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Limnology and Oceanography, Vol. 39, No. 3 (May, 1994), 486-492.

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Differential effects of zooplankton species on ciliate community structure

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Abstract

An in situ bioassay experiment using *Diacyclops bicuspidatus thomasi*, *Daphnia rosea*, *Diatomus novamexicanus*, and *Holopedium gibberum* single-species treatments was conducted to assess the influence of these zooplankters on the ciliate community structure of Castle Lake, California. At peak ambient abundances for adult individuals, these zooplankters all strongly depressed ciliate population growth rates. The ranking of the zooplankton-imposed ciliate death rates, from least to most severe, was *Holopedium* << *Daphnia* = *Diatomus* <<< *Diacyclops*. The ranking of ciliate-taxa-response death rates to the zooplankton treatments was *Halteria* = *Mesodinium* < *Askenasia* = *Urotricha* = (*Askenasia* <) *Strobilidium* << *Strombidium*. As total ciliate abundance was depressed by the zooplankton treatments, the relative frequency of the small ciliates (~5,000 μm^3) increased, and the relative frequency of the larger ciliates (~20,000 μm^3) decreased. These results suggest that both seasonal and long-term shifts in zooplankton community structure have the potential to dramatically alter the dynamics and structure of ciliate communities.

Zooplankton can potentially affect ciliate communities through direct predation and (or) exploitative and interference competition. Zooplankton predation on ciliates probably functions as an important link between the microbial community (bacteria, picoplankton, and flagellates) and higher trophic level zooplanktivores (i.e. fish). Further, it has been shown that at least *Daphnia* gain substantial nutritional benefit from consuming ciliates (Wickham et al. 1993). Despite this, very little research has examined the link between ciliates and zooplankton. Several studies have found ciliates to seasonally form a large portion of the total zooplankton biomass (e.g. Nauwerck 1963; Pace and Orcutt 1981; Pace 1985). Due to the high metabolic rates of ciliates, relative to rotifer and crustacean zooplankton, ciliates may play an important role in determining overall rates of grazing, nutrient regeneration, secondary production, etc.

and may be particularly important during seasonal periods when they are most abundant (Weisse et al. 1990).

Those studies which have examined ciliate-zooplankton interactions found that increasing total zooplankton (Porter et al. 1979; Arndt and Nixdorf 1991; Carrick et al. 1991) and *Daphnia* biomass (Gilbert 1989; Pace and Funke 1991; Wickham and Gilbert 1991, 1993) decreased total ciliate abundance and community growth rates. The influence of crustacean zooplankton predation on natural ciliate communities, however, remains largely unknown. For example, virtually nothing is known about zooplankton interspecies differences in predation on or competition with ciliates or about ciliate interspecies differences in susceptibility to zooplankton interactions. The statement of Pace (1981, p. 1115) that “the relative importance of predators as regulators of distribution and abundance [of ciliates] remains to be elucidated” is essentially unchallenged today. Even in marine ecosystems, where zooplankton predation on ciliates is well documented (Stoecker and Capuzzo 1990), very little is known about intraspecific differences in zooplankton grazing effects on ciliate community composition and dynamics. Since it is known that different zooplankton species

Acknowledgments

K.W. and M.T.B. contributed equally to this study. We thank S. Threlkeld, H. Arndt, and two anonymous reviewers for their comments to an earlier version of this study.

This study was funded by National Science Foundation grants BSR 90-06623 and BSR 89-18448 to C.R.G.

have vastly different feeding modes and food preferences (DeMott 1990) and it is also known that many ciliate species have strong jumping responses (Tamar 1979)—similar to the predator avoidance strategies of some zooplankters—one can predict a priori that crustacean zooplankters will differ in their effects on ciliate communities and that ciliate species will differ in their responses to zooplankton interactions.

The present study examines the individual effects of the crustacean zooplankters *Diacyclops bicuspidatus thomasi*, *Daphnia rosea*, *Diaptomus novamexicanus*, and *Holopedium gibberum* on the early-summer ciliate community of Castle Lake, California. Crustacean abundances representative of peak adult levels previously noted in the lake (Brett and Goldman in prep.) were used in this experiment. Knowledge of the zooplankton species-specific influences on ciliates is important because one can predict a priori that individual zooplankton species differ in their capacity to influence the distribution and abundance of ciliates and because crustacean zooplankton and ciliated protozoans are a key link in determining whether energy is efficiently transferred from the microbial community to the classic food chain (nutrients, algae, zooplankton, planktivores, piscivorous fish). Zooplankton communities typically undergo seasonal shifts in species composition which could in turn influence ciliate community dynamics. Furthermore, the crustacean zooplankton of the lake has undergone a pronounced overall shift during the last 5 yr, with reduced representation of *Diaptomus* and *Daphnia* and increased representation of *Diacyclops* (Brett and Goldman in prep.).

