



## Nordic Society Oikos

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Source: *Oikos*, Vol. 67, No. 2 (Jun., 1993), pp. 257-263

Published by: [Blackwell Publishing](#) on behalf of [Nordic Society Oikos](#)

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## Relative importance of nutrient availability and food chain for size and community composition in phytoplankton

Lars-Anders Hansson and Stephen R. Carpenter

Hansson, L.-A. and Carpenter, S. R. 1993. Relative importance of nutrient availability and food chain for size and community composition in phytoplankton. – *Oikos* 67: 257–263.

In a field experiment, algal community structure and size distribution were assessed at different grazing pressure and nutrient supply. Our aim was to study the interactive effects of food web composition and nutrients on algal community structure. High grazing reduced algal biomass and cell numbers, but had no consistent effect on algal size, except at extremely high *Daphnia* abundance, which promoted large, filamentous, algal forms. At high fish predation, the grazer assemblage altered towards small, less efficient grazers (copepods, *Bosmina*), but no trend in algal size was recorded. In enclosures with low grazing and low nutrient supply, algal cell concentration, but not chlorophyll, was as high as in corresponding enclosures with nutrient supply, indicating the importance of food web structure. Algal size was reduced by nutrient supply, which promoted dominance by small, fast growing, algal forms.

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Early limnology mainly focused on abiotic factors and their effects on biota (Persson et al. 1988), but during the sixties and seventies all parts of ecology, including limnology, were influenced by the idea that competition was the main factor in determining ecosystem structure. Later, predation and grazing were invoked more frequently, but eventually it became obvious that not one factor alone determines the number and species composition of organisms in an ecosystem. It also seemed clear that a change in predation pressure may not only affect the prey, but effects may “cascade” far down in the food web (Hairston et al. 1960, Hrbáček 1962, Oksanen et al. 1981, McQueen et al. 1986, Carpenter et al. 1987, Persson et al. 1988). Although effects of trophic cascades and abiotic factors have been demonstrated repeatedly, there is still confusion about the relative importance of abiotic factors (e.g. nutrient supply), competition and predation when they act simultaneously in natural systems.

The increasing interest in interactions between abiotic and biotic factors includes the idea that nutrient

richness influences food chain length and therefore the nature of trophic cascading (Fretwell 1977, Persson et al. 1988). Some experimental studies have suggested that grazing effects on phytoplankton are strongest in oligotrophic systems (McQueen et al. 1986), whereas others state that the low density zooplankton assemblage in oligotrophic lakes has a negligible impact on phytoplankton, and that food web effects are strongest in lakes of intermediate productivity (Elser and Goldman 1991). Theory suggests that variability and destabilization of the phytoplankton assemblage are most likely at high nutrient supply, while the level of nutrients necessary for destabilization increases with grazing intensity (Carpenter 1992). All these ideas depend on the interactions between algae and contrasting zooplankton communities at different nutrient levels. Very little is known about these interactions. The aim of our study has been to assess the response in algal community structure and size at different grazing pressure and different nutrient supply. The study was performed as a field experiment, where we altered the nutrient supply

Accepted 15 October 1992

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(i.e. changed the system from the bottom of the food web), as well as the predation pressure on grazing zooplankton (changed the system from the top of the food web). The experimental design (low and high nutrient concentration, crossed with low and high predation pressure on zooplankters), allowed us to evaluate interactive effects of predation, grazing and nutrient supply on biomass, genera composition and size distribution of algae and zooplankters.

It may be predicted that in the absence of predation on zooplankton, nutrient addition will increase phyto- and zooplankton biomasses, although a growing zooplankton population with large individuals will eventually damp algal biomass development. Furthermore, models predict that large zooplankters promote an algal community dominated by large phytoplankters (Carpenter and Kitchell 1984). On the other hand, if fish are allowed to prey upon the zooplankters, zooplankter size will be reduced, and the grazer community altered towards smaller, less efficient grazers, promoting dominance by smaller phytoplankters (Carpenter and Kitchell 1984). Since zooplankters regenerate nutrients by grazing (Sterner 1986), it may be predicted that at high grazing pressure, the amount of available phosphorus will be higher than at low grazing pressure.

