

**Shifts in Phytoplankton Size Structure and Community Composition During Grazing by Contrasting Zooplankton Assemblages**



Ann M. Bergquist; Stephen R. Carpenter; John C. Latino

*Limnology and Oceanography*, Vol. 30, No. 5 (Sep., 1985), 1037-1045.

Stable URL:

<http://links.jstor.org/sici?sici=0024-3590%28198509%2930%3A5%3C1037%3ASIPSSA%3E2.0.CO%3B2-O>

*Limnology and Oceanography* is currently published by American Society of Limnology and Oceanography.

---

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/limnoc.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

---

JSTOR is an independent not-for-profit organization dedicated to creating and preserving a digital archive of scholarly journals. For more information regarding JSTOR, please contact [support@jstor.org](mailto:support@jstor.org).

## Shifts in phytoplankton size structure and community composition during grazing by contrasting zooplankton assemblages<sup>1</sup>

Ann M. Bergquist, Stephen R. Carpenter, and John C. Latino<sup>2</sup>

Department of Biology, University of Notre Dame, Notre Dame, Indiana 46556

### Abstract

Contrasting zooplankton assemblages consistently produced different compositional shifts in a phytoplankton community. Two experiments in 120-liter enclosures were used to assess the responses of the algae to two different-sized zooplankton communities. Grazing by a mixture of small copepods, *Bosmina longirostris*, and rotifers led to increased growth of phytoplankters with greatest axial linear dimensions <25  $\mu\text{m}$  and ratios of surface area to volume <2.6, such as *Chlamydomonas* and Chlorococcales. Larger phytoplankton taxa such as *Asterionella formosa*, *Closteriopsis longissimus*, and *Synedra* sp. declined in the presence of small zooplankters. In contrast, a mixture of large zooplankters dominated by *Daphnia pulex* and *Diaptomus oregonensis* caused declines in phytoplankters with greatest axial linear dimensions <60  $\mu\text{m}$  and ratios of surface area to volume <2.75, while larger algae such as *Aphanocapsa* and *Dinobryon* increased. Discriminant analyses showed that volume and surface area were the most effective characters for determining the response of algae to grazers. Zooplankton community structure was important in determining the responses of algal assemblages to grazing.

Body and cell size are factors frequently involved in discussions of plankton dynamics. Size distributions of herbivorous zooplankton are regulated by predation (Hall et al. 1976). Several allometric relationships suggest that systematic shifts in zooplankton size distribution should in turn alter the phytoplankton size distribution (Carpenter and Kitchell 1984): the range of cell sizes ingested depends on zooplankter size (Burns 1968; Gliwicz 1980); nutrient excretion rates are size-specific (Peters and Rigler 1973; Ejsmont-Karabin 1983); and cell size influences rates of algal nutrient uptake (Shuter 1978; Smith and Kalf 1982), growth (Banse 1976, 1982), and sinking (Walsby and Reynolds 1980).

Nevertheless, the importance of cell size in the grazing response of algal communities is not clearly understood. The size range of particles ingested depends on zooplankter size (Burns 1968; Gliwicz 1980), but within the ingestible range selectivity is more complex and varies among zooplankton taxa (Peters and Downing 1984). In grazing experiments with mixed assemblages, algal re-

sponses appear to be size-related (Porter 1977), but the importance of size has not been compared directly with that of other algal properties such as spines, mucilage, and coloniality, which may mitigate grazing losses (Sournia 1982). Lehman and Sandgren (1985) emphasized that the response of algae to zooplankton is a net result of grazing loss and of growth, which may be stimulated by recycled nutrients. They noted that grazing responses were not strictly size-dependent. When some algal taxa responded differently from one experiment to the next, the differences were attributed to changes in zooplankton size. Much of the apparent variability in algal responses to grazing may be due to differences in zooplankton size or species composition. However, the effects of contrasting zooplankton assemblages on a single phytoplankton assemblage have not been compared experimentally.

In our experiments we sought answers to two important unresolved questions about the relationship of grazing to algal size. First, how effective is cell size vs. other morphological characteristics in predicting the response of algae to grazing? Second, are algal responses and their relationship to cell size familiar for contrasting zooplankton assemblages? To address these questions, we determined species-specific and size-specific

<sup>1</sup> A contribution from the University of Notre Dame Environmental Research Center, supported by the Houston Endowment and NSF grant BSR 83-08918.

<sup>2</sup> Present address: IBM Chemical Environmental Analysis 1, East Fishkill, New York 12533.

responses of phytoplankton to grazing. Like Lehman and Sandgren (1985), who used 3–4-day experiments, we used brief experiments (5 days). Periods of a few days characterize changes in algal species' growth and loss rates in lakes (Lehman and Sandgren 1985), yet are shorter than the intervals over which grazing rates change significantly (Harris 1980; Carpenter and Kitchell 1984). Time-course experiments confirm that changes in density of species and size classes plateau in a few days, while zooplankton biomass can be held essentially constant and enclosure effects appear minimal (Lehman 1979; Lehman and Sandgren 1985; Bergquist in prep.). We examined the responses of algal community composition and size distribution to grazing by two natural zooplankton assemblages with contrasting size distributions, at zooplankton densities comparable to those found in patches in the lakes. Discriminant analyses compared the usefulness of size-related variables and other morphological characters for predicting responses of algae to grazers.

