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Nutrient limitation of phytoplankton production in Alaskan Arctic foothill lakes

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Abstract

We used 54 enrichment bioassays to assess nutrient limitation (N, P) of ^{14}C uptake by natural phytoplankton assemblages in 39 lakes and ponds in the Arctic Foothills region of Alaska. Our purpose was to categorize phytoplankton nutrient status in this under-represented region of North America and to improve our ability to predict the response of primary production to anticipated anthropogenically mediated increases in nutrient loading. Experiments were performed across several watersheds and included assays on terminal lakes and lakes occupying various positions in chains (lakes in series within a watershed and connected by streams). In total, 89% (48 of 54) of the bioassays showed significant stimulation of ^{14}C primary production by some form of nutrient addition relative to unamended controls. A significant response was observed following enrichment with N and P, N alone and P alone in 83, 35 and 22% of the bioassays, respectively. In experiments where N and P proved stimulatory, the influence of N alone was significantly greater than the influence of P alone. Overall, the data point to a greater importance for N than P in regulating phytoplankton production in this region. The degree of response to N and P enrichment declined as the summer progressed and showed no relationship to irradiance or water temperature, suggesting secondary limitation by some micronutrient such as iron as the summer advanced. Phytoplankton nutrient status was often consistent across lakes within a watershed, suggesting that watershed characteristics influence nutrient availability. Lakes in this region will clearly show increased phytoplankton production in response to anthropogenic activities and anticipated changes in climate that will increase nutrient loading.

Introduction

The study of phytoplankton nutrient (N and P) deficiency is central to modern limnology (e.g., Schindler, 1988). Phosphorus is generally considered to limit phytoplankton production and standing crop in lacustrine ecosystems based on the robust relationship between P loading and lake trophic status derived from a largely temperate database (Dillon & Rigler, 1974; Schindler, 1978; Vollenweider, 1976) and the demonstrated control of phytoplankton standing stock and group composition by P in whole-lake nutrient enrichment studies (Schindler, 1977). However, a recent assessment of the published literature for nutrient enrichment experiments led Elser et al. (1990) to conclude that the P-paradigm was not universally applicable and that N limitation was more prevalent in oligotrophic North American lakes than previously believed.

Scarcity of data has previously excluded high latitude lakes from consideration in general models of nutrient deficiency. In particular, only Vincent and Vincent (1982a,b) and Priscu (1995) conducted detailed bioassay studies on phytoplankton nutrient limitation in Antarctic lakes. Moreover, the few previous studies in the Alaskan arctic include only short-term bioassays in coastal tundra thaw ponds (Kalff, 1971) and an Arctic Foothill lake (Toolik Lake) (Whalen & Alexander, 1986a), mesocosm experiments in Toolik Lake (O'Brien et al., 1992) and batch culture bioassays and

fertilization experiments in two Arctic Foothill ponds (McCoy, 1983). Results from arctic waters were variable, but simultaneous addition of N and P usually gave the best response in terms of increased phytomass or ^{14}C assimilation. However, frequent stimulation by N alone, but not P alone (Whalen & Alexander, 1986a) at least suggests that N cannot be discounted as the primary control on phytoplankton productivity in these characteristically oligotrophic lakes.

The Alaskan arctic will be heavily impacted by global change. General Circulation Models predict a 4°C increase in summer air temperature (Mitchell et al., 1993), while increased thawing of the permafrost has already been noted (Lachenbruch & Marshall, 1986). Moreover, a worldwide increase in atmospheric N deposition has resulted from agricultural intensification and fossil fuel combustion in developed countries (Galloway et al., 1995). Finally, increased recreational activity is expected with the recent public opening of the Dalton Highway, the only road in the Alaskan arctic. Accelerated slumping and erosion from thawed permafrost and recreational activity will increase N and P loading to lacustrine ecoystems via rivers and runoff, while N will be directly deposited to lake surfaces from the atmosphere.

Our current, incomplete understanding of nutrient limitation of phytoplankton production in Alaskan arctic waters and anticipated regional-scale changes clearly point to a need for a comprehensive regional assessment of the current nutrient status of lakes and ponds. Consequently, this study was aimed at extending the database for phytoplankton nutrient status to this under-represented region of North America and at providing information essential to improving predictive capabilities for the response of Alaskan arctic lakes to future climatic and anthropogenic influences. To meet these objectives, we conducted 54 short-term nutrient (NO_3^-, NH_4^+, urea-N, PO_4^{3-}) enrichment experiments on 45 lakes and ponds across several watersheds and occupying a variety of landscape positions. We attempted to relate nutrient status and the degree of response (percent increase in ^{14}C uptake relative to unenriched controls) to these variables as well as other environmental measurements (irradiance, temperature, ambient N and P concentrations).

Site description

The Toolik Lake region (68°N, 149°W) is located 20 km north of the Alaska's Brooks Range at about 750 m elevation (Fig. 1). Regional access is provided by the Dalton Highway, an undeveloped roadway which was constructed in conjunction with the trans-Alaska oil pipeline and currently serves as the only road in the Alaskan arctic. This area is typical of the 95 000 km^2 Arctic Foothills region of Alaska. Briefly, permafrost is continuous, the landscape is treeless, snow cover persists for 7–9 months, and rivers cease to flow during winter. Lakes and ponds are surrounded by tussock tundra, wet sedge tundra or dwarf shrub communities. Ridge tops and other well-drained sites are composed of drier heath tundra. The mean annual air temperature is −6°C, while precipitation averages 20 cm annually, with about 40% falling as snow (Ping et al., 1998). Regional physiography and vegetation physiognomy are fully described elsewhere (Wahrhaftig, 1965; Walker et al., 1994).

