

## Change of microplankton community structure in response to fertilization of an arctic lake

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### **Abstract:**

Microplankton in an oligotrophic arctic lake were assessed by direct counts for one summer prior to nutrient additions and three summers during which inorganic nitrogen and phosphorus were added to the lake at approximately ten times ambient loading rates. Protozoa increased significantly in both number and biomass following fertilization, and community structure changed from dominance by oligotrichs prior to fertilization to dominance by the bacterivorous peritrich *Epistylis rotans* in the second and third years of fertilization. Rotifer abundance and biomass was not significantly different among summers, although one species, *Conochilus natans* that had not been seen previously, was present during the second and third year of fertilization. By the third year of fertilization both protozoan and rotifer biomass had declined from peak levels, while crustacean zooplankton nauplius abundance had increased suggesting the emergence of top-down regulatory controls as the lake became eutrophic.

**Key words:** arctic lakes, rotifers, protozoans, microplankton, fertilization Abstract

### **Article:**

#### **Introduction**

Two prevailing concepts of regulatory control in aquatic ecosystems are the bottom-up effects of nutrients (e.g. Schindler, 1978; Pace, 1986) and the top-down effects of predation leading to cascading trophic interactions (Carpenter et al., 1985). The bottom-up effect of nutrients may be envisioned as setting the upper limits of biomass that any trophic entity within the system can attain. It functions by increasing the biomass of primary producers which leads to subsequent increases in herbivore and carnivore biomass. Changes in community structure may also occur as a result of bottom-up regulation, for example when eutrophication of aquatic systems leads to blooms of various algal types. O'Brien et al. (1992) note, however, the evidence for regulation of trophic levels beyond primary producers is inconsistent, especially in arctic lakes.

Cascading trophic interactions (top-down regulation) are hypothesized to work in a different fashion. An alteration of the top trophic level leads to a reciprocal response by its prey, which leads to similar reciprocal responses in the prey's food resource and so on. For example, in a simple system, an increase in predatory fish should result in reductions of zooplanktivorous fish, an increase in herbivorous zooplankton, and a reduction of phytoplankton. Carpenter & Kitchell (1992) have noted that the trophic cascade hypothesis is only one of a number of factors that regulates community structure, and that impacts are often damped out with increasing distance from the trophic level of primary manipulation. They also note that questions of scale (both physical and temporal) are critical to proper understanding of trophic cascade impacts. Sanders et al. (1992) have suggested that predator controls are likely to be more important in eutrophic systems than those with limited nutrients and production. A recent review of microbial food webs in temperate lakes (Riemann & Christoffersen, 1993) supports this view.

Most studies of ecosystem response to either top-down or bottom-up manipulations have focused on aggregated taxonomic groupings which presumably comprise trophic levels and data are generally reported as biomass

increases or decreases. Many studies have also ignored the heterotrophic microbial components of aquatic systems, and even fewer studies have addressed changes in the structure of heterotrophic microplankton communities, despite evidence of the significant role they play in carbon and nutrient cycling (cf. Pace & Funke, 1991). Thus, Stockner & Porter (1988) suggested that understanding the responses of heterotrophic microplankton was essential to interpretation of ecosystem responses in manipulative studies.

A few studies have provided insight and raised intriguing questions regarding regulatory controls on microbial food web components. Pace & Funke (1991) studied the response of microplankton communities to short term (4 day) nutrient and predator manipulations in microcosms in two oligotrophic northern temperate lakes. They found significant increases in microplankton biomass in response to fertilization, but noted that no significant top-down response of microplankton was induced by predator manipulation. Consistent with Carpenter & Kitchell (1992), they concluded that trophic cascades are truncated at the level of protozoans. Hoffmann & Höfle (1993) followed changes in microbial food webs in mesocosms in a eutrophic lake with added DOC. They suggested that increased DOC led directly to increases in bacteria and protozoans, followed by an increase in algae as a result of nutrient release due to protozoan grazing. This was followed in turn by increases in two rotifer species that grazed on the algae. Berninger, et al. (1993) used frequent sampling and time-series analyses to identify trophic relationships among microbial components of a hypereutrophic freshwater pond. They found evidence of strong predator-prey interactions within the microbial food which suggested an efficient link to higher trophic levels.