We thank J. and M. Elser, G. Sprules, and an anonymous referee for comments; J. Lehman for suggestions; R. Greene for verifying plankton identifications; and Mr. and Mrs. O. J. Stewart for help and hospitality at the field station.

#### Study sites

Peter and Tuesday Lakes are small (2.4 and 1.2 ha), but relatively deep (19 and 21 m) brown-water lakes. They are about 1 km apart, in section 36, T45N R42W, Gogebic Co., Michigan, on the University of Notre Dame Environmental Research Center properties. These lakes and their plankton have been described elsewhere (Schmitz 1958; Stross and Hasler 1960; Kitchell and Kitchell 1980).

The two lakes have very different fish communities (J. F. Kitchell and J. R. Hodgson per. comm.) and consequently distinct zooplankton assemblages. Peter Lake, which supports largemouth bass (*Micropterus salmoides*), has no zooplanktivorous fish, and the zooplankton is dominated by large *Daphnia pulex* and *Diatomus oregonensis*. Its phytoplankton is dominated by large unicellular algae such as *Micrasterias* as well

as colonial forms such as *Sphaerocystis schroeteri*. Tuesday Lake has a fish fauna which consists of three zooplanktivores: mudminnows (*Umbra limi*), redbelly dace (*Chrosomus eos*), and finescale dace (*Chrosomus neogaeus*). Its zooplankton is dominated by rotifers and small cladocerans and copepods. Its phytoplankton is generally smaller than that of Peter Lake and is dominated by unicellular Chlorococcales.

#### Materials and methods

We did two experiments using the contrasting zooplankton communities of Peter and Tuesday Lakes. In each experiment nine 120-liter polyethylene enclosures suspended from bicycle inner tubes were floated in Tuesday Lake and filled with lake water filtered through 75- $\mu\text{m}$ -mesh Nitex net, which removed 82% of the ambient animals. The remaining animals were small rotifers and nauplii (49 animals liter<sup>-1</sup> in experiment 1 and 27 animals liter<sup>-1</sup> in experiment 2). These were the only animals in the control bags, to which no additional zooplankters were added. Zooplankters from each lake were collected and concentrated by vertical hauls (80- $\mu\text{m}$  mesh). Some small rotifers were not collected, but the mesh size was chosen to maximize the nets' efficiencies of removing or concentrating zooplankton without substantially altering phytoplankton assemblages or zooplankton biomass. The entire water column to a depth of 12 m was sampled in Peter Lake, but only epilimnetic (3 m) hauls were made in Tuesday Lake. Zooplankters were acclimated overnight to lake surface temperature. 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 in Peter Lake was determined by sampling the water column with a clear Van Dorn bottle at 1.0-m intervals to a depth of 12 m. In Tuesday Lake, the water column was sampled at 0.5-m intervals to a depth of 3 m; this marked the bottom of the thermocline and zooplankters were absent below this depth. Samples from each lake were filtered through a 75- $\mu\text{m}$ -mesh Nitex net, pooled, and enumerated. Zooplankton biomasses were estimated by drying at 100°C for 96 h

and weighing triplicate 250-ml samples of zooplankters concentrated by tows and by counting the number of individuals in a fourth 25-ml sample for each lake. Concentrations were calculated as animals per liter and dry weight biomass per liter.

In experiment 1 (31 July–4 August 1982) zooplankton from Peter Lake was added to three bags to give concentrations of 2.348 mg liter<sup>-1</sup> (5.2 times mean lakewide concentration). Tuesday Lake zooplankton was added to another three bags to yield concentrations of 0.515 mg liter<sup>-1</sup> (3.9 times mean epilimnion concentration). The high zooplankton densities were used to elicit strong, rapid responses from the phytoplankton while minimizing enclosure effects. The densities are similar to the concentrations of zooplankters aggregated in patches in the lakes. Three bags did not receive zooplankton and served as controls.

This experimental design was repeated in experiment 2 (9–13 September 1982). Zooplankton additions from Peter Lake were 1.600 mg liter<sup>-1</sup> (4.8 times mean lakewide concentration) and from Tuesday Lake were 0.299 mg liter<sup>-1</sup> (4.3 times mean epilimnion concentration). These biomasses were <70% of those used in experiment 1.

Bags were stirred before sampling. A 500-ml initial and final water sample and 300-ml phytoplankton sample were collected from each bag and from Tuesday Lake with a clear Van Dorn bottle at 0.5-m depth. Subsamples for phytoplankton counts were preserved in Lugol's solution. Triplicate zooplankton samples totaling 9.6 liters were pooled, filtered through 75- $\mu$ m-mesh Nitex net, and preserved with Formalin. Zooplankters were counted until the standard error was <10% of the mean for each sample and measured under a dissecting microscope.