Methods

Lake water was collected at 1-, 3-, and 5-m depth and passed through an 83- μ m mesh screen to remove large zooplankton. Twenty-five 10-liter Cubitainers were incrementally filled with this screened lake water. The individual zooplankton species treatments were created by adding ~ 15 *Diacyclops*, 15 *Daphnia*, 15 *Diaptomus*, or 3 *Holopedium* liter⁻¹ to each of five separate Cubitainers. The removal (control) treatment consisted only of screened lake water. The Cubitainers were incubated at 5-m depth in Castle Lake. The experiment be-

gan on 13 June 1991 and ended 8 d later on 21 June. The temperature at 5-m depth was 13°C at the beginning of the experiment and 15°C at the end. The seasonal average for light penetration at 5 m is $23 \pm 4.6\%$ (± 1 SD) of surface values. A more detailed description of the lake is given by Goldman and de Amezaga (1984).

At the end of the experiment, samples for crustacean zooplankton enumeration were taken by pouring 6 liters of each treatment replicate through an 83- μ m screen and preserving with a Lugol's and sucrose solution. One liter of unfiltered water preserved with Lugol's solution was collected for ciliate, rotifer, and nauplii enumeration. Zooplankton juveniles and adults were counted and their biomass calculated from previously determined dry weights for these size classes of Castle Lake zooplankton (Redfield 1979). Ciliates were counted by concentrating the 1 liter of sample preserved in Lugol's solution to a small volume by simple sedimentation for 3 d and counting under an inverted light microscope by the Utermöhl technique. For the removal, *Daphnia*, *Diaptomus*, and *Holopedium* treatments, 500 ml of the sample was counted; the entire sample was counted for the *Diacyclops* treatment. These samples were counted within 4 months of collection and were stored at room temperature until enumeration. Because the ciliates were identified to genera, some taxa reported may contain several species. Individual ciliate biovolume was determined by measuring the length and maximal width for 10–40 individuals of each genera and assuming a prolate spheroid shape.

Data analyses

We used the difference between the ciliate population growth rates in the control and the zooplankton species treatments to calculate mortality associated with our zooplankton treatments: $r_{\text{control}} - r_{\text{treatment}} = d_{\text{zooplankton}} (d_z)$, where r is the logistic growth rate, d is the population death rate, and $r = b - d$ (b is the population birth rate). This variable d_z has the advantage of eliminating several extrinsic sources of variability, including differences in average abundances for the different ciliate taxa and differences in growth rates between ciliate taxa in response to the environmental characteristics of our experimental vessels. These

Table 1. Zooplankton abundance (ind. liter⁻¹), biomass ($\mu\text{g DW liter}^{-1}$), and fecundity (eggs adult ♀^{-1}) in the removal and zooplankton treatments. Initial and final observations are given, values presented are mean ± 1 SD. (DW—dry weight.)

Treatment	Abundance		Biomass		r (biomass change d^{-1})	Fecundity	
	Initial	Final	Initial	Final		Initial	Final
Removal			6.2	13 \pm 4.0	0.085 \pm 0.037		
<i>Diacyclops</i>	13.7	7.6 \pm 1.3	36	58 \pm 9.6	0.058 \pm 0.023	11	1.8 \pm 0.49
<i>Daphnia</i>	15.2	33.8 \pm 6.2	121	180 \pm 34	0.046 \pm 0.023	2.0	0.30 \pm 0.076
<i>Diaptomus</i>	15.2	12.7 \pm 0.7	55	66 \pm 4.6	0.023 \pm 0.009	1.2	0.71 \pm 0.13
<i>Holopedium</i>	2.8	14.0 \pm 2.1	43	150 \pm 23	0.155 \pm 0.020	5.5	0.88 \pm 0.17

differences were reflected in the pronounced differences in taxa-specific growth rates in our control treatments. Strictly speaking, this approach is only valid when $b_{\text{treatment}} = b_{\text{control}}$, which would not be true in cases of exploitative competition. Fortunately, any loss of potential birth rate due to exploitative competition is reflected in an equivalent overestimate of the true d_z . Thus, d_z expresses variation associated with real mortality due to predation or interference competition and inequities in the realized birth rates ($b_{\text{treatment}} \neq b_{\text{control}}$) due to exploitative competition. The parameter d_z does not, however, reflect mortality unrelated to the zooplankton treatments (i.e. background mortality).

