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SPECIES-DEPENDENT EFFECTS OF ZOOPLANKTON ON PLANKTONIC ECOSYSTEM PROCESSES IN CASTLE LAKE, CALIFORNIA[1]

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Abstract. Freshwater zooplankton communities typically undergo pronounced seasonal succession and often show dramatic responses to external factors such as changes in zooplanktivore abundance. For this reason it is important to assess how common zooplankton species differ in their grazing impacts on planktonic ecosystems. To accomplish this we used single-species treatments with *Diacyclops bicuspidatus thomasi, Daphnia rosea, Diaptomus novamexicanus,* and *Holopedium gibberum* in situ in Castle Lake, California. These taxonomically diverse zooplankters differ markedly in feeding modes and typical seasonal population dynamics. We measured the response of nutrient concentrations, bacterioplankton abundance, phytoplankton species composition and biomass, primary production, a grazing index (phaeophytin/chlorophyll *a*), and microzooplankton to our single-species treatments.

The filter-feeding cladocerans *Daphnia* and *Holopedium* and the raptorial filter-feeding calanoid copepod *Diaptomus* showed several effects typical of herbivorous zooplankton. These included increasing dissolved nutrient concentrations, decreasing algal biomass and the abundance of several common algae, increasing a grazing index, increasing the ratio of bacterial to algal biomass, as well as depressing ciliate microzooplankton abundance. The raptorial cyclopoid copepod *Diacyclops* was apparently exclusively predaceous as it decimated the ciliate and rotifer microzooplankton, but had no notable effect on the other measured parameters relative to zooplankton-free controls. *Diacyclops* had the greatest effect on the microzooplankton and *Daphnia* and *Diaptomus* had the greatest effect on inorganic nutrients and characteristics of the phytoplankton. *Holopedium* had qualitatively similar but weaker impacts compared to *Daphnia* and *Diaptomus.* None of the zooplankton treatments had an effect on bacterioplankton abundance, nor did grazing by any of these zooplankters increase total algal primary production. Our results suggest differences in the grazing effects of common freshwater zooplankton can be pronounced and indicate that both seasonal succession and long-term shifts in the zooplankton community structure should have marked effects on microzooplankton competitors and prey, the phytoplankton, and nutrient cycling.

Key words: Castle Lake; Daphnia; Diacyclops; Diaptomus; *grazing impacts;* Holopedium; *planktonic ecosystem; zooplankton.*

Introduction

Herbivores can influence the structure and dynamics of plant communities by preferentially removing specific plants or parts of plants, by regenerating nutrients, and by competitively suppressing other herbivores. These direct effects can in turn result in a myriad of indirect effects, which can dramatically alter the structure and dynamics of ecosystems, often in unforeseen ways (Paine 1992). Most investigations of grazing effects on plant communities have used enclosure/exclosure designs with a dominant herbivore or all herbivores. These studies are able to determine the influence of herbivores on plant communities, and in ecosystems where there are only one or a few main herbivores this may be sufficient. However, many herbivore communities are extremely dynamic, with the species composition of the community shifting mark-

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edly both seasonally and long term. This is particularly true of freshwater zooplankton communities. In cases where the herbivore community is dynamic, it is imperative to gain insights into how different herbivores impact plant communities.

Research actually assessing species-specific grazing impacts has generally examined aquatic systems and has concentrated on a few ecosystem types (e.g., rocky intertidal zones, coral reefs, and streams). The behavior and impact of different herbivores varies markedly from system to system. Terrestrial research has shown grazers often attack different parts of plants or attack the same plants at different times of the year (e.g., Karban and Strauss 1993); further, it is widely known that phytophagous insects often attack only one host plant species when many potential host species are available. Working in the marine intertidal zone, Fletcher (1987) and Paine (1992) found some grazers had very strong negative impacts on algal biomass or recruitment, while other grazers had no impact or a positive impact on the algae. Research on Caribbean coral communities showed urchins have a much greater impact on attached algae than do herbivorous fishes (e.g., Morrison 1988). Studies on stream insects have shown pronounced differences between species in grazing impacts on periphytic algal communities. In some cases different insect species completely changed the periphyton species composition or dramatically altered the pattern of algal distribution (e.g., DeNicola et al. 1990, Feminella and Resh 1991).

While some research on zooplankton has specifically examined species-specific effects on the phytoplankton (Knisely and Geller 1986), most studies have used treatments with or without zooplankton (Lehman and Sandgren 1985, Bergquist and Carpenter 1986) or contrasted large-size vs. small-size dominated zooplankton communities (Vanni 1987, Cyr and Pace 1993). With the exception of Knisely and Geller (1986), these studies do not indicate how zooplankton species shifts drive changes in the planktonic ecosystem.

Much of the past research on species differences in grazing effects, particularly the stream research, has emphasized the importance of feeding behavior and morphology in ultimately explaining subsequent interspecies differences. The taxonomically diverse zooplankters examined in the present investigation represent a broad range of feeding strategies, from the raptorial cyclopoid copepod *Diacyclops,* to the raptorial and filtering calanoid copepod *Diaptomus* and the exclusively filter-feeding cladocerans *Daphnia* and *Holopedium.* DeMott (1986) and DeMott and Moxter (1991) demonstrated that zooplankton have varying abilities to discriminate between potential food particles of similar morphology based on taste. Rotifers were found to be the most selective followed by copepods, while cladocerans (and particularly *Daphnia*) usually fed nonselectively. Hessen (1985) concluded that the ability to retain small particles was strongly correlated with filtering comb morphology, with zooplankters having fine combs selecting the smallest particles. Simply based on feeding strategy, one could predict that these zooplankters would have markedly different effects on the species composition of the algae, rates of phytoplankton primary production, nutrient regeneration, competitors, etc. Crustacean zooplankton species are also known to differ dramatically in behavior, life history characteristics, growth response to resources, susceptibility to algal toxins and elemental composition (Lynch 1980, Lampert and Muck 1985, Stich 1989, Andersen and Hessen 1991, Lundstedt and Brett 1991). Thus one can predict a priori that different zooplankton species will have distinct effects on the entire planktonic ecosystem.

To contribute to the understanding of zooplankton species impacts on planktonic ecosystems, we used *Diacyclops bicuspidatus thomasi, Daphnia rosea, Diaptomus novamexicanus,* and *Holopedium gibberum,* the four most common crustacean zooplankton in Castle Lake, California. The zooplankton community of Castle Lake is very dynamic seasonally in terms of total community biomass and species contributions to biomass. Further, the zooplankton community of Castle Lake has recently shifted structure in response to fish community manipulations, which resulted in increased zooplanktivory due to increased abundance of golden shiners (*Notemigonus crysoleucas*). During our whole-lake manipulation, the zooplankton community shifted from biomass dominance by *Daphnia* and *Diaptomus,* and seasonally *Holopedium,* to dramatically increased representation of *Diacyclops* and decreased representation by *Daphnia* and *Diaptomus.* During the time that the fish community was manipulated and the zooplankton community structure changed, water transparency declined and phytoplankton primary production increased (J. J. Elser, *personal observation*).

