

Primary Research Paper

## Effects of a whole-lake, experimental fertilization on lake trout in a small oligotrophic arctic lake

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### Abstract

We tested whether increased phosphorus and nitrogen concentrations would affect a lake trout (*Salvelinus namaycush*) population in a small oligotrophic lake with a benthically dominated food web. From 1990 to 1994, nitrogen and phosphorus were added to Lake N1 (4.4 ha) at the arctic Long-Term Ecological Research site in Alaska. We used mark/recapture methods to determine the lake trout population size, size structure, recruitment, and individual growth from 1987 to 1999. Data were also collected on water chemistry and food availability. Fertilization resulted in increased pelagic primary productivity, chlorophyll *a*, turbidity, snail density, and hypoxia in summer and winter. Lake trout density was not affected by the manipulation however growth and average size increased. Recruitment was high initially, but declined throughout the fertilization. These results suggest that lake trout were affected through increased food availability and changes to the physical characteristics of the lake. During fertilization, hypoxia near the sediments may have killed over-wintering embryos and decreased habitat availability. Although lake trout responded strongly to increased nutrients, loss of recruitment might jeopardize lake trout persistence if arctic lakes undergo eutrophication.

### Introduction

Eutrophication is one of the major problems facing freshwater ecosystems (Hasler, 1947; Carpenter et al., 1998; Smith et al., 1999). Nutrient enrichment in aquatic ecosystems from anthropogenic changes in land use such as deforestation, construction, and agriculture, lead to increased phosphorus and nitrogen in streams and lakes

(Carpenter et al., 1998). Arctic Alaska, characterized by low human density and oligotrophic lakes, is also susceptible to eutrophication. Recent studies have indicated that nutrients trapped in the permafrost could be released due to atmospheric warming (Rastetter, 1996).

Eutrophication leads to a series of biotic and abiotic changes in lakes. Nutrients entering lakes lead to increased primary production, algal

biomass, and changes to algal species composition (Dillon & Rigler, 1974; Schindler, 1974; Schindler et al., 1974; Stockner & Shortreed, 1988), all of which result in decreased water transparency (Goldman, 1988; Budy et al., 1998). As organisms die, they sink to the bottom where bacterial decomposition releases nutrients and decreases oxygen content in the hypolimnion (Tanner, 1952; Lehman, 1988; Hecky et al., 1994). Although increased primary production can result in increased secondary production (Brett & Goldman, 1997; Budy et al., 1998) the strength of the response to nutrient addition decreases with each subsequent trophic level (McQueen, 1990; Brett & Goldman, 1996; Micheli, 1999). In addition to causing increased productivity at higher trophic levels, eutrophication can affect community structure (Schindler et al., 1974; Kyle et al., 1988; Smith et al., 1999). As oligotrophic lakes undergo eutrophication, oligotrophy-tolerant fish species such as salmonids and coregonids are replaced by more eutrophy-tolerant species such as perch and cyprinids (Hasler, 1947).

Whole-lake experimental fertilization is a useful tool to examine the importance of bottom-up control of aquatic food webs (Schindler & Fee, 1974). Nutrient availability determines the potential productivity of an ecosystem whereas the species composition, and more specifically, the identity of the top-consumers, determines the realized productivity (Carpenter et al., 1985). The response of lakes to nutrient additions is affected by the trophic status, trophic structure, and the physical and chemical condition of the water and lake sediments (Schindler, 1974; Carpenter et al., 1985; Elser et al., 1990).

Arctic lakes are good systems in which to examine the effects of nutrient enrichment because they are relatively pristine and are nutrient limited. Lakes on the North Slope of the Brooks Range in arctic Alaska are typically small (<100 ha) and oligotrophic (Kling et al., 1992). Concentrations of nitrogen and phosphorus are low and limit primary productivity (Hobbie, 1980; Whalen & Cornwell, 1985; Miller et al., 1986; Levine & Whalen, 2001). In some lakes, phosphorus is bound to iron and magnesium in the sediment further restricting phosphorus availability to biota (Prentki et al., 1980; Cornwell & Kipphut, 1992). Mean primary

productivity in arctic lakes during summer is  $29 \mu\text{g C m}^{-2} \text{d}^{-1}$  (Levine and Whalen, 2001). Most of the annual nutrient load enters the lakes with spring meltwater (Whalen & Cornwell, 1985), and, primary production peaks at ice-out and decreases throughout the summer (Miller et al., 1986).

Additionally, food webs of arctic lakes in the vicinity of Toolik Lake, Alaska, are simple and trophic structure is controlled by fish (Gettel, 1998; Hershey et al., 1999). Lake trout (*Salvelinus namaycush*) are found in deep lakes (max. depth >8 m, Hershey et al., 1999) and feed on fish and invertebrates, particularly the snail *Lymnaea elodes* (O'Brien et al., 1979; McDonald & Hershey, 1989; Merrick et al., 1991, 1992; Sierszen et al. 2003). The presence of lake trout affects the size structure and abundance of *Lymnaea* and the distribution of slimy sculpin (*Cottus cognatus*) populations (Hershey, 1990; Merrick et al., 1991, 1992; Hanson et al., 1992; McDonald & Hershey, 1992). The presence of lake trout induces a strong trophic cascade (*sensu* Carpenter et al., 1985) through control of sculpin (Hanson et al., 1992; McDonald & Hershey, 1992) and *Lymnaea*. Sculpin affect chironomid density and species composition (Hershey, 1985). In the presence of lake trout, chironomid density, biomass, and species diversity is higher (Goyke & Hershey, 1992).

For the last two decades, experiments at the arctic Long-Term Ecological Research (LTER) site have examined the possible effects of increased nutrient inputs into aquatic ecosystem (e.g., Peterson et al., 1985; O'Brien et al., 1992; Peterson et al., 1993), but implications of fertilization for lake trout have not previously been evaluated. O'Brien et al. (1992) found nutrient additions to limnocorrals in Toolik Lake resulted in increased pelagic primary productivity and microbial, algal, and zooplankton density, but benthic organisms not respond. In 1985, Lake N2 was divided with a plastic curtain and one side fertilized with inorganic phosphorus and nitrogen at 5 times the natural load (Hershey, 1992; O'Brien et al., 2005). In response, primary productivity, phytoplankton biomass (M. C. Miller, personal communication), respiration at the water-sediment interface (Sugai & Kipphut, 1992), and density of snails (Hershey, 1992) increased although chironomid density and slimy sculpin growth did not change (Hershey, 1992).

