

# Comparisons of Phytoplankton and Epilithic Algae of Selby Lake – Gates of the Arctic National Park and Preserve, Alaska

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## ABSTRACT

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Selby Lake in Gates of the Arctic National Park and Preserve was assessed as oligotrophic due to measurements of low nutrient concentrations and resultant low planktonic biomass as total chlorophyll. An orthograde oxygen profile in early summer also indicated an oligotrophic condition. Total nitrogen averaged about  $0.4 \mu\text{g} \cdot \text{L}^{-1}$  and total phosphorus about  $4 \mu\text{g} \cdot \text{L}^{-1}$ , resulting in a TN:TP ratio of about 100, which indicated the planktonic algae were probably limited by phosphorus. Nutrient stimulation bioassays confirmed this. Nitrogen alone was not stimulating to plankton algal growth, but nitrogen and phosphorus added together in the bioassays stimulated growth more than just phosphorus, as is often found in oligotrophic lakes. Aerial observation of Selby Lake and similar nearby lakes had indicated that epilithic benthic algal biomass was probably relatively high because the extensive shallows were visibly green. When recent growth in the ice-scour zone ( $< 2 \text{ m}$ ) was sampled in early July, the whole lake average standing crop of epilithic algae was estimated as approximately equal to the whole lake standing crop of phytoplankton. Biomass was greater near inlets than away from inlets. Epilithic algal biomass varied inversely with the temperature of inlets and directly with the inlets' total nitrogen concentration. Root zone fixation of atmospheric nitrogen by alders may be the source of N in the enriched inlets, and cold inlets probably plunge to the lake bottom, bathing the epilithic algae with nutrients. The importance of benthic algae in clear-oligotrophic lakes with extensive shallows need to be recognized.

Key Words: phytoplankton, epilithic algae, arctic lake, nitrogen, phosphorus.

Algal biomass of arctic lakes is relatively unstudied, despite the existence of thousands of arctic lakes in the Nearctic (Hobbie 1980). The few published studies of phytoplankton of U.S. arctic lakes (Hobbie 1964, Hobbie et al. 1972, Miller et al. 1986) found peak biomass as chlorophyll was typically  $< 3 \mu\text{g} \cdot \text{L}^{-1}$ . Nutrient stimulation experiments with arctic lake phytoplankton indicated phosphorus limitation (Hobbie 1980, Jones et al. 1990), nitrogen limitation (LaPerriere and Jones 1991), and phosphorus and nitrogen co-limitation (Miller et al. 1986) in various lakes.

Benthic algal production and biomass in these systems can be large relative to that of phytoplankton

(LaPerriere and Jones 1991). At the Barrow (AK) ponds, a production of  $14 \text{ g C} \cdot \text{m}^{-2}$  was measured for the benthic algae, in contrast to only  $1 \text{ g C} \cdot \text{m}^{-2}$  for phytoplankton (Hobbie 1984). Aerial observations of very clear Alaska lakes revealed visible rings of benthic algae (LaPerriere and Jones, 1988, pers. obs.). While studying the phytoplankton of Itkillik Lake in 1989, LaPerriere and Jones (1991) made a rough estimate of the relative biomass of benthic algae, measured the biomass of the phytoplankton, and found nearly equal amounts per square meter of entire lake area. These preliminary calculations suggested that benthic algae could be an important source of carbon in these oligotrophic

systems and are not routinely measured in trophic state assessments.

Little is known about controlling influences on benthic algae (Lowe 1996). In Quebec Eastern Township lakes, Cattaneo (1987) found a significant relation between total phosphorus (TP) sampled in the littoral and benthic algal cell volume but not with chlorophyll content. Her greatest standing crop averaged slightly under  $100 \text{ mg chl a} \cdot \text{m}^{-2}$ . She made no nitrogen measurements at sampling sites but suspected that nitrogen might be related to benthic algal growth, especially in lakes with low total nitrogen (TN) to TP ratios. In a temperate lake (Lake Chelan, WA) benthic algae study, Jacoby et al. (1991) found a strong relation between soluble reactive phosphorus and benthic algal biomass at the sampling site, suggesting the importance of local nutrient enrichment on benthic algal growth. Loeb and Reuter (1981), in a study of five oligotrophic temperate lakes, found the dominant epilithic periphyton were non-nitrogen fixers (in contrast to those of the sublittoral zone) and "appear to depend on external nitrogen sources for their production."

Selby Lake on the south slope of the Brooks Range in northwestern Alaska provided an ideal setting for

comparing lake algae in these two compartments for standing crop and controlling influences. Selby Lake has extensive shallows (Fig. 1) that provide habitat for benthos. Over 40% of the lake area is  $< 8 \text{ m}$ .

