

Long-term response and recovery to nutrient addition of a partitioned arctic lake

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SUMMARY

1. To study the bottom-up linkages in arctic lakes, we treated one side of a partitioned lake with inorganic nitrogen and phosphorus for a 6-week period each summer for 6 years starting in the summer of 1985. We took a variety of weekly measurements to determine the impact of the nutrient loading on the lake and continued weekly measurements for 2–6 years after the cessation of nutrient loading to observe the recovery of the treated side. The loading rates ($2.91 \text{ mmol N m}^{-2} \text{ day}^{-1}$ and $0.23 \text{ mmol P m}^{-2} \text{ day}^{-1}$) were five times the calculated loading rates for Toolik Lake, located nearby.
2. In all 6 years of nutrient addition, phytoplankton biomass and productivity were greater in the treated sector than the reference sector. In the first 4 years of nutrient addition there was no flux of phosphorus from the mineral-rich sediments. This changed in the last 2 years of nutrient addition as phosphorus was released to the lake.
3. The response of the animal community to increased plant production was mixed. One of the four macro-zooplankton species (*Daphnia longiremis*) increased in number by about twofold in the first 5 years. However, the copepod *Cyclops scutifer* showed no response during the treatment phase of the study. The benthic invertebrate response was also mixed. After a 2-year lag time the snail *Lymnaea elodes* increased in the treated lake sector but chironomids did not.
4. Ecosystem response to fertilisation was not controlled solely by nutrient addition because phosphorus was not recycled from the sediments until the last 2 years of nutrient addition. Phytoplankton still showed the effects of nutrient addition in the recovery period and the hypolimnion of the treated sector was still anaerobic starting at 6 m in 1996.

Keywords: eutrophication, metal-rich sediments, nutrient loading, phytoplankton, zooplankton

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Introduction

A major theme in freshwater ecology is determining whether lake ecosystems and their resident populations are regulated from the top down by predators (Brooks & Dodson, 1965; Paine, 1966; Carpenter, Kitchell & Hodgson, 1985; Tessier & Woodruff, 2002) or from the bottom up by nutrient supply (Schindler, 1974; Pace & Cole, 2000; Beisner, Dent & Carpenter, 2003). The study of bottom-up control has a long history in lake studies, perhaps beginning with Naumann (1919) who found that lakes rich in nutrients developed dense and unique phytoplankton communities. In more recent times, with the advent of modern detergents and their attendant polyphosphates, the eutrophication of lakes became a serious pollution problem (National Academy of Sciences, 1969). Several classic studies showed that phosphorus and possibly nitrogen were responsible for the problem (Edmondson, 1972; Schindler, 1974). At about the same time a strong empirical relationship was developed between the degree of phosphorus loading to a lake and the density of summer phytoplankton populations (Vollenweider, 1968; Smith, 1990).

It is clear from our past work on nutrient additions to limnocorrals (O'Brien *et al.*, 1992) and several nutrient addition studies of arctic lakes (Jansson, 1978; Holmgren, 1984; Welch, Legault & Kling, 1989) that arctic lakes respond to the addition of nutrients in a manner similar to temperate lakes. However, many arctic lakes seem to be either nitrogen-limited or nearly co-limited by phosphorus and nitrogen (Smith *et al.*, 1984; Levine & Whalen, 2001; Squires & Lesack, 2002). In fact, Ostrofsky & Rigler (1987) found a different relationship between chlorophyll and phosphorus in subarctic lakes than Rigler and his colleagues had found in temperate lakes (Dillon & Rigler, 1974). This may be because of the fact that, at least in the Toolik region of arctic Alaska, the sediment of the lakes strongly adsorbs phosphorus (Cornwell, 1987; Cornwell & Kipphut, 1992) moving lakes towards a nitrogen limitation.

Most studies of the effects of nutrient addition to arctic and subarctic lakes have focused on the response of only the phytoplankton (Jansson, 1978; McCoy, 1983; Jansson *et al.*, 2001), assuming perhaps that zooplankton and other herbivores and detritivores increase in density with increasing phytoplankton density. However, in temperate-lake studies the

response of zooplankton to nutrient addition is variable: increasing (O'Brien *et al.*, 1992; Carpenter *et al.*, 1996; Johnston *et al.*, 1999), showing no change (Cuker & Hudson, 1992) or decreasing (O'Brien & deNoyelles, 1972; Malley, Chang & Schindler, 1988).