The entire phytoplankton sample from each bag was settled for 3 days, and the concentrated sample was subsampled into Sedgwick-Rafter cells. At least four preparations were examined for each bag. Phytoplankton was identified according to Prescott (1962). The only phytoplankton taxa collected in zooplankton tows (*Micrasterias* sp., *S. 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 each sample. Greatest axial linear dimension (GALD) and the shortest axis perpendicular to it were also measured. Twenty specimens of each alga were measured in detail so that volumes and surface areas could be estimated. Algal shapes were approximated by composite geometric models (Pip and Robinson 1982). Surface areas and volumes for colonial or filamentous algae were determined for the entire algal unit, and the number of cells per unit was recorded.

For each algal taxon in each treatment (control, Peter, or Tuesday) in each experiment, final density was compared to initial density by Student's *t*-test (2 df). To test for grazing effects, we compared the mean final concentration (counts from three replicate bags) for each algal taxon from each zooplankton treatment (Peter or Tuesday) in each experiment to the final mean concentration (counts from three replicate bags) of that alga in the control treatment (*t*-test, 4 df). Taxa with significant responses to grazing were classified as "increasers" or "decreasers." Discriminant function analysis was used to determine whether algal morphology and size-related characters could be used to distinguish between increasing and decreasing algal taxa under grazing by each of the two zooplankton assemblages. Nine algal characteristics were used as classification variables. Five of these (cell wall, projections, motility, gelatinous covering, and armor) were recorded as present or absent for each taxon. The remaining four (volume, surface area, GALD, and cells per algal unit) were logarithmically transformed.

### Results

The zooplankton assemblages differed substantially. The major species in Peter Lake were *D. pulex* and *D. oregonensis*, while Tuesday Lake was dominated by rotifers and smaller cladocerans and copepods (Table 1). Consequently, the zooplankton size distributions in the two treatments differed markedly (Fig. 1). Tuesday Lake zooplankters were substantially smaller, the majority <0.5 mm long. The Peter Lake

Table 1. Initial composition (animals per liter  $\pm$  SE) of zooplankton added to bags by experiment and lake source. Taxa are arranged by body length from longest to shortest. Minor species each constitute  $<1\%$  of the sample.

	$\bar{x} \pm SE$	
	Exp. 1	Exp. 2
<b>Peter Lake</b>		
<i>Daphnia pulex</i>	68 $\pm$ 6.0	28 $\pm$ 3.5
<i>Holopedium gibberum</i>	—	4 $\pm$ 0.5
<i>Diaptomus oregonensis</i>	80 $\pm$ 6.1	36 $\pm$ 2.2
<i>Eucyclops</i> sp.	9 $\pm$ 0.8	12 $\pm$ 1.0
<i>Asplanchna priodonta</i>	2 $\pm$ 0.1	4 $\pm$ 0.3
<i>Cyclops varicans rubellus</i>	9 $\pm$ 0.7	16 $\pm$ 0.9
<i>Chydorus</i> sp.	3 $\pm$ 0.4	—
Copepodites	27 $\pm$ 0.9	30 $\pm$ 0.8
Nauplii	53 $\pm$ 3.2	29 $\pm$ 2.6
<i>Keratella cochlearis</i>	39 $\pm$ 1.9	35 $\pm$ 2.0
Minor species	6 $\pm$ 0.9	8 $\pm$ 1.1
Total	296	202
<b>Tuesday Lake</b>		
<i>Diaphanosoma leuchtenbergianum</i>	—	6 $\pm$ 0.6
<i>Diaptomus</i> sp.	11 $\pm$ 0.8	7 $\pm$ 0.9
<i>Cyclops varicans rubellus</i>	22 $\pm$ 2.0	19 $\pm$ 1.5
<i>Trichocerca cylindrica</i>	99 $\pm$ 7.3	51 $\pm$ 4.6
<i>Bosmina longirostris</i>	55 $\pm$ 5.8	51 $\pm$ 5.3
<i>Trichocerca multicornis</i>	23 $\pm$ 1.8	26 $\pm$ 2.1
Copepodites	44 $\pm$ 2.2	52 $\pm$ 1.9
<i>Polyarthra vulgaris</i>	199 $\pm$ 14.1	64 $\pm$ 5.8
Nauplii	144 $\pm$ 12.0	84 $\pm$ 7.9
<i>Keratella cochlearis</i>	409 $\pm$ 28.3	199 $\pm$ 12.6
Minor crustaceans	22 $\pm$ 2.4	13 $\pm$ 3.0
Minor rotifers	77 $\pm$ 8.5	71 $\pm$ 6.9
Total	1,105	643

assemblage was dominated by much larger zooplankton, with many *D. pulex*  $>2.0$  mm long. Although animal densities were much lower in the Peter Lake bags (Table 1), the zooplankton biomass was much greater. In experiment 1 the biomass of the larger Peter Lake zooplankton was 4.56 times that of the smaller animals of Tuesday Lake. In experiment 2 the biomass was 5.35 times as great.

