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Date:

2022-12-01

Citation:

Myrstener, M., Fork, M. L., Bergström, A. K., Puts, I. C., Hauptmann, D., Isles, P. D. F., Burrows, R. M. & Sponseller, R. A. (2022). Resolving the Drivers of Algal Nutrient Limitation from Boreal to Arctic Lakes and Streams. *Ecosystems*, 25 (8), pp.1682-1699. <https://doi.org/10.1007/s10021-022-00759-4>.






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Resolving the Drivers of Algal Nutrient Limitation from Boreal to Arctic Lakes and Streams

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ABSTRACT

Nutrient inputs to northern freshwaters are changing, potentially altering aquatic ecosystem functioning through effects on primary producers. Yet, while primary producer growth is sensitive to nutrient supply, it is also constrained by a suite of other factors, including light and temperature, which may play varying roles across stream and lake habitats. Here, we use bioassay results from 89 lakes and streams spanning northern boreal to Arctic Sweden to test for differences in nutrient limitation status of algal biomass along gradients in colored dissolved organic carbon (DOC), water temperature, and nutrient concentrations, and to ask whether there are distinct patterns and drivers between habitats. Single nitrogen (N) limitation or primary N-limitation with secondary phosphorus (P) limitation of algal biomass was the most com-

mon condition for streams and lakes. Average response to N-addition was a doubling in biomass; however, the degree of limitation was modulated by the distinct physical and chemical conditions in lakes versus streams and across boreal to Arctic regions. Overall, algal responses to N-addition were strongest at sites with low background concentrations of dissolved inorganic N. Low temperatures constrained biomass responses to added nutrients in lakes but had weaker effects on responses in streams. Further, DOC mediated the response of algal biomass to nutrient addition differently among lakes and streams. Stream responses were dampened at higher DOC, whereas lake responses to nutrient addition increased from low to moderate DOC but were depressed at high DOC. Our results suggest that future changes in nutrient availability, particularly N, will exert strong effects on the trophic state of northern freshwaters. However, we highlight important differences in the physical and chemical factors that shape algal responses to nutrient availability in different parts of aquatic networks, which will ultimately affect the integrated response of northern aquatic systems to ongoing environmental changes.

Key words: nutrient limitation; lake; stream; nitrogen; phosphorus; phytoplankton; periphyton.

Received 13 August 2021; accepted 5 March 2022

Supplementary Information: The online version contains supplementary material available at <https://doi.org/10.1007/s10021-022-00759-4>.

Author Contributions: All authors contributed to the conception of the ideas and approaches and collection of the data herein. MM and MLF performed analyses, generated figures, and co-wrote the manuscript with input from all of the other authors.

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HIGHLIGHTS

- Algal N limitation is widespread across freshwaters in northern Sweden.
- Controls on nutrient limitation differ between habitats and regions.
- Global change will differentially influence northern streams versus lakes.

INTRODUCTION

Arctic and boreal landscapes are currently exposed to multiple environmental changes that directly or indirectly impact the physical and chemical properties of aquatic ecosystems. In particular, ongoing climate warming (Kendrick and others 2018), declines in atmospheric deposition (Isles and others 2018), and land use change (Lucas and others 2016) all have the potential to increase or decrease the supply of nitrogen (N) and phosphorus (P) to northern waters. Aquatic ecosystem responses to these changes depend largely on the nature and degree of nutrient limitation relative to other potential constraints on primary production imposed by thermal (Van Vliet and others 2013) and light (Karlsson and others 2009) regimes. At catchment scales, responses to changing nutrient supply may also differ among lake and stream environments, which vary in biotic structure, habitat geometry, and strength and nature of connections to surrounding soils and wetlands (Stanley and others 1990; Francoeur and others 2001). Yet, while lakes and streams show broadly similar nutrient limitation status (Elser and others 2007), factors that shape the patterns and strength of limitation across these ecosystems are poorly understood.

Both lakes and streams are sensitive to environmental change in surrounding landscapes, but fundamental differences between these systems may modulate how they respond to altered nutrient supplies from land. For example, the majority of primary productivity in most small streams occurs on the bottom by periphytic algae (Minshall 1978), whereas productivity in lakes and larger rivers is partitioned between benthic and pelagic habitats (Ask and others 2009). In addition, benthic algae in streams are continuously supplied with nutrients mostly derived from catchment soils (Hynes 1975), whereas in lakes, phytoplankton and especially periphyton may be more reliant on nutrients resuspended and/or remineralized internally from sediments (Hansson 1992; Blumenshine

and others 1997). Indeed, the general conditions for internal nutrient recycling also differ between these systems (Essington and Carpenter 2000). In lakes, recycling is promoted by longer water residence times (René Brooks and others 2014), which at the same time weaken the direct link to dissolved resources supplied from catchment soils when compared to running waters.

Differences in the physical environment between lotic and lentic systems may interact with resource supply to further influence patterns of autotrophic nutrient limitation. For any aquatic system, light (Hill and others 2009) and thermal (Francoeur and others 1999) conditions can constrain the capacity of primary producers to take advantage of available nutrients. In running waters, light availability is dynamic, regulated in space and time by canopy cover (Hill and Dimick 2002), channel orientation (Julian and others 2008), and the optical properties of water in wider/deeper systems (Kirk 1994). By comparison, canopy shading is rarely an issue for lakes, and instead light availability is primarily dependent on depth and the optical properties of water (Ask and others 2009). Similarly, streams and lakes often have distinct thermal regimes arising from differences in incident light, water volume, and groundwater influences (Caissie 2006). Finally, obvious differences between lakes and streams in terms of water flow can further influence the strength of nutrient limitation (King and others 2014). Compared to lakes, the dominance of advective flow in streams may reduce limitation by supporting a continuously high flux of nutrients to biofilm surfaces (Peipoch and others 2016), decreasing constraints imposed by slow diffusive fluxes to primary producers (Larned and others 2004). However, very high flows may scour periphytic communities or smother them in deposited material and thereby create time periods of reduced nutrient demand (Biggs 1995). Overall, these physical differences mean that primary producer responses to similar changes in nutrient concentration among stream and lake habitats may not be simple and/or unidirectional across inland water networks.

Ongoing increases (de Wit and others 2016) or decreases (Kendrick and others 2018) in dissolved organic carbon (DOC) inputs from soils may also differentially influence the strength of nutrient limitation faced by primary producers in northern streams versus lakes. In lakes, colored DOC can exert strong controls on primary production through simultaneous influences on nutrient availability (positive association) and light availability (negative association). Specifically, nutrients

transported with or as part of DOC can increase nutrient availability (Salonen and others 1992), but because colored DOC also absorbs light, it has the potential to induce light limitation of primary productivity at high concentrations (Bergström and Karlsson 2019; Kelly and others 2018; Seekell and others 2015). However, for northern, shallow streams, the negative effects of DOC on primary producers that result from decreased light availability appear less important than the positive influences of increased nutrient availability (Myrstener and others 2018; Burrows and others 2021). DOC can further exert effects on primary productivity in lakes by increasing near surface water temperature (Read and Rose 2013), cooling deeper waters (Solomon and others 2015; Warren and others 2017) and decreasing thermocline depth (Strock and others 2017). Yet again, such effects on the physical environment are not likely to be pronounced in streams, where stratification is rare and temperature is more closely connected to groundwater inputs, discharge, canopy cover, and air temperature (Van Vliet and others 2011; Wondzell and others 2019).

