



Light and nutrient control phytoplankton biomass responses to global change in northern lakes

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Abstract

Global change affects terrestrial loadings of colored dissolved organic carbon (DOC) and nutrients to northern lakes. Still, little is known about how phytoplankton respond to changes in light and nutrient availability across gradients in lake DOC. In this study, we used results from whole-lake studies in northern Sweden to show that annual mean phytoplankton biomass expressed unimodal curved relationships across lake DOC gradients, peaking at threshold DOC levels of around 11 mg/L. Whole-lake single nutrient enrichment in selected lakes caused elevated biomass, with most pronounced effect at the threshold DOC level. These patterns give support to the suggested dual control by DOC on phytoplankton via nutrient (positively) and light (negatively) availability and imply that the lakes' location along the DOC axis is critical in determining to what extent phytoplankton respond to changes in DOC and/or nutrient loadings. By using data from the large Swedish Lake Monitoring Survey, we further estimated that 80% of northern Swedish lakes are below the DOC threshold, potentially experiencing increased phytoplankton biomass with browning alone, and/or combined with nutrient enrichment. The results support the previous model results on effects of browning and eutrophication on lake phytoplankton, and provide important understanding of how northern lakes may respond to future global changes.

KEYWORDS

dissolved organic carbon, nitrogen, phosphorus, phytoplankton, whole-lake nutrient enrichment experiments

1 | INTRODUCTION

Nutrient poor northern lakes dominate the population of lakes globally (Downing et al., 2006; Karlsson et al., 2009; Lewis, 2011) and these ecosystems are under pressure from global change (Creed et al., 2018). Increased loadings of terrestrial colored dissolved organic carbon (DOC) attributed to recovery from acidification (Monteith et al., 2007), and/or climate- and land-use changes (de Wit et al., 2016; Finstad et al., 2006; Kritzberg, 2017; Larsen, Andersen, & Hessen, 2011), result in browning of many of these lakes. Intensified land use (i.e., forestry and agriculture), and utilization of fertilizers and fossil fuels (Hessen, Andersen, Larsen, Skjelvåle, & Wit, 2009; Isles, Creed,

& Bergström, 2018; Kreutzweiser, Hazlett, & Gunn, 2008; Vitousek, 1997) further elevate nutrient loadings. Despite these broad and large-scale environmental changes operating on northern lakes, our knowledge of how browning alone or combined with nutrient enrichment affect these ecosystems is incomplete, which limit our ability to predict their future conditions (Creed et al., 2018; Solomon et al., 2015).

Understanding controls on phytoplankton biomass development is essential to our ability to assess global-change impacts on lake ecosystems. Phytoplankton play a key role in elemental cycles and support of lake food webs (Jansson, Persson, DeRoos, Jones, & Tranvik, 2007; Sterner & Hessen, 1994) and although changes in

both colored DOC and nutrient input are expected to affect their development, there is a paucity of information about how these changes will operate at the whole-lake scale. In northern lakes, colored DOC of terrestrial origin is a main factor controlling light conditions (Karlsson et al., 2009), which can be an important factor constraining phytoplankton biomass development especially in more humic lakes (Carpenter, Cole, Kitchell, & Pace, 1998; Jones, 1992; Thrane, Hessen, & Andersen, 2014). In addition, terrestrial DOC inputs promote development of heterotrophic bacteria (Hessen, 1985; Jansson, Bergström, Drakare, & Blomqvist, 2001), which may outcompete phytoplankton for limiting inorganic nutrients, thereby constraining their development even further in addition to poor light conditions (Jansson et al., 2007).

On the other hand, terrestrial DOC input can be positive for phytoplankton by the concomitant input of nutrients as nitrogen (N) and phosphorus (P) to lakes (Jones, 1992; Solomon et al., 2015), and by causing carbon dioxide (CO₂) supersaturated lake water (Jansson, Karlsson, & Jonsson, 2012). Although phytoplankton biomass is generally stimulated by nutrient supply, few whole-lake nutrient enrichment experiments exist in northern lakes. Phytoplankton development and their response to limiting nutrient enrichment is commonly tested in short-term bioassay enclosure experiments which usually test nutrient limiting conditions per se as being incubated at sufficient light levels (Bergström, Faithfull, Karlsson, & Karlsson, 2013; Bergström, Jonsson, & Jansson, 2008; Elser et al., 2009). These types of enclosure experiments do not therefore assess the interacting effect between, for example nutrient- and light availability that takes place on a whole-lake scale (cf. Schindler, 1998), and additionally lack some ecological realism by neglecting predation and CO₂ diffusion from the surrounding lake water and the atmosphere (Jansson et al., 2012; Schindler, 1977). Hence, it is still unclear which of these environmental factors that are most important in regulating phytoplankton development on whole-lake scale, which prohibits our assessments of global-change impacts (e.g., browning and/or enhanced nutrient input) on northern lakes.