The grazing response variables examined in the present study were dissolved inorganic nitrogen (DIN), soluble reactive phosphorus (SRP), the ratio of DIN/SRP, bacteria cell abundance, bacteria biovolume per algal biovolume, algal community structure and biovolume, phaeophytin per chlorophyll *a,* ^{14}C uptake, ^{14}C uptake per unit algal carbon, and ciliate and rotifer abundance. DIN and SRP are measures of zooplankton nutrient regeneration, the ratio of DIN to SRP is a measure of the nature of nutrient cycling and may determine the direction of algal succession (Sterner et al. 1992), the ratio of phaeophytin (a chlorophyll breakdown product) to chlorophyll *a* is an index of grazing (Carpenter and Bergquist 1985), ^{14}C uptake is a measure of total primary production, and ^{14}C uptake per unit algal carbon is a measure of relative primary production.

METHODS

To test the differential grazing effects of the four most common zooplankters in Castle Lake on microzooplankton competitors, the phytoplankton, primary production, the bacterioplankton, and nutrient cycling, we removed all larger zooplankton from lake water using a screen and created individual species treatments by adding a previously determined number of individuals to each experimental vessel. Differences between each zooplankton species treatment and a zooplankton-free control treatment were considered either direct or indirect effects of the zooplankton species tested. The length of the experiment, 8 d, was sufficient to allow trends to develop for the microzooplankton, which have generation times of a few days to a week, but short enough to still detect trends among short-term processes such as nutrient regeneration.

Lake water was collected at 1, 3, and 5 m depth and passed through a 83-μm mesh screen to remove large zooplankton. Twenty-five 10-L cubitainers were incrementally filled with this screened lake water. The individual zooplankton species treatments were created by adding $\approx$15 *Diacyclops,* 15 *Daphnia,* 15 *Diaptomus,* or 3 *Holopedium*/L to each of five separate cubitainers. We used individual zooplankter abundances in our species treatments, which were similar to high abundances seen for those species in Castle Lake. This was done in order to provide sufficiently high treatment abundances to detect a treatment effect and to assure that our results were still biologically meaningful. The experiments were started with mainly adult or late-stage juvenile zooplankters, but by the end of the experiment all treatments were dominated (in terms of biomass) by juveniles of the treatment species. The adult individuals used to start the experiment had mean dry masses of 2.6, 3.6, 8.0, and 15.4 μg/individual for *Diacyclops, Diaptomus, Daphnia,* and *Holopedium,* respectively. The removal (control) treatment consisted of screened lake water added to five cubitainers.

The cubitainers were incubated at 5 m depth in Castle Lake. The experiment was started on 13 June 1991 and ended 8 d later on 21 June 1991. The temperature at 5 m depth was 13° and 15°C at the beginning and end of the experiment, respectively. The seasonal average for light penetration at 5 m is 23 ± 4.6% (± 1 SD) of surface values. For a more detailed description of Castle Lake, see Goldman and de Amezaga (1984).

At the end of the experiment, samples for crustacean zooplankton enumeration were taken by pouring 6 L of each treatment replicate through a 83-μm mesh screen and preserving with a Lugol's and sucrose solution. One litre of unfiltered water preserved with Lugol's was collected for ciliate, rotifer, and nauplii enumeration; 125 mL of sample water, also preserved with Lugol's, was collected for phytoplankton species identification and enumeration. Ten millilitres of sample water were preserved with 2% formalin for bacteria cell counts. One litre of unpreserved sample water was collected for analyses of nitrate, ammonia, SRP, chlorophyll *a,* phaeophytin, and ^{14}C incorporation. Water intended for nutrient and pigment analyses was screened through a 83-μm mesh within 1 h after collection to remove large zooplankton.

Zooplankton juveniles and adults were enumerated and their biomass calculated using previously determined dry masses for these size classes of Castle Lake zooplankton (Redfield 1979). The rate of zooplankton biomass change for the treatment zooplankters was calculated according to the logistic growth equation using the initial and final treatment zooplankter biomass and an 8-d sampling interval. Ciliates were counted by concentrating the 1 L of Lugol's preserved sample to a small volume by sedimentation for 3 d and counting under an inverted light microscope using the Utermöhl technique. For the removal, *Daphnia, Diaptomus,* and *Holopedium* treatments, 500 mL of the sample was counted, while the entire sample was counted for the *Diacyclops* treatment. These samples were counted within 4 mo of collection and were stored at room temperature until enumeration. Algae were also enumerated using the Utermöhl technique. Algal biovolume was estimated from cell abundances and species cell biovolume values for Castle Lake and Lake Tahoe algae (Elser and Goldman 1991; D. Hunter, *unpublished data*). Epifluorescence microscopy of acridine-orange stained and formalin-fixed samples was used to count bacteria (Hobbie et al. 1977). Sterile water was used to prepare the stain, and blanks were run for each counting session.

Ammonia was quantified using the phenolhypochlorite method (Solórzano 1969). Nitrate, plus nitrite, was analyzed using a diazotization-coupling reaction (Strickland and Parsons 1972). SRP was measured by the phosphomolybdate method (American Public Health Association 1976). Chlorophyll *a* and phaeophytin concentrations were determined using the fluorometric method with acid correction for degradation products (Strickland and Parsons 1972) after freezing for 48 h and extracting with methanol in the dark at 4°C for 24 h (Marker et al. 1980). Primary production determinations were made at the end of the experiment, with one light bottle for each replicate of each treatment and one composite dark bottle for each treatment. This was done by placing 250-mL water samples in clear glass bottles inoculated with 185 kBq (5 μCi) $H^{14}CO_3$. Bottles were suspended at 5 m depth for $\approx$4 h, after which their contents were filtered onto 0.4-μm Millipore filters. The filters were placed in a gas proportional detector to measure ^{14}C. Dissolved inorganic carbon concentration was determined by infrared analysis of subsamples placed in evacuated blood-collection tubes and preserved with chloroform (Roberts and Smith 1988).

DATA ANALYSES

Since we had a possible covariation between our zooplankton species treatments and the zooplankton biomasses of these treatments, i.e., there were systematic differences in the zooplankton biomass between

TABLE 1. Crustacean zooplankton abundance, dry biomass, and fecundity in the removal and zooplankton treatments. Initial and final observations are given, values presented are mean ± 1 SD. Abundance estimates do not include nauplii.

Treatment	Initial individuals (ind./L)	Initial biomass (μg/L)	Initial percent nauplii	Initial fecundity (eggs/♀♀)*	Final individuals ind./L	Final biomass (μg/L)	Final percent nauplii	Final fecundity (eggs/♀♀)*	Rate of biomass change per day
Removal	...	3.8	100	...	...	8.5 ± 3.2	97 ± 4	...	0.095 ± 0.045
Diacyclops	13.7	33	11	11	7.6 ± 1.3	58 ± 9.6	70 ± 11	1.8 ± 0.49	0.067 ± 0.023
Daphnia	15.2	120	3	2.0	33.8 ± 6.2	175 ± 33	5 ± 3	0.30 ± 0.076	0.046 ± 0.023
Diaptomus	15.2	52	7	1.2	12.7 ± 0.7	63 ± 3.3	34 ± 4	0.71 ± 0.13	0.022 ± 0.007
Holopedium	2.8	40	9	5.5	14.0 ± 2.1	145 ± 23	4 ± 1	0.88 ± 0.17	0.160 ± 0.020

* ♀♀ = adult females.