Materials and methods

Experimental

Bioassay experiments were performed across several watersheds and included assays on terminal lakes and lakes occupying various positions in chains (Fig. 1). The Toolik Lake watershed (I-Series, S-Series, Ne-Series, and E-1) was sampled most frequently. For the purpose of analyzing land cover trends, the Toolik Lake watershed was further divided between lakes which drain soils south of Toolik (I-Series) and lakes which drain soils southwest of Toolik (S-series including I-Swamp). The next most frequently sampled watershed included six lakes which flow into the Sagavanirktok River (Lakes GTH 60, 61, 74, 94, 96, and 97). Lakes GTH 99, 103 and 104 are all located within a third watershed that ultimately flows into the Itkillik River. Three watersheds which empty into the Sagavanirktok River were sampled twice (Island Lake and Galbraith Lake, Lakes GTH 108 and 109, and Fog Lakes 1 and 4). Another watershed sampled twice (Lakes E-5 and E-6) empties into the Kuparuk River. Lake GTH 110, which flows into the Toolik River, and Lakes GTH 42 and N-2 ,which both flow into the Itkillik River, were lone representatives of their respective watersheds. Finally, several terminal lakes were examined including S-1, S-2, S-4, N-1, GTH 98, and Exp. Lake. A total of 45 lakes and ponds were sampled. Toolik Lake (Fig. 1) was sampled on five occasions during the 1998 and 1999 field seasons. Lakes I-4, I-5, N2-R, N2-T, and E-1 were each sampled twice

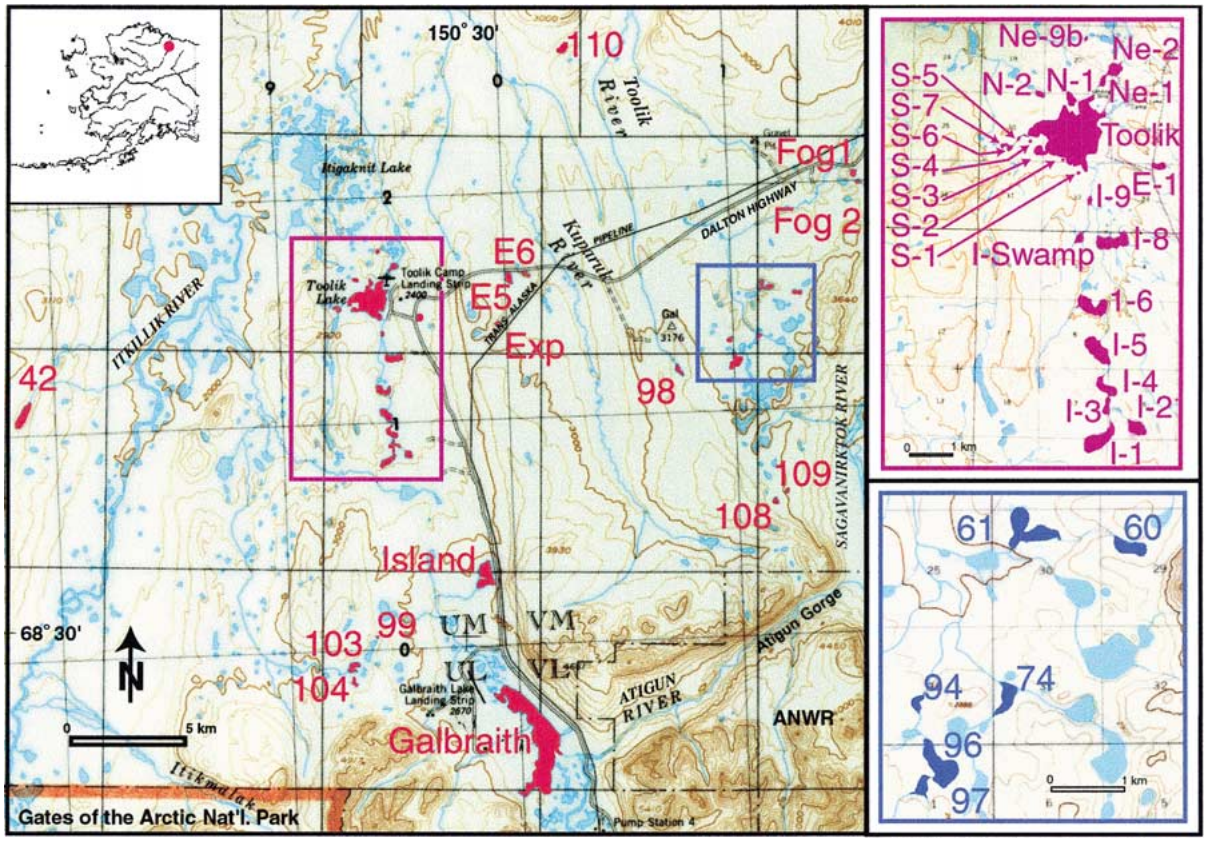

Figure 1. Location of the study site. Sampled lakes are named and highlighted.

and the other 39 lakes were sampled one time each. Toolik Lake and lakes within a 5-km radius were accessed by foot while more remote lakes were accessed by helicopter.