## Methods

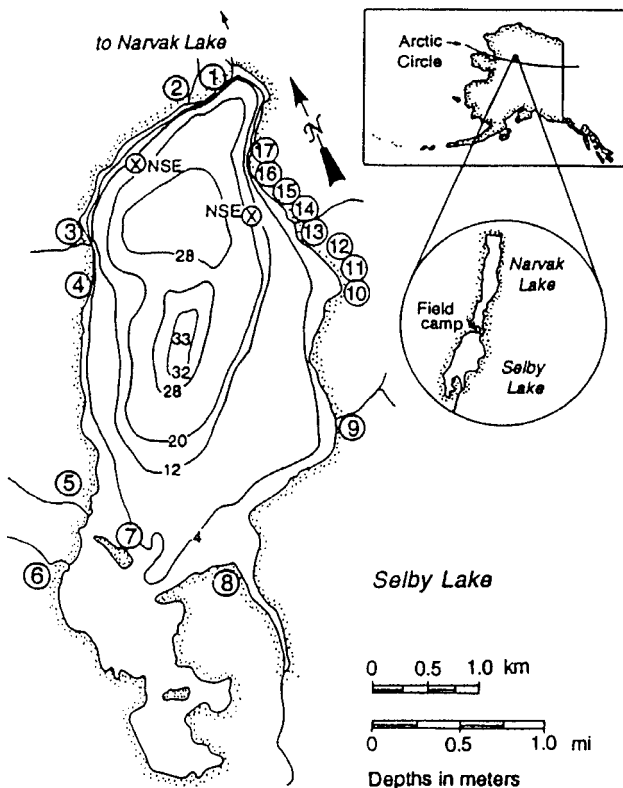
### *Site Description*

Selby Lake ( $66^{\circ}52'N$ ,  $155^{\circ}40'W$ ) is located on the south-facing slopes of the Brooks Range in Gates of the Arctic National Park and Preserve. It lies at an altitude of about 145 m in the upper Kobuk River drainage and is thought to have been formed by retreat of the Itkillik I glaciation more than 65,000 years B.P. (Reanier and Anderson, undated). The lake occupies  $10.2 \text{ km}^2$ , and the watershed, which includes Narvak Lake ( $8.6 \text{ km}^2$ ), is  $280.9 \text{ km}^2$  (the watershed of Narvak Lake is  $234.3 \text{ km}^2$ ). The Angayucham Mountains influence the morphometry of the upper, deeper part of Selby Lake ( $Z_{\text{max}} = 28 \text{ m}$ ) (Reanier and Anderson, undated). The lake is impounded by a moraine to the south [David Swanson (1997), University of Alaska Fairbanks, pers. comm.].

### *Pelagic Conditions and Phytoplankton*

Phytoplankton sampling on Selby Lake was conducted on July 8, 1993. Discrete samples were collected for chlorophyll and nutrient analyses using a 2-L Van Dorn sampler on a marked wire-line. These samples were emptied into 1-L cubitainers and placed in a cooler until they could be prepared for analyses. Dissolved oxygen and temperature profiles were measured with a YSI Model 56 dissolved oxygen meter (air calibrated). On July 21, 1993, the lake was again sampled during a synoptic survey of lakes in Gates of the Arctic National Park and Preserve. Profiles of temperature and oxygen were taken with a YSI 3800 multimeter, and integrated nutrient and phytoplankton samples were taken with a weighted 13-mm (i. d.) Tygon tube lowered to twice the Secchi depth. All samples for planktonic chlorophyll analysis were prepared by filtering 1-L samples through a Gelman GF/C glass-fiber filter and were stored over desiccant until processed at the laboratory for chlorophyll.

Triplicate samples for total and dissolved N and P were placed into acid-washed screw-cap culture tubes at the field laboratory; nitrogen samples were preserved with  $20 \mu\text{L}$  of 50% sulfuric acid per 10-mL sample. Filtrate from the chlorophyll test (GF/C filters) was used to measure total dissolved N and P. All nutrient



**Figure 1.**—Bathymetry of Selby Lake, Gates of the Arctic National Park and Preserve, Alaska (after Reanier and Anderson, undated). Circled numbers are locations of sites sampled for periphyton and water quality characteristics, July 1993. Sites of nutrient stimulation experiments are marked NSE.

samples underwent persulfate digestion at the laboratory, and the molybdate blue species of phosphorus produced in the ascorbic acid method (Prepas and Rigler 1982) was read on a Milton Roy 1201 spectrophotometer. Nitrogen was read as nitrate directly on the persulfate-digested samples by the second-derivative spectroscopy method of Crumpton et al. (1992).

