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## LIMNETIC HERBIVORY: EFFECTS ON PHYTOPLANKTON POPULATIONS AND PRIMARY PRODUCTION<sup>1</sup>

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**Abstract.** Population-level and ecosystem-level responses of phytoplankton to grazing by zooplankton were determined in nutrient-enriched and unenriched enclosures in Peter Lake, Michigan. Species-specific net growth rates were determined, and chlorophyll *a*, primary production (PPR), and alkaline phosphatase activity (APA) were determined for each of three size categories of phytoplankton: <22  $\mu\text{m}$ , 22–75  $\mu\text{m}$ , >75  $\mu\text{m}$ . Thirteen of 16 dominant algal taxa were nutrient limited. Zooplankton reduced APA, an indicator of nutrient deficiency. Growth rates of grazed, nutrient-limited algae (<30  $\mu\text{m}$ ) increased at low levels of zooplankton biomass, but decreased at higher biomass levels. Growth rates of larger (>30  $\mu\text{m}$ ) nutrient-limited algae increased or did not change as zooplankton biomass increased. These species-specific responses resulted in four- to fivefold changes in chlorophyll concentration and PPR. Overall, the stimulatory effect of nutrient regeneration by zooplankton overrode losses due to grazing, and caused net increases in phytoplankton biomass and productivity.

**Key words:** algal growth rates; alkaline phosphatase activity; grazing; herbivory; Michigan; nutrient cycling; primary production; size-structure; zooplankton.

### INTRODUCTION

Ecologists disagree about the relevance of population phenomena to ecosystem processes, reflecting the dichotomy between reductionist and holist views in ecology (McIntosh 1985). In phytoplankton ecology, there are two largely distinct bodies of literature, one emphasizing population dynamics and species replacement sequences (e.g., Reynolds 1984), the other emphasizing nutrient cycling and production (e.g., Peterson 1980). Theoretical viewpoints also diverge. O'Neill and Giddings (1979) argue that interactions among phytoplankton species are compensatory and largely irrelevant to primary production. In contrast, Carpenter and Kitchell (1984) present a model of size-structured plankton assemblages that yields large changes in primary production due to interactions at the population level. The key difference between these models is the inclusion by Carpenter and Kitchell (1984) of size-specific growth, nutrient uptake, and grazing.

Zooplankton have at least two counteracting effects on phytoplankton: grazing, which reduces algal standing crop, and nutrient regeneration, which can stimulate algal growth. Therefore, the net response of algae to grazing is not intuitively clear. At the species level, for some taxa standing crops are depressed by grazing, for some they are increased, and for others they are unaffected (Porter 1973, Bergquist et al. 1985, Lehman and Sandgren 1985). Community responses such as chlorophyll *a* concentration and primary productivity in relation to zooplankton abundance have been studied, but with conflicting results. Some experimenters

found that heavy grazing depressed primary production (Andersson et al. 1978, Henrikson et al. 1980, Lynch and Shapiro 1981, Elliott et al. 1983). Other studies detected little or no effect of herbivory on primary productivity (Coveney et al. 1977). Other results showed positive correlations between the density of grazers and chlorophyll *a* concentration (O'Brien and DeNoyelles 1974) or primary productivity (Korstad 1980). The conflicting results suggest that there is a unimodal response of primary productivity to zooplankton grazing. The conflicting data may represent opposite sides of the response curve (Carpenter and Kitchell 1984). The unimodal productivity response has been demonstrated in periphyton (Cooper 1973, Flint and Goldman 1975, Seale 1980, Gregory 1983) and terrestrial grasslands (McNaughton 1979), but has never been shown to occur in planktonic assemblages. Moreover, few grazing studies of lake phytoplankton have monitored both individual species and whole-assemblage responses.

We studied responses of individual species and the phytoplankton assemblage simultaneously to examine the relationships of population responses and primary production. Zooplankton biomass and nutrient levels were manipulated in bags to determine subsequent responses of individual phytoplankton taxa as well as chlorophyll *a* concentration, alkaline phosphatase activity, and carbon fixation rates in three size fractions of algae. We hypothesized that species-specific responses of the algae would correspond to changes in chlorophyll concentration and primary production, consistent with the model of Carpenter and Kitchell (1984). Alternatively, if chlorophyll *a* concentration and primary production remained static despite species-specific responses, the results would lend credence to the view that population dynamics are relatively unimportant in the context of ecosystem phenomena.

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## STUDY SITE

Peter Lake is a kettle-hole lake located at the University of Notre Dame Environmental Research Center in Section 36, T45N R42W, Gogebic County, Michigan. The watershed was logged >70 yr ago and is now forested with northern hardwoods. The lake is relatively deep (mean depth 8 m, maximum depth 19 m) for its surface area (2.4 ha) (Stross 1958). Epilimnetic pH is <7, and surface water alkalinity ranges from 160 to 260  $\mu\text{mol/L}$ . Light intensity is 1% of surface levels at 6–8 m. Peter Lake is infertile. In the epilimnion, total P ranges from 0.2 to 0.6  $\mu\text{mol/L}$ , and total N ranges from 4 to 6.3  $\mu\text{mol/L}$  (concentrations exclude most zooplankton; S. R. Carpenter et al., *personal observation*).

## MATERIALS AND METHODS

Cylindrical 120-L bags composed of 0.15 mm polyethylene floated by bicycle inner tubes were open at the water's surface and closed at the bottom. Twelve bags were anchored  $\approx 3$  m apart in random order in shallow (1.5 m) water. Each bag was filled with 120 L of epilimnetic lake water filtered through a 75- $\mu\text{m}$  mesh Nitex net to remove the majority of grazers. This procedure removed >95% of the zooplankton biomass in all cases, although small numbers of rotifers and copepod nauplii did slip through the net. A smaller mesh size could not be used since the object was not only to remove zooplankters, but also to retain as much as possible of the natural phytoplankton size distribution. The chosen mesh size struck a balance between efficiency of zooplankton removal and the need to include large phytoplankters in the initial algal complement of each enclosure.