The goal of this work was twofold. First, to determine the impact of nutrient addition to an arctic lake with strong phosphorus adsorbing sediments. Second, to determine which components of an arctic lake food web would respond to the increased phytoplankton and resulting detritus. In this paper, we present the results of a 6-year study of nitrogen and phosphorus addition to a partitioned lake in arctic Alaska. We also analysed the recovery of the treated section of the lake for from 2 to 6 years. We examined the chemical response of both sediments and open water and the biological response of pelagic and benthic organisms to nutrient addition.

Methods

Site description

Lake N-2, where this research was conducted, is located in arctic Alaska (68°38'27"N, 149°37'30"W) in the northern foothills of the Brooks Mountains about 1 km northwest of the Toolik Lake Research Station (see http://ecosystems.mbl.edu/arc/data_doc/lakes/lakedescriptions/laken2.html for an aerial view of the lake and some data). It is an oligotrophic kettle lake with an area of 1.8 ha, a maximum depth of 10.7 m (Fig. 1), a catchment area of 9 ha, and very

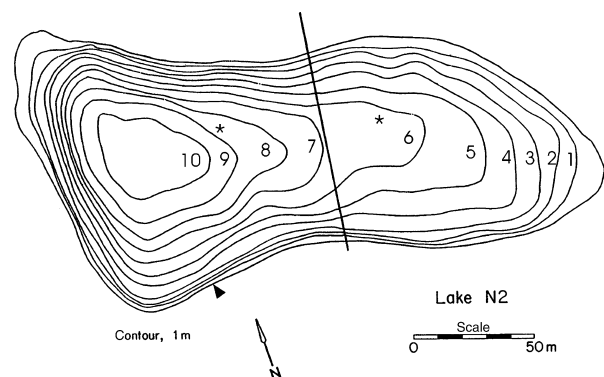


Fig. 1 A morphometric map of Lake N-2. The stars indicate the approximate main sampling station in each sector of the lake. The triangle indicates the point where the tube delivering the nutrients entered the lake. The solid, straight line indicates the position of the curtain.

little surface inflow for most of the summer. The lake is ice-covered for 8 months of the year and from mid-June through August is thermally stratified with the surface waters reaching a maximum temperature of 18 °C in some years.

The lake has very low phosphorus levels of 0.1 $\mu\text{mol L}^{-1}$ or less and inorganic nitrogen of 0.2–0.5 $\mu\text{mol L}^{-1}$. This results in clear water with Secchi disk transparencies up to 6 m in late summer. The low levels of nutrients lead to low levels of phytoplankton biomass and productivity; photic zone chlorophyll *a* averages 1.2 $\mu\text{g L}^{-1}$ and total summertime primary productivity is only about 2 g C $\text{m}^{-2} \text{year}^{-1}$ (Miller *et al.*, 1986; Hobbie *et al.*, 1995). The phytoplankton are sparse and small and most are flagellates belonging to the Chrysophyceae, Cryptophyceae and Dinophyceae. Bacteria numbers are around $2 \times 10^6 \text{ mL}^{-1}$, and are similar to those found in nearby lakes. Pelagic crustacean zooplankton densities range from 10 to 30 L^{-1} , with only four species commonly present: *Daphnia longiremis* (Sars), *Bosmina longirostris* (O. F. Muller), *Diaptomus pribilofensis* (Juday & Muttkowski) and *Cyclops scutifer* (Sars). These are the species most common to the region (O'Brien *et al.*, 2004). The microplankton consists of rotifers, mainly *Polyarthra vulgaris* (Carlin), *Keratella cochlearis* (Bory de St Vincent) and *Kellicottia longispina* (Kellicott). The benthic community in Lake N-2 is dominated by the snail *Lymnaea elodes* (Say) and a sparse community of chironomids. There are two fish species: the benthic-dwelling slimy sculpin *Cottus cognatus* (Richardson), and arctic grayling *Thymallus arcticus* (Pallas).

Thus the lake has a simple food web with three clearly herbivorous zooplankton species, the two cladocerans and *D. pribilofensis*, that would be expected to respond to increased phytoplankton. Cyclopoid copepods are thought to be predaceous (Wetzel, 2001) and thus might not respond directly to increased phytoplankton. Chironomids are thought to be limited by predation from sculpin (Hershey, 1985a), and so would not be likely to respond to increased food resources (Hershey, 1985b), while snails are food limited (Cuker, 1983) and should respond.