In this study we examined the effect of fertilization on the lake trout (*Salvelinus namaycush*) population in Lake N1, a small oligotrophic lake at the arctic LTER site. Specifically, we tested the null hypothesis that fertilization would have no effect on the population size, size structure, recruitment, and growth of lake trout. We monitored these parameters over a 13-year period including pre-, during, and post-fertilization of the lake. Although the main goal of this project was to examine the strength of the bottom up response, the results also have implications for fisheries management as fertilization has been suggested as a tool to increase fish production in arctic Alaskan lakes.

## Methods

### *Study site*

Lake N1 is located at the Arctic LTER site on the north slope of the Brooks Range in Alaska (68° 38' 25" N, 149° 36' 20" W). It has an area of 4.4 ha (Kling et al., 1992) and maximum depth of 14 m (average depth = 3.9 m) (Bettez et al., 2002). The lake consists of two basins of roughly equal area, of which, the southern basin is shallower (max. depth = 6 m). The temperature and oxygen characteristics of Lake N1 are similar to other lakes in the region (Kling et al., 1992). The ice-free period extends from mid-June to late September and average epilimnetic temperature in July is 12 °C (Bettez et al., 2002). Temperature of the hypolimnion remains near 4 °C and is characterized by oxygen concentration greater than 6 mg/l. Hypoxic conditions are limited to a thin layer (<1 m) at the water-sediment interface. Lake N1 contains a simple assemblage of 4 fish species; lake trout (*Salvelinus namaycush*), Arctic grayling (*Thymallus arcticus*), burbot (*Lota lota*), and slimy sculpin (*Cottus cognatus*).

### *Nutrient additions*

Inorganic nitrogen and phosphorus were added to Lake N1 in the summers of 1990 through 1994. In 1990, 1991, and 1992, ammonium nitrate (2.5 mmol N m<sup>-2</sup> day<sup>-1</sup>; 144.7 Kg N year<sup>-1</sup>) and phosphoric acid (0.199 mmol P m<sup>-2</sup> day<sup>-1</sup>;

19.47 l year<sup>-1</sup>) were added from late June to early August. This annual loading rate is 4 times that for nearby Toolik Lake was selected based on the results of previous experiments in the area (Hershey, 1992; O'Brien et al., 1992). Due to the development of a thick hypolimnetic anoxic layer in Lake N1 during 1993 and 1994, nitrogen and phosphorus additions were reduced. Total additions in the summer of 1993 and 1994 were at a rate of 1.7 mmol N m<sup>-2</sup> day<sup>-1</sup> and 0.136 mmol P m<sup>-2</sup> day<sup>-1</sup>, 68% of previous additions.

Physical, chemical, and biotic parameters were sampled each summer to assess the response of lake N1 to the fertilization. We measured Secchi depth, thermal profile, and oxygen profile weekly and chlorophyll *a* and primary productivity bi-weekly from late June through early August. All methods followed the arctic LTER lakes sampling protocol ([www.mbl.edu/html/ECOSYSTEMS/lterhtml/arc.html](http://www.mbl.edu/html/ECOSYSTEMS/lterhtml/arc.html)). Briefly, temperature and oxygen were measured each meter from the surface to the bottom at the deepest part of the lake. In 1989–1992, oxygen was measured with a YSI model 57 oxygen meter and temperature was measured with a YSI model 33 conductivity meter. In 1993–1998, oxygen and temperature were measured with a Hydrolab SVR(-DL Surveyor3 data logger. Water samples for chlorophyll *a* and primary productivity analysis were collected at the surface, 1, 3, 5, 8, and 12 m. Chlorophyll *a* determination was by fluorometric analysis after acetone extraction (modified from Wetzel & Likens, 1979). Primary productivity was measured by <sup>14</sup>C uptake method (modified from Wetzel & Likens, 1979). In 1986, 1990–1993, 1995, 1998, and 1999, density of the snail *Lymnaea elodes* was measured in mid-summer. *Lymnaea elodes* within 0.5-m of a 10-m transect in 3–5 m of water were counted by a diver.

### *Fish sampling*

From 1987 to 1999, lake trout (*Salvelinus namaycush*) were collected by angling. Fish were typically collected through the ice using ice-fishing gear rigged with light line and 1/16th to 1/8th ounce plastic-covered lead jigs tipped with salted fish. Upon capture, each fish was measured (total length in mm), weighed (grams), individually identified with a tag (if >200 mm TL), and released. In 1993, experimental gillnets were fished

from 28 July to 2 August. Twenty-four lake trout were collected and sacrificed for aging by otolith analysis. Because gillnetting was more efficient at capturing smaller-sized lake trout than was angling, fish collected by gillnetting were not included in analyses of population size, population size structure, or recruitment. In 1999, 14 of the fish collected by angling were sacrificed for age determination.

No tagging had been conducted in Lake N1 prior to this study. In 1987 and 1988, fish were marked using Floy juvenile tags (Floy Tag Inc., Seattle WA, USA) attached by monofilament to the skin below the base of the dorsal fin. From 1989 to 1994, individually numbered Floy anchor tags (Floy Tag Inc., Seattle WA, USA) were used. The Floy anchor tags were inserted below the base of the dorsal fin. Inserted tags were gently tugged to assure that the anchor was hooked securely behind the inter-muscular bones. In response to high rates of anchor tag loss (>25%), beginning in 1993 fish were tagged with passive integrated transponder (PIT) tags (Biomedic Data Systems). The PIT tags were injected into the flesh at the base of the dorsal fin and the adipose fin was clipped as a visible mark that the fish had been PIT tagged. Both Floy anchor tags and PIT tags were used in 1993 through 1994. After 1994, all fish (including fish carrying anchor tags) were tagged with PIT tags.

Upon capture, each fish was inspected for the presence of a tag or scar tissue in the area of tag insertion. The presence of a tag scar was used as an indicator that the fish had previously been tagged, but the tag had been lost. Although tag-scarred fish could not be identified individually, they were counted as recaptured fish for the determination of recruitment. For this study, we considered each year as a sample, therefore, only the data from the first capture of each fish in each year was included in analyses.

For analysis of the lake trout population, we grouped the data into three time periods. Pre-fertilization was from 1987 to 1990. We included data collected in 1990 with the pre-fertilization data because most fish were collected prior to the initiation of fertilization in late June, 1990. Fish collected in 1991–1995 were grouped in the fertilization period. The fish sample from 1995 was included in the fertilization period

because it was the first collection after the last summer of fertilization. The post-fertilization period was from 1996 to 1999.