A previous report notes the general agreement of microplankton response in arctic lakes to increased nutrient loading with the paradigm of bottom-up regulatory control (Ruble, 1992). This paper reports changes in community structure and abundance of heterotrophic microplankton over a three year period in response to nutrient additions to highly oligotrophic Lake N-1 at the Arctic Long Term Ecological Research site (LTER) at Toolik Lake, Alaska. We began this study with two simple hypotheses: (1) heterotrophic microplankton would increase in response to nutrient additions; and (2) top-down effects would follow fertilization as predicted from cascading trophic interactions, i.e., once production increased at the highest trophic level, we should begin to see a top-down impact of increased predation.

## Materials and methods

### Study site

The Arctic 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 highly oligotrophic systems (Miller et al., 1986) with varying zooplankton and fish populations (O'Brien et al., 1979; Kling et al., 1992b). Most data presented here are from Lake N-1 which has been characterized by Kling et al., (1992b). It is 4.4 hectares in area with a maximum depth of 14 m in one basin, although half the lake is only about 2 m in depth. Typically, algal communities in these oligotrophic arctic lakes are dominated by small chrysophytes, dinoflagellates, and cryptophytes (O'Brien et al., in press). Zoo-plankton commonly found in Lake N-1 include the herbivore *Diatomus pribaifensis*, the carnivore *Cyclops scutifer*, and the larger but much less abundant predator *Heterocope septentrionalis* (O'Brien et al., 1979; Kling et al., 1992b). Fish in N-1 include lake trout, burbot, arctic grayling, and slimy sculpin (Hanson et al., 1992). At least eight species of chironomids are found in the benthos (Kling et al., 1992b). Lake N-1 has been fertilized since 1990 by weekly additions of inorganic nitrogen and phosphorus at rates (3 mM N m<sup>-2</sup> d<sup>-1</sup> as (NH<sub>4</sub>)<sub>2</sub>SO<sub>4</sub> and 0.23 mM P m<sup>-2</sup> d<sup>-1</sup> as H<sub>3</sub>PO<sub>4</sub>) which are about 5 to 10 times the normal nutrient loading during the summer (July 1—August 15).

Climate is a major constraint at the arctic LTER site. The region is underlain by permafrost and has mean annual temperatures of —9 °C (monthly means —32 °C to 12 °C). Annual precipitation is about 31 cm, with about half falling as rain from late May through September. Ice cover up to 2 m thick generally thaws in late June and reforms in late September or October.

## Methods

Water samples were collected during summers (1989—1992) by Van Dorn sampler at the surface and at depths of 1, 3, 5, 8, and occasionally 12 m in Lake N-1. Two liters of sample water were then gently concentrated to 60 ml by reverse flow through a 20  $\mu\text{m}$  net (Dodson & Thomas, 1964). Cold glutaraldehyde was added as a preservative to 1% final concentration and samples were stored under refrigeration (4  $^{\circ}\text{C}$ ). Live samples were also examined to assure that glutaraldehyde was an appropriate preservative and to aid in identification.

Samples were enumerated following the procedure of Baldock (1986). Briefly, an aliquot of the concentrated sample was stained with 0.25% Rose Bengal solution, and then drawn onto an 8.0  $\mu\text{m}$  pore white cellulose acetate filter under gentle vacuum. Filters were examined under a compound microscope after mounting on slides in a 43% sucrose solution. The entire surface area of the filter was scanned at 100 $\times$  or 200 $\times$  and individual microplankton identified. Magnification up to 400 $\times$  was used to aid in identification as necessary. Taxonomic guides to protozoa (Lee et al., 1985) and rotifers (Ruttner-Kolisko, 1974) were used to identify organisms to genus and in some cases species. Crustacean zooplankton nauplii were enumerated but not taxonomically identified, although nearly 100% of zooplankton biomass is comprised of *Diaptomus pibilofensis* and *Cyclops scutifer* (J. O'Brien, Univ. of Kansas, personal communication). For comparing microplankton across years or lakes, counts from samples on each day were integrated over the entire water column to provide mean values. Carbon biomass of microplankters was estimated for individual taxa (Table 1) based on measured sizes and literature values (Ruttner-Kolisko, 1977; Pauli, 1989; Putt & Stoecker, 1989).