Chlorophyll filters from planktonic samples were extracted in hot ethanol (Sartory and Grobbelaar 1984), and samples were analyzed for total chlorophyll (i.e., not corrected for phaeopigments) on a fluorometer (Knowlton 1984). Secchi disk transparency was measured using a standard 20-cm weighted disk of alternating black-and-white quadrants.

### *Nutrient Stimulation Experiments*

Lake planktonic algal stimulation bioassay experiments were conducted at two locations on Selby Lake (Fig. 1) in early July 1993. Near-surface water was placed into 10-L cubitainers. Triplicate containers were treated with nitrogen (adding  $75 \mu\text{g} \cdot \text{L}^{-1}$  using ammonium nitrate), with phosphorus (adding  $5 \mu\text{g} \cdot \text{L}^{-1}$  using sodium orthophosphate), with both nitrogen and phosphorus together at the above concentrations, and with no nutrient additions as controls.

The cubitainers were attached to an anchored, buoyed line at one-half of the Secchi depth (4 to 5 m) and allowed to incubate at ambient conditions for 4 or 5 days. When retrieved, the cubitainers were returned to the field laboratory in dark containers, and replicate samples were immediately filtered through GF/C glass-fiber filters and treated as all other planktonic chlorophyll samples.

### *Littoral Conditions and Epilithic Algae*

Sites for epilithic algae sampling on Selby Lake (Fig. 1) were accessed July 8-13, 1993. Positions were located with a Sony Pyxis global positioning system and marked on a topographic map (1:63,360). At each inlet site, the inlet flow was estimated from the width, average depth, and an estimate of surface velocity. Temperature and pH were measured at the mouth of inlets, and in the littoral area of sites without inlets, using a Ciba-Corning Checkmate handheld meter. Grab samples were taken within inlets or in littoral areas of non-inlet sites in 1-L cubitainers for cation and nutrient analyses and into 100-mL Nalgene bottles for color and turbidity analyses. Water samples were placed in an insulated cooler for storage until analyzed or prepared for analysis back at the field camp. Apparent color (unfiltered) was read on a HACH test kit (Model CO-1), and turbidity

was read on a HACH Model 16800 Portablab-turbidimeter (nephelometer). Field preparation of nutrient samples and their analyses were conducted as described above for phytoplankton work. Cation samples were poured into 60-mL acid-washed polypropylene bottles and acidified with 0.1 mL of 50% sulfuric acid. Major cations were analyzed by flame spectroscopy at the laboratory.

Epilithic algae samples were taken near 11 of 14 inlet sites and at 3 additional non-inlet sites on Selby Lake (Fig. 1). Inlet Site 5 was not sampled because it was scoured from high flow with sand flowing from the inlet. The blue line on the topographic map between our Sites 13 and 14 was not a single channel as shown, but instead there was diffuse flow through the shoreline gravels from Sites 11 through 17. There was negligible inlet flow at Sites 13 and 14, and they were not sampled. These samples were taken by a skin-diver (wearing a dry suit) who randomly chose 7 to 12 rocks from the bottom and swam pairs of them to shore, holding them upright. All epilithic algae samples were collected in the zone where the water depth was 0 to 2.2 m – where we expected only new seasonal growth because of scour of the bottom by moving ice during breakup (Hobbie 1973). Algal growth was observed to extend out from shore to approximately 8 m water depth, but depths past 2.2 m were not sampled because of the difficulty of free-diving much past 2 m.

Chlorophyll samples were removed from an area  $4.5 \times 10^{-4} \text{ m}^2$ , delineated by pressing a U.S. 25¢ coin to the rock and scrubbing all surrounding algae away with a brush and squirt bottle. Then the delineated spot of algae was brushed and washed onto a glass-fiber GF/A-E filter and vacuum filtered at less than 20 cm of mercury using a hand pump. One milliliter of saturated  $\text{MgCO}_3$  was added to the water in the filtration head to help keep the sample alkaline. Filters were stored over desiccant in opaque airtight containers until brought to the laboratory, where they were frozen until analyzed. Filters were ground in 90% (v/v) acetone and analyzed by spectrophotometry using the trichromatic formulae (APHA et al. 1989). Because we could not freeze samples in the field, we could not correct total chlorophyll to true chlorophyll by measuring and subtracting phaeopigments on samples that might have had inactive and dead algal cells.