#### *Population size and recruitment estimates*

Due to high rates of tag loss for Floy juvenile and Floy anchor tags, the data violated the assumptions of standard methods of population estimation (Petersen, Schnabel, Jolly-Seber). We used an alternative method of population estimation (Manly & Parr, 1968) that is based on the Peterson method but eliminates fish that might have experienced tag loss from the capture probability calculation (J. Nichols, Patuxent Wildlife Research Center, 11510 American Holly Drive, Laurel, MD 20708–4017, personal communication). The method uses a subset of the tagged fish to estimate capture probability in each year. The subset included those fish caught before year  $t$  and recaptured after year  $t$ , (e.g., if  $t = 1990$ , the subset includes fish tagged prior to 1990 and recaptured at some time after 1990), to calculate the capture probability in year  $t$  ( $p_t$ ). The proportion of fish from the subset that was captured in the sample for year  $t$  was our capture probability. In this way, fish that experience tag loss are not included in the subset and do not influence the calculation of capture probability or result in subsequent overestimation of population size. The population estimate for year  $t$  ( $N_t$ ) was then calculated by equation (1) where  $p_t$  is the capture probability in year  $t$  and  $n_t$  is the number of lake trout captured in the sample in year  $t$ .

$$N_t = n_t/p_t \quad (1)$$

Because young-of-the-year lake trout are extremely difficult to capture in arctic lakes, we used the number of fish entering the catchable size-class (>200 mm) each year as a measure of recruitment. Recruitment into the catchable size-class was calculated by the non-parametric method of Robson & Flick (1965). This method has been used previously to assess recruitment in lake trout populations (Burr, 1990, 1997). Briefly, this method orders the fish by length and examines the distribution of unmarked fish between marked fish. This method assumes that fish of a given size have equal probability of being marked, therefore,

there should be an equal number of unmarked fish between each marked fish in the series. If there are significantly more unmarked fish between smaller marked fish than larger marked fish, recruitment into the catchable size-class is occurring.

In the Robson & Flick method (Robson & Flick, 1965; Seber, 1982), fish are sorted by length from shortest to longest and each marked fish is labeled as  $L_i$  where  $i$  is from 1 to  $R$  ( $R$  = the total number of marked fish). The total number of unmarked fish in a sample is  $U$  and the number of unmarked fish in each interval between marked fish is recorded and labeled as  $U_i$  where  $i$  is from 1 to  $R+1$ . The expected value ( $u_i$ ) is  $U/R+1$ . If  $U_i$  is significantly higher than expected ( $u_i$ ), it is assumed to be due to recruitment. The procedure sequentially tests each interval starting with  $U_1$  and continuing until an interval is detected without any recruits. Equation (2) is used to determine the probability of collecting  $U_1$  unmarked fish in the first interval. Note that in equation (2) the function inside of the parentheses is not division but is the mathematical term choose.

$$P[U_1 \geq u_1] = \frac{\binom{R+U-u_1}{R}}{\binom{R+U}{R}} \quad (2)$$

If  $U_i$  is significantly higher than expected, the sample contains new recruits to the population. To test whether  $U_2$  contains any recruits,  $U_1$  and  $L_1$  are removed from the data set and the procedure repeated on the new reduced dataset. Because the intervals containing recruits are removed from the next analysis, the expected  $u_i$  will be lower and should be closer to the true average number of unmarked non-recruits in each interval. The analysis is repeated on subsequent intervals (removing  $U_i$  and  $L_i$  each time) until an interval ( $U_x$ ) of unmarked fish is tested and found not to be significantly greater than expected.

If ties occur between marked fish or the proportion of marked individuals is high in the population, intervals should be pooled (Robson & Flick, 1965; Seber, 1982). The combined interval  $S_k$  will contain some number of intervals. As intervals are pooled it will change  $R$  also as

marked fish between the combined intervals are removed from consideration. The tail probability of  $S_k$  is given in equation (3).

$$\sum_{r=0}^{k-1} \binom{S_k+r-1}{r} \binom{R+U-S_k-r}{R-r} / \binom{R+U}{R} \quad (3)$$

The next step in the procedure determines how many fish in each interval are non-recruits. At this point in the analysis, all the intervals containing new recruits have been identified and have all been removed from the data set. Because no new recruits were detected in the last interval tested ( $U_x$ ), the calculated expected for  $u_i$  is presumed to be the true value for the entire sample (including  $U_1$  through  $U_{x-1}$ ) and is used to determine the number of recruits in each interval which contain recruits (i.e.,  $U_1$  through  $U_{x-1}$ ). The total recruitment for the sample is the sum of recruitment for each interval in which significant recruitment was detected ( $U_1 - u_x + U_2 - u_x + \dots$  to  $U_{x-1} - u_x$ ).

### Growth

We constructed a capture history, including weight and total length, for each fish. Relative growth rates based on weight (%weight gain year<sup>-1</sup>) and total length (%length gain year<sup>-1</sup>) were calculated for fish caught in two or more years. Many lake trout were not captured each year and therefore had missing data in their capture history. We used linear interpolation to estimate the weight and length of fish in years they were not captured. If more than 3 years occurred between capture events for an individual fish, growth for that time interval was not included in the analysis.

We used a one-way ANOVA to test the null hypothesis that there was no difference in relative growth before, during, and after fertilization. Because fish were monitored over multiple years, many spanning more than one treatment period, the overall data set does not meet the criterion for independence. To meet the assumption of independence, we included in this analysis only the relative growth in the first year each individual fish was monitored. Relative growth of fish first captured in pre-fertilization (1987–1989), fertilization (1991–1994), and post-fertilization (1996–1998) were included in the analysis.

Examination of the mean relative growth for each year indicated that there was a time lag between when the treatment changed and when lake trout relative growth changed. We did not include in the analysis data from 1990, the first year of fertilization, or 1995, the first year of the post-fertilization period.

Because growth is generally lower in larger, mature fish (Moyle & Cech, 1988), we examined the mean initial weight of fish included in the relative growth analysis. We used a one-way ANOVA to test the hypothesis that there was no difference in the initial weight of fish from the three treatment periods used in the relative growth analysis. If the fish used to measure growth were larger in one period, the relative growth in that period would be expected to be lower due to differences in the size of fish measured.