Because 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 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 d_z as a dependent variable. The interaction term for this regression was not significant ($P = 0.453$), so we could conclude that our slopes were not significantly different and proceed with the full ANCOVA. We conducted a full ANCOVA with zooplankton treatment and ciliate taxa as independent variables and zooplankton biomass as a concomitant variable. We tested the effect of the individual zooplankton treatments on the ciliate growth rates by running a single-factor ANOVA with zooplankton treatment as the independent vari-

able and the residuals of a single-factor ANOVA (across ciliate taxa) as the dependent variable; that is, we first corrected for variation associated with ciliate taxa before we tested for differences between zooplankton species treatments. Individual zooplankton species treatments were declared significantly different based on the results of Dunnett t -tests. We conducted a similar analysis to determine differences in ciliate taxa-specific responses to the zooplankton treatments.

Results

The four zooplankton treatments (*Diacyclops*, *Daphnia*, *Diaptomus*, *Holopedium*) were started with individual abundances roughly equivalent to peak abundances previously noted for these species in Castle Lake (Table 1). During the experiment, biomass increased and fecundity decreased in each treatment. The increase in biomass in all treatments was due to recruitment of juveniles. Between 82 and 94% of the biomass in each treatment was from the treatment species; the remaining biomass was almost exclusively the rotifer *Polyarthra vulgaris* and copepod nauplii.

Seven ciliate taxa were commonly found in the samples from this experiment: *Strobilidium*, *Strombidium*, *Urotricha*, *Halteria*, *Mesodinium*, *Lagynophrya*, and *Askenasia* (Fig. 1). Each of these taxa (except *Urotricha*) increased in abundance from the start to the end of the experiment in the removal treatment. The full ANCOVA with zooplankton species treatments and ciliate taxa as independent category variables and zooplankton biomass as a concomitant variable showed strong and highly significant model effects for zooplankton species treatment, ciliate taxa response, and the interaction between zooplankton treatment and ciliate response and an insignificant