Partitioning the Lake

In 1985, Lake N-2 was partitioned using a fibreglass-reinforced polyethylene curtain that had 10-cm diameter tubes sewn in both the top and bottom. Styrofoam

strips for flotation and a 1.4-cm diameter nylon rope were inserted in the top tube while the bottom tube was weighted with a heavy chain. The curtain was pulled across the lake near the middle of the long axis of the lake (Fig. 1) and secured to both shores.

Nutrient addition

Nutrients were added continuously each summer from 1985 to 1990 to the surface of the middle of the downstream (west) section of the lake. Additions were started on 1 July (12 July in 1985) and ended in mid-August. Nitrogen was added as NH_4NO_3 at a rate of 2.91 $\text{mmol N m}^{-2} \text{day}^{-1}$ (3.64 $\text{mmol N m}^{-2} \text{day}^{-1}$ in 1985) and phosphorus was added as phosphoric acid at a rate of 0.23 $\text{mmol P m}^{-2} \text{day}^{-1}$ (0.28 $\text{mmol P m}^{-2} \text{day}^{-1}$ in 1985). Annual rates of nutrient addition were 131 mmol m^{-2} of nitrogen and 10.4 mmol m^{-2} of phosphorus. These loading rates were approximately five times the estimated annual total N and P loading rate of nearby Toolik Lake (Whalen & Cornwell, 1985). In the summer of 1988, ^{15}N was added as $^{15}\text{NH}_4\text{Cl}$ to both sectors of the lake during the duration of the non-labelled nutrient addition. The loading varied with the sector to compensate for sector volume, with the reference sector receiving 16.1 mg per ^{15}N day and the treated sector receiving 47.9 mg day^{-1} (Kling, 1994).

Physical and chemical pelagic measurements

Physical and chemical measurements were made weekly at a central station in each sector of the lake (Fig. 1). Vertical oxygen and temperature profiles were measured using a YSI model 57 m and probe. Water samples for nutrient analysis were collected with a Van Dorn sampler at depths of 1, 3, 5 and 6 m in the reference sector and 1, 3, 5 and 8 m in the treated sector. The methods used to measure these chemicals are given in Wetzel & Likens (1979).

Biological pelagic measurements

Water samples to determine chlorophyll *a* concentrations were taken weekly at the same depth as for nutrients. To be consistent between both sectors of the lake, the chlorophyll *a* analysis used only the measurements from 0, 1, 3 and 5 m from each sector of the lake. The chlorophyll *a* samples were filtered

through Gelman A/E glass fibre filters. Material retained on the filters was extracted in 90% acetone for 24 h and the extract analysed by fluorescence (Wetzel & Likens, 1979). Pelagic primary production was determined at the same depths using a 24 h *in situ* ^{14}C incubation as described by Miller *et al.* (1986). Again only depths 0, 1, 3 and 5 m were used to analyse the primary productivity and hence we do not report these data in areal units.

The detailed methods used for microplankton collection are given in Rublee & Bettez (2001). Lake water from 1 m was concentrated by reverse flow filtration through a 20 μm mesh net and the microplankton preserved in glutaraldehyde.

Crustacean zooplankton densities were determined weekly using a 30-cm diameter, 335- μm mesh net. Replicate 6 m vertical hauls were taken from the main station in each sector of the lake. Zooplankton were preserved in the field with a mixture of 100% ethyl alcohol and 4% formalin, mixed roughly 1 : 1 with the sample. Arctic grayling density and growth rates were not assessed reliably because the few fish that were tagged moved between sectors of the lake.

Benthic animals measurements

The methods used for benthic animal collection and analysis are given in Hershey (1992). Three groups were sampled: chironomids by using an Ekman dredge, snails by using SCUBA divers counts, and sculpin using jar traps.

Benthic chemical measurements

Sediment-water fluxes of inorganic nitrogen and phosphorus were measured in clear or opaque Plexiglas benthic chambers (Sugai & Kipphut, 1992). The chambers covered 0.2 m² of sediment and enclosed 42–52 l of water and were stirred by a 1 rpm motor. The nutrients were analysed using standard colorimetric techniques given in Wetzel & Likens (1979).