All lakes were sampled via an inflatable raft with the exception of Toolik Lake, which was sampled from an aluminum boat. Mid-lake samples from a depth of about 1-m and free of larger zooplankton (filtered through 210-μm Nitex mesh) were dispensed into clear, 1-l polyethylene carboys which were transported to the Toolik Lake Field Station in opaque polyethylene bags. Within 6 h of collection, carboys were amended with: (a) 3 μM KNO_3–N; (b) 3 μM NH_4Cl–N; (c) 3 μM $(NH_2)_2CO$–N; (d) 0.5 μM KH_2PO_4–P; (e) 3 μM NH_4Cl–N and 0.5 μM KH_2PO_4–P; or (f) no addition (control) such that each treatment was quadruplicated. Urea-N (treatment [c]) was included as a nutrient amendment because NH_4^+–N and NO_3^-–N concentrations were frequently at or below detection limits and urea-N can constitute a significant fraction of the total N uptake by marine (McCarthy et al., 1977) and fresh water (Mitamura & Saijo, 1985) phytoplankton. A shore-side incubator at Toolik Lake was used to acclimate the samples to the altered nutrient environment for 6 h at the surface lake temperature. A subsample from each carboy was then transferred into a clear, 73-ml polystyrene bottle and an additional subsample from one randomly selected carboy for each treatment was dispensed into an opaque bottle of similar size. Each bottle was then amended with 90 kBq $NaH^{14}CO_3$ (specific activity, 2.0 GBq mmol^{-1}) and all bottles were incubated for 24 h in a floating incubator located 50 m offshore in Toolik Lake. Both the shore-side and floating incubators were covered with neutral density screen to exclude 50% of surface irradiance. Experiments were terminated by filtration (<12 cm Hg) of the entire contents through Gelman Metricel GN-6 (0.45 μm pore size) cellulose ester filters. Following a 5-ml rinse with deionized water, filters were air-dried and assayed for radiocarbon incorporation into the particulate fraction by liquid scintillation spectrometry.

Assays for phytoplankton nutrient status are not standardized and all techniques are subject to criti-

cism (reviewed by Elser et al., 1990). Size and time scales range from bottle to whole lake and from hours to season while response is measured by ^{14}C uptake or change in biomass or community composition. Our experimental protocol represents a compromise among the availability of helicopter support, weight constraints in foot and air transport of samples and gear, the desire to process samples as rapidly as possible following collection, the capacity of our incubators and the goal of sampling as many lakes as possible. However, results given here are directly comparable to many previous studies, as short-term ^{14}C assimilation is one of the most commonly used community response variables (Elser et al., 1990)

Supporting physical, chemical and biological measurements were made on water collected from each lake. Alkalinity was determined potentiometrically using a Gran titration. Duplicate chlorophyll *a* (Chl *a*) determinations were made fluorometrically on filter-trapped (Gelman GFC glass fiber filters) particulate material extracted for 24 h in a 90% acetone solution buffered with $MgCO_3$ (Parsons et al., 1984). Samples for nutrient analysis were filtered (0.45-μm pore diameter), stored frozen, and later analyzed for NO_3^-–N (+ NO_2^-–N), NH_4^+–N and soluble reactive phosphorus (SRP) by automated flow injection analysis using the Cu–Cd reduction, phenol hypochlorite, and antimony-phospho-molybdate complexation methods, respectively (Parsons et al., 1984). The precision of repeated analyses (n=10) of all nutrients at a concentration of 0.2 μM N or P was <10%. All methods are described in detail in Whalen & Alexander (1986a).

Calculations and statistical analysis

Dissolved inorganic carbon concentrations were calculated from alkalinity determinations and temperature-corrected acidity constants (Stumm & Morgan, 1996), assuming infinite dilution. Inorganic carbon uptake was calculated as the difference between light and dark bottle estimates by applying an isotope correction factor of 1.06 (Wetzel & Likens, 1991).

The influence of nutrient additions on radiocarbon uptake within each experiment was evaluated by single factor analysis of variance. Multiple comparisons of treatment means were performed by Tukey's least significant difference procedure. Untransformed data in all cases satisfied assumptions of normality and homoscedasticity. Treatment responses were compared between lakes using paired *t*-tests. Relationships between variables were assessed by correlation or linear regression analysis. Statistical analysis was performed using the SPSS statistical package for personal computers. A significance level of α=0.05 was used for all tests.

Results

Biological and chemical analyses reflect the oligotrophic nature of arctic lakes and ponds. The concentration of dissolved inorganic nitrogen (DIN; NH_4^+–N plus NO_3^-–N) was generally low but highly variable (Table 1). The NH_4^+–N concentration was higher than NO_3^-–N concentration in 76% (41 of 54) of lake samples. Soluble reactive phosphorus was consistently below the analytical detection limit of 0.03 μM. Overall, the lakes were relatively shallow, showing an average maximum depth of about 9 m and including a number of small tundra ponds approximately 1 m deep. The Chl *a* concentration in 42 of 45 lakes was <3 μg l^{-1}, pointing to a generally low phytomass. Accordingly, ^{14}C assimilation was low in bioassay controls, ranging from 6 to 101 μg C l^{-1} day^{-1} and averaging 29 μg C l^{-1} day^{-1}.

Overall, 89% (48 of 54) of the bioassay experiments showed significant stimulation of ^{14}C primary production relative to controls by some form of nutrient enrichment (Table 2). A significant response was observed to N and P addition in 83% (45 of 54) of the bioassays. At least one form of nitrogen (NO_3^-–N, NH_4^+–N, or urea-N) proved stimulatory in 35% of the bioassays. Ammonium was the most effective nitrogenous nutrient, producing a significant increase in radiocarbon uptake in 28% of the bioassays. Urea-N was slightly less stimulatory, significantly enhancing phytoplankton production in 21% of the bioassays. Nitrate was stimulatory in 17% of the bioassays, but was tested on only 23 dates due to logistical constraints. Phosphorus enrichment gave significantly enhanced radiocarbon uptake in 22% of the bioassays. The degree of response, measured as the percent change in ^{14}C assimilation relative to unamended controls, was highly variable both among experiments and among treatments within an experiment. The maximum stimulation for each treatment was 41% for NO_3^-–N, 98% for NH_4^+–N, 54% for urea-N, 69% for PO_4^{3-}–P, and 258% for NH_4^+–N and PO_4^{3-}–P, with the average stimulation for each treatment indicated in Fig. 2. When the entire data were averaged, N and P was clearly the most effective treatment.

