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Community structure and bottom-up regulation of heterotrophic microplankton in arctic LTER lakes

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Abstract

Microplankton community structures and abundance was assessed in lakes at the Toolik Lake LTER site in northern Alaska during the summers of 1989 and 1990. The microplankton community included oligotrich ciliates, but rotifers and zooplankton nauplii comprised greater than 90% of total estimated heterotrophic microplankton biomass. Dominant rotifer taxa included *Keratella cochlearis*, *Kellicottia longispina*, *Polyarthra vulgaris*, *Conochilus unicornis* and a *Synchaeta* sp. Microplankton biomass was lowest in highly oligotrophic Toolik Lake ($< 5\ \mu gC\ l^{-1}$ at the surface) and highest (up to $55\ \mu gC\ l^{-1}$) in the most eutrophic lakes, experimentally fertilized lakes, and fertilized limnocorrals, consistent with bottom-up regulation of microplankton abundance.

Introduction

Recognition of the potential trophic significance of the microbial loop (Azam *et al.*, 1983; Porter *et al.*, 1985) has generated considerable study of heterotrophic nanoplankton (2–20 μm) and microplankton (20–200 μm) in aquatic ecosystems (e.g. Stockner & Porter, 1988). Heterotrophic nano- and microplankton graze on bacteria (Hobbie & Helfrich, 1988; Sanders *et al.*, 1989) and small autotrophs (Stockner & Porter, 1988; Rublee & Gallegos, 1989; Gallegos, 1990). Thus, the microplankton represent a potentially important trophic link from bacterial utilization of dissolved organics and algal utilization of inorganics to zooplankton and higher order consumers.

The significance of the microbial loop to higher trophic levels remains uncertain. From an energy and carbon standpoint, numerous studies confirm bacterivory and algal consumption in freshwaters (e.g. Sherr & Sherr, 1984; Sanders *et al.*, 1989) and that microplankton can be consumed by crustacean zooplankton (e.g. Williamson & Butler, 1986). Nevertheless, many investigators suggest that the microbial loop acts as an energy sink (cf. Pomeroy & Wiebe, 1988), since insertion of new trophic levels must result in respiratory losses as energy passes along them. However, if the microbial loop acts primarily as a 'salvage pathway' by returning dissolved organic carbon (which otherwise would be lost by excretion and decomposition) back into grazing food webs, then regardless of the conversion efficiency, the microbial loop represents a net addition to resources available to the higher trophic levels. Further, the role of the microbial loop in recycling nutrients and regulating microbial populations may actually stimulate bacterial and algal production (Porter *et al.*, 1985).

Regulation of microbial populations is thought to be dependent on both bottom-up and top-down controls. Bottom-up regulation is represented by

food resources which appear to set limits on the attainable biomass within aquatic systems (cf. Pace, 1984; McQueen *et al.*, 1989). Top-down regulation is represented by predators which are known to control population abundance (see e.g. Hobbie & Helfrich, 1988).

Arctic freshwater ecosystems may be ideal sites to study aspects of the microbial loop. Reduced diversity of organisms in arctic freshwaters relative to temperate systems (Hobbie, 1973) should make it easier to determine interactions and thus regulation and impact of microbial loop components. Here I report data on microplankton abundance and distribution from some lakes of the LTER site at Toolik Lake, Alaska, during the summers of 1989 and 1990, and discuss bottom-up control of heterotrophic microplankton populations.

Materials and methods

The Toolik Lake LTER site (68° N, 149° W) is located in the northern foothills of the Brooks Mountain Range of Alaska. The site includes a number of ponds and lakes which have been under study for over a decade. These lakes are naturally oligotrophic systems with varying zooplankton and fish populations. Most data presented here are from eight lakes of the Toolik LTER site (Table 1), some of which have been experimentally manipulated (nutrient or fish additions). Additional data are reported from an experimental study conducted in limnocorrals within Toolik Lake during 1989.