Each zooplankton assemblage changed little between experiments. Although densities were lower in experiment 2 than in experiment 1 for both treatments (Fig. 1),

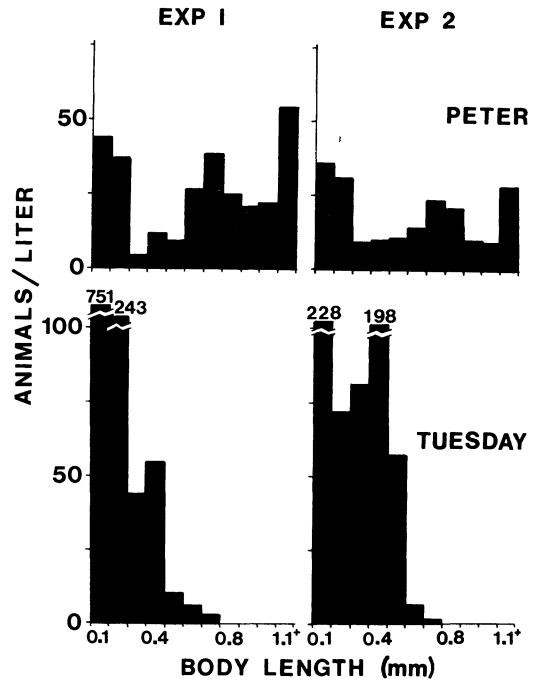


Fig. 1. Initial abundances (animals per liter) by size class of zooplankton added to bags in experiments 1 and 2.

species composition remained similar (Table 1). *Daphnia pulex*, the largest grazer in Peter Lake, dropped in abundance from 23% of the assemblage in experiment 1 to  $<14\%$  in experiment 2, and consequently, the size distribution of Peter Lake zooplankton shifted to slightly smaller classes (Fig. 1). Rotifers comprised 73% of the animals in the Tuesday Lake assemblage in experiment 1 and 64% in experiment 2. The Tuesday Lake zooplankton showed increases in its larger size classes in experiment 2.

Bag-to-bag variability within treatments was small in both experiments. Coefficients of variation for algal units per milliliter in sets of three replicate bags were 14.5–21.3% in experiment 1 and 8.7–17.5% in experiment 2. Consequently, standard errors were small relative to the means ( $<12.3\%$  in all cases) and 65 of 126 tests for algal response gave significant results (Table 2).

The contrasting zooplankton assemblages in both experiments consistently caused opposite shifts in phytoplankton size distribution (Fig. 2). Large phytoplankters ( $>100$

Table 2. Phytoplankton responses by major algal taxon arranged from shortest to longest average GALD. Bags with Peter Lake zooplankton—P; bags with Tuesday Lake zooplankton—T; bags without zooplankton—C. D—Decreaser ( $P < 0.05$ ); I—increaser ( $P < 0.05$ ); N—no significant change; A—absent. Responses in columns P and T are relative to control densities and column C responses are relative to initial lake density.

	Exp. 1			Exp. 2		
	P	T	C	P	T	C
Chlorococcales (unicellular, nonmotile)	D	I	I	D	I	I
<i>Chlamydomonas</i>	D	I	I	D	I	N
<i>Cosmarium</i> sp.	N	N	N	D	N	N
<i>Scenedesmus quadricauda</i>	D	N	I	D	I	I
<i>Euglena</i> sp.	D	D	N	A	A	A
<i>Tetraedron regulare</i>	A	A	A	D	N	I
<i>Cerasterias staurastroides</i>	A	A	A	I	N	I
<i>Euglena gracilis</i>	N	D	D	N	N	D
<i>Gleodinium</i> sp.	D	D	N	A	A	A
<i>Aphanocapsa</i> sp. (GALD < 60 $\mu\text{m}$ )	D	D	N	D	N	N
<i>Frustulia</i> sp.	N	N	N	N	N	I
<i>Staurastrum</i> sp.	N	N	I	N	N	N
<i>Microcystis incerta</i>	N	N	I	A	A	A
<i>Perdinium limbatum</i>	N	D	D	D	D	D
<i>Dinobryon</i> spp. (GALD < 70 $\mu\text{m}$ )	I	N	N	N	N	N
<i>Schroderia setigera</i>	D	D	N	A	A	A
<i>Tabellaria</i> sp.	N	N	N	N	N	I
<i>Aphanocapsa</i> sp. (GALD $\geq$ 60 $\mu\text{m}$ )	I	N	D	I	N	N
<i>Asterionella formosa</i>	N	D	I	N	D	N
<i>Closteriopsis longissimus</i> (GALD < 110 $\mu\text{m}$ )	A	A	A	N	N	D
<i>Chryso-sphaerella longispina</i>	I	N	D	A	A	A
<i>Dinobryon</i> spp. (GALD $\geq$ 70 $\mu\text{m}$ )	I	N	D	I	N	N
<i>Synedra</i> sp.	A	A	A	I	D	N
<i>Fragillaria crotonensis</i>	A	A	A	I	N	N
<i>Zygonema</i> sp.	A	A	A	I	N	D
<i>Closteriopsis longissimus</i> (GALD $\geq$ 110 $\mu\text{m}$ )	N	D	N	I	N	D
<i>Mougeotia</i> sp.	A	A	A	I	N	D