## Results

### *Pelagic Conditions and Phytoplankton*

Selby Lake had a thermocline on July 8, 1993, but this had disappeared 2 weeks later when the lake

warmed during an unusually hot period (Fig. 2). In both profiles, dissolved oxygen was orthograde, or at least nearly uniformly distributed with depth, showing the oligotrophic condition of this pristine waterbody. Nutrient and chlorophyll profiles conducted on July 8, 1993 (Fig. 3), showed higher phytoplankton concentration at about 8 to 14 m depth (a metalimnetic peak). Lower temperatures may also explain greater dissolved

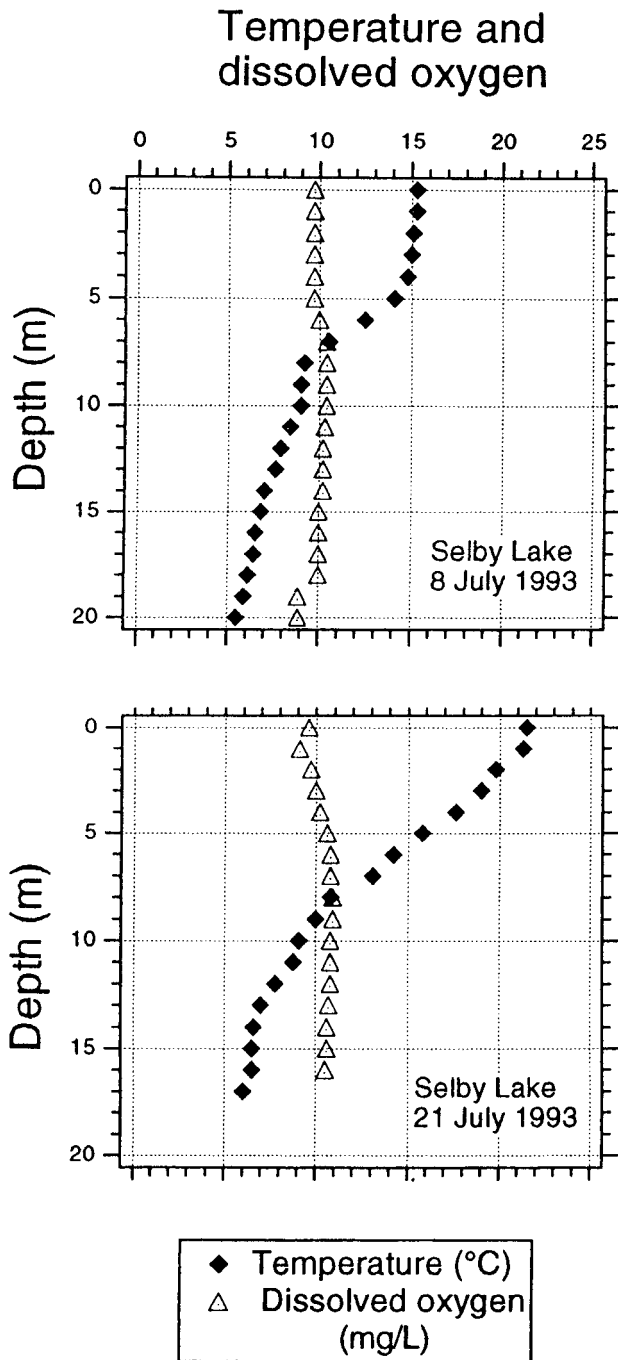


Figure 2.—Profiles of temperature and dissolved oxygen, Selby Lake, Gates of the Arctic National Park and Preserve, Alaska, July 1993.

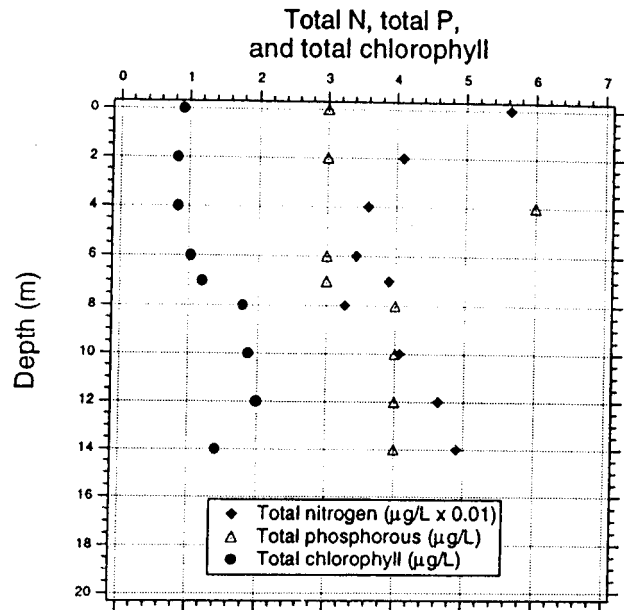


Figure 3.—Nutrient—total N and total P, and total chlorophyll profiles of Selby Lake, Gates of the Arctic National Park and Preserve, Alaska, July 8, 1993.

oxygen between 4 to 15 m on July 21, 1993 (Fig. 2). Total phosphorus and total nitrogen also increased at or near this metalimnetic chlorophyll maximum (Fig. 3). When corrected for the area of lake underlain by particular depths, the whole lake density of phytoplankton was  $14 \text{ mg} \cdot \text{m}^{-2}$  as total chlorophyll in Selby Lake.

