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TROPHIC CASCADES AND COMPENSATION: DIFFERENTIAL RESPONSES OF MICROZOOPLANKTON IN WHOLE-LAKE EXPERIMENTS

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Abstract. Food webs in three lake basins were manipulated by altering fish communities to either reduce or increase the abundance of *Daphnia.* These basins were subsequently fertilized with nitrogen and phosphorus for two years. We tested three predictions about the response of heterotrophic flagellates, ciliates, and rotifers (collectively, microzooplankton) derived from prior studies. We predicted that (1) microzooplankton would increase with lake fertilization, (2) lakes with abundant *Daphnia* would have lower increases in microzooplankton, and (3) both increases in resource availability *and* suppression by *Daphnia* would determine microzooplankton dynamics. Contrary to the first prediction, microzooplankton did not increase with fertilization relative to the reference lake, except in the low-*Daphnia* system. The second prediction was supported, as *Daphnia* prevented microzooplankton from increasing in the fertilized lakes with the strength of the *Daphnia* effect being greater than anticipated. Because of this strong effect, microzooplankton dynamics were in all but one case most strongly related to suppression by *Daphnia* rather than to a combined effect of resources and suppression. The microzooplankton communities were differentially affected by the trophic cascade. Heterotrophic flagellates appeared to be limited by a variety of predators. Even in the low-*Daphnia* fertilized lake, mortality was apparently high. Ciliates and rotifers increased in the low-*Daphnia* fertilized lake and were strongly suppressed otherwise. These experiments indicate that small-scale, short-term experiments and larger-scale comparative analyses may be inadequate for assessing the strength of trophic interactions. The potential for community-level responses, not well assessed except at the ecosystem scale, may alternatively dampen or enhance the impacts of trophic cascades in food webs.

Key words: ciliates; Daphnia; *ecosystem experiments; flagellates; lakes; rotifers; trophic cascades; zooplankton.*

INTRODUCTION

Predicting the outcome of food web interactions is complicated in at least two ways. First, behavioral, physiological, and morphometric responses of individuals often act to ameliorate predation, thus limiting the impact of one trophic group upon another (Sih 1987, Polis et al. 1996). In addition, changes in food webs may ramify through trophic networks, creating complex dynamics among the trophically linked populations (Abrams et al. 1996). These individual and population responses can engender indeterminate and often surprising results (Brown et al. 1986, Yodzis 1988). While it is possible to quantify the direct and indirect effects of food web perturbations on populations experimentally (Morin et al. 1988, Wootton 1994) or with modeling approaches (Pimm 1991), the generality of these responses for specific types of communities is usually unknown. Nevertheless, strong food web interactions can also result in dramatic and predictable trophic-level responses (Paine 1980). Such interactions have been well documented in lakes where trophic cascades originating from piscivorous and planktivorous fishes determine the size structure of zooplankton communities, which may in turn influence phytoplankton biomass (Carpenter et al. 1985).

Compensatory responses may also dampen the action of trophic cascades. For example, in studies of lake food webs, simple predictions about lower trophic levels are not always upheld when fish populations are experimentally manipulated, because of changes in the intensity of vertebrate and invertebrate predation on zooplankton as well as changes within phytoplankton communities (e.g., Carpenter and Kitchell 1993). Strong effects of zooplankton on phytoplankton hinge most often on the presence or absence of large species of the cladoceran *Daphnia* (Leibold 1989, Carpenter and Kitchell 1993). When large *Daphnia* are abundant, phytoplankton are often suppressed relative to their abundance in the absence of a large grazer (Pace 1984, Mazumder 1994, Carpenter et al. 1996). These interactions, however, occur within a food web of multiple pathways dictated by the trophic diversity of microorganisms as well as interactions involving other zooplankton and fish (Porter 1996). Included within these pelagic food webs are flagellated and ciliated protozoa

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and rotifers, which are both abundant and important constituents of the plankton community in terms of secondary production and nutrient cycling (Stockner and Porter 1988). These organisms, referred to collectively here as microzooplankton, can also be simultaneously potential competitors and prey of *Daphnia*.

Previous studies have documented the importance of system productivity and predators as regulators of the abundance, biomass, and composition of microzooplankton communities. Heterotrophic flagellate, ciliate, and rotifer abundances increase across gradients of primary production, and simple regression models predict these changes (Pace 1986, Sanders et al. 1992, Gasol and Kalff 1995). Zooplankton predators also limit microzooplankton abundance and may regulate their dynamics (Pace and Funke 1991, Riemann and Christoffersen 1993, Burns and Schallenberg 1996). *Daphnia* kill, consume, and compete for food with microzooplankton, with the largest species having the greatest effect (Gilbert 1988*a*, *b*, Wickham and Gilbert 1991, 1993, Jürgens 1994). Microzooplankton populations are typically reduced to very low densities in enclosure experiments with high *Daphnia* populations (Pace and Funke 1991, Christoffersen et al. 1993, Jürgens et al. 1994, Marchessault and Mazumder, *in press*). Microzooplankton mortality is much higher in lakes with species of *Daphnia* of mean adult body lengths of 1 mm, ~10 mg dry mass (Pace and Vaqué 1994). Negative correlations have also been observed between the abundance of *Daphnia* and heterotrophic flagellates within and among lakes (Güde 1988, Weisse et al. 1990, Gasol and Vaqué 1993). As for phytoplankton, *Daphnia* appears to be a key genus that when present may strongly limit the abundance and biomass of microzooplankton (Pace and Funke 1991, Jürgens 1994). Lake trophic cascades arising from piscivorous fish should suppress microzooplankton by enhancing *Daphnia*. There is also the possibility, however, for compensation, as microzooplankton species resistant to predation may come to dominate communities when *Daphnia* is abundant. For example, some rotifers are less susceptible to *Daphnia* because of size, elongated spines, sturdy loricas, or rapid escape responses (Gilbert 1988*a*, *b*, Jack and Gilbert 1993).

Understanding of the interactions of microzooplankton, *Daphnia*, and lake trophic conditions is based on experimental studies in enclosures over relatively short periods of time (days to weeks), or alternatively, on among-lake comparisons. There is uncertainty about whether the results from experimental and comparative studies extrapolate to predict the results of food web changes in lakes. For example, enclosure studies may exaggerate *Daphnia* effects because populations increase to unusually high densities when fish predation is eliminated (Pace and Cole 1994). Further, short-term experiments may not allow sufficient time for compensatory mechanisms that ameliorate predatory effects. Comparative studies, while describing general patterns of variation, may provide only weak predictions about changes within individual systems. Food web disturbances of whole lakes bridge the uncertainties associated with comparative and enclosure studies, allowing tests at key scales of interest—lakes and years (Carpenter and Kitchell 1993).

Two common disturbances to lake food webs arise from increases in nutrient loading and shifts in fish communities that alter trophic cascades. Here, we explore the joint effects of nutrient loading and food web structure on microzooplankton in whole-lake experiments carried out over four years. Fish manipulations were designed to either suppress or enhance the abundance of *Daphnia* (Carpenter et al. 1996). Lakes with and without *Daphnia* were then fertilized during the final two years of the experiment. We ask here if we can predict at least qualitatively the net responses of microzooplankton to the combined manipulations by examining three general predictions. First, microzooplankton should increase with fertilization based on the comparative studies documenting increased abundances across gradients from oligotrophic to eutrophic systems. Second, increases should be reduced in fertilized lakes with sustained high *Daphnia* populations based on experimental results and the comparative study of heterotrophic flagellates by Gasol and Vaqué (1993). The literature is not specific, however, about what abundance of *Daphnia* constitutes a "high" population. The third prediction concerns the relative importance of resources vs. suppression by *Daphnia* in determining abundance. The literature cited above suggests that both factors are important, and we test this prediction by fitting time series of microzooplankton dynamics with models that include measures of resources and *Daphnia*.

METHODS

Study sites and lake experimental manipulations

Experiments were carried out in Paul, Peter, and Long lakes, located at the University of Notre Dame Environmental Research Center in Gogebic County, Michigan. Whole-lake manipulations and results for phytoplankton, zooplankton, and bacteria have been reported elsewhere (Carpenter et al. 1996, Pace and Cole 1996) and are only briefly summarized here.

All three lakes are relatively small (<5 ha), steep-sided basins that stratify strongly during the May–September period considered in this study. Long Lake was divided in the spring of 1991 into three basins using two neoprene curtains drawn top to bottom, across narrow portions of the lake. We studied two of these basins and hereafter refer to them as East and West Long lakes, for convenience. While these basins were chosen for their similarity in physical, chemical, and biological conditions, they diverged during the course of the experiment and responded quite differently to the manipulations as described below. We therefore consider

TABLE 1. Sampling frequency and depths for measurements of the abundance of heterotrophic flagellates, ciliates, and rotifers in the experimental lakes.