$\mu\text{m}$ ), which included colonial and filamentous as well as unicellular algae, responded to grazing by Peter Lake zooplankton by increasing in density, while smaller algae (<20  $\mu\text{m}$ ) were severely depressed in numbers. Small algae (<20  $\mu\text{m}$ ) increased in density in bags with Tuesday Lake zooplankton, and densities of large algae (>100

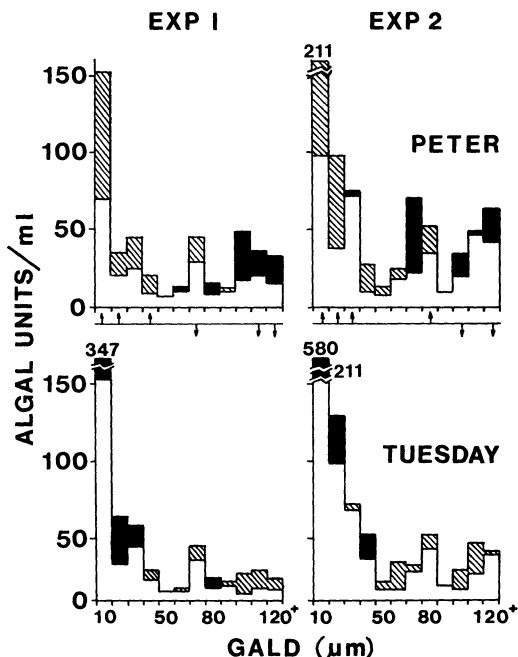


Fig. 2. Final phytoplankton concentrations by size class for each experiment. Bar with arrows shows change with time by size class in control bags. Arrows appear only for significant ( $P \leq 0.05$ ) changes and the orientation reflects the direction of the change. Key: solid bars—increase above control level, hatched bars—decrease below control level. Pooled SE  $\pm 7.9$  for experiment 1 and  $\pm 9.5$  for experiment 2.

$\mu\text{m}$ ) fell below control levels. Results were similar in both experiments.

Comparisons of initial and final phytoplankton densities in control bags showed that small size classes increased during the experiment, while large size classes decreased (Fig. 2). These trends were magnified in bags with Tuesday Lake zooplankton, but reversed in bags with Peter Lake zooplankton. In the latter bags, phytoplankters with values of GALD <20  $\mu\text{m}$  declined in density while phytoplankters with values of GALD >100  $\mu\text{m}$  increased in density during both experiments.

Comparisons of final phytoplankton densities in control bags with ambient Tuesday Lake conditions at the end of each experiment gave some indication of enclosure effects on the organisms. Small algal taxa (<20  $\mu\text{m}$ ) were generally in higher concentrations in control bags than in the lake at the end of experiment 1, but similar at the end of

experiment 2. Large algal taxa tended to be reduced in number in both experiments in the bags. Two algal taxa did not appear to grow well in the bags under any circumstances: *Euglena gracilis* and *Peridinium limbatum*.

Of the 27 common algal taxa, 22 responded significantly to at least one of the zooplankton treatments (Table 2). Three taxa (*Aphanocapsa* sp., *Closteriopsis longissimus*, and *Dinobryon* spp.) showed significant size shifts during one or more experiments. These taxa were divided into size classes that responded differently to grazing, and in subsequent analyses we treated these size classes as distinct groups with respect to response to grazing. No algal taxa increased under grazing by either zooplankton assemblage, but some, such as small *Aphanocapsa* sp. and *P. limbatum*, decreased with both treatments. *Chlamydomonas* and small unicellular chlorococcalean algae decreased in density with large grazers, but increased in bags with small zooplankters. Eight of the taxa showed no change in density when exposed to Tuesday Lake zooplankton, but increased in density in bags with Peter Lake grazers; all of these except *Cerasterias staurastroides* had GALD values  $>60 \mu\text{m}$ . Only five taxa showed no response to either treatment.

In Tuesday Lake bags, 15 of the 16 significant responses to grazing occurred when there was either no significant change in the control bags or grazers amplified the growth response in control bags (i.e. the increase in grazed bags was greater than the increase in the control bags, or the decrease in grazed bags was greater than the decrease in control bags) (Table 2). However, in 12 of 26 cases Peter Lake zooplankton reversed the growth responses observed in controls. Final densities after grazing by Peter Lake zooplankton significantly exceeded initial densities for large *Aphanocapsa*, *Chrysosphaerella longispina*, large *C. longissimus*, large *Dinobryon*, and *Mougeotia* in all cases where these phytoplankters were enhanced over the controls. Significant declines in density during experiments with Peter Lake zooplankton were recorded for *Chlamydomonas*, Chlorococcales, and *Scenedesmus quadricauda*. Three taxa (*Asterionella for-*

*mosa*, *Tetraedron regulare*, and *Zygonema*) changed significantly relative to the controls even though their densities did not change significantly during grazing by Peter Lake zooplankton, because controls showed statistically significant changes during the experiment (Table 2).