Zooplankters to be used in bags were collected and concentrated by vertical hauls of a plankton net (80- $\mu\text{m}$  mesh netting). Tows were made from 12 m since large *Daphnia pulex* were usually found in the hypolimnion. *Chaoborus* spp. were removed from the tows. Zooplankters were acclimated to surface water temperatures overnight. Dead or injured animals (<10% of the total number of cladocerans collected) were removed before the zooplankters were added to the bags.

Ambient zooplankton concentration was determined by sampling with a clear 3.2-L van Dorn bottle at 1.0-m intervals to a depth of 12 m. These samples were filtered through a 75- $\mu\text{m}$  mesh Nitex net, pooled, and counted. Efficiencies for the 80- $\mu\text{m}$  mesh plankton net were calculated from the depth-integrated densities of each species.

The experiment was conducted 3–7 July 1984. Several earlier experiments comparable to this one showed that incubations of 4 d produced significant responses in treatment bags, while bags with ambient zooplankton remained similar to the open lake (Bergquist 1985). Six bags received nutrient additions of 16  $\mu\text{mol/L}$  phosphorus (as  $[\text{NH}_4]_2\text{PO}_4$  and  $\text{KH}_2\text{PO}_4$ ) and 16  $\mu\text{mol/L}$

nitrogen (as  $[\text{NH}_4]_2\text{HPO}_4$  and  $\text{NaNO}_3$ ), which were sufficient to maintain concentrations of at least 1  $\mu\text{mol/L}$  dissolved  $\text{PO}_4\text{-P}$  and 7  $\mu\text{mol/L}$   $\text{NH}_4\text{-N}$  and  $\text{NO}_3\text{-N}$  throughout the experiment (Bergquist 1985). The remaining six bags were not enriched with nutrients. After all experimental bags were in place and filled, zooplankton were added to each set of bags at five densities (0.5 $\times$ , 1 $\times$ , 3 $\times$ , 6 $\times$ , and 9 $\times$  ambient lakewide zooplankton concentration); in addition, there was a control enclosure to which no zooplankton were added. Zooplankton aliquots (dry mass) ranged from 0.326 mg/L (in 0.5 $\times$  bags) to 5.877 mg/L (in 9 $\times$  bags). High zooplankton densities were used to elicit strong, rapid responses from the phytoplankton while minimizing enclosure effects. Five- to 10-fold variations in zooplankton biomass, comparable to variations among the bags, are common in Peter Lake due to patchiness and vertical migration (M. Dini and S. Carpenter, *personal observation*). The bags were stirred daily.

Initial and final water samples from enclosures and from Peter Lake were collected using a clear van Dorn bottle. 300-mL subsamples were preserved with Lugol's solution for phytoplankton counting. Screened (75- $\mu\text{m}$  mesh) samples for determining total phosphorus (TOTP) concentration were quickly frozen. For determining total nitrogen (TOTN) concentration, concentrated sulfuric acid was added to screened samples to bring the pH to below 2 (American Public Health Association 1981). In this study, TOTN and TOTP do not include N and P in particles >75  $\mu\text{m}$ . Zooplankton in enclosures were sampled with a 28-L Schindler-Patalas plankton trap, and preserved with formalin for subsequent counting. Water samples for determining chlorophyll *a* (CHL *a*), concentration, primary productivity (PPR), alkaline phosphatase activity (APA), alkalinity, and pH were collected, screened (125- $\mu\text{m}$  mesh), and briefly held in the dark in closed ice chests until prepared for incubation or returned to the lab for analysis.

TOTN concentration was determined by the micro-Kjeldahl technique using the phenol-hypochlorite ammonia method (Wetzel and Likens 1979). TOTP concentration was determined by the ascorbic acid method following persulfate digestion (American Public Health Association 1981). Alkalinities were determined by the total inflection point method (Gran 1952). Dissolved inorganic carbon (DIC) concentration was calculated from alkalinity and pH data (Wetzel and Likens 1979).

Fluorometric CHL *a* determinations corrected for pheopigments were made after filters (Whatman GF/F) were frozen and homogenized and pigments were extracted in 100% methanol (Strickland and Parsons 1968, Marker et al. 1980). APA was determined fluorometrically in the field laboratory using methylumbelliferyl-phosphate as the substrate (Pettersson 1980). Samples were run at pH 8.5 in Tris-HCl buffer at 0.2 mol/L and 19.5°C. Fluorescence was read at 5- to 10-min intervals for 30 to 45 min. Final concentrations of

methylumbelliferyl-phosphate were saturating (15  $\mu\text{mol/L}$ ). Blanks were run using boiled lake water.

Phytoplankton photosynthesis in duplicate subsamples was determined by the radiocarbon method. DCMU was added to control bottles (Legendre et al. 1983). Bottles (125 mL), each containing 185 kBq of  $\text{NaH}^{14}\text{CO}_3$ , were incubated for 6 h at midday at a depth of 0.75 m. Algae were collected on Whatman GF/F filters for liquid scintillation counting.

Chlorophyll *a* and PPR (for all enclosures), and APA (1  $\times$ , 6  $\times$ , and control enclosures) were determined for three size classes of phytoplankton. These were separated by pouring the samples through a fractionation tower consisting of 75- $\mu\text{m}$  (top) and 22- $\mu\text{m}$  (middle) Nitex mesh nets, and a GF/F glass fiber filter (bottom). For CHL *a* and PPR the plankters retained by the mesh nets were then carefully rinsed onto separate GF/F glass fiber filters. This gave three phytoplankton fractions: L = >75  $\mu\text{m}$ , M = 22–75  $\mu\text{m}$ , and S = <22  $\mu\text{m}$ . Ultraplankton was rare in Peter Lake, and <1% of total CHL *a* could pass through a GF/F glass fiber filter. APA was determined for the same three size fractions and a dissolved (<0.45  $\mu\text{m}$ ) fraction.