Table 1. Morphometric, chemical, and biological data for lakes in the Arctic Foothills region of Alaska. Nonmorphometric means (± 1 SEM) are reported for samples collected at 1 m. Data for lakes sampled on more than one occasion were averaged

Variable	Mean (SE)	Maximum	Minimum	*N*
Maximum depth (m)	8.8 (1.1)	33	1.0	43
Area (ha)	25.2 (13.7)	422	0.3	32
Alkalinity (meq l^{-1})	0.75 (0.09)	2.35	0.05	45
Temperature (°C)	13.7 (0.4)	17.5	5.0	45
pH	7.5 (0.1)	8.4	6.6	45
Chlorophyll *a* (μg l^{-1})	1.5 (0.1)	5.1	0.2	45
Primary production (μg C l^{-1} day^{-1})[a]	29 (3)	101	6.5	45
NH_4^+-N (μM)	0.55 (0.08)	2.70	b.d.[b]	45
NO_3^--N (μM)	0.34 (0.1)	4.90	b.d.	45
PO_4^{3-}-P (μM)	b.d.	b.d.	b.d.	45

[a]Primary production calculated from control bioassay bottles. [b]b.d.= below detection limit of 0.05, 0.05, and 0.03 μM for NO_3^-N, NH_4^+–N, and PO_4^{3-}–P, respectively.

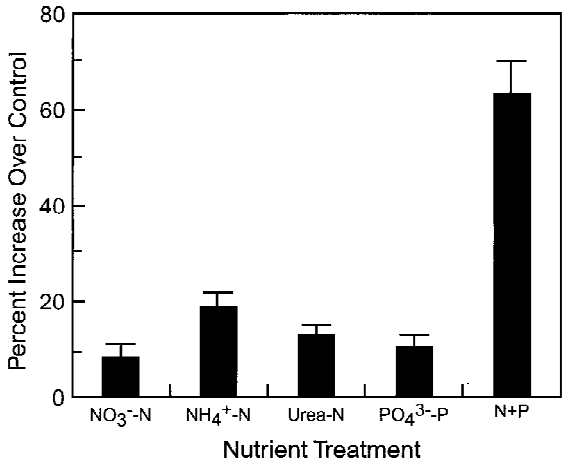

Figure 2. Average (±1 SEM) response of phytoplankton ^{14}C primary production to nutrient enrichment in 54 bioassay experiments performed in lakes in the Northern Foothills region of the Alaskan arctic.

Morris & Lewis (1988) have identified five distinct and interpretable responses that occur with respect to ^{14}C uptake by phytoplankton *relative to unfertilized controls* during nutrient enrichment bioassays: (a) no significant difference in ^{14}C uptake between the control and the treatments (no limitations); (b) increases *exclusively* in treatments simultaneously enriched with N and P (concurrent limitation; 'N&P'); (c) increases following separate applications of N alone *and* P alone (reciprocal limitation; 'N/P'); (d) increases in treatments containing P alone and not N alone (P limitation); and (e) increases in treatments containing N alone, but not P alone (N limitation). Within this context, concurrent limitation (N&P) was the most common response, occurring in 43% of the 54 bioassays (Table 2). Nitrogen limitation was indicated in 24% of the bioassays, while P limitation, reciprocal limitation and no limitation were each observed in 11% of the bioassays. Thus, N was a limiting factor in 78% of total experiments, either alone (N limitation) or in combination with P (N&P or N/P). This frequency distribution of nutrient status remained essentially unchanged when lakes that were sampled on more than one occasion were excluded from the analysis (Fig. 3).

Regional and watershed-scale analysis of the data showed several trends with respect to nutrient status of the phytoplankton communities. When all 54 experiments were considered, the degree of stimulation to the most favorable N source (NO_3^-–N, NH_4^+–N or urea-N) was significantly higher than that resulting from PO_4^{3-}–P enrichment, 23% versus 10%. Moreover, when only concurrently limited lakes were considered (n=22), the stimulatory effect of the most favorable N source remained significantly higher than the influence of PO_4^{3-}–P enrichment, 13% versus 1%. Lakes draining the southern portion of the Toolik watershed (I-Series) and the watershed which includes GTH Lakes 60, 61, 74, 94, 96, and 97 (Fig. 1) showed significantly higher responses to N than P enrichment. Lakes draining the western component of the Toolik watershed (S Series and I-Swamp) were predominately P-limited. Lakes classified as P-limited had significantly higher alkalinities (1.30 versus 0.67 meq l^{-1}) than lakes classified otherwise. Phosphorus limited lakes were also, as a group, relatively shallow.

Table 2. Phytoplankton nutrient limitation for lakes in the Arctic Foothills region of Alaska as determined by nutrient enrichment experiments. Categories of nutrient status include: concurrent limitation (N&P); nitrogen limitation (N); phosphorus limitation (P); reciprocal limitation (N/P); and no limitation (none). A significant increase in phytoplankton production relative to the control (no addition) is indicated by an asterisk (∗) associated with the treatment