We investigated the drivers of variation in nutrient limitation of aquatic primary producers using results from 244 nutrient limitation bioassays from 89 streams and lakes across northern Sweden. This region encompasses steep gradients in climate, differences in dominant catchment vegetation (from coniferous forests to high elevation tundra), and variation in stream and lake water chemistry (Sponseller and others 2014; Isles and others 2018). We leveraged bioassay data with the objective of identifying the relative importance of background nutrient supply versus other physical (light and temperature) and chemical (DOC) factors that could shape patterns of nutrient limitation among biomes (boreal to Arctic) and between habitats (streams and lakes; benthic and pelagic). While our data draw from multiple studies that have generally emphasized aquatic N limitation for specific system types, we focus here on how the predictors of these patterns differ across ecosystem types. This lies at the core of understanding how northern freshwaters will respond to ongoing environmental change.

METHODS

Site Description

We compiled published bioassay data from 57 individual lakes and 32 individual streams sampled at different times of the year and at different locations/depths. These include 18 periphyton experi-

ments in lakes, 132 lake phytoplankton experiments, and 94 stream periphyton experiments, all spanning boreal to Arctic regions of northern Sweden, to a total of 244 assays (Table S2). Boreal sites are distributed around 64°N and mainly represent conifer-dominated catchments. The remaining sites are situated above the Arctic circle around 68°N and include a few streams and lakes in coniferous forest landscapes but with the majority located in the Fennoscandian highland landscapes (Virtanen and others 2016). Despite land cover differences, we grouped all sites around 68°N in the analyses because of their clear separation from boreal sites (see Figure 1) and this group is hereafter referred to as 'subarctic'. This group also includes Arctic sites based on the Arctic boundaries defined by the Arctic Monitoring and Assessment Programme on the basis of elevation, vegetation, and occurrence of permafrost (AMAP 1998). Therefore, to acknowledge the full range of sites from boreal to Arctic, we use phrases like "spanning boreal to Arctic" as well.

Our study sites encompass large gradients in physical and chemical variables (Table 1), with minimal direct human activities, except for forest management. Stream sites are shallow (< 0.5 m) first to third order (majority first–second order) systems in forested (coniferous or birch forest) or tundra landscapes. All studied lakes are relatively small, with areas ranging 1–35 ha, and some have been limed as part of national water quality programs. All bioassays were performed in ice-free conditions from May to September with the majority of assays in June to August. Detailed information of methods, sampling and analysis procedure are available in the original papers (Bergström and others 2008, 2013, 2015; Burrows and others 2021; Fork and others 2020a; Isles and others 2020; Myrstener and others 2018).

Nutrient Diffusing Substrates in Streams and Lake Benthic Zones

Stream and lake benthic periphyton nutrient limitation was evaluated using nutrient diffusing substrates (NDS). All NDS were prepared according to Tank and others (2006) with plastic cups and porous ceramic tops. All N treatments consisted of 0.5 M NaNO₃, stream P treatments were 0.5 M KH₂PO₄ or K₂HPO₄, and lake (benthic) P treatments consisted of 0.05 M KH₂PO₄ + 0.05 M K₂HPO₄. Replicates (4–5) of each treatment were deployed for 17–20 days in the streams and for 50 days in the lakes. For the lake experiments, nutrient-infused agar was replaced halfway

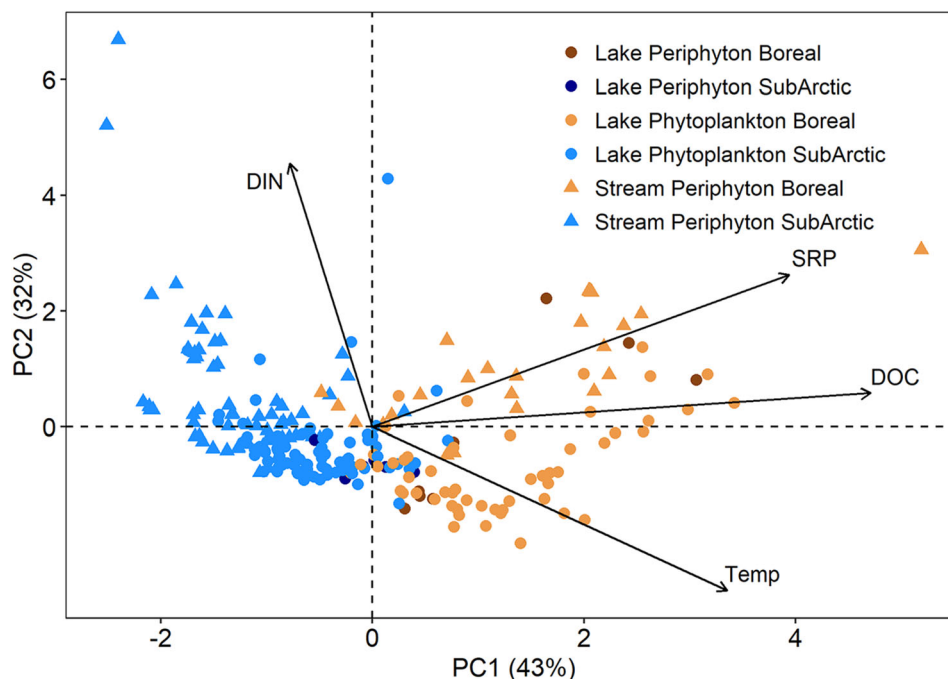


Figure 1. Principal component analysis of the physical and chemical parameters of all sites visualizing differences in lakes (circles) vs streams (triangles), and boreal (brown) vs subarctic (blue) freshwaters. Together, PC1 and PC2 explain 75% of the total variance in multi-dimensional space for these physical and chemical parameters.

Table 1. Physical and Chemical Characteristics of The Six Habitat Groups of Lakes and Streams

	Lake periphyton		Lake phytoplankton		Stream periphyton	
	Subarctic	Boreal	Subarctic	Boreal	Subarctic	Boreal
n	9	9	80	57	64	32
Temperature (°C)	14.4 ± 2	16.7 ± 5	12.0 ± 3	18.3 ± 4	7.5 ± 4	10.9 ± 2
Incoming PAR (mol m ⁻² d ⁻¹)	18.8 ± 4	12.7 ± 7	N.A	N.A	12.2 ± 7	4.7 ± 3
DIN (µg N·L ⁻¹)	4.7 ± 3	4.5 ± 10	6.0 ± 22	6.8 ± 11	13.8 ± 48	21.2 ± 14
SRP (µg P·L ⁻¹)	2.1 ± 0	1.9 ± 4	1.0 ± 1	1.5 ± 3	0.8 ± 2	5.1 ± 3
DOC (mg C·L ⁻¹)	3.9 ± 2	9.2 ± 4	4.7 ± 2	11.8 ± 4	2.6 ± 2	15.9 ± 6

For temperature, light, and DOC, values shown are mean ± SD; for DIN and SRP, values are median ± SD. n equals number of assays in each group. Incoming PAR represents photosynthetically active radiation in the water and is presented as the accumulated daily incoming light. DIN is dissolved inorganic nitrogen, DOC dissolved organic carbon and SRP soluble reactive phosphorus. Lake periphyton PAR was modeled based on absorbance and incoming light, as described in the Supplementary Information. Because lake phytoplankton experiments were designed to provide non-limiting light conditions, PAR was not measured in these experiments (denoted by N.A).

through the deployment to ensure continuous nutrient diffusion for the full period (Fork and others 2020a). Stream NDS were deployed at 10–20 cm depth and lake NDS were deployed at 0.1–1 m depth. After retrieval, chlorophyll-*a* (chl-*a*) was either analyzed directly using a BenthosTorch (bbe Moldaenke, Germany) or frozen at –80 °C and analyzed spectrophotometrically (Steinman and others 2017) after acetone extraction, with acidification correction for pheophytins. Total chl-*a* estimates from the BenthosTorch typically compare well with conventional spectroscopic methods

(Kahlert and McKie 2014), especially on thin biofilms (Echenique-Subiabre and others 2016). Regardless, our emphasis on nutrient response ratios, as opposed to total concentrations, reduces the influence of any potential differences in chl-*a* analysis.