## Material and methods

### Site description

Long Lake (Michigan, USA; N46°13', 89°32'W) is an unproductive forest lake consisting of two basins, each with a maximum depth of 14 m. The two basins are connected by a littoral zone where the depth rarely exceeds 3 m. In a flat area of this littoral zone, at a water depth of 2.5 m, 12 enclosures were built, each with a diameter of 2.0 m (volume 7.8 m<sup>3</sup>). The enclosures were made of reinforced plastic sheets, welded to a cylindrical shape with a heat gun. To stabilize the construction, three iron bar rings were attached to the top, middle and bottom sections of each enclosure. The enclosure rings were tied to wooden posts driven into the sediment.

### Experimental design

Low (ambient) and high nutrient concentrations were crossed with low and high grazing pressure in a 2 × 2 factorial design. Each of the four treatments 00 (no nutrients/no fish predation), 0F (no nutrients/fish predation), N0 (nutrients/no fish predation), and NF (nutrients/fish predation) were replicated three times and randomly allocated to the 12 enclosures. The inside walls of each enclosure were brushed twice a week to retard algal colonization on the walls, and thereby reduce this enclosure effect.

Fish were used to keep the abundance of grazing zooplankters low. Similar biomasses of fish were put in nylon cages (0.4 m<sup>3</sup>) inside all enclosures. Six of the twelve enclosures (0F and NF treatments) had fish cages with coarse mesh (3 mm mesh size), allowing fish to prey upon zooplankters, whereas six cages (00 and N0 treatments) had fine net (0.2 mm) releasing the zooplankton from predation pressure, but still exposing enclosures to fish excretion (Threlkeld 1987). Fish are known to affect nutrient dynamics, and thereby algal growth, in three ways: (a) by excreting nutrients (Threlkeld 1987); (b) by feeding on the sediment surface (Lamarra 1974); and (c) by altering size structure, and therefore excretion rates of the zooplankton assemblage (Vanni and Findlay 1990). Our design with the same amount of caged fish in each enclosure excludes differences between treatments caused by excretion and sediment feeding, allowing us to focus on nutrient dynamics caused by predation.

Once every 10th d fish were removed from enclosures and treated with Prolong<sup>TM</sup> (Nitrofurazone) to reduce infection by fungi. This treatment kept death rate among fish below 1% a day. After treatment (1 h) fish from the small mesh size cages were put in the coarse net cages and vice versa, a procedure intended to smooth out any differences in excretion and predation rate among fish individuals. In the beginning of the experimental period the amount of fish was not sufficient to reduce *Daphnia* abundance in the treatments with nutrient addition (NF), and *Daphnia* were therefore screened with a 125 µm plankton net. No screening was necessary after 31 July. Fish abundance in the cages was increased from 2 (10–21 June), 4 (21–28 June), 6 (28 June–20 July), and finally to 8 (20 July–18 Aug.). Species used were yellow perch (*Perca flavescens*), rock bass (*Ambloplites rupestris*) and common shiner (*Notropis cornutus*), constituting 70%, 19% and 11%, respectively (by numbers). The mean size for perch was 86.5 mm (SD 13.6), for rock bass 62.8 mm (SD 25.6) and for shiner 80.1 (SD 13.2). At the end of the experiment, biomass in each enclosure corresponded to about 200 kg fish/ha.

Phosphorus (KH<sub>2</sub>PO<sub>4</sub>, 3.33 g) and nitrogen (NH<sub>4</sub>Cl, 14.89 g) were added every 10th d to six of the enclosures, yielding a total addition of 20.0 g KH<sub>2</sub>PO<sub>4</sub> (4.7 g P) and 89.3 g NH<sub>4</sub>Cl (23.6 g N) per enclosure during the experiment.