Years	Lake	Group	Depth	Frequency
1988–1990	PL, PR	H. flagellates	Epi, Meta	Weekly
1989–1990	EL, WL	H. flagellates	Epi	Weekly
1991–1994	All	H. flagellates	Epi, Meta	Biweekly
1990–1994	All	Ciliates	Epi	Weekly
1988	PL, PR	Rotifers	Epi	Weekly
1989–1990	PL, PR	Rotifers	Epi, Meta	Weekly
1989–1990	EL, WL	Rotifers	Epi	Weekly
1991–1994	All	Rotifers	Epi, Meta	Weekly

Notes: PL = Paul Lake, PR = Peter Lake, EL = East Long Lake, and WL = West Long Lake; Epi = epilimnion, and meta = metalimnion, as defined in *Methods*. "Biweekly" means every other week.

and treat East Long, West Long, and Peter as separate experimental lakes in this paper. Paul Lake served as an unmanipulated reference ecosystem, as in past studies (Carpenter and Kitchell 1993).

In May 1991, fish were removed from Peter Lake by electroshocking, angling, and finally by adding rotenone. The lake was restocked with zooplanktivorous fishes, principally golden shiners (*Notemigonus crysoleucas*), which were maintained throughout the experiment. This lake served as the "planktivore lake," as piscivorous fishes were absent and planktivorous fish abundant. The fish community of West Long Lake was dominated by piscivorous bass (*Micropterus salmoides* and *M. dolomieu*) and had few planktivorous fish of any kind. Curtain placement in East Long Lake resulted in an unexpected change. Inflowing groundwater moves across organically rich sediments within the littoral zone of the East Long basin while in the West Long basin littoral sediments have a higher sand content (Christensen et al. 1996). As a consequence of curtaining, dissolved organic carbon (DOC), acidity, and water color increased in East Long Lake (Christensen et al. 1996). Accompanying these changes, fish populations declined and both piscivory and planktivory were negligible for most of the experiment (J. F. Kitchell et al., *unpublished data*).

Beginning in 1993, Peter, East Long, and West Long lakes were enriched with liquid fertilizer. Nutrients were added at a central station daily from late May through early September in 1993 and 1994. Phosphorus was added as PO_4, and nitrogen was added as NH_4NO_3 at a N:P ratio of 25:1 by atoms. Loading rates were adjusted to provide similar mass loading per epilimnion volume in each experimental lake (Carpenter et al. 1995, 1996).

Sampling and counting methods

Flagellates, ciliates, and rotifers were sampled at different frequencies and depths during the years 1988–1990 and consistently for all the study lakes during the experimental period of 1991–1994 (Table 1). Data from 1988–1990 serve as additional information for evaluating responses of the experimental lakes, especially their responses to fertilization in 1993 and 1994. Each lake was sampled weekly at a central station from mid-May to early September. Water samples for heterotrophic flagellates, ciliates, and rotifers were taken with a 2-L Van Dorn bottle at the surface, 1 m, and 2 m depths. These samples were pooled to constitute an epilimnetic sample representative of the surface mixed layer. A second sample was taken from the metalimnion, defined as either the oxygen maximum (when present) or the depth of greatest temperature change.

Duplicate subsamples of 10–20 mL were withdrawn from water samples for preservation and subsequent counting of heterotrophic flagellates. Samples were stained with proflavin, preserved with cold glutaraldehyde (1% final solution), filtered onto 1.0-μm filters with gentle vacuum (<13.3 kPa), and stored in a freezer. Counts were made at 600× magnification by scanning strips until at least 50 cells were counted for each filter.

Subsamples of 100 mL were taken for ciliates. Samples were preserved with a 1% final concentration of Lugol's solution and counted with an inverted microscope at 150× magnification. Subsamples of 1–2 L for rotifers were filtered through a 20-μm sieve, preserved in cold 4% sucrose–formalin solution, and counted with an inverted microscope at 100× magnification.

We tested whether the responses of protozoans and rotifers were related to changes in phytoplankton and crustacean zooplankton. Methods for sampling and analysis of phytoplankton and zooplankton are described in Carpenter and Kitchell (1993) and Carpenter et al. (1996). Samples for phytoplankton analysis were taken weekly in each lake from late May to early September using a Van Dorn bottle. Chlorophyll *a* corrected for pheopigments was measured weekly at six depths ranging from 1 to 100% irradiance in each study lake. We calculated chlorophyll concentrations for the mixed layer (0–2 m) to correspond with the depths for the epilimnetic protozoan and rotifer samples and to serve as an index of overall primary production for the lakes. Note that the chlorophyll concentrations for the 0–2 m layer are closely correlated with the volumetric chlorophyll concentrations averaged to the 5% light level reported by Carpenter et al. (1996). Zooplankton were sampled by duplicate vertical hauls of a calibrated net. Species were identified and enumerated. Lengths were measured, and biomass was estimated using published length-dry mass relationships, as summarized in McCauley (1984).

Analysis of the ecosystem experiments

Interpretations of the ecosystem experiments are based on trends in the experimental lakes (East, West, and Peter) relative to the reference lake (Paul) and on time series analyses. We first tested whether protozoans and rotifers increased when the lakes were fertilized, using randomized intervention analysis (Carpenter et al. 1989). Randomized intervention analysis (RIA) compares differences between a reference and experimental lake before and after manipulation. The probability of nonrandom change associated with the manipulation is calculated by iterative randomization of the time series and repeated calculation of before and after manipulation differences to generate a distribution of difference values. RIAs were based on all data for the period of 1988–1994.

Two factors were manipulated in the whole-lake experiments—nutrient loading and food web structure. We examined whether changes in resources and predation brought about by these manipulations were related to temporal variation in microzooplankton. We considered phosphorus input per unit epilimnetic volume as a measure of resource availability to the plankton, because phosphorus was limiting (see *Results*) and related to variability in primary production, phytoplankton biomass, and bacterial productivity (Carpenter et al. 1996, Pace and Cole 1996). To assess the effects of the food web manipulation, we used the mean size of crustacean zooplankton. Mean size of crustaceans reflects measurements of length for all species and stages of copepods and cladocerans including juveniles; this index has been useful for assessing the effects of zooplankton on phytoplankton in these and other lakes (Pace 1984, Carpenter and Kitchell 1993, Carpenter et al. 1996). In our experiments shifts in crustacean size reflected the differences in food web treatments and the dynamics of *Daphnia* (see *Results*).

Time series models were fit for the period 1991—1994 because this encompassed the focal period for the experimental manipulation considered here, and because time series data for the various groups were consistent over this interval (Table 1). Time series analyses employed weekly data (ciliates, rotifers) or data collected every other week (flagellates) over the 4-yr period. Missing values in the time series were estimated using linear interpolation. Because of trends in the time series due to fertilization of the lakes, data were first "differenced," meaning the first value of the series was subtracted from the second value, the second value from the third value, and so on. This procedure detrends the data, creating a time series of differences with a mean near zero (Wei 1990). The differenced model analyzes how perturbations away from zero in the predictor variable result in perturbations away from zero in the response variable.

The time series models can be cast in a form analogous to least squares regression. We fit the weekly log-transformed and differenced data for the microzooplankton time series (MZ_t) to a model that included differenced predictor variables (R = resources and Z = crustacean zooplankton) and lagged prior values (MZ_{t-x}) of the microzooplankton series.

$$\mathrm{MZ}_t = a + B_1R_{t-x} + B_2Z_{t-y} + B_3\mathrm{MZ}_{t-z} + e_t. \quad (1)$$

The fitted coefficients B_1, B_2, and B_3 account for the effects of resources, zooplankton, and serial correlation respectively, while a is a constant, e_t is a series of uncorrelated residuals, and t is time. Lags between the predictor and microzooplankton series, denoted by x and y, were usually zero, and the lag for serial correlation, denoted by z, was typically one time unit.

We also considered two additional variables, chlorophyll and *Daphnia* biomass. These represent potentially important covariates driving the response of microzooplankton. In particular, *Daphnia* biomass represents a more direct metric for assessing the specific effects of *Daphnia* than the index of crustacean size used above. Autocorrelations on the differenced time series of the dependent and independent variables were first estimated. Appropriate autocorrelation models were fit, and cross-correlation functions were calculated on these filtered time series. We also fit models using these covariates as predictors to microzooplankton time series using Eq. 1.

Models and cross-correlations were calculated using the ARIMA procedure in SAS (SAS Institute 1988), following the methods presented in Wei (1990). Criteria used to compare models were residual error, standard deviations of parameters, autocorrelation functions, cross-correlations, and analyses of residuals.

Results

Nutrient enrichment of the three fertilized lakes increased phytoplankton and zooplankton biomass (Carpenter et al. 1996). For example, in Peter Lake, mean chlorophyll *a* concentrations for the two fertilization years were two- to six-fold higher than observed for the two years prior to fertilization (Table 2). Chlorophyll concentrations were relatively constant in the reference lake, Paul (Table 2) and similar to those observed in earlier years (Carpenter and Kitchell 1993). *Daphnia pulex* and *D. rosea* dominated zooplankton biomass of East and West Long in most years, especially with fertilization of the lakes (Table 2). *Daphnia* populations increased at least three-fold during the two fertilization years in East and West Long lakes (Table 2). This upward shift in *Daphnia* abundance was much greater than the interannual variability observed in Paul Lake (Table 2). Average body lengths of *Daphnia* were greatest in West Long and were ~1 mm in East Long and Paul lakes (Table 2). Peter Lake had

TABLE 2. Means of chlorophyll *a* and *Daphnia* abundance, size, and percentage of total zooplankton biomass for each year in the reference lake (Paul) and three experimental lakes. Lakes were fertilized in 1993 and 1994. Chlorophyll is a volumetric average to the depth of 5% light. Means for Peter Lake in 1994 were split to contrast the first half of the season (1994*a*), when *Daphnia* abundance was low, with the second half of the season (1994*b*), when *Daphnia* increased to high abundance.