The interacting effect of DOC, affecting both nutrient (positive) and light (negative) availability implies promotions of nonlinear relationships between phytoplankton development and lake DOC (Seekell, Lapierre, & Karlsson, 2015) and has been one explanation for the unimodal curved relationships shown for northern lakes (Ask et al., 2009; Hanson, Bade, Carpenter, & Kratz, 2003; Solomon et al., 2015). Modeled results, validated with empirical data, suggest that although enhanced single limiting nutrient availability per unit of DOC should promote pelagic primary production the unimodal curved relationship with DOC persists (Kelly, Solomon, Zwart, & Jones, 2018). However, these model results have not been tested by whole-lake enrichment experiments of phytoplankton biomass production. Hence, it remains to be assessed to what degree the decrease in phytoplankton biomass with DOC could be counteracted or even reversed by nutrient enrichment, and to what extent increased DOC mitigates the effects of added nutrients on phytoplankton biomass development on a whole-lake scale.

Here we use data from natural and fertilized lakes in arctic and boreal Sweden to assess the patterns and controls of phytoplankton biomass across gradients in nutrients and DOC on a whole-lake scale. Based on these results, we then used data from the large Swedish Lake Monitoring Survey to make projections of phytoplankton development in response to enhanced DOC and nutrient loadings for the northern Swedish lake population. We found that phytoplankton biomass expressed unimodal curved relationships with lake DOC, peaking in biomass during reference and single nutrient enriched conditions at threshold DOC levels of 11–12 mg/L. Phytoplankton biomass was consistently higher after single nutrient enrichment with most pronounced biomass increases at the threshold DOC levels. We also estimated that 80% of northern Swedish lakes are below these DOC thresholds. Our results are in line with model predictions (cf. Kelly et al., 2018) and suggest consistent patterns in phytoplankton biomass development in northern lakes, with shifts from nutrient to light limitation with increasing lake DOC, and that this trade-off between light and nutrient availability determines their magnitude in response to nutrient enrichment. Overall, we report compelling evidence for how northern lakes will respond to future global changes such as lake browning and eutrophication.

2 | MATERIALS AND METHODS

2.1 | Site description

We compiled data from whole-lake inorganic nutrient enrichment experiments ($n = 5$ lakes) and seasonal lake studies ($n = 11$ lakes; where 4 lakes functioned as reference lakes for the nutrient-enriched lakes) conducted in northern boreal and arctic Sweden. Data included published data (Deininger, Faithfull, & Bergström, 2017; Holmgren, 1983; Jansson, Jonsson, Andersson, & Karlsson, 2010; Karlsson, Jonsson, & Jansson, 2001) and unpublished data ($n = 2$ lakes) (Bergström unpublished data) (Table S1). The regions have low-N deposition (wet-dissolved inorganic N (DIN) deposition of $<200 \text{ kg km}^{-2} \text{ yr}^{-1}$ and $<100 \text{ kg km}^{-2} \text{ yr}^{-1}$) (Bergström et al., 2013, 2008), and except for forestry (mainly concerns boreal lakes) anthropogenic influences on the lakes are negligible. The lake catchments consist mainly of open mires and coniferous forests (boreal) or mountain birch (*Betula pubescens*) (sub-alpine arctic). Boreal lakes usually stratify from mid-May until mid-to-late September whereas, for the arctic lakes, some stratify from mid-June until early September, and some remain unstratified over summer. Lakes included are small, shallow, vary in color, DOC, and nutrient content (Tables S1–S2). The lakes have different food web structures, some with fish and some without (Table S1).

2.2 | Whole-lake fertilization experiments

Short-term bioassays have shown that northern Swedish lakes have primarily N- (boreal) and N- to NP-limited (arctic) phytoplankton (Figure S1). Thus, N (and P) are regarded as key nutrients to assess

the potential control of phytoplankton biomass by nutrients. For the boreal region, we used data from three experimental lake pairs selected at three DOC levels (ca 7 mg/L, 11 mg/L and 20 mg/L) where one lake in each pair served as a control lake and the other as an N-enrichment lake. The experiment had one reference year (2011, all lakes) and two impact years (2012, 2013, with N enrichment in 3 of 6 lakes) (Deininger et al., 2017; Klaus et al., 2018). N in the form of dissolved potassium nitrate (KNO_3 , in 2012) and concentrated nitric acid (16 M HNO_3 in 2013) were added equally across the surface of the fertilized lakes. To mimic leaching events following high-flow events in winter and spring (cf. Bergström et al., 2008), the whole-water column was fertilized once during ice cover through holes evenly distributed over the lake surface drilled through the ice (late March 2012, early April 2013). Fertilization then took place once in every 2 weeks during the whole-growing season from onset of stratification in late May/early June until late August. In 2013, fertilization was additionally performed every week in the high-DOC lake, due to its shorter water residence time. The areal artificial DIN loading to the boreal lakes was for Fisklösan (DOC ca 7 mg/L): $1 \text{ g N m}^{-2} \text{ yr}^{-1}$; for Lapptjärn (DOC ca 11 mg/L): $1.1 \text{ g N m}^{-2} \text{ yr}^{-1}$ and for Nedre Björntjärn (DOC of ca 20 mg/L): $1.8 \text{ g N m}^{-2} \text{ yr}^{-1}$ (Klaus et al., 2018).