Statistical analysis

The primary productivity and chlorophyll *a* measurements were analysed using Friedman's test with each date-depth combination used for a block (Sokal & Rohlf, 1995). This was used rather than Wilcoxon's test since it did not require the assumption of a

symmetric distribution. One-sided tests were used for chlorophyll *a* and primary productivity since there was a clear expectation about the direction of the treatment effect. For each zooplankton species and each year, the four densities (two from each sector of the lake) for each date were ranked, and the ranks for each sector of the lake were summed over all dates. This statistic is similar to that used in Friedman's test, which could have been used instead after averaging all pairs of replicate densities. Using our method allowed us to use all density values directly. A computer program was written to exactly calculate the *P*-value for each sum of ranks. Two-sided tests were used for the statistics for the zooplankton because there was no clear expectation about the direction of the difference between the two sides.

Results

Physical and chemical pelagic response

There were no obvious physical differences between the two sectors of the lake even after 6 years of treatment except in decreasing Secchi disk depths. These changes tightly correlated with the phytoplankton response and are not reported. The levels of inorganic phosphorus and nitrogen were always at or below detection even in the treated sector and thus are not reported.

Biological pelagic response

The addition of nitrogen and phosphorus caused a substantial increase in sestonic biomass in the treated sector of the lake. For all treatment years and the first three recovery years (1985–1993), the yearly average chlorophyll *a* values (Fig. 2) were very significantly higher on the treated side ($P < 0.001$). The treated side was still significantly higher in 1994 ($P < 0.05$) and 1996 ($P < 0.01$), but not 1995. Mean annual chlorophyll *a* increased during the treatment phase with the highest concentration occurring in 1990, the last year of treatment. Mean annual chlorophyll *a* declined rapidly after cessation of nutrient addition. By 1992, values were down to less than some reference values observed during treatment. The chlorophyll *a* concentrations in the reference sector increased during the treatment phase, possibly indicating some back-transport of nutrients from the treated sector or simply

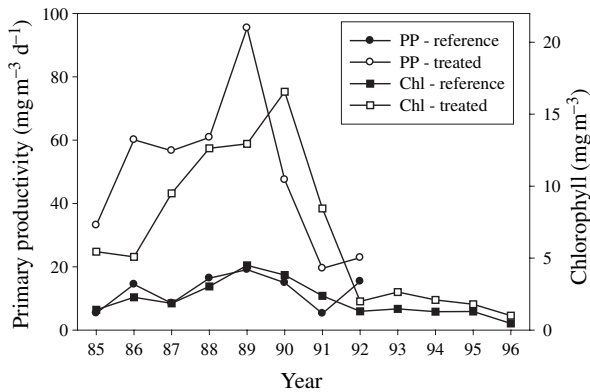


Fig. 2 Annual means of pelagic chlorophyll *a* (reference dark squares, treated open squares) and annual means of primary productivity (reference dark circles, treated open circles).

natural variation. Primary productivity (Fig. 2) was significantly higher on the treated side for all the years primary productivity was measured 1985–1992 ($P < 0.01$ for 1985 and 1989, $P < 0.001$ for all other years). Rates of primary productivity on the treated side peaked in 1989 rather than 1990, the last year of treatment and the peak chlorophyll year.

The complete results of the microplankton response is given in (Ruble & Bettez, 2001). The microzooplankton responded to the nutrient loading with increased biomass, especially of rotifers, to about twice the density of that in the reference sector ($20 \mu\text{g C L}^{-1}$) as the reference sector (Ruble & Bettez, 2001). Rotifers continued to be generally denser in the treated side than in the reference side through 1996,

although much less dense than in 1989, averaging $5.8 \mu\text{g C L}^{-1}$ during the 6 years of recovery.

The response of the four crustacean species of zooplankton to the experimental addition of nutrients and increased phytoplankton biomass was complex. The population density of *D. longiremis* was significantly higher in the treated sector compared to the reference sector in every year of treatment except 1990, although the levels of significance varied (Table 1). The density of *D. longiremis* in the treated sector was significantly greater in four of the six post-treatment years as well. In four of the six treatment years the population density of *D. pribilofensis* was significantly different on the two sides, but it was higher on the treated side in 1986–1988, and on the reference side in 1990 (Table 1). In the post-treatment years there was only 1 year during which there was a significant difference, being higher on the treated side in 1995.