We can draw no conclusions about grazing of algal taxa that did not change significantly (N in Table 2). These taxa usually were rare ( $<5$  per ml) or showed high bag-to-bag variability. Therefore we excluded these taxa from discriminant analyses intended to compare the effects of selected morphological features on grazing response.

Standardized discriminant function coefficients consistently weighed volume and surface area more heavily than other characteristics in determining responses of algae to grazing (Table 3). The presence or absence of a cell wall was also of some importance in responses of algae to Peter Lake zooplankton. The variable armor was important for Peter Lake bags in experiment 1: most of the increasers had loricas or similar covering, while only one of the decreasers was so protected. Projections were important in the response to Tuesday Lake zooplankton in experiment 1: three decreasers but no increasers had this trait.

Each discriminant function was quite successful in classifying algal taxa as increasers or decreasers. In experiment 1, classification was 100% correct. In experiment 2, correct classifications were obtained for 14 of the 15 algae in bags with Peter Lake zooplankton. The misclassified alga was *C. staurastroides*, a small projection-bearing phytoplankter. The discriminant function for Tuesday Lake zooplankton in experiment 2 successfully classified 5 of 6 algal taxa. The only misclassified alga was *S. quadricauda*, a small increaser with spines.

Algal community data are commonly summarized by the GALD value (which is easily measured), the ratio of surface area to volume (S:V), or both. Although the GALD value varies 3–4 orders of magnitude among phytoplankters, S:V usually varies only about tenfold and is apparently conserved (Lewis 1976; Reynolds 1984). Because untransformed S:V (dimensions:  $\text{length}^{-1}$ ) decreases with increasing cell size,

Table 3. Characters used in the discriminant analyses and the values of their standardized discriminant function coefficients. Within a column, the highest coefficients (by absolute value) correspond to the variables that were most influential in distinguishing between taxa that increased or decreased under grazing. Bags with Peter Lake zooplankton—P; bags with Tuesday Lake zooplankton—T.

Character	Exp. 1		Exp. 2	
	P	T	P	T
Volume	-3.340	26.195	4.245	1.094
Surface area	3.317	-18.752	-3.518	0
Cell wall	-1.055	-4.726	0.788	0
Projections	0.670	15.090	0.237	0.251
GALD (greatest axial linear dimension)	-0.663	0	-0.673	0
Motility	-0.442	2.842	0.382	-0.358
Gelatinous sheath or mucilage	0.901	-2.129	-0.211	0.061
Armor (plates or shell)	1.531	-0.219	-0.210	0
Cells per algal unit	0	0	0.204	0

shape and size are confounded. Differences in shape, which may be important in grazing responses, can be investigated with Vogel's (1981) dimensionless  $S:V$  (square root of surface area divided by cube root of volume).

We plotted dimensionless  $S:V$  against GALD to assess the relationship to grazing responses (Fig. 3). Shape was conserved in these phytoplankton assemblages: dimensionless  $S:V$  varied only twofold, GALD more than tenfold. Effects of algal size and shape on response to grazing were strikingly different for the two zooplankton assemblages. In enclosures with Peter Lake zooplankton, 13 of 14 decreasing taxa had  $S:V < 2.75$  and  $GALD < 60 \mu\text{m}$ ; the single exception was *Schroderia setigera*. All of the increasers except *C. staurastroides* had a GALD value  $> 60 \mu\text{m}$ . On the other hand, in bags with Tuesday Lake zooplankton, increasers had  $S:V < 2.6$  and  $GALD < 25 \mu\text{m}$ . *Euglena* sp. was very close to this threshold, but, like the larger *E. gracilis*, was a decreaser.

### Discussion

Our experiments showed that phytoplankton taxa and size classes respond differently to different zooplankton communities. Grazing by two zooplankton assemblages that had very different size distributions consistently elicited opposite shifts in phytoplankton size distribution (Figs. 2, 3). Small taxa increased in density when grazed by small zooplankton, but de-

creased in density when grazed by large zooplankton. Conversely, large phytoplankters became less abundant in the presence of small zooplankters, but increased in density in the presence of large zooplankters. These shifts are consistent with observed differences in the summer phytoplankton of Peter and Tuesday Lakes (Bergquist et al. unpubl. data).