Water samples were collected by Van Dorn sampler at the surface and at depths of 1, 3, 5, 8, 12, 16, and 20 m or to the deepest depth of shallower lakes. Two liters of sample were then gently concentrated to 60 ml by reverse flow through a 20 μm net (Dodson & Thomas, 1964). Glutaraldehyde was added as a preservative to 1% final concentration and samples were stored refrigerated until counted. Live samples were also examined to assure that glutaraldehyde was an appropriate preservative and so that microplankton could be identified after preservation.

Samples were enumerated following the procedure of Baldock (1986). An aliquot of the concentrated samples (5–20 ml, depending on particle concentration of sample) was stained with 0.25% Rose Bengal solution, and then drawn onto an 8.0 μm pore cellulose acetate filter under gentle vacuum. Filters were mounted on slides in a 43% sucrose solution and examined under a compound microscope. The entire surface area of the filter was scanned at 100× or 200× and individual microplankton identified. Magnification up to 400× was used to aid in identification as necessary. Taxonomic guides to protozoa (Jahn *et al.*, 1979; Lee *et al.*, 1985) and rotifers (Ruttner-Kolisko, 1974) were used to identify organisms. Nauplii were enumerated but not taxonomically identified. Carbon biomass was estimated based

Table 1. Characteristics of Toolik LTER study lakes.

Lake	Depth (max)	Chlor a[1] ($\mu g\,l^{-}$)[1]	Description
Toolik	25 m	1.69	Highly oligotrophic control lake.
E–1	12 m	4.65	No manipulation, abundant small grayling
N–1	12 m	5.09	Lake trout present, fertilization of lake begun in 1990
N–2	7 m	3.46(C) 12.81(F)	No fish, lake divided by plastic curtain, one side fertilized (N + P), 1985–1990.
I–6	12 m	0.26	No manipulation, in Toolik watershed.
I–8	8 m	0.31	Lake trout removed, in Toolik watershed.
S–6	6 m	1.07	Lake trout added beginning in 1986.
S–7	4 m	0.26	No manipulation, few fish.

[1] Chlorophyll values are time and depth integrated means from 2 (I–6, I–8) to 9 (Toolik, N–1, N–2) samples from these lakes. (Data from M.C. Miller, Univ. of Cincinnatti)

on measured sizes and literature values (Ruttner-Kolisko, 1977; Pauli, 1989; Putt & Stoecker, 1989).

The experimental study conducted in limnocorrals was a follow-up to previous work reported in this volume (O'Brien *et al.*, 1992) and details will be presented elsewhere (G. Kipphut & S. Whalen, in prep.). Briefly, 1 mole nitrogen, as either nitrate or ammonia, was added in a single dose to 5 m^3 limnocorrals on July 4, 1989. The corrals were sampled three times during the summer for microplankton, once immediately prior to nitrogen amendments and twice afterwards. Data from the limnocorrals is reported as the average values from 1 and 4 m samples.

Results

The microplankton observed in lakes of the Toolik LTER site included ciliated protozoans, rotifers, and crustacean zooplankton nauplii. Most ciliates were small oligotrichs (< 50 μm in largest dimension) of the genera *Halteria*, *Strombidium* and *Strobilidium*. A *Vorticella* sp. was also present and dominated in a few samples. Other protozoans were rarely seen. Four species of rotifers dominated the microplankton: *Keratella cochlearis*, *Kellicottia longispina*, *Polyarthra vulgaris* and *Conochilus unicornis*. Five additional species were occasionally observed: *Keratella quadrata*, *Ascomorpha* (*Chromogaster*) *ecaudis*, *Filinia terminalis*, *Gastropus stylifer*, and an unidentified *Synchaeta* sp.