Nutrient Bioassays in Lake Pelagic Zones

Lake phytoplankton nutrient limitation was evaluated using bioassay enclosures. In each case, lake water was filtered (50 µm mesh size) to exclude

grazers. Transparent polyethylene containers (20L) or clear polyethylene bottles (500 mL or 250 mL) were treated with N, P, or N + P (hereafter NP) as NH_4NO_3 and KH_2PO_4 with a N/P molar ratio of 23:1. 99 lake phytoplankton assays (75% of total phytoplankton assays) were sampled and incubated in the epilimnion at depths corresponding to 1/2 surface light (0.5 to 1.5 m depth) for 3–4 days (Bergström and others 2008; Isles and others 2020). Thirty-three phytoplankton assays (25% of total phytoplankton assays) were instead incubated in light chambers with light and temperature conditions corresponding to the lakes from which they were sampled ($85\text{--}150 \mu\text{mol m}^{-2} \text{s}^{-1}$, Bergström and others 2013, 2015). These chamber-incubated bottles were shaken during a 48-h incubation. After incubation, water was filtered onto GF/F filters, extracted in ethanol, and analyzed on a spectrofluorometer (PerkinElmer, LS45). All lake phytoplankton assays were designed to have sufficient light to enable a response to the nutrient additions.

Physical and Chemical Variables

Information on background dissolved N, P, and DOC concentrations, and temperature was available for all sites. Soluble reactive phosphorus (SRP) and dissolved inorganic nitrogen (DIN) are not perfect proxies for assessing bioavailable pools (Soares and others 2017), but neither total P nor total dissolved N were universally available in the compiled datasets and therefore we use SRP and DIN here. Water samples for DOC and dissolved nutrients (DIN as nitrate + ammonium, and SRP) were filtered using GF/F filters or 0.45- μm cellulose acetate filters. Stream temperature and light were continuously measured using HOBO pendant loggers (Onset Computer Corporation, Borne, USA), while lake temperatures were recorded at the deployment using an YSI ProDO sensor (Yellow Springs, OH, USA). Because lake phytoplankton assays were designed to provide sufficient light conditions (cf. above) to test for nutrient limitation, precise light data were not available from these experiments.

Data Analysis

To explore the physical and chemical gradients within our study systems, we performed a principle component analysis (PCA) using universally available variables including temperature, DIN, SRP and DOC. The first two components together explain 75% of the variance in the data and this analysis was used to group the data into six main ‘habitat’

groups differentiated by region and habitat type: both boreal and subarctic (including Arctic tundra sites) lake periphyton, stream periphyton and lake phytoplankton (Table 1 and Figure 1).

We used natural-log transformed response ratios (RR_x) according to Elser and others (2007), to identify the presence and strength of nutrient limitation in individual bioassays. Response ratios were obtained by dividing each individual chl- α treatment response by its corresponding control. We used one-sample t-tests to assess whether RR_N and RR_P were different from zero (that is, different from the control), indicating nutrient limitation. We also compared differences between treatment effects (RR_N , RR_P , and RR_{NP}) using a fixed-effects model with a subsequent post hoc test (Tukey HSD). Detailed results of these analyses are available in Table S1. We considered a significant increase ($p \leq 0.01$) in only N or P alone without additional increases in NP indicative of single limitation. A significant increase in N or P alone as well as a significant increase in NP compared to the first limiting nutrient was defined as primary and secondary co-limitation. Finally, a simultaneous significant increase in both N and P alone was defined as dual N and P co-limitation.

To address our objective of assessing differences in nutrient limitation across gradients of nutrient supply and physical conditions, we explored potential thresholds in the bivariate relationships between RR_N versus DIN and RR_N versus temperature using a resampling approach. Specifically, we compared the maximum RR_N in a subset of the data above a candidate DIN threshold to the maximum in each of 1000 random samples (with replacement) of the whole dataset (with each sample having the same number of observations as the subset above/below the threshold). When the maximum value in the subset was less than the maximum in 95% of the resampled sets, we considered the candidate significant. We tested candidate thresholds every $1 \mu\text{g L}^{-1}$ from $5 \mu\text{g L}^{-1}$ DIN to the maximum concentration where there were at least 10 experiments with higher DIN concentration (that is, $68 \mu\text{g L}^{-1}$ for periphyton and $29 \mu\text{g L}^{-1}$ for phytoplankton). The reported DIN threshold is the lowest DIN concentration for which the bioassays conducted in waters above that concentration had a significantly lower RR_N than a subset from the whole dataset. Put more simply, we found the lowest DIN concentration threshold at which the most N-limited sample above the threshold was significantly less N-limited than a random subset of the entire data. We repeated this entire procedure 1000 times using random samples of 75% of the

dataset to get a distribution of thresholds. We analyzed the DIN threshold for phytoplankton and stream periphyton separately. We used a similar approach to identify a threshold in RR_N response to temperature, using subsets of the data below a given temperature (ranging from 4–15° C for periphyton and 10–22° C for phytoplankton, such that the minimum temps had at least ten colder experiments and maxima had at least ten warmer). In this case, we report the greatest significant temperature as the threshold.

To more broadly assess the chemical and physical drivers of nutrient limitation across and within habitats, we performed path analysis using the *cfa*-function of the Lavaan package (Latent Variable Analysis, Rosseel 2012) in R 3.5.0 (R Core Team 2018). Path analysis is designed to account for collinearity between variables, as compared to multiple regression models. Based on the low prevalence of P-limitation (on average only 10% increase in chl-*a* in P treatment compared to control, $p = 0.5$), we did not analyze this response further but instead focused on analysis of RR_N and RR_{NP} . For the path analyses, we included water temperature, daily PAR (for stream assays only), and background concentrations of DIN, SRP and DOC as potential drivers for RR_N or RR_{NP} . Further, for this analysis only, we set all negative RR_N (7% of cases) and RR_{NP} (7% of cases) to zero (that is, no response) because the interpretation of negative response ratios, especially for P, is still subject to scientific debate and may represent true variability in nutrient limitation (that is, inhibition effects) or methodological issues (Tank and Dodds 2003; Tanaka and others 2014).

We performed a series of path analyses to address our objective of understanding how controls on nutrient limitation vary by region and habitat. We performed this analysis using the entire data set ($n = 244$) and then individually on the subarctic lake phytoplankton ($n = 79$), boreal lake phytoplankton ($n = 53$), subarctic stream periphyton ($n = 62$), and boreal stream periphyton ($n = 32$) habitat groups (Table S2). We excluded lake periphyton ($n = 18$, of which 9 were different depths within the same lake) from the individual sets of our path analysis because of the low number of true replicates in this single study. Path analysis provides a test of overall predictive ability of the model (that is, R^2), while also revealing the direction and significance of linkages between predictors and response variables (described by path coefficients) and among the predictors (using Pearson correlations). We focused on these different coefficients to compare and contrast the drivers of

nutrient limitation among habitat groups and across the region.