the different treatments (Table 1), we first examined the relationship between zooplankton species and biomass for our independent variables. The first step in this analysis was a test for constancy of slopes, which can be determined by examining the interaction term of a regression with zooplankton species treatment and zooplankton biomass as independent variables and the parameter values as dependent variables. In 8 of 10 cases we could assume that our slopes were not significantly different and proceeded with a full analysis of covariance (ANCOVA); that is, the probability value for our interaction term was not significant ($P > 0.05$). We then conducted full ANCOVAs with zooplankton treatment as an independent variable and zooplankton biomass as a concomitant variable. Individual zooplankton species treatments were declared significantly different from the control treatment based on the results of two-tailed Dunnett *t* tests. The ratio data (DIN/SRP, phaeophytin per chlorophyll *a*, relative primary production, bacteria biovolume per algal biovolume) were arcsine transformed while the remaining data (DIN, SRP, bacteria cell abundance, algal community structure and biovolume, total primary production, and ciliate and rotifer abundance) were $\log_{10}(X + 1)$ transformed. A multidimensional scaling procedure was carried out using SYSTAT version 4.0 (Wilkinson 1988) with transformed data (observation − parameter mean/parameter standard deviation), using the covariance option within the correlation module to generate similarity indices, and the multidimensional scaling module to generate a two-dimensional similarity plot. Multidimensional scaling is a clustering strategy using full dimensions, in this case two, whereas many other clustering strategies (e.g., dentograms) utilize more than one but less than two dimensions. The purpose of this procedure was to obtain an objective measure of similarity or dissimilarity between and within the treatments based on the results obtained for the measured parameters.

RESULTS

The four zooplankton treatments (*Diacyclops, Daphnia, Diaptomus, Holopedium*) began with individual abundances roughly equivalent to peak abundances previously noted for these species in Castle Lake (M. T. Brett, *personal observations*) (Table 1). Over 94% of the zooplankton biomass in each treatment consisted of the treatment species, with the remaining biomass made up almost exclusively of nauplii. During the experiment, biomass increased and fecundity decreased in each zooplankton species treatment. The increase in biomass in all treatments was due to the recruitment of juveniles, i.e., juveniles comprised 10–20% of treatment species biomass at the beginning of the experiment and generally >50% of treatment biomass at the end of the experiment.

The results of the ANCOVA analyses, with zooplankton species treatment as an independent variable and zooplankton biomass as a concomitant variable showed that the zooplankton species term was significant for every parameter presented in Table 2, while the zooplankton biomass term was significant in only one case (i.e., for the ratio of bacterial to algal biomass). In this case the variability explained by the biomass term was small, 12.2% of the sum of squares, compared to the variability explained by the zooplankton species term, 50.6% of the sum of squares. Thus, in general, our experimental results reflected the effect of zooplankton species treatments and not the disparities in zooplankton biomass between treatments.

While our ANCOVA analysis suggests zooplankton biomass was responsible for only a small portion of the treatment responses noted, relative to treatment zooplankter species, this does not mean that our results were unaffected by disparities in zooplankton biomass between treatments. For example, the *Diacyclops* and *Diaptomus* had final biomasses approximately one-third of those for the *Daphnia* and *Holopedium* treatments. Thus one would have logically expected greater treatment impacts in the *Diacyclops* and *Diaptomus* had they had the same biomass as the *Daphnia* and *Holopedium* treatments.

In order to mathematically compensate for disparities in zooplankton biomass between the different treatments we calculated zooplankton-induced deviation rates from the zooplankton-free control treatment. These treatment deviation rates were calculated for each zooplankton treatment and for all measured parameters according to the logistic growth equation, i.e., parameter : treatment deviation rate = [ln(treatment : replicate value) − ln(control mean)]/8. These values were then corrected for disparities in treatment biomass by multiplying the parameter : treatment deviation rate by the ratio of the zooplankton biomass in the *Daphnia* treatment and the zooplankton biomass in the *Diacyclops* and *Diaptomus* and *Holopedium* treatments. Treatment biomasses were normalized to the *Daphnia* values because *Daphnia* is the most commonly investigated freshwater zooplankter and because the *Daphnia* treatment achieved the highest biomass during this experiment. This data manipulation assumes that the relationship between the deviation rate and treatment zooplankton biomass is linear; this is probably true in most but not all cases (Carrick et al. 1991). In essence this approach is saying: if a hypothetical deviation rate is 0.30 and 0.10 in the *Daphnia* and *Diaptomus* treatments, respectively, and the *Daphnia* treatment had a 3 times greater biomass than did the *Diaptomus* treatment then the biomass corrected deviation rates would be 0.30 and 0.30 in the *Daphnia* and *Diaptomus* treatments, respectively. Instead of concluding that the responses to the two zooplankton species were different, correcting for biomass leads to the conclusion that the responses were similar. Since this data manipulation makes an assumption that may not be true (i.e., a linear relation between response and zooplankton biomass), we did not conduct a formal statistical analysis of these data.

The biomass-adjusted deviation rates (Table 3) suggest *Daphnia* had the greatest negative impact on total phytoplankton biovolume and enriched DIN (relative to SRP) the most of the zooplankton species tested. *Diaptomus* had the greatest positive impact on SRP concentrations, the ratio of phaeophytin to chlorophyll, and most strongly enriched SRP (relative to DIN) of the zooplankters tested. *Daphnia* and *Diaptomus* had similar strong positive impacts on DIN concentrations, relative primary production, and the ratio of bacteria to phytoplankton biovolume. *Diacyclops* very strongly depressed rotifer (almost exclusively *Polyarthra vulgaris*) and ciliate abundance, but had no notable effect on dissolved nutrients, the phytoplankton, or bacterioplankton relative to the control treatment. *Holopedium* generally had similar but weaker impacts, compared to *Daphnia* and *Diaptomus*, on all of the measured parameters (Table 3).

TABLE 2. Results of an ANCOVA for the various parameters, with zooplankton species as a category variable and zooplankton biomass as a concomitant variable. The interaction probability value refers to the test for constancy of slopes.

Source of variation	SS	df	*F* ratio	*P*
	DIN*			
Zooplankton species	0.625	4	8.79	0.0003
Zooplankton biomass	0.012	1	0.69	0.4177
Error	0.336	19	···	···
Interaction	···	···	···	0.9850
	SRP†			
Zooplankton species	0.442	4	3.98	0.0165
Zooplankton biomass	0.007	1	0.25	0.6257
Error	0.528	19	···	···
Interaction	···	···	···	0.0390
	DIN/SRP			
Zooplankton species	12.0	4	15.88	0.0001
Zooplankton biomass	0.11	1	0.56	0.4646
Error	3.59	19	···	···
Interaction	···	···	···	0.8540
	Phytoplankton biomass			
Zooplankton species	0.416	4	8.48	0.0004
Zooplankton biomass	0.027	1	2.17	0.1572
Error	0.233	19	···	···
Interaction	···	···	···	0.0750
	Phaeophytin/chlorophyll			
Zooplankton species	0.090	4	5.29	0.0050
Zooplankton biomass	0.004	1	0.85	0.3690
Error	0.081	19	···	···
Interaction	···	···	···	0.5770
	^{14}C/phytoplankton			
Zooplankton species	0.00083	4	3.25	0.0340
Zooplankton biomass	0.00022	1	3.41	0.0810
Error	0.00122	19	···	···
Interaction	···	···	···	0.2040
	Bacteria			
Zooplankton species	0.0228	4	4.26	0.0126
Zooplankton biomass	0.0005	1	0.36	0.5537
Error	0.0255	19	···	···
Interaction	···	···	···	0.3780
	Bacteria/phytoplankton			
Zooplankton species	0.164	4	6.34	0.0020
Zooplankton biomass	0.038	1	6.30	0.0210
Error	0.123	19	···	···
Interaction	···	···	···	0.2320
	Ciliates			
Zooplankton species	4.850	4	83.36	0.0001
Zooplankton biomass	0.037	1	2.54	0.1296
Error	0.247	17	···	···
Interaction	···	···	···	0.2060
	Rotifers			
Zooplankton species	4.194	4	26.29	0.0001
Zooplankton biomass	0.139	1	3.49	0.0780
Error	0.718	17	···	···
Interaction	···	···	···	0.0220

* DIN = dissolved inorganic nitrogen.