Microplankton assemblages demonstrated similar temporal and spatial patterns of distribution among lakes, but species composition and biomass varied. Results from Toolik Lake and the control side of Lake N-2 (Figs 1, 2) serve to demonstrate these patterns. The highest protozoan abundance was usually found during late June, the beginning of the ice-free season. Initially, protozoans were more numerous than rotifers (100 to 1000 l^{-1}, compared to 10–300 rotifers l^{-1} at the surface), but rotifer biomass was usually larger than protozoan biomass because of their larger individual size. Protozoan abundance and biomass declined rapidly in all lakes after the initial peak. Secondary peaks in numbers were evident in some lakes, but protozoan biomass generally remained low (< 0.5 μg C l^{-1}). An exception to this pattern was found in Toolik Lake in 1990, where a late summer peak of ciliates was found in the upper 3 m of the water column.

Rotifer abundance and biomass was generally low early in the summer, and increased to peak values during mid July to early August in all lakes. Maximum rotifer abundance (3000 individuals l^{-1}) was found at 3 m in the fertilized side of Lake N-2 on July 20, 1989. Nauplius biomass generally equalled or exceeded rotifer biomass and tended to increase during the summer. Over all lakes, protozoan abundance decreased with depth ($r = -0.25$, $p < 0.01$), $n = 497$), rotifer abundance showed no significant correlation with depth ($r = -0.07$, $p = 0.14$, $n = 497$), and nauplius abundance showed a positive correlation with depth ($r = 0.15$, $p < 0.01$, $n = 497$).

Although seasonal patterns were similar for all lakes, absolute abundance and biomass of microplankton varied by more than an order of magnitude among the lakes (Fig. 3). Oligotrophic Toolik Lake consistently had the lowest microplankton biomass, generally less than 4 μg C l^{-1}. Lakes E-1 and N-2 are more productive than Toolik and microplankton biomass was generally an order of magnitude higher, reaching values as high as 55 μg C l^{-1} (Lake E-1, 8 m, July 19, 1989).

The distribution of rotifer species varied over time and depth. For example, in Lake E-1 in 1989, the peak abundance of rotifers was initially found in the epilimnion (0–3 m) during June and early July. Increases in number of individuals at 5–11 m depths resulted in displacement of the peak abundance to the hypolimnion by mid July. Three rotifer species demonstrated significant positive correlations with depth in Lake E-1 (*Kellicottia longispina*, $r = 0.21$, $p < 0.05$, $n = 93$; *Polyarthra vulgaris*, $r = 0.49$, $p < 0.01$, $n = 93$; and *Filinia terminalis*, $r = 0.48$, $p < 0.01$, $n = 93$). This pattern varied among lakes, however. For example, in Toolik Lake, both *K. longispina* and *P. vul-*