Zooplankton were counted in a gridded Petri dish under a dissecting microscope until the standard error was <10% of the mean. Zooplankters were identified to species and their body lengths (exclusive of spines and setae) were measured with an ocular micrometer. Juvenile copepods (nauplii and copepodites) were tabulated separately. Zooplankter biomasses were estimated using the length-to-mass regression of Peters and Downing (1984).

Each phytoplankton sample was allowed to settle and then quantitatively subsampled into Sedgwick-Rafter cells. A minimum of four preparations was examined for each sample. Phytoplankton were identified according to Prescott (1962). All phytoplankton taxa collected with zooplankton tows (e.g., *Micrasterias* sp., *Sphaerocystis Schroeteri*) were excluded from further analyses. Other algal taxa were counted under an inverted microscope until the standard error was <10% of the mean for the sample. The greatest axial linear dimension (GALD) and the shortest axis perpendicular to GALD were also measured.

Net phytoplankton daily growth rates (*g*) for each algal taxon initially present in sufficient numbers for reliable abundance estimates were computed for each enclosure by:

$$g = \ln(N_f/N_i)/\Delta t,$$

where  $N_i$  is initial algal units per millilitre,  $N_f$  is final algal units per millilitre, and  $\Delta t$  is 4 d, the duration of the experiment (Lehman and Sandgren 1985). For each algal taxon, the six enclosures without nutrient additions were used to calculate a linear regression (with 95% confidence intervals) of net algal growth rate vs. the logarithm of zooplankton concentration. Taxa for which the regression of *g* on zooplankton concentration

had a significantly negative slope were considered to have decreased under grazing. Regressions were calculated using a quadratic model when the data suggested a nonlinear response to zooplankton abundance. To determine if an alga was nutrient-limited, net algal growth rates in enriched and unenriched bags were compared by pairwise *t* test. Correlations of other variables with zooplankton biomass were calculated from the enclosures with zooplankton additions.

## RESULTS

### Zooplankton

*Daphnia pulex*, *Holopedium gibberum*, and *Diaptomus oregonensis* dominated the biomass of the zooplankton assemblage (Table 1). Zooplankton survivorship (ratio of final to initial biomass) decreased with increasing zooplankton biomass (Table 1;  $r = -0.929$ ,  $P < .001$ ). Survivorship was generally higher in bags receiving nutrient additions, but not significantly so ( $t = 0.915$ ,  $P > .38$ ). The distribution of biomass among size classes remained similar to initial conditions except for losses in the largest size classes (>1.0 mm). Increased losses with increasing zooplankton density were largely due to high mortality of *Holopedium gibberum*.

### Community responses of phytoplankton

TOTP and TOTN concentrations in particles <75  $\mu\text{m}$  increased significantly with zooplankton concentration in nutrient-enriched bags (TOTP:  $r = 0.972$ ,  $P < .01$ ; TOTN:  $r = 0.915$ ,  $P < .05$ ). Over the full range of zooplankton concentrations, TOTP increased 4% and TOTN increased 10.5%. In unenriched bags, only TOTN increased significantly with increasing zooplankton concentration ( $r = 0.981$ ,  $P < .01$ ), a 20% change over the range of zooplankton additions. Apparently the zooplankton P added to unenriched bags remained in particles >75  $\mu\text{m}$ , which were removed by screening prior to analysis.

In each nutrient-enriched enclosure total CHL *a* concentration was greater than in its corresponding unenriched counterpart (Fig. 1). In both enriched and unenriched bags, CHL *a* concentration was significantly positively correlated with zooplankton concentration (Fig. 1). Ratios of CHL *a* concentration to both TOTP and TOTN concentrations significantly increased with zooplankton biomass concentration in all cases (Fig. 1). The elevation of CHL *a* concentration in enriched control bags was due to increases in edible algae (mainly *Chlamydomonas*, chlorococcales, and *Cryptomonas*) in the S and M (<75  $\mu\text{m}$ ) size classes (see Size-fractionated Responses).

Total APA and total specific APA (i.e., APA per unit CHL *a*) were both significantly lower in enriched than in unenriched enclosures (Fig. 2), indicating that the nutrient enrichments decreased phosphorus limitation. In addition, specific APAs were inversely related to

TABLE 1. Initial and final zooplankton composition and mean body length for bags with 1 × ambient lake zooplankton concentration in the experiment.\*

Taxon	Zooplankton composition				Mean body length (mm)
	Initial		Final		
	(animals/L)	% of inds.	(animals/L)	% of inds.	
<i>Daphnia pulex</i>	13.5	11.7	11.4	9.1	1.64
<i>Daphnia rosea</i>	0.9	0.8	0.7	0.5	1.31
<i>Holopedium gibberum</i>	11.8	10.2	8.8	7.0	1.23
<i>Diaptomus oregonensis</i>	13.3	11.5	12.8	10.2	0.90
<i>Cyclops varicans rubellus</i>	3.3	2.9	3.0	2.4	0.83
Copepodites	15.2	13.2	16.3	13.0	0.61
Nauplii	8.9	7.7	7.0	5.6	0.45
<i>Polyarthra vulgaris</i>	22.8	19.7	36.6	29.1	0.41
<i>Gastropus stylifer</i>	18.3	15.8	20.2	16.1	0.37
<i>Keratella</i> spp.	4.5	3.9	6.7	5.3	0.23
Miscellaneous	3.0	2.6	2.1	1.7	0.73
Total	115.5		125.6		

\* Biomasses of individual zooplankters were estimated using the length-to-mass regression of Peters and Downing (1984). Species biomass was then calculated from density and mean individual biomass.

zooplankton concentration (Fig. 2), indicating a decline in phosphorus limitation as zooplankton biomass increased.