† SRP = soluble reactive phosphorus.

The treatment responses for the individual algal species were generally not as strong as the total phytoplankton biovolume response to the zooplankton treatments (Table 4). This is mainly because *Peridinium inconspicuum*, which strongly dominated total algal biomass, showed a strong response to grazing by *Diaptomus, Holopedium,* and *Daphnia,* while many of the rarer algal species only showed a strong response to grazing by *Daphnia.* Of the 10 algal species found in at least 80% of the samples, *P. inconspicuum, Arthrodesmus* sp., *Scenedesmus bijuga, Oocystis* sp., *Dictyosphaerium pulchellum, Rhodomonas minuta, Microcystis flos-aquae,* and small flagellates had reduced abundances in the *Daphnia* treatment. Of the common

TABLE 3. Zooplankton biomass adjusted treatment rates of deviation from controls. Values presented are mean ± 1 SD. Values for the removal treatment were not adjusted for zooplankton biomass.

Treatment	DIN*	SRP†	DIN/SRP	Algal biovol.	Phaeo./chl.
Removal	0.000 ± 0.062	0.000 ± 0.028	0.000 ± 0.062	0.000 ± 0.027	0.000 ± 0.017
Diacyclops	−0.017 ± 0.286	0.000 ± 0.028	−0.017 ± 0.286	0.030 ± 0.033	0.005 ± 0.065
Diaptomus	0.299 ± 0.098	0.115 ± 0.079	−0.428 ± 0.107	−0.109 ± 0.087	0.154 ± 0.079
Holopedium	0.086 ± 0.041	0.073 ± 0.049	−0.115 ± 0.055	−0.103 ± 0.037	0.048 ± 0.032
Daphnia	0.252 ± 0.054	0.057 ± 0.078	0.120 ± 0.037	−0.185 ± 0.078	0.045 ± 0.014

* DIN = dissolved inorganic nitrogen.
† SRP = soluble reactive phosphorus.

algae, *P. inconspicuum* and *Rhodomonas minuta* were most consistently reduced by zooplankton grazing. If these values were adjusted for disparities in zooplankton biomass between the different treatments, the expected impacts of the *Diacyclops, Diaptomus,* and *Holopedium* treatments would only be slightly greater.

A multidimensional scaling of the data presented in Figs. 1, 2, 3, and 4 shows that the zooplankton species treatments resulted in four distinguishable groupings (Fig. 5). One grouping each was noted for the control, *Diacyclops,* and *Daphnia* treatments and a fourth structure for the *Diaptomus* and *Holopedium* treatments combined. DIN, algal abundance, and the ratios of phaeophytin/chlorophyll *a*, ^{14}C uptake/algal carbon and bacterial biovolume/algal biovolume significantly loaded on Dimension 1, while bacteria biovolume, and ciliate and rotifer abundance significantly loaded on Dimension 2.

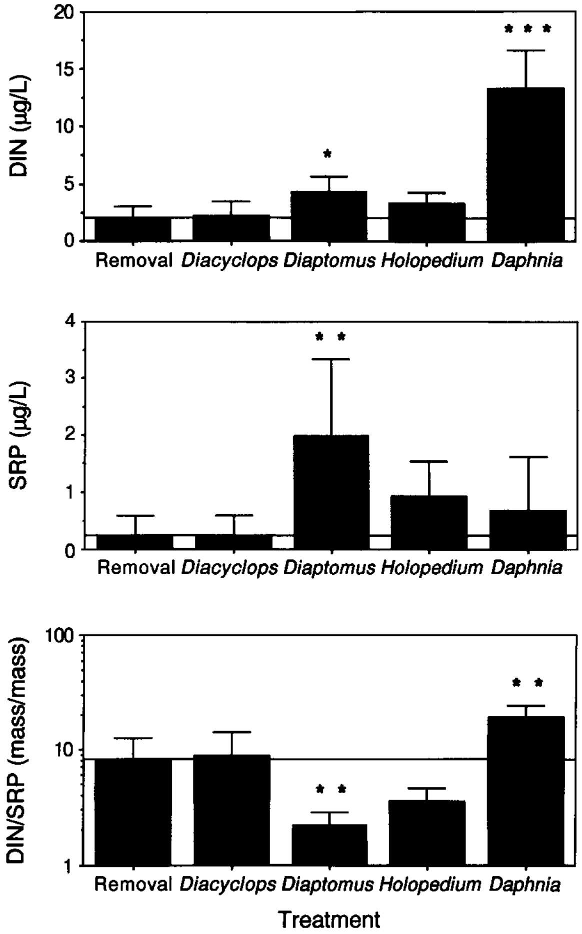

FIG. 1. The response of dissolved inorganic nitrogen (DIN), soluble reactive phosphorus (SRP), and the ratio of DIN/SRP to the zooplankton species treatments. The values presented are mean ± 1 SD, the Dunnett *t* test probabilities are $^*P < 0.05$, $^{**}P < 0.01$, and $^{***}P < 0.001$.

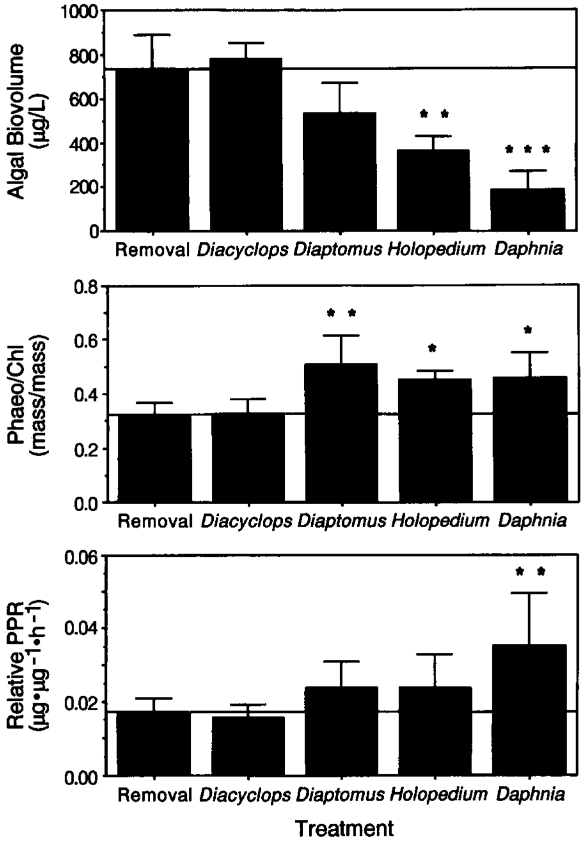

FIG. 2. The response of phytoplankton biovolume, the ratio of phaeophytin to chlorophyll *a*, and the ratio of CO_2 uptake to algal biomass to the zooplankton species treatments. Algal carbon content was assumed to be 16% of biovolume. See Fig. 1 for explanation of symbols. PPR = primary production.

TABLE 3. Continued.