Fish sacrificed in 1993 and 1999 were aged by otolith analysis. Sagittal otoliths were mounted in epoxy and transverse thin sections containing the nucleus were cut with a low-speed saw. The thin section was ground with 600 grit wet/ dry sandpaper and polished with 0.03  $\mu\text{m}$  alumina oxide slurry. Annuli were counted at 100 $\times$  magnification. We tested for homogeneity of slopes to examine differences in relationships of weight and age and length and age between fish collected in 1993 and 1999.

## Results

During the five summers of fertilization, the Secchi depth decreased and pelagic primary productivity and Chlorophyll *a* concentration increased (Fig. 1). Little change occurred in the mean epilimnetic temperature or oxygen concentration during the study. Anoxia at the water-sediment interface developed during fertilization and the thickness of the anoxic layer increased from 1991 to 1994. By late summer in 1994, oxygen levels throughout the hypolimnion were  $<2$  mg/l (Fig. 2). Beginning in 1995, the first year post-fertilization, Secchi depth, primary productivity, and chlorophyll *a* concentrations returned to pre-fertilization levels (Fig. 1). The thickness of the anoxic layer in the hypolimnion decreased throughout the post-fertilization period. Density

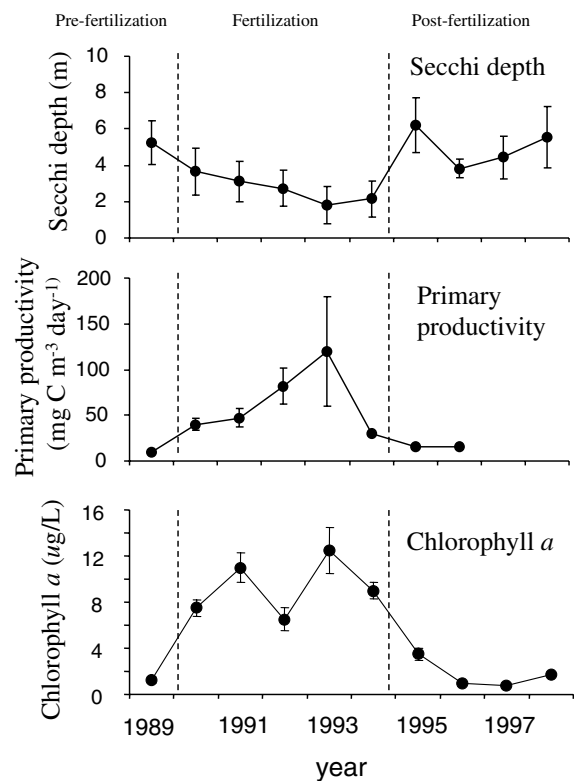


Figure 1. Mean yearly summer secchi depth (m), chlorophyll *a* ( $\mu\text{g/l}$ ), and primary productivity ( $\text{mg C m}^{-3} \text{ day}^{-1}$ ) in Lake N1 during three experimental periods. Error bars show the standard deviation of the mean.

of the snail *Lymnaea elodes*, the main food source for lake trout in small arctic lakes, increased during fertilization (Fig. 3), and in contrast to primary productivity and chlorophyll, snail density remained elevated during much of the post-fertilization period.

From 1987 to 1999, we attached 300 tags to lake trout. Sixty of these fish had tag scars indicating that they had been previously tagged (Table 1). Excluding these re-tagging events, we tagged 240 individual lake trout. By 1996, over 75% of the population had been tagged. This number increased to 90% in 1999.

The estimated density (Manly & Parr, 1968) of lake trout in Lake N1 varied between 15.5 to 27.3 fish/ha from 1990 to 1998 (Table 1). Population estimates from mark/recapture studies are beset by high error rates when sample sizes are low. The broad range in the estimates reflects that fact that the method is sensitive to small sample size combined with the problem of tag loss.

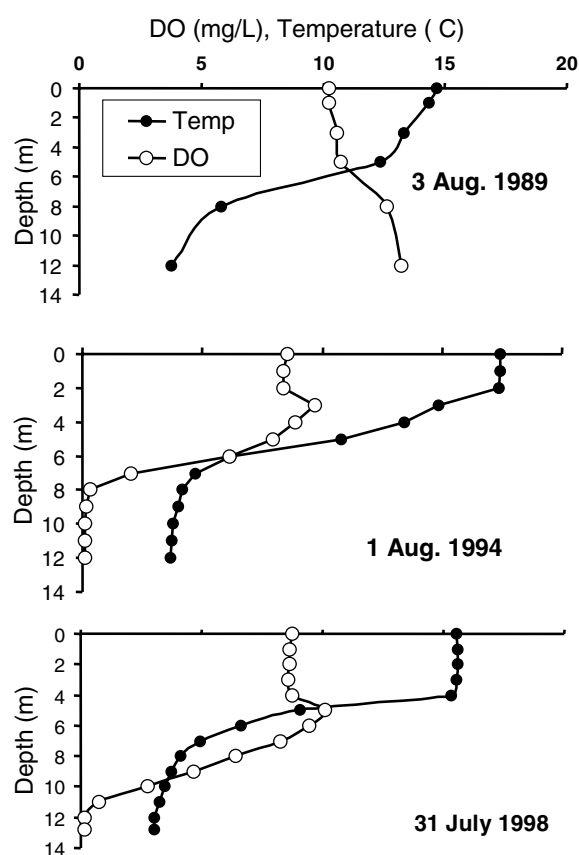


Figure 2. Representative temperature ( $^{\circ}\text{C}$ ) and dissolved oxygen (mg/l) profiles from Lake N1. Profiles are representative of late summer conditions during the pre-fertilization (3 Aug. 1989), fertilization (1 Aug. 1994), and post-fertilization (31 July 1998) periods.

Recruitment of lake trout to the catchable size-class (total length  $>200$  mm) in Lake N1 showed a downward trend from 1990 to 1995 and ceased altogether from 1996 to 1998 (Table 1). Too few fish were recaptured in 1988 and 1989 to calculate recruitment of fish. In 1990, 23 of the 42 unmarked fish were new recruits. Recruitment occurred each year until 1996 when 0 of 13 unmarked fish were new recruits. Too few fish were caught in 1997 to calculate recruitment. In 1998, 0 of 4 unmarked fish were new recruits. Of the 3 unmarked fish captured in 1999, 2 were new recruits.