Total PPR increased significantly with zooplankton concentration in unenriched bags, but not in enriched enclosures (Fig. 3). PPR and specific PPR (i.e., PPR per unit CHL *a*) were both higher in enriched bags than in unenriched ones (Fig. 3). However, specific PPR increased significantly with zooplankton concentration in unenriched bags and decreased significantly in enriched bags. Specific PPR was limited by P in unenriched bags, and by grazing in enriched bags. PPR per unit TOTP was higher in unenriched bags and increased with zooplankton concentration, while PPR per unit TOTP in enriched bags remained low and stable (Fig. 3). Similarly, PPR per unit TOTN increased with zooplankton concentration in unenriched bags. In enriched enclosures PPR remained stable and higher than in the unenriched bags (Fig. 3).

#### Size-fractionated responses

Within each size class, CHL *a* responses to zooplankton concentration were similar for the two nutrient treatments (Fig. 4). CHL *a* in fractions M and L significantly increased with increasing zooplankton concentration in all cases (Table 2, Fig. 4). On the other hand, CHL *a* in S fraction phytoplankters was significantly negatively correlated with zooplankton concentration in enriched enclosures (Table 2). In unenriched bags CHL *a* in the S fraction declined steadily after an increase from the 0.5 × to the 1 × enclosure.

For each of the three size fractions, APA was lower in nutrient-enriched bags than in the corresponding unenriched bags, with the exception of fraction M in the control bags (Fig. 5). APA declined with increasing zooplankton concentration in all algal size fractions in the nutrient addition treatment. In the unenriched bags, the APA response was more variable. APA of the dissolved phytoplankton fraction was high compared with

that of other fractions, and appeared to increase with increasing zooplankton concentration in enriched enclosures, but not in unenriched ones (Fig. 5).

Specific APA was clearly lower in enriched than in unenriched enclosures in each algal size fraction (Fig. 5; note different scales). The most striking trend was a decline in specific APA of the L fraction as zooplankton

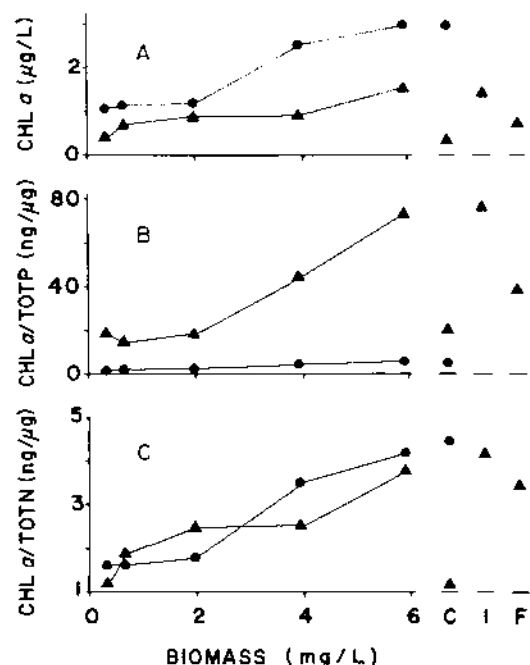


FIG. 1. CHL *a* concentrations versus zooplankton biomass concentration. ● = nutrient-enriched enclosures (N+), ▲ = unenriched enclosures (N-), C = enclosures without zooplankton, I = initial and F = final lake concentrations. (A) CHL *a* (N+,  $r = 0.969$ ,  $P < .01$ ; N-,  $r = 0.940$ ,  $P < .05$ ). (B) CHL *a* total phosphorus (N+,  $r = 0.967$ ,  $P < .01$ ; N-,  $r = 0.965$ ,  $P < .01$ ). (C) CHL *a* total nitrogen (N+,  $r = 0.969$ ,  $P < .01$ ; N-,  $r = 0.928$ ,  $P < .05$ ).

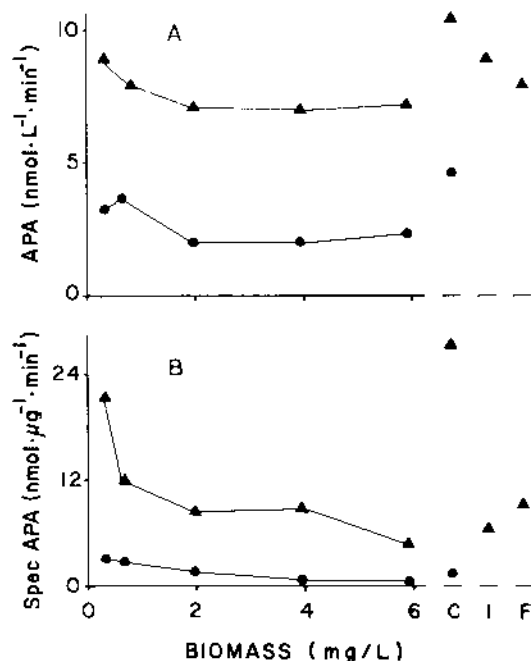


FIG. 2. Alkaline phosphatase activity (APA) and specific APA versus zooplankton biomass concentration. Key as in Fig. 1. (A) APA ( $\text{PO}_4$  flux; N+,  $r = -0.635$ ,  $P > .05$ ; N-,  $r = 0.708$ ,  $P > .05$ ). (B) specific APA ( $\text{PO}_4$  flux per unit chlorophyll  $a$ ; N+,  $r = -0.916$ ,  $P < .05$ ; N-,  $r = -0.923$ ,  $P < .05$ ).

concentration increased. Specific APA was highest in the L fraction in all enclosures, but specific APA in fraction S in control enclosures was also elevated over enclosures with zooplankton.

