

The key role of nitrogen in boosting algal growth in Arctic rivers

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Abstract

Increasing nutrient loads are impairing water quality and ecological status of aquatic ecosystems globally, but their effects on Arctic freshwaters remain less studied. Nutrients in Arctic freshwaters are increasing due to expanding anthropogenic land use and climate change induced alterations in nutrient leaching and transport. Also increased occurrences of non-native semelparous Pacific pink salmon (*Oncorhynchus gorbuscha*) in the northern European rivers can enhance nutrient availability. These additional nutrients may be readily available for aquatic primary producers in often inherently (ultra-)oligotrophic Arctic freshwaters. We used an experimental field set-up with nutrient diffusing substrates to study temporal and spatial differences in the response of primary producers to increased phosphorus (P) and nitrogen (N) levels in Arctic rivers. Additional NO₃-N enhanced algal growth (chlorophyll-*a* (Chl-*a*) amount) of epilithic biofilm. PO₄-P alone had no effect, indicating N as the primary limiting factor for algal growth. This was particularly evident in autumn while early summer showed evidence for secondary P limitation. The response to nutrient additions was mostly dictated by the background availability of inorganic N. Our results suggest that Arctic rivers are highly sensitive to nutrient additions, especially N. Thus, any increase in nutrients can boost algal growth causing cascading effects throughout Arctic ecosystems.

Key words: benthic algae, Chl-*a*, nitrogen limitation, nutrient enrichment, river network, stream biofilm

Introduction

Increasing nutrient loads are one of the major reasons for the impairment of water quality and ecological status of aquatic ecosystems globally (Vörösmarty et al. 2010; Grizzetti et al. 2012; Lemm et al. 2021). For example, far less than half of European surface water bodies reach “good ecological status” required by the European Water Framework Directive (EEA 2023) mainly due to land use pressures, such as settlement, agriculture, and forestry, which are the main sources of nutrient loads (Dudgeon 2014; Marttila et al. 2020) together with atmospheric pollution (EEA 2024). Their effects on freshwater biodiversity and ecosystem health are reported mainly from densely populated and exploited regions, whereas Arctic areas, usually with considerably less intensive land use, are underrepresented in the monitoring of ecological changes (Heino et al. 2020). Despite the low level of anthropogenic land use compared to more southerly areas, Arctic regions are not immune to global environmental changes such as anthropogenic alterations in nutrient concentrations (e.g., Choudhary et al. 2016). Even minor changes in nutrient availability may induce considerable changes in ecological processes of freshwater systems such as primary production and decomposition (Nelson et al. 2013; Ferreira et al. 2015) or

in the community characteristics of primary producers (e.g., taxonomic richness and evenness; Nelson et al. 2013). These changes at the lowest trophic levels can cascade to upper levels in freshwater food webs (Smith et al. 1999; Price et al. 2019; Canning and Death 2021). Therefore, research on the effects of additional nutrients in Arctic areas under major environmental change is urgently needed.

The magnitude of climate change is more evident in the Arctic region than elsewhere on the globe (Serreze and Barry 2011; Meredith et al. 2019). The average rise in air temperature in Arctic regions during the last four decades has been reported recently to be four times faster than the global average (Rantanen et al. 2022). In addition, climate change induced warming is weakening the strong seasonality of Arctic air temperature profiles (Xu et al. 2013), possibly lengthening the growing season. Since the 1970s, annual precipitation in the Arctic has increased by more than 9%, and precipitation falling as rain by 24% (AMAP 2021) directly impacting the runoff from land to water systems (Rawlins and Karmalkar 2024). Rivers and lakes freeze later in the year, their ice cover is thinner and lasts for a shorter time (AMAP 2021; Blåfield et al. 2024). Climate change has also been associated with alterations in the amount of snowfall (Bintanja and

Andry 2017), in the timing and duration of snowmelt events (Hinzman et al. 2020; Mudryk et al. 2023) as well as rain on snow events (Serreze et al. 2021).

These climatical transitions can alter nutrient availability in aquatic ecosystems via multiple pathways. Changes may happen in both total concentrations and in temporal patterns of nutrient availability. For example, a more benign climate and greater accessibility of remote areas can lead to intensified anthropogenic land use in the Arctic regions (Meredith et al. 2019; Heino et al. 2020). Increase of total precipitation and changes in its timing, both alone and together with intensified land use, will enhance leaching, hydrological connectivity, and transport of solutes from terrestrial catchments to aquatic environments (Spence et al. 2015; Croghan et al. 2024); whereas increased frequency and intensity of droughts can trigger seasonal shifts in dissolved organic carbon and nutrient concentrations (Gómez-Gener et al. 2020; Tiwari et al. 2022). Climate warming has also been linked to the thawing of arctic permafrost (Aalto et al. 2018), with subsequent release of ancient, stored compounds (Toohey et al. 2016; Kendrick et al. 2018). In addition to physical pathways, causes for altering water chemistry in Arctic regions may also be biological. In the Barents region, for example, the ongoing mass invasion of the non-native pink salmon (*Oncorhynchus gorbuscha*) (Dunmall et al. 2025) is likely to increase nutrient availability. The life cycle of this semelparous fish species is anadromous, i.e., divided into a river phase for spawning and hatching and a sea phase for growing and maturation, but unlike native fish, its life cycle spans only 2 years culminating in mass deaths of the whole generation soon after spawning (Heard 1991). Consequently, considerable amounts of sea derived nutrients can be released to the rivers both from pink salmon's spawning behavior and the decaying carcasses. For example, after Pacific salmon (*Oncorhynchus* sp.) spawning runs in their native distribution areas, Chaloner et al. (2007) reported, on average, 7× higher $\text{NH}_4\text{-N}$ and 4× higher soluble reactive phosphorus values, and Holtgrieve and Schindler (2011), on average, 2× higher total nitrogen (N) and 4× higher total phosphorus (P) values compared to the control concentrations.