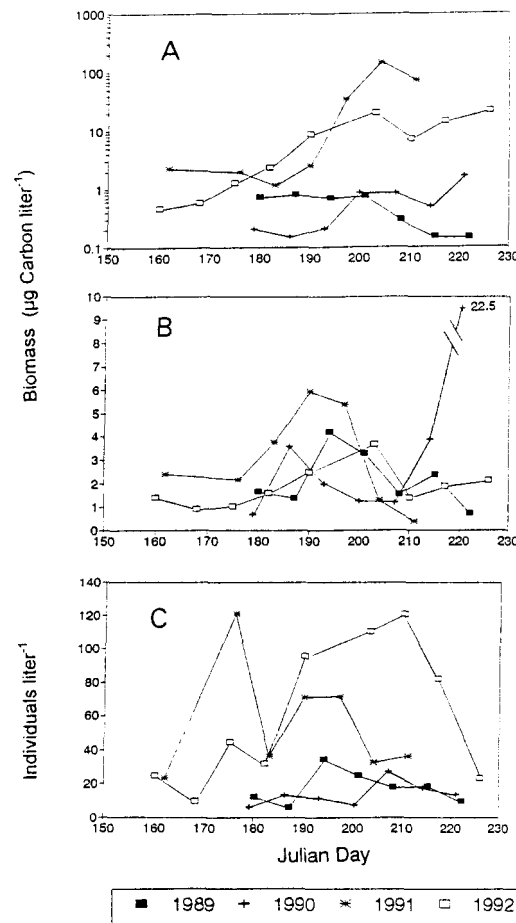


Fig. 1. Microplankton response to fertilization of Lake N-1. In all panels, (■) represents prefertilization data from 1989. Fertilization began during summer 1990 (+) and continued during 1991 (\*), and 1992 (□) A. Protozoan biomass, note log scale. B. Rotifer biomass. C. Nauplius abundance.

Five other lakes at the LTER site which were sampled at least three times per year and at least two different years during the period 1989-1991 were used as reference lakes for comparative purposes (Carpenter, 1989). Data were analyzed by non-parametric statistical tests after rank transformation (SAS, 1988).

## Results

Counts of microplankton in Lake N-1 during 1989 were similar to those found in other lakes at the arctic LTER site (Rublee, 1992), characterized by: low abundance of protozoans with peak biomass  $<1 \mu\text{g C l}^{-1}$ , during the first half of the summer; mean rotifer biomass  $<2\text{-}3 \mu\text{g C l}^{-1}$ , with peak abundance in mid to late summer; and estimated crustacean nauplius biomass about twice that of the rotifers with a similar mid to late summer season peak abundance. Mean protozoan abundance was  $148 \text{ ind l}^{-1}$ ; (range, 72-238, coefficient of variation, 50.3%), which corresponded to a biomass of about  $0.5 \mu\text{g C l}^{-1}$ . Oligotrich ciliates of the genera *Halteria*, *Strombidium*, and *Strobilidium* were the most common protozoans observed, comprising  $>96\%$  of the protozoan community on each sampling date. Mean rotifer abundance was  $97 \text{ individuals l}^{-1}$  (range 31-190, CV 54.7%) with *Keratella cochlearis* and *Conochilus unicornis* comprising  $>95\%$  of the individuals observed. This corresponded to an estimated mean biomass for rotifers of  $2.2 \mu\text{g C l}^{-1}$ . Mean nauplius abundance was  $18 \text{ ind l}^{-1}$  (range 6-34, CV 54.0%).

Table 1. Organism to carbon conversion factors ( $\text{ng C individual}^{-1}$ ) for microplankton in Lake N-1.

Protozoans	ng C	Rotifers	ng C
<i>Strombidium</i> (20–30 $\mu\text{m}$ )	0.5	<i>Keratella cochlearis</i>	18.0
(31–45 $\mu\text{m}$ )	1.3	<i>Keratella quadrata</i>	24.5
(>45 $\mu\text{m}$ )	3.5	<i>Kellicottia longispina</i>	15.3
<i>Halteria</i> (15–25 $\mu\text{m}$ )	0.6	<i>Polyarthra vulgaris</i>	19.9
(26–45 $\mu\text{m}$ )	3.9	<i>Synchaeta</i> sp.	51.0
(>45 $\mu\text{m}$ )	11.0	<i>Conochilus unicornis</i>	25.8
<i>Strobilidium</i>	11.0	<i>Conochilus natans</i>	40.0
<i>Epistylis</i>	4.0		
<i>Vorticella</i>	9.1		
Misc.	2.5		

