Changes in abundance, composition and controls within the plankton of a fertilised arctic lake

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Summary:

1. An oligotrophic arctic lake was fertilised with inorganic nitrogen and phosphorus as $(NH_4)_2$ NO_3 and H_3PO_4 for five summers. The loading rate was 1.7–2.5 mmol N m^{-2} day^{-1} and 0.136–0.20 mmol P m^{-2} day^{-1} which is two to three times the annual loading of lakes in the area. The heterotrophic microzooplankton community was enumerated during the experiment as well as 1 year pre- and post-treatment.

2. The structure of the microplankton community changed from a nutrient limited system, dominated by oligotrich protozoans and small-particle feeding rotifers, to a system dominated by a succession of peritrich protozoans and predatory rotifers. These peritrich protozoans and predatory rotifers were not present prior to fertilisation and never constituted more than a small fraction of the biomass in other lakes at the research site. The average biomass of the rotifers and protozoans was more than seven and a half times larger by the end of fertilisation than it was initially.

3. Because of the increases in numbers of individuals in these new taxa, the structure of the microbial food web changed. When fertilisation stopped, most parameters returned to prefertilisation levels within 1 year.

Keywords: arctic rotifers, fertilisation, microplankton, protozoans

Article:

Introduction

Aquatic communities are regulated by both top down and bottom up controls. Bottom up control assumes systems are resource limited, and that any increase in resources, such as nutrients, results in a subsequent increase in primary production followed by increases at higher trophic levels (Schindler, 1978; Pace, 1986). The top down theory of control proposes that predators regulate population structure and prey densities, resulting in cascading interactions (Brooks & Dodson, 1965; Carpenter et al., 1985) in which prey species are reciprocally affected by changes in predator densities.

Several studies of the bottom up control of arctic aquatic systems have been conducted at the Arctic Long-term Ecological Research (LTER) site in Alaska. These include microcosms (2–6 m^3) in 1991 and 1994 (Hobbie et al., 1999), 'limnocorrals' (60 m^3) (O'Brien et al., 1992) and lake fertilisations (Rublee & Bettez, 1995). In each of these experiments there was a bottom up response resulting in an increase in primary productivity and algal biomass. Bacterial, and subsequently, heterotrophic nanoflagellate and microplankton numbers all increased in relation to reference populations.

There have been numerous studies investigating predator–prey (top down) interactions at all trophic levels within the classic food web. Flagellates have been shown to have an impact on bacterial numbers in arctic (Hobbie & Helfrich, 1988; O'Brien et al., 1992), as well as temperate systems (Sanders et al., 1989; Weiss, 1990; Berninger et al., 1991). Nanoflagellate numbers have been shown to be affected by ciliates (Weiss, 1990), which in turn are a food source for rotifers (Gilbert & Jack, 1993) and, when abundant, nauplii as well (Burns & Gilbert, 1993). Clodocerans and calanoid copepods can control ciliate numbers (Gilbert, 1989; Pace & Funke, 1991; Wickham & Gilbert, 1991) while other protozoans can be an important food source of metazoan

zooplankton (Sanders & Wickham, 1993; Wickham, 1995). Rotifers have also been shown to be a food resource for many of the mesoplankton species such as Cladocera, Cyclopoda and Calanoida (Williamson, 1983 and references therein). Zooplankton numbers, species composition and size are affected by the presence and densities of planktivorous fish (O'Brien et al., 1979, 1992, 1997; Carpenter et al., 1985; Christoffersen et al., 1993).

Previous studies at this site have demonstrated the importance of nutrient inputs to arctic lake food webs and the importance of predator–prey interactions among bacteria, heterotrophic nanoflagellates and microplankton; (Hobbie & Helfrich, 1988; O'Brien et al., 1992; Rublee & Bettez, 1995; Hobbie et al., 1999), as well as those between zooplankton and fish (O'Brien et al., 1997), and lake trout and snails (Hershey, 1990). The purpose of this paper is to expand on a previous report describing changes in the microplankton community as a response to 3 years of whole lake fertilisation (Rublee & Bettez, 1995), which saw the protozoan community respond with increased abundance of the small peritrich Epistylis rotans (≈10-fold), resulting in their dominance during the second and third year of fertilisation. The rotifer biomass, however, did not change significantly from prefertilisation levels, although there was an increase in the abundance of two taxa, *Concochilus natans* and a *Synchaeta* spp.