The density response of *B. longirostris* was significant in only two of the treatment years, and the treated side was higher in density only in 1986 (Table 1). During the post-treatment years, there was a significant difference in *B. longirostris* density only in 1992, when the reference sector population was greater than the treated sector population. At no time during the treatment years was there a significant difference in the population densities of *C. scutifer* (Table 1). However, in four of the six post-treatment years, the density was significantly greater in the treated sector. In fact, the highest densities of *C. scutifer*

Table 1 Average densities (number L^{-1}) of zooplankton species in reference and treated sides of the lake during (1985–1990) and after (1991–1996) treatment

Year	<i>D. longiremis</i>		<i>D. pribilofensis</i>		<i>B. longirostris</i>		<i>C. scutifer</i>	
	Reference	Treated	Reference	Treated	Reference	Treated	Reference	Treated
85	7.82	12.87*	2.95	4.24	2.06	2.01	13.24	16.78
86	4.59	9.87***	2.18	6.92***	1.01	3.09**	8.06	8.39
87	6.52	10.06*	4.73	10.08**	0.22	1.32	6.85	6.55
88	5.51	13.28*	3.86	11.26***	0.47	0.77	6.90	6.94
89	5.15	10.45**	4.86	7.29	0.62	2.47	11.59	14.03
90	7.32	5.32	10.78	7.04*	4.48	1.36***	14.79	16.41
91	3.27	2.54	3.70	4.32	0.40	0.30	2.75	3.41
92	0.53	2.44***	1.50	1.27	0.53	0.04***	5.70	9.79***
93	2.74	3.97*	2.34	2.93	1.33	0.95	6.63	10.49***
94	5.57	5.88	5.42	4.71	3.24	2.99	9.52	9.58
95	3.21	5.24***	2.97	4.94*	1.90	3.55	9.34	30.20***
96	1.49	5.45**	3.58	5.37	2.06	1.72	7.99	22.78***

Asterisks indicate level of significance: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

observed in the entire study occurred in 1995 and 1996 in the formerly treated sector.

Benthic biological response

The complete results for the benthic biological response is given in Hershey (1992). There are only two major invertebrate groups in the benthos of the lake: *Lymnaea* snails and chironomids. At the start of the experiment *Lymnaea* densities were higher in the reference sector of the lake but by 1987 and 1988 the densities in the treated sector were almost twice those in the reference sector and significantly different (Hershey, 1992). Chironomid densities were also higher on the reference side in 1985, but unlike the snails, this remained so throughout the experiment. While there was no numerical response from the chironomids there were community changes. By the end of the nutrient addition phase of the experiment, the treated sector was dominated by individuals in the genus *Phaenopsectra* rather than the Orthocladids that had been the original dominant group (Hershey, 1992). Sculpin length, weight, age and growth rate did not differ between reference and treated sectors of the lake.

Benthic chemical response

Nutrient addition had significant effects on the depletion of oxygen and flux of nutrients between sediments and overlying water. Oxygen consumption by the sediments caused oxygen depletion deep in the lake, which extended to shallower water in later years of treatment. Figure 3 shows the depth for which O_2 concentration was $3 \text{ mg } O_2 \text{ L}^{-1}$ in late summer of each year (above this depth there was more O_2 and below there was less) in the treated sector of the lake. Low-oxygen water extended from below 9 m in 1985 to just below 6 m by 1988. The depth of low oxygen remained similar for the rest of the study. The reference section of the lake rarely showed low oxygen concentrations.

The fluxes of ammonium from the sediments did not increase at a smooth rate; there was a marked increase during the summer of 1987, and then further increases through 1990 (Fig. 4). The ammonium flux remained at near 1990 levels during the recovery years (except for 1994 and 1995). Despite the increases in ammonium fluxes, phosphorus fluxes from the

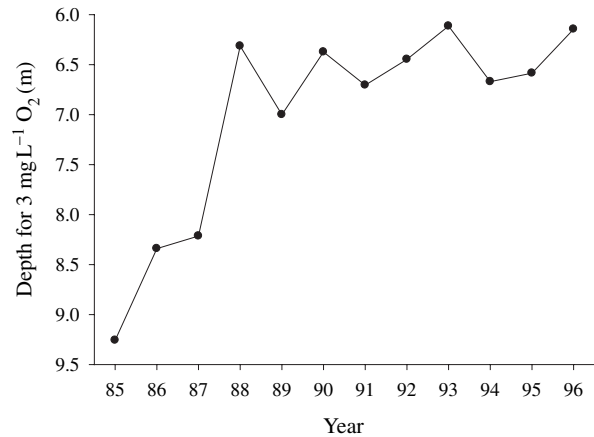


Fig. 3 The annual shallowest depth with oxygen at least $3 \text{ mg } O_2 \text{ L}^{-1}$ in late summer.