The PPR trends observed in size-fractionated phytoplankton were similar to those observed for CHL  $a$  (Figs. 4 and 6). PPR of the two larger algal size classes (M and L) increased significantly with zooplankton concentration in both enriched and unenriched treatment bags (Table 2, Fig. 6). PPR was always greater in class M than in L. PPR in the S fraction in enriched bags was inversely proportional to zooplankton concentration (Table 2, Fig. 6). In unenriched bags PPR in the S fraction first increased and then decreased as zooplankton concentration increased. A quadratic regression model for these data was significant ( $R^2 = 0.983$ ,  $P < .017$ ).

Ratios of PPR to CHL  $a$ , TOTP, and TOTN concentrations were more complicated. Specific PPR generally declined with increasing zooplankton concentration in nutrient-enriched bags, and specific PPR was higher for the L than for the M algal fraction (Fig. 7). There were no significant trends of specific PPR with zooplankton concentration in unenriched enclosures (Table 2). Productivity was high in fraction L. PPR per unit TOTP in enriched bags exhibited the same significant trends observed for PPR (Table 2, Figs. 6 and 7). In unenriched bags PPR/TOTP increased with increasing zooplankton concentration in fractions M and

L, but in the S fraction this response was irregular. The trends of PPR/TOTN related to zooplankton concentration were identical to the PPR results for all three algal size classes (Figs. 6 and 7).

#### Species-specific responses

Phytoplankters in Peter Lake were strikingly nutrient limited (Table 3). Over 80% of the most abundant taxa responded significantly to the addition of nitrogen and phosphorus. Two of the three taxa that were not nutrient limited (*Crucigenia quadrata* and *Chlamydomonas*) were small ( $\text{GALD} < 20 \mu\text{m}$ ). It may be that other nanoplankton were not nutrient limited, since it was not always possible to identify specimens to species. However, the growth of microflagellates and nonmotile chlorococcales, as groups, was stimulated by nutrient addition. The third alga not limited by nutrients was a heterocystous cyanophyte, *Anabaena circinalis*. The data on this phytoplankter were equivocal. *A. circinalis* increased in enriched enclosures with very high zooplankton concentrations and also in the enriched control enclosures.

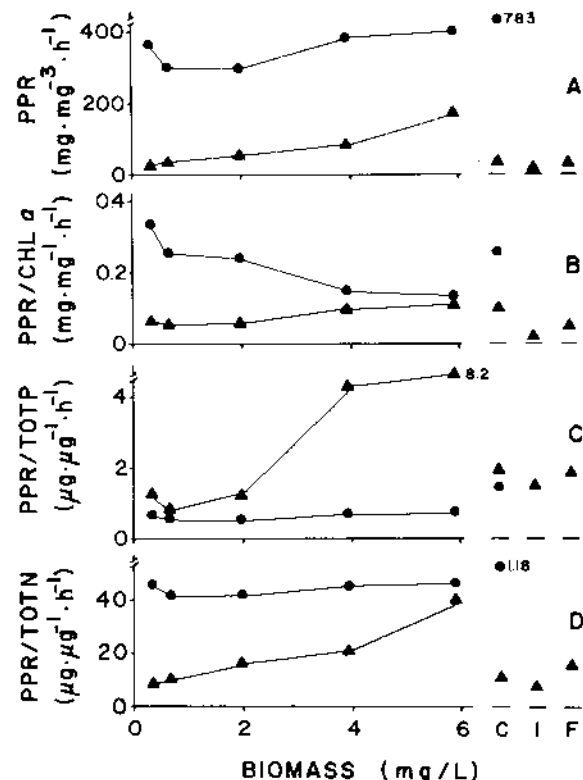


FIG. 3. Primary productivity measured as carbon (PPR) relationships with zooplankton biomass concentration. Key as in Fig. 1. (A) PPR (N+,  $r = 0.724$ ,  $P > .05$ ; N-,  $r = 0.966$ ,  $P < .01$ ). (B) specific PPR (PPR per unit chlorophyll  $a$ ; N+,  $r = -0.935$ ,  $P < .05$ ; N-,  $r = 0.960$ ,  $P = .01$ ). (C) PPR total phosphorus (N+,  $r = 0.648$ ,  $P > .05$ ; N-,  $r = 0.959$ ,  $P < .05$ ). (D) PPR total nitrogen (N+,  $r = 0.493$ ,  $P > .05$ ; N-,  $r = 0.973$ ,  $P < .01$ ).

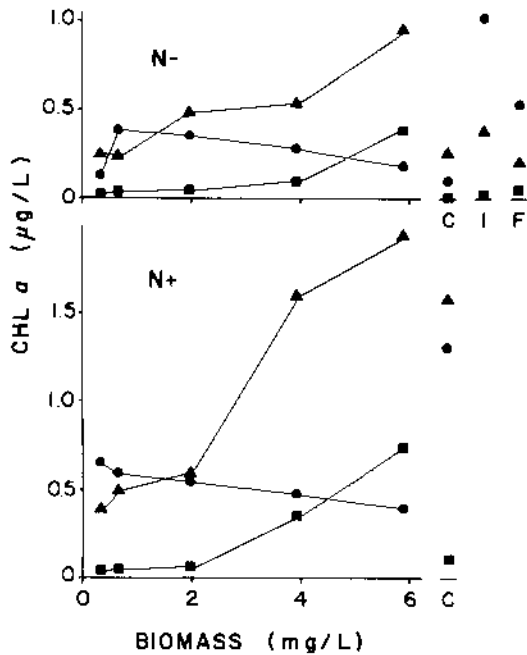


FIG. 4. Chlorophyll *a* concentrations in three size classes of phytoplankton for unenriched (N-) and enriched (N+) lake enclosures, versus zooplankton biomass concentration. Key: ● = fraction S (<22  $\mu\text{m}$ ), ▲ = fraction M (22–75  $\mu\text{m}$ ), and ■ = fraction L (>75  $\mu\text{m}$ ). C = enclosures without zooplankton, I = initial and F = final lake concentrations.