Especially changes in N and P availability are interesting as these affect the rate of primary production across the biosphere, even though there can be substantial variation in the responses among ecosystem types (Elser et al. 2007; Harpole et al. 2011). Being inherently oligotrophic and among the least productive ecosystems, the biota in arctic rivers could be expected to readily respond to increased availability of nutrients. Epilithic algae are the key primary producers in northern rivers (Quesada et al. 2008) and their growth is usually limited by nutrients but also by the amount of light, substrate availability, and flow velocity (Stevenson et al. 1996). Based on the River Continuum Concept (RCC; Vannote et al. 1980), algal productivity (and thus the role of autochthonic resources in stream food webs) is lower in narrow headwater streams than in larger rivers, mainly due to limited light availability in streams with a dense riparian canopy. The northernmost arctic areas are completely treeless but the decrease in canopy cover and tree size is gradual as trees can grow as dwarfs or in restricted low-altitude areas such

as river valleys and stream shores. Recent decades have also shown gradual increase of shrub cover in Arctic landscapes related to climate warming (Sturm et al. 2001; Myers-Smith et al. 2011). Thus, even though the arctic river ecosystems may differ from their boreal counterparts regarding the applicability of RCC due to differences in riparian vegetation, some spatial and stream size dependent differences in light availability can still be expected. Also, the amount of light in the Arctic is extremely seasonal, being highest during summer and decreasing towards autumn, as the length of the day (daylight hours) drops from 24 h to approximately 12 h from June to September. In addition, riverbed scouring caused by increased discharge and suspended sediments during the snowmelt-induced spring flood can detach biofilm from benthic substrates (Biggs et al. 1999; Hoyle et al. 2017), leading to seasonal differences in the amount of epilithic algae.

The aim of this research was to study the reactivity of epilithic primary producers to additional nutrients across a network of various sized Arctic rivers at the two extremes of the growing season: early summer and autumn. We expected to see an overall increase in algal growth (Chl-*a* accrual) due to nutrient additions (Hypothesis 1; *H1*), but the magnitude of response was hypothesized to vary depending on the season (i.e., higher in early summer vs. autumn; *H2*) and river size (i.e., higher in larger rivers vs. smaller streams; *H3*) due to expected differences in light availability. In addition, the strongest responses to nutrient additions were expected to be seen at the most oligotrophic sites (*H4*). To test for these effects, we established a field experiment using nutrient diffusing substrates (NDS) replicated across (i) two time periods (early summer vs. autumn), and (ii) 18 stream/river sites located within the arctic Teno River catchment and varying from 1st to 6th order in size.

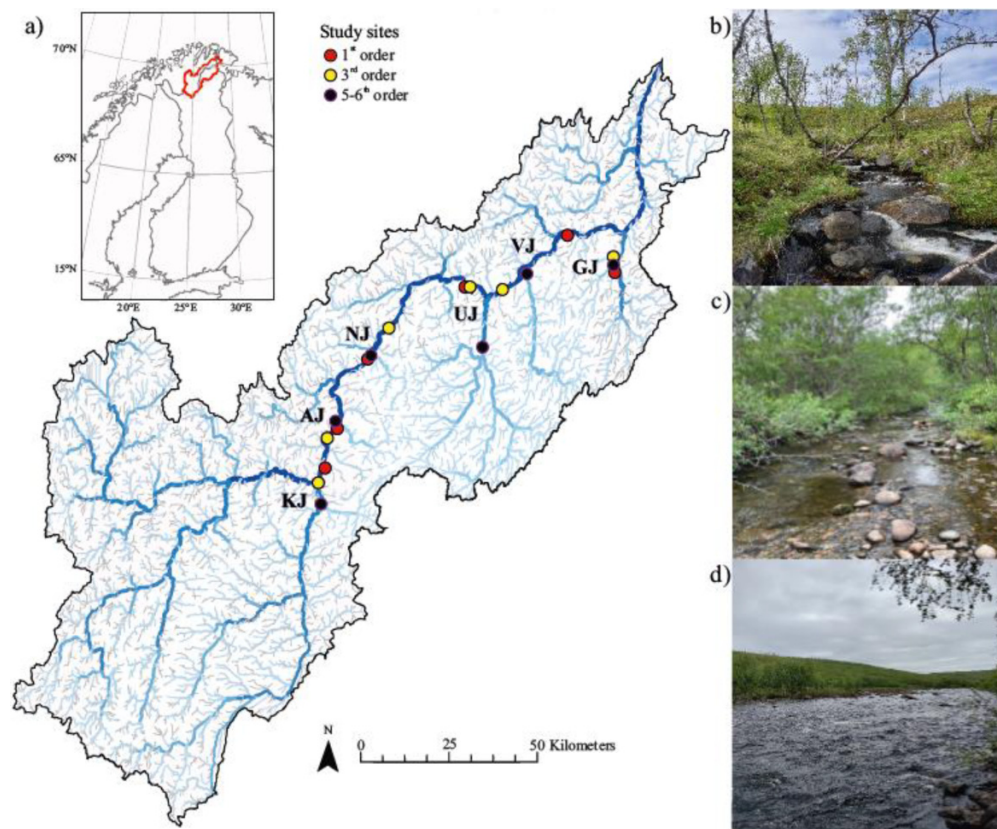
Materials and methods

Study sites

The study was conducted within the Teno (a.k.a. Tana or Deatnu) River catchment in northernmost Finland. Teno River is an Arctic/subarctic border river located between Finland and Norway and draining into the Barents Sea. Its total catchment area is 16 400 km² and total river length 360 km. The annual mean discharge is 177 m³s⁻¹, but spring floods peak up to 2000–3000 m³s⁻¹ (Jelovica et al. 2024). The annual precipitation ranges from ca. 300 to 500 mm and mean air temperature from ca. 0 to -3 °C (Koster et al. 2005). The average length of the terrestrial thermal growth season is 105–125 days/year. Lower latitudes of the area are dominated by arctic-alpine terrestrial vegetation with typical tree species being mountain birch (*Betula pubescens* ssp. *czerepanovii*) and a few willow species (*Salix* sp.), whereas at higher altitudes, vegetation consists of treeless tundra. Streams in the area are typically inherently ultraoligotrophic with circumneutral water (Tolonen et al. 2017).