The biomass of microplankton in Lake N-1 showed no significant change during the first year of fertilization of Lake N-1 (Duncan's Multiple Range Test), but after the first year, the patterns of response were different for the three major taxa (protozoans, rotifers and crustacean nauplii, Fig. 1). Protozoan biomass (Fig. 1A) showed a significant three order of magnitude increase up to  $150 \mu\text{g C l}^{-1}$  during the second and third years of fertilization (ANOVA on rank transformed data,  $F = 11.19$ , 3,27 d.f.,  $p < 0.01$ ; Duncan's Multiple Range Test grouped 1991 and 1992 together, in a different group from 1991 and 1992). Rotifer biomass (Fig. 1B) showed no significant difference among any years (ANOVA on rank-transformed data,  $F = 0.42$ , 3,27 d.f.,  $P < 0.36$ ), despite a pronounced increase on the last sampling date of 1990, the first year of fertilization. The abundance of crustacean nauplii (Fig. 1C) increased significantly by about 3 to 4 times pre-fertilization levels during the second and third year of fertilization ( $F = 9.07$ , 3,27 d.f.,  $p < 0.01$ ; 1989 and 1990 were grouped together in a Duncan's Multiple Range Test as were 1991 and 1992).

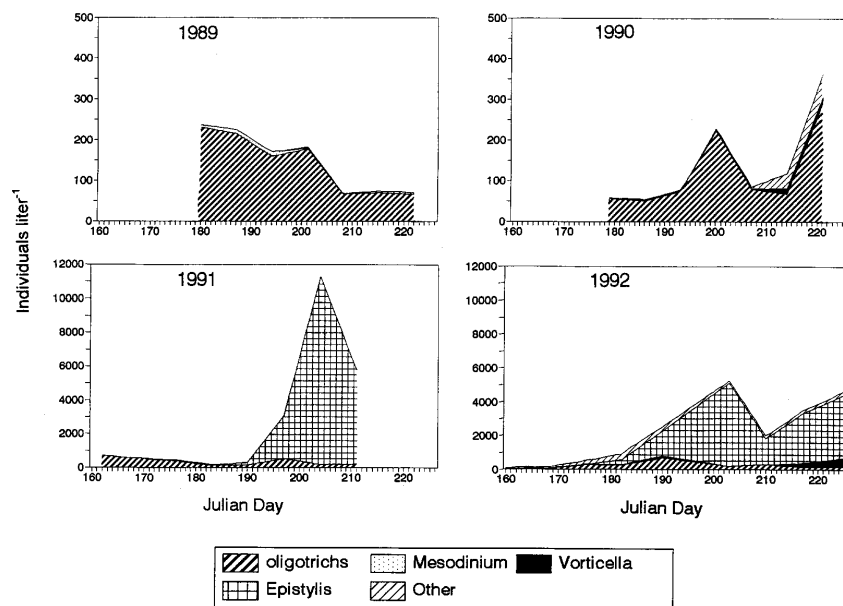


Fig. 2. Protozoan community structure in Lake N-1, 1989–1992. Note change in scale of Y-axis in years 1991 and 1992.

Mean values of microplankton abundance and biomass were compared to similar data from five other lakes at the LTER site, including both sides of Lake N-2, a lake which had been divided by a plastic curtain and fertilized on one side (O'Brien et al., in prep.). Duncan's multiple range tests on rank transformed data indicated that protozoan abundance and biomass in Lake N-1 during 1991 and 1992 was significantly higher than in other lakes (including N-1 in 1989 and 1990). The abundance and biomass values for rotifers and nauplii were not significantly different from those found in other arctic LTER lakes.

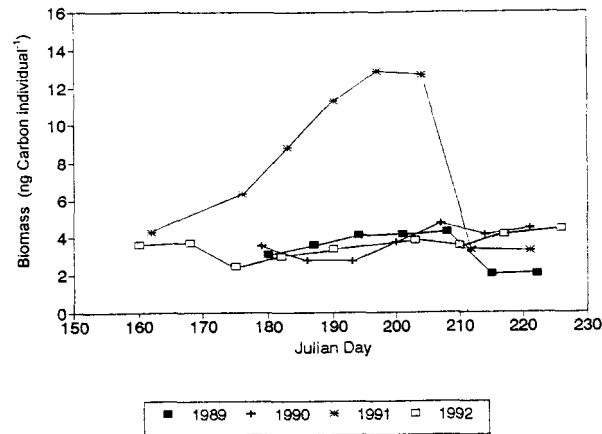


Fig. 3. Mean size of protozoans in the plankton of Lake N-1, 1989-1992.