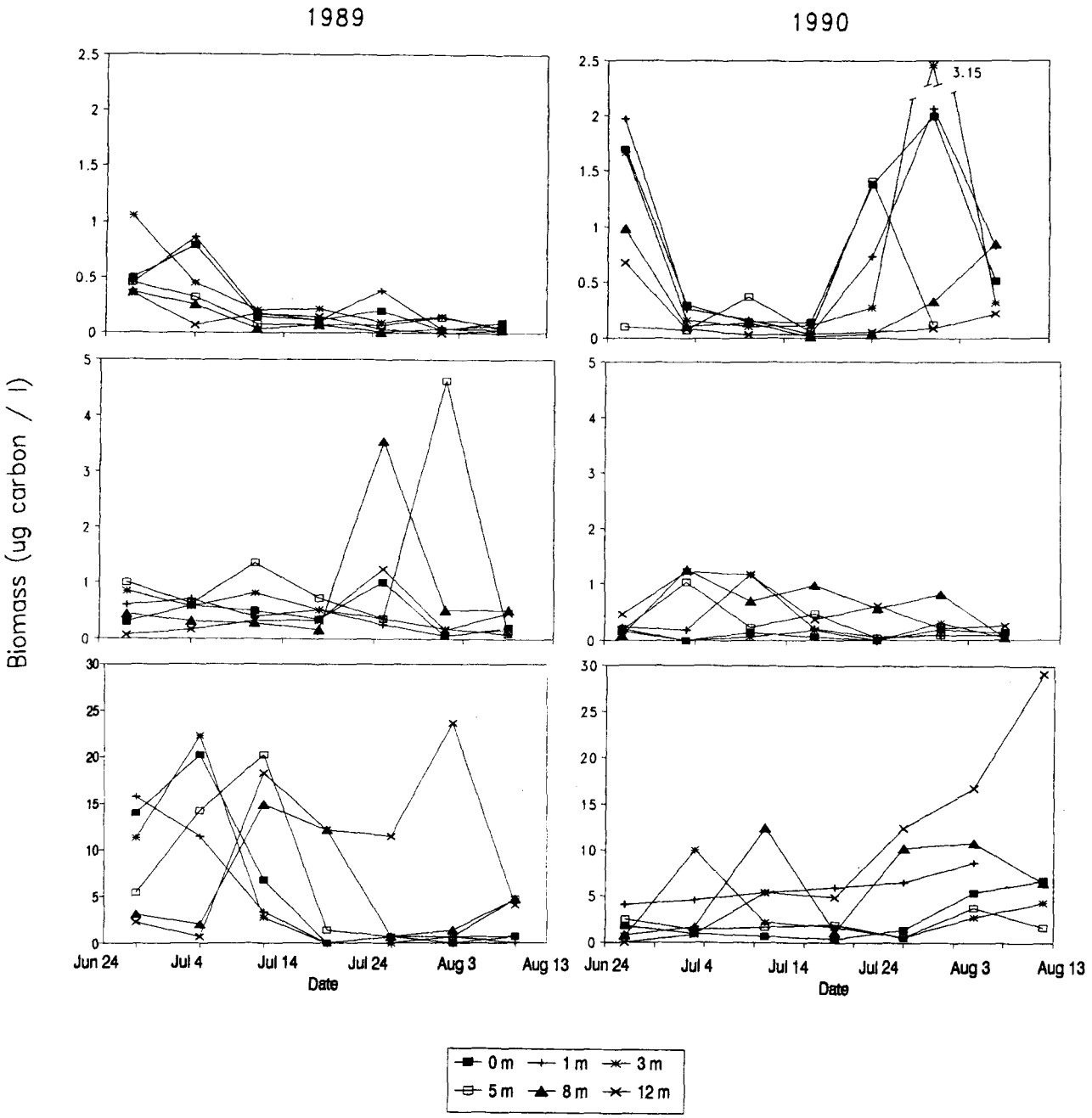

Fig. 1. Microplankton abundance at depths in Toolik Lake, Alaska. Upper panels: ciliate biomass in 1989 and 1990. Middle panels: rotifer biomass in 1989 and 1990. Lower panels: nauplius biomass in 1989 and 1990. Note scale difference for different taxa.

garis demonstrated significant negative correlations with depth ($r = -0.36$, $p < 0.01$, $n = 118$; and $r = -0.27$, $p < 0.01$, $n = 118$, respectively).

In the limnocorral experiment, total microplankton abundance appeared dependent upon trophic status. Addition of either nitrate or