Lake	Date	NO_3^-–N	NH_4^+–N	Urea-N	PO_4^{3-}–P	N&P	Status
Toolik	6/21/98					∗	N&P
Toolik	7/20/98		∗	∗		∗	N
Toolik	8/17/98					∗	N&P
Toolik	8/22/98					∗	N&P
Toolik	8/3/99	na[a]	∗	∗		∗	N
I-1	7/30/98					∗	N&P
I-2	7/24/98					∗	N&P
I-3	7/27/98					∗	N&P
I-4	7/11/98	na				∗	N&P
I-4	8/18/98					∗	N&P
I-5	8/8/98					∗	N&P
I-5	7/5/99	na	∗	∗	∗	∗	N/P
I-6	8/4/98					∗	N&P
I-8	7/14/98	∗	∗			∗	N
I-9	7/18/98					∗	N&P
I-Swamp	8/13/98				∗	∗	P
S-1	6/28/98					∗	N&P
S-2	8/12/98					∗	N&P
S-3	7/7/99	na				∗	N&P
S-4	7/9/99	na				∗	P
S-5	7/9/99	na			∗	∗	P
S-6	7/2/98	∗			∗	∗	N/P
S-7	7/23/98				∗	∗	P
N-1	7/17/98		∗	∗		∗	N
N-2R	7/4/98		∗		∗	∗	N/P
N-2R	7/31/99	na				∗	N&P
N-2T	7/7/98	∗				∗	N
N-2T	7/31/99	na	∗	∗	∗	∗	N/P
Ne-1	7/27/99	na					none
Ne-2	7/27/99	na				∗	N&P
Ne-9B	8/2/98					∗	N&P
E-1	7/13/98					∗	N&P
E-1	6/28/99	na	∗	∗		∗	N
Exp	7/9/98	∗		∗		∗	N
E-5	7/11/99	na	∗			∗	N
E-6	8/3/99	na				∗	N&P
GTH 42	6/30/99	na				∗	P
GTH 60	6/29/99	na	∗	∗		∗	N
GTH 61	6/29/99	na	∗			∗	N
GTH 74	6/29/99	na				∗	N&P
GTH 94	6/22/99	na				∗	N&P
GTH 96	6/22/99	na				∗	N&P
GTH 97	6/22/99	na					none
GTH 98	6/24/99	na	∗	∗		∗	N
GTH 99	6/25/99	na					none
GTH 103	6/25/99	na	∗			∗	N
GTH 104	6/25/99	na					none
GTH 108	7/1/99	na					none
GTH 109	7/1/99	na				∗	N&P
GTH 110	7/1/99	na	∗	∗		∗	N
Island	7/13/99	na		∗	∗	∗	N/P
Galbraith	7/13/99	na	∗		∗	∗	N/P
Fog L. 1	7/28/99	na					none
Fog L. 4	7/28/99	na			∗		P

[a] na = not assayed.

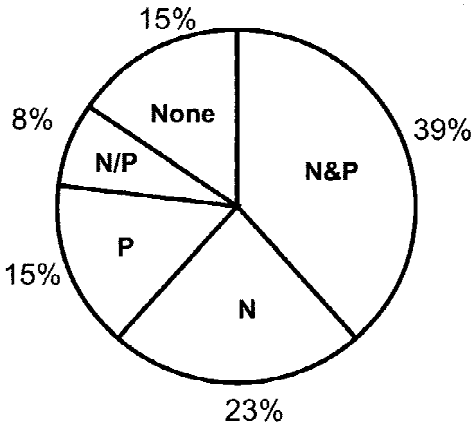

Figure 3. Frequency distribution for categories of nutrient limitation of phytoplankton production in 39 lakes in the Arctic Foothills region of Alaska where bioassay experiments were performed one time only. Categories include: concurrent limitation (N&P); nitrogen limitation (N); phosphorus limitation (P); reciprocal limitation (N/P); and no limitation (none).

All had a mean depth <4 m, except Lake 42 (33 m). The epilimnetic DIN:SRP ratio is commonly used as an indicator of nutrient limitation, but has limited utility in arctic lakes because inorganic nutrient concentrations are frequently at or below detection limits. Nonetheless, NO_3^-–N concentrations (most easily and accurately determined) showed a relationship to N-limitation. The average NO_3^-–N concentration was significantly lower in N-limited than other lakes (0.06 versus 0.43 μM).

Samples receiving the N&P treatment presumably become limited by some other environmental factor beyond N and P. However, physical factors were not limiting as the degree of stimulation from this treatment was independent of irradiance (r=0.01) and temperature (r=0.28) when the entire data were considered. Instead, results of time series bioassays in Toolik Lake suggest that the degree of the response to N&P enrichment may be seasonal. The stimulatory effect of N&P amendment progressively decreased throughout the summer while the lake was thermally stratified (Fig. 4a–c), but increased dramatically in mid- to late August as the thermocline approached the lake bottom or was destroyed (Fig. 4d–e).

Logistic constraints prevented repeated sampling of many lakes to assess seasonal differences in nutrient status of the phytoplankton communities. Accordingly, analysis of within-lake temporal trends was limited to Toolik Lake (above) and five lakes sampled on two dates (I-4, I-5, N2-R, N2-T, and E-1). Temporal deviations in nutrient limitation were evident in four

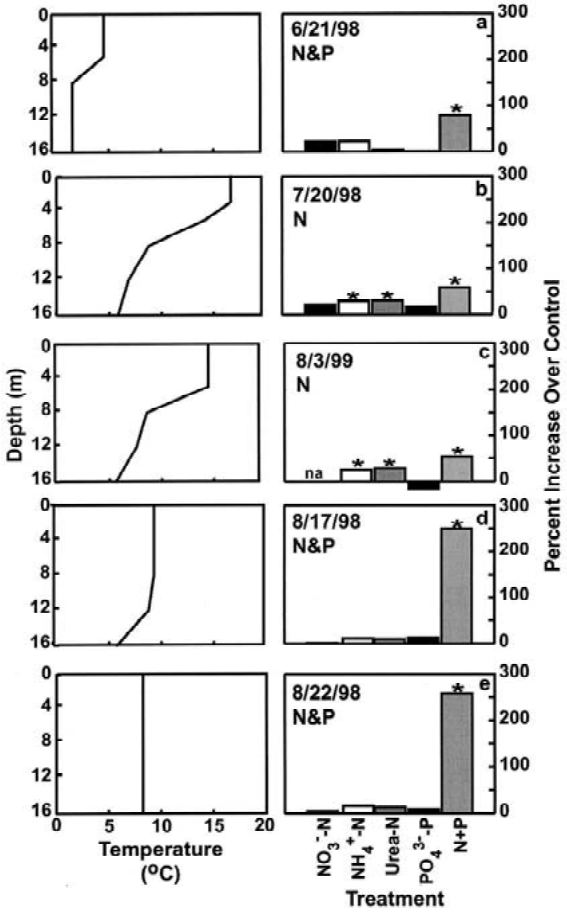

Figure 4. Influence of thermal regime (left panels) on nutrient bioassay responses (right panel) in Toolik Lake. Treatments showing significantly elevated ^{14}C primary production relative to controls are indicated by an asterisk (∗). The sample date and nutrient status are indicated within each panel.

of these five lakes (Table 3). Toolik Lake, sampled on five occasions, was concurrently limited on three sampling dates and N-limited on two (Fig. 4). In all of these cases of multiple (≥2) observations, stimulatory treatments always involved N addition.