Relative PPR	Bacteria	Bact./phyto.	Ciliates	Rotifers
0.000 ± 0.027	0.000 ± 0.023	0.000 ± 0.045	0.000 ± 0.021	0.000 ± 0.031
−0.033 ± 0.100	0.052 ± 0.055	0.022 ± 0.057	−1.180 ± 0.169	−1.140 ± 0.494
0.112 ± 0.096	0.054 ± 0.037	0.163 ± 0.099	−0.370 ± 0.137	−0.135 ± 0.223
0.046 ± 0.054	0.017 ± 0.015	0.121 ± 0.034	−0.126 ± 0.049	−0.087 ± 0.084
0.093 ± 0.070	−0.018 ± 0.008	0.167 ± 0.083	−0.240 ± 0.078	−0.048 ± 0.046

DISCUSSION

The zooplankters tested in this experiment can be divided into two broad ecological categories: (1) the carnivorous *Diacyclops* and (2) the omnivorous *Daphnia, Diaptomus,* and *Holopedium* (Figs. 1–4). The raptorial *Diacyclops* decimated the ciliate and rotifer microzooplankton, but had no notable effect on nutrient concentrations, bacterioplankton, phytoplankton, or primary production relative to zooplankton-free controls. The filter-feeding cladocerans *Daphnia* and *Holopedium* and the raptorial and filter-feeding calanoid copepod *Diaptomus* showed several effects typical of herbivores, such as increasing dissolved nutrient concentrations and decreasing algal biomass. However, these species also depressed microzooplankton abundance, particularly that of ciliates. None of the zooplankton treatments had an effect on bacterioplankton abundance. Multidimensional scaling, a fully two-dimensional clustering strategy, revealed four different planktonic ecosystem structures in response to our zooplankton species treatments. The removal, *Diacyclops,* and *Daphnia* treatments formed independent structures, while the *Diaptomus* and *Holopedium* treatments combined to form a fourth independent structure (Fig. 5). These results confirm that shifts in zooplankton community species composition should in and of themselves result in shifts in overall planktonic ecosystem structure.

In Castle Lake *Diacyclops* and *Holopedium* generally have their peak abundances in early summer, while the population peaks for *Daphnia* and *Diaptomus* can occur any time during the summer. Thus there could be regular shifts in the intensity of zooplankton–phytoplankton or zooplankton–microzooplankton interactions (e.g., due to *Diacyclops* and *Holopedium*) or erratic fluctuations in these interactions due to normal unpredictable population peaks for *Daphnia* and *Diaptomus.* Our results suggest the shift in crustacean zooplankton community structure, caused by our prior manipulation of the fish community, can be expected to have profound effects on the dissolved nutrient concentrations, phytoplankton, bacteria, and microzooplankton of Castle Lake. The increase in *Diacyclops* and decrease in *Daphnia* and *Diaptomus* abundance noted during the last several years should cause the crustacean zooplankton assemblage to change from primarily a grazer-dominated community to a community with much more carnivory. Consistent with these predictions, whole-lake monitoring (J. J. Elser, *personal observation*) has shown that water clarity (an inverse measure of algal biomass) decreased and total primary production increased at the same time that the zooplankton community structure shifted in Castle Lake.

Since our experiments were conducted during only one time period, one can question to what extent they are representative of the entire summer season. Research on the clear water phase (Lampert et al. 1986) has shown that the overall effect of zooplankton grazing on planktonic ecosystems is dependent on the composition of the algae, with strong zooplankton effects

TABLE 4. Algal species biovolume, μg/L, in each of the zooplankton species treatments, mean biovolume ± 1 SD is presented. Statistical differences were determined using two-tailed Dunnett *t* test results of logarithmically transformed data. Only data for those species observed in at least 80% of the samples are given.

	Removal	*Diacyclops*	*Diaptomus*	*Holopedium*	*Daphnia*
Peridinium inconspicuum	251 ± 37	278 ± 45	153 ± 19*	104 ± 33***	29.5 ± 23***
Arthrodesmus sp.	36.3 ± 8.9	37.2 ± 6.4	35.3 ± 8.7	28.0 ± 4.8	24.3 ± 11.3*
Scenedesmus bijuga	23.8 ± 14	25.6 ± 7.5	21.7 ± 15.9	9.2 ± 5.7	2.1 ± 3.0**
Oocystis sp.	9.2 ± 3.7	6.2 ± 5.5	6.6 ± 2.1	7.8 ± 2.6	4.7 ± 2.8*
Small flagellates	6.5 ± 2.9	5.7 ± 1.3	5.7 ± 1.5	5.5 ± 2.0	2.1 ± 1.1**
Dictyosphaerium pulchellum	4.1 ± 2.0	5.2 ± 5.1	5.7 ± 2.8	5.0 ± 2.6	1.2 ± 1.3*
Rhodomonas minuta	1.6 ± 0.9	2.0 ± 0.4	0.6 ± 0.1**	0.4 ± 0.2***	0.05 ± 0.03***
Synedra sp.	0.63 ± 0.12	1.34 ± 0.43**	1.00 ± 0.36	0.42 ± 0.13	0.51 ± 0.35
Microcystis flos-aquae	0.58 ± 0.37	0.38 ± 0.22	0.40 ± 0.22	0.41 ± 0.25	0.08 ± 0.10*
Dinobryon bavaricum	0.58 ± 0.39	0.33 ± 0.29	0.23 ± 0.30	0.47 ± 0.51	0.17 ± 0.14

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

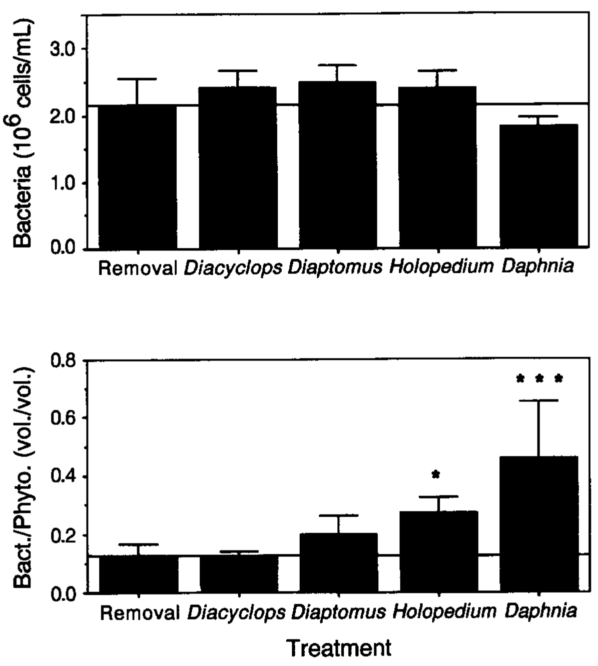

FIG. 3. The response of bacteria cell abundance and the ratio of bacterial biovolume to algal biovolume to the zooplankton species treatments. The volume of each bacteria cell was assumed to be 0.04 μm^3. See Fig. 1 for explanation of symbols.