Lake	Year	Chlorophyll (μg/L)	*Daphnia* (no./L)	*Daphnia* size (mm)	*Daphnia* %
Paul	1991	4.66	1.80	0.97	14
	1992	4.40	2.29	0.98	8
	1993	4.97	0.32	0.92	2
	1994	4.39	4.22	1.09	16
East	1991	5.68	0.40	1.16	10
	1992	7.90	3.99	0.97	18
	1993	19.71	24.35	1.06	72
	1994	11.42	34.87	1.13	76
West	1991	5.62	3.60	1.20	67
	1992	4.47	4.63	1.09	43
	1993	12.20	16.47	1.25	90
	1994	12.37	21.17	1.26	83
Peter	1991	3.36	0.12	1.12	1
	1992	5.17	0.01	†	<1
	1993	19.73	0.03	1.07	<1
	1994*a*	9.90	0.02	0.72	<1
	1994*b*	14.44	74.90	0.89	64

† Too few animals to estimate.

planktivorous fish and low *Daphnia* populations throughout most of the 4-yr period (Table 2). A variety of rotifers and small crustaceans dominated zooplankton biomass from 1991 to mid-1994. Declines in planktivore populations in Peter Lake during 1994, however, were followed by a large increase in *Daphnia rosea* along with some *D. pulex* and *D. dubia* (Carpenter et al. 1996). During the final half of the sampling season, *Daphnia* dominated zooplankton biomass in Peter Lake (Table 2).

Did microzooplankton increase in the fertilized lakes?

We consider this question by testing if an individual group became more abundant when lakes were fertilized in 1993 and 1994 relative to the reference lake. In Figs. 1–3 we present the annual means and standard errors for each group in each lake. Error bars are shown to provide an estimate of variability, but are not appropriate for comparisons among means because of autocorrelation in the time series.

Heterotrophic flagellates.—Heterotrophic flagellate abundances varied from 10^5 to 10^7 cells/L. Average flagellate abundances were in the range of $<1–4 \times 10^6$ cells/L, with highest abundances in 1993 for all lakes including the unfertilized reference lake, Paul (Fig. 1). Flagellates in the fertilized lakes did not increase relative to the reference lake except for the metalimnion of Peter Lake. In this case Paul Lake averaged over 2

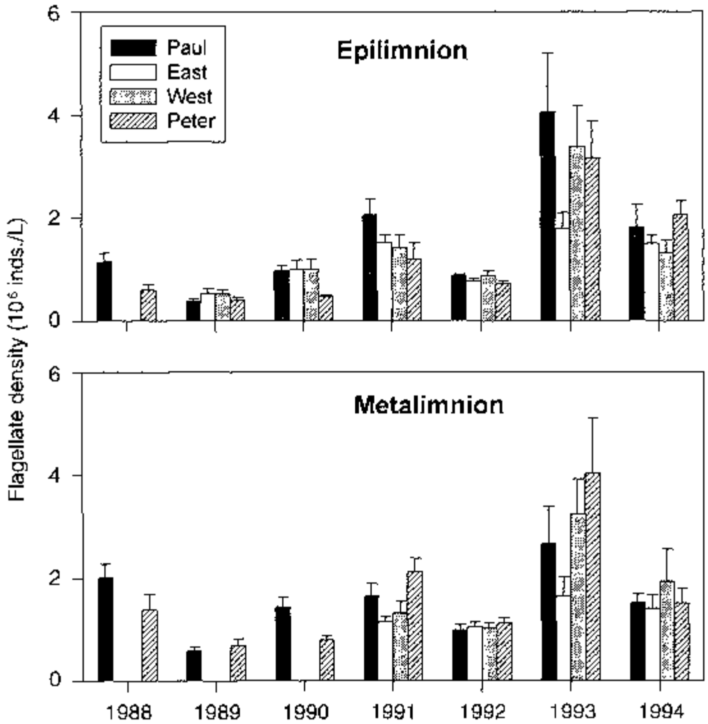

FIG. 1. Annual mean abundance (+1 SE) of epilimnetic and metalimnetic heterotrophic flagellates in the reference lake (Paul) and the experimental lakes (East, West, and Peter).

TABLE 3. Randomized intervention analysis (RIA) to test for changes in abundances of heterotrophic flagellates, ciliates, and rotifers in the experimental lakes (East, West, and Peter) relative to the reference lake (Paul).

Lake	Group	Depth	D_{pre}	D_{post}	P	df
East	Flagellates	Epi	115 000	1 311 000	0.004	50
		Meta	200 000	572 000	0.39	33
West	Flagellates	Epi	110 000	589 000	0.34	50
		Meta	158 000	−500 340	0.19	33
Peter	Flagellates	Epi	386 000	330 000	0.85	82
		Meta	204 000	−674 000	0.014	82
East	Ciliates	Epi	110	1 790	0.024	72
West	Ciliates	Epi	1 840	1 190	0.297	72
Peter	Ciliates	Epi	−90	−7 350	0.001	79
East	Rotifers	Epi	−334	−140	0.33	88
		Meta	−416	−169	0.42	66
West	Rotifers	Epi	−202	244	0.044	88
		Meta	−228	344	0.002	66
Peter	Rotifers	Epi	133	−492	0.008	113
		Meta	116	−1 378	<0.001	99

Notes: Epi = epilimnion; Meta = metalimnion. D_{pre} and D_{post} are the mean differences in numbers per liter (Paul − Experimental) before (1988–1992) and after (1993–1994) fertilization with nutrients. P is the two-tailed probability that $D_{post} - D_{pre}$ is significantly different from zero.

$\times 10^5$ more flagellates/L prior to fertilization, while Peter Lake had over 6×10^5 more flagellates/L after fertilization (Table 3). This was a large and significant shift in the relative abundance of flagellates. However, a similar positive increase in flagellate abundance was not observed in the other lakes. In East Long Lake, flagellates actually decreased relative to Paul Lake after fertilization (Table 3).

Ciliates.—Mean ciliate abundances were ≤4400 cells/L in all lakes except Peter Lake during 1993–1994 (Fig. 2). Ciliates increased strongly in Peter Lake in response to fertilization (Fig. 2, Table 3). In East Long Lake, ciliate densities declined with fertilization relative to Paul Lake (Table 3). Differences between East Long Lake and Paul Lake were trivial prior to fertilization, but Paul Lake had on average 1790 more ciliates/L after East Long was fertilized.

Rotifers.—Mean rotifer abundances varied from <100 to >2000 individuals/L (Fig. 3). Rotifer abundances increased in Peter Lake in both the epilimnion and metalimnion. Note that rotifers began increasing in 1991 when minnows were added to the lake, 2 yr prior to fertilization (Fig. 3). No such trend was evident in either East or West Long lakes (Fig. 3). RIA confirmed that there were large positive shifts in rotifer abundance in Peter Lake relative to Paul Lake with fertilization (Table 3). In East Long Lake, no significant change was observed, while in West Long Lake, rotifers decreased relative to the reference lake (Table 3).

In summary, microzooplankton did not increase in all the fertilized lakes as predicted. Only in Peter Lake were significant increases observed relative to the unfertilized reference lake.

Was the abundance of Daphnia *related to changes in microzooplankton with fertilization?*

The evidence for an effect of *Daphnia* on heterotrophic flagellates is equivocal. Flagellates were most abundant in the reference lake during 1993 when *Daphnia* abundances were low (Table 2, Fig. 1). However, flagellates were most abundant in all other lakes in 1993, and in some of these lakes, *Daphnia* was also abundant (Table 2). The relative decline during the fertilization period in epilimnetic flagellates in East Long Lake could have been related to the abundant populations of *Daphnia* observed in this lake during 1993 and 1994 (Table 2). The relative increase in flagellates in the metalimnion of Peter Lake, especially in 1993,

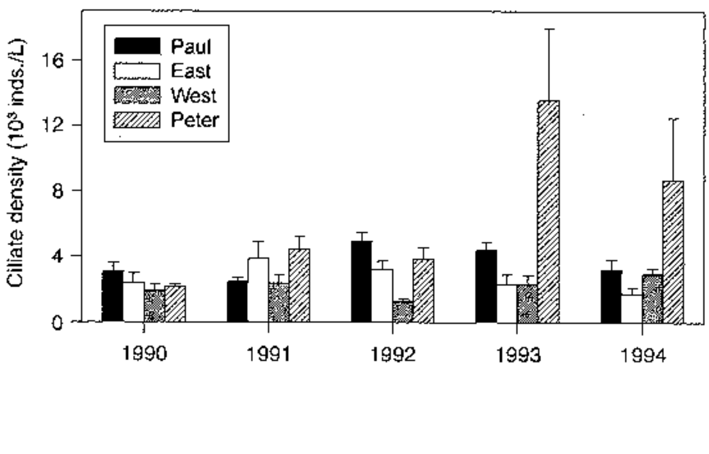

FIG. 2. Annual mean abundance (+1 SE) of epilimnetic ciliates in the reference lake (Paul) and the experimental lakes (East, West, and Peter).