Finally, to better understand the potential influence of DOC on patterns of limitation, we used path analysis to evaluate the drivers of RR_{NP} for 1) all lake + stream periphyton bioassays ($n = 112$) and 2) subsets of lakes divided into high DOC ($> 9.6 \text{ mg C}\cdot\text{L}^{-1}$, $n = 36$) and low DOC ($< 9.6 \text{ mg C}\cdot\text{L}^{-1}$, $n = 94$). Two lakes had DOC of exactly $9.6 \text{ mg C}\cdot\text{L}^{-1}$ and were therefore excluded from the path analysis. The $9.6 \text{ mg C}\cdot\text{L}^{-1}$ cutoff largely, but not entirely, separated boreal and subarctic sites and was selected by iteratively searching all possible breakpoints for the lowest mean square error in a piecewise linear regression for the relationship between DOC and RR_{NP} . This $9.6 \text{ mg C}\cdot\text{L}^{-1}$ cutoff is further supported by data from northern lakes that suggest this is roughly the concentration where DOC transitions from a nutrient source for phytoplankton to a factor that reduces light availability and inhibits phytoplankton growth (Hanson and others 2003; Solomon and others 2015). Importantly, our analysis did not aim to identify a particular DOC threshold but instead aimed to compare predictors of nutrient limitation between classes of lakes with low and high DOC concentrations. We focused these analyses on RR_{NP} because we were interested in the effects of DOC when macronutrient demand has been satisfied (as compared to using single nutrient addition responses).

RESULTS

Physical and Chemical Habitat

There was large variability in physical and chemical conditions among sites and across boreal to Arctic regions. Overall, water temperature varied from 1 to 25 °C, light from 1 to $39 \text{ mol}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$, DIN from < 1 to $176 \text{ }\mu\text{g N}\cdot\text{L}^{-1}$, SRP from 0 to $14 \text{ }\mu\text{g P}\cdot\text{L}^{-1}$ and DOC from 1 to $33 \text{ mg C}\cdot\text{L}^{-1}$ (Table 1). Results from the PCA showed little overlap in the physical and chemical conditions of boreal and subarctic freshwaters (Figure 1). Boreal lakes and especially streams had higher and more variable concentrations of SRP (4 vs. $1 \text{ }\mu\text{g}\cdot\text{L}^{-1}$, $p < 0.01$) and DOC (13 vs. $4 \text{ mg C}\cdot\text{L}^{-1}$, $p < 0.01$) compared to subarctic counterparts. Boreal waters also tended to be warmer and receive less light than subarctic sites (16 vs. 10 °C, $p < 0.01$ and PAR 9 vs. $15 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$, $p < 0.01$). Finally, there was also a separation in the physical and chemical properties between stream and lake habitats (Figure 1). When comparing all lakes to all streams, average DIN

tended to be higher in streams than lakes (31 vs. 11 $\mu\text{g}\cdot\text{L}^{-1}$, $p < 0.01$), while lakes were on average warmer (15 vs. 9 $^{\circ}\text{C}$, $p < 0.01$) and received more light (14 vs. 10 $\text{mol m}^{-2} \text{d}^{-1}$, $p < 0.01$) (Table 1).

Nutrient Limitation Status

Across habitats and regions, N-addition caused a greater increase in chl- α than P-addition. On average, chl- α nearly doubled in response to N (mean $\ln\text{RR}_N = 0.5$) and tripled with NP (mean $\ln\text{RR}_{NP} = 0.9$). There was a negative response to N- or NP-addition in 7% of bioassays (Figure 2). The average response to P-addition including all bioassays was a 10% increase in chl- α (but this was not statistically different from zero, $p = 0.5$), and 8% of P assays had positive responses that exceeded 10%, while 54% of the responses to P-addition were negative (though individual experiments were not statistically analyzed, Table S1). Notably, negative responses were present in all different treatments (N, P, and NP), all types of habitats (lake periphyton, phytoplankton and stream periphyton) and in both types of experimental approaches (NDS surfaces and bottles). Across regions, lake phytoplankton displayed primary N-limitation with secondary limitation by P, as marked by significantly higher responses to NP than N (Figure 2). In addition, single N-limitation without secondary response to P was seen in boreal stream periphyton and all lake periphyton. Finally, subarctic stream periphyton displayed dual co-limitation among sites but with a greater degree of N limitation

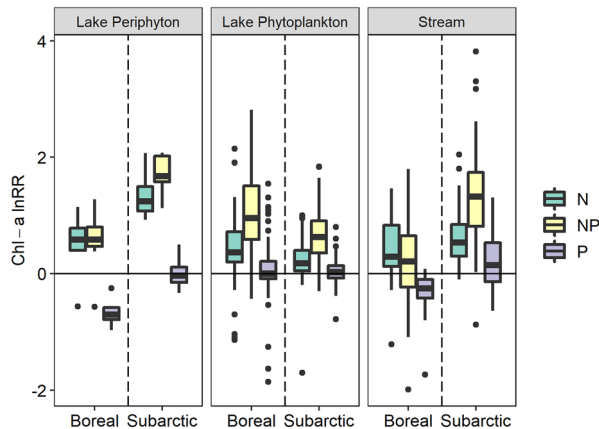


Figure 2. Response to nutrient treatments given as natural logarithm (\ln) transformed values. A $\ln\text{RR}$ of 0.7 equals a doubling in chl- α compared to the control, and values below 0 equal a negative response in chl- α compared to the control. Error bars represent 95% confidence intervals, and individual dots are outliers outside the 95% confidence interval.

(mean $\text{RR}_N = 0.6$, $p < 0.01$) as compared to P (mean $\text{RR}_P = 0.2$, $p < 0.01$). Dual co-limitation also occurred for some boreal lake phytoplankton bioassays (concurrent responses to each of N and P alone) as well as primary P-limitation in individual subarctic lakes. Although limitation status was not statistically evaluated within individual experiments in this study, results are available in the individual papers as well as the raw data of this study (<https://doi.org/10.5281/zenodo.6127581>).

Overall Controls on Chl- α Responses to N- and NP-Addition

The dominant controls on RR_N and RR_{NP} were different among habitats and regions, resulting in relatively low explanatory power of models including all data (path analysis $r^2 \text{RR}_N = 0.11$ and $r^2 \text{RR}_{NP} = 0.24$). DIN concentrations did, however, have an overall effect on RR_N , with lower responses to N in sites with higher DIN concentrations (Figure 3a), consistent with primary N-limitation at most sites. Our resampling approach identified thresholds in the response to added N at around 21 $\mu\text{g N}\cdot\text{L}^{-1}$ DIN (periphyton: 95% CI = [9, 42] with mean = 21.3 $\mu\text{g N}\cdot\text{L}^{-1}$; phytoplankton: 95% CI = [12, 29] with mean = 21.7 $\mu\text{g N}\cdot\text{L}^{-1}$; Figure 3a). In water bodies with ambient DIN concentrations above these thresholds, we rarely observed high RR_N values (above $\text{RR}_N = 2$), indicating that DIN saturation of algal production demand is common above these thresholds. In addition, we identified statistically significant temperature thresholds in the responses to added N (Figure 3b). For phytoplankton, there was a threshold at 10 $^{\circ}\text{C}$ below which we never observed strong responses to added N. In contrast, periphyton responded strongly to N-additions across nearly all temperatures (Figure 3b), although we did identify a threshold at 11.1 $^{\circ}\text{C}$ above which responses to N addition were enhanced in periphyton. We found similar patterns between response ratios and physical and chemical drivers for NP treatments (Figure S1).