Four types of algal responses to zooplankton were observed (Fig. 8): (A) reduced, (B) enhanced (net growth rate increased with zooplankton concentration), (C) neither reduced nor enhanced, and (D) enhanced and grazed (unimodal). Only two small, abundant taxa, *Chlamydomonas* and nonmotile chlorococcales, exhibited significant negative linear responses to zooplankton biomass (Table 3). However, responses of both of these taxa fit a parabolic model more closely than a linear model, suggesting that they belonged in the unimodal category. These were not the only grazed taxa. Several taxa (*Oocystis*, *Cerasterias staurastroides*, *Dactylococcopsis smithii*, *Chroococcus limneticus*) had higher *g* in the enriched control bag than in enriched bags with low zooplankton concentrations, suggesting that they were grazed. These taxa account for the difference between the enriched control bag and the enriched 0.5  $\times$  zooplankton bag in medium-fraction chlorophyll (Figs. 1 and 4). Finally, all taxa that exhibited unimodal responses were grazed, at least at high zooplankton concentrations (Table 3).

A few taxa (all small algae) exhibited unimodal responses to zooplankton grazing. These algae increased with zooplankton concentration at relatively low zooplankton abundances, but decreased at higher zooplankton concentrations. Significant quadratic regression models were found for microflagellates (Table 3) and *Cryptomonas* (Table 3, Fig. 8D). *Cryptomonas* increased in abundance in previous experiments at Pe-

TABLE 2. Correlation coefficients for CHL *a* concentration, primary productivity (PPR), and selected PPR ratios, versus zooplankton concentration in enriched (N+) and unenriched (N-) bags by phytoplankton size fraction.†

		CHL <i>a</i>	PPR	PPR/ CHL <i>a</i>	PPR/ TOTP‡	PPR/ TOTN‡
N+	S	-0.984 **	-0.986 **	-0.974 **	-0.984 **	-0.980 **
	M	0.966 **	0.938 *	-0.732 NS	0.964 **	0.927 *
	L	0.963 **	0.975 **	-0.946 *	0.974 **	0.975 **
N-	S	-0.226 NS	0.055 NS	0.157 NS	0.482 NS	-0.080 NS
	M	0.958 **	0.916 *	0.783 NS	0.922 *	0.922 *
	L	0.895 *	0.973 **	0.611 NS	0.966 **	0.980 **

† S = small (<22  $\mu\text{m}$ ); M = medium (22–75  $\mu\text{m}$ ); L = large (>75  $\mu\text{m}$ ).

‡ TOTP = total phosphorus; TOTN = total nitrogen.

\* .05  $\geq P > .01$ ; \*\* .01  $\geq P > .001$ ; NS = not significant.

ter Lake zooplankton concentrations of up to 5  $\times$  ambient (Bergquist 1985). Additionally, the quadratic term improved the regression model for *Chlamydomonas* (Table 3) and for nonmotile chlorococcales (Table 3),

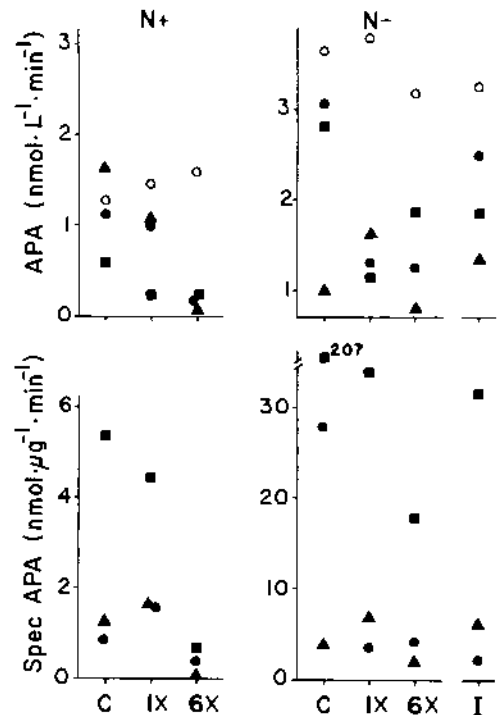


FIG. 5. Alkaline phosphatase activity (APA) and specific APA (APA per unit chlorophyll *a*) of four size classes of phytoplankton for selected bags (controls, 1  $\times$ , and 6  $\times$  ambient lakewater concentrations) and initial (I) lake conditions. Left: nutrient-enriched enclosures (N+); right: unenriched enclosures (N-). ○ = APA of dissolved (<0.45  $\mu\text{m}$ ) fraction. Key to other symbols as in Fig. 4.

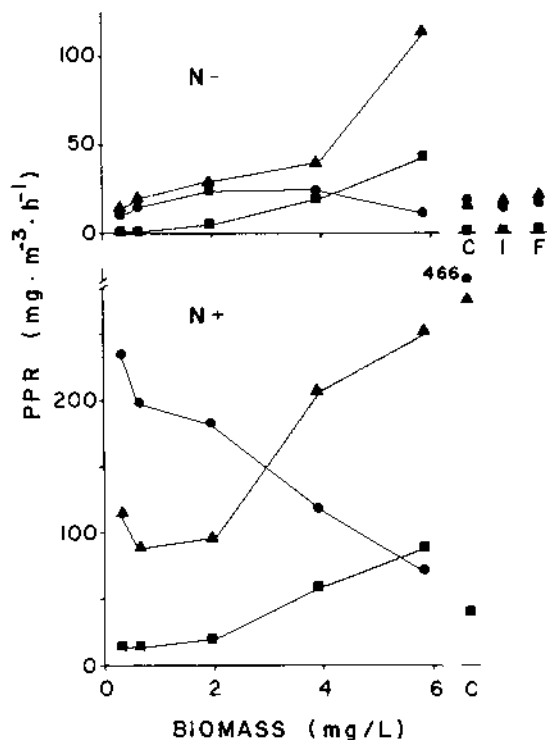


FIG. 6. Primary productivity measured as carbon (PPR) for three size classes of phytoplankton, versus zooplankton biomass concentration in unenriched enclosures (N-) and enriched enclosures (N+). Key to symbols as in Fig. 4.

suggesting that these taxa exhibited unimodal responses.