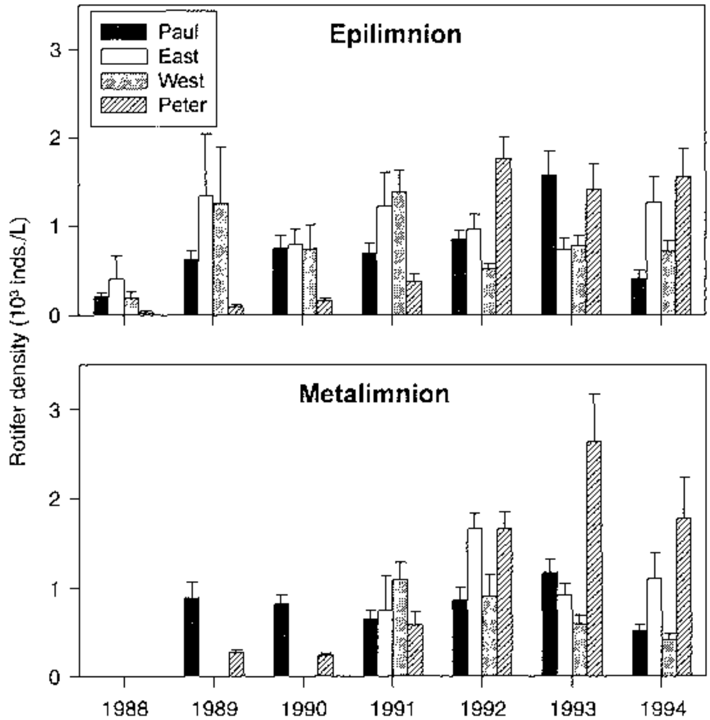

FIG. 3. Annual mean abundance (+1 SE) of epilimnetic and metalimnetic rotifers in the reference lake (Paul) and the experimental lakes (East, West, and Peter).

is consistent with fertilization and low abundances of *Daphnia*. Flagellate abundances, however, were not clearly related either to fertilization or to changes in *Daphnia* (Fig. 2).

Ciliate abundances were related to the presence or absence of *Daphnia* resulting from the experimental manipulations. Ciliates increased during 1993 in Peter Lake, a system where *Daphnia* abundance was low except for late 1994 (Table 2). Ciliates did not increase in East or West Long lakes where *Daphnia* was abundant during the fertilization years (Table 2). The relationship between *Daphnia* and ciliates can be further illustrated by examining dynamics in East Long Lake in 1993 and Peter Lake in 1994 (Fig. 4). In East Long Lake abundances of ciliates were relatively high in May when *Daphnia* densities were low but declined as *Daphnia* increased (Fig. 4a). Ciliate densities remained below 2000 individuals/L for the remainder of the sampling period while *Daphnia* abundances typically exceeded 15 individuals/L (Fig. 4a). In Peter Lake there was a marked increase of ciliates to a peak of 66 000 individuals/L in late June and then a rapid decline. After the decline, ciliates remained at lower abundances while the *Daphnia* population increased exponentially (Fig. 4b). The dynamics of *Daphnia* and ciliates for these two lake years indicate that ciliates probably cannot exceed abundances of 5000 individuals/L when *Daphnia* densities are in the range of 10–100 individuals/L.

Rotifers were also related to the abundance of *Daphnia*. Rotifers did not increase in either East or West Long lakes with fertilization (Fig. 3). Changes in rotifer abundance in Peter Lake were associated with the absence of *Daphnia* beginning in 1991 (Fig. 3). Further evidence of a negative effect of *Daphnia* on rotifers in Peter Lake is provided by the outbreak of *Daphnia* observed in the second half of 1994. Rotifers declined in both the epilimnion and metalimnion to <1000 individuals/L as *Daphnia* increased from <1 to >100 individuals/L (Fig. 5).

Were microzooplankton dynamics determined by resources and by crustacean zooplankton?

Phosphorus additions were immediately incorporated by the plankton in the fertilized lakes and phosphate never accumulated indicating phosphorus remained a limiting nutrient during the experiments (Carpenter et al. 1996). Phosphorus loading, therefore, served as an index of resource availability.

Previous analyses have also indicated that crustacean size is an index of grazing on phytoplankton that is independent of the changes in zooplankton biomass that accompany higher nutrient loading (Carpenter and Kitchell 1993). Here, we also use crustacean size as a measure of effects on the microzooplankton based on numerous studies of the effects of crustaceans, particularly *Daphnia*, on flagellates, ciliates, and rotifers (see *Introduction*). Crustacean zooplankton may negatively

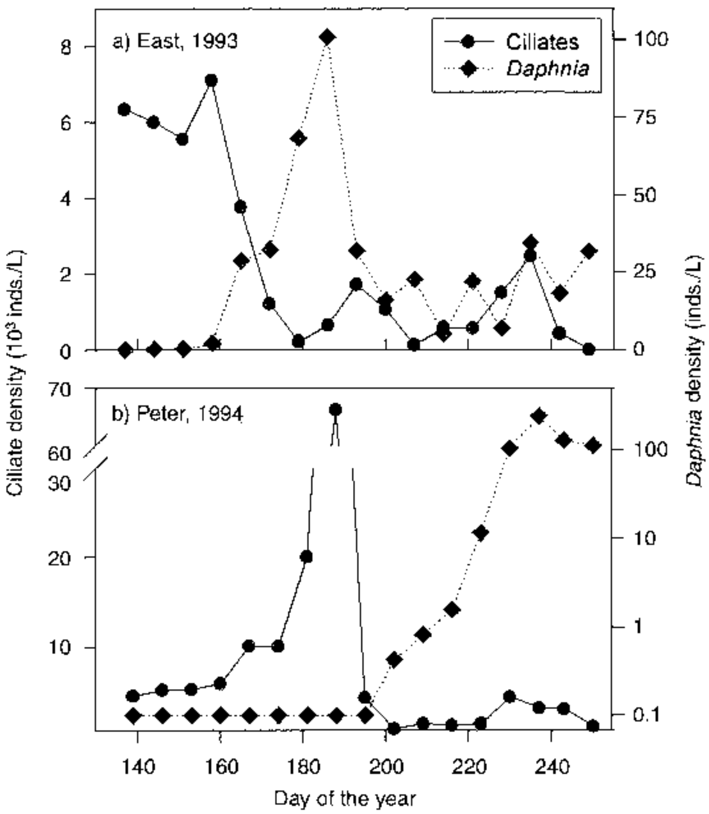

FIG. 4. Weekly dynamics of ciliates and *Daphnia* in East (1993) and Peter (1994) lakes.

affect microzooplankton in three ways: direct predation, mortality resulting when microzooplankton contact crustacean feeding structures but are not ingested, and exploitative competition for food (Gilbert 1988*a*). Our analyses of dynamics do not distinguish among these processes, and so we refer below to negative crustacean and/or *Daphnia* effects as suppression.

The range of crustacean sizes among the experi-

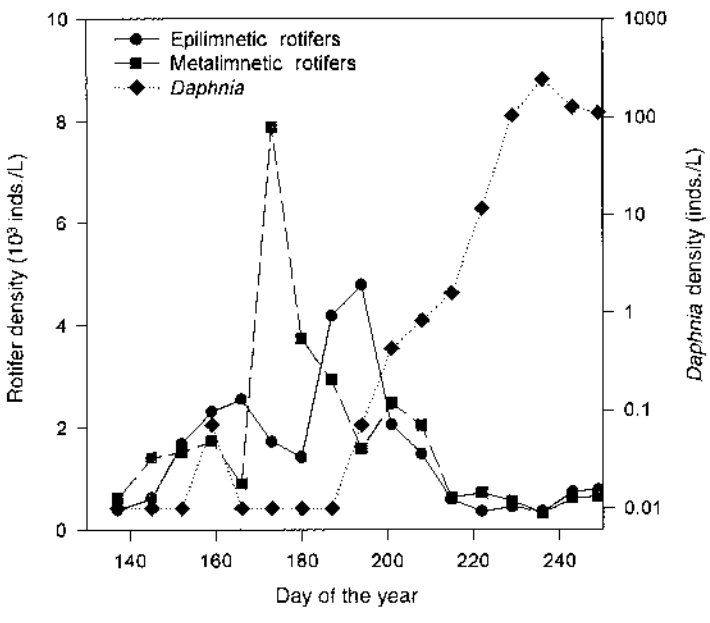

FIG. 5. Weekly dynamics of rotifers and *Daphnia* in Peter Lake during 1994.

TABLE 4. Time series models for flagellate, ciliate, and rotifer abundance as in Eq. 1. Average crustacean zooplankton size (B_2) was the predictor variable. The effect of serial correlation for the microzooplankton response series is denoted by B_s. For each model the parameter estimates with standard deviations, approximate t values, lags, and standard deviations of the residuals (s) are shown.