Possible explanations for the contrasting size shifts of the phytoplankton are differences in grazing selectivity (Peters and

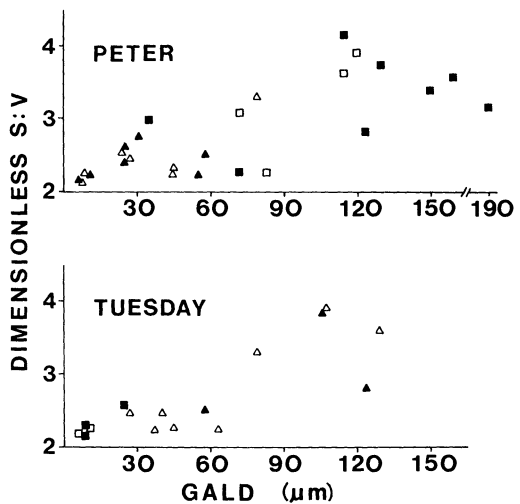


Fig. 3. Dimensionless  $S:V$  (square root of surface area divided by cube root of volume) vs. GALD (greatest axial linear dimension) for algal taxa significantly ( $P \leq 0.05$ ) increasing or decreasing under experimental conditions. Key:  $\Delta$ —exp. 1 decreaser;  $\blacktriangle$ —exp. 2 decreaser;  $\square$ —exp. 1 increaser,  $\blacksquare$ —exp. 2 increaser.

Downing 1984) and nutrient recycling rate (Peters 1983) between our experimental zooplankton assemblages. Neither process affects algae of different sizes equally. Models of size-structured plankton communities predict shifts to small algae at low biomass of small grazers and shifts to larger algae as grazer size or biomass increase (Carpenter and Kitchell 1984), consistent with our experimental results. However, further experiments are needed to distinguish the effects of nutrient recycling and selective grazing in natural plankton.

Algal size was the most reliable predictor of algal responses in our experimental treatments of differing zooplankton assemblages (Table 3, Fig. 3). The misclassified algal taxa can be explained by other morphological characteristics. *Cerasterias staurastroides*, despite its small size, was an increaser in bags with Peter Lake zooplankton; its tetragonal shape composed of four projections suggests that the alga was difficult for grazers to handle. Large algae are often attenuate in shape to preserve a favorable ratio of surface area to volume (Reynolds 1984); these algae, with large GALD values but relatively small volume, increased in abundance in the presence of Peter Lake zooplankton. The major algal increasers in Porter's (1973, 1976) experiments were gelatinous green algae, many of which were colonial. No increasing algae met this description in our experiments, although colonies of *Aphanocapsa* (a cyanophyte)  $>60 \mu\text{m}$  in GALD increased in number.

The erroneous classification of *S. quadricauda* indicates that the effectiveness of spines as a grazing deterrent depends on the relative size of the grazer and alga. *Scenedesmus quadricauda* (GALD  $<25 \mu\text{m}$ ) consistently decreased in the presence of large zooplankton, but increased in the presence of small zooplankton in experiment 2. The discriminant function for small zooplankton in experiment 2 misclassified *S. quadricauda* because two *Euglena* species, similar in size to *S. quadricauda* but without spines, decreased. Apparently spines prevented grazing by the small zooplankton but not by the large zooplankton. Gifford et al. (1981) showed that a spinose form of a small diatom ( $<25 \mu\text{m}$ ) was similarly grazed pref-

erentially by a large marine calanoid copepod.

Our study shows that particle size distributions are closely coupled to grazing dynamics in plankton communities. In a statistical sense, size explained much of the variance in algal community response to grazing. This observation is consistent with theoretical results showing dependence of phytoplankton size distributions on both biomass and size distribution of zooplankton (Carpenter and Kitchell 1984). Models of size-dependent energy flow that neglect nutrient recycling by herbivores (Sheldon et al. 1977; Silvert and Platt 1980) may not be adequate for predicting consequences of limnetic alga-grazer interactions for size structure.

Our results have practical consequences for lake management techniques that manipulate food webs to decrease algal density (Shapiro 1980). In our study, large grazers promoted the growth of large algae. This is similar to the effect of *D. pulex* on colonial *Aphanizomenon flos-aquae* in eutrophic lakes (Lynch 1980) and may involve nutrient transfer through zooplankton from small to large algae. Such size shifts can alter Secchi disk transparency (Edmondson 1980) and productivity (Carpenter and Kitchell 1984). Consequences of food web manipulations may best be understood in terms of size structure shifts; certainly such experiments are a useful context in which to test ideas about the dynamics of size structure in plankton.

## References

- BANSE, K. 1976. Rates of growth, respiration, and photosynthesis of unicellular algae as related to cell size—a review. *J. Phycol.* **12**: 135–140.
- . 1982. Cell volumes, maximal growth rates of unicellular algae and ciliates, and the role of ciliates in the marine pelagial. *Limnol. Oceanogr.* **27**: 1059–1071.
- BURNS, C. W. 1968. The relationship between body size of filter-feeding Cladocera and the maximum size of particle ingested. *Limnol. Oceanogr.* **13**: 675–678.
- CARPENTER, S. R., AND J. F. KITCHELL. 1984. Plankton community structure and limnetic primary production. *Am. Nat.* **124**: 159–172.
- EDMONDSON, W. T. 1980. Secchi disk and chlorophyll. *Limnol. Oceanogr.* **25**: 378–379.
- EJSMONT-KARABIN, J. 1983. Ammonia nitrogen and