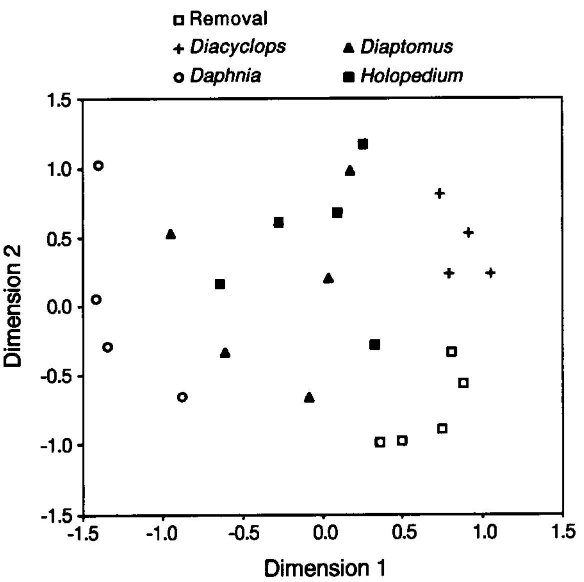

FIG. 5. Multidimensional scaling plot based on the planktonic community structure data presented in Fig. 1. The similarity matrix for this plot was generated using the covariance module of SYSTAT, using raw data transformed by subtracting the overall mean from the observation and dividing this product by the overall standard deviation. The purpose of this procedure was to obtain an objective measure of similarity or dissimilarity between and within the treatments based on the results obtained for the measured parameters.

expected when the phytoplankton is dominated by edible algae (e.g., diatoms and flagellates) and weak effects expected when the phytoplankton is dominated by grazing-resistant colonial forms or algae of poor nutritional quality (e.g., blue-greens) (Kerfoot et al. 1988). Generally speaking, the phytoplankton community of Castle Lake is rarely dominated by colonial forms, with the exception of a late-summer deep layer *Dinobyron* maximum, so zooplankton are likely to have a greater impact on the algae of this lake than in either ultra-oligotrophic or hypereutrophic lakes (Elser and Goldman 1991).

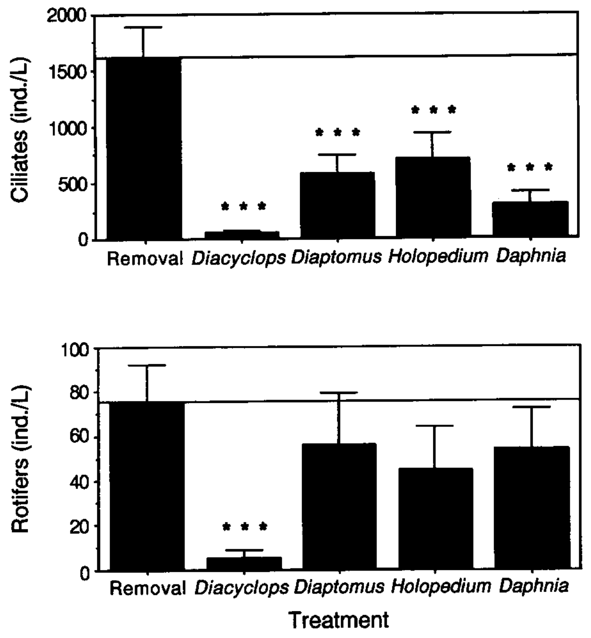

FIG. 4. The response of rotifer and ciliate abundance to the zooplankton species treatments. See Fig. 1 for explanation of symbols.

Classic characterizations such as carnivore and herbivore may not be completely appropriate for freshwater zooplankton, which are probably all omnivores to a greater or lesser extent. We know, for example, that *Diacyclops* severely depressed ciliate and rotifer microzooplankton abundance and had no notable effect on the algae, bacteria, or nutrient cycling, but we do not actually know whether *Diacyclops* only consumed microzooplankton. Regardless, the apparent effect of *Diacyclops* was exclusively that of a carnivore. This result was obtained despite the fact that much of the final zooplankton biomass in the *Diacyclops* treatment was composed of nauplii that are generally thought to be more herbivorous than cyclopoid copepodites and adults. Similarly, *Daphnia, Diaptomus,* and *Holopedium* may have reduced microzooplankton abundance through interference (direct physical interactions) or exploitative competition and not actually consumed them (Gilbert 1989), but their apparent roles were those of omnivores. Wickham and Gilbert (1993), however, suggest *Daphnia* suppression of microzooplankton is due to interference and direct predation as opposed to exploitative competition. Certainly none of the zooplankters we examined could be classified as exclusively herbivorous based on our experimental results. Classic definitions are further complicated by the fact that a major component of planktonic ecosystems (i.e., the protozoa) are often mixotrophic, that is, they consume particles such as bacteria or small algae and can photosynthesize. Any animal that consumes a mixotroph should therefore be an omnivore. More than anything else, our results probably suggest that strict definitions such as carnivory and herbivory may not be completely relevant in planktonic ecosystems, where food particle selection by zooplankton is generally based on prey size, particle detection, taste, etc. (DeMott and Moxter 1991) and is probably only marginally constrained by whether the particle in question is auto- or heterotrophic.

The results of our ANCOVA analyses indicate that in each case there was a significant zooplankton species effect, while the zooplankton biomass term was only significant in one case, i.e., the ratio of phytoplankton to bacteria biomass. These results indicate that different zooplankters have varying effects on the parameters measured, but they say nothing about the relative importance of zooplankton species vs. zooplankton biomass in influencing planktonic ecosystem processes and structure. This is because there was little variation in zooplankton biomass within zooplankton species treatments, although there was variation between treatments. Namely, the *Daphnia* and *Holopedium* treatments had final biomasses ≈3 times larger than those for the *Diaptomus* and *Diacyclops* treatments. Had we used identical zooplankton biomasses for each treatment, we would have expected greater effects in the *Diaptomus* and *Diacyclops* treatments. Clearly, this experiment was not designed to assess the importance of zooplankton biomass for any of the zooplankton species tested. Elser and Goldman (1991) examined the relative importance of *Daphnia* and ambient zooplankton biomass on Castle Lake phytoplankton. They observed that experimental gradients of either ambient Castle Lake zooplankton or *Daphnia* caused reductions in algal biomass and increases in dissolved ammonia and relative primary production with increasing biomass.

When adjusted for dissimilarities in zooplankton biomass between zooplankton species treatments our data suggest *Daphnia* and *Diaptomus* had grazing impacts of similar magnitudes, while *Holopedium* had qualitatively similar but weaker grazing impacts. In general these species influenced planktonic ecosystem structure in a manner expected from trophic cascade theory (Carpenter et al. 1985), that is, these zooplankters increased free nutrient concentrations, depressed phytoplankton community biomass, increased relative primary production, and depressed microzooplankton abundance (Figs. 1–4). *Daphnia* also reduced the abundance of the algae *Peridinium inconspicuum, Arthrodesmus* sp., *Scenedesmus bijuga, Oocystis* sp., *Dictyosphaerium pulchellum, Rhodomonas minuta, Microcystis flos-aquae,* and small flagellates. In similarly designed studies, Pace and Funke (1991) found *Daphnia pulex* usually reduced ciliate abundance, occasionally reduced chlorophyll *a* concentrations and heterotrophic flagellate abundance, and had no effect on bacterial abundance and production. Wickham and Gilbert (1991) showed *Daphnia pulex* generally reduced rotifer and ciliate growth rates, while *Bosmina longirostris* and *Daphnia galeata mendotae* had little influence on microzooplankton. None of the zooplankton species examined in their experiments had a significant effect on phytoplankton or bacterial abundance.

Of all the treatments, *Diacyclops* had the greatest effect on the ciliate and rotifer microzooplankton (Fig. 4). This result should be qualified with a few caveats. Namely, since we removed many other zooplankters such as nauplii, *Bosmina,* and juvenile *Daphnia,* which could have conceivably been the preferred prey for *Diacyclops,* from the lake water before starting the experiment, our results may not actually reflect the true effect of *Diacyclops* predation on typical zooplankton communities. Further, many prey species avoid predation by decreasing spatial overlap with their main predators (Williamson and Stoeckel 1990). However, since we enclosed both the microzooplankters and *Diacyclops* we prevented this possible prey escape mechanism. Our results probably exaggerated the typical effect of *Diacyclops* predation on microzooplankton communities.

