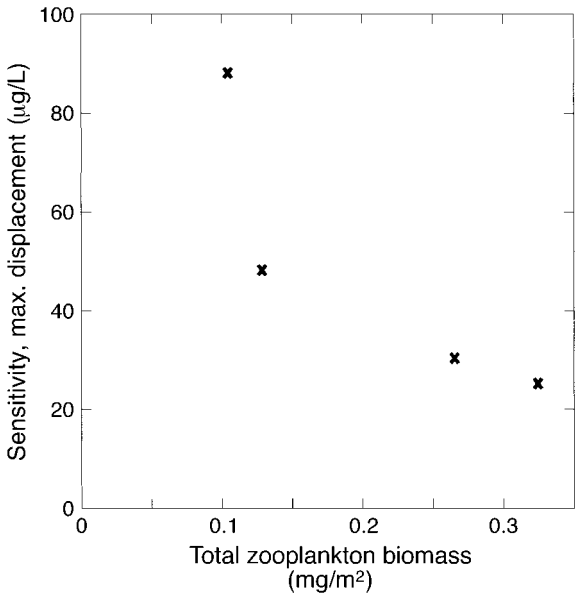

FIG. 12. Effect of total zooplankton biomass on phytoplankton sensitivity to large nutrient pulses.

low in the pond without fish throughout 1994, especially in the period immediately before the large nutrient pulse. Because grazing rates are positively related to total zooplankton biomass (Cyr and Pace 1992), it is not surprising that phytoplankton responses to the large nutrient pulse were smaller in the pond with more zooplankton biomass. In our experiment, sensitivity declined with increasing zooplankton biomass (Fig. 12), consistent with the observation that zooplankton biomass, and not size structure, can sometimes be the major factor controlling changes in phytoplankton biomass (Lampert and Taylor 1985, Lampert 1988, Cyr and Pace 1992).

Our results therefore suggest that grazer size structure is an informative predictor of phytoplankton sensitivity to small nutrient pulses, but that other factors need to be incorporated into predictions for larger perturbations. In particular, if large zooplankton are not dominant, then grazers may not be able to buffer phytoplankton responses from large pulse events. Instead, zooplankton biomass, and perhaps species-level differences in the composition of either the phytoplankton or zooplankton communities, may play a role in how phytoplankton respond to large pulses. It also seems likely that there may be some perturbations that are too large for the grazing effects of zooplankton (due to either size structure or biomass) to adequately regulate phytoplankton responses.

Does grazer size structure affect phytoplankton return rate following nutrient pulses?

We also tested the hypothesis that phytoplankton in lakes with large-bodied zooplankton tend to recover more slowly from pulses of nutrients than phytoplankton in lakes without large grazers. We were unable to test this hypothesis for the small nutrient pulse, since the pond without fish remained within the reference state following this pulse in both years. However, there were detectable differences in return rate for the large nutrient pulse, despite theoretical predictions that differences in recovery times between food web treatments can be quite small (<25 d) (DeAngelis et al. 1989, Cottingham and Carpenter 1994). Recovery from both the small and large nutrient pulses was relatively rapid: the number of days outside of the prediction limits, even in the large-pulse scenarios, was usually <1 mo. This agrees well with the recovery times of ~10–30 d predicted by models (Carpenter et al. 1992, Cottingham and Carpenter 1994).

In both 1994 and 1995, phytoplankton biomass in the pond with fish recovered more quickly from the large nutrient pulse than phytoplankton in the pond without fish, consistent with expectations derived from simulation models (Fig. 1) and experiments in other ecosystems (Steinman et al. 1991). The greater return rate in ponds with small zooplankton is likely to be due to allometric differences between large-bodied and small-bodied grazers. For example, smaller zooplankton species have a shorter life cycle and greater intrinsic rates of increase (Allan 1976), both of which could allow smaller zooplankton to have faster numerical responses to a large increase in phytoplankton (Vanni 1987). *Daphnia* populations, on the other hand, cannot consistently increase quickly enough to control summer bloom formation, particularly blooms of cyanobacteria (Dawidowicz 1990, Gliwicz 1990, Reynolds 1994). Some of this lack of grazing control of cyanobacteria may be due to low food quality (Gulati and DeMott 1997), an issue we could not directly address in this study, since cyanobacteria were not abundant in our ponds.

Implications

The design of our experiment reflects a compromise between our ability to replicate the experimental units and the capacity of the experimental units to adequately encompass the physical, chemical, and biological properties of a natural system (Levin 1992, Carpenter et al. 1998, Schindler 1998). In this study, we chose to represent a high degree of ecological realism at the expense of rigorous replication and control. For example, we used two nearby lakes as partial controls for background environmental variability. Comparison of time series from the experimental ponds with the reference lakes clearly demonstrated that our manipulations moved the phytoplankton communities of Monday and Wednesday ponds to a parameter space outside the natural variation observed in similar lakes nearby. To test for pond-specific responses to nutrient pulses that were not due to grazer community manipulations, we switched the fish treatments between ponds in the two years of the experiment. In theory, this unconventional

type of replication should satisfy all of the primary goals of experimental replication, i.e., to assess the repeatability of experimental effects, discern the treatment effects from natural variation, estimate the variance of response parameters, and test for the significance of responses to manipulation (McAllister and Peterman 1992).

Because the contrasts in grazer size structure were weak in 1994, we have only one good estimate of the effect of grazer size structure on phytoplankton stability to nutrient perturbations. Results from 1995 supported the hypotheses that larger grazers decrease phytoplankton sensitivity to nutrient pulses, but also decrease return rates. Thus, we have shown that grazer size structure can alter the stability properties of phytoplankton. However, because our experimental design consciously made a trade-off between ecological realism and generality, we cannot generalize the results of our experiments to all other aquatic systems without performing additional experiments in other systems. Nonetheless, our study clearly demonstrates how the proposed relationship between community structure and stability can be evaluated in field experiments, and points the way toward further empirical work to confirm whether the effects of grazer size structure on phytoplankton stability will hold more generally.

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