In total, 18 spatially independent study sites were selected from the Teno River catchment area based on their location and size (Fig. 1) so that the final set included an equal number

Fig. 1. (a) Location of the study catchment and the study sites. Different size classes are shown with different colors. Letters refer to the closest 5–6th order river based on which each site is coded. Codes and river names are given in Table S1. Photos (b–d) provide examples of each size class: 1st (VJ-1: Gorrehatája), 3rd (VJ-3: Gárnjájohka), and 5–6th (VJ-6: Vetsijoki) order streams, respectively (© Kaisa-Leena Huttunen & Aino Erkinaro). Basemap data sources: opendatasoft (*world-administrative-boundaries*, 08/22), National Land Survey of Finland (*topographic database*, 08/22), Norwegian Mapping Authority (*dtm10_utm33*, 08/22).



of 1st, 3rd, and 5–6th order rivers, and that these size classes were spatially interspersed. Direct human impact in the area is minimal and spatially limited (agriculture 0%–0.02%, urban area (i.e., artificial substrates) 0%–3.2%; Table S1).

Nutrient addition experiment and field measurements

We used NDS, i.e., cups filled with nutrient-amended agar and topped with a substrate mimicking stone surface (e.g., Tank et al. 2007), to test the reactivity of epilithic algal communities to additional nutrients and, consequently, to identify the resources limiting algal growth in Arctic rivers. The experiment was conducted in 2022 and replicated at the same study sites twice, early summer (June–July) and autumn (August–September), to study potential seasonal differences in biological responses to nutrient availability. Due to the differences in the introduction success of odd and even year pink salmon populations (Dunmall et al. 2025), the mass invasions in Europe are occurring only in odd years. Thus, there was no real pink salmon impact on nutrient availability during the experiment in 2022.

NDS were prepared following the instructions by Tank et al. (2007), with minor adjustments. Forty milliliters plastic tubes were filled full either with plain agar (control) or with agar en-

riched with 0.5 mol/L NaNO₃ (N treatment), 0.5 mol/L KH₂PO₄ (P treatment), or both 0.5 mol/L NaNO₃ and 0.5 mol/L KH₂PO₄ (N + P treatment). Porous ceramic tiles (5.9 cm²) allowing steady diffusion of nutrients were placed on top of the agar-filled cups and attached firmly with plastic lids with a spherical hole in the middle, leaving the upper surface of the tiles available for biofilm formation. Four replicates of each treatment were prepared for each site and attached as sets of all four treatments in a random order within each block to two steel L-bars per site, covered with a plastic foil and stored in dark until reaching the field sites.

L-bars were attached firmly to the stream bottom selecting optimal habitats for epilithic algal growth and ensuring the similarity of water depth and stream velocity across sites as well as feasible. A HOBO logger (Onset Computer Corporation, Borne, USA) was attached to one of the L-bars at each site to measure water temperature and light availability once an hour during the experiment. Water depth and velocity (Schiltknecht MiniAir 20; Schiltknecht, Gossau, Switzerland) on top of the tiles were measured at each L-bar location in both the beginning and end of the experiment. NDS cups were incubated in the rivers for 23–26 and 25–29 days in early summer (13 June to 13 July 2022) and autumn (15 August to 16 September 2022), respectively. Duration from 3 to 4 weeks was used to ensure biofilm formation and the sufficiency of

diffusing nutrients. After each incubation period tiles were removed from the cups, placed to individual zip-bags, and stored in a dark cold box until freezing to -20°C within the same day.

Water samples were collected from each site on both occasions ($n = 18 + 18$) from the water column to describe in situ nutrient availability. Water samples were frozen and analyzed later for pH, nitrogen (dissolved $\text{NO}_2 + \text{NO}_3$, NH_4) and phosphorus (dissolved PO_4) following the Finnish standards. $\text{NO}_2 + \text{NO}_3$ and NH_4 were summed to present dissolved inorganic nitrogen (DIN). Additional site-specific hydromorphological measurements were conducted to describe the study sites. These included (i) assessment of substrate size distribution (simplified Wentworth scale: sand (<2 mm), gravel (2–16 mm), pebble (16–64 mm), small cobble (64–128 mm), large cobble (128–256 mm), boulder (256–400 mm), and bedrock (>400 mm)) from 10 randomly positioned $0.5 \text{ m} \times 0.5 \text{ m}$ plots to obtain dominant substrate size and substrate diversity (Simpson's D); (ii) estimates of bryophyte cover (%) from the same plots; and (iii) water depth and stream velocity measurements from 20 spots distributed along five cross-sections. Replicated measurements were summarized to site-specific averages and coefficients of variation for each variable.

In addition, site-specific grazing pressure was evaluated based on the proportion (dry weight) of scraper or collector-gatherer invertebrates which may use epilithic algae as nutrition. These data were obtained from a separate study based on 2 min kick net sampling for stream macroinvertebrates from the same sites (Palomäki 2024).

Laboratory protocol

Chl-*a* amount was used as a measure of epilithic algal growth. To obtain Chl-*a* we used acetone extraction following closely the protocol presented in Steinman et al. (2017). Thawed tiles were placed to clean containers, submerged to 10 mL of 90% MgCO_3 -buffered acetone, sealed tightly and stored in $+4^{\circ}\text{C}$ dark conditions. After 24 h, the tiles were removed from the containers. The remaining liquid containing Chl-*a* pigment was poured to centrifuge tubes and centrifuged for 6 min. Sample absorbance was measured at wavelengths of 664 and 750 nm using a spectrophotometer (UV-1700 PharmaSpec, Shimadzu, Japan). After the first measurements, 0.1 mL of 1 mol/L HCl was added to the sample and absorbance was re-measured at wavelengths of 665 and 750 nm to obtain corrections for pheophytins (Steinman et al. 2017).