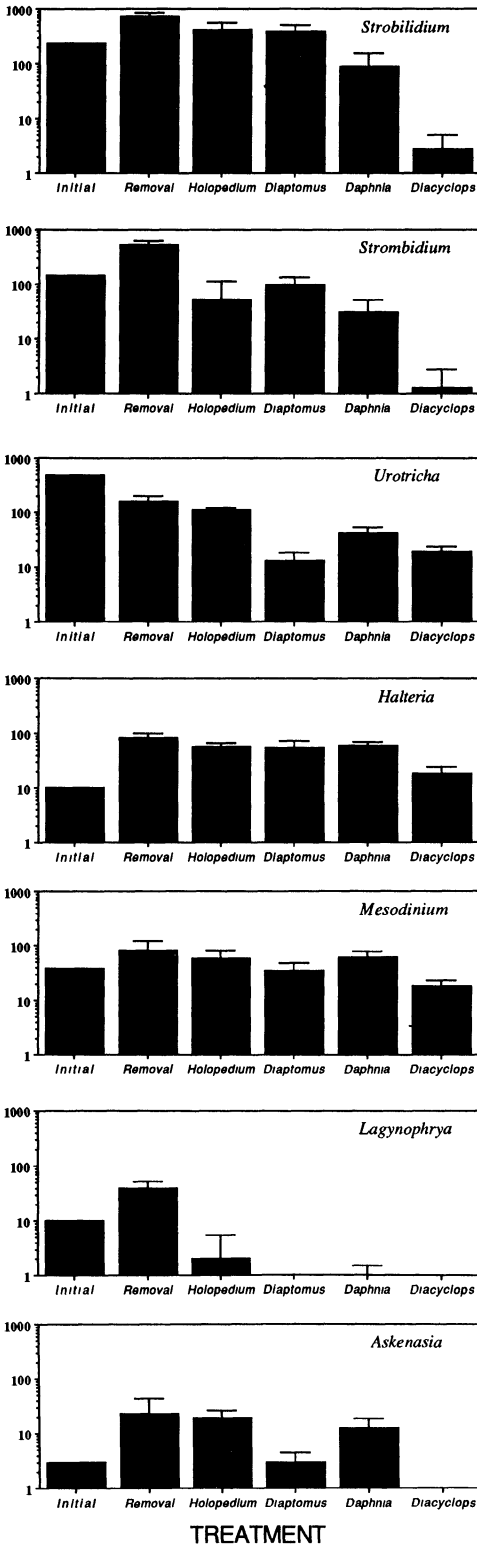


Table 2. Results of ANCOVA analysis with d_z as the dependent variable and zooplankton species treatment and ciliate taxa as independent category variables and zooplankton biomass as an independent concomitant variable.

Source	SS	df	F-ratio	P
Zooplankton species	0.845	3	66.68	0.000
Ciliate taxa	1.520	5	72.00	0.000
Zooplankton ciliate	1.029	15	16.25	0.000
Zooplankton biomass	0.015	1	3.47	0.066
Error	0.350	83		

effect for zooplankton biomass (Table 2). Dunnett *t*-tests conducted on the residuals of a single-factor ANOVA across ciliate taxa showed that *Holopedium* had the least severe effect on ciliate death rates followed by *Daphnia* and *Diaptomus*, which in turn had much less severe effects than did *Diacyclops* (Fig. 2). Dunnett *t*-tests conducted on the residuals of a single-factor ANOVA across zooplankton treatments showed that *Halteria* and *Mesodinium* were least depressed by interactions with zooplankton, followed by *Askenasia* = *Urotricha*, then by *Strobilidium*, and finally by *Strombidium*, which was most strongly depressed by zooplankton (Fig. 3). Strictly speaking, the results presented in Figs. 3 and 4 are only generalizations because the interaction term for the full ANCOVA was significant, indicating that the real nature of zooplankton ciliate interactions were taxa-specific.

If the ciliate abundance data are pooled into large (*Strobilidium*, *Strombidium*, and *Lagynophrya*) and small (*Urotricha*, *Halteria*, and *Mesodinium*) ciliates (Table 3), there is a very strong correlation between ln(total ciliate abundance) and the proportion of large ciliates across all treatments and replicates (Fig. 4). Furthermore, each of the large ciliates was significantly positively correlated with ln(total ciliate abundance), while each of the small ciliate genera was negatively correlated with ln(total ciliate abundance) (Table 3).

We compared the d_z for phytoplankton (Brett et al. in prep.) with the d_z for ciliates to determine whether exploitative competition may

Fig. 1. Ciliate taxa abundance, in individuals liter⁻¹, for the control and four zooplankton species treatments. Initial values refer to the ciliate abundances measured at the start of the experiment. Values are mean ± 1 SD.

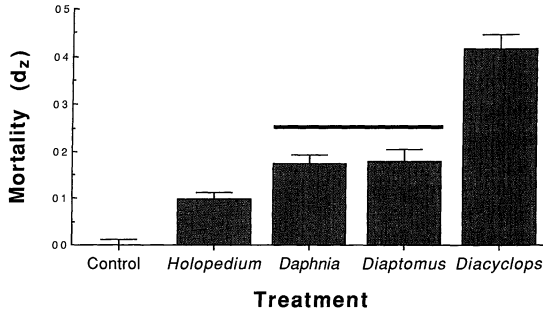


Fig. 2. Zooplankton species treatment-induced death rates (d_z). Values presented are mean death rate across all observations (0.208) plus the residual (± 1 SE) of a single-factor ANOVA across ciliate taxa (i.e. these values are corrected for variation associated with ciliate taxa). Individual zooplankton species treatments were declared significantly different based on the results of Dunnett t -tests. The horizontal bar indicates treatments that were not significantly different from each other.

have occurred. The d_z for phytoplankton as a percentage of d_z for ciliates was 0% for *Diacyclops*, 31% for *Diaptomus*, 80% for *Daphnia*, and 81% for *Holopedium*. If we assume that the algal concentrations in the experimental vessels were below the incipient limiting level (ILL) for ciliates and that ciliate growth is linearly depressed below the ILL, then we can speculate that exploitative competition may have been significant in the *Daphnia* and *Holopedium* treatments. However, these results could also suggest that *Daphnia* and *Holopedium* consumed ciliates at a slightly higher rate than they consumed algae.