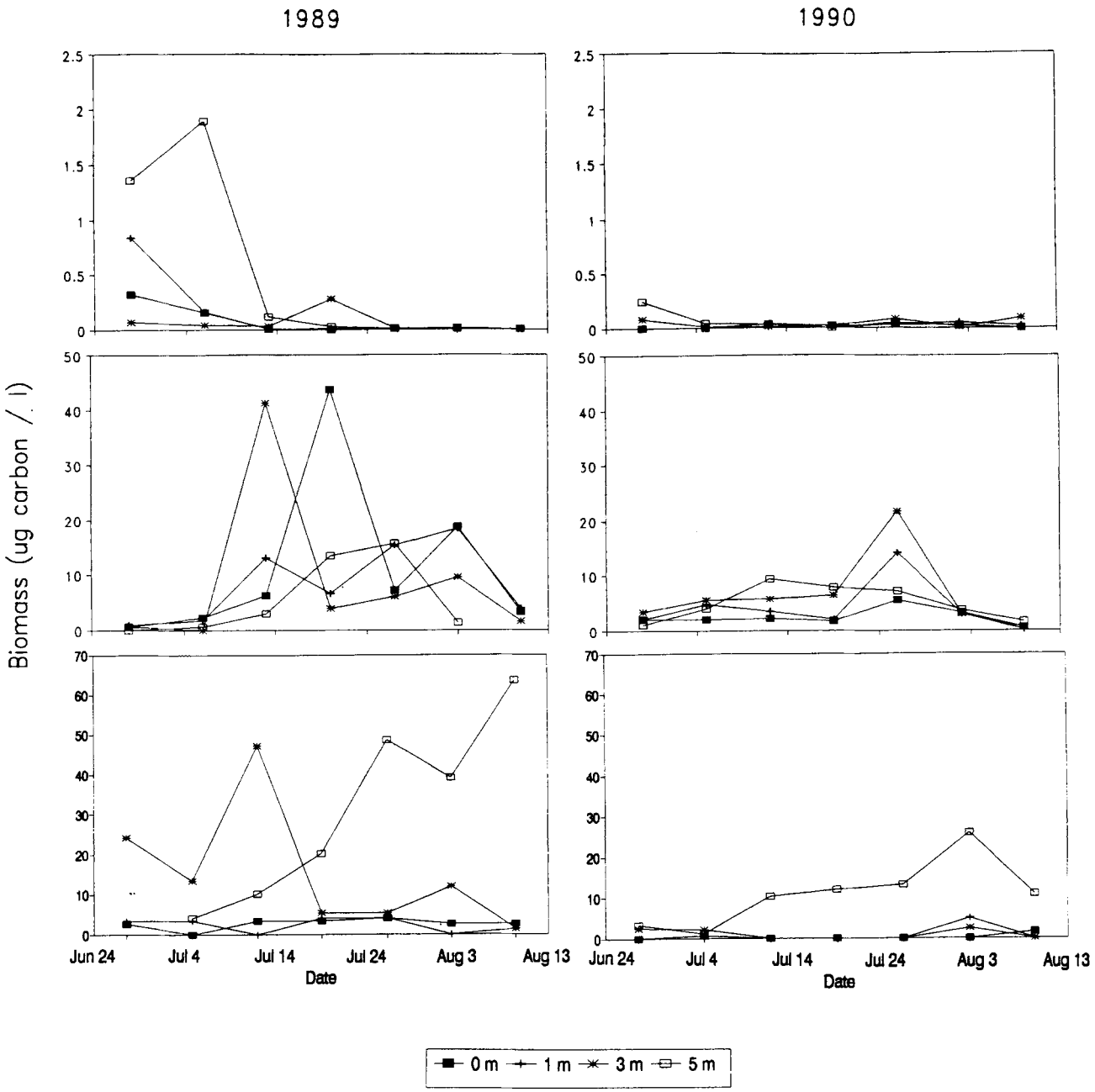

Fig. 2. Microplankton abundance at depths in Lake N-2, control side. Upper panels: ciliate biomass in 1989 and 1990. Middle panels: rotifer biomass in 1989 and 1990. Lower panels: nauplius biomass in 1989 and 1990. Note scale difference for different taxa.

ammonia resulted in dramatic increases in primary producer biomass as measured by chlorophyll *a* and was followed by increased microplankton biomass (Fig. 4). Although the relationship of microplankton biomass to chlorophyll concentration also suggested a similar dependence on primary producers, the correlation was not significant for those lakes where data on