Region- and Habitat-Specific Controls on Responses to Nutrients

Boreal to Arctic algal biomass responses to N were mediated by distinct drivers (Figure 4). In boreal systems, the response to N was controlled mainly by nutrient availability. Specifically, the path analysis for boreal streams suggested that relatively high background SRP concentrations across sites (Table 1) gave rise to single N-limitation (Figure 2)

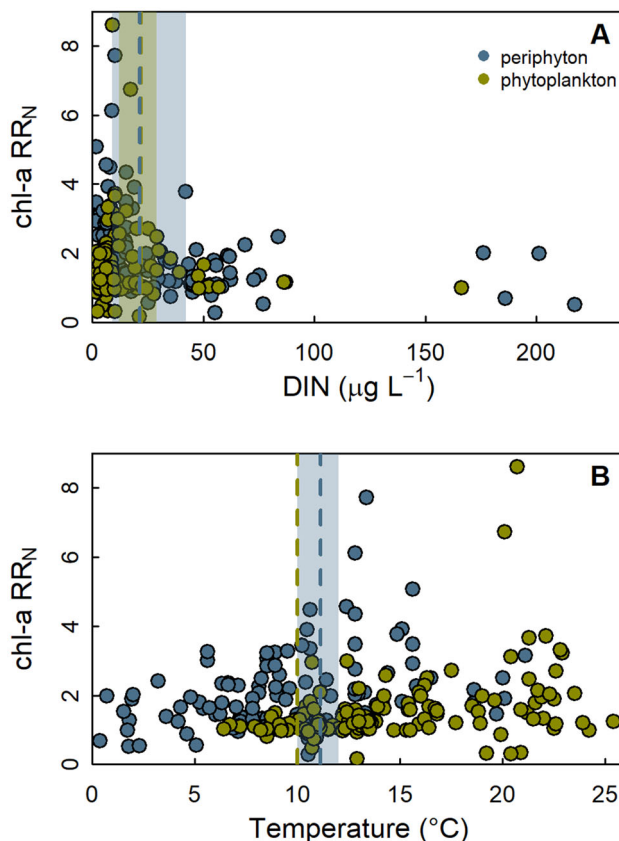


Figure 3. Relationship between chl- α response to N-addition and dissolved inorganic nitrogen (DIN, panel **a**) and temperature (panel **b**). Thresholds of RR_N maxima for both **a** DIN and **b** temperature are marked with dashed vertical lines and 95% confidence intervals are indicated by shaded rectangles. In **a**, the threshold for both periphyton and phytoplankton is approximately $21 \mu\text{g N}\cdot\text{L}^{-1}$. In **b** the 95% confidence interval around the temperature threshold for phytoplankton (green dashed line) is very narrow around the threshold at $10 \text{ }^\circ\text{C}$. Note that for visual reasons, RR_N is untransformed.

and a clear negative relationship between DIN concentrations and both RR_N and RR_{NP} (path coefficient = -0.67 for RR_N and RR_{NP} ; Figure 4a). In boreal lakes, more variable SRP concentrations and consistently low DIN concentrations resulted in primary N-limitation but relatively greater occurrence of secondary P-limitation or dual co-limitation. For these lakes, phytoplankton responses to added N and NP increased with the availability of SRP (coefficients = 0.49 and 0.29 for RR_N and RR_{NP} , respectively) and at warmer temperatures (coefficients = 0.29 and 0.64 ; Figure 4b).

In subarctic freshwaters, large variability in DIN concentration and overall low SRP concentrations (Table 1) resulted in both primary N- and primary P-limitation for individual lakes and streams. As such, nutrient availability was less predictive of RR_N and RR_{NP} in this region. For subarctic streams, temperature was the main factor controlling RR_N (Figure 4c, path coefficient = 0.32). For subarctic lakes, there was a negative influence of DIN on the

response to added N (Figure 4d, path coefficient = -0.32), but this was strongly influenced by two high DIN lakes. When these sites were omitted from the analysis, temperature was the only significant control on RR_N , similar to subarctic streams. For all subarctic sites, responses to NP were mainly related to variability in water temperature; notably, the effect of DOC concentration on RR_{NP} was negative in subarctic streams (path coefficients = -0.30) and positive in subarctic lakes (path coefficient = 0.25).

The effect of DOC on responses to added nutrients, and its relationship to other physical and chemical drivers, differed among regions and habitats (Figure 4). In lakes, the main effect of DOC was mediated through increased temperature, while the role of DOC as a driver in streams was mediated through nutrient concentrations (positive relationship with SRP in boreal and negative with DIN in subarctic, Figure 4). To assess these roles in more detail, we explored output from path analyses

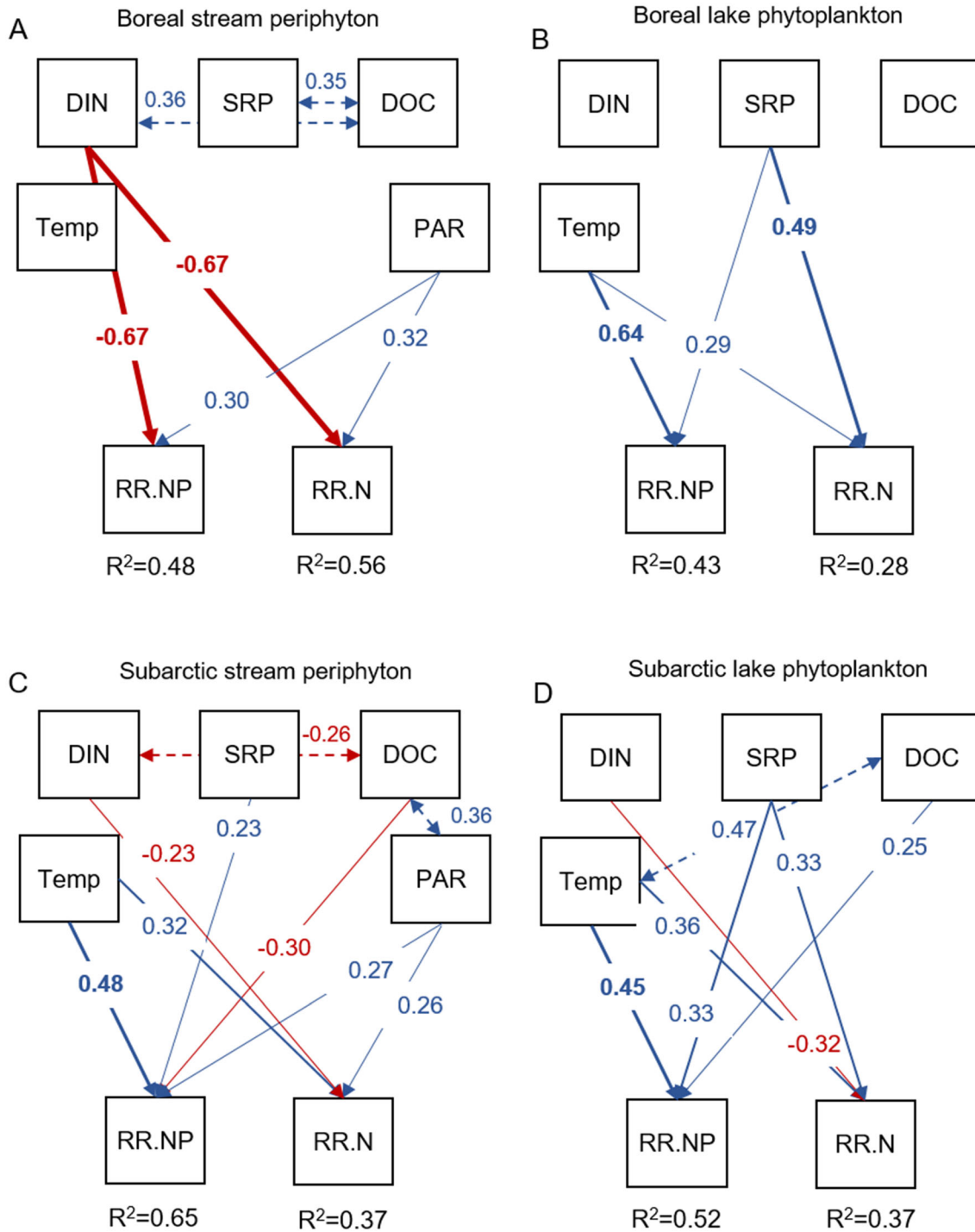


Figure 4. Results from the path analyses. Arrows between predictors (dashed lines: temperature, DIN, SRP, DOC and PAR) represent Pearson correlations at $p \leq 0.01$ (note that correlation between DIN and DOC is plotted behind SRP). Arrows from predictors to response variables (solid lines: RR_{NP} and RR_N) represent path coefficients at $p \leq 0.05$. Red arrows are negative relationships and blue arrows are positive relationships. To visually highlight the strongest relationships, bold lines represent Pearson correlations and path coefficients above 0.4.