Chl-*a* amount was calculated with the following formula (Steinman et al. 2017):

$$\text{Chl-}a \text{ } (\mu\text{g}/\text{cm}^2) = 26.7 \times [(A_{664} - A_{750}) - (A_{665} - A_{750})] \times (V/a) \times L$$

where 26.7 is the absorbance correction for acetone extraction, *A* is the absorbance at a certain wavelength before (A_{664}) or after acidification (A_{665}), *V* is the volume of acetone used in the extraction (mL), *a* is the tile area (cm^2), and *L* is the length of light path through cuvette (cm). The obtained values were divided by the number of incubation days

to standardize the among-site differences in the duration of in-stream incubation.

Statistical analyses

We used one-way Analysis of variance (ANOVA) with Tukey's HSD for pairwise comparison to study the site-specific differences in algal growth (Chl-*a* accrual) among nutrient treatments, separately for early summer and autumn sampling (*H1*). Paired *t* test and one-way ANOVA were used to test for the differences in light availability between seasons and size classes, respectively. A three-way repeated ANOVA (Fig. S1) was used to test for the effects of season and/or stream size on responses to nutrient additions (*H2*, *H3*). For this purpose, relative responses (i.e., $\log(\text{treatment/control})$) were used instead of absolute values. In this way, the responses to nutrient additions were normalized across rivers by scaling relative to control (i.e., ambient) Chl-*a* amounts (Tank and Dodds 2003), accounting for the potential site-specific differences in algal growth.

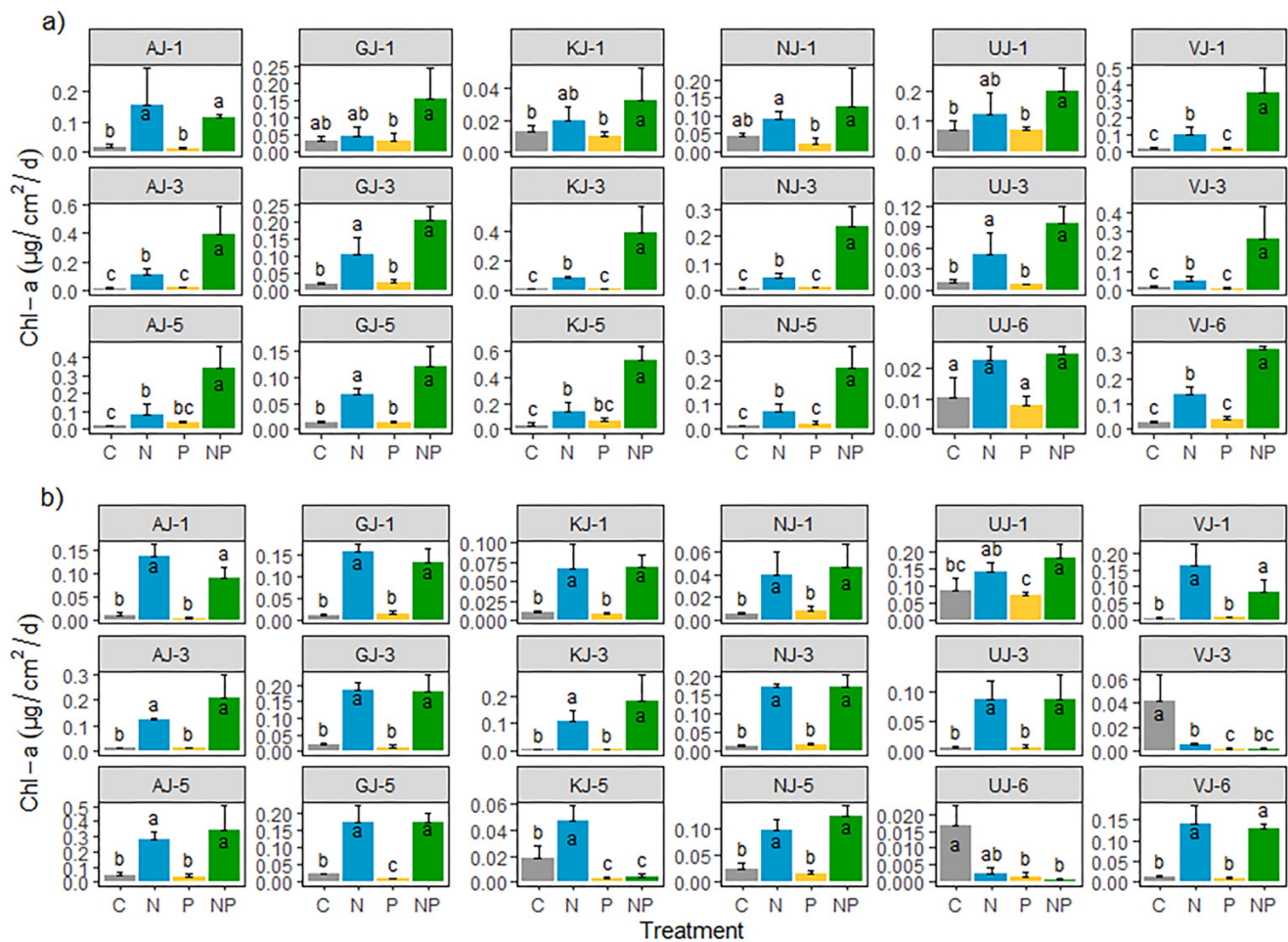
Univariate regressions were used to link the responses to differences in original nutrient availability in the water column, separately for both seasons (*H4*). In addition, multiple regression based on multimodel inference and Akaike information criterion (package MuMIN ver. 1.46.0 in R; Bartón 2022) was used to study further the effect of local environmental variables on site-specific responses for nutrient additions. The explanatory variables for multiple regressions included catchment size, stream velocity, light availability, water temperature, and water column DIN and PO_4 . Prior to multiple regressions, variation inflation factor (VIF) was calculated to test for multicollinearity among explanatory variables. All included variables had $\text{VIF} < 5$ and were thus used in the modeling. Importance values, calculated separately for each explanatory variable as summed weights across all models including a certain variable, was used to compare their relative importance (Burnham and Anderson 2002; Johnson and Omland 2004).