### Sampling procedure

Samples from the enclosures were taken five times from 10 June to 18 August 1990. The sampling days were: 10 June (day 161); 27 June (day 178); 25 July (206); 3 August (day 215); and 18 August (230). Samples for zooplankton enumeration, and phytoplankton chlorophyll and numbers were taken from 0–2 m water depth with a plastic pipe (52 mm). Three pipesful (total 12 l) were put together in a bucket and mixed. Thereafter, 4 l were filtered for zooplankton counts, 4 l for phyto-

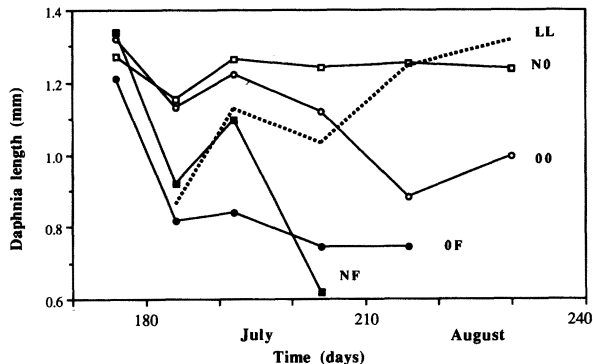


Fig. 1. Mean length of *Daphnia* (mm) over time in Long Lake (LL) and in the four treatments 00 (no nutrients/no fish predation); 0F (no nutrients/fish predation); N0 (nutrients/no fish predation); NF (nutrients/fish predation). No *Daphnia* occurred in NF after 25 July (day 205) and in 0F after 3 August (day 216).

plankton enumeration and species determination, and 0.1 to 2.2 l for chlorophyll determination.

The zooplankton samples were filtered through an 80  $\mu\text{m}$  net and fixed with Lugol's solution for later counting and length measurements. Biomass ( $\mu\text{g l}^{-1}$ ) was calculated from length-weight regressions according to Bottrell et al. (1976). Phytoplankton samples were concentrated through a 10  $\mu\text{m}$  net and fixed with Lugol's solution for later counting and determination of genera.

Algal chlorophyll samples were filtered on GF/C filters, which were frozen prior to extraction in methanol (Marker et al. 1980). Readings were made on a Turner 450 Fluorometer. Nutrient samples for phosphate and total phosphorus were sampled in surface water (0–20 cm) and analysed on a Technicon Autoanalyzer II.

Samples for algal counting and measuring were mounted in HPMA (2-hydroxypropyl methacrylate) according to Crumpton (1987). Algal cells were counted at 200 times magnification and the Greatest Axial Linear Dimension (GALD) was measured on at least 20 individuals of each species. A pooled size index was calculated as the mean GALD of all cells or colonies of the five most abundant genera. Specifically,

$$\text{Size index} = (\sum C_i \times \text{GALD}_i) / (\sum C_i)$$

where  $C_i$  is the concentration and  $\text{GALD}_i$  is the size of genus  $i$ . The size index was used to compare effects of grazing and nutrient addition on phytoplankton size distributions.

A repeated measure analysis of variance was carried out to assess the effect on algal and zooplankton abundances of nutrient addition and fish predation on zooplankton. The analysis was performed using SYSTAT (Wilkinson 1988), following the guidelines of Gurevitch and Chester (1986).

## Results

At the end of the experimental period the concentration of available phosphorus ( $\text{PO}_4$ ) was below 1  $\mu\text{g/l}$  in the 00 and 0F treatments (no nutrients/no fish predation and no nutrients/fish predation, respectively). At the end of the experiment there was a difference in mean phosphate ( $\text{PO}_4\text{-P}$ ) concentrations between the N0 and NF treatments (200.9  $\mu\text{g/l}$  (SD 14.0) and 134.9  $\mu\text{g/l}$  (SD 12.6) respectively;  $t = 10.23$ ;  $p < 0.001$ ).