Near-surface concentrations of nutrients and chlorophyll (Table 1) at the start of nutrient stimulation bioassay experiments (NSEs) were similar to those obtained for the depth profile (Fig. 3) performed between the two NSE sites. When depth-integrated samples were taken 2 weeks later at the northeast end of Selby Lake during a synoptic survey of lakes in Gates of the Arctic National Park and Preserve, conditions were still similar. At that time chlorophyll *a* averaged  $1.31 \pm 0.02$  (mean  $\pm$  1 std. dev.) ( $n = 3$ ), TN averaged  $374 \pm 229$  ( $n = 3$ ), and TP averaged  $4 \pm 2 \mu\text{g} \cdot \text{L}^{-1}$  ( $n = 3$ ).

### Nutrient Stimulation Experiments

Phosphorus limitation of the phytoplankton was indicated by large TN:TP ratios ( $\geq 100$ , Table 1), and this finding was confirmed by the results of nutrient stimulation bioassay experiments (Table 2). When nitrogen and phosphorus were added together, there was additional stimulation above that achieved with phosphorus alone. This secondary response to nitrogen probably resulted from ammonium being the cation in the nitrogen additions (Knowlton and Jones 1996).

**Table 1.**—Initial conditions for nutrient stimulation experiments, Selby Lake (July 7-8, 1993), Gates of the Arctic National Park and Preserve, Alaska.

Location	TN ( $\mu\text{g} \cdot \text{L}^{-1}$ )	TP ( $\mu\text{g} \cdot \text{L}^{-1}$ )	TN:TP	chl ( $\mu\text{g} \cdot \text{L}^{-1}$ )	Secchi (m)
Selby N	350	2	175	1.0	8.5
Selby E	314	3	105	1.8	8.8

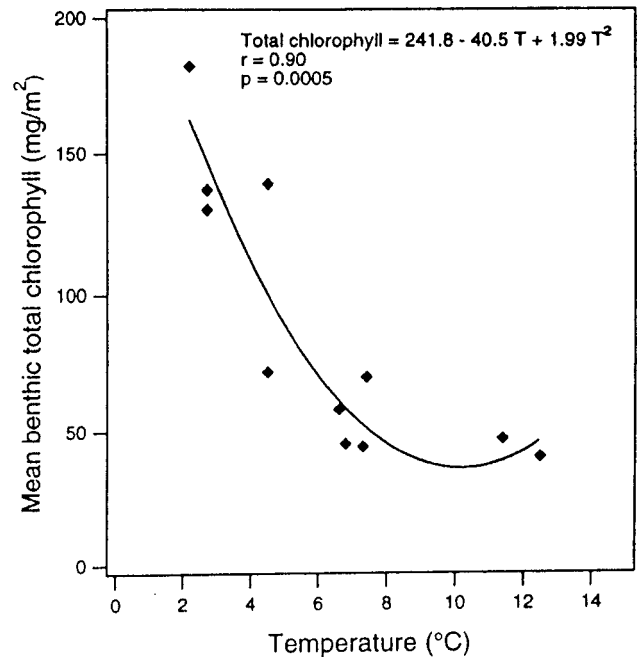
### *Littoral Conditions and Benthic Algae – Selby Lake*

Biomass of periphyton (as total chlorophyll) was quite variable with the standard deviation of values at a site equal to 45 to 112% of the mean. Median values of sites located near inlets ranged from 28 to 178  $\text{mg} \cdot \text{m}^{-2}$  and averaged 70  $\text{mg} \cdot \text{m}^{-2}$  ( $n = 11$ ; Table 3), while median values at sites located away from inlets ranged from 29 to 46  $\text{mg} \cdot \text{m}^{-2}$  and averaged 40  $\text{mg} \cdot \text{m}^{-2}$  ( $n = 3$ ). We estimated that about 75% of the littoral was not influenced by inlets; therefore, the weighted overall average (station median) periphyton density measured was 42  $\text{mg} \cdot \text{m}^{-2}$ . We assumed this value was conservatively representative of the lake to 8 m of depth, the visible extent of epilithic algae because chlorophyll was still increasing with depth at 2 m, where we stopped

**Table 2.**—Ratios of final to initial chlorophyll obtained from nutrient stimulation bioassay experiments in Selby Lake, Gates of the Arctic National Park and Preserve, Alaska (July 7-12, 1993). Results underlined by a continuous line are not significantly different by Duncan's multiple range test ( $\alpha = 0.05$ ). (C = control, +P = phosphorus added, +N = nitrogen added, +N & P = nitrogen and phosphorus added).