Changes in both protozoans and rotifers over the four years included changes in community structure as well as abundance (Fig. 2). During the first summer of fertilization, the protozoan community was similar to that in 1989, dominated by oligotrichs, and with low abundances of *Mesodinium* and *Vorticella campanula*. In 1991, the increase in protozoan biomass was attributable to a mid to late summer bloom of the colonial peritrich *Epistylis rotans*, which had not been seen in previous years. *Epistylis* was also present in 1992, but at about half the level of the previous year. *Vorticella*, usually attached to colonial bluegreen algae or crustacean exoskeletons, was also more common during the third year of fertilization. Additionally, there was a change in the mean size of protozoans during the second year of fertilization (Fig. 3). This change was characterized by a significant increase in the mean size of ciliates during 1992 (one-way ANOVA by ranks,  $F = 4.43$ , 3,27 d.f.,  $p < 0.01$ ). This increase could not be attributed to the *Epistylis rotans* bloom, however, since the mean estimated biomass of *Epistylis* ( $4 \text{ ng C ind}^{-1}$ ) was similar to the mean protozoan size of other years. The change was attributable to the appearance large ( $>60\text{-}70 \mu\text{m}$  in length) oligotrichs, *Strombidium* and *Strobilidium*. During the third year of fertilization the mean size of ciliates returned to pre-fertilization levels.

Rotifer community structure also changed somewhat during this study (Fig. 4). In 1989, *Conochilus unicornis* and *Keratella cochlearis*, rotifers which feed on small particles (Dumont, 1977; Pourriot, 1977), comprised  $>90\%$  of total rotifer biomass on all sampling dates. During the first year of fertilization, *C. unicornis* comprised 80-90% of the rotifer biomass until mid summer, when a *Synchaeta* sp. and *Polyarthra vulgaris*, which feed on protozoans and flagellated algae (Dumont, 1977; Pourriot, 1977) increased in abundance. *Synchaeta* continued to increase in abundance until it comprised greater than 90% of rotifer biomass on the last sampling date of 1990. During the second year of fertilization, *Polyarthra vulgaris* was most common on the first two sampling dates, and an additional rotifer species, *Conochilus natans*, which had not been seen in previous summers, appeared. By midsummer, *C. unicornis* again became the dominant rotifer, comprising  $>90\%$  of rotifer biomass. In late summer, *C. unicornis*, *Kellicottia longispina*, *Keratella cochlearis*, and *Polyarthra vulgaris* were all commonly observed. In the third summer of fertilization *Kellicottia longispina*, *Keratella quadrata*, and *Keratella cochlearis* were dominant during the first half of the summer; *Conochilus unicornis* and *Synchaeta* were most common during late summer.

## Discussion

Previous studies at the Arctic LTER site included fertilization and fish density manipulations of limnocorrals (O'Brien et al., 1992) and fertilization of one-half of a naturally oligotrophic lake (Lake N-2) which had been

divided by a plastic curtain and from which most fish had been removed (O'Brien et al., in preparation). The 'bottom-up' responses to fertilization included increases in nutrient pools and increased biomass of phytoplankton, nanoflagellates, benthic algae and submerged vegetation, benthic insects, and crustacean zooplankton (after a 1-2 year lag). There was also evidence of top-down regulation, manifested in apparent selection favoring small zooplankton when fish were present (O'Brien et al., 1992). Microplankton were not studied in either the limnocorrals or in lake N-2 prior to 1989 (the 3rd year of fertilization of N-2). However, microplankton abundance in lake N-2 during 1989 and 1990 was the highest of any lake at the LTER site during those years, with values on the experimental side significantly higher than on the control side, and short duration experiments in limnocorrals also suggested a strong positive response to fertilization (Ruble, 1992).