on phytoplankton RR_{NP} in low versus high DOC lakes across the entire study area (Figure 5a and b). Overall, RR_{NP} was notably different between sites

of high vs. low DOC. In low DOC lakes ($< 9.6 \text{ mg C}\cdot\text{L}^{-1}$), DOC had a positive effect on phytoplankton RR_{NP} (path coefficient = 0.23), which was linked to

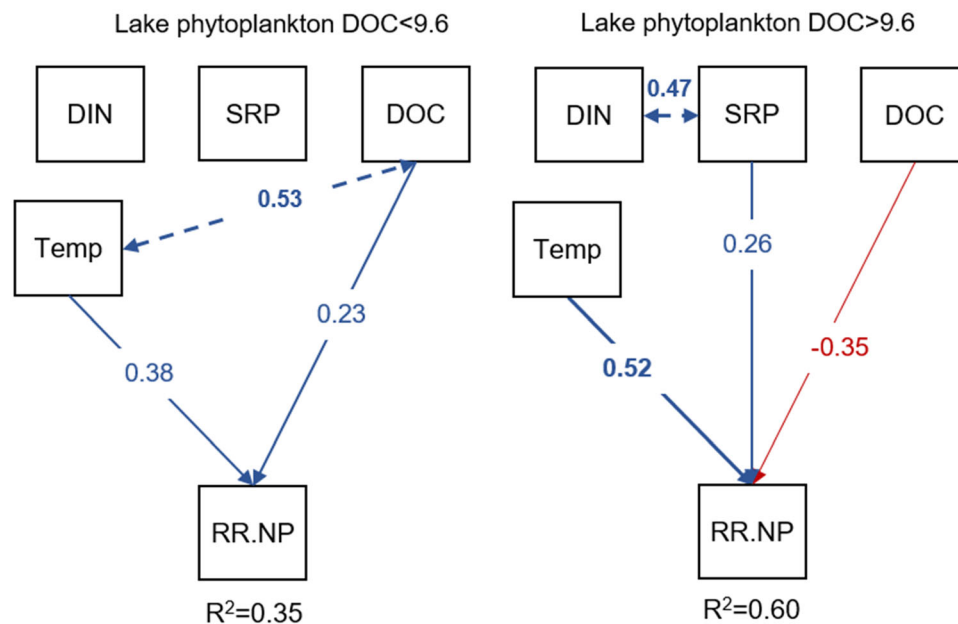


Figure 5. Path analyses of chl- α responses to NP (RR_{NP}) of low DOC lake phytoplankton ($DOC < 9.6\text{ mg C}\cdot\text{L}^{-1}$), high DOC lake phytoplankton ($DOC > 9.6\text{ mg C}\cdot\text{L}^{-1}$). Arrows between predictors (dashed lines: temperature, DIN, SRP, DOC and PAR) represent Pearson correlations at $p \leq 0.01$. Arrows from predictors to response variables (solid lines, RR_{NP} and RR_N) represent path coefficients at $p < 0.05$. Red arrows are negative relationships and blue arrows are positive relationships. To visually highlight the strongest relationships, bold lines represent Pearson correlations and path coefficients above 0.4.

positive relationships between DOC and temperature (Pearson's $r = 0.53$). By comparison, in high DOC lakes ($> 9.6\text{ mg C}\cdot\text{L}^{-1}$), DOC was negatively related to RR_{NP} (path coefficient = -0.35). For periphyton (Figure S2), DOC was strongly negatively associated with RR_{NP} (path coefficient = -0.51), presumably through a positive correlation with SRP (Pearson's $r = 0.73$) and secondarily through a negative association with light (Pearson's $r = 0.55$). Note that both incident light and DOC concentration in the streams are highly associated with canopy cover along the regional gradient from boreal to Arctic sites.

DISCUSSION

Our integration of bioassay data highlights single or primary N-limitation, with secondary P-limitation, as the most common 'status' for algae in streams and lakes from boreal to subarctic Sweden. Overall, these patterns are consistent with N-limitation of terrestrial productivity across boreal (Högberg and others 2017) and subarctic (Hicks and others 2021) Sweden, and with the growing recognition that N-limitation is common across oligotrophic freshwaters, despite theory that suggests these systems

should progress toward P-limitation (Scott and others 2019). Also, the observed transition from single and primary N-limitation in boreal regions to a greater occurrence of NP co-limitation in subarctic regions was previously reported from lake bioassays (Bergström and others 2013) and is in line with whole-lake nutrient enrichment experiments across northern Sweden (Bergström and Karlsson 2019), but appears even more pronounced for stream periphyton. Our results also generally reveal broad similarities in the strength of nutrient limitation among lakes and streams, suggesting that the physical properties of running waters that could in theory alleviate limitation (for example, greater advective flux of nutrients, King and others 2014) were insufficient given the very low background concentrations of N and P across these systems. Despite these similarities, lakes and streams were distinguished by the sets of physical and chemical variables that predicted the response to added nutrients. Such differences have landscape- and regional scale implications for how nutrients are processed and transported in northern inland waters.

Drivers of Nutrient Limitation for Aquatic Autotrophs in Boreal and Subarctic Sweden

Our analysis provides insight into the physical constraints that modify algal responses to nutrient supply in northern lakes and streams. First, warmer systems had stronger overall responses to added nutrients, similar to what has been reported for boreal and subarctic sites in the individual studies (Bergström and others 2013; Myrstener and others 2018). This temperature effect was clearer for phytoplankton, which showed notably weak responses to N-addition below 10 °C. A few of these low temperature lake bioassays were P-limited (see Figure S1, Bergström and others 2013), which may explain the low RR_N 's. In other instances, however, low RR 's at temperatures below the 10 °C threshold may reflect true physiological constraints on phytoplankton; for example, from decreased enzymatic activity induced by low temperatures (Markager and others 1999). This threshold value is significant given that epilimnetic temperatures below 10 °C are common in Arctic lakes (Granéli and others 2004; Bonilla and others 2005), particularly during shoulder seasons when nutrients may be elevated (Lougheed and others 2011). For stream periphyton, we found a similar threshold at 11.1 °C, but differences in the strength of limitation above and below this temperature were less strong, implying relatively higher tolerance of especially Arctic periphyton to extremely low temperatures (Tang and others 1997). In contrast to thermal effects, we observed less influence of light on responses to nutrient addition, but phytoplankton bioassays were not designed to test this influence (see Methods). Incident light was important for boreal forest streams, where canopy shading is often dense (Burrows and others 2021), and it clearly influenced benthic algal responses in DOC-rich boreal lakes (Fork and others 2020a). Not surprisingly, light limitation was less common for subarctic streams, many of which drain tundra landscapes with little to no canopy cover. For these streams, variation in temperature is likely to play a more important role than light as driver of algal response to changing nutrient supplies, as least throughout the summer growing season (Myrstener and others 2018).