The zooplankton community consisted of *Daphnia* sp., copepods, *Bosmina* sp., *Holopedium* sp., and *Polphemus* sp., but was always dominated by *Daphnia* and/or copepods, although *Bosmina* constituted 20% (by numbers) in NF treatments at the end of the experimental period. There were no initial length differences in *Daphnia* between enclosures (Fig. 1; Kruskal-Wallis one-way analysis of variance;  $H = 3.32$ ; NS). *Daphnia* length was constant around 1.25 mm in the N0 treatment during the whole investigation period. In the

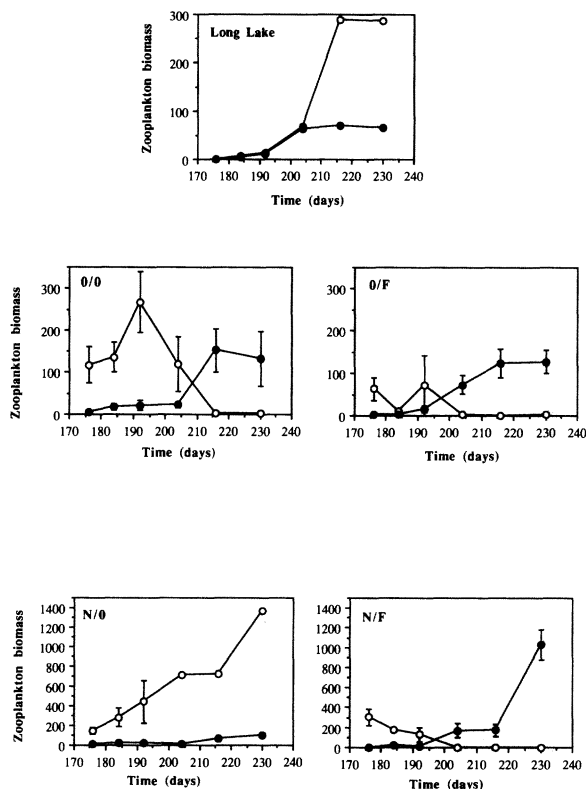


Fig. 2. *Daphnia* (open symbols) and copepod (closed symbols) biomasses ( $\mu\text{g/l}$ ; dry mass) over time in Long Lake and in the four treatments 00 (no nutrients/no fish predation); 0F (no nutrients/fish predation); N0 (nutrients/no fish predation); NF (nutrients/fish predation). Mean values  $\pm 1$  SD are given. The number of replicates is three, except in N0 from 25 July (day 205), due to fish that by mistake entered one replicate. Note that in the NF treatment *Daphnia* were initially screened due to too low number of fish. After 31 July (day 211) no screening was necessary.

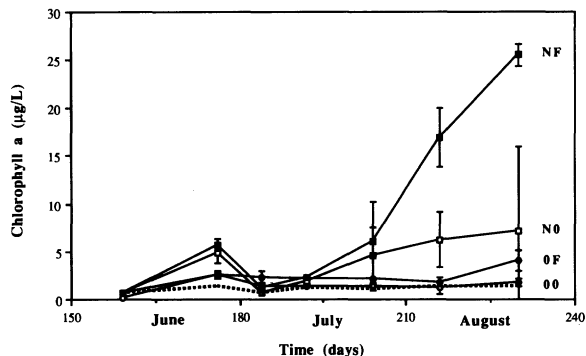


Fig. 3. Chlorophyll *a* development over time in Long Lake (dotted line) and in the four treatments 00 (no nutrients/no fish predation); 0F (no nutrients/fish predation); N0 ( nutrients/no fish predation); NF (nutrients/fish predation). Mean values  $\pm$  1 SD are given for each treatment. At the last sampling date  $n=2$  for NF (due to a rip in the plastic of one enclosure) and N0 (due to a fish added accidentally to one enclosure)

treatment where zooplankters suffered from predation (0F and NF), *Daphnia* were smaller (mean 0.80 mm) than in treatments without predation (mean 1.27 mm) ( $p < 0.030$ ; Mann-Whitney U-test). There was also a tendency towards decreased size in the 00 compared to N0 treatments, although differences were only significant on day 217 (3 Aug.) ( $t = 4.57$ ,  $p < 0.050$ ).