Group	Depth	B_2	1 SD	t	Lag	B_s	1 SD	t	Lag	s
Flagellates	Epi	−0.236	0.136	−1.74	0	0.647	0.067	9.72	1	0.283
	Meta	−0.301	0.126	−2.38	0	0.662	0.066	10.07	1	0.265
Ciliates	Epi	−0.550	0.138	−3.98	0	0.776	0.040	19.42	1	0.364
Rotifers	Epi	−0.315	0.143	−2.19	3	0.186	0.062	3.00	3	0.353
	Meta	−0.343	0.152	−2.26	0	0.178	0.061	2.91	1	0.359

Note: An absolute t value > 1.96 is significant at $P < 0.05$.

mental lakes reflected the food web manipulations as primarily shown by the abundance and dynamics of *Daphnia*. Crustaceans were small (mean <0.4 mm) in Peter Lake except in late 1994. Mean annual sizes ranged from 0.260 to 0.352 mm for 1991–1993, and were 0.339 mm in the first half of 1994 but increased to 0.572 mm with the large increase in *Daphnia* (Table 2). Mean sizes were relatively small in East Long Lake during the first year (0.363 mm), but *Daphnia* dominated in subsequent years with consequent increases in mean size (range of annual means: 0.629–0.956 mm). West Long Lake also was dominated by large crustaceans, with annual mean sizes ranging from 0.470 to 0.660 mm.

Phosphorus loading was unrelated to the temporal variation of the microzooplankton groups. Coefficients for phosphorus loading (B_1) in the joint time series models all had associated t values <1.96 and hence were not significant by our criteria (analyses not shown). Furthermore, cross-correlations between phosphorus loading and microzooplankton at lags 0, 1, 2, and 3 were either not significantly greater than zero or

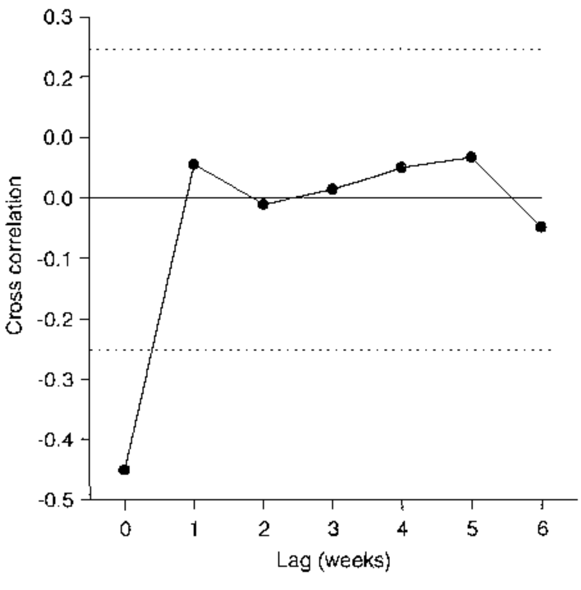

FIG. 6. Cross correlations at differing lags between time series of ciliates and *Daphnia* in East Long Lake (1991–1994).

were negative, with two exceptions (positive cross-correlations at lag 1 for ciliates, lag 2 for epilimnetic flagellates).

Crustacean size was significantly related to microzooplankton dynamics, with the exception of epilimnetic flagellates (Table 4). The models were consistent for the five cases (Table 4) and explained a substantial amount of the temporal variation for ciliates (predicted vs. observed: $r = 0.52$, $P < 0.0001$) and rotifers (epilimnetic, $r = 0.71$, $P < 0.0001$; metalimnetic, $r = 0.70$, $P < 0.0001$). Model fits for flagellates were significant, but residual variation was high (epilimnetic $r = 0.41$, $P < 0.0001$; metalimnetic $r = 0.36$, $P < 0.0001$). Overall, these models indicate that week-to-week increases in zooplankton size were associated with decreases in the abundance of flagellates, ciliates, and rotifers.

Changes in crustacean size had an immediate effect on metalimnetic flagellates, ciliates, and metalimnetic rotifers (lags = 0). There was, however, a 3-wk lag between changes in crustacean size and rotifer abundance (Table 4). We cannot explain this lag, but one possibility is that large crustaceans reduce food available to rotifers, causing lagged declines in abundance. Overall, the dynamics of microzooplankton appear to be primarily regulated by the suppressive effects of larger crustacean zooplankton (i.e., *Daphnia*).

To further explore this conclusion, we considered chlorophyll and *Daphnia* biomass as potential covariates with microzooplankton dynamics. Differenced time series were filtered to remove autocorrelation, and cross-correlations were calculated. Cross-correlations with magnitude $>2/n^{0.5}$ are considered different from zero (Chatfield 1989). Fig. 6 is a representative cross-correlation function for ciliates and *Daphnia* biomass in East Long Lake. Note the strong negative cross-correlation at lag zero, indicating that increases in *Daphnia* biomass were associated with declines in ciliates and that correlations with *Daphnia* biomass lagged 1–6 wk were near zero. Fig. 7 summarizes lag zero cross-correlations for epilimnetic flagellates, ciliates, and rotifers with the covariates chlorophyll and *Daphnia* biomass. Similar patterns were observed for metalimnetic flagellates and rotifers (data not shown). Note that 9 of the 12 possible correlations with chlorophyll were positive, but only three were significant—flagellates in East and West Long lakes and ciliates in

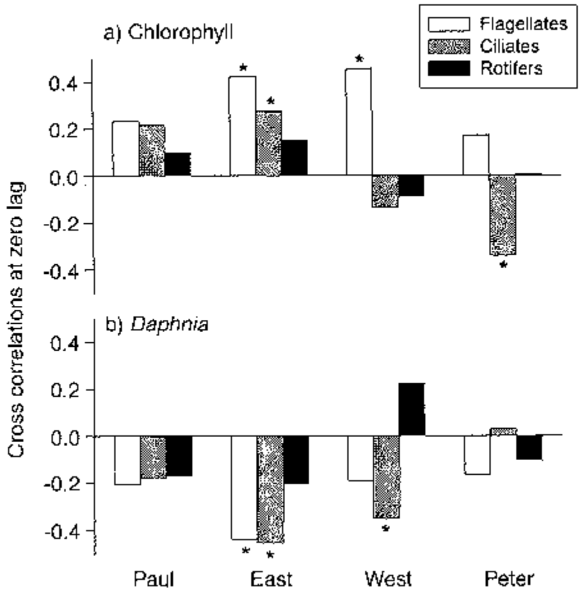

FIG. 7. Cross correlations at zero lag between time series of chlorophyll or *Daphnia* and microzooplankton in each lake for the period 1991–1994. Asterisks denote correlations significantly ($P < 0.05$) greater than zero.

East Long Lake (Fig. 7). The significant negative correlation between ciliates and chlorophyll in Peter Lake suggests that ciliates might have become important grazers in this system (Fig. 7).

Correlations between microzooplankton and *Daphnia* biomass were negative in 10 of 12 cases, but only 3 were significant. These significant negative correlations were observed in East Long Lake for flagellates and ciliates and in West Long Lake for ciliates. There was also a significant negative correlation between rotifers and *Daphnia* in West Long Lake at lag 1 ($r = -0.341$).

We also fit time series models combining data from all lakes using chlorophyll and *Daphnia* biomass as predictor variables, following Eq. 1. In all but one case, the best models were based only on *Daphnia* biomass at zero lag (Table 5). For epilimnetic flagellates, a joint model including chlorophyll and *Daphnia* provided the best fit. For this model, flagellates (F) at time t were related to chlorophyll (C) and *Daphnia* biomass (D) as follows:

$$F(t) = 0.001 + 0.676F(t - 1) + 0.280C(t) - 0.070D(t) \quad (2)$$

where t ratios associated with the coefficients for chlorophyll and *Daphnia* were 3.40 and -3.11 respectively. Thus, only for epilimnetic flagellates were both resources and the suppressive effects of zooplankton, as represented by chlorophyll and *Daphnia*, respectively, the best predictors of dynamics. In agreement with the models based on zooplankton size (Table 4), microzooplankton dynamics for all other cases were negatively correlated with changes in *Daphnia* biomass, and models based on the differenced *Daphnia* biomass time series provided the best fits for dynamics (Table 5).

DISCUSSION

Evaluation of predictions

We predicted that all microzooplankton groups would increase with fertilization in the three experimental lakes but that increases would be lower in lakes with *Daphnia*. While there was a trend of increasing abundance of flagellates from 1988 to 1994 in the experimental lakes, these increases were not significantly different from changes observed in the unfertilized reference lake, with the exception of metalimnetic flagellates in Peter Lake. Ciliates and rotifers only increased in Peter Lake where *Daphnia* density was generally low. In the case of rotifers in Peter Lake, increases appeared to precede fertilization and to coincide with the removal of *Daphnia* in 1991.

The average size of crustaceans, which was also related to *Daphnia* biomass, had a strong effect on the responses of all the microzooplankton groups, in agreement with the idea that *Daphnia* would be important in determining responses. The magnitude of the suppression of microzooplankton, however, was greater than predicted given the 2–6 fold increases in phytoplankton biomass that resulted from lake fertilization (Table 2).

We also predicted that microzooplankton dynamics would be correlated with metrics of both resource availability and crustacean zooplankton suppression. This was only true for epilimnetic flagellates, where the best time series model included chlorophyll and *Daphnia* biomass. In all other cases, dynamics were best explained by models based on zooplankton size or *Daphnia* biomass. Models based on size and biomass were nearly equivalent in predictive power and especially in the case of rotifers, they explained a substantial amount of the temporal variation ($r = 0.7$ for predicted vs. observed variation in all cases). Microzooplankton depend on a variety of resources, which are not perfectly

TABLE 5. Time series models for flagellate, ciliate, and rotifer abundance, as in Eq. 1. *Daphnia* biomass (B_{Daph}) was the predictor variable. Other statistics are as in Table 4.

