Lake characteristics influence recovery of microplankton in arctic LTER lakes following experimental fertilization

By: Parke A. Rublee & Neil D. Bettez

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Abstract:
Lakes N-1 and N-2 at the Arctic Long Term Ecological Research site at Toolik Lake, Alaska, U.S.A. were fertilized with nitrogen and phosphorus for 5 and 6 years, respectively. The response and recovery of the microplankton community (protozoans, rotifers and crustacean nauplii) differed in the two lakes. Microplankton biomass in Lake N-1 increased five-fold while that in Lake-N-2 only doubled, despite larger nutrient additions to N-2. Microplankton community structure in Lake N-1 shifted toward dominance by few taxa, while the community in Lake N-2 maintained diversity. Finally, the recovery of Lake N-1 to near prefertilization microplankton biomass levels was rapid, while Lake N-2 showed at least a 1-year lag in recovery. These differences appear to be related to differences in the structure of lake sediments.
Key words: microplankton, arctic lakes, eutrophication, rotifers

Article:
Introduction
Alaskan arctic aquatic ecosystems are of interest because the arctic region is expected to undergo significant global climate change (e.g. Lachenbruch & Marshall, 1986; Abelson, 1989; Schindler et al., 1990). The impact of increased temperature and altered rainfall is expected to lead to changes in the physical, chemical, and biological character of the relatively pristine lakes and streams in this region (McDonald et al., 1996; Rouse et al., 1997; Hobbie et al. In Press). Since microbial communities are characterized by rapid metabolism and short life cycles, they include organisms that could demonstrate rapid response to environmental change.

Previously, we have reported on the increased biomass and species changes of the microplankton community in response to increased nutrient (N and P) loadings in artificially divided Lake N-2 (Rublee, 1992), and in Lake N-1 (Rublee, 1998; Rublee & Bettez, 1995). In this paper, we report observations that demonstrate subtle differences in the recovery of the microplankton community after fertilization of the lakes stopped.

Site description
The arctic LTER site lies in the northern foothills of the Brooks Mountain range of Alaska (68° N, 149° W). The area is a region of arctic tundra, underlain by permafrost, with an average annual temperature of about -9 °C and low rainfall. Lakes are covered by up to 2 m of ice from late September to mid-June. The site has been under study for 25 years, although microplankton populations have been monitored only since 1989. Lakes are of glacial origin and generally highly oligotrophic. More complete descriptions of Toolik and other LTER lakes can be found in O'Brien (1992) and O'Brien et al. (1997).

Methods
We sampled from three lakes: two of these Lake N1 and Lake N-2 were subject to experimental nutrient loading and the third one, Toolik Lake, served as a reference lake (Table 1). Water samples (2-l) collected weekly from a depth of 1 m by a Van Dorn bottle from June to August were concentrated to 60 ml by reverse flow filtration

through a 20 μm mesh net. Glutaraldehyde was added to a final concentration of 1% for fixation. For enumeration, 5–20 ml of the concentrated sample was stained with rose bengal for 10–15 min (Baldock,1986), followed by observation under a light microscope at 100–400 × magnification for identification and enumeration. Biomass (as μg carbon l^{-1}) was derived from literature values (cf. Rublee, 1992)

Table 1. Description of lakes sampled

Name	Area (ha)	Depth (m)	Description of lake/manipulation
Toolik	150	25	Ultra-oligotrophic reference lake.
N - 2	2	7	Divided lake: treatment side fertilized a 5× natural loading, 1985–1990. Highly oligotrophic prior to fertilization.
N - 1	4	12	Whole lake fertilized at 4× natural loading, 1990–1994. Highly oligotrophic prior to fertilization.

Results

Microplankton biomass in Toolik Lake varied from 3 to 9 μg C l^{-1} from 1989 to 1999 (Fig. 1). Rotifers averaged 15% (range 7–22%) of the biomass of the microplankton over the 11 year sampling period. Both Lake N-1 and the fertilized side of Lake N-2 demonstrated a clear response to the nutrient amendment. In Lake N-1, microplankton mean biomass increased five-fold during fertilization from a mean value of 11 μg C l^{-1} to 50 μg C l^{-1}(Fig. 1). Microplankton populations shifted from a mixed assemblage to one dominated by the rotifer *Conochilus unicornis* during the first- year of fertilization, to peritrich protozoans during the second year of fertilization, the rotifers *Synchaeta* and *Polyarthra* during the third year of fertilization, and finally to a dominance of *Trichocerca* species in the fourth and fifth years (for details see Rublee & Bettez, 1995). The biomass of micro-plankton returned to near prefertilization levels in the first year following fertilization. Although biomass of rotifers was higher during years of fertilization, the proportion of microplankton biomass comprised by rotifers was similar during fertilized (average 30%, range 3–71%) vs non-fertilized years (average 26%, range 3–65%).

The microplankton community in Lake N-2, a divided lake (reference and treatment sides) was followed during 1989 and 1990, the last 2 years of fertilization, and for 9 additional years (Fig. 1). The average biomass of the microplankton in Lake N-2 during the years of fertilization was 20 μg C l^{-1}, about twice the average value found in the control side of Lake N-2. The microplankton community was a mixed assemblage of ciliate and peritrich protozoans and rotifers. No individual taxon comprised more than about 20% of the biomass of the community, and the rotifer assemblage was similar to that in unfertilized control lakes, mostly composed of *Keratella cochlearis, K. quadrata, Kellicotia longispina* and *Polyarthra* and *Conochilus* species. After fertilization ceased, biomass in the treatment side of Lake N-2 returned to prefertilization levels after a one to two year lag (Fig. 1).