Copepod size also decreased in presence of predators, but differences were not significant before the last sampling occasion ( $t = 10.51$ ;  $p < 0.001$ ), when mean lengths were 0.41 and 0.65 mm with and without fish predation, respectively. *Bosmina* followed the same trend and ended up with a mean length of 0.29 and 0.36 mm in treatments with and without fish predation, respectively ( $t = 5.25$ ;  $p < 0.010$ ). In the lake, the mean length of *Daphnia* increased from 0.85 to 1.25 mm during the investigation period, whereas copepods showed no trend and varied between 0.25 and 0.60 mm.

The biomass of copepods was similar in the lake and in all treatments except with both nutrients and fish

Table 1. Repeated measures analysis of variance on the effect of nutrient addition (00 and 0F vs N0 and NF) and fish predation (00 and N0 vs 0F and NF) on the biomasses of phytoplankton (as chlorophyll) and zooplankton. The data were log transformed to make the residuals approach a normal distribution. One of the N0 enclosures and the data from the last sampling occasion (day 230) were removed from the analysis due to missing values.

	Zooplankton		Chlorophyll	
	F	p	F	P
Nutrients	5.20	0.056	14.9	0.006
Fish predation	10.4	0.015	7.99	0.026
Nutrient $\times$ Fish	0.48	0.510	0.49	0.506

Table 2. Algal size index, and *Daphnia* and copepod biomasses ( $\mu\text{g/l}$ ) in Long Lake from 10 June to 18 August 1990.

Date	Size index	<i>Daphnia</i>	Copepod
10 June	52	—	—
27 June	58	0	1
25 July	39	67	63
3 August	42	289	69
18 August	32	286	64

predation (NF), where copepods reached high numbers (997 individuals/l) and biomasses of up to 1.3 mg/l (Fig. 1). In the lake and in N0 treatments *Daphnia* increased in abundance and finally reached mean biomasses of 286 and 1400  $\mu\text{g/l}$ , respectively (Fig. 2). In all other treatments (00, 0F, NF) no *Daphnia* were present at the end of the experimental period.

Chlorophyll *a* values were always below 5  $\mu\text{g/l}$  in treatments with no nutrient addition, and always below 3  $\mu\text{g/l}$  in the lake (Fig. 3). Although the same amount of nutrients were added to N0 and NF, chlorophyll *a* concentrations differed between the last two sampling occasions ( $t = 7.59$ ;  $p < 0.010$  and  $t = 4.10$ ;  $p < 0.100$  (in this last sampling  $n = 4$  due to a rip in the plastic of one NF enclosure and mistaken introduction of fish to a N0 replicate).

There was a significant nutrient effect on chlorophyll concentration ( $p < 0.006$ ; Table 1), and also an effect, although not significant, on zooplankton biomass ( $p < 0.056$ ; Table 1). Fish predation on zooplankton significantly affected both phytoplankton and zooplankton biomasses ( $p < 0.026$ ; Table 1). We did not detect any significant interactive effects from nutrients and fish predation ( $p > 0.500$ ; ANOVA; Table 1).

The five dominating algal taxa, forming the base for the size index calculations, usually constituted more than 90% and always more than 70% of the cell numbers, and ranged in size (GALD) between 13.2  $\mu\text{m}$  (*Peridinium pusillum*) and 644.4  $\mu\text{m}$  (unidentified filamentous species). A decreasing trend in algal size index (Table 2) was found in the lake due to a shift from dominance by medium sized (*Synura*, *Gymnodinium*, *Gonyostomum*, *Dinobryon*; mean GALD 64  $\mu\text{m}$ ) to small sized (*Merismopedia*, *Sphaerocystis*; mean GALD 29  $\mu\text{m}$ ) algal groups. Enclosures without nutrient addition (00; 0F) were at the end of the experimental period dominated (usually more than 90% by numbers) by *Pseudoanabena* (91  $\mu\text{m}$ ) or *Dictyosphaerium* and *Dinobryon* together (46 and 155  $\mu\text{m}$ , respectively). These relatively large algae caused an increase in the size index (Table 3). With one exception (enclosure 6 which became dominated by filamentous genera), enclosures with nutrient addition became dominated by the genera *Cryptomonas* (24  $\mu\text{m}$ ; Fig. 4) and *Dictyosphaerium* (46  $\mu\text{m}$ ; Fig. 5). At the end of the season these genera comprised more than 85% of the algal individuals, considerably reducing size indexes (Table 3). Size indexes