In this paper we report longer-term results, which include two additional years of fertilisation and 1 year postfertilisation, as well as data on phytoplankton and zooplankton which have not been previously reported. This paper also highlights the importance of long-term measurements when conducting whole lake manipulations because changes in species composition and food web structure may not occur until after several years of manipulation.

Methods

Study site

The Arctic LTER site is located in the northern foothills of the Brooks Mountain Range of Alaska (68°38′ N, 149°43′ W). The area has been under study since 1975, and a LTER site since 1987. Average annual temperature is –9 °C and annual precipitation is 20–40 cm with approximately 50% occurring as rain between May and September (Arctic LTER data base, unpublished data). The area is underlain by continuous permafrost and was last glaciated 12 000– 14 000 years ago, during the Itkillik II glaciation of northern Alaska (Brown & Kreig, 1983).

Lake N1 is one of several lakes at the Arctic LTER research site that is undergoing long-term manipulation and measurement. Lake N1 was fertilised at two to three times the annual loading of Toolik lake for five summers (1990–1994) with inorganic nitrogen as $(NH_4)_2\ NO_3$, and inorganic phosphorus as H_3PO_4. The N : P ratio remained constant at 12.5, throughout the experiment while the fertilisation level decreased in the last 2 years. In the first 3 years of the experiment (1990, 1991 and 1992), 2.5 mmol N m^{-2} day^{-1} and 0.199 mmol P m^{-2} day^{-1} were added. In the last 2 years (1993 and 1994), 1.7 mmol N m^{-2} day^{-1} and 0.136 mmol P m^{-2} day^{-1} were added.

Lake N1 is typical of many lakes in the region in both size and species composition. It is a dimictic kettle basin lake, although for several years during the study it was monomictic. Lake N1 is 4.8 ha in area, with a volume of 1.72×10^5 m^3, a maximum depth of 14 m and a mean depth of 3.9 m. The lake is ice-free from mid-June until late-September, after which ice forms up to 2 m thick. The average summer temperature is 12 °C in the epilimnion and 5.1 °C in the hypolimnion.

Four fish species are present in lake N1: lake trout (*Salvelinus namaycush*), arctic grayling (*Thymallus arcticus*), burbot (*Lota lota*) and slimy sculpin (*Cottus cognatus*) (Hanson et al., 1992). The mesozooplankton community is predominantly composed of *Diaptomus pribilofensis* and *Cyclops scutifer*, but also contains *Daphnia middendorphiana, D. longiremis, Bosmina longirostris, Holopedium gibberum, Polyphemus pediculus* and *Heterocope septentrionalis* in much lower numbers (O'Brien et al., 1979). Lake N1 was oligotrophic prior to fertilisation (Miller et al., 1986). The pretreatment summer average primary productivity was 10.27 mg C m^3

day^{-1}, and the chlorophyll *a* concentration was 1.13 μg chlorophyll *a* L^{-1}.

Methods

Weekly samples and measurements were taken each summer throughout the experiment as well as 1 year pre and post-treatment to measure physical, chemical and biological parameters. Water samples were collected at the surface and at depths of 1, 3, 5, 8 and 12 m with a Van Dorn sampler (Wildco, Buffalo, NY, USA) for microplankton, chlorophyll and primary productivity resulting in between 36 and 60 samples taken each summer. Composite samples of mesozooplankton and algae were also taken weekly.

Collection of microplankton (nominally 20–200 lm) involved concentrating 2 L of water by reverse flow filtration using a 20-μm Nitex (Small Parts, Inc, Miami Lakes, FL, USA) net (Dodson & Thomas, 1964). The final volume of 60 mL was preserved with glutaraldehyde to a final concentration of 1%. All samples were stored refrigerated until they were enumerated using direct counts according to the method of Baldock (1986). Briefly, a known volume was stained with Rose Bengal, drawn onto an 8.0-μm pore cellulose acetate filter, which was then mounted in 47% sucrose solution. The entire filter surface was examined at 100× to 400× magnification and individual protozoans and rotifers were identified to genus and if possible to species using taxonomic guides to protozoa (Corliss, 1979; Lee et al., 1985) and rotifers (Ruttner-Kolisko, 1974); zooplankton nauplii were simply enumerated. Carbon biomass of rotifers and protozoans were calculated from measured sizes and literature values (Ruttner-Kolisko, 1977; Pauli, 1989; Putt & Stoecker, 1989).