Selby North, July 7-12 (initial chl = 1.0 $\mu\text{g}/\text{L}$ )				
C	+N	+P	+N & P	
1.4	1.5	2.6	3.5	
Selby East, <sup>a</sup> July 8-12 (initial chl = 1.8 $\mu\text{g}/\text{L}$ )				
C	+N	+P	+N & P	
0.8	0.8	1.2	1.4	

<sup>a</sup>Eliminating an apparent outlier from each of the three replicates of two treatments resulted in the P-treatment at 140% of initial and the N & P treatment at about 160% of the initial chlorophyll. The multiple-range test then evaluates  $C = N < P = N \& P$ .



**Figure 4.**—Relation of mean epilithic algal biomass (as total chlorophyll) at inlet sites around Selby Lake and inlet temperature, July 1993.

sampling. When multiplied by the area of the lake subtended by the 8-m contour and divided by the area of the lake, the whole-lake average density was estimated as 20  $\text{mg} \cdot \text{m}^{-2}$  (as total chlorophyll), about equal to the standing crop estimate of phytoplankton.

Epilithic algae were at greater density near colder inlets (Table 3 and Fig. 4;  $r = 0.90$ ,  $p = 0.0005$ ) than near warmer inlets ( $n = 11$ ). The best single-variable model was with log-transformed temperature ( $r = 0.83$ ,  $p = 0.0009$ ). Patches of filamentous algae were seen near these cold inlets. Those inlets with greater epilithic algae density also had greater total nitrogen (Table 3 and Fig. 5;  $r = 0.62$ ,  $p = 0.0237$ ). No significant relation with total phosphorus and benthic algal density was found. Total nitrogen was not significantly correlated with inverse temperature.

In all but one inlet, total phosphorus measurements (Table 3) were greater than initial conditions at the lake surface at the start of nutrient stimulation experiments (Table 1). Most inlet total phosphorus values were greater than maximum measurements at various depths in the lake (Fig. 3), where they may simply have reflected the concentration of phytoplankton. Total nitrogen concentrations of the inlets were also mostly greater than initial conditions of the nutrient stimulation experiments, and half of the inlet concentrations were greater than maximum measurements at various depths in the lake.

**Table 3.—Inlet characteristics, Selby Lake, Gates of the Arctic National Park and Preserve, Alaska, July 8–13, 1993.**

Inlet	Mean Epilithic Algal Biomass (mg·m <sup>-2</sup> as chl)	pH	Temp. (°C)	Approximate Flow (ft <sup>3</sup> ·sec <sup>-1</sup> )	Color (units)	Turbidity (NTU)
2	45	5.35	6.8	4.0	11	0.34
3	70	6.81	7.4	40	<1	0.53
4	58	6.63	6.6	0.1	120	0.40
5	— <sup>a</sup>	5.62	6.8	53	13	0.33
6	47	6.57	11.4	4.0	27	0.26
9	40	6.77	12.5	1.5	89	0.60
10	44	6.58	7.3	0.6	44	0.16
11	130	6.94	2.7	4.0	19	0.22
12	139	6.87	4.5	4.5	11	0.04
15	182	6.74	2.2	1.5	14	0.10
16	137	6.62	2.7	1.5	17	— <sup>b</sup>
17	72	6.57	4.5	4.0	63	0.40

<sup>a</sup> no samples taken because of scouring and sand and gravel deposition from inlet

<sup>b</sup> dash means datum not measured

Inlet	TP (µg·L <sup>-1</sup> )	TN (µg·L <sup>-1</sup> )	TN:TP	Ca (mg·L <sup>-1</sup> )	Mg (mg·L <sup>-1</sup> )	K (mg·L <sup>-1</sup> )	Na (mg·L <sup>-1</sup> )
2	7	277	40	1.70	0.74	<0.01	0.61
3	3	127	42	1.42	0.58	0.03	0.42
4	8	550	69	2.96	1.28	<0.01	0.55
5	5	173	35	2.08	0.96	0.06	0.48
6	5	633	127	4.62	1.91	0.14	0.64
9	12	403	34	18.8	3.46	0.04	1.87
10	5	380	76	35.9	4.52	0.10	4.22
11	5	797	159	7.44	2.84	0.20	0.66
12	6	1067	178	7.74	2.35	0.20	1.44
15	5	727	145	8.31	2.27	0.16	1.63
16	4	587	147	6.70	3.15	0.12	1.34
17	4	457	114	6.14	2.27	0.06	1.08