Table 3. Final algal size index and *Daphnia* and copepod biomasses ( $\mu\text{g/l}$ ; 18 August) for treatments with and without nutrient addition (N0, NF and 00, 0F, respectively). Size index differs between treatments with and without nutrient addition ( $t_9 = 15.28$ ;  $p < 0.001$ ; enclosure 6 was excluded from the t-test due to extremely high *Daphnia* biomass and dominance by filamentous algae).

No nutrient addition					Nutrient addition				
	No.	Index	D	C		No.	Index	D	C
0/0	4	77	2	156	N/0	6	143	2357	115
	7	52	5	237		10	26	376	95
	8	86	2	2		11	32	2	8
0/F	1	62	5	128	N/F	2	24	0	962
	5	73	0	80		3	27	0	767
	12	71	0	172		9	45	0	1316

differed between enclosures with and without nutrient addition at the last sampling date ( $t = 15.28$ ;  $p < 0.001$ ).

The eventual increase in abundance of *Dinobryon*, *Peridinium* and *Dictyosphaerium* was a characteristic phenomenon in the 0F treatments (no nutrients/low grazing), and these genera finally comprised 91% of the cell/colony number in the 0F treatments (Fig. 6). Total cell/colony numbers were similar in 00, NF and the lake, whereas enclosures with low grazing pressure contained about three times higher cell/colony numbers (Fig. 6).

## Discussion

In enclosures with an excess of nutrients and where zooplankton were protected from fish predation, *Daphnia* became dominant. On the other hand, copepods were only slightly affected by predation from fish: they became smaller, but maintained high numbers. With one exception (NF 18 August), copepods were unaffected by nutrient addition. Most probably this was a result of differences in life-cycles, size and behaviour. Copepods develop slowly and therefore take some time

to respond to increased resources, whereas *Daphnia* are able to produce several generations in a short time. Copepods were never abundant when *Daphnia* occurred in high numbers. The striking final difference in copepod biomass between N0 and NF treatments suggests some sort of interactions between *Daphnia* and copepods. A possibility is that large *Daphnia* filter-feed on naupliar stages of copepods, thereby inhibiting population growth. Alternatively, *Daphnia* feeding may damage nauplii in the way it damages rotifers (Gilbert 1988).

Although the final zooplankton biomass was similar in the NF and N0 treatments (Fig. 1), the zooplankton community, and thereby the grazing pressure on phytoplankton, was completely different. Similarly, 00 and 0F treatments both ended up with zooplankton biomasses around  $150 \mu\text{g/l}$ , suggesting that a certain nutrient level is able to support a certain biomass of zooplankters.

The Copepod-*Bosmina* complex in treatment NF resulted in high algal numbers and chlorophyll values, whereas a high number of *Daphnia* in treatment N0 was

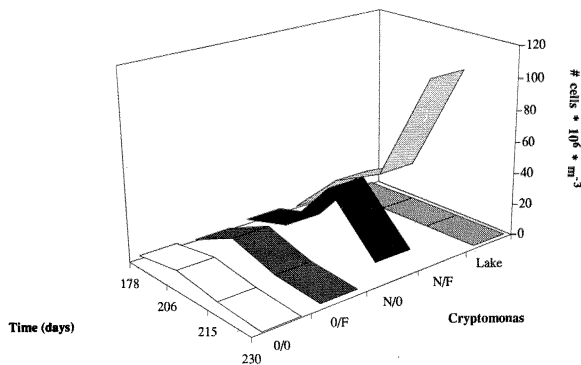


Fig. 4. Cell numbers ( $\times 10^6 \times \text{m}^{-3}$ ) of *Cryptomonas* sp. over time in Long Lake and in the four treatments from 27 June (day 178) to 18 August (day 230) 1990. The figure shows low numbers in the lake and in 00 and 0F treatments, whereas *Cryptomonas* dominated in the N0 and NF treatments. The final difference between N0 and NF is attributed to differences in grazing pressure.