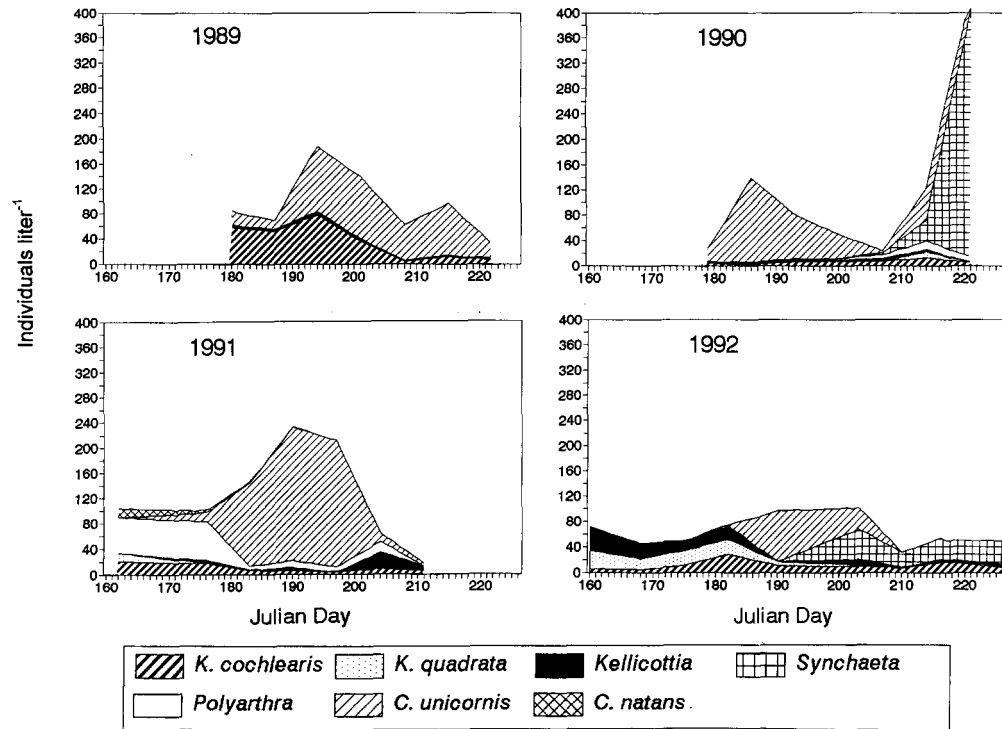


Fig. 4. Rotifer community structure in Lake N-1, 1989-1992.

As expected, nutrient additions to Lake N-1 resulted in increased microbial biomass, consistent with the first hypothesis we addressed. However, the increase was attributable primarily to one species of protozoan, and secondarily to crustacean nauplii, but not to rotifers. These responses are probably best explained by aggregating species into 'functional' taxonomic groupings. Phytoplankton responded to fertilization by increased abundance of the dominant, small, single-celled algae during the first year of fertilization and a shift toward colonial forms and filamentous blue-greens during the second and especially the third year of fertilization (M. Miller, Univ. of Cincinnati, personal communication). Additionally, based on limnocorral studies in Toolik Lake (Hobbie & Helfrich, 1988) both heterotrophic and autotrophic nanoflagellates increased. The microplankton community response during the first year of fertilization (1990) appeared to be an increase in the abundance of extant species (such as the oligotrichs, Fig. 2) and their predators (e.g. Synchaeta, Fig. 4). Thus, there was minimal change in food web structure during the first summer of fertilization.

During the second summer of fertilization (1991), a shift in food web structure toward dominance by bacterivorous taxa became apparent. Early in the summer *Polyarthra vulgaris*, a predator on flagellated algae (Dumont 1977, Pourriot 1977), was the dominant rotifer (Fig. 4), but by midsummer *Conochilus unicornis* which feeds effectively on bacteria and particles less than 10  $\mu\text{m}$  (Dumont, 1977; Pourriot, 1977) became the dominant rotifer at higher abundance than in previous years (Fig. 4). By late summer, *Epistylis rotans*, a bacterivorous colonial peritrich reached densities greater than  $10^4 \text{ l}^{-1}$  (Fig. 2), equivalent to a biomass of over  $100 \mu\text{g C l}^{-1}$  (Fig. 1). Finally, crustacean nauplii were found at higher abundance during 1991, than in 1989 or 1990 (Fig. 1).