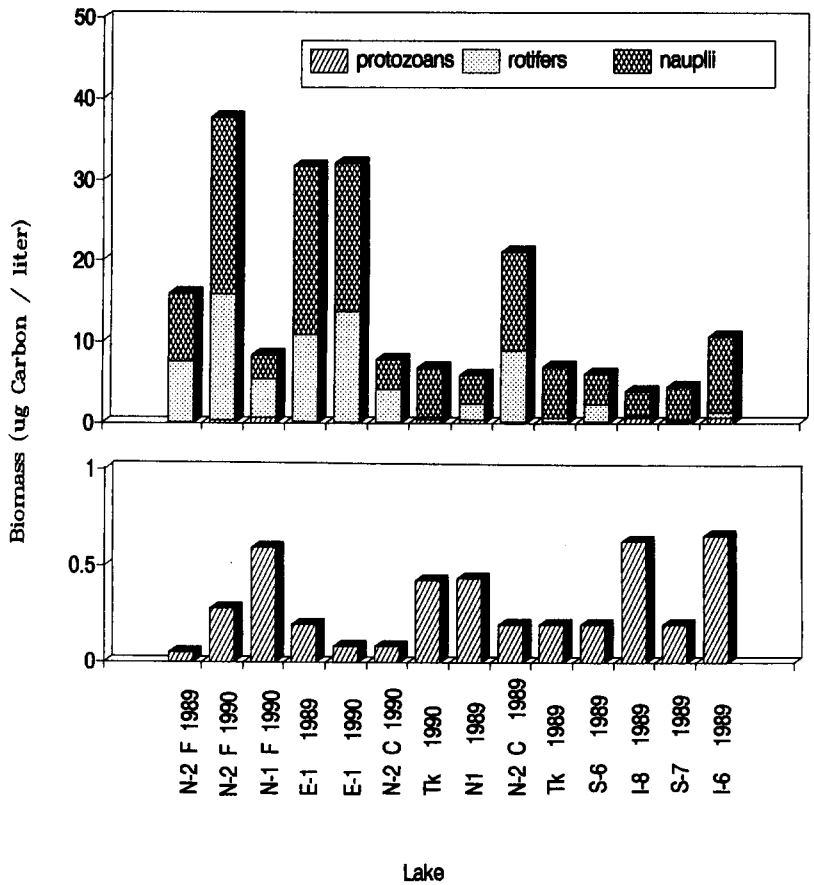

Fig. 3. Mean values for abundance of microplankton taxa in Toolik LTER lakes, 1989 and 1990. Upper, total microplankton biomass. Lower, protozoan biomass in expanded scale. Lakes are arranged in trophic spectrum from mesotrophic to oligotrophic based on chlorophyll *a* concentrations. Designation F indicates experimentally fertilized lakes and C indicates control side of N-2.

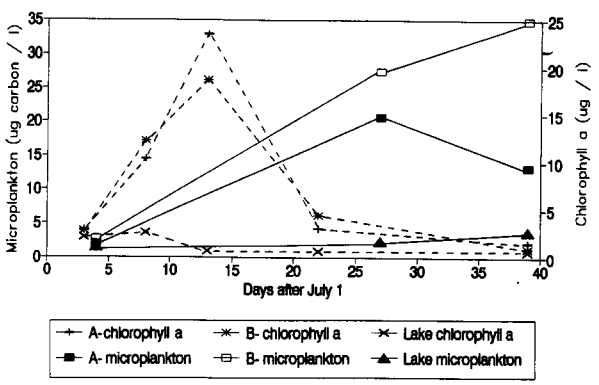

Fig. 4. Limnocorral experiment. Dashed lines represent chlorophyll *a*; Solid lines represent microplankton biomass. Limnocorral A fertilized with ammonia. Limnocorral B fertilized with nitrate. Lake samples adjacent to limnocorrals are control.

microplankton biomass and chlorophyll concentrations were available ($r = 0.337$, NS, $n = 8$).

Discussion

Previous studies provide limited information on heterotrophic microplankton in arctic freshwaters. Several studies report species lists of rotifers from arctic lakes (e.g. Moore, 1978; Chengalath & Koste, 1989), and the rotifer species reported here appear to be common to the plankton of Alaskan arctic lakes. Moore (1978) also noted the presence of ciliated protozoa, including the tintinnid *Codonella cratera*, in a series of eighteen arctic and subarctic lakes. No tintinnids were seen in lakes at the Toolik LTER site during this study.