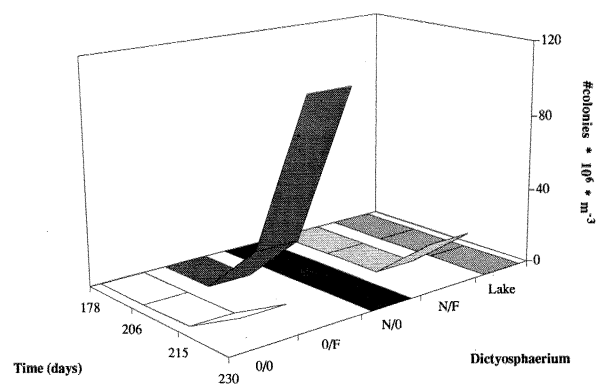


Fig. 5. Cell numbers ( $\times 10^6 \times \text{m}^{-3}$ ) of *Dictyosphaerium* sp. over time in Long Lake and in the four treatments from 27 June (day 178) to 18 August (day 230) 1990. The figure shows a moderate increase in cell numbers in 00 and NF treatments, whereas *Dictyosphaerium* completely dominated in 0F treatments.

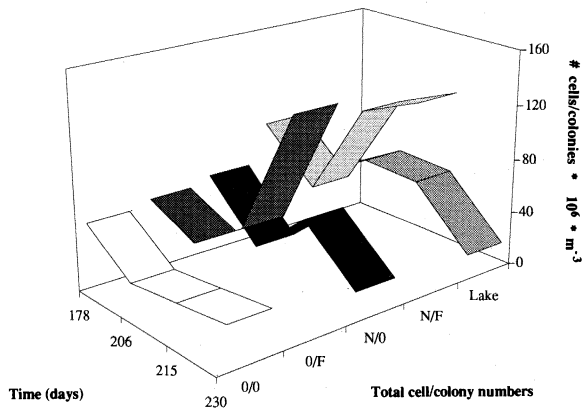


Fig. 6. Total cell numbers ( $\times 10^6 \times m^{-3}$ ) over time in Long Lake and in the four treatments from 27 June (day 178) to 18 August (day 230) 1990. The figure shows comparable amounts of cells in the lake and in the treatments with high grazing (00 and N0), but high and similar cell numbers in treatments where algae were released from grazing.

associated with considerable reduction in phytoplankton chlorophyll and cell numbers (Figs 3 and 6). Although treatments N0 and NF received the same amount of nutrients, chlorophyll values and algal cell numbers differed considerably, indicating that the food web composition markedly affected algal biomass development.

Another effect of high grazing rate may be the higher portion of available phosphorus in the N0 compared to the NF enclosures. This difference suggests that the grazing rate was higher than algal growth rate, leaving more available phosphorus in the water.

In late August the enclosures with nutrient addition were dominated by small cryptomonads (GALD 24  $\mu m$ ), resulting in low size index. The only exception was one of the N0 replicates where 35% of the cells were filamentous, considerably increasing the size index. This enclosure had the highest abundance of large *Daphnia* (170 individuals/l), with a biomass more than eight times higher than in the lake (2357 compared to 286  $\mu g/l$ ), which fits well with theory (Carpenter and Kitchell 1984) and experimental studies (Bergquist et al. 1985), where a high abundance of large zooplankton is predicted to cause a shift towards large, inedible phytoplankters (in this case filaments). However, in the enclosure with the second highest *Daphnia* biomass (376  $\mu g/l$ , slightly higher than the lake), small algal species (mainly *Cryptomonas*) still dominated. Hence, at extremely high *Daphnia* abundance the predictions from theory are corroborated, but at high natural abundances there was no trend towards higher size indexes, although *Daphnia* was the dominating zooplankton. Theory also predicts a zooplankton population dominated by small species (copepods and *Bosmina*) to promote a community of small phytoplankton (Carpenter and Kitchell 1984). In enclosures with fish predation

*Daphnia* disappeared and the zooplankton community became dominated by small copepods and *Bosmina*, but no trend towards smaller sized algae was recorded.