While our experiment was not designed to explicitly test whether large body sized zooplankters have greater grazing impacts, as is commonly thought, a few observations are obvious. For example, *Diacyclops,* which was the smallest sized zooplankter examined (and which also had the smallest biomass), had the greatest impact on the microzooplankton, while *Daphnia* and *Diaptomus* generally had greater impacts on the measured parameters than the larger sized *Holopedium.* In contrast, Pace (1984) found that zooplankton biomass explained little residual variability for total phosphorus to chlorophyll relationships, while mean zooplankton biomass explained a significant amount of residual variability. Similarly, Vanni (1987) found an increase in mean zooplankton size and total community biomass, due to reduced fish predation, resulted in a decrease in total algal biomass, reductions in the abundance of edible algae, and a shift towards grazing-resistant algae. However, a more comprehensive investigation (90 zooplankton communities from 28 lakes) of the importance of zooplankton size (Cyr and Pace 1993) found only a weak relationship ($r^2 = 0.15$) between mean zooplankter body mass and zooplankton community grazing rate. These authors suggested grazing differences among zooplankton taxa may be a potentially important source of variability in this relationship. This is supported by observations of particle selection, which show far greater differences between zooplankton taxa than simple body size relations would suggest (Hessen 1985, DeMott 1986, DeMott and Moxter 1991).

To examine nutrient cycling and experimentally test the predictions of stoichiometric theory (Sterner et al. 1992), we measured the effects of the different zooplankton species on the DIN/SRP ratio (Fig. 1). *Diaptomus* disproportionately increased SRP relative to DIN, resulting in a low DIN/SRP ratio in this treatment. In contrast, *Daphnia* increased DIN relative to SRP, resulting in a high DIN/SRP ratio. These observations are consistent with recent work on the stoichiometry of N and P recycling by crustacean zooplankton (Sterner et al. 1992). According to stoichiometric theory, animals with low body N:P ratios should recycle nutrients at high N:P ratios relative to their food, while high N:P animals should regenerate at low ratios. Andersen and Hessen (1991) reported that *Daphnia* had a characteristically low N:P ratio and *Diaptomus* had a high N:P ratio. Our results for *Diacyclops* (no difference from the control treatment) are also consistent with stoichiometric theory since it is predicted that carnivores will consume food with elemental ratios similar to their own. This means carnivores will excrete few nutrients and these nutrients will be excreted at the ratio at which they were consumed (Brett 1993). Since *Holopedium* has a low body N:P ratio (Andersen and Hessen 1991), stoichiometric theory predicts this species will regenerate nutrients at a high N:P ratio, however, in contrast to theory, our data suggested that *Holopedium* regenerated relatively more SRP than DIN. Thus our results support stoichiometric predictions for three of the four zooplankters examined.

In contrast to many terrestrial investigations, our study did not show stimulation of total primary production in any of the zooplankton species treatments (in fact it was depressed in the *Daphnia* and *Holopedium* treatments), however relative primary production was stimulated in the *Daphnia* treatment (Fig. 2). Total primary production is algal production per volume lake water while relative primary production is algal production per unit algal biomass. Since zooplankton grazing should release nutrients, grazing could in theory stimulate the growth of those algal cells not grazed provided the algal community is nutrient limited. Thus grazing may depress total community production but stimulate the relative production of the surviving plants. The results of the present experiment showing depressions of total primary production and stimulation of relative primary production in some treatments are in contrast to those of Bergquist and Carpenter (1986), who found that total primary production was positively correlated with zooplankton biomass in grazing experiments. However, our findings are essentially the same as those of Svensson and Stenson (1991), who found reductions in total primary production and increases in relative primary production, and Uehlinger and Bloesch (1987), who found reductions in total primary production in response to zooplankton grazing. The present study is also consistent with two previous experiments from Castle Lake (Elser and Goldman 1991, Elser 1992), which found that ambient concentrations of zooplankton decreased total primary production and increased relative primary production. Thus zooplankton grazing does not usually stimulate total phytoplankton primary production, but it may often increase relative primary production.

Similar to phytoplankton, planktonic bacteria are limited by nutrients (particularly phosphorus) and are grazed by heterotrophic flagellates, ciliate and rotifer microzooplankton, and crustacean zooplankton. Since bacteria are generally smaller than algae they are thought to be grazed more by heterotrophic flagellates and microzooplankton, while algae are usually assumed to be grazed mostly by the larger crustacean zooplankton. Unlike most algae, bacteria derive their energy from the breakdown of organic compounds. Crustacean zooplankton may depress bacteria abundance by directly consuming them. In contrast, crustacean zooplankton may also stimulate bacterial standing stocks by depressing phytoplankton biomass thereby reducing nutrient competition between bacteria and algae, by depressing microzooplankton bacteria grazers, and by releasing organic compounds while feeding. The measured bacterial abundances for the four zooplankton treatments were never significantly different from the zooplankton removal treatment (Fig. 3). However, the *Diacyclops, Diaptomus,* and *Holopedium* treatments stimulated bacterial standing stock sufficiently and the *Daphnia* treatment depressed algal standing stock enough to result in the *Daphnia* treatment having significantly lower bacterial cell abundance than observed in the *Diacyclops, Diaptomus* and *Holopedium* treatments ($P < 0.01$). These data could be used to argue against a direct coupling between crustacean zooplankton grazing and bacterial abundance, in agreement with Pace and Funke (1991) and Wickham and Gilbert (1991) and in contrast to Riemann and Søndergaard (1986), if we use the control treatment as a frame of reference. However, if we base our conclusions on differences between the zooplankton treatments, there is evidence that *Daphnia* grazing may have reduced bacterial standing stocks, while *Diacyclops, Diaptomus,* and *Holopedium* stimulated the bacterioplankton. The latter conclusions are at least consistent with the feeding morphologies of these zooplankters (Hessen 1985), i.e., *Daphnia* are able to filter the smallest particles. Since *Daphnia* depressed phytoplankton biomass much more than they depressed bacteria abundance, *Daphnia* actually shifted the ratio between bacterial and algal biomass in the direction of the bacteria to a far greater extent than did the other zooplankton treatments. This result may reflect food preferences and feeding morphologies or it may simply be due to the fact that *Daphnia* also depressed micozooplankton, and possibly other heterotrophs, which are important consumers of bacteria.

The present investigation indicates the raptorial cyclopoid copepod *Diacyclops* was mainly carnivorous and decimated the microzooplankton. The filter-feeding cladocerans *Daphnia* and *Holopedium* and the raptorial and filter-feeding calanoid copepod *Diaptomus* were apparently omnivorous. These species regenerated nutrients, and depressed phytoplankton food and microzooplankton competitors. Coupled with our field observations indicating *Diacyclops* has greatly increased its abundance and *Daphnia* and *Diaptomus* have decreased their abundances during time preceding these experiments, our experimental results suggest Castle Lake should have entered a period in which grazing on the microzooplankton increased markedly, and phytoplankton biomass and total primary production increased. Consistent with these predictions, whole-lake monitoring (J. J. Elser, *personal observation*) has shown that water clarity (a measure of algal biomass) decreased and total primary production increased at the same time that the zooplankton community structure shifted in Castle Lake. These observations suggest seasonal and interannual changes in crustacean zooplankton community structure, brought about by interactions with planktivore communities or due to normal seasonal succession, should in turn have profound influences on the structure of the planktonic ecosystems.