Group	Depth	B_{Daph}	1 SD	t	B_s	1 SD	t	Lag	s
Flagellate	Meta	−0.085	0.022	−3.81	0.619	0.068	9.05	1	0.257
Ciliates	Epi	−0.141	0.026	−5.44	0.747	0.043	17.27	1	0.354
Rotifers	Epi	−0.077	0.030	−2.56	0.241	0.061	3.49	3	0.352
Rotifers	Meta	−0.055	0.032	−1.74	0.188	0.061	3.07	1	0.360

represented by either phosphorus loading or chlorophyll. Nevertheless, these two variables are strong indicators of overall lake productivity, correlated with microzooplankton abundance in among-lake comparisons, and should be indicative of the actual food available to these organisms. We conclude that regulation of microzooplankton by *Daphnia* was very strong while resource regulation was weak.

In summary, the prediction that *Daphnia* would limit increases was supported, with the caveat that the limitation was even stronger than expected. Fertilization in East and West Long lakes resulted in increased *Daphnia* biomass and consequently in suppression of microzooplankton sufficient to prevent *any* net increases. We initially projected that an increase in microzooplankton would occur in these lakes but that the increase would be substantially lower than in the low-*Daphnia* fertilized lake (Peter Lake). Thus, the microzooplankton and *Daphnia* did not have a linear response to the fertilization, indicating that our predictions in aggregate were too simplistic, and illustrating the complexity of predicting food web responses.

Flagellate responses

One of the most surprising results was the lack of an increase in flagellates in any of the fertilized lakes. Flagellate abundance typically increases with increases in bacteria, based on data from a variety of pelagic systems (Sanders et al. 1992, Gasol 1994). Further, bacterial abundance and production are positively correlated with primary production and phytoplankton biomass (Bird and Kalff 1984, Cole et al. 1988). In the experimental lakes, bacterial productivity increased with fertilization, but abundance did not (Pace and Cole 1996). Flagellates may have partially consumed the increased bacterial production, although in lakes dominated by *Daphnia* we have calculated that most of the increase in bacterial production was consumed by this cladoceran (Pace and Cole 1996).

Standing stocks and estimated feeding rates of potential flagellate predators also suggest that mortality was high. Large *Daphnia* graze on heterotrophic flagellates in the 1–10 μm size range at rates of ~1 $mL \cdot animal^{-1} \cdot h^{-1}$ (Sanders et al. 1994, Jürgen 1994). In East and West Long lakes, average *Daphnia* densities (Table 2) were sufficient to clear 0.4–0.8 $L \cdot L^{-1} \cdot d^{-1}$. These indirect estimates of feeding agree well with the flagellate mortalities of 0.5–1 d^{-1} we have previously measured for communities with average *Daphnia* sizes of 1 mm and above (Pace and Vaqué 1994). Even in Peter Lake when *Daphnia* was at low abundance, increases in flagellates may have been inhibited by alternative predators such as ciliates, rotifers, and small-bodied cladocerans, which are all effective flagellate consumers (Weisse 1991, Sanders et al. 1994). For example, using the average abundance of ciliates and rotifers in Peter Lake during 1993 and assuming filtering rates on flagellates of 0.05 and 0.005 $mL \cdot organism^{-1} \cdot h^{-1}$, respectively (Sanders et al. 1994), ciliates and rotifers in combination could have cleared the epilimnion of flagellates three times per day. These clearance rates exceed flagellate growth rates reported for in situ conditions on the order of 0.1–1 d^{-1} (e.g., Sherr et al. 1984, Pace and Vaqué 1994) and are comparable to maximum rates of 2–4 d^{-1} typically measured in cultures (Sherr and Sherr 1994).

Predation was apparently high, limiting the potential for a net increase in flagellates. However, in prior experiments, flagellates in field enclosures without *Daphnia* increased in abundance relative to enclosures containing *Daphnia* (Riemann 1985, Christoffersen et al. 1993, Pace and Funke 1991). Extrapolation from these enclosure experiments did not predict the responses of flagellates in our experiments. Instead, in the whole-lake experiments, predation by a variety of consumers appeared sufficient to limit flagellate populations. These results agree with measurements in Lake Constance by Weisse (1991), indicating that rotifer and ciliate consumption limits flagellates during much of the year. Flagellate abundances are typically constrained within an order of magnitude. For the lakes studied here, despite the large changes in primary production, 90% of the observations were in about a five-fold range ($6.6–34 \times 10^5$ and $7.4–32 \times 10^5$ cells/L for epi- and metalimnetic flagellates, respectively). Our results suggest that heterotrophic flagellate densities vary in a rather narrow range because of tight constraints imposed by a suite of predators.

Daphnia *effects on ciliates and rotifers*

As with flagellates, the net responses of ciliates and rotifers represent the balance between population growth and mortality. Differences in the annual means, patterns of abundance within years (i.e., Figs. 4 and 5), and the time series models strongly implicate *Daphnia* as limiting ciliates and rotifers in the whole-lake experiments. In Peter Lake ciliates increased in mean abundance four-fold with fertilization in 1993. Similarly, rotifers became much more abundant in Peter Lake after the removal of *Daphnia*. For example, epilimnetic rotifers were on average eight times more abundant during 1991–1992 than in the prior two years and were 12 times more abundant when the lakes were fertilized (1993–1994). In the experimental lakes where *Daphnia* dominated zooplankton biomass (East and West Long), neither ciliates nor rotifers increased in abundance.

Was mortality due to either direct consumption or damage by *Daphnia* sufficient to account for the responses of rotifers and ciliates in the high-*Daphnia* systems? Filtration rates by *Daphnia pulex* feeding on planktonic ciliates are ~15 $mL \cdot animal^{-1} \cdot d^{-1}$ (Jack and Gilbert 1993). These rates imply specific mortalities of 0.2–0.5 d^{-1} for ciliates in East Long Lake at the average *Daphnia* densities observed in 1993 and 1994. These estimates also agree well with direct measures of ciliate mortality in the range of 0.2–0.6 d^{-1} for communities with average *Daphnia* sizes of 1 mm and above (Pace and Vaqué 1994). Maximum ciliate growth rates are on the order of 1–3 d^{-1} (Sherr and Sherr 1994), but realized growth rates are typically lower (0.1–1 d^{-1}) and in the range of mortality due to *Daphnia*. These rates suggest, but do not prove, that the primary effect of *Daphnia* on ciliates was via consumption or feeding-induced mortality rather than by exploitative competition.

Daphnia may have also caused considerable mortality in rotifers. *Daphnia pulex* densities as low as 5 animals/L can result in mortalities comparable to maximum growth rates in rotifers such as *Keratella cochlearis* (Gilbert 1988*b*). Again, estimates of mortality based on these feeding rates agree well with direct measures of rotifer mortality in the range of 0.05–0.5 d^{-1} for communities with average *Daphnia* sizes of 1 mm and above (Pace and Vaqué 1994). Rotifers, however, are most strongly affected by largest-bodied *Daphnia* (individuals in the 1.5–2 mm size range). There were *Daphnia* of this size in the experimental lakes, and it is likely that they exerted significant mortality on some of the most susceptible populations, but it is not possible to infer that community-level effects were determined primarily by mortality. Further, in some cases, the time series analyses indicate that the negative effects of *Daphnia* on rotifers were lagged (e.g., West Long), which is more consistent with the possibility that *Daphnia* was limiting rotifers by suppressing their resources over time rather than by the more immediate effects of direct mortality.

Compensatory responses within microzooplankton communities

In this study we have considered responses of microzooplankton groups based on taxonomic affiliations that are also related to size. Within groups, however, species replacements might compensate for limitations imposed by predators. For example, species resistant to *Daphnia* predation might replace more susceptible species so that flagellates, ciliates, or rotifers in aggregate would increase with fertilization, even in lakes with abundant *Daphnia*. The capacity for such compensatory changes varies among the three groups.

Because the heterotrophic flagellates are dominated by small cells (<10 μm), there is probably little potential for shifts to species resistant to predation. One possibility is that species with high growth rates might be favored when predation is intense. However, little is know about differential growth rates among flagellates, and flagellate species cannot be identified with conventional counting techniques.

Some ciliates have escape mechanisms that may reduce predation, and larger ciliates also experience lower predation rates (Jack and Gilbert 1993). Defensive mechanisms of ciliates seem to be less effective against larger cladocerans like *Daphnia pulex* and *D. rosea*, which dominated the experimental lakes, suggesting that the potential for compensatory changes within this community was low. Throughout the study, ciliate communities in all lakes were numerically dominated by oligotrichs. Average total abundance during 1990–1994 ranged from 80 to 90% in the reference lake (Paul) and from 57 to 85%, 61 to 89%, and 57 to 85% in the experimental lakes (East Long, West Long, and Peter, respectively). There were no obvious trends in the changes in abundance among years related to the experiments. Ciliates were also primarily in the 20–40 μm size range, and we did not observe shifts to dominance by larger species.