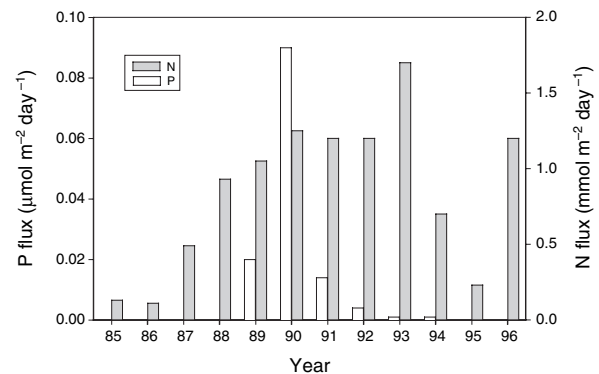


Fig. 4 The average daily fluxes of inorganic nitrogen (shaded bars) and phosphorus (white bars) from the sediments of the treated sector of the lake.

sediments were not measurable until the last 2 years of nutrient addition and then declined to below detection by 1995 (Fig. 4).

Discussion

Biological pelagic response

There were no physical or chemical effects of nutrient loading on the fertilised sector of the lake that were not attributable to the stimulation of phytoplankton growth and build-up of phytoplankton biomass. Clearly the addition of nitrogen and phosphorus stimulated phytoplankton growth. This has been found in other arctic and subarctic lakes. Nutrients from sewage greatly stimulated primary production

in a high arctic lake (Schindler *et al.*, 1974). In more experimental approaches three lakes in northern Sweden (68°N) were fertilised with phosphorus or nitrogen and then both nitrogen and phosphorus (Jansson, 1978): when fertilised with phosphorus alone, mean summer biomass of phytoplankton was eight times greater than in the reference lake, however, when fertilised with both nitrogen and phosphorus the phytoplankton biomass was 60 times that of the reference lake (Jansson, 1978). In a similar experiment in the central Canadian Arctic (63°N), the study lakes seemed to be phosphorus-limited but required both nitrogen and phosphorus addition for increased phytoplankton production (Welch *et al.*, 1989). Two small, humic lakes in northern Sweden showed no plankton response to phosphorus addition but did respond to nitrogen addition. Also in Sweden in Lake Erken, Vrede *et al.* (1999) found the limitation by phosphorus and nitrogen changed seasonally.

Ostrofsky & Rigler (1987) found a different regression relationship between spring total phosphorus and summer chlorophyll *a* in subarctic lakes than had been found for temperate lakes (Dillon & Rigler, 1974). Thus arctic lakes seem to differ from temperate lakes in that they may be nitrogen-limited, or if phosphorus-limited a nitrogen limitation may ensue with the addition of just a little phosphorus (Levine & Whalen, 2001). However, Elser, Marzolf & Goldman (1990) and Maberly *et al.* (2002) showed that many temperate lakes seem to behave in this same way.

At the beginning of the summers of 1986 and 1987, prior to the commencement of nutrient addition but about 2 weeks after ice-out, the chlorophyll *a* concentrations in the treated sector were low and virtually identical (within 5%) to those in the reference sector. But in the beginning of 1988 and 1989, prior to the commencement of nutrient addition, the chlorophyll concentration in the treated sector was more than twice that in the reference sector. These are the summers when we first observed some phosphorus flux from the sediments in the treated sector (Fig. 4). The lack of carry-over early in the experiment may be because of the high nutrient adsorbing properties of the lake sediments, similar to Toolik Lake (Cornwell, 1987) and other lakes (Houser, Carpenter & Cole, 2000). The observed carry-over later in the experiment indicated that maybe the nutrient addition saturated the phosphorus binding capacity of the sediments. Alternatively, the anoxic condition in the hypolimnion

for several summers may have finally reduced enough iron to allow phosphorus release (Lijklema, 1980).