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LITERATURE CITED

American Public Health Association. 1976. Standard methods for the examination of water and wastewater. American Public Health Association, Washington, D.C., U.S.A.

Andersen, T., and D. O. Hessen. 1991. Carbon, nitrogen, and phosphorus content of freshwater zooplankton. Limnology and Oceanography **36**:807–813.

Bergquist, A. M., and S. R. Carpenter. 1986. Limnetic herbivory: effects on phytoplankton populations and primary production. Ecology **67**:1351–1360.

Bogdan, K. C., and J. J. Gilbert. 1987. Quantitative comparison of food niches in some freshwater zooplankton. Oecologia **72**:331–340.

Brett, M. T. 1993. Comment on "Possibility of N or P limitation for planktonic cladocerans: an experimental test" (Urabe and Wantanabe) and "Nutrient element limitation of zooplankton production" (Hessen). Limnology and Oceanography **38**:1333–1337.

Carpenter, S. R., and A. M. Bergquist. 1985. Experimental tests of grazing indicators based on chlorophyll-*a* degradation products. Archiv für Hydrobiologie **102**:303–317.

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

Carrick, H. J., G. L. Fahnenstiel, E. F. Stoermer, and R. G. Wetzel. 1991. The importance of zooplankton-protozoan trophic couplings in Lake Michigan. Limnology and Oceanography **36**:1335–1346.

Cyr, H., and M. L. Pace. 1993. Allometric theory: extrapolations from individuals to communities. Ecology **74**:1234–1245.

DeMott, W. R. 1986. The role of taste in food selection by freshwater zooplankton. Oecologia **69**:334–340.

DeMott, W. R., and F. Moxter. 1991. Foraging on cyanobacteria by copepods: responses to chemical defenses and resource abundance. Ecology **72**:1820–1834.

DeNicola, D. M., C. D. McIntire, G. A. Lamberti, S. V. Gregory, and L. R. Ashkenas. 1990. Temporal patterns of grazer–periphyton interactions in laboratory streams. Freshwater Biology **23**:475–489.

Elser, J. J. 1992. Phytoplankton dynamics and the role of grazers in Castle Lake, California. Ecology **73**:887–902.

Elser, J. J., and C. R. Goldman. 1991. Zooplankton effects on phytoplankton in lakes of contrasting trophic status. Limnology and Oceanography **36**:64–90.

Feminella, J. W., and V. H. Resh. 1991. Herbivorous caddisflies, macroalgae, and epilithic microalgae: dynamic interactions in a stream grazing system. Oecologia **87**:247–256.

Fletcher, W. J. 1987. Interactions among subtidal Australian sea urchins, gastropods, and algae: effects of experimental removals. Ecological Monographs **57**:89–109.

Gilbert, J. J. 1989. The effect of *Daphnia* interference on a natural rotifer and ciliate community: short-term bottle experiments. Limnology and Oceanography **34**:606–617.

Goldman, C. R., and E. de Amezaga. 1984. Primary productivity and precipitation at Castle Lake and Lake Tahoe during twenty-four years, 1959–1982. Internationale Vereinigung für theoretische und angewandte Limnologie, Verhandlungen **22**:591–599.

Hessen, D. O. 1985. Filtering structures and particle size selection in coexisting Cladocera. Oecologia **66**:368–372.

Hobbie, J. E., R. J. Daley, and S. Jasper. 1977. Use of Nuclepore filters for counting bacteria by fluorescence microscopy. Applied and Environmental Microbiology **33**: 1225–1228.

Karban, R., and S. Y. Strauss. 1993. Effects of herbivores on growth and reproduction of their perennial host, *Erigeron glaucus*. Ecology **74**:39–46.

Kerfoot, W. C., C. Levitan, and W. R. DeMott. 1988. *Daphnia*–phytoplankton interactions: density-dependent shifts in resource quality. Ecology **69**:1806–1825.

Knisely, K., and W. Geller. 1986. Selective feeding of four zooplankton species on natural phytoplankton. Oecologia **69**:86–94.

Lampert, W., W. Fleckner, H. Rai, and B. E. Taylor. 1986. Phytoplankton control by grazing zooplankton: a study on the clear-water phase. Limnology and Oceanography **31**: 478–490.

Lampert, W., and P. Muck. 1985. Multiple aspects of food limitation in zooplankton communities: the *Daphnia-Eudiaptomus* example. Ergebnisse der Limnologie **21**:311–322.

Lehman, J. T, and C. D. Sandgren. 1985. Species-specific rates of growth and grazing loss among freshwater algae. Limnology and Oceanography **30**:34–46.

Lynch, M. 1980. The evolution of cladoceran life histories. Quarterly Review of Biology **55**:23–42.

Lundstedt, L., and M. T. Brett. 1991. Differential growth rates of three cladoceran species in response to mono- and mixed-algal diets. Limnology and Oceanography **36**:159–165.

Marker, A. F., C. A. Crowther, and R. J. M. Gunn. 1980.

Methanol and acetone as solvents for estimating chlorophyll-*a* and phaeopigments by spectrophotometry. Ergebnisse der Limnologie **14**:52–69.

Morrison, D. 1988. Comparing fish and urchin grazing in shallow and deeper coral reef algal communities. Ecology **69**:1367–1382.

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.

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

Paine, R. T. 1992. Food-web analysis through field measurements of per capita interaction strength. Nature **355**: 73–75.

Redfield, G. W. 1979. Temporal variation in diel vertical migration and the ecology of zooplankton in Castle Lake, California. Dissertation. University of California, Davis, California, U.S.A.

Riemann, B., and M. Søndergaard. 1986. Carbon dynamics in eutrophic temperate lakes. Elsevier, New York, New York, U.S.A.

Roberts, D. G., and D. M. Smith. 1988. Infrared gas analysis of both gaseous and dissolved CO_2 in small volume marine samples. Limnology and Oceanography **33**:135–140.

Solórzano, L. 1969. Determination of ammonia in natural waters by the phenolhypochlorite method. Limnology and Oceanography **14**:799–801.

Sterner, R. W., J. J. Elser, and D. O. Hessen. 1992. Stoichiometric relationships among producers, consumers and nutrient cycling in pelagic ecosystems. Biogeochemistry **17**: 49–67.

Stich, H. B. 1989. Seasonal changes of diel vertical migrations of crustacean plankton in Lake Constance. Archiv für Hydrobiologie (Supplement) **83**:355–405.

Strickland, J. D. H., and T. R. Parsons. 1972. A practical handbook of seawater analysis. Second edition. Bulletin of the Fisheries Research Board of Canada **167**.

Svensson, J.-E., and J. A. E. Stenson. 1991. Herbivoran impact on phytoplankton community structure. Hydrobiologia **226**:71–80.

Uehlinger, U., and J. Bloesch. 1987. The influence of crustacean zooplankton on the size structure of algal biomass and suspended and settling seston (biomanipulation in limnocorrals II). Internationale Revue der gesamten Hydrobiologie **72**:473–483.

Vanni, M. J. 1987. Effects of nutrients and zooplankton size on the structure of a phytoplankton community. Ecology **68**:624–635.

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.

Wilkinson, L. 1988. SYSTAT: the system for statistics. SYSTAT, Evanston, IIllinois, U.S.A.

Williamson, C. E., and M. E. Stoeckel. 1990. Estimating predation risk in zooplankton communities: the importance of vertical overlap. Hydrobiologia **198**:125–131.