Discussion

This study is one of the most comprehensive regional investigations of nutrient limitation to phytoplankton production. Remarkably, nutrient addition consistently stimulated phytoplankton production in lakes occupying a variety of landscape positions across several watersheds. Although supporting morphometric data are limited to mean depth and surface area, the

Table 3. Temporal changes in nutrient status of phytoplankton communities for lakes in the Arctic Foothills region of Alaska sampled on two dates. Categories of nutrient status include concurrent limitation (N&P), nitrogen limitation (N) and reciprocal limitation (N/P).

Lake	Observation 1	Time frame	Observation 2
I-4	N&P	Season	N&P
I-5	N&P	Year	N/P
E-1	N&P	Year	N
N2-R	N/P	Year	N&P
N2-T	N	Year	N/P

wide range of values for these parameters (Table 1) suggest highly variable hydraulic residence times and nutrient loading rates in the study lakes. Nutrient enrichment failed to significantly stimulate phytoplankton ^{14}C production in only six of the 54 experiments. Five of the six cases of no nutrient limitation occurred in headwater lakes, suggesting that nutrients from the watershed are quickly incorporated into the aquatic phytomass and become increasingly depleted as water progresses down a lake chain. Hough & Thompson (1996) similarly reported that nutrient availability (especially DIN) declined downstream in a chain of lakes in Michigan.

Bioassays most frequently indicated concurrent nutrient limitation (Fig. 3). Responses that meet the definition of concurrent limitation have been reported previously in temperate regions (Axler et al., 1994; Dodds & Priscu, 1990; Morris & Lewis, 1988; Suttle & Harrison, 1988; White & Payne, 1977; White et al., 1985) and are common in oligotrophic systems (Dodds et al., 1989). Concurrent limitation is indicative of extreme shortages of both N and P (White & Payne, 1977) and represents a situation in which cellular N:P ratios are near critical values for a large proportion of the phytoplankton community (Morris & Lewis, 1988). Phytoplankton assemblages composed of a relatively small number of closely related species with similar N and P kinetic abilities are most likely to exhibit concurrent limitation (Morris & Lewis, 1988). Low concentrations of dissolved inorganic nutrients (Table 1) and low and seasonally invariant kinetic constants for DIN assimilation in arctic phytoplankton assemblages (Whalen & Alexander, 1986b) are consistent with the observed prevalence of concurrent nutrient limitation in these lakes.

The role of N limitation was greater than anticipated. Nitrogen was limiting or co-limiting (N&P, N/P) in 78% of all experiments. Additionally, the degree of stimulation following nutrient addition was significantly greater in N-enriched than in P-enriched bioassays. Typically, N limitation is associated with eutrophic temperate lakes and tropical lakes (Hecky & Kilham, 1988) but has also been documented in less productive lakes (Goldman, 1981; Morris & Lewis, 1988; Reuter et al., 1993; White et al., 1985). The stimulatory effect of DIN and urea-N on primary production found here is in agreement with previous reports from a comprehensive study in Toolik Lake which show persistent N limitation, (Whalen & Alexander, 1986a; Whalen & Cornwell, 1985) as well as consistently low summer concentrations of DIN (Whalen & Alexander, 1986b) and infer by a mass balance approach the extensive utilization of dissolved organic-N to meet nutritional requirements of phytoplankton (Whalen & Cornwell, 1988).

Strict P limitation was observed in only six lakes, although a synergistic effect between N and P was evident throughout the summer. In 84% of all experiments, additions of N & P resulted in a higher degree of response than when these nutrients were added individually. Similar observations elsewhere (Diaz & Pedrozo, 1996; Elser et al., 1990; McCoy, 1983; White & Payne, 1977) are usually interpreted to indicate that the elimination of limitation by the addition of one nutrient quickly leads to the depletion of the other. Generally, N is believed to function as a secondary nutrient capable of producing a synergistic effect in the presence of P (Dodds et al., 1989; Elser et al., 1990). This contrasts with our observation that the primary limiting nutrient in concurrently limited lakes was N rather than P, and may reflect regional differences in factors regulating nutrient supply (e.g., plant cover, bedrock composition).

Like P limitation, reciprocal limitation was observed in six lakes. Reciprocal limitation has been interpreted to indicate that different components of the phytoplankton community are limited by N or P (Morris & Lewis, 1988). This phenomena can result from differences among species in optimum nutrient ratios for growth (Hecky & Kilham, 1988). Diaz & Pedrozo (1996) reported that low concentrations of both nutrients limited phytoplankton growth in ultraoligotrophic lakes in Argentina and that the addition of either nutrient stimulated growth. The relative infrequency of reciprocal limitation here suggests a fundamental physiological similarity of phytoplankton communities throughout the study area.

Ammonium was a more effective stimulant of ^{14}C primary production than NO_3^-–N (Fig. 2), consistent with both a previous report (Whalen & Alexander, 1986b) that NH_4^+–N was the preferred form of DIN by arctic phytoplankton and the lack of widespread evidence for preferential utilization of NO_3^-–N over NH_4^+–N by phytoplankton. However, N limitation here was significantly correlated with low NO_3^-–N concentrations and showed no relationship to NH_4^+–N levels. Similarly, White et al. (1985) noted an association between low NO_3^-–N concentrations and the stimulatory effect of added NH_4^+–N and concluded that NO_3^-–N concentrations reasonably approximated DIN availability. Likewise, we believe that the best indicator of ambient DIN here may be the NO_3^-–N concentration and that the absence of a relationship between NH_4^+–N concentrations and N limitation likely stems from the difficulty of accurately measuring NH_4^+–N at the limit of detection levels (reviewed by Aminot et al., 1997).