The rotifer community probably has the greatest potential to undergo changes to species either resistant to, or alternatively, relatively undefended against predators. Rotifer spines, loricas, and escape behaviors all confer protection against cladocerans, and some rotifers are invulnerable due to their large size (Gilbert 1988*a*). A full analysis of the changes in the rotifer community is beyond the scope of this paper. Nevertheless, the dominant rotifers we observed before the manipulations were typically species of *Keratella, Polyarthra, Conochilus,* and *Trichocerca*. All of these species are variously defended against predators. These rotifers remained among the dominant species in all lakes throughout the experiment. In addition, we observed increases in the predatory rotifer, *Asplanchna* sp., whose biomass became dominant in the zooplankton community in some cases when *Daphnia* biomass was low. We did not, however, observe strong shifts in the rotifer community toward species that were relatively undefended (e.g., *Synchaeta* spp.) in Peter Lake when *Daphnia* was at low abundance. It is likely that defended rotifers were still favored in Peter Lake because they remained exposed to other potential predators such as copepods.

Trophic cascades and microzooplankton

Trophic cascades are significant but also variable features of lake food webs, driven by predator-prey interactions among fishes and between fishes and zooplankton. While cascades are often viewed as occurring among trophic levels, microzooplankton and *Daphnia* occupy the same trophic level in the sense that both consume the same food resources. Trophic cascades, thus, are more accurately viewed as predation that influences the dynamics and biomass of size-based trophic groups within ecosystems. Trophic cascades not only move down food chains but also sideways.

We used *Daphnia* as an indicator of the result of trophic cascades in this study, which is reasonable in the case of Peter and West Long lakes, where planktivores and piscivores dominated, respectively. In East Long Lake all fish populations declined during the experiment (see *Study sites*, above), resulting in extremely low planktivory and, correspondingly, in an increase of *Daphnia*. From this perspective, East Long Lake behaved like a piscivore-dominated system.

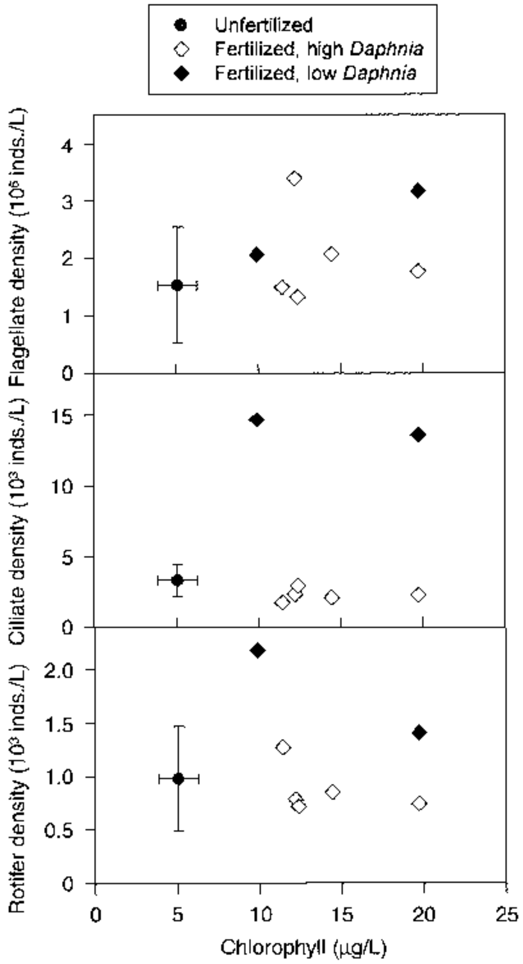

FIG. 8. Mean abundances of epilimnetic microzooplankton and chlorophyll. Solid circles are the means (±1 SD) of annual abundance for all unfertilized lake-years (Paul, 1991–1994; East, West, Peter, 1991–1992). Open diamonds are fertilized lakes with high *Daphnia* densities, including East Long (1993–1994), West Long (1993–1994), and Peter (second half of 1994; see Table 2). Closed diamonds are fertilized lakes with low *Daphnia* densities (Peter 1993 and first half of 1994, see Table 2).

Trophic cascades may extend from the largest to smallest organisms, but are generally truncated at some level by compensatory interactions that dampen predator-prey effects (Hunter and Price 1992, Strong 1992). Even in lakes, complex food web interactions mediated by increases in previously rare species as well as shifts in species interactions within trophic guilds may limit cascading effects (Mazumder et al. 1992, Elser et al. 1995). Within the microzooplankton community studied here, different net outcomes were observed that reflect strong, modest, and dampened effects of cascading trophic interactions. Fig. 8 illustrates the net response of flagellates, ciliates, and rotifers in the three experimental lakes during the two fertilization years (1993 and 1994), along with averages for all lakes prior to fertilization. Data for Peter Lake in 1994 were split into high and low *Daphnia* periods following Table 1. The net response of flagellates was not determined primarily by a trophic cascade mediated by *Daphnia*, because average flagellate abundances were independent of *Daphnia* density in the fertilization years (Fig. 8a). Flagellates are limited by a suite of predators, so trophic cascades associated with *Daphnia* appear to simply result in replacement of one set of predators by another. In contrast, ciliates show a strong effect of the trophic cascade. Abundances were three-fold greater in the fertilized, low-*Daphnia* lake. At high *Daphnia* densities, ciliate abundances were similar to the unfertilized condition despite large increases in chlorophyll (Fig. 8b). *Daphnia* was clearly able to suppress ciliates. Rotifers were also on average more abundant in fertilized lakes with low *Daphnia* (Fig. 8c), but the effect of *Daphnia* was more modest. Responses of rotifer communities are likely more variable because of the variety of species and potential responses (Gilbert 1988*a*, *b*). Nevertheless, even within this community, the potential for compensatory changes to alleviate the strong effects of *Daphnia* was limited.

Trophic cascades suppressed two of the three groups of microzooplankton. Direct suppression is possible in lake plankton because *Daphnia* feeds on a wide range of organisms and thereby focuses food web productivity on itself (Pace et al. 1990). This dominance of consumption is a characteristic of systems evidencing strong cascades (Strong 1992). Net responses of the third group (flagellates) were most likely stabilized by alternative predators such as ciliates and rotifers in Peter Lake. This evidence for the equivalence of predators represents a form of indirect compensation (Lawton and Brown 1993, Frost et al. 1995). Indirect compensation through the mechanism of alternative predators may be a common feature of food webs and could be especially important for microorganisms where the potential for functional compensation at both the predator and prey level is likely to be high.

Conclusions

In summary, *Daphnia* has the potential to completely prevent increases in the abundance of microzooplankton when lakes are eutrophied. Predicting either the dynamics or average biomass of microzooplankton requires data on both primary productivity and zooplankton community structure.

Because trophic cascades are variable, predicting the outcome of food web changes will be, at best, difficult and highly probabilistic. Even in the well-studied plankton communities considered here, our qualitative predictions were too simplistic. Trophic cascades differentially affected the microzooplankton. The potential for community-level responses may alternatively dampen or enhance the impacts of trophic cascades in food webs. The potential for community-level change may not be well assessed either in short term experiments or in ecosystem comparisons. Identifying the key indicators of trophic cascades, such as *Daphnia,* and the key groups most strongly affected, such as ciliates and rotifers, is an essential step toward describing the models to predict the conditions promoting, and consequences of, trophic cascades.

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Literature Cited

Abrams, P. A., B. A. Menge, G. G. Mittelbach, D. A. Spiller, and P. Yodzis. 1996. The role of indirect effects in food webs. Pages 371–395 *in* G. A. Polis and K. O. Winemiller, editors. Food webs: integration of patterns and dynamics. Chapman and Hall, New York, New York, USA.

Bird, D. F., and J. Kalff. 1984. Empirical relationships between bacterial abundance and chlorophyll concentration in fresh and marine waters. Canadian Journal of Fisheries and Aquatic Sciences **41**:1015–1023.

Brown, J. H., D. W. Davidson, J. C. Munger, and R. S. Inouye. 1986. Experimental community ecology: the desert granivore system. Pages 41–62 *in* J. Diamond and T. J. Case, editors. Community ecology. Harper and Row, New York, New York, USA.

Burns, C. W., and M. Schallenberg. 1996. Relative impacts of copepods, cladocerans, and nutrients on the microbial food web of a mesotrophic lake. Journal of Plankton Research **18**:683–714.

Carpenter, S. R., D. L. Christensen, J. J. Cole, K. L. Cottingham, X. He, J. R. Hodgson, J. F. Kitchell, S. E. Knight, M. L. Pace, D. M. Post, D. E. Schindler, and N. Voichek. 1995. Biological control of eutrophication in lakes. Environmental Science and Technology **29**:784–786.

Carpenter, S. R., T. M. Frost, D. Heisey, and T. K. Kratz. 1989. Randomized intervention analysis and the interpretation of whole ecosystem experiments. Ecology **70**:1142–1152.

Carpenter S. R., and J. F. Kitchell, editors. 1993. The trophic cascade in lakes. Cambridge University Press, Cambridge, UK.

Carpenter, S. R., J. F. Kitchell, K. L. Cottingham, D. E. Schindler, D. L. Christensen, D. M. Post, and N. Voichek. 1996. Chlorophyll variability, nutrient input and grazing: evidence from whole-lake experiments. Ecology **77**:725–735.

Carpenter, S. R., J. F. Kitchell, and J. R. Hodgson. 1985. Cascading trophic interactions and lake productivity. BioScience **35**:634–639.