Zooplankton samples were collected by replicate vertical 10 m tows using a 30-cm diameter plankton net with 335 μm mesh plankton netting. Samples were preserved in an alcohol/formalin solution until they were processed. Mesozooplankton samples were enumerated by species, with the entire sample surveyed for the three large species: *Daphnia middendorphiana, H. septentrionalis* and *H. gibberum*, while a sub sample of 1 or 2 mL was used for the other species.

Standard limnological methods were used to collect and analyse other samples. Chlorophyll *a* samples were collected on either 47 mm Gelman A/E (Pall Life Sciences, Ann Arbor, MI, USA) or Whatman GF/C (Whatman, Clifton, NJ, USA) glass fibre filters. Filters were placed in 10 mL of 90% acetone and extracted in the dark for 24 h before chlorophyll was measured using a fluorometer. Phytoplankton primary production was estimated using a ^{14}C method, modified from Wetzel & Likens (1991). From 1989 to 1994 bottles were incubated *in-situ*; in 1995 bottles were incubated in nearby Toolik Lake or a lakeside incubator.

Results

The abundance of microplankton during the summer of 1989, prior to fertilisation, and the changes in community composition during the first 3 years of fertilisation (1990–1992) have been reported previously (Rublee & Bettez, 1995). Briefly, prior to fertilisation, lake N1 was similar to other lakes at the Arctic LTER site with respect to species composition and nutrient pools (Kling et al., 1992), with low levels of autotrophs, generally dominated by small algae (average primary production, 10.27 mg C m^3 day^{-1}; average chlorophyll *a*, 1.13 μg L^{-1}), while the ciliated protozoan population was composed mainly of the oligotrich ciliates *Strombidium, Strobilidium*, and *Halteria* spp. with an average protozoan density of 142 individual L^{-1} and a biomass of 0.48 μg C L^{-1}. Rotifers were mostly smaller planktonic species (*Conochilus unicornis* and *Keratella cochlearis*), capable of ingesting small-particles with an upper size of 10– 12 μm (Dumont, 1977) although eight other species were occasionally found as well. The rotifers comprised an average of 34% of the microplankton biomass, with a density of 91.3 individuals L^{-1} and 2.1 μg C L^{-1}. The average biomass of the zooplankton nauplii in 1989 was 3.6 μg C L^{-1}. Prior to fertilisation, the mesozooplankton community was dominated by the large zooplanktivorous copepod *H. septentrionalis* with densities of 0.05 individual L^{-1} in early July, which increased to 0.13 individual L^{-1} by early August.

The addition of nutrients, beginning in 1990, stimulated primary productivity and algal biomass relative to both untreated lakes and lake N1 in 1989. The average annual values for primary productivity and chlorophyll *a* for lake N1 ranged from 25.7 to 104.9 mg C m^3 day^{-1} for the primary productivity and 5.9–11.2 μg chlorophyll *a* L^{-}

^{1} over the 5-year experimental period (Fig. 1a). The highest measured primary productivity was 1091 mg C m^{3} day^{-1}, which occurred on 12 July 1993 during a bloom of Cyanobacteria. The highest chlorophyll value was 36.5 µg chlorophyll *a* L^{-1}, which occurred the following week on 19 July 1993.