All statistical analyses were run in R (ver. 4.1.0; R Core Team 2021). Data normality and equality of variances were tested with Shapiro–Wilk and Levene's tests, respectively, and transformations ($\log(x + 1)$) were used if needed to improve data distribution.

Results

Nutrient additions led to an overall increase in algal growth (Chl-*a* accrual) at all study sites in both seasons, but there were differences between treatments and seasons in the magnitude of responses. P alone did not differ from the control in either season, whereas N alone or N and P together mainly did (Fig. 2). However, site-specific responses to nutrient treatments seemed to differ between the seasons. In early summer the amount of Chl-*a* was highest in the N + P treatment, differing significantly from all other treatments at most of the sites in intermediate and large rivers but only at one of the small streams (VJ-1; Fig. 2a); whereas in autumn N alone had an equally strong effect than N and P together independent of river size (Fig. 2b). Chl-*a* accumulation on unamended con-

Fig. 2. The amount of Chl-*a* ($\mu\text{g}/\text{cm}^2/\text{day}$) in different treatments (C = control, N = nitrogen, P = phosphorus, NP = nitrogen + phosphorus), separately for each study site in (a) early summer and (b) autumn. Different letters above the bars indicate statistical differences ($p < 0.05$) between the treatments using log-transformed data. Note that the scale of the y-axis differs between the sites. For both seasons the rivers are in size order so that the the upmost row presents small (1st order) streams, middle row intermediate (3rd order), and the lowest row the largest (5–6th order) rivers.



control tiles were greatest in small streams in early summer, and lowest in small streams in autumn (Fig. 2, Fig. S2).

As expected, light availability was higher during the early summer study period compared to autumn (Fig. S3; $t_{17} = 4.48$, $p < 0.001$ for $\log(x + 1)$ transformed data), supporting our background assumption of seasonal differences in the overall response to nutrient treatments (H2). Similarly, there were differences in light availability among stream size classes on both seasons (Fig. S2; $F_{2,15} = 10.72$, $p = 0.001$ in early and $F_{2,15} = 7.51$, $p = 0.006$ in autumn). The largest rivers had the highest light intensity, supporting the background assumption of the strongest response in biomass accrual in larger rivers with the least light limitation (H3). However, although relative responses to nutrient additions differed clearly between the treatments (Fig. 3), there were no significant main effects of the seasons or the size classes (Table 1). The treatment*season interaction was significant; however, supporting the site-specific results of seasonal differences in responses of algal biomass to the N treatment. Based on post hoc pairwise comparisons, the difference between N and

N + P treatments was not significant in autumn ($t_{17} = 1.43$, $p = 0.516$) while all other pairwise treatment comparisons in both seasons were significant ($p < 0.001$).

In addition to among-group differences, we tested whether the relative responses to nutrient additions were related to the original in situ nutrient concentrations (H4), focusing only on N and N + P treatments since the responses to P alone did not differ from the control. In early summer there was a clear trend of decreasing relative response with increasing DIN concentration in the water column, both for N ($R^2 = 0.31$, $p = 0.017$) and N + P ($R^2 = 0.42$, $p = 0.004$) treatments, but no similar relationship regarding availability of PO_4 (Figs. 4a and 4b). In autumn, the relative responses to N or N + P treatments were not related to water column DIN nor to PO_4 (Figs. 4c and 4d).

We also used multimodel inference to test whether some other environmental variables instead of, or in addition to, river size (linked to light conditions) or background water column nutrient availability explained the site-specific relative responses. The best explanatory models for the early-summer

Fig. 3. Relative responses (i.e., $\log(\text{treatment}/\text{control})$) of algal biomass accrual to different nutrient treatments separately for each size class in (a) early summer and (b) autumn. Boxes show medians and quartiles, whiskers the range ($\pm 1.5 \times$ the interquartile range) and black dots the outlying data points. Each box is based on site-specific averages for each season and treatment (i.e., $n = 6$).

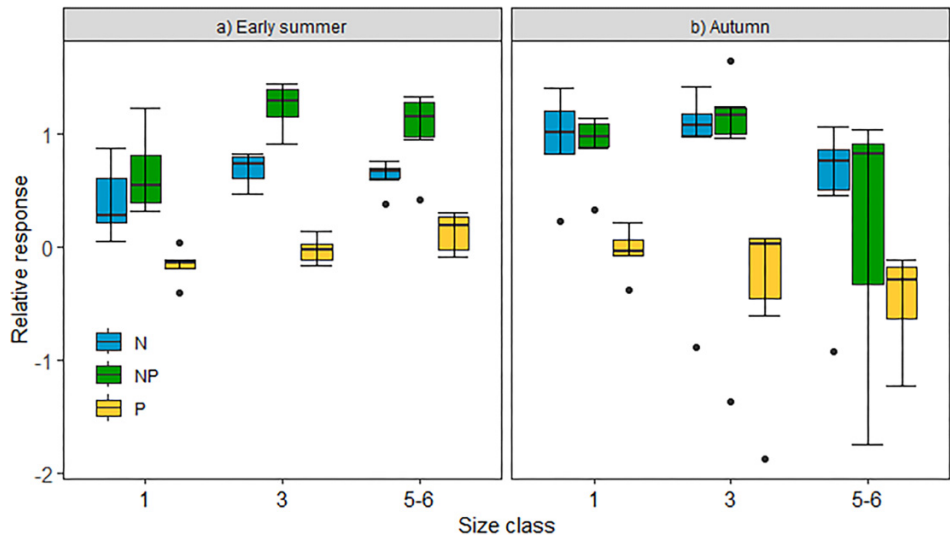


Table 1. Results of ANOVA for the effects of size class, treatment, season, and their interactions.