Because nutrient concentrations steadily decrease in arctic lakes following ice-out (Miller et al., 1986; Whalen & Alexander, 1986b; Whalen & Cornwell, 1985), it was expected that the degree of the bioassay response to N&P would increase throughout the summer period of thermal stratification, indicating increasingly severe nutrient limitation (Reuter et al., 1993; Vincent et al., 1984). Consequently, the progressive decrease in stimulation of ^{14}C uptake by the N&P treatment in Toolik Lake during the summer period of thermal stratification (Fig. 4a–c) was surprising and is contrary to the observation by Goldman et al. (1993) that peak bioassay responses in oligotrophic Lake Tahoe occurred during thermal stratification. Mixing events typically relieve cellular shortages of N and P by returning nutrients from the hypolimnion, thereby eliminating the stimulatory response of nutrient addition (Lebo et al., 1994; Reuter et al., 1993; Vincent et al., 1984). However, marked stimulation by N&P in Toolik bioassays when the lake was nearly or completely mixed (Fig. 4d,e) suggests that hypolimnetic accumulation of nutrients during summer stratification is inadequate to significantly enhance phytoplankton primary productivity when circulated into surface waters. This is consistent with both the lack of a nutricline (Whalen & Alexander, 1986b) and the ability of Toolik sediments to act as a strong sink for PO_4^{3-}–P and NH_4^+–N regenerated in surficial layers (Whalen & Cornwell, 1985).

In concert, the progressive decrease in the degree of the bioassay response to N&P addition during summer stratification and highly enhanced response during circulation suggest that a deficient micronutrient was re-supplied from the hypolimnion to the phytoplankton during mixing, while the N&P treatment supplied necessary macronutrients. This corroborates well the observation that phytoplankton in nutrient-amended limnocorrals in Toolik Lake never completely exhausted the available N or P in the first year of fertilization and that some other control mechanism, aside from zooplankton grazing, was limiting (O'Brien et al., 1992).

Two lines of evidence point to dissolved iron (DFe) as a candidate secondary limiting nutrient in Toolik Lake during summer stratification. First, the annual riverine influx of total iron (TFe) and dissolved iron (DFe) into Toolik Lake is largely delivered during the first 7–10 days of stream flow in the spring (Cornwell, 1983). Second, seasonal analysis of water column concentrations of TFe and DFe show highest surface water concentrations ($\sim$0.45 μM) in August, following overturn (Cornwell, 1983). Although the highly oxidizing environment at the Toolik sediment–water interface presents a barrier to extensive upward diffusion of DFe into the water column (Cornwell & Kipphut, 1992), sufficient DFe may be regenerated in or released into hypolimnetic waters to meet phytoplankton requirements when the lake water freely circulates, unlike the situation for N and P. Recently, phytoplankton primary productivity in Lake Erie was shown to be limited by low DFe bioavailability when pelagic waters were thermally stratified (Twiss et al., 2000). Secondary limitation by DFe or some other micronutrient as the summer progresses may be common in the Arctic Foothills, as the pooled bioassay data for all lakes shows a generalized decrease in the degree of the stimulatory effect of the N&P treatment with increasing time since the onset of thermal stratification. Despite the circumstantial evidence pointing to DFe as a secondary limiting factor to phytoplankton production, other micronutrients cannot be discounted. For instance, Axler et al. (1980) demonstrated enhanced $H^{14}CO_3^-$ and $^{15}NO_3^-$ uptake by natural phytoplankton communities in oligotrophic Castle Lake in response to Mo addition. Clearly, additional experiments involving micronutrient additions are needed to directly determine the existence and cause of apparent secondary nutrient limitation late in the growing season in arctic lakes.

The degree of the response to N&P addition was unrelated to irradiance during the incubation period. In fact, many of the greatest stimulatory responses

were recorded during relatively cloudy days. Similarly, O'Brien et al. (1992) reported that nutrient-enriched limnocorrals in Toolik Lake never became light-limited, despite Chl *a* concentrations 10–15 times greater than in unfertilized reference corrals. Collectively, these observations and the consistent stimulatory effect of nutrient amendment point to the importance of N and P and possibly micronutrients such as Fe in regulating phytoplankton production in Arctic Foothill lakes. More specifically, N supply appears to be crucial as it was limiting or co-limiting in 72% of the lakes that were sampled one time only (Fig. 3). Further, the limited evidence showing seasonal or annual variations with respect to within-lake nutrient status (Fig. 4 and Table 3) also consistently showed limitation or co-limitation by N.

The degree of response to N&P addition was also unrelated to water temperature during the incubation period. However, this result must be evaluated cautiously. Most of the observations clustered around the summer maximum (Table 1) and site-to-site variations in response may obscure a statistical effect over a narrow temperature range. Previous investigators have reported for polar lakes a strong photosynthetic response to temperature (Rae & Vincent, 1998) and unusually low quantum yield (Markager et al., 1999), which was attributed to a combination of low temperature and nutrient stress. Photosynthetic carbon uptake by phytoplankton is governed by the interaction of cellular physiology and environmental influences such as nutrient supply and temperature. Additional experiments are needed to determine the relationship between water temperature and degree of the photosynthetic response to nutrient enrichment.