The strong phosphorus adsorption by the sediments may also account for the almost threefold increase in average annual chlorophyll *a* as the experiment progressed. We can estimate the expected chlorophyll *a* by analysing the results of 33 lake or limnocorral nutrient-addition years (O'Brien *et al.*, 1992). These experiments used six different phosphorus loading rates between 0.1 and 1 g P m⁻² year⁻¹. The regression of the average annual chlorophyll *a* for the first year of these experiments (omitting the present lake, N-2) yields an expected chlorophyll in µg L⁻¹ $12.2 \times P^{0.85}$. The first 2 years of the N-2 experiment the chlorophyll levels were 73 and 79% of this expected value. These low chlorophyll *a* values probably indicate uptake of phosphorus by the sediments before the phytoplankton could take it up. In subsequent years the chlorophyll *a* was above the expected value, getting greater with each year and as high as 250% of expected in the last year of nutrient addition. This probably reflected phosphorus being recycled from the sediments, as shown in Fig. 4.

In terms of phytoplankton biomass, as assessed by chlorophyll *a*, the treated sector of the lake recovered fairly rapidly. By 1995 the chlorophyll *a* concentrations in the treated sector were very similar to the reference sector prefertilisation concentrations (Fig. 2). Most recovery data in other areas of the Arctic are studies in which domestic sewage input is stopped or reduced. The chlorophyll *a* concentration fell to 30% 7 years after sewage input ceased in Lake Norrviken in central Sweden (Ahlgren, 1978). Likewise the chlorophyll *a* concentration in a subarctic chain of lakes in northern Quebec fell 70–80% 8 years after the sewage input was reduced by 80% (Choulik & Moore, 1992). Thus the fertilised sector of Lake N-2 may have recovered faster than other arctic and subarctic lakes. Again, this is likely because of the high concentrations of iron and manganese in the sediments.

The response of the macrozooplankton to nutrient addition was mixed (Table 1). Only *D. longiremis* consistently had increased densities in the treated sector of the lake and *D. pribilofensis* had significantly higher densities in the treated sector three of the six treatment years. Two species, *B. longirostris* and *D. pribilofensis*, had a significant reversed response in which the density in the reference sector was higher than the

treated sector in 1990 (Table 1). We believe that this is an anomalous result because of high densities of dinoflagellates in the treated sector. The dinoflagellates could either have been a poor food source or have clogged the plankton net resulting in lower apparent densities. We tested this second hypothesis in the summer of 1991 when the dinoflagellates were still present by comparing the zooplankton density sampled with the vertically towed net versus samples collected by a vertically lowered pump. The pump sampled *D. pribilofensis* and *C. scutifer* with 153% efficiency compared with the net, so the net is probably underestimating these species in the presence of dinoflagellates in 1990 and 1991.

One of the more interesting trends with the zooplankton response to nutrient addition is the case of *C. scutifer*. *Cyclops scutifer* showed no response to nutrient addition during the treatment phase of the experiment, yet in four of the 6 years during the recovery phase the densities of *C. scutifer* were significantly higher in the previously treated sector compared with the reference sector. There is little known of the feeding of cyclopoid copepods. However, in the ^{15}N addition experiment (Kling, 1994), the ^{15}N was incorporated into the seston, and with a time delay, into all of the pelagic zooplankton. By the end of the summer *D. longiremis* had the same ^{15}N composition as the seston showing it to be a strict herbivore. *Cyclops scutifer* had much less ^{15}N than the seston suggesting that it may feed on detritus, acquire food from the microbial food loop, or be predaceous. However, recent work on the vertical distribution of *C. scutifer* in Toolik Lake has shown that the vast majority of individuals of *C. scutifer* occupy the lower portions of the lake (C. Johnson, personal communication). If a similar distribution was present in Lake N-2, then epilimnetic phytoplankton would not have been directly available to *C. scutifer* and one would expect *C. scutifer* to load up the ^{15}N more slowly than the species dwelling in the epilimnion.