Size structure of the lake trout population changed throughout the experiment (Table 2, Fig. 4). During the pre-fertilization period, mean total length of fish captured was 385.8 mm and

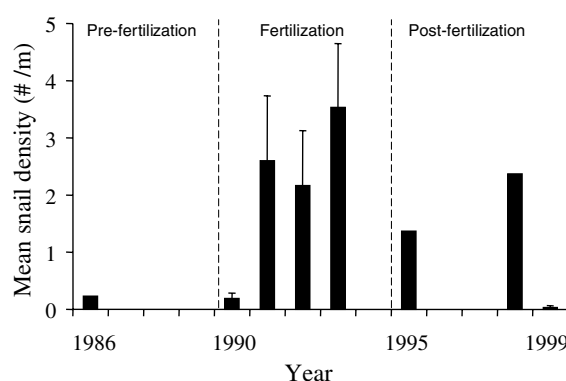


Figure 3. Mean density of snails (*Lymnaea elodes* and *Valvata-lewisii*) in Lake N1 from 1986 to 1999. Snails were counted in mid summer by a diver swimming along 10 m transects (area =  $10\text{ m}^2$ ). Standard error bars are given for years in which more than one transect was sampled. No samples could be collected in 1994 due to high turbidity. Data are not available for 1987–1989, 1996 and 1997.

mean weight was 537.7 g (Table 2). The mode of the size structure occurred at the 300–349 mm total length size-class (Fig. 4). Mean total length and weight were 389.9 mm and 561.7 g, respectively, during the fertilization period and the modal length was approximately 400 mm. Mean total length and mean weight declined from 1991 to 1993 and increased in 1994 and 1995. The mean total length and weight continued to increase during post-fertilization, during which, mean total length was 483.4 mm and mean weight was 1068.9 g (Table 2). During post-fertilization, the mode of the size structure was in the 450–499 mm size-class and less than 5% of individuals were smaller than 400 mm (Fig. 4).

Analyses of growth based on weight and length were similar, therefore, we report only the results based on weight. Mean relative growth (%weight gain  $\text{year}^{-1}$ ) was low from 1987 to 1990, increased from 1991 to 1994, and declined thereafter (Fig. 5). Relative growth was negatively related to initial weight ( $r^2 = 0.48$ ,  $p < 0.0001$ ). Statistical analyses could not be performed on these data because the growth rates of individuals were measured in more than one year, so yearly mean values are not independent. To statistically compare the relative growth among treatment periods, we used only the relative growth measure for the first year in which each fish was monitored. The relative growth was significantly higher during

the fertilization period (1991–1994) than during pre-fertilization (1987–1989) and post-fertilization (1996–1998) (ANOVA:  $F_{2,75} = 7.727$ ,  $p = 0.001$ , Fig. 6). The initial weight of lake trout used in this

analysis was similar during pre-fertilization and fertilization but was significantly higher during post-fertilization (ANOVA:  $F_{2,75} = 9.330$ ,  $p < 0.001$ , Fig. 6).

Table 1. Number of tagged and unmarked lake trout captured in Lake N1 each year and population and recruitment estimates

Year	Number of fish captured				Recapture prob. ( $p$ )	Est. population (sd) (number ha <sup>-1</sup> )	Est. recruitment (number ha <sup>-1</sup> )
	total	recaps	(scarred)	Unmarked			
1987	20	0	(0)	20	–	–	NA
1988	7	1	(0)	6	1/3	0.33	4.77 (3.6)
1989	12	1	(1)	11	0/0	–	–
1990	48	6	(0)	42	1/2	0.5	21.8 (15.3)
1991	57	14	(4)	43	0/0	–	–
1992	73	31	(19)	42	3/3	1	16.6 (0)
1993	51	30	(9)	21	6/9	0.67	17.4 (3.8)
1994	41	29	(16)	12	6/14	0.43	21.7 (6.2)
1995	60	36	(11)	24	17/27	0.63	21.7 (2.7)
1996	57	44	(0)	13	35/42	0.83	15.5 (0.7)
1997	5	4	(0)	1	2/48	0.04	27.3 (14.6)
1998	42	38	(2)	4	15/29	0.52	18.5 (2.6)
1999	35	32	(0)	3	–	–	–

Recaptured fish includes fish that were tag scarred. Recapture probability is based on the subset of fish that were tagged prior to, and captured subsequent to, the year of interest (modified method from Manly & Parr, 1968; see text). Recapture probability is the number of fish in the subset captured divided by the total number in the subset. Estimated recruitment to the catchable size class (> 200 mm) was calculated using the method of Robson and Flick (1965).

Table 2. Mean and standard deviation (sd) for length, weight of lake trout from Lake N1

year	number	total length (mm)		weight (g)	
		mean	(sd)	mean	(sd)
1987	20	365.2	(75.23)	469.9	(319.3)
1988	7	376.4	(90.5)	516.1	(413.5)
1989	12	381.2	(60.0)	518.3	(268.1)
1990	48	397.2	(70.0)	574.0	(337.0)
<b>Pre-fertilization total</b>	<b>87</b>	<b>385.8</b>	<b>(71.7)</b>	<b>537.7</b>	<b>(328.0)</b>
1991	57	388.3	(65.5)	528.4	(286.1)
1992	73	367.4	(67.2)	442.8	(258.2)
1993	50	362.5	(68.8)	441.8	(273.2)
1994	41	404.7	(67.2)	609.4	(287.5)
<b>Fertilization total</b>	<b>221</b>	<b>389.9</b>	<b>(69.3)</b>	<b>561.7</b>	<b>(317.1)</b>
1995	60	439.9	(45.4)	842.1	(299.4)
1996	57	471.3	(32.1)	997.1	(232.5)
1997	5	502.0	(17.3)	1234.0	(171.1)
1998	42	494.6	(19.0)	1150.6	(155.4)
1999	36	486.9	(64.2)	1063.7	(303.0)
<b>Post-fertilization total</b>	<b>200</b>	<b>483.4</b>	<b>(41.0)</b>	<b>1068.7</b>	<b>(246.9)</b>

Mean relative growth and initial weight were calculated for the subset of the population (number) that was tagged and subsequently recaptured.