Discussion

This experiment showed strong crustacean zooplankton species-level effects on total ciliate abundance, with *D. bicuspidatus thomasi*, *D. rosea*, *D. novamexicanus*, and *H. gibberum* all strongly depressing total ciliate abundance. In addition, the ciliate taxa differed strongly in their responses to interactions with zooplankton (Figs. 1–3). Previous research has shown negative relationships between *Daphnia* or zooplankton community biomass and total ciliate abundance or growth rates (e.g. Arndt and Nixdorf 1991; Carrick et al. 1991; Pace and Funke 1991). While the present experiment generally confirms these findings, our results suggest that zooplankton species differ in their propensity to depress ciliate abundance and that ciliate taxa differ in their sus-

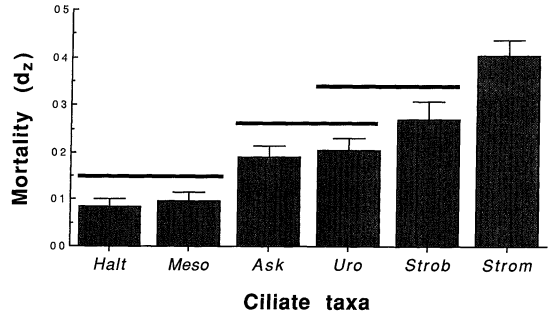


Fig. 3. Ciliate taxa response death rates (d_z). Details as Fig. 2, but across zooplankton species treatments (i.e. values are corrected for variation associated with the zooplankton treatments).

ceptibility to interactions with zooplankton. Further, there is evidence (i.e. the highly significant interaction term of our full ANCOVA) that the exact nature of zooplankton ciliate interactions is taxa-specific; for example, the escape responses used by the various ciliate taxa (i.e. jumping) may be effective against certain zooplankters but not against others. These results all suggest that seasonal succession in the crustacean zooplankton community may be a strong determinant of ciliate community dynamics and composition.

The cyclopid copepod *Diacyclops* clearly had the strongest effect on ciliates, followed by *Daphnia* and *Diaptomus* and then by *Holo-*

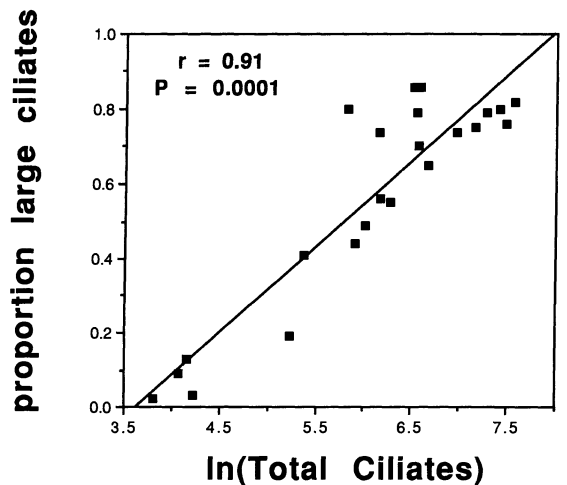


Fig. 4. Correlation between $\ln(\text{total ciliates})$ and the proportion large ciliates ($> 17,000 \mu\text{m}^3$) in the total ciliate community. Sizes and correlation with $\ln(\text{total ciliates})$ are given for each ciliate taxa in Table 3.

Table 3. Results of size measurements for the common ciliate taxa and correlations of proportion community composition with $\ln(\text{total ciliates})$ for these taxa. The average mortality due to zooplankton interactions (d_i) presented as mean ± 1 SE.

	Volume (μm^3)	Length (μm)	d_i (± 1 SE)	Correlation coefficient	<i>P</i>
<i>Mesodinium</i>	5,000	22.4	0.096 \pm 0.019	-0.88	0.0001
<i>Urotricha</i>	5,060	26.6	0.203 \pm 0.028	-0.75	0.0001
<i>Halteria</i>	5,270	22.2	0.084 \pm 0.016	-0.91	0.0001
<i>Askenasia</i>	11,500	31.5	0.191 \pm 0.022	0.21	0.3441
<i>Strombidium</i>	17,700	37.3	0.404 \pm 0.034	0.74	0.0001
<i>Lagynophrya</i>	20,500	52.8	—	0.64	0.0011
<i>Strobilidium</i>	22,500	40.5	0.269 \pm 0.039	0.77	0.0001