Discussion

Despite annual variability shown in microplankton values in Toolik Lake, and in the reference side of Lake N-2, there were pronounced responses of the microplankton community to nutrient additions. Differences in the response and recovery of Lake N-1 and Lake N-2 included: (1) a much greater increase in biomass in Lake N-1 as compared with Lake N-2, despite a heavier nutrient loading regime in Lake N2; (2) decrease in the diversity of microplankton in Lake N-1 to a community dominated by a single or few protozoan or rotifer taxa; and (3) slower return of Lake N-2 to prefertilization levels of microplankton biomass.

The differences in response of Lake N-1 and N-2 to fertilization are likely the result of the character of the bottom sediments. Soils in this region are characterized by high iron content, which strongly adsorbs phosphorus (Prentki et al., 1980; Kipphut, 1988; Cornwell & Kipphut, 1992; Sugai & Kipphut, 1992). Thus, in Lake N-2, which has a relatively thick layer of sediment, phosphorus was adsorbed onto sediments during the earlier years of fertilization, effectively reducing the loadings to the pelagic. However, by 1989 and for several years after fertilization ceased, there was a net flux of phosphorus out of sediments (cf. Sugai & Kipphut, 1992;

Hobbie et al., In Press) which appears to have had the effect of extending the term of nutrient enrichment in this lake. This effect was minimal in Lake N-1, which has a rocky bottom and a very thin layer of sediment. Microplankton are affected indirectly by the supply of nutrients through phytoplankton growth, which provides food for microplankton.

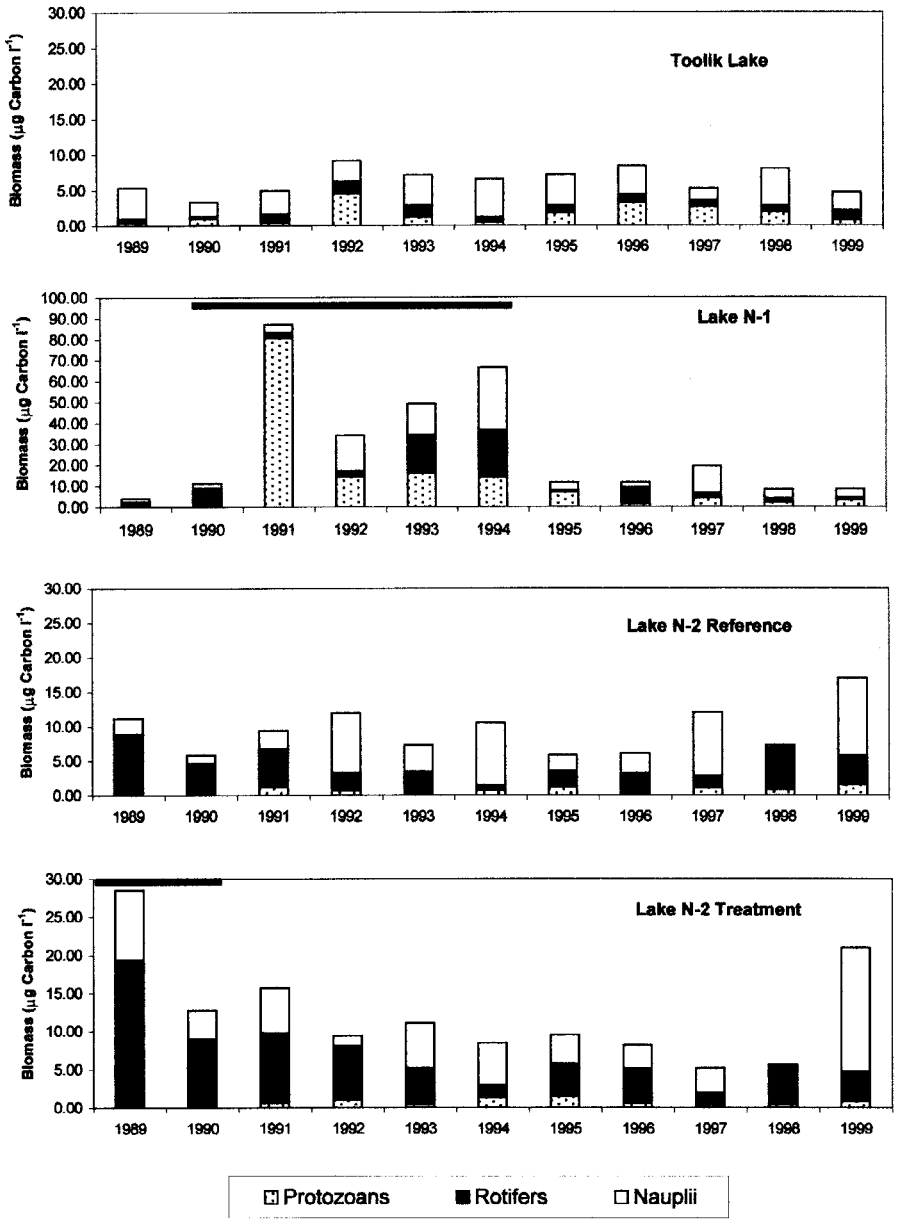

Figure 1. Microplankton biomass at 1 m depth in Arctic LTER lakes, 1989–1999. Horizontal bars indicate periods of experimental fertilization of lakes N-1 and N-2.

In summary, relatively subtle differences in lake structure may contribute to differential responses of aquatic organisms to environmental change. Thus, designing studies to determine response to global warming or other perturbations must take into account any unique characteristics of study sites.

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