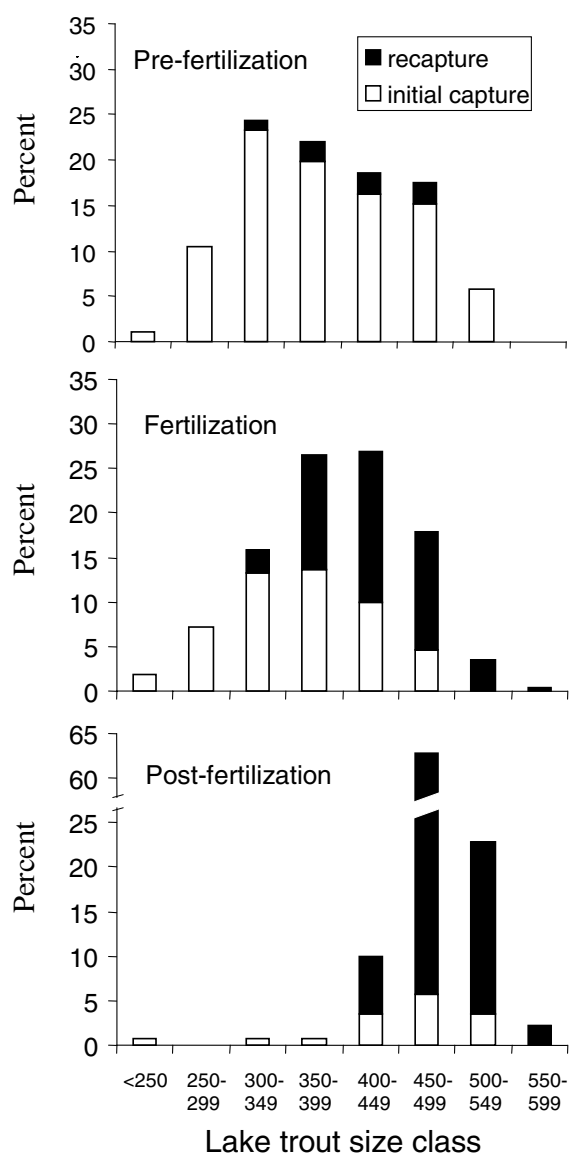


Figure 4. Size structure of the lake trout population in Lake N1 during pre-fertilization (1987–1990), fertilization (1991–1995), and post-fertilization (1996–1999). Open area of column represents untagged fish and closed area represents tagged fish (i.e., recaptured fish).

The relationships of weight to age and length to age differed for lake trout collected in 1993 and 1999 (Fig. 7), the 2 years for which otolith analysis was possible. The year by age interaction terms in the test of homogeneity of slope analysis was significant for the weight to age ( $F = 6.4$ ;  $p = 0.0191$ ) and length to age ( $F = 20.37$ ;  $p = 0.0002$ ) analyses indicated that the slopes of

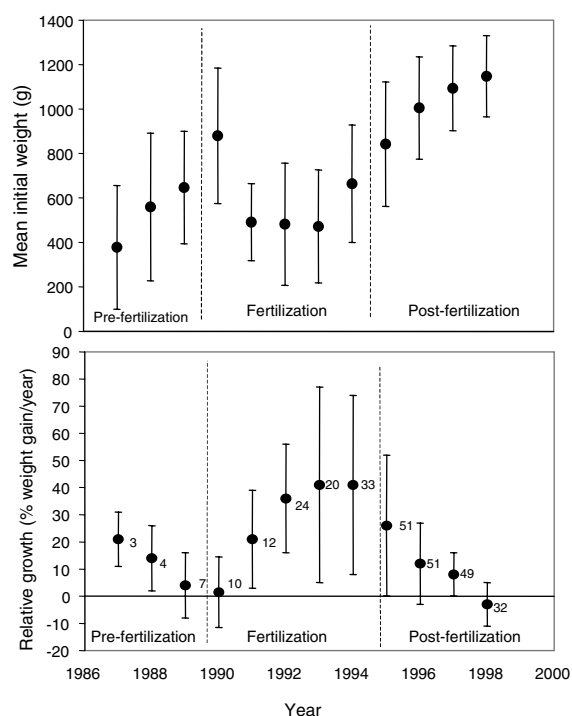


Figure 5. Mean annual initial weight (g) and relative growth (% weight gain  $\text{yr}^{-1}$ ) of lake trout in Lake N1 before, during, and after, experimental fertilization. Error bars indicate the standard deviation of the mean.

the lines differed between the 2 years. Lake trout in 1999 were longer and heavier at a given age than fish in 1993.

## Discussion

Changes to the size structure of the lake trout population in Lake N1 can be explained by changes in growth and recruitment to the catchable size-class (>200 mm). During the pre-treatment period, the lake trout population was comprised mainly of medium-sized, slow-growing fish, which is typical for lake trout in small lakes at the arctic LTER site (Lienesch et al., unpublished data). Even though relative growth quadrupled after fertilization began (Fig. 6), mean fish size did not change appreciably because recruitment to the catchable size-class was high (Table 1). As fertilization progressed, recruitment declined and mean lake trout size increased accompanied by a decline of mean relative growth (Fig. 5). After fertilization ended, recruitment stopped and relative growth was not different than

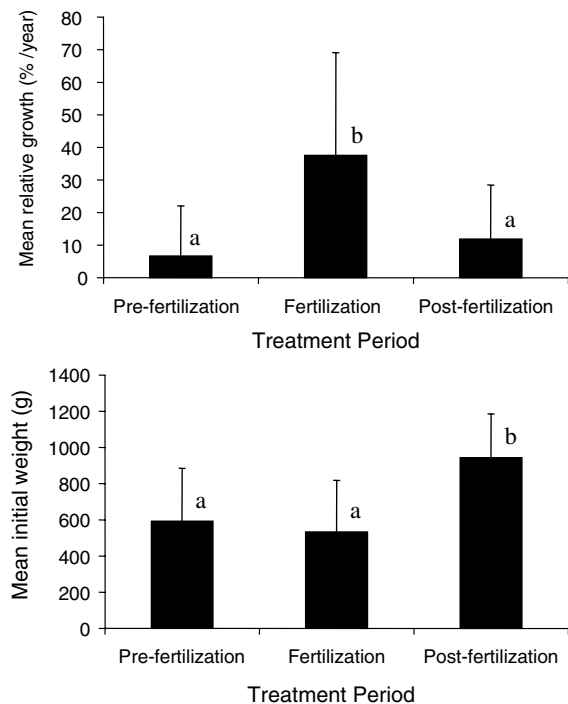


Figure 6. Comparisons of initial weight (g) and relative growth (% weight gain/yr) of lake trout in Lake N1 during pre-fertilization (1987–1989), fertilization (1991–1994), and post-fertilization (1996–1999). Relative weight was calculated for the first year each individual fish was monitored (see text). Initial size data is from fish used in the relative weight analysis. Error bars indicate the standard deviation of the mean. Periods marked with different letters indicate significant differences as determined by pairwise mean comparisons with a Bonferroni correction.

pre-fertilization levels even though fish size was greater. Although relative growth declined sharply throughout post-fertilization, mean lake trout size remained high due to lack of recruitment of small fish to the catchable size-class.