The lack of response of some of the zooplankton species to added nutrients and increased phytoplankton is not surprising. In a number of studies the response of zooplankton to added nutrients has been variable. In some studies there has been an increase in zooplankton density with added nutrients (Carpenter *et al.*, 1996; Johnston *et al.*, 1999). In an arctic limnocorral study, O'Brien *et al.* (1992) found that added nutrients did stimulate increased *Daphnia* biomass but

only in the third year of the study. In another limnocorral study, Qin & Culver (1995) found that added nutrients increased phytoplankton biomass but not zooplankton biomass. However, quite a few studies have found that zooplankton actually decrease with added nutrients (O'Brien & deNoyelles, 1972; Malley *et al.*, 1988; Hann, Leavitt & Chang, 1994). In the classic study of Lake Washington, Edmondson (1991) found that *Daphnia* recolonised the lake and became abundant with reduction in eutrophication. These results of poor zooplankton response to increased nutrients are consistent with Porter, Gerritsen & Orcutt (1982), who found that *D. magna* (Straus) survived, grew and reproduced best at moderate algal concentrations rather than at high algal concentrations. It appears that the response of zooplankton to fertilisation depends as much on changes in amount and type of food source, and possibly to the effects of zooplankton distribution within the water column, as it does to simple increased primary production.

Benthic biological response

In the treated sector of the lake snail densities increased but chironomid densities did not (Hershey, 1992). The responses of benthic invertebrates to increased planktonic algal production in other nutrient addition studies have not been consistent. In 20 arctic and subarctic lakes there was a positive correlation between the number of chironomids and phytoplankton production (Moore, 1978). Yet in another study, increases in attached and planktonic algae did not influence chironomid density but did have strong effects on oligochaete density (Moore, 1980). In a 6-year fertilisation study, Welch, Jorgenson & Curtis (1988) found that emerging chironomid biomass responded quickly but variably to increased phytoplankton production.

Benthic chemical response

There was a marked increase in sediment-water chemical interactions in response to the addition of nutrients to the epilimnion. Within the hypolimnetic sediments, fluxes of ammonium and phosphorus to the water column increased more than 10-fold after 6 years of fertilisation (Fig. 4). Although we do not have good estimates of seston settling rates, the increases in nutrient fluxes are almost certainly because of the sinking and subsequent decomposition

of phytoplankton from the epilimnion. This recycling of nitrogen and phosphorus probably played some role in the slow year-to-year increase in chlorophyll concentrations and primary production rates that were observed in the treated sector during the first 5 years of nutrient addition (Fig. 2). Decomposition of organic matter in the hypolimnetic sediments is also the likely cause of the partial or complete anoxia that was observed within the deeper portions of the water column in the treated sector. The depth to water with $3 \text{ mg O}_2 \text{ L}^{-1}$ or lower gradually grew shallower through the first 4 years of nutrient addition and then remained essentially unchanged for the rest of the study (Fig. 3). A factor contributing to low summer oxygen concentration is the poor spring mixing of many arctic lakes. These lakes, including N-2, commonly thermally stratify very soon after ice-out and rarely fully mix in the spring.

Although fluxes of both N and P increased in response to nutrient addition, P fluxes appear to be much more strongly influenced by the iron and manganese rich nature of the lake sediments. During the period when nutrient addition was occurring, increases in P fluxes were delayed relative to N flux. Likewise, P fluxes declined more quickly than N fluxes when fertilisation ended (Fig. 4). Our hypothesis to explain these observations is that P is much more tightly bound by the sediments relative to N. Only when sufficient iron had been reduced did P fluxes increase. This apparently occurred in 1989, after 4 years of fertilisation (Fig. 4). It is important to realise that if lake sediments contain a lot of iron, as lake N-2 sediments do, it takes quite a bit of time to reduce them to the point where phosphorus is released (Lijklema, 1980). The P fluxes declined immediately after cessation of nutrient addition and this is somewhat puzzling because the hypolimnion remained anoxic throughout the recovery period. One possibility is the large flux in 1990 represented most of the added phosphorus and with nutrient addition discontinued there was no longer a large store of phosphorus to generate much flux of phosphorus. Thus the phosphorus flux greatly declined. Nitrogen fluxes declined much more slowly than P fluxes.

Conclusions

The response of the animal groups in the lake confirms much of our understanding of arctic food

webs. Most of the macro- and micro-zooplankton are food limited in that three of the macrozooplankton species did respond to increased phytoplankton in at least some of the treatment years and the microplankton responded. However, *C. scutifer* did not respond during treatment indicating that this species is likely not a strict herbivore although it likely dwelling in the hypolimnion makes interpretation difficult. It is thought that sculpin predation regulates chironomid densities and the lack of numerical response of either chironomids or sculpin is consistent with this idea. However, the increase in snail abundance indicates that they may be food resource limited as has been proposed previously.

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