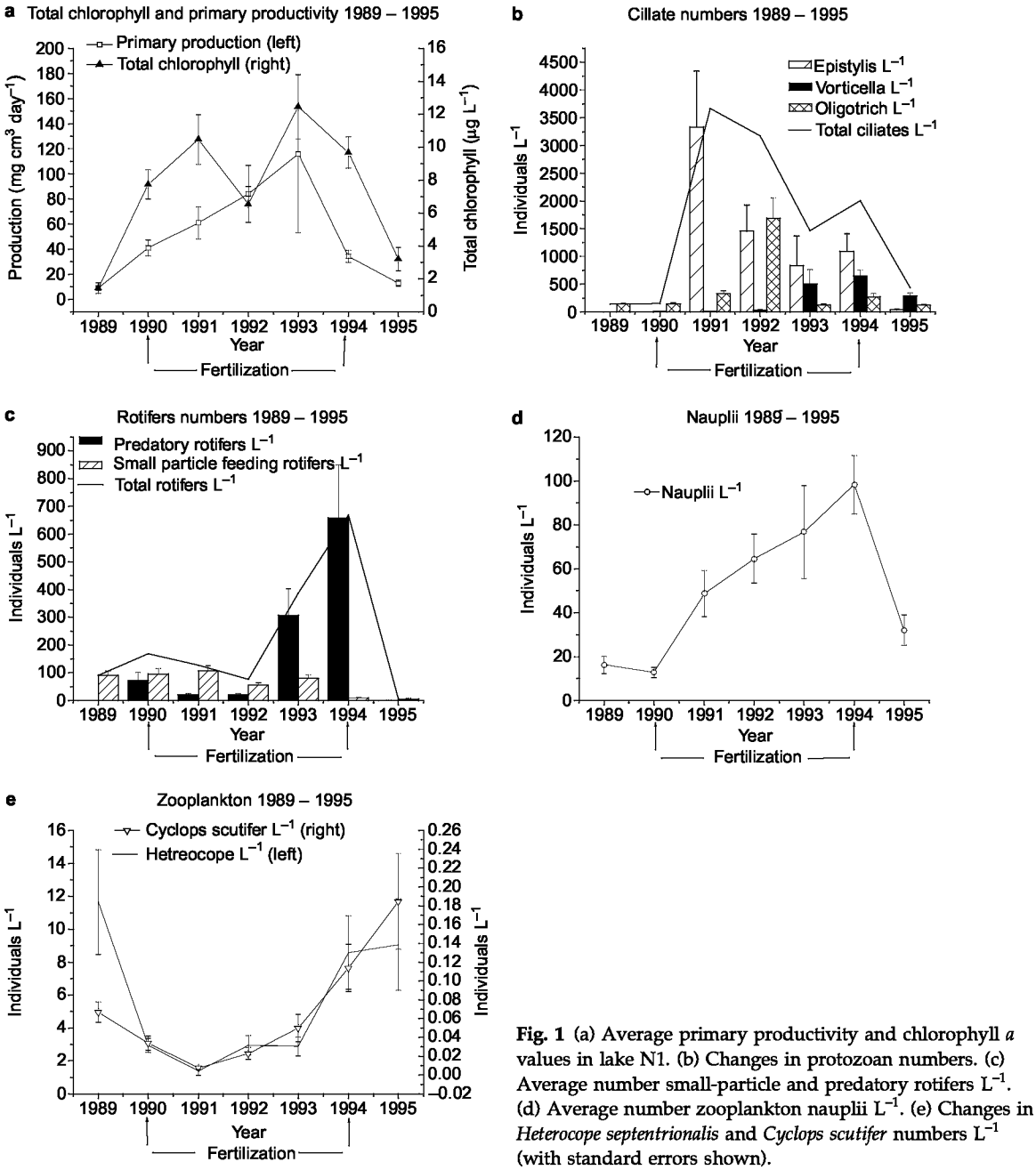

Fig. 1 (a) Average primary productivity and chlorophyll *a* values in lake N1. (b) Changes in protozoan numbers. (c) Average number small-particle and predatory rotifers L^{-1}. (d) Average number zooplankton nauplii L^{-1}. (e) Changes in *Heterocope septentrionalis* and *Cyclops scutifer* numbers L^{-1} (with standard errors shown).

With fertilisation, the algal community in lake N1 shifted from one composed primarily of small autotrophs to one characterised by larger 1, 2 and 4-celled colonial algae or filamentous Cyanobacteria. In the second and third years of fertilisation 1991 and 1992, *Coelosphaerium minimum* (Cyanobacteria), *Synecocystis* (Cyanobacteria), *Ceratium* (Dinophyta), *Oocystis* (Chlorophyta), *Chroococcus* (Cyanobacteria), *Cryptomonas* (Cryptophyta) and *Asterionella*, and *Cyclotella* (Baillariophyta) were present. In 1994, a nitrogen fixing Cyanobacteria, *Anabaena* sp., appeared.

As reported earlier in Rublee & Bettez (1995), microplankton populations varied both temporally and spatially. The distribution patterns of *E. rotans* within the water column as well as over the summer illustrate the patterns seen in other taxa of mesozooplankton and microplankton. This seasonal and spatial variability is responsible for most of the error associated with each yearly mean (Fig. 1a-e). *Epistylis* abundance generally increased through the early summer, peaking in mid-July, and then decreased for the remainder of the summer (Fig. 2a).