## Discussion

The oligotrophic condition typical of most arctic lakes (Hobbie 1964, 1984) was displayed in Selby Lake by the orthograde dissolved oxygen profiles and by the low nutrient and plankton biomass concentrations. Low nutrients in arctic lakes are the result of decreased weathering due to cold temperatures and particularly to the permafrost (Welch and Legault 1986) that is

continuous in the watershed outside the thaw bulb of the lake (Brewer 1958).

The biomass of phytoplankton of Selby Lake was low and comparable to published estimates for other oligotrophic arctic lakes (Hobbie 1973, 1984; Miller et al. 1986; Jones et al. 1990; Kling et al. 1992). Surface concentrations of plankton chlorophyll, which were determined for nutrient stimulation experiments, however, would be somewhat low for representing whole lake conditions. Because of the prevalence of

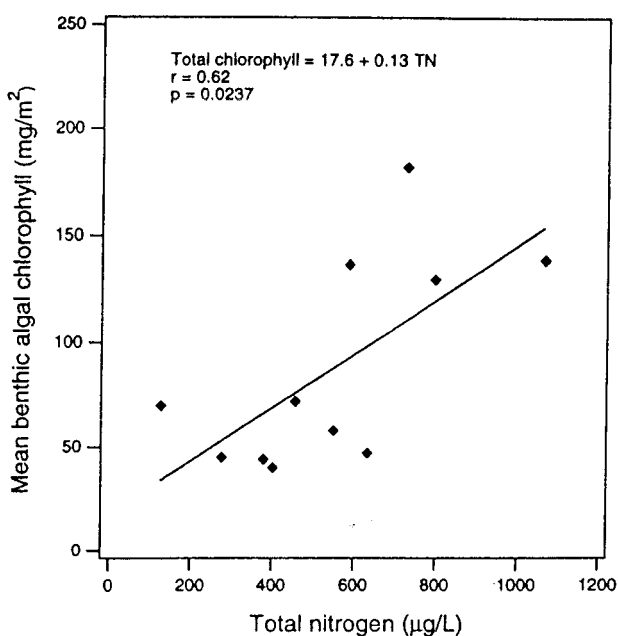


Figure 5.—Relation of mean epilithic algal biomass (as total chlorophyll) at inlet sites around Selby Lake and total nitrogen in the inlet, July 1993.

deep chlorophyll peaks in arctic lakes in general (Miller et al. 1986, Jones et al. 1990, LaPerriere and Jones 1991) and in Selby Lake (Fig. 3), the synoptic survey measurements of algal biomass in lakes of Gates of the Arctic National Park and Preserve were measured with an integrating tube sampler (Hanna and Peters 1991) after 1992.

The phytoplankton of Selby Lake was phosphorus limited. This was expected from the high nitrogen to phosphorus ratio measured. Given the high TN:TP values in this lake, the secondary response to N was not expected. It may have been in response to ammonium additions rather than a shortfall of N (Knowlton and Jones 1996). Similar experiments in nearby Walker Lake (Jones et al. 1990) using potassium nitrate did not result in a secondary response to N. Because of the oligotrophic nature of this lake, it is presumed that the sediments do not become anoxic, even during the long duration of the ice cover of arctic winter; therefore, sediments do not release phosphorus after sedimentation. This condition was measured at Toolik Lake in the Arctic Foothills of the north side of the Brooks Range (Cornwell 1987). We have recently observed that arctic lakes with bare rock slopes at the water's edge receive large amounts of fine sediment with adsorbed phosphorus during snowmelt. We have also observed that this snowmelt sediment settles out within a week or so. In the shallowest lakes, however, especially those on the Arctic Slope and in the Arctic Foothills, sediment is resuspended by mixing when associated

with frequent windstorms. There, nitrogen may be limiting.

The benthic algal biomass was approximately equal to the phytoplankton biomass when both were expressed as average concentrations over the whole lake area. This is undoubtedly due to the relatively gentle slope of the euphotic zone of Selby Lake as well as to the high clarity of the water and resultant deep light penetration (Lundgren 1978). Benthic algae represent a functional zone not routinely measured in lake studies (Lowe 1996), nor is this compartment considered in lake trophic state assessments. Data from Selby Lake suggest benthic algal biomass can be quantitatively important in shallow arctic lakes with low fertility and resultant high clarity, and that phytoplankton biomass measurements would greatly underestimate the areal biomass of algae. Canfield et al. (1983) demonstrated the importance of nutrients and carbon associated with macrophytes in determining the trophic state of macrophyte-dominated lakes in Florida as compared to classification of such lakes using only phytoplankton measurements from the open water.