Changes to mean relative growth in a population can sometimes be attributed to changes in mean size of fish in the population because growth is inversely related to size (Moyle & Cech, 1988). We noted an increase in relative growth during the fertilization period compared to both pre-fertilization and post-fertilization. If the change in relative growth was due to changes in fish size, we would expect to find a smaller average size in the population (i.e., if there is a decrease in fish size it should be accompanied by an increase in relative growth rate). The size of individuals used to compare growth rates between

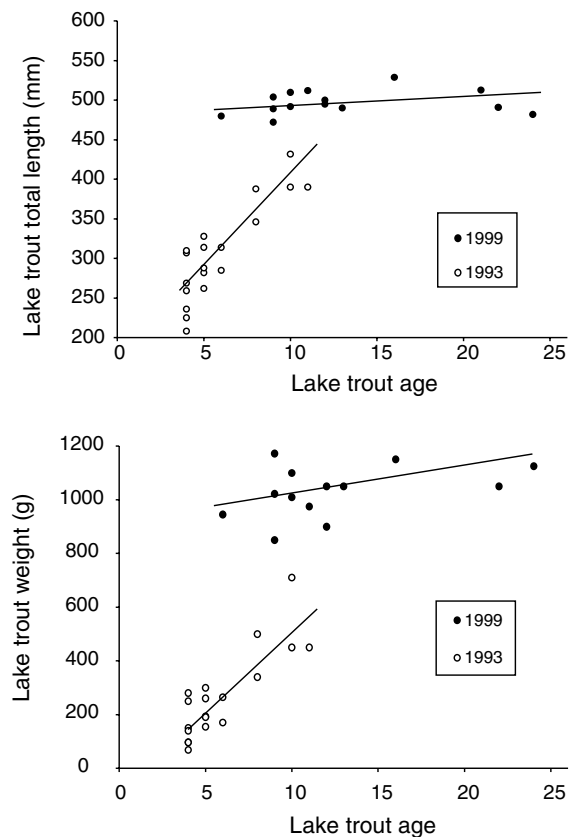


Figure 7. Weight at age and length at age for lake trout collected from Lake N1 in 1993 and 1999, the two years when age data were available.

periods did not change between the pre-fertilization and fertilization period. Therefore, the increased growth during the fertilization period was not an artifact of changes in size, but likely a result of increased food availability. Growth rate decreased from fertilization to post-fertilization, consistent with the inverse growth to size relationship. Although relative growth rate of fish post-fertilization was not significantly different from that from pre-fertilization, the mean initial weight of post-fertilization fish was significantly higher than that for pre-fertilization fish indicating that growth rates at the end of the experiment were still elevated.

Lake trout growth increased concurrently with increased food availability in Lake N1. Snail density increased by an order of magnitude during fertilization (Fig. 3). Although snail density in 1986 and 1990 was similar to that of other lake trout lakes ( $<0.2 \text{ m}^{-2}$ ; Hershey, 1990; Merrick et al.,

1991), in 1992 to 1995 it was between 2 and 4 m<sup>-2</sup>, which is typical of lakes without lake trout (Hershey, 1990). Snails are a major food source for lake trout in arctic lakes (O'Brien et al., 1979; McDonald & Hershey, 1989; Merrick et al., 1991; 1992; Sierszen et al., 2003) and snail density is typically controlled by lake trout predation (Hershey, 1990; Merrick et al., 1991, 1992). In lakes without lake trout, snails are limited by food availability (Hershey, 1992). High snail density during fertilization indicated snail productivity exceeded lake trout consumption despite the increase in lake trout growth. Predation on snails by lake trout may have been limited by visibility during fertilization. Water clarity in Lake N1 was so low in 1994 that divers could not see the bottom well enough to measure snail density. Because lake trout are visual feeders we can safely assume they also would have reduced ability to detect prey. Increased lake trout growth during, and immediately after, the fertilization period indicates that lake trout were food limited prior to the manipulation.

Other changes to the biota of N1 occurred during fertilization. Algal biomass and microplankton abundance increased and microplankton species composition shifted from small herbivores toward large predators (Ruble, 1992; Bettez, 1996; Bettez et al., 2002). Zooplankton density, especially for cladocerans, increased toward the end of the fertilization period and then returned to pre-fertilization levels after nutrient additions ended (Bettez et al., 2002). Although arctic food webs are dominated by benthic productivity (Hershey et al., 1999; Sierszen et al., 2003), adult lake trout will utilize zooplankton under certain conditions (Martin, 1952; Vander Zanden et al., 1999). Zooplankton are important prey for young-of-the-year (YOY) lake trout (McDonald et al., 1992) and growth and survival of YOY lake trout depends on availability of zooplankton (McDonald et al., 1992, 1996). In arctic lakes, YOY and small juvenile lake trout (<200 mm TL) may be restricted to sub-optimal near-shore habitats to avoid predation by adult lake trout (McDonald et al., 1992). In Lake N1, increased cladoceran density and decreased vulnerability to predation due to increased turbidity may have resulted in higher growth and survivorship of YOY and juvenile lake trout.

The density of lake trout in N1 was relatively stable from 1990 to 1999 (15–25 fish ha<sup>-1</sup>) and was similar to values reported for other small lakes (Healey, 1978; Martin & Olver, 1980; Burr, 1997; Mills et al., 2002) and to other lakes at the arctic LTER site (Lake NE12, Lienesch et al., unpublished data). Although our ability to monitor population size was limited by tag loss early in the study and the inherent limitations of mark-recapture population estimates (Koper & Brooks, 1998), there was no evidence of an increase from the 1990 population estimate due to the fertilization.

Lake N1 did not experience high recruitment to the catchable size-class as a result of increased food availability (Table 1, Fig. 3). High food availability usually results in high growth and survivorship of juveniles (LaBrasseur et al., 1978; Stockner, 1987) and eventually, higher recruitment and increased population size. Although recruitment was high early in the fertilization period, it declined from 1993 to 1995 and recruitment ceased during the post-fertilization period (1996 to 1999). If it takes approximately 3 years with a high growth rate for lake trout to exceed 200 mm total length, the lack of recruitment in 1996 through 1998 corresponds to a reduction of lake trout from the 1993 to 1995 year-classes.