	Df	F value	p value
Size class	2, 15	0.33	0.722
Treatment	2, 30	128.75	<0.001
Season	1, 15	0.99	0.334
Size \times treatment	4, 30	2.17	0.097
Size \times season	2, 15	2.76	0.095
Treatment \times season	2, 30	16.47	<0.001
Size \times treatment \times season	4, 30	0.95	0.447

Note: Statistically significant ($p < 0.05$) p values are highlighted in bold.

responses to N and N + P treatments included light intensity and water column DIN, the magnitude of the response decreasing with availability of in situ nutrients and light limitation. DIN concentration had the highest importance value of these two for both treatments (Tables 2a and 2b). In autumn, the relations of treatment responses to explanatory variables were dictated by three outlier sites (KJ-5, UJ-6, and VJ-3) with unexpectedly low Chl-*a* concentrations (Fig. 2b) and higher proportion of scraper or collector-gatherer invertebrates compared to other sites on average (Table S1). When including these sites, responses to N or N + P additions were best explained by the catchment size with weaker responses in larger rivers (Tables 2c and 2d). When the outlier samples were excluded, there were no statistically significant explanatory models for either treatment.

Discussion

Impairment of water quality due to excess of nutrients has been identified as one of the key reasons for biodiversity loss and for weakening of ecological status of aquatic

ecosystems (Vörösmarty et al. 2010; Lemm et al. 2021). Being inherently oligotrophic and among the least productive ecosystems globally, the northernmost rivers may be especially prone to additional nutrient inputs resulting from human activities and climate change through multiple pathways. On the other hand, strong oligotrophy may lead to a situation where neither N nor P addition alone is sufficient to boost autotrophic productivity, thus increasing the likelihood of nutrient colimitation at high latitudes (Harpole et al. 2011). Here we studied the sensitivity of Arctic rivers to climate-change associated nutrient additions by measuring the reactivity of epilithic primary producer biomass accrual rate to additional major nutrients in a spatially and temporally replicated field experiment. The results showed that nitrogen was the key limiting factor for algal growth, independent of sampling season (early summer vs. autumn) or river size (1st to 6th order). The magnitude of the response was dependent on the ambient DIN concentration, being greatest at the most oligotrophic sites, but only in early summer.

Both N (alone) and N + P (together) treatments increased algal growth, whereas P (alone) treatment did not differ from the control showing that nitrogen is the key limiting nutrient for epilithic algal growth in these northernmost European rivers. As such, our results support the findings by Myrstener et al. (2018) and Burrows et al. (2021), from similar types of field experiments stating that biofilm activity and biomass accrual were persistently N limited along a climate gradient in Arctic Sweden. Together these results contrast with the expectation of nutrient colimitation at high latitudes (Harpole et al. 2011; Myrstener et al. 2022), the widespread, but potentially biased view (e.g., Elser et al. 2007) of overall P limitation in freshwaters, and with observations from lotic field experiments in Alaska reporting enhanced algal growth as a response to PO_4 additions (Slavik et al. 2004; Kendrick and Huryn 2015; Covino et al. 2021). Similar to other studies in

Fig. 4. Relative responses to N and N + P treatments in relation to background water column dissolved inorganic nitrogen (DIN) (a), (c) and PO₄ (b), (d) concentrations in early summer (above) and in autumn (below). Solid and dashed lines denote statistically significant ($p < 0.05$) and non-significant linear regressions, respectively. Note that the scale of the x-axis and y-axis partly differs among the plots. For the visual purposes, one site with outlying DIN concentration in autumn (i.e., 31 $\mu\text{g/L}$, see Table S1) was removed from the autumn plot.