The number of *Epistylis* individuals' L^{-1} also decreased with sample depth (Fig. 2b) with the density of individuals being negatively correlated with depth over all years (r = -0.230, $P < 0.01$).

The contribution of individual ciliate taxa within the ciliate communities changed over the course of the experiment (Fig. 1b). Prior to fertilisation and in the first year of the experiment (1989-1990) oligotrichs were the dominant species in the ciliate community. In the second and third year of the experiment (1991- 1992) because of increased abundance of the previously rare protozoan *E. rotans* the total number of ciliated protozoans increased to its highest level during the experiment. In the last 2 years of the experiment (1993-1994) *Epistylis* numbers decreased while *Vorticella* numbers reached their peak. In 1995, the first postfertilisation year, the protozoan community appeared to be returning to its prefertilisation character as *Epistylis* became rare and *Vorticella* populations declined.

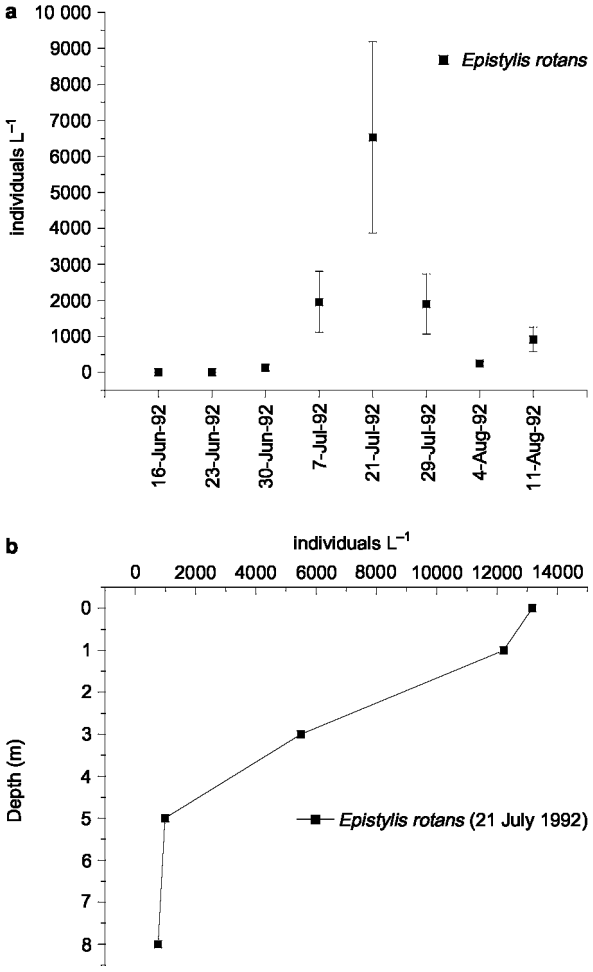

Fig. 2 (a) Average number of *Epistylis rotans* individuals L^{-1} in the water column in 1992 (with standard errors shown). (b) Number of *Epistylis rotans* individuals' L^{-1} within the water column on 21 July 1992.

The effect of fertilisation on the rotifer population differed by species and functional group (Fig. 1c). In the first 4 years of fertilisation (1990-1993) there was no statistically significant change in the number or biomass of the predominant rotifer species present prior to fertilisation; these consumed primarily small algal particles. However, in the next 2 years (1994 and 1995) the numbers and biomass of these species did show a significant decrease from the prefertilisation levels found in 1989 (unpaired t-test, P = 0.0016 with 16 d.f in 1994 and P = 0.0020 with 15 d.f in 1995). In contrast, the numbers and biomass of predatory rotifers increased significantly over the course of the experiment, with predatory rotifers eventually accounting for 98% of the mean total rotifer number and biomass in 1994 (Fig. 1c).

The changes in numbers and biomass of predatory rotifers were because of increased abundance of two species,

Synchaeta and *Trichocerca*. In 1990, *Synchaeta* numbers in specific samples, such as 9 August 1990 at 1 m, increased to as much 832 individual L^{-1} and accounted for as much as 72% of the rotifer population. In 1991 and 1992 the number of *Synchaeta* decreased and, although higher than 1989 levels, never constituted more than 50% of the population on any single date. In 1993 the predatory rotifer *Trichocerca*, which was rarely found in earlier samples, appeared and accounted for 68% of the total rotifer biomass that summer. In the following year, which was the final year of fertilisation, the number of *Trichocerca* increased to a peak of 5703 individuals L^{-1} and accounted for 98% of the total rotifer biomass for the summer.