Several other studies report biomass of microplankton in addition to identifying dominant taxa. Hobbie, Kalff, and Holmgren (unpublished data) reported six rotifer species, and biomass in the range of 0.1–0.4 mg m^{-3} for Lakes Peters and Schrader in May through July, 1968. These values represented 1% or less of the total zooplankton biomass. In Wolf Lake they found higher rotifer biomass, 1.9–5.8 mg m^{-3} over the same period, which represented up to 2% of the total zooplankton biomass. In ultra oligotrophic Char Lake, Rigler *et al.* (1974) reported annual abundance of *Keratella cochlearis*, the second most common zooplankter, to range from $0–5 \times 10^4$ individuals m^{-2} for the 27.5 m deep lake. Production of the rotifers was estimated to represent about 1% of the production of the dominant zooplankter, *Limnocalanus macrurus*. They also noted the abundance of ciliated protozoans, 0–10.3 individuals ml^{-1}, and estimated their production to exceed that of *Keratella*.

The values reported in this study for rotifer abundance and biomass are slightly higher, and in Lakes E-1 and the fertilized side of N-2, significantly higher, than most earlier studies of arctic lakes. Several factors may contribute to this. First, sampling by reverse flow filtration, the method used in this study, is less likely to damage and more likely to retain small rotifers than sampling by net tows. Second, Lakes E-1 and N-2 (fertilized) are smaller, more eutrophic systems than Char, Peters, and Schrader lakes and thus higher microplankton biomass is not unexpected.

One previous report has addressed protozoans in Toolik Lake. In that study, Hobbie & Helfrich (1988) studied heterotrophic nanoflagellates (2–20 μm in length). They found $1–2 \times 10^3$ cells ml^{-1} during July and August 1984 in Toolik Lake and control limnocorrals. They also noted that in fertilized limnocorrals, peaks of nanoflagellate abundance (up to 6.5×10^3 ml^{-1}) were found 6–7 days after peaks in bacterial numbers, suggesting a clear pattern of predator control of bacteria. These heterotrophic flagellates as well as small ciliates are taxa that were not enumerated in the current study. Preserved samples of lake water viewed in settling chambers with an inverted microscope included numerous small protozoans (e.g. 10–25 μm heliozoans) and larger myxotophic flagellates (e.g. *Dinobryon* spp.) that may be abundant but are not quantitatively retained by the reverse-flow method that was used in this study.

One goal of the LTER program is to assess the importance of bottom-up and top-down regulation in lakes (see O'Brien *et al.*, 1992). Pace (1986) presented compelling evidence for bottom-up regulation of microplankton biomass in a series of temperate Canadian lakes, and the results of this study are generally consistent with the hypothesis that biomass of a trophic level is positively correlated with bottom-up factors (food resources). For example, a comparison of the control and fertilized sides of N-2 (Fig. 3) and the limnocorral experiment (Fig. 4) indicate that bottom-up inputs lead to increased microplankton biomass, as would be predicted from temperate studies (e.g. Pace, 1986; Beaver & Crisman, 1989).

Despite general agreement of increased total microplankton biomass with increased trophic status, changes in the microplankton community structure in this study are not entirely consistent with observations of microplankton community response to changing trophic status by Pace (1986) in Quebec lakes or by Beaver & Crisman (1989) in temperate Florida lakes. Pace (1986) found little change in community structure across the trophic spectrum, and both Pace and Beaver & Crisman (1989) reported increased abundance of ciliates with increasing trophic status. In this study, the biomass of rotifers as well as the contribution of rotifers to total microplankton declined as primary producer biomass declined, while protozoans demonstrated no clear pattern (Fig. 3). It is likely, however, that chlorophyll *a*, alone, is a poor estimator of microplankton food resources in these systems. For example, the highest protozoan biomass was found in lakes N-1, Toolik, I-6, and I-8. Each of these lakes may be characterized as having small phytoplankton, probably dominated by cryptophytes, chrysophytes and centric diatoms. This compares with lower protozoan biomass in lakes N-2 and E-1, systems richer in nutrients where large phyto-

plankton dominate, including larger flagellates and dinoflagellates which do not represent food resource available to the small oligotrich protozoans.