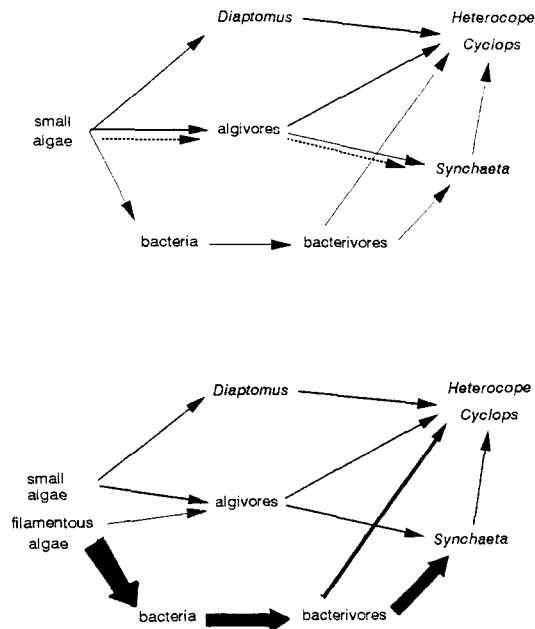


Fig. 5. Response of microbial food web to fertilization in Lake N-1 at the arctic LTER site. Upper panel: Food web structure prior to and during first year of fertilization (1989–1990). Width of solid arrows indicates relative importance of pathway prior to fertilization. Dashed arrow represent increased interactions during first year of fertilization. Lower panel: Food web structure during second and third years of fertilization (1991–1992). Note addition of filamentous algae and that while strength of traditional grazing interactions has not decreased, the pathway through bacteria has increased dramatically. Bacterivores include: heterotrophic and mixotrophic nanoflagellates, *Epistylis rotans* and *Vorticella campanula*. Algivores include oligotrich ciliates, rotifers (*Keratella* spp., *Kellicottia longispina*, *Polyarthra vulgaris*, *Conochilus* spp.).

During the third summer of fertilization (1992) there may be evidence of top-down regulatory effects on microbial populations, as expected by our second hypothesis, although the evidence is not strong. First, protozoan biomass was again dominated by *E. rotans*, but abundance was only one-half of that during the previous year (Fig. 2). Second, mean rotifer abundance was the lowest of any year, suggesting that zooplankton predators had an impact on rotifer population densities. Third, nauplius abundance attained the highest level seen during the four year study period (Fig. 1).

From a trophic perspective, nutrient additions at the arctic LTER site appeared to have led to a shift in food web structure from high dependency on direct utilization of primary production to one with greater dependence on indirect utilization of photosynthetically fixed carbon via the heterotrophic microbial components during the first three years of fertilization (Fig. 5). This interpretation, though speculative, is consistent with observations of Rieman & Christoffersen (1993) who noted that importance of the microbial loop increases relative to grazing pathways with increasing levels of productivity in temperate lakes. They also noted that the role of predatory controls probably is more important in eutrophic lakes. During the first two years of this study, bottom-up controls clearly impact microplankton abundance. By the third year of fertilization, however, top-down controls may begin to exhibit regulation as evidenced by declines in protozoan and rotifer abundance over previous years, and increased numbers of crustacean nauplii.

Our results to date emphasize the importance of long-term studies in evaluating the responses of microbial communities to large-scale manipulations (cf. Carpenter & Kitchell, 1992), and support the recommendations of Stockner & Porter (1988) that microbial interactions must be assessed in detail in order to understand the role microbial food webs play in both stable and perturbed aquatic ecosystems. Aggregation of microbial taxa into groups that supersede functional levels may lead to erroneous conclusions regarding the regulatory controls. This becomes especially problematic with microbial components of food webs since they may occupy more than one trophic level and since the number of potential trophic interactions increases dramatically as the

diversity of microbial communities is increased. The experimental manipulation of Lake N-1 is continuing, and should help in unraveling the long-term microbial response to fertilization. We expect to see continued change if increases in the higher trophic levels indeed begin to exert regulatory feedback on zooplankton and microbial populations. In particular, this should provide an interesting empirical test of the observation by Pace & Funke (1991) in short term experiments that top-down impacts are truncated at the level of protozoans.