The net growth rates of several algal taxa (mostly larger ones) that were nutrient limited significantly increased as zooplankton concentration increased (Table 3, Fig. 8B). The growth rate of *Anabaena circinalis* also significantly increased (Table 3); although it was not shown to be nutrient limited, its growth may have been limited at some grazer concentrations (control, 6×, and 9×). Of these grazer-enhanced taxa, *Cerasterias staurastroides*, *Dinobryon*, *Anabaena*, and *Closteriopsis longissima* had shown positive responses to zooplankton additions in previous experiments (Bergquist 1985, Bergquist et al. 1985).

DISCUSSION

Nutrient limitation was common among the major algal taxa (Table 3). CHL *a* concentration and PPR increased and specific APA decreased in all three algal size fractions in response to enrichment at ambient levels of zooplankton biomass. Community responses to nutrient enrichment at all levels of zooplankton biomass were identical to the size-fractionated responses: CHL *a*, PPR, and specific PPR increased with nutrient addition, and specific APA decreased.

Responses to grazing were more complex. Although four distinct kinds of species-specific responses were observed, all but three taxa fell into one of two cate-

gories: nutrient limited, but not reduced by grazers (10 taxa), or nutrient limited and grazed (3 taxa) (Table 3). The latter category included only smaller (<30 μm) taxa, while the former included the majority of the M and L fraction algae. In Peter Lake virtually all of the algal biomass could be assigned to one of these two response groups. Gliwicz (1975) observed similar size fractionated algal responses when phytoplankton were grazed by increasing numbers of *Daphnia pulex*. When the zooplankton composition is known, algal size is a reliable predictor of responses to grazing (Bergquist et al. 1985).

Some nutrient-limited phytoplankton taxa increased as zooplankton biomass increased, while others were unaffected. Large reductions in specific APAs of L fraction algae suggested that the increased growth rates of taxa in the L fraction were due to phosphorus regeneration by zooplankton. Zooplankton transferred nutrients from smaller grazed algae or bacteria to the larger phytoplankters. The consequence was increased CHL *a* and PPR in fractions M and L as zooplankton biomass increased. Algae accounting for this increase were *Cerasterias staurastroides*, *Dinobryon sertularia*, *Closteriopsis longissima*, *Anabaena circinalis*, and, at low zooplankton concentrations, *Cryptomonas*.

For grazed, nutrient-limited taxa in unenriched bags, the effect of the zooplankton on the phytoplankton had

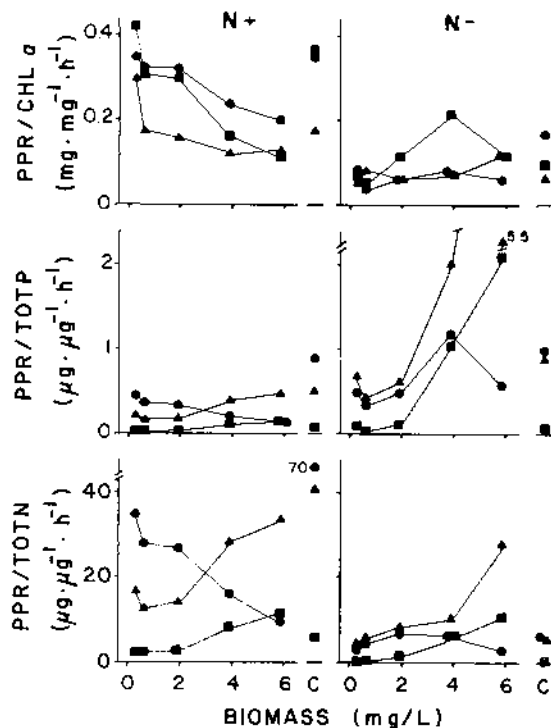


FIG. 7. PPR (primary productivity, measured as carbon) ratios for three size classes of phytoplankton, versus zooplankton biomass concentration in enriched (N+, left) and unenriched (N-, right) bags. CHL *a* = chlorophyll *a*, TOTP = total phosphorus, TOTN = total nitrogen. Key to symbols as in Fig. 4.

TABLE 3. Growth rate responses of major algal taxa to zooplankton grazing. + = significant response ( $P \leq .05$ ) and 0 = nonsignificant response.

Algal size class*	Mean GALD†	Taxon	Nutrient limitation	Linear response‡		Unimodal response§
				Decrease	Increase	
S	6	microflagellates	+	0	0	+
	6	nonmotile chlorococcales	+	+	0	+
	7	<i>Crucigenia quadrata</i>	0	0	0	
	8	<i>Chlamydomonas</i>	0	+	0	+
	18	<i>Selenastrum minutum</i>	+	0	0	
M	29	<i>Cryptomonas</i>	+	0	0	+
	31	<i>Cosmarium</i> sp.	+	0	0	
	41	<i>Oocystis</i> sp.	+	0	0	
	42	<i>Cerasterias staurastroides</i>	+	0	+	
	47	<i>Dactylococcopsis smithii</i>	+	0	0	
	52	<i>Chroococcus limneticus</i>	+	0	0	
	66	<i>Gloeocystis</i> sp.	+	0	+	
L	87	<i>Dinobryon sertularia</i>	+	0	+	
	105	<i>Dinobryon cylindricum</i>	+	0	0	
	116	<i>Closteriopsis longissima</i>	+	0	+	
	127	<i>Anabaena circinalis</i>	0	0	+	

\* S = small (<22  $\mu\text{m}$ ); M = medium (22–75  $\mu\text{m}$ ); L = large (>75  $\mu\text{m}$ ).

† GALD = greatest axial linear dimension.

‡ Responses to grazing were determined by linear regression of the net growth rates of algae in unenriched bags against zooplankton concentration.