The response of the microplankton community in Lake N-1 to fertilization provides additional insight into regulation of microplankton community structure. During 1989, the seasonal pattern of microplankton abundance in Lake N-1 was typical, and similar to that of Toolik Lake (Fig. 1). After whole lake fertilization of N-1 was begun in 1990, algal biomass increased and protozoan abundance showed 4-fold increase during later summer, due to both an increase in number and mean size of individual ciliates (Fig. 5). Additionally, the species composition, but not biomass, of the rotifer assemblage in Lake N-1 changed: during 1989, the rotifer assemblage was dominated by rotifers which could be termed small-particle feeders such as *Conochilus unicornis*, *Keratella* spp., and *Kellicottia longispina*, which feed mainly on small phytoplankton (Hutchinson, 1967). These species also dominated during the early summer of 1990, but by August, 'predatory rotifers', *Synchaeta* sp. and *Polyarthra vulgaris* which consume flagellates, ciliates and other rotifers (Hutchinson, 1967), comprised more than 80% of the rotifer assemblage in Lake N-1 (Fig. 6). The development of these predatory rotifer populations may be a response to the increase in protozoans which can serve as a food resource. These data also suggest interactions within the

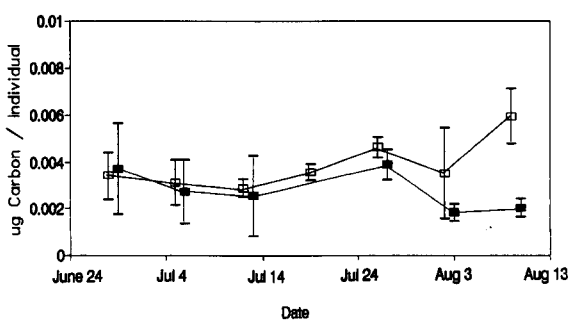

Fig. 5. Individual ciliate protozoan biomass, Lake N1, 1989 (filled square) and 1990 (open square). Values are mean (± SD) of samples taken at 5 depths (0, 1, 3, 5, and 8 m) on each sampling date.

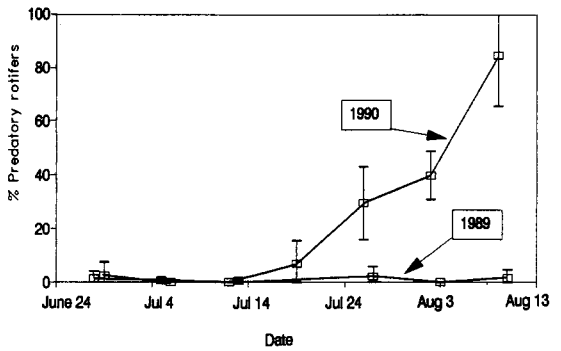

Fig. 6. Percentage of predatory rotifers (*Synchaeta* + *Polyarthra*) in Lake N-1, 1989 and 1990. Values are mean (± SD) of samples taken at 5 depths (0, 1, 3, 5, and 8 m) on each sampling date.

microbial food web which may represent a transient response as the lake system shifts toward a new equilibrium community, since predatory rotifers were not dominant in any of the other lakes studied.

Other types of regulation of microplankton also occur in these lakes. O'Brien *et al.* (1979) have noted that crustacean zooplankton community structure in arctic lakes varies considerably, and the highest abundance of rotifers was found in lakes (N-2, E-1) where the predaceous copepod *Heterocope septentrionalis* is absent. Additionally, Neill (1989) has pointed out that *Daphnia* spp. may inhibit herbivorous rotifers by interference competition, and in arctic lakes such as Lake N-1, where herbivorous zooplankton populations of *Daphnia*, *Bosmina*, and *Diaptomus* are highest, such controls may be important when food resources are limiting. Continued study of grazing interactions in control and experimentally manipulated arctic LTER lakes will aid in understanding the regulation and importance of the microbial loop in lake systems.

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