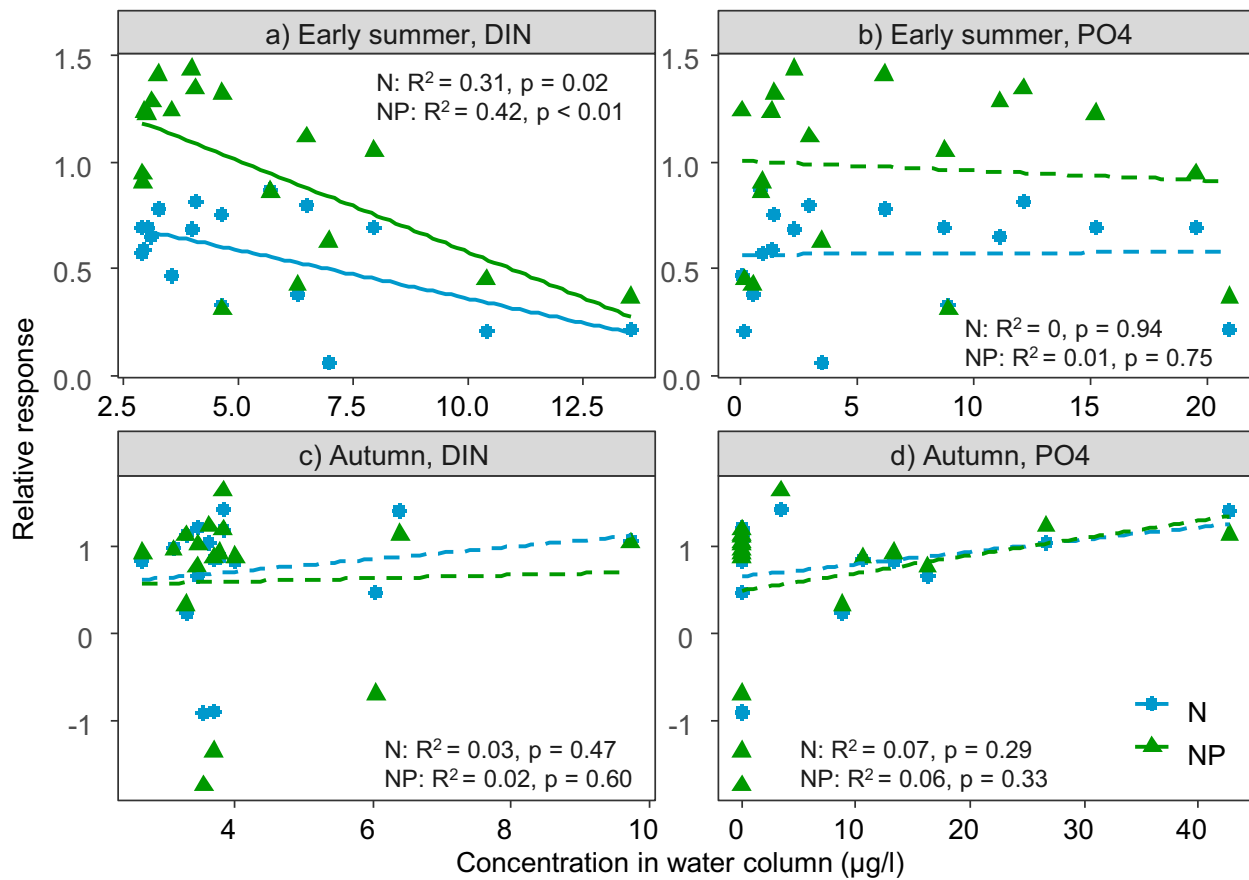


Table 2. Standardized regression coefficients for the best models ($\Delta\text{AICc} < 2$) explaining mean responses to N or N + P treatments in early summer (a, b) and autumn (c, d).

	Catchment size	DIN	PO ₄	Light intensity	Water temp.	Stream velocity	Adj. R ²	ΔAICc
a) Early summer N	x	−0.55	x	x	x	x	0.26	0
	x	−0.41	x	0.36	x	x	0.34	0.23
	x	x	x	0.52	x	x	0.23	0.76
Importance:	0.19	0.65	0.14	0.53	0.15	0.2		
b) Early summer N + P	x	−0.65	x	x	x	x	0.38	0
	x	−0.56	x	0.23	x	x	0.39	1.89
Importance:	0.29	0.9	0.13	0.27	0.18	0.17		
c) Autumn N	−1.11	x	x	x	x	0.71	0.41	0
Importance:	0.93	0.21	0.21	0.12	0.13	0.69		
d) Autumn N + P	−0.58	x	x	x	x	x	0.30	0
	−1.01	x	x	x	x	0.54	0.37	0.21
Importance:	0.91	0.15	0.18	0.13	0.14	0.43		

Note: x denotes that a predictor variable was not included in that model. The overall importance, i.e., summed weights across all candidate models is presented for each predictor. The highest importance value is highlighted in bold. AIC, Akaike information criterion.

the northernmost European rivers (e.g., Docherty et al. 2018; Myrstener et al. 2018; Burrows et al. 2021), P alone was not sufficient to boost biomass accrual and, in a few cases, P addition seemed to even inhibit algal growth. The negative effects

of P additions in NDS experiments have sometimes been suggested to be an artefact due to methodological issues such as incubation time, salt type, and agar preparation (Beck et al. 2017; Pastor et al. 2020). However, this artefact effect seems

unlikely in cases where secondary (or serial; sensu Harpole et al. 2011) P limitation (i.e., significantly higher responses to N + P additions compared to N alone) has been reported from the same experiments. The Swedish tundra streams were shown to be secondarily P limited (Myrstener et al. 2018) similar to streams in NE Greenland (Docherty et al. 2018). In our research, secondary P limitation was also observed, but only in early summer when the responses to N + P treatments at most of the intermediate and large river sites were greater than to N alone. In autumn the responses to N and N + P additions were equal independent of the stream size indicating single N limitation. Thus, even though there were no significant (main effect) differences between the seasons, seasonality influenced site-specific responses to N and P additions, as importance of N limitation increased towards autumn. Similarly, Myrstener et al. (2018) observed stronger responses to N additions towards autumn, possibly linked to simultaneously decreasing DIN concentrations.

One important factor potentially limiting autotrophic productivity and explaining the differences in nutrient treatment responses is light availability (Beck et al. 2017). Thus, we expected to see differences in the magnitude of responses between size classes and seasons due to the assumed stream-size and season related differences in light conditions. There were indeed clear differences in light availability between the size classes and also between sampling seasons, but not in the responses to nutrient additions. This differs from Burrows et al. (2021) who also reported seasonal differences in algal biomass responses to nutrient additions, linking the absence of treatment responses in late season to light limitation in boreal forest streams. However, while we did not observe overall differences between seasons or size classes in the relative responses of algal growth to nutrient additions, light intensity was included in some of the best explanatory models in multiple regressions. Light increased the magnitude of the responses, but it was mostly of secondary importance and included in the models only in early summer. This discrepancy between our ANOVA and regression results is probably due to the high within group variability in light availability especially in early summer (Fig. S3). Some streams and rivers, independent of their size class, were surrounded by unexpectedly dense mountain birch and willow forests, while others had only a few scattered trees or treeless tundra vegetation in their riparian zones (Figs. 1b–1d). This represents normal variation in the subarctic–arctic border vegetation and, consequently, hints to finer-scale among-site differences in limiting factors (Jarvie et al. 2018; Myrstener et al. 2018; Burrows et al. 2021).