§ Unimodal responses were determined by a quadratic regression model when nonlinear responses to zooplankton were observed.

both negative (grazing) and positive (nutrient recycling) aspects. Nutrient recycling stimulated algal growth in all size classes, but with increased zooplankton biomass, grazing on fraction S became increasingly more intense. Heavy grazing caused declines in species growth rates and PPR at the highest zooplankton biomasses. The unimodal response in PPR of the S fraction algae reflected the sum of the two zooplankton effects: nutrient recycling, which stimulated algal growth at low levels of zooplankton biomass, and grazing losses, which reduced standing crop as zooplankton grazing pressure intensified. All taxa that responded unimodally were nutrient limited, except *Chlamydomonas*. The quadratic model for *Chlamydomonas* gave only a marginal improvement over the linear model. It was not clear that *Chlamydomonas* increased significantly between the two lowest zooplankton biomasses, but it clearly declined significantly with further increases in zooplankton biomass.

Grazed algae responded quite differently in enriched bags. CHL *a* concentration and PPR of fraction S and species-specific growth rates steadily declined due to grazing with increasing zooplankton biomass. APA data indicated that enrichment alleviated phosphorus limitation. Therefore, phosphorus recycling by zooplankton had less effect in the enriched bags than in the unenriched bags. Apparently, the monotonic decline in enriched bags represents only the right-hand side of the full unimodal curve. In similar experiments in more productive lakes where nutrient limitation was less prevalent, linear decreases in net algal growth rates with increased zooplankton concentration were frequently observed (Lehman and Sandgren 1985).

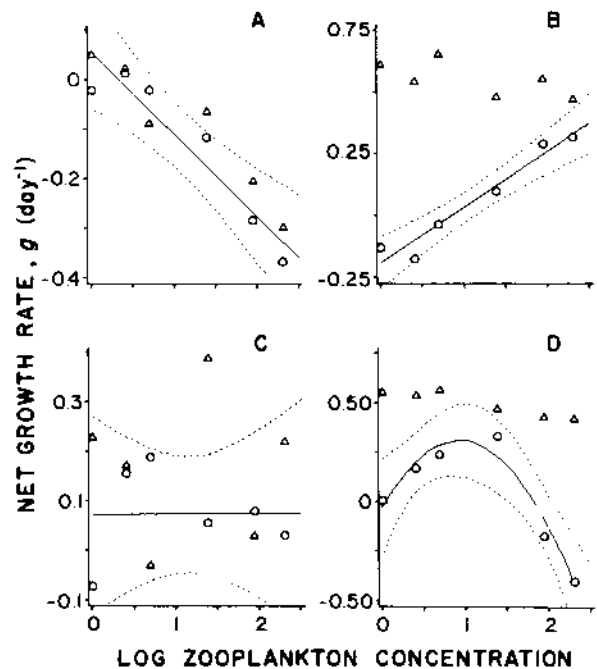


FIG. 8. Net algal daily growth rates ( $g$ ) versus log zooplankton concentration (multiples of ambient lake concentration) for selected species. O = unenriched bags (N-),  $\Delta$  = enriched bags (N+). (A) *Chlamydomonas* ( $r^2 = 0.892$ ,  $P = .0045$ ). (B) *Cerasterias staurastroides* ( $r^2 = 0.947$ ,  $P = .0011$ ). (C) *Crucigenia quadrata* ( $r^2 = 0.000$ ,  $P = .987$ ). (D) *Cryptomonas* ( $R^2 = 0.942$ ,  $P = .0123$ ). (A), (B), and (C) show linear regression lines with 95% confidence intervals calculated for unenriched-enclosure  $g$  values. (D) shows a quadratic regression line with 95% confidence intervals calculated for unenriched enclosures.

A unimodal response of algae to grazers has not been reported previously for plankton systems. The stimulatory effect of zooplankton on edible algal taxa explains the paradoxical co-occurrence of small flagellates and large grazers observed in other food web manipulation experiments (Lynch and Shapiro 1981, Shapiro and Wright 1984). Such small, grazed, nutrient-limited taxa actually increased in abundance in bags with low concentrations of zooplankters.

Total CHL *a* and total PPR responses reflected the dominance of this assemblage by nutrient-limited, ungrazed phytoplankters. The significant increases in total CHL *a* and total PPR as zooplankton biomass increased were independent of changes in nutrient concentration. CHL *a*: nutrient ratios increased significantly with zooplankton biomass in all cases (Fig. 1). In unenriched enclosures specific PPR, PPR/TOTP, and PPR/TOTN also increased significantly (Fig. 3). We infer that the rate of nutrient cycling increased, which enabled the algae to fix more carbon per unit nutrient.

Species-specific responses translated into major changes in total system-level variables: nearly a four-fold increase in total CHL *a* and nearly a fivefold increase in total PPR from ambient to 9× enclosures. Apportionment of CHL *a* and PPR among algal size classes changed with zooplankton density, indicating that reallocation of limiting nutrients among algal populations had direct effects on system-level variables. These results indicate that system responses can be represented as an overall consequence of population-level processes. In particular, population interactions (such as selective grazing by zooplankton) that redistribute nutrients and chlorophyll among algal size classes have major effects on PPR. The results support a hierarchical view of limnetic PPR: nutrient loads establish the potential production, and population interactions set actual production by allocating limiting nutrients among populations with different metabolic capacities.

The population- and system-level responses reported here occurred over short time scales of a few days. Over longer time scales, responses in lakes will not reach equilibrium because zooplankton populations fluctuate temporally and spatially, in response to zooplanktivory and other factors independent of food supply. This study shows that both algal species composition and phosphorus limitation respond to grazing intensity, and that primary production is consequently altered. These compositional changes are potentially compensatory, and could increase or decrease total ecosystem productivity. This great range of dynamic possibilities may explain the enormous variability exhibited in phytoplankton production.

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