## References

- Baldock, B. M., 1986. A method for enumerating protozoa in a variety of freshwater habitats. *Microb. Ecol.* 12: 187-191.
- Berninger, U.-G., S. A. Wickham & B. J. Finlay, 1993. Trophic coupling within the microbial food web: a study with fine temporal resolution in a eutrophic freshwater ecosystem. *Freshwat. Biol.* 30: 419-432.
- Carpenter, S. R., 1989. Replication and treatment strength in whole-lake experiments. *Ecology* 70: 453-463.
- Carpenter, S. R., J. F. Kitchell & J. R. Hodgson, 1985. Cascading trophic interactions and lake productivity. *Bioscience* 35: 634- 639.
- Carpenter, S. R. & J. F. Kitchell, 1992. Trophic cascade and biomanipulation: Interface of research and management - a reply to the comment by DeMelo et al., *Limnol. Oceanogr.* 37: 208-213.
- Dodson, A. & W. Thomas, 1964. Concentrating plankton in a gentle fashion. *Limnol. Oceanogr.* 9: 455-459.
- Dumont, H. J., 1977. Biotic factors in the population dynamics of rotifers. *Arch. Hydrobiol. Beih. Ergebn. Limnol.* 8: 98-122.
- Hanson, K. L., A. E. Hershey & M. E. McDonald, 1992. A comparison of slimy sculpin (*Cottus cognatus*) populations in arctic lakes with and without piscivorous predators. *Hydrobiologia* 240 (Dev. Hydrobiol. 78): 189-202.
- Hobbie, J. E. & J. V. K. Helfrich III, 1988. The effect of grazing by microprotozoans on production of bacteria. *Archiv. Hydrobiol. Beih.* 31: 281-288.
- Hoffman, W. & M. G. H6fle, 1993. Rotifer population dynamics in response to increased bacterial biomass and nutrients: a mesocosm experiment. *Hydrobiologia* 255/256 (Dev. Hydrobiol. 83): 171-175.
- Kling, G. W., B. Fry & W. J. O'Brien, 1992a. Stable isotopes and planktonic trophic structure in arctic lakes. *Ecology* 73: 561-566.
- Kling, G. W., W. J. O'Brien, M. C. Miller & A. E. Hershey, 1992b. The biogeochemistry and zoogeography of lakes and rivers in arctic Alaska. *Hydrobiologia* 240 (Dev. Hydrobiol. 78): 1-14.
- Lee, J. J., S. H. Hunter & E. C. Bovee (eds), 1985. An illustrated guide to the protozoa. *Soc. Protozool.*
- Miller, M. C., G. R. Hater, P. Spatt, P. Westlake & D. Yaekel, 1986. Primary production and its control in Toolik Lake, Alaska. *Arch. Hydrobiol./Suppl.* 74, 1: 97-131.
- O'Brien, W. J., C. Buchanan & J. F. Haney, 1979. Arctic zooplankton community structure: Exceptions to some general rules. *Arctic* 32: 237-247.
- O'Brien, W. J., A. E. Hershey, J. E. Hobbie, M. A. Huller, G. W. Kip-phut, M. C. Miller, B. Moller & J. R. Vestal, 1992. Control mechanisms of arctic lake ecosystems: A limnocorral experiment. *Hydrobiologia* 240 (Dev. Hydrobiol. 78): 143-188.
- O'Brien, W. J., M. Bahr, A. Hershey, J. Hobbie, G. Kipphut, G. Kling, H. Kling, M. McDonald, M. Miller & P. A. Rublee, 1995. The Limnology of Toolik Lake, In Milner & Oswood (eds), *Alaskan Freshwaters*. Springer-Verlag. In press.
- Pace, M. L., 1986. An empirical analysis of zooplankton community size structure across lake trophic gradients. *Limnol. Oceanogr.* 31: 45-55.
- Pace, M. L. & E. Funke, 1991. Regulation of planktonic microbial communities by nutrients and herbivores. *Ecology* 72: 904-914.
- Pauli, H.-R., 1989. A new method to estimate individual dry weights of rotifers. *Hydrobiologia* 186/187 (Dev. Hydrobiol. 52): 355- 361.
- Pourriot, R., 1977. Food and feeding habits of Rotifera. *Arch. Hydrobiol. Beih. Ergebn. Limnol.* 8: 243-260.
- Putt, M. & D. K. Stoecker, 1989. An experimentally determined carbon:volume ratio for marine `oligotrichous' ciliates from estuarine and coastal waters. *Limnol. Oceanogr.* 34: 1097-1104.
- Rieman, B. & K. Christoffersen, 1993. Microbial trophodynamics in temperate lakes. *Mar. Microb. Food Webs* 7: 69-100.



- Rublee, P. A., 1992. Community structure and bottom-up regulation of heterotrophic microplankton in arctic LTER Lakes. *Hydrobiologia* 240 (Dev. Hydrobiol. 78): 133-142.
- Ruttner-Kolisko, A., 1974. Plankton rotifers. Biology and taxonomy. *Die Binnengewasser*, Suppl. Vol. XXVI, part 1.
- Ruttner-Kolisko, A. 1977. Suggestions for biomass calculation of plankton rotifers. *Arch. Hydrobiol.* 8: 71-76.
- SAS Institute, Inc., 1988. SAS/STAT User's Guide, Release 6.03 Edition. Cary, NC.
- Sanders, R. W., D. A. Caron & U.-G. Berninger, 1992. Relationships between bacteria and heterotrophic nanoplankton in marine and fresh waters: an inter-ecosystem comparison. *Mar. Ecol. Progr. Series.* 86: 1-14.
- Schindler, D. W., 1978. Factors regulating phytoplankton production and standing crops in the world's freshwaters. *Limnol. Oceanogr.* 23: 478-486.
- Stockner, J. G. & K. G. Porter, 1988. Microbial food webs in freshwater planktonic ecosystems. In S. R. Carpenter (ed.), *Complex Interactions in lake communities*. Springer-Verlag, NY: 69-83.