Landscape position may influence chemical and biological characteristics of lakes (Hershey et al., 1999; Kratz et al., 1997). Arctic terrestrial plant communities show differing abilities to sequester and release nutrients, such that vegetation cover can regulate nutrient delivery to a lake (Shaver et al., 1991). Arctic Foothill lakes with relatively high concentrations of NO_3^-–N are frequently surrounded by dry acidic tundra and glacial till deposits, while lakes with lesser concentrations of NO_3^-–N are associated with shrub tundra and other alluvial deposits (C. Richards, University of Minnesota-Duluth; unpublished). Accordingly, we expected P limitation in watersheds dominated by dry acidic tundra. A surveyed component of the watershed containing the S-Series Lakes (Fig. 1) was comprised of 57.1% dry acidic tundra and 11.4% glacial till deposits (C. Richards, unpublished). Of the five lakes assayed within this surveyed area, three were P-limited (S-4, S-5, S-7), one showed reciprocal limitation (S-6), and one was concurrently limited (S-3) (Table 2). Clearly, these limited observations are in agreement with our current understanding of landscape influences on lake ecology in this region and point to vegetation cover as a promising predictor of phytoplankton nutrient status.

Nutrient status appeared to be somewhat consistent within watersheds reinforcing the concept that the surrounding landscape influences nutrient delivery to lakes (Table 2 and Fig. 1). The I-Series lakes exhibited concurrent limitation in most bioassay experiments and showed significantly greater responses to N than P enrichment. The watershed containing lakes GTH 60, 61, 74, 94, 96, and 97 also showed a significantly greater response to N than P enrichment. In contrast, the S-Series (which includes I-Swamp) was predominately P-limited. Several qualitative observations also support consistency of nutrient status within watersheds, but limited sample size precludes rigorous statistical analysis. First, both Fog Lakes showed larger responses to P than N enrichment, although only Fog 4 was P-limited. Second, Galbraith and Island Lakes both showed reciprocal limitation and a greater response to P than N addition. Third, the chain containing lakes GTH 99, 103, and 104 showed N limitation in one case (GTH 103) and no limitation in the other lakes, but the degree of response was higher overall for N additions. Finally, lakes GTH 108 and 109 were both more responsive to N than P, although neither was categorized as N-limited.

Our experiments give for the most part a single indication of the short-term photosynthetic response of natural Arctic phytoplankton assemblages from several lakes to a single level of macronutrient addition. Data must be cautiously interpreted for several reasons. First, in some instances, enrichment with inorganic P (Lean & Pick, 1981) or N (Turpin et al., 1988) may temporarily suppress carbon fixation as energy is directed toward acquisition of the limiting nutrient. Second, containment overemphasizes the importance of nutrient limitiation while minimizing the potential influence of other limiting factors (Elser & Kimmel, 1986). Third, these experiments provide no information with respect to the magnitude and duration of changes in community growth (e.g., increase in Chl *a*) or species composition in response to fertilization (Hecky & Kilham, 1988). This information is best provided by long term ecosystem- or mesocosm-level experiments that incorporate complex

interactions such as recycling and competition that occur in natural ecosystems (Taylor et al., 1995).

Despite methodological shortcomings, results of this study provide the first information to identify and qualitatively predict the impact of global change on water quality and phytoplankton primary productivity in arctic lakes. Ice core records from South Greenland indicate that anthropogenic emissions have increased atmospheric N deposition in remote regions of the Northern Hemisphere (Mayewski et al., 1990). Accelerated, anthropogenically driven N deposition has consistently led to enhanced primary production and a shift in community composition to undesirable, bloom-forming species in N-sensitive coastal temperate waters (reviewed by Paerl, 1997). Inasmuch as Arctic Foothill lakes respond best to N when a single nutrient is added, these waters are likely increasing in phytoplankton production and will continue to do so in response to deposition of remotely generated DIN. Lakes may ultimately shift dominance from N- or co-limitation to strong P limitation, a phenomenon that was documented by Goldman et al. (1993) for ultraoligotrophic Lake Tahoe following years of increased N loading from fossil fuel combustion. Lakes rarely showed no response to nutrient addition. Therefore, increased nutrient delivery as a consequence of increased slumping, erosion and thawing of the permafrost in warmer predicted future climates (Mitchell et al., 1993; Rowntree, 1997) or as a result of increasing recreational activity will also increase phytoplankton productivity. A decrease in hypolimnetic O_2 in response to warmer water temperatures (Hobbie et al., 1999) and longer thaw season (Mitchell et al., 1993; Rowntree, 1997) may in some cases facilitate internal nutrient loading, which is currently inconsequential in lake nutrient budgets (Whalen & Cornwell, 1985, 1988).

Conclusions

A regional survey of lakes in the Arctic Foothills region of Alaska most often showed concurrent (N&P) nutrient limitation of phytoplankton production in short-term nutrient bioassay experiments. Strict N limitation was observed more frequently than P limitation and the degree of response to N alone was significantly greater than the degree of response to P alone in concurrently limited lakes, suggesting that N was generally more important than P in regulating phytoplankton production. The degree of response to nutrient additions showed an unexpected, generalized decrease throughout the summer period of thermal stratification, suggesting secondary limitation of phytoplankton production by some micronutrient such as iron. The degree of response to nutrient additions was unrelated to irradiance and water temperature pointing to the overwhelming influence of nutrient availability as a control of phytoplankton production in these lakes. Phytoplankton nutrient status was often consistent across lakes within a watershed, suggesting that watershed characteristics influence nutrient availability. Lakes in this region will clearly show increased phytoplankton production in response to anthropogenic activity and anticipated changes in climate that will increase nutrient loading.

Currently, information is lacking with regard to phytoplankton community composition for these lakes. Future research should be directed toward acquiring a long-term database for both phytoplankton production and species composition in a few representative lakes to better document the effects of global change and increased recreational activity on this component of the lake ecosystem. Additionally, we recommend that future experiments include simultaneous assessment of growth response bioassays, physiological assays and nutrient deficiency indices to more firmly establish the extent and seasonality of nutrient limitation of phytoplankton production in this region.

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