Chatfield, C. 1989. The analysis of time series. Chapman and Hall, New York, New York, USA.

Christensen, D. L., S. R. Carpenter, K. L. Cottingham, S. E. Knight, J. P. LeBouton, D. E. Schindler, N. Voichek, J. J. Cole, and M. L. Pace. 1996. Pelagic responses to changes in dissolved organic carbon following division of a seepage lake. Limnology and Oceanography **42**:553–559.

Christoffersen, K., B. Riemann, A. Klysner, and M. Søndergaard. 1993. Potential role of fish predation and natural populations of zooplankton in structuring a plankton community in eutrophic lake water. Limnology and Oceanography **38**:561–573.

Cole, J. J., S. Findlay, and M. L. Pace. 1988. Bacterial production in fresh and saltwater: a cross-system overview. Marine Ecology Progress Series **43**:1–10.

Elser, J. J., C. Luecke, M. T. Brett, and C. R. Goldman. 1995. Effects of food web compensation after manipulation of rainbow trout in an oligotrophic lake. Ecology **76**:52–69.

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. G. Jones and J. H. Lawton, editors. Linking species and ecosystems. Chapman and Hall, New York, New York, USA.

Gasol, J. M. 1994. A framework for the assessment of top-down vs. bottom-up control of heterotrophic nanoflagellate abundance. Marine Ecology Progress Series **113**:291–300.

Gasol, J. M., and J. Kalff. 1995. Patterns in the top-down versus bottom-up regulation of heterotrophic nanoflagellates in temperate lakes. Journal of Plankton Research **17**:1879–1903.

Gasol, J. M., and D. Vaqué. 1993. Lack of coupling between heterotrophic nanoflagellates and bacteria: a general phenomenon across aquatic systems? Limnology and Oceanography **38**:657–665.

Gilbert, J. J. 1988*a*. Suppression of rotifer populations by *Daphnia*: A review of the evidence, the mechanisms, and the effects on zooplankton community structure. Limnology and Oceanography **33**:1286–1303.

———. 1988*b*. Susceptibilities of ten rotifer species to interference from *Daphnia pulex*. Ecology **69**:1826–1838.

Güde, H. 1988. Direct and indirect influences of crustacean zooplankton on bacterioplankton of Lake Constance. Hydrobiologia **159**:63–73.

Hunter, M. D., and P. W. Price. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. Ecology **73**:724–732.

Jack, J. D., and J. J. Gilbert. 1993. Susceptibilities of different-sized ciliates to direct suppression by small and large cladocerans. Freshwater Biology **29**:19–29.

Jürgens, K. 1994. The impact of *Daphnia* on microbial food webs—a review. Marine Microbial Food Webs **5**:27–37.

Jürgens, K., J. M. Gasol, R. Massana, and C. Pedrós-Alió. 1994. Control of heterotrophic bacteria and protozoans by *Daphnia pulex* in the epilimnion of Lake Ciso. Archiv für Hydrobiologie **131**:55–78.

Lawton, J. H., and V. K. Brown. 1993. Redundancy in ecosystems. Pages 255–270 *in* E. Detlef-Schulze and H. A. Mooney, editors. Biodiversity and ecosystem function. Springer-Verlag, New York, New York, USA.

Leibold, M. A. 1989. Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. American Naturalist **134**:922–948.

Marchessault, P., and A. Mazumder. *In press.* Grazer and nutrient impacts on epilimnetic ciliate communities. Limnology and Oceanography.

Mazumder, A. 1994. Patterns of algal biomass in dominant odd- vs. even-link lake ecosystems. Ecology **75**:1141–1149.

Mazumder, A., W. D. Taylor, D. R. S. Lean, and D. J. McQueen. 1992. Partitioning and fluxes of phosphorus: mechanisms regulating the size-distribution and biomass of plankton. Archiv für Hydrobiologie, Ergebnisse der Limnologie **35**:121–143.

McCauley, E. 1984. The estimation of the abundance and biomass of zooplankton in samples. Pages 228–265 *in* J. A. Downing and F. H. Rigler, editors. A manual on methods for the assessment of secondary productivity in fresh waters. Blackwell Scientific, Oxford, UK.

Morin, P. J., S. P. Lawler, and E. A. Johnson. 1988. Competition between aquatic insects and vertebrates: experimental measures of interaction strength and higher order interactions. Ecology **69**:1401–1409.

Pace, M. L. 1984. Zooplankton community structure, but not biomass, influences the phosphorus-chlorophyll *a* relationship. Canadian Journal of Fisheries and Aquatic Sciences **41**:1089–1096.

———. 1986. An empirical analysis of zooplankton community structure. Limnology and Oceanography **31**:45–55.

Pace, M. L., and J. J. Cole. 1994. Comparative and experimental approaches to top-down and bottom-up regulation of bacteria. Microbial Ecology **28**:181–193.

Pace, M. L., and J. J. Cole. 1996. Regulation of bacteria by resources and predation tested in whole lake experiments. Limnology and Oceanography **42**:1448–1459.

Pace, M. L., and E. Funke. 1991. Regulation of planktonic microbial communities by nutrients and herbivores. Ecology **72**:904–914.

Pace, M. L., G. B. McManus, and S. E. G. Findlay. 1990. Plankton community structure determines the fate of bacterial production in a temperate lake. Limnology and Oceanography **35**:795–808.

Pace, M. L., and D. Vaqué. 1994. The importance of *Daphnia* in determining mortality rates of protozoans and rotifers in lakes. Limnology and Oceanography **39**:985–996.

Paine, R. T. 1980. Food webs: linkage, interaction strength and community infrastructure. Journal of Animal Ecology **49**:667–685.

Pimm, S. L. 1991. The balance of nature? University of Chicago Press, Chicago, Illinois, USA.

Polis, G. A., R. D. Holt, B. A. Menge, and K. O. Winemiller. 1996. Time, space, and life history: influences on food webs. Pages 435–460 *in* G. A. Polis and K. O. Winemiller, editors. Food webs: integration of patterns and dynamics. Chapman and Hall, New York, New York, USA.

Porter, K. G. 1996. Integrating the microbial loop and the classic food chain into a realistic planktonic food web. Pages 51–59 *in* G. A. Polis and K. O. Winemiller, editors. Food webs: integration of patterns and dynamics. Chapman and Hall, New York, New York, USA.

Riemann, B. 1985. Potential importance of fish predation and zooplankton grazing on natural populations of freshwater bacteria. Applied and Environmental Microbiology **50**:187–193.

Riemann, B., and K. Christoffersen. 1993. Microbial trophodynamics in temperate lakes. Marine Microbial Food Webs **7**:69–100.

Sanders, R. W., D. A. Caron, and U.-G. Berninger. 1992. Relationships between bacteria and heterotrophic nanoplankton in marine and fresh waters: an inter-ecosystem comparison. Marine Ecology Progress Series **86**:1–14.

Sanders, R. W., D. A. Leeper, C. H. King, and K. G. Porter. 1994. Grazing by rotifers and crustacean zooplankton on nanoplanktonic protists. Hydrobiologia **288**:167–181.

SAS Institute. 1988. SAS/ETS user's guide. SAS Institute Incorporated, Cary, North Carolina, USA.

Sherr, E. B., and B. F. Sherr. 1994. Bacterivory and herbivory: key roles of phagotrophic protists in pelagic food webs. Microbial Ecology **28**:223–235.

Sherr, B. F., E. B. Sherr, and S. Y. Newell. 1984. Abundance and productivity of heterotrophic nanoplankton in Georgia coastal waters. Journal of Plankton Research **6**:195–202.

Sih, A. 1987. Predators and prey lifestyles: an evolutionary and ecological overview. Pages 203–224 *in* W. C. Kerfoot and A. Sih, editors. Predation: direct and indirect impacts on aquatic communities. University Press of New England, Hanover, New Hampshire, USA.

Stockner, J. G., and K. G. Porter. 1988. Microbial food webs in freshwater planktonic ecosystems. Pages 69–83 *in* S. R. Carpenter, editor. Complex interactions in lake communities. Springer-Verlag, New York, New York, USA.

Strong, D. R. 1992. Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. Ecology **73**:747–754.

Wei, W. W. S. 1990. Time series analysis. Addison-Wesley, New York, New York, USA.

Weisse, T. 1991. The annual cycle of heterotrophic freshwater nanoflagellates: role of bottom-up and top-down control. Journal of Plankton Research **13**:167–185.

Weisse, T., H. Müller, R. M. Pinto-Coelho, A. Schweizer, D. Springmann, and G. Baldringer. 1990. Response of the microbial loop to the phytoplankton spring bloom in a large prealpine lake. Limnology and Oceanography **35**:781–794.

Wickham, S. A., and J. J. Gilbert. 1991. Relative vulnerabilities of natural rotifer and ciliate communities to cladocerans: laboratory and field experiments. Freshwater Biology **26**:77–86.

Wickham, S. A., and J. J. Gilbert. 1993. The comparative importance of competition and predation by *Daphnia* on ciliated protists. Archiv für Hydrobiologie **126**:289–313.

Wootton, J. T. 1994. Predicting direct and indirect effects: an integrated approach using experiments and path analysis. Ecology **75**:151–165.

Yodzis, P. 1988. The indeterminancy of ecological interactions. Ecology **69**:508–515.