Instead of light, the magnitude of the response to nutrient additions was mostly dictated by the background availability of inorganic nitrogen in the water column. As expected, the most oligotrophic sites showed the greatest response to N or N + P additions (see also Beck et al. 2017; Ardón et al. 2021; Myrstener et al. 2022). Interestingly, and similar to light availability, this response was observed only in the early summer, supporting further the importance of seasonal variation not only in the role of the key nutrients but also in other environmental conditions for algal growth (Myrstener et al. 2018; Burrows et al. 2021). In the autumn, the magnitude of

the response was related to catchment size. This pattern of the larger rivers showing weaker responses was fully dictated by three outlier sites with unexpectedly low Chl-*a* concentrations compared to other sites or early-summer samples. These sites seemed to differ from the other sites by having a higher proportion of scraper (UJ-6: 70%) or collector-gatherer invertebrates (VJ-3: 42%, KJ-5: 37%) than all other sites on average (4% and 25%, respectively), which may have resulted in higher biofilm consumption by benthic invertebrates and consequently to a deviating outcome (Hillebrand 2002). However, the inclusion or exclusion of the outlier samples did not affect other main interpretations of the results. Overall, the background availability of nitrogen was clearly more important than phosphorus in dictating the magnitude of responses to nutrient additions. Elser et al. (2007) suggested that terrestrial tundra vegetation responds more strongly to N than P additions because tundra soils are relatively young, contain less organic matter, and have higher natural P supply from soil and bed rock compared to lower latitudes. As the streams drain their water from the surrounding soils, the same might hold also for aquatic ecosystems. For example, in the early summer, small rivers can have relatively higher snowmelt-induced soil water runoff from adjacent terrestrial landscapes (Croghan et al. 2023; Noor et al. 2023), leading to increased carbon and nutrient concentrations (Croghan et al. 2024) compared to larger rivers. This could be, at least partly, the reason why smaller streams showed no signs of secondary P limitation. Indeed, the smallest rivers in early summer had the highest algal growth on unamended control tiles suggesting less constrained early season productivity compared to later season and larger rivers. However, this does not explain the observed absence of secondary P limitation in autumn independent on the river size. There may be some environmental variables, like light availability (Burrows et al. 2021), that mask P limitation, but it may also reflect seasonal differences in the overall availability of P (Weintraub 2011; Shogren et al. 2019), in our case better autumnal availability, in relation to its need in arctic river ecosystems.

The recently increased numbers of the non-native semelparous pink salmon (Sandlund et al. 2019) may increase nutrient concentrations in Arctic rivers. Especially NH₄-N and P concentrations can be expected to increase in (and downstream of) pink salmon spawning areas (Chaloner et al. 2007; Holtgrieve and Schindler 2011). In its native range, in rivers draining to north Pacific Ocean and adjacent regions of the Bering Sea and Arctic Ocean, the marine-derived nutrients released from pacific salmon are utilized by primary producers in both aquatic and terrestrial ecosystems, as indicated by, for example, $\delta^{15}\text{N}$ values, and increased algal and salmonberry (*Rubus spectabilis*) fruit production (Wipfli et al. 1999; Bartz and Naiman 2005; Rüegg et al. 2020; Siemens et al. 2020). Based on our results, nitrogen alone is sufficient to boost algal growth especially in autumn. As pink salmon spawning and consequent mass decay of fish carcasses in our study area occurs from August to September (i.e., overlapping the autumn sampling period in this experiment), algal growth could increase markedly due to pink salmon presence, resulting in localized benthic algal blooms. In addition, since

pink salmon mass occurrences are expected to increase especially NH_4^+ compared to NO_3^- (Chaloner et al. 2007), even stronger responses may be possible, as of these two, NH_4 is in theory more readily used by algae (Glibert et al. 2016). As pink salmon occurrence is expected to increase the availability of P as well, it seems unlikely that these systems would shift from N to P limitation. Nutrient enrichment may also change the structure of primary producer communities by, for example, favoring certain taxa and decreasing diversity (Slavik et al. 2004; Gudmundsdottir et al. 2013; Huttunen et al. 2020). Considering the key role of benthic algae in arctic river ecosystems (Stevenson et al. 1996), cascading effects across the food web, such as increased secondary productivity of stream invertebrates (Neijns et al. 2024) and changes in community composition of consumers (Canning and Death 2021), may be expected. In addition to primary productivity, other microbial activity (e.g., decomposition) is likely to be enhanced by additional nutrient availability, with further impacts on nutrient cycling (Gulis et al. 2004; Ferreira et al. 2015; Biasi et al. 2017).

Advanced understanding of the temporal and spatial range of potential climate-change induced alterations in nutrient availability is required for evaluating their ecological effects. Especially temporally replicated studies aiming to widen the seasonal scale from spring thaw until freezing would be crucial for the comprehensive understanding of the seasonality of in-stream nutrient availability and the temporal patterns of algal responses to additional nutrients (e.g., Kendrick and Huryn 2015; Covino et al. 2021). In addition, long-term and reach-scale nutrient manipulations is needed to confirm whether conclusions from smaller scale NDS experiments hold at larger scales, or whether differences in study scale could explain the sometimes-contrasting results of P and N limitation in Arctic streams (Slavik et al. 2004; Ardón et al. 2021). This information on varying nutrient availability and its ecological consequences is especially crucial for Arctic regions that are experiencing severe environmental changes yet remain largely underrepresented in ecological research. As a result, there is a lack of research-based information needed for predicting future changes of these vulnerable ecosystems.

Acknowledgements

We thank Anton Pajukoski, Veera Kohtamäki, Aino Juutinen, and Taika Lehtimäki for laboratory and field assistance; Research Council of Finland via grant No. 356403 and 347662, ARCI Advancing Arctic Collaborations and Biodiverse Anthropocenes research programmes, Kvantum Institute (University of Oulu) and Kone Foundation for funding; and Oulanka Research Station for water chemistry analyses.

Article information

History dates

Received: 22 November 2024

Accepted: 19 March 2025

Accepted manuscript online: 31 March 2025

Version of record online: 6 May 2025

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Data availability

Data generated and analyzed during this study are available in the Dryad repository (DOI:10.5061/dryad.1zcrjdg2w), <https://doi.org/10.5061/dryad.1zcrjdg2w>.

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Competing interests

The authors declare there are no competing interests.

Supplementary material

Supplementary data are available with the article at <https://doi.org/10.1139/as-2024-0074>.

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