Despite evidence that temperature and light influence the strength of limitation, variation in background nutrient concentration of streams and lakes was the main factor controlling bioassay responses within and across the region, as observed in other northern settings (Levine and Whalen

2001). We show that N-limitation prevailed across aquatic systems up to a background concentration of about 21 $\mu\text{g DIN L}^{-1}$, with error estimates extending this threshold to 30 and 40 $\mu\text{g DIN L}^{-1}$ for phytoplankton and periphyton, respectively. Although there is uncertainty around this putative threshold, it is still considerably lower than that reported for more P rich rivers of the midwestern USA, which saturate closer to 100 $\mu\text{g DIN L}^{-1}$ (Reisinger and others 2016), and for smaller streams elsewhere (for example, 50 $\mu\text{g DIN L}^{-1}$; Grimm and Fisher 1986). The lower threshold value observed across our sites likely reflects the relative ease of satisfying algal N demand in these cold, low P, and low productivity systems. In fact, while some form of N-limitation is clearly common across our sites, the threshold past which N demand is met is notably low compared to global freshwater concentrations of DIN, and suggests modest increases in N supply could alter limitation status in this region (for example, Myrstener and others 2020).

Despite the overall importance of N in these streams and lakes, there were differences in the occurrence and relative strength of N- and P-limitation between habitats and regions, which could be attributed to their distinct physical and chemical features. For example, DOC-rich boreal streams generally had higher SRP concentrations and displayed single N-limitation with no secondary responses to P. The magnitude of RR_N across these streams was mainly driven by the variation in background DIN concentrations. By comparison, SRP in boreal lakes was more variable and sometimes below detection, and DIN was universally low. Here, the strength of RR_N was positively correlated with SRP concentrations and phytoplankton more often experienced secondary limitation by P as compared to the more P-rich boreal streams. Based on these observations, we suggest that the occurrence of primary N- versus NP co-limitation for boreal aquatic ecosystems is driven by regional differences in P rather than N availability. This hypothesis is mechanistically linked to the often strong, positive association between DOC and P-supply to boreal surface waters (for example, Jansson and others 2001). For DOC-rich streams, this association appears to sustain sufficient P-supply to benthic algae. In boreal lakes, however, concentrations of both nutrients are relatively low, which increases the likelihood that phytoplankton responses to N are constrained by, and sometimes secondarily limited by, P availability.

Relationships between bioassay responses and background nutrients at subarctic sites clearly dif-

ferred from the boreal sites. For these higher latitude lake phytoplankton and stream periphyton, both primary N- and primary P-limitation occurred, and systems were more often co-limited by the two nutrients, as is commonly reported for aquatic systems globally (Elser and others 2007). Given the variation in limitation status among habitats, temperature emerged as the only universal driver of responses to N across subarctic sites. Further, in contrast to boreal sites, N appear the more important nutrient in determining the occurrence of N- versus P-limitation. This difference is likely due to the larger variability in DIN concentrations observed across our subarctic and Arctic sites relative to boreal sites. Although many of these sites are oligotrophic, some individual lakes and streams can be relatively DIN rich, either by receiving inputs of NO_3 via deep alluvial groundwater (Myrstener and others 2020; Weih 1998), or if they are located in high elevation zones with poor soil development and thus low soil N retention capacity (Bergström and others 2013). Throughout the subarctic to Arctic region, these individual systems with relatively high DIN can drive very localized and differential N- and P-responses in an otherwise strongly N-limited landscape (Myrstener and others 2020).

The Role of DOC

The effects of DOC on aquatic production can be related to DOC-associated nutrients, light attenuation, and/or altered thermal regimes (Solomon and others 2015; Olson and others 2020). Here we demonstrate that these various mechanisms also

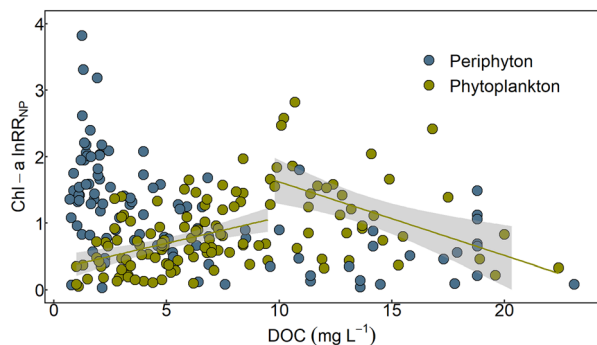


Figure 6. Relationship between chl- α response ratio to NP ($\ln\text{RR}_{\text{NP}}$) and DOC in lake phytoplankton and stream + lake periphyton. Lines represent a piecewise linear regression with a DOC threshold of 9.6 mg C L^{-1} for phytoplankton. Lines are significant at $p < 0.01$ with $R^2 = 0.31$. The slope for the low DOC RR_{NP} is 0.085, and the slope for the high DOC RR_{NP} is 0.111. Shaded area represents the 95% confidence interval for each line.

drive differences in responses to nutrient addition. Path analysis results suggest the relative importance of these mechanisms differed between lakes and streams. In streams, higher concentrations of DOC led to depressed responses to nutrient addition across the full range of observed concentrations (Figure 6), likely through a positive association between DOC and nutrient concentrations (Figure 4a), but also potentially through covariation with canopy cover and light (Burrows and others 2021). Similarly, for phytoplankton in high DOC lakes ($> 9.6 \text{ mg C L}^{-1}$, mainly boreal lakes), DOC and nutrient response ratios were negatively related (Figure 5). Light absorption by DOC could drive this negative relationship by decreasing light availability and thus constraining autotrophic responses to greater nutrient availability (for example, Bergström and Karlsson 2019; Holgersson and others 2021). Despite efforts to control for the light environment in field incubations of phytoplankton, light levels may not have been saturating in all lakes. However, an alternative mechanism for the lower nutrient responses observed at high DOC concentrations may be DOC-associated pools of organic N and/or P. Organic nutrients can represent a large fraction of the bioavailable nutrient pool in DOC-rich waters (Soares and others 2017) and could potentially reduce demand for added nutrients in bioassays.

For low DOC lakes ($< 9.6 \text{ mg C L}^{-1}$, mainly subarctic lakes), DOC and nutrient responses were positively related, ostensibly because DOC was associated with increased surface water temperature that promoted higher rates of growth in autotrophs (Edwards and others 2016, Figure 5a). Although the connection between DOC and water temperature is supported by the path analysis, it is not clear whether this arises from direct effects of DOC (for example, by absorbing more radiation, Read and Rose 2013) or reflects covariation in temperature and DOC resulting from some other factor (for example, regional landscape position). Regardless, the positive effect of DOC on RR_{NP} across this set of lakes is the opposite of what would be expected if DOC-associated nutrients were the main factor controlling this response. Further, the apparent unimodal relationship between phytoplankton nutrient responses and DOC concentration (Figure 6) differs from the responses of lake (benthic) periphyton across some of the same lakes, which show a monotonic decrease in RRs across a similar range of DOC concentrations (Fork and others 2020a). Therefore, predicting whole-lake responses to changing DOC is more complicated than may be assumed from observations of indi-

vidual habitats. Ultimately, patterns of phytoplankton nutrient limitation status recapitulated the patterns in primary productivity along gradients of DOC (the hump-shape; Hanson and others 2003; Seekell and others 2015; Bergström and Karlsson 2019). Phytoplankton in northern Fennoscandian lakes are the most productive at moderate levels of DOC (around 10 mgL^{-1} , Bergström and Karlsson 2019) which we show is also where they are the most nutrient limited and thus where changes in inorganic nutrients will have the greatest effect on algal biomass.