- inorganic phosphorus excretion by the plankton rotifers. *Hydrobiologia* **104**: 231–236.
- GIFFORD, D. J., R. N. BOHRER, AND C. M. BOYD. 1981. Spines on diatoms: Do copepods care? *Limnol. Oceanogr.* **26**: 1057–1061.
- GLIWICZ, Z. M. 1980. Filtering rates, food size selection, and feeding rates in cladocerans—another aspect of interspecific competition in filter-feeding zooplankton. *Am. Soc. Limnol. Oceanogr. Spec. Symp.* **3**: 282–291. New England.
- HALL, D. J., S. T. THRELKELD, C. W. BURNS, AND P. H. CROWLEY. 1976. The size-efficiency hypothesis and the size structure of zooplankton communities. *Annu. Rev. Ecol. Syst.* **7**: 177–208.
- HARRIS, G. P. 1980. Temporal and spatial scales in phytoplankton ecology. Mechanisms, methods, models, and management. *Can. J. Fish Aquat. Sci.* **37**: 877–900.
- KITCHELL, J. A., AND J. F. KITCHELL. 1980. Size-selective predation, light transmission, and oxygen stratification: Evidence from the recent sediments of manipulated lakes. *Limnol. Oceanogr.* **25**: 389–402.
- LEHMAN, J. T. 1979. Physical and chemical factors affecting the seasonal abundance of *Asterionella formosa* in a small temperate lake. *Arch. Hydrobiol.* **87**: 274–303.
- , AND C. D. SANDGREN. 1985. Species-specific rates of growth and grazing loss among freshwater algae. *Limnol. Oceanogr.* **30**: 34–46.
- LEWIS, W. M. 1976. Surface-volume ratio: Implications for phytoplankton morphology. *Science* **192**: 885–887.
- LYNCH, M. 1980. *Aphanizomenon* blooms: Alternate control and cultivation by *Daphnia pulex*. *Am. Soc. Limnol. Oceanogr. Spec. Symp.* **3**: 299–304. New England.
- PETERS, R. H. 1983. The ecological implications of body size. Cambridge.
- , AND J. A. DOWNING. 1984. Empirical analysis of zooplankton filtering and feeding rates. *Limnol. Oceanogr.* **29**: 763–784.
- , AND F. H. RIGLER. 1973. Phosphorus release by *Daphnia*. *Limnol. Oceanogr.* **18**: 821–839.
- PIP, E., AND G. G. ROBINSON. 1982. A study of the seasonal dynamics of three phycoperiphytic communities using nuclear track autoradiography. 1. Inorganic carbon uptake. *Arch. Hydrobiol.* **94**: 341–371.
- PORTER, K. G. 1973. Selective grazing and differential digestion of algae by zooplankton. *Nature* **244**: 179–180.
- . 1976. Enhancement of algal growth and productivity by grazing zooplankton. *Science* **192**: 1332–1334.
- . 1977. The plant-animal interface in freshwater ecosystems. *Am. Sci.* **65**: 159–170.
- PRESCOTT, G. W. 1962. Algae of the western Great Lakes area. Brown.
- REYNOLDS, C. S. 1984. The ecology of freshwater phytoplankton. Cambridge.
- SCHMITZ, W. R. 1958. Artificially induced circulation in thermally stratified lakes. Ph.D. thesis, Univ. Wis. 110 p.
- SHAPIRO, J. 1980. The importance of trophic-level interactions to the abundance and species composition of algae in lakes, p. 105–116. *In* J. Barica and L. R. Mur [eds.], *Hypertrophic ecosystems*. Junk.
- SHELDON, R. W., W. H. SUTCLIFFE, JR., AND M. A. PARANJAPE. 1977. Structure of the pelagic food chain and relationship between plankton and fish production. *J. Fish. Res. Bd. Can.* **34**: 2344–2353.
- SHUTER, B. J. 1978. Size dependence of phosphorus and nitrogen subsistence quotas in unicellular organisms. *Limnol. Oceanogr.* **23**: 1248–1255.
- SILVERT, W., AND T. PLATT. 1980. Dynamic energy-flow model of the particle size distribution in pelagic ecosystems. *Am. Soc. Limnol. Oceanogr. Spec. Symp.* **3**: 754–763. New England.
- SMITH, R. E., AND J. KALFF. 1982. Size-dependent phosphorus uptake kinetics and cell quota in phytoplankton. *J. Phycol.* **18**: 275–284.
- SOURNIA, A. 1982. Form and function in marine phytoplankton. *Biol. Rev.* **57**: 347–394.
- STROSS, R. G., AND A. D. HASLER. 1960. Some lime-induced changes in lake metabolism. *Limnol. Oceanogr.* **5**: 265–272.
- VOGEL, S. 1981. *Life in moving fluids*. Princeton.
- WALSBY, A. F., AND C. S. REYNOLDS. 1980. Sinking and floating, p. 371–412. *In* I. Morris [ed.], *Physiological ecology of phytoplankton*. Univ. Calif.

Submitted: 14 May 1984

Accepted: 9 April 1985