The response of mesozooplankton to the fertilisation experiment varied, both by year and species. The abundance of zooplankton nauplii increased fourfold over the course of the fertilisation (Fig. 1d). *Heterocope septentrionalis* increased during the fertilisation, while *C. scutifer* had lower values posttreatment than prior to fertilisation (Fig. 1e). In the first year of the fertilisation *P. pedunuclus* densities reached as high as 19.7 individuals L^{-1}, but they were not present in samples for the remainder of the experiment. Neither *Daphnia* species in N1 showed significant increases until the last year of the fertilisation or the first year of the recovery. In the last year of fertilisation the average number of *Daphnia longiremis*, was 0.019 individuals L^{-1}, which was almost four times greater than numbers present prior to fertilisation. In the first year of the recovery *D. middendorphiana* reached densities as high as 3.5 individuals L^{-1} up from the previous high of 0.285 before and during fertilisation.

In 1995 the first year of the recovery many parameters returned to near pretreatment levels. Primary productivity and chlorophyll a in lake N1 dropped by almost 60% from 25.67 mg C m^3 day^{-1} and 7.52 μg chlorophyll *a* L^{-1} in 1994 to 11.27 mg C m^3 day^{-1} for primary productivity and 3.26 μg chlorophyll *a* L^{-1} in 1995 (Fig. 1a). The secchi depth increased to 7.9 m, which was greater than any pretreatment measurement. Although the ciliated protozoan population was still predominantly com-posed of peritrichs (*Epistylis*, and *Vorticella*), their numbers and biomass declined to levels below those of the previous 4 years (Fig. 1b). Oligotrich ciliate abundance returned to prefertilisation levels (Fig. 1b), although their biomass remained above their prefertilisation levels because individuals were much larger with 76% greater than 50 pm and their average biomass being six times greater than in 1989 (Table 1). The rotifer population declined to below prefertilisation levels but its composition returned to being dominated by small-particle feeding rotifers, which comprised 90% of the average rotifer population number and biomass in 1995 (Fig. 1c). Predatory rotifer abundance in the summer of 1995 was 0.60 individuals L^{-1}, which was similar to prefertilisation levels of 0.5 individuals L^{-1}.

Discussion

The microbial components of aquatic communities are important in nutrient cycling and energy flow and as a result have been the focus of many studies concerning both top down and bottom up controls. Although it is now accepted that much of the organic carbon in lakes is processed through microbial interactions (e.g. Fenchel, 1988; Porter et al., 1988) it has been suggested that oligotrophic aquatic environments contain insufficient energy to support bacterivorous ciliates and rotifers (Hall et al., 1976; Fenchel, 1980; Beaver & Crisman, 1982; Pace, 1982,1986). In these oligotrophic arctic lakes, bacterial production roughly equals grazing by heterotrophic nanoflagellates (Hobbie et al., 1999). Because bacterial production is low, the only bacteriovores present in significant numbers are the heterotrophic nanoflagellates, which are preyed upon by a small population of predatory rotifers. Therefore the microplankton and mesoplankton, whose numbers are low by temperate standards, do not exert a top down control on heterotrophic nanoflagellates (Hobbie et al., 1999).

The result of this is a microplankton community in these oligotrophic lakes composed primarily of oligotrich ciliates and small particle feeding rotifers, both of which feed upon bacteria as well as the autotrophic nanoflagellates predominant in these lakes. In turn, these microplankton are consumed directly by mesozooplankton, and to a lesser extent, predatory rotifers. Because their abundances are low, none of the constituents of the microplankton in these oligotrophic lakes return a substantial amount of biomass to higher trophic levels. The net result is that the microplankton do not appear to play a significant role as a link to higher trophic levels in the oligotrophic lakes at the Arctic LTER (Rublee, 1992).

With fertilisation however, the structure of the microbial food web in N1 changed. The food web shifted from one that was controlled by the limited biomass of the autotrophic and heterotrophic pico and nanoplankton to one that was driven by detritus and excess algal biomass, which resulted from increases in both primary productivity, and the proportion of inedible filamentous algae.