The measured biomass of benthic algae of Selby Lake was high in comparison to literature values. Mean annual chlorophyll *a* on natural substrates from 2 m in Lake Tahoe (Loeb 1986) was approximately 19 mg · m<sup>-2</sup>, compared to about 42 mg · m<sup>-2</sup> from 0 to 2.2 m in Selby Lake. Jacoby et al. (1991) found benthic algae of oligotrophic Lake Chelan near the enrichment of nutrients from inlets at 0.5 m to average about 22 mg · m<sup>-2</sup> chlorophyll *a* in May and September 1987 and about 9 mg · m<sup>-2</sup> in July. Average concentrations calculated for the total area of Lake Taupo (Hawes and Smith 1994) were 0.3 to 2 mg · m<sup>-2</sup> compared to 20 mg · m<sup>-2</sup> over the whole surface area of Selby Lake. However, Lake Taupo is a large lake (more than 500 km<sup>2</sup>) and has an extensive surface area underlain by water too deep to grow benthic algae. Those depths in Selby Lake are under a small proportion of the lake's surface area. The lake immediately above Selby – Narvak Lake – was formed from a deeply glaciated valley ( $Z_{\max} = 114$  m). It was observed to have epilithic algae to the same depth as Selby Lake, but due to lake morphometry, it lies under little of the whole lake area and is relatively less important (LaPerriere, unpubl. data).

The distribution of benthic algae was uneven in the littoral of Selby Lake, being greater in the influence of inlets, and especially greater near colder inflows and those with elevated nitrogen. Correlation of water quality characteristics with benthic algal biomass led to speculation on the causes of the high concentrations observed near certain inlets. The inverse relationship of benthic algal biomass with temperature has been observed before in cold regions. Van Nieuwenhuysen

(1983) found an increase in subarctic stream benthic algal growth efficiency as temperatures fell late in the growing season. An Antarctic stream scientist (Hansson 1992) has also reported an inverse relationship between standing crop of benthic algae and temperature.

The direct relation of benthic algal standing crop with nitrogen concentration may be due to a phenomenon described at Toolik Lake. Whalen and Alexander (1986) speculated that the benthic algae rapidly utilized the nitrogen entering the lake from the surroundings that flowed in approximate to the sediments in spring. We observed that the few cold and nitrogen-rich inlets often were braided through gravels with thick alder (*Alnus crispus*) growth where they entered the lake. Alders support microrhiza in the root zone that fix atmospheric nitrogen. The inverse relation between temperature and local standing crop near inlets suggests physical delivery of nutrients by higher density cold water flowing along the lake sediments and plunging toward the bottom waters (Vincent et al. 1991). In the influence of cold inlets, benthic algal mats would be bathed by nutrients from the catchment, whereas in other regions of the littoral zone, benthic growth might largely rely on nutrient conditions in the sediments (Lowe 1996) and more weakly on those of the epilimnion.

Studies of colonizing epilithic algae in streams have shown a direct relation between nutrient conditions and biomass accrual (Lohman et al. 1991). At the time of our sampling, new growth of epilithic algae (as chlorophyll) was correlated with total nitrogen in the inlets, but not with total phosphorus. This empirical evidence for possible nitrogen limitation is consistent with observations in certain streams (Grimm and Fisher 1986, Lohman et al. 1991, LaPerriere 1995). However, given that the primary nutrient limiting phytoplankton was phosphorus, it raised the possibility that algae in the phytoplankton and in the benthos can be regulated by different elements within a single lake. Because the evidence is thus far only correlative, the nature of the reliance of benthic algae on nitrogen should be investigated experimentally (Pringle 1987).

The importance of benthic algae in the understanding of lakes has certainly been underemphasized to date (Lowe 1996). Heckey and Hesslein (1995) conclude from their stable isotope studies that top predators in temperate and arctic lakes were equally dependent on planktonic and benthic algal carbon. O'Brien et al. (1997) also concluded in their recent book chapter on the limnology of Toolik Lake that the fish community obtains most of its food from the benthic food web, which was attributed to the absence of forage fish. Overall, our findings suggest that epilithic algae might assume equal importance to planktonic algae in clear, arctic lakes with extensive shallows and

that they should be given additional consideration in the study of the importance and function of lake primary producers.

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