The lack of recruitment during post-fertilization, and the associated skewed size structure (Fig. 4), is typical for lake trout in arctic lakes. Lake trout populations in the arctic are typically old and slow-growing (Johnson, 1972, 1976; Burr, 1997), and age and size structure are stable over time (Johnson, 1976) unless the population is disturbed by fishing pressure (McDonald & Hershey, 1989). Mills et al. (2002) studied lake trout populations in 9 small lakes (16–54 ha) in the Experimental Lakes Area, Ontario, and found recruitment was very stable among year-classes. Many large (>100 ha) arctic lakes are dominated by large (>600 mm) lake trout (Johnson, 1972, 1976; M. E. McDonald, unpublished data) but 4.4 ha Lake N1 did not contain any fish greater than 550 mm and 1400 g prior to fertilization. There is a general trend for smaller lake trout (<400 mm) to constitute a larger proportion of the total population in smaller lakes (Burr, 1990).

One hypothesis to explain the loss of recruitment in Lake N1 is that high predation rates by adult lake trout and burbot (*Lota lota*) may have

eliminated fish <200 mm from the population. During fertilization, increased food availability resulted in higher growth for lake trout and high primary productivity greatly reduced visibility (Fig. 1). Small fish (<200 mm) developing during this period may have been at reduced risk to predation, even though there were more large (>500 mm), potentially piscivorous, lake trout in the population. In the first summer post-fertilization, visibility returned to pre-fertilization levels thereby increasing the vulnerability of small fish to predation. Young-of-the-year and juvenile lake trout may have been forced back into the physical refugia of rock crevices, resulting in lower growth rates. It is possible that lake trout in Lake N1 were successfully spawning throughout the experiment but the young produced in 1993–1995 were eaten by adults during the post-fertilization period, before they reached the catchable size-class.

The most likely hypothesis to explain the loss of lake trout recruitment involves hypoxic conditions that developed during fertilization. Lake trout spawn in the fall over clean rocky substrate and the eggs over-winter in interstitial spaces in the reef (Martin & Olver, 1980). Salmonid eggs can be killed by burial in sediment or from hypoxic conditions resulting from decomposition of organic matter in sediment (Sly, 1988; Ventling-schwank & Livingstone, 1994; Casselman, 1995; Manny et al., 1995). The distribution of lake trout and other salmonids is limited by oxygen availability (Ryan & Marshall, 1994) and hypoxia has been implicated as a major factor responsible for recruitment failure of lake trout and other salmonids in other lakes undergoing eutrophication (Tanner, 1952; Schindler et al., 1974; Casselman, 1995; Cornelius et al., 1995; Manny et al., 1995; Noakes & Curry, 1995; Evans et al., 1996). During fertilization of Lake N1, high deposition of organic matter onto the spawning grounds may have resulted in increased biological oxygen demand and subsequent death of over-wintering lake trout eggs.

Fertilization of Lake N1 resulted in hypoxia in the hypolimnion during summer stratification and ultimately throughout the water column in winter. Prior to nutrient enrichment, the hypolimnion was oxygen rich (Fig. 2). As fertilization progressed, a hypoxic layer developed on the bottom and expanded upward each summer. In 1993 and 1994,

the upper boundary of the low oxygen layer approached the thermocline. In addition to creating a thick hypoxic layer during the summer, winter hypoxia became more pronounced. In 1993 and 1994, measurements taken before ice out showed low oxygen levels (<6 mg/l) throughout the water column. This indicated that respiration occurring throughout winter was further depleting oxygen. After fertilization ended, winter hypoxia no longer occurred and summer hypoxia declined. The year-classes with failed recruitment, 1993 through 1995, would have been produced during the worst years of hypoxia in Lake N1.

Although we experimentally fertilized Lake N1, lakes in the arctic may soon experience nutrient enrichment through the effects of global warming. Current models predict global warming to have great effects on arctic ecosystems (Oechel et al., 1997). Global warming models predict the mean air temperature will increase 3–6 °C (e.g. Lachenbruch & Marshall, 1986; Schlesinger & Mitchell, 1987; Grotch, 1988; Abelson, 1989) resulting in a thicker active layer (i.e., soil above permafrost) (Kane et al., 1991; Chapin et al., 1995). Rastetter (1996) predicts that nutrients currently bound in permafrost will be released and eventually be transported to aquatic ecosystems. In addition, increased epilimnetic water temperatures associated with global warming would also have negative effects on bioenergetics of juvenile and YOY lake trout (McDonald et al., 1992, 1996). The combined effects of increased epilimnetic temperatures and increased nutrient inputs will most certainly have negative effects on lake trout populations.

Nutrient addition has been used as a fisheries management tool to increase fish production and to restore production in lakes experiencing oligotrophication. Some lakes that historically received nutrient inputs from the marine environment through anadromous salmonids have become nutrient poor as salmonid populations declined. Other lakes may have lost nutrients due to fish harvest. Fertilization has been successfully used to replace nutrients in such lakes and has resulted in increased growth and survivorship of juvenile salmonids (Nelson, 1958; LaBrasseur et al., 1978; Stockner, 1987; Kyle et al., 1997).

Although we detected increased lake trout growth during the fertilization period, long-term damage to the population, through the loss of

recruitment or winter-kill, may out-weigh the short-term benefits. Alternating between short (1–2 year) fertilization periods and extended recovery periods (3–5 years), may be successful in stimulating fish growth while avoiding the hypoxia problems we experienced during our 5-year fertilization period. The different responses of Lake N1 and Lake N2 (Hershey, 1992), where nutrients were added at a higher loading rate yet response from the biota was weaker than in Lake N1, indicate that there is great variability in the response of arctic lakes to fertilization. Lakes should be individually assessed for susceptibility to fertilization before any management plan including fertilization is implemented.

### Conclusions and implications

We have shown that arctic lakes can exhibit a strong bottom up response to increased nutrient loading. Primary production, snail density, and zooplankton density increased after fertilization. Lake trout, the top predator in many arctic lakes, had higher growth and larger mean size after the fertilization. Indirect effects, either mediated by predation, hypoxic conditions, or a combination of the two, resulted in low recruitment of young lake trout to the catchable size-class. Eutrophication may threaten the existence of lake trout populations in small arctic lakes. Although our fertilization period ended before winter-kill occurred in Lake N1, extended periods of fertilization and associated hypoxic conditions during ice-cover, could extirpate lake trout populations. Arctic lakes are very nutrient limited and may be endangered by development in the arctic, global warming, or intentional fertilization of lakes in an attempt to stimulate fish production.

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