Table 1 Percent protozoans, peritrichs, rotifers and nauplii of microplankton biomass and percentage of oligotrichs that were >50 μm 1989–95

Year	Peritrichs	Other ciliates	Rotifers	Nauplii	Oligotrichs >50 μm
1989	0.09	7.8	33.7	58.5	33.18
1990	0.48	6.7	62.1	30.7	37.94
1991	32.2	34.0	7.4	26.4	39.63
1992	19.4	27.0	7.2	46.4	2.83
1993	20.2	21.2	14.5	44.1	43.34
1994	19.3	21.7	16.4	42.7	73.38
1995	17.5	35.9	1.0	45.7	76.92

The first component of the microplankton to respond to the changes in the algal community was the peritrich ciliates, which are bacteriovores. They showed the largest change in biomass of any component of the microplankton, with the average number of individuals 675 times higher in 1991 than in the first year of fertilisation and more than 5500 times higher than prior to fertilisation (Fig. 1b). Peritrichs comprised more than 20% of the microplankton biomass and replaced rotifers as the second largest component of the microplankton.

The rotifers *Synchaeta* and *Polyarthra*, both of which feed on flagellated algae (Dumont, 1977; Pourriot, 1977), were responsible for changes in rotifer numbers during the first 2 years (1990 and 1991) of the experiment. However, the large increases in rotifer numbers did not begin until 1993 with the appearance of the predatory Trichocercidea rotifers. Trichocercidea have been found in a wide variety of periphytic environments, with a few semiplanktonic species, which can act as indicators of eutrophy and usually invade because of increased primary productivity (Pejler & Berzins, 1993). Pourriot (1970) proposes that the occurrence of trichocercids is restricted by organisms on which they feed (especially chrysophytes) or by the substrates on which they deposit their eggs, usually filamentous algae.

Copepod nauplii, except for the first 2 years of fertilisation, comprised the largest component of the microplankton biomass, 26–58% (Table 1). There was a 1 year lag in the response of the zooplankton nauplii to fertilisation and a 3–4 years lag in the appearance of increased numbers of adult mesozooplankton. Other fertilisation experiments at the LTER (O'Brien et al., 1992), and whole lake fertilisations in sub-arctic Sweden (Persson et al., 1997) have also seen delayed responses of adult zooplankton. In these cold arctic environments, crustacean zooplankton have only one reproductive cycle each year, thus, the fertilisation response lags until the following summer. One possible explanation for the longer response, which occurred in our system, could be the blooms of *cyanobacteria* that occurred in 1992 and 1993. Cladoceran zooplankton have been shown to be inhibited by toxic by-products associated with blue green algal blooms (Gentile, 1971), thus, blooms of *cyanobacteria* in 1992 and 1993 could account for the lack of response until 1994 in *B. longirostris* and *D. longiremis* populations as well as the *D. middendorphiana* populations which did not increase until after fertilisation ended in 1995. Decreases in numbers of *D. pribilofensis* are potentially due to predation by *H. septentrionalis*, which increased in numbers throughout the experiment.

There have been several other whole lake experiments that have investigated changes in rotifers and mesozooplankton caused by fertilisations. Experimental Lakes Area (ELA) lake 227 was fertilised with N and P for 5 years from 1969 to 1974, and two lakes in the Koukkel area in northern Swedish Lapland were fertilised with either N, P, or N and P for 4 years from 1972 to 1975. In ELA lake 227 fertilisation resulted in increased primary production and algal biomass but had a negative effect on zooplankton and rotifer biomass and species diversity. These reductions were most likely the result of changes in oxygen and pH, which had an adverse effect on the rotifer and zooplankton populations (Malley et al., 1988). In the Swedish experiment fertilisation also resulted in increased algal biomass with parallel increases in particulate carbon and bacterial biomass.

However, except for an increase in *C. unicornis* in the fourth year of fertilisation, no significant changes in maximal abundance and mean biomass occurred (Persson, 1977).

This paper highlights the importance of long-term experiments in understanding the response of the microbial food web to fertilisation. With an additional 2 years of fertilisation, the structure of the microbial web is markedly different. The first 3 years of fertilisation saw significant increases in primary producers and peritrich protozoan numbers, but no great change in the rotifer population, and a decline in the numbers of mesozooplankton. The last 2 years of the experiment saw decreasing numbers of peritrich protozoans, and increases in the numbers of predatory rotifers, and nauplii zooplankton along with increases in the two largest species of zooplankton. This shift in the microbial food from oligotrichs and small particle feeding rotifers to bacteriovores and finally to predatory rotifers would not have been evident had the experiment been carried out for a shorter period.

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