In short term experiments in small containers (125 l) the hypothesis that algal size increases with size and numbers of large grazers was corroborated (Bergquist et al. 1985). In our study performed in larger (7900 l), and more complex experimental systems (open to the sediment, longer experimental period), we were not able to illustrate the shift towards larger algal forms, except at extremely high densities of large grazers (170 individuals/l; 2359  $\mu g/l$ ). Furthermore, the natural grazer community in Long Lake (final *Daphnia* abundance 27 individuals/l; 286  $\mu g/l$ ) was not able to increase the algal size index. Instead, the size index showed a decreasing trend during the season as the number of *Daphnia* increased (Table 2). On the other hand, increased nutrient supply reduced algal size significantly, irrespective of if the grazer community was dominated by small copepods and *Bosmina* or by large *Daphnia* (Table 3). In an analysis of algal size trends in experimental lakes over 7 years, Carpenter et al. (in press) found no consistent relationships between zooplankton and phytoplankton size, contrary to the theory of Carpenter and Kitchell (1984). Our experiment supports the result of their whole-lake studies.

The abundance of *Dictyosphaerium* increased in 00, 0F and NF treatments, which coincided with the reduction in *Daphnia* abundance in these treatments. In N0 and in the lake, where *Daphnia* was abundant, only few *Dictyosphaerium* occurred, suggesting that grazing by *Daphnia* inhibited dominance by *Dictyosphaerium*. *Cryptomonas* sp. responded heavily to nutrient addition, but the abundance was reduced in the presence of *Daphnia* (N0; Fig. 4), although its dominance persisted (72% of total cell numbers at the end of the experimental period).

Fish predation effects cascaded down to phytoplankton, clearly illustrating the links between trophic levels. Similarly, nutrient addition affected not only phytoplankton, but also zooplankton biomass, but no significant interactive effects of nutrient addition and fish predation on phytoplankton and zooplankton biomasses were recorded (Table 1). Hence, from our experiment we cannot conclude that high nutrient supply can offset the effects of grazing, as has been suggested from field studies (Hansson 1992). However, it should be noted that the technical problems in two of the enclosures (see text to Fig. 3), reduced the data set considerably since repeated measures ANOVA is unable to handle scattered missing values (the whole last sampling occasion and one of the treatments had to be omitted from the statistical analysis). The risk of making a Type II error is therefore increased, suggesting that additional studies have to be performed before any conclusions can be made about the possible interactions between food web structure and nutrient supply.

Final total cell numbers were similar (Fig. 6) in enclou-

tures with and without nutrient addition, resulting in seven times higher chlorophyll content per cell/colony in treatment with than without nutrient addition. This high chlorophyll content may be due to self shading or to different species composition.

High nutrient concentrations seems to alter the algal community towards dominance by small, fast growing groups, and grazing seems to damp the exponential population growth. Furthermore, when algae are released from grazing (as in 0F), the number of cells/colonies reached values as high as if nutrients were provided (Fig. 6), although the algal community was completely different (dominated by *Dictyosphaerium* and *Dinobryon* instead of by *Cryptomonas*).

Our experiment suggests that aggregated ecosystem variables (zooplankton biomass, chlorophyll, and phosphorus concentration) have simpler, more predictable responses to manipulation than phytoplankton community composition or size structure. Community responses may simply be more complex and variable than ecosystem responses. The regularities of allometry suggest that phytoplankton communities may behave predictably when viewed from the perspective of size structure (Carpenter and Kitchell 1984), much as the size perspective crystallized understanding and predictability of zooplankton communities (Brooks and Dodson 1965). Our findings suggest, however, that even size dynamics of phytoplankton are complex.

*Acknowledgements* – This study was supported with grants from the Swedish Natural Science Research Council (NFR; to LAH) and the US National Science Foundation (NSF; to SRC; BSR-86-04996). The study was performed at the Univ. of Notre Dame Environmental Research Center. We thank M. Vanni for valuable comments on the manuscript.

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