pedium, which had the weakest effects on ciliates (Fig. 2). These experimental results indicate that the shift in crustacean community composition noted in Castle Lake during the last 5 yr (Brett and Goldman in prep.)—i.e. increased representation of *Diacyclops* and decreased representation of *Daphnia* and *Diaptomus*—should in turn result in an overall crustacean zooplankton community with increased negative effects on the ciliate community due to direct-predation or exploitative and interference competition. Our results contradict the assertion of Carrick et al. (1991) that the species composition of the zooplankton community had little influence on ciliates. Our results are, however, consistent with those of Wickham and Gilbert (1991) who found strong differences in crustacean zooplankton species impacts on ciliates, with *Daphnia pulex* consistently strongly depressing ciliate abundance, the smaller *Daphnia galeata mendotae* having an intermediate effect, and *Bosmina longirostris* having no impact.

We also found pronounced differences between ciliate taxa in their overall responses to zooplankton interactions (Fig. 3); in addition, \ln -transformed total ciliate abundance was strongly positively correlated with the proportion of large ciliates across all treatments and replicates (Fig. 4), while the small ciliates were negatively related to total ciliate abundance and the large ciliates were positively related to total ciliate abundance (Table 3). Our results are essentially the opposite of those obtained by Carrick et al. (1991) and Wickham and Gilbert (1993), who found small ciliates and flagellates were more likely to be suppressed by interactions with crustacean zooplankton than were larger protozoans. Similar to our study, however, Arndt and Nixdorf (1991) found that

larger ciliates were more affected by zooplankton than were smaller ones. Our results do not necessarily indicate that larger ciliates were preferentially selected by crustacean zooplankton. These results could merely reflect the fact that small ciliates generally have higher cell division rates than do larger ciliates. Theoretically, even random exploitation will shift communities toward increased representation of taxa with high cell division rates.

The dramatic depressions in ciliate abundance noted in each crustacean species treatment suggest crustacean zooplankton, especially *Diacyclops*, can effectively transfer energy incorporated in ciliates to higher trophic levels, such as planktivorous fish. It must be said, however, that the experimental design we used does not allow us to rule out other explanations (e.g. exploitative or interference competition) for the declines in ciliate abundance noted in the zooplankton treatments. Thus, crustaceans may negatively impact ciliate communities but not assimilate energy from them, in which case the crustacean zooplankton would not function as a link between ciliates and zooplanktivores. In the present study, exploitative competition can be ruled out for the *Diacyclops* treatment, since phytoplankton community and species abundance and bacteria abundance were nearly identical between the removal and *Diacyclops* treatments. Exploitative competition may have been important in the *Daphnia* and *Holopedium* treatments because phytoplankton biomass was depressed at nearly the same rate as was ciliate abundance (81 and 80%, respectively) in these treatments. These results could mean, alternatively, that *Daphnia* and *Holopedium* selected ciliates at slightly higher rates than algae. Wickham and Gilbert (1993) used

an experimental design which was more appropriate for determining the role of exploitative competition (i.e. with and without *Daphnia* and added algae) and concluded that exploitative competition probably did not occur, although predation and interference competition did.

The initial and final removal ciliate abundances noted in this study are outliers relative to published relationships between chlorophyll *a* and ciliates liter⁻¹ (Pace 1985). When the experiment started, we observed 920 ciliates liter⁻¹; we expected 4,700 ciliates liter⁻¹ based on the observed chlorophyll concentrations in the surface waters of Castle Lake (1.7 µg liter⁻¹) at that time. If our experimental results are valid, however, we can explain the unusually low ciliate abundances noted in the initial samples by intense predation from *Diacyclops*, which has seen its abundance increase dramatically in Castle Lake during the last several years (Brett and Goldman in prep.).

Our experimental results showed the abundance of planktonic ciliates was reduced by crustacean zooplankton. This suggests that the zooplankters *Daphnia*, *Diatomus*, *Holopedium*, and especially *Diacyclops* may be able to efficiently transfer energy between the ciliate community and higher trophic levels, such as planktivorous fish. There were also strong zooplankton species effects on both ciliate abundance and community structure, which suggests that interactions with crustacean zooplankton may be a driving force behind ciliate community structure and seasonal succession.

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Submitted: 19 August 1992

Accepted: 18 May 1993

Amended: 19 July 1993