Implications for Environmental Change

Variation in nutrient response ratios of aquatic primary production provides insight into the potential effects of ongoing physical and chemical changes in northern waters that conventional ecosystem productivity measures may miss. First, observed N-limitation of primary production across these systems indicates that future changes in N concentrations will have direct and widespread effects on the productivity of phytoplankton and periphyton. However, the variation in limitation status and in drivers of limitation strength between sites and regions suggests that catchments in Northern Sweden will respond differently to future changes in N and P inputs. Several studies in northern Fennoscandia indicate that declining nutrient supplies to aquatic systems (that is, oligotrophication) is a dominant current trend (for example, Lucas and others 2016; Huser and others 2018; Isles and others 2018). Based on our results, we suggest that declining P in northern Sweden (Huser and others 2018) will have the strongest effects on subarctic habitats, because of more prevalent NP- and P-limitation. In boreal aquatic ecosystems, by comparison, productivity will mainly be sensitive to changes in DIN supply, due to persistent supplies of DOC-associated P and more widespread single N-limitation. However, evidence that N is declining faster than P in many northern lakes (Isles and others 2018) suggests that we might see increasing shifts toward single N-limitation, or as concentrations become extremely low, dual N- and P-limitation. In any case, lower background concentrations of DIN and SRP in lakes than streams, likely driven by the effects of longer residence times and elevated water temperature, suggest oligotrophication effects may, on average, be more severe in these ecosystems. Importantly, in a global perspective, P-limitation may be increasingly exacerbated in other parts of the boreal and Arctic biomes, particularly where ongoing permafrost

thaw is enhancing N supply while decreasing P supply to aquatic systems (Kendrick and others 2018). In this context, the effects of thawing permafrost are likely more localized in the Fennoscandian Arctic due to the patchy and discontinuous nature of permafrost cover in the region (Gisnås and others 2017).

The often strong nutrient limitation of northern aquatic ecosystems will likely dampen the ability of primary producer communities to respond positively to increasing temperatures (Levine and Whalen 2001; Myrstener and others 2018). However, it is possible that warming could alleviate this issue for N by promoting accelerated rates of biological N fixation (Huisman and others 2018), and studies of lake benthic communities in northern Sweden do report high abundance of potentially N fixing cyanobacteria (Diehl and others 2018). However, for stream periphyton and lake phytoplankton in this region, cold temperatures and very low concentrations of P and/or ferric iron are likely to constrain this process (Downing and others 2001; Molot and others 2014). In fact, assessments of phytoplankton communities from lakes across this region suggest very low relative abundance of cyanobacteria (Jansson and others 2001; Deinger and others 2017). Regardless, our bioassay data show that the ability of primary producers, and particularly lake phytoplankton, to take advantage of elevated nutrient supply can be strongly modulated by temperature. Further, we do know that lake surface-temperatures are increasing globally (O'Reilly and others 2015), but lake benthic zones are generally cooling (Bartosiewicz and others 2019). For more remote regions, stream temperature change is relatively understudied and therefore it is hard to make predictions for broad-scale temperature effects on nutrient limitation.

Finally, increases in DOC (that is, browning) have been one of the more dramatic changes observed in boreal aquatic systems over the last decades (Finstad and others 2016; Fork and others 2020b), while decreases of the same have been observed for some Arctic rivers (Kendrick and others 2018). From a nutrient standpoint, browning of freshwaters seems to have the strongest, positive effect P concentrations and therefore may amplify N-limitation (Isles and others 2020). Our results support this through the occurrence of single N-limitation at the highest DOC sites. Increasing DOC concentrations may thus have positive effects on primary producers in subarctic and Arctic sites which are more likely to have some form of P-limitation, yet are still far from DOC thresholds that correspond to strongly reduced light availability

(Holgerson and others 2021). Overall, because ongoing environmental changes are simultaneously altering concentrations of DOC (De Wit and others 2016), nutrients (Isles and others 2020), and temperature (Houser 2006) in northern lakes and streams, better understanding how these factors interact to shape nutrient limitation is crucial for predicting future lake and stream productivity.

Toward an Integrated Understanding of Northern Freshwater Nutrient Limitation

One challenge to integrating results across systems and studies is that stream and lake bioassays are conducted using different approaches. Notably, differences in experiment duration and the methods used to supply nutrients may limit our ability to synthesize findings across studies. Yet, despite a wide range in incubation times (3 to 50 days), we observed no indication that bioassay duration influenced the identity of limiting nutrient or strongly affected the strength of nutrient limitation, similar to other meta-analyses of experiments across terrestrial and aquatic ecosystems (Elser and others 2007) and in streams specifically (Ardón and others 2020). Another challenge to integrating findings concerns differences in assay construction. Phytoplankton bioassays are based solely on the organisms collected, whereas NDS experiments are open and measure organisms that colonize a new substrate, and therefore may not select equally for all algal taxa in a given system. Different methods may also be associated with unique biases. For example, P-inhibition in stream studies has been ascribed to heating treatment solutions during construction of NDS (Tanaka and others 2014; Beck and Hall 2018), which were used here for periphyton but not phytoplankton experiments. However, our results show a similar magnitude of P-inhibition for phytoplankton bioassays. In fact, we observed occasions of nutrient inhibition in response to all nutrient treatments, habitats, and types of incubations, and similar responses have been reported across aquatic and terrestrial settings (for example, Elser and others 2007). Collectively, such observations suggest that inhibition is not always a methodological artefact but can also arise from other biological or ecological mechanisms, potentially including the cost of dealing with extremely high relative nutrient supply (for example,

Elser and others 2016), and/or shifts in the composition of autotrophic communities with enrichment (for example, Jansson and others 1996; Vizza and others 2018). Regardless, differences in the approaches to studying nutrient limitation in lakes versus streams limit our ability to integrate responses to changing nutrients supply across inland water networks.

Despite these challenges, integrating assessment of lake and stream nutrient limitation of aquatic primary production is necessary to gain a landscape-scale understanding of ecosystem processes that underpin carbon and nutrient cycling. Hydrologic connectivity among these habitats is especially high in boreal and Arctic waters (Fergus and others 2017), but we seldom acknowledge the importance of such connections for cycling of elements at landscape scales. Here we show consistent N-limitation of primary production in streams and lakes across boreal to Arctic Sweden, which creates competition for DIN between connected freshwater ecosystems. Such competition for a shared resource is not universal: in the Upper Guadalupe River system (Texas, USA), Stanley and others (1990) reported differential nutrient limitation in rivers (mainly N-limited) and connected reservoirs (mainly P-limited). The broader significance of shared versus unshared resource limitation for ecological processes and biogeochemical cycling across connected aquatic habitats remains to be explored. More practically, integrated lake and stream nutrient limitation studies may help us further differentiate biologically relevant drivers from methodological artefacts, as well as separate habitat-specific (benthic/pelagic) from system-specific (lake/stream) effects (Francoeur and others 2001; Elser and others 2007). In the present case, exploring patterns of autotrophic nutrient limitation across streams and lakes that are vulnerable to ongoing global change may help us predict the future of northern aquatic networks.

ACKNOWLEDGEMENTS

We acknowledge the support for laboratory analyses from the Chemical Biological Centre (KBC-group) at Umeå University.

FUNDING

Open access funding provided by Umea University.

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DATA AVAILABILITY

The data described in this manuscript are archived in the Zenodo repository (<https://doi.org/10.5281/zenodo.6127581>).

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