For the arctic region, we used data from whole-lake fertilization experiments in the Kuokkel area conducted in the 1970s (Holmgren, 1983). We compiled data from three sub-alpine arctic lakes where one lake served as a control (Stugsjön 1971–1975) and two lakes as enrichment lakes (Magnusjaure, Hymenjaure). For Magnusjaure, 1973 was a control year, followed by 1 year with single N enrichment (1974), and then by 1 year with enrichment of N and P combined (1975). For Hymenjaure, 1971 was a control year, followed by 3 years of single P enrichment (1972–1974) and then by 1 year of enrichment with N and P combined (1975). The fertilization procedure was similar between lakes. Lakes were fertilized every week from the beginning of June until late August/early September where the fertilizers were spread equally across the lake surfaces. Ammonium nitrate was used for N- and phosphoric acid (H_3PO_4) was used for P fertilization. The annual artificial nutrient loadings were for the lake Magnusjaure: 3.9 g N m^{-2} (1974), 0.3 g P m^{-2} plus 4.6 g N m^{-2} (1975), and for the lake Hymenjaure: 0.09 g P m^{-2} , 0.25 g P m^{-2} , 0.31 g P m^{-2} (1972, 1973, 1974) and 0.3 g P m^{-2} plus 3.9 g N m^{-2} (1975), respectively (Holmgren, 1983).

2.3 | Lake sampling and analysis of physical, chemical, and biological parameters

We used seasonal means for physical, chemical, and biological parameters which were measured and sampled during the open-water season between June and early September (Deininger et al., 2017; Holmgren, 1983; Jansson et al., 2010; Karlsson et al., 2001). Composite samples for chemical and biological parameters were taken from the mid-epilimnion (stratified) or the whole-water column (unstratified). Subsamples were taken from the composite

samples for analyses of water chemistry and phytoplankton biomass. Lake water was analyzed for DOC, dissolved inorganic nitrogen (DIN), that is, NO_2^- -N, NO_3^- -N, and NH_4^+ -N, total nitrogen (TN) and total phosphorus (TP). For detailed analytical procedures see (Deininger et al., 2017; Holmgren, 1983; Jansson et al., 2010; Karlsson et al., 2001). For lakes Stugsjön, Hymenjaure, and Magnusjaure the DOC concentrations were estimated using linear regression analysis between TN and DOC ($n = 22$, $r^2 = 0.71$, $p < 0.001$) using data from Jansson et al. (2010) and Bergström et al. (2015).

Temperature and photosynthetic active radiation (PAR) profiles in the lakes were measured using handheld probes. The vertical light extinction coefficient (k_d) was calculated as the slope of the linear regression of the natural logarithm of PAR versus depth. For lakes Stugsjön, Magnusjaure, and Hymenjaure, the k_d was estimated using linear regression analysis between DOC and k_d ($n = 16$, $r^2 = 0.95$, $p < 0.001$) using data from Karlsson et al. (2001), Bergström et al. (2015), and Deininger et al. (2017). The mean PAR irradiance for the mixed layer (I_m), which is a dimensionless estimate for the light climate, was calculated according to Karlsson et al. (2009). The I_m was also converted (i.e., $1:I_m$) when assessing how light availability declines with enhanced DOC content since I_m numbers, unlike k_d numbers, otherwise declines with reduced light availability (cf. Table S2). When comparing these estimates for our small and relatively shallow lakes, they illustrate in a similar way how light availability (i.e., I_m and $1:k_d$) declines across lake DOC gradients (Figure S2) and were also highly related to each other ($n = 16$, $r = 0.96$, $p < 0.05$).

Samples for phytoplankton biomass were preserved with Lugol's iodine solution and counted using inverted phase contrast microscopy and identified to genus level and species level where possible. Bio-volumes were calculated using biometry measurements and geometrical formulas and transformed to biomass ($\mu\text{g/L}$ wet weight) by assuming a density of 1 g/cm^3 (Deininger et al., 2017; Holmgren, 1983; Jansson et al., 2010). Phytoplankton biomass was then converted to C equivalents by assuming a C content of 22% for cyanophytes, 16% for chlorophytes, and 11% for other phytoplankton (Blomqvist, Bell, Olofsson, Stensdotter, & Vrede, 1995). Hence, for clarification, the dataset subsequently comprise of summer mean values for phytoplankton biomass (and other parameters presented) for control lakes in 1971 (Stugsjön), 1998–1999 (lakes 10–14; $n = 5$), 2011–2013 (Nästjärn, Mångstenjärn, Övre Björntjärn; $n = 9$), 2012 (Lillsjölidjärnen, Stortjärnen; $n = 2$), and for the reference years for the treatment lakes in 1971 (Hymenjaure), 1973 (Magnusjaure), and 2011 (Fisklösan, Lapptjärn, Nedre Björntjärn; $n = 3$) (i.e., in total during un-fertilized reference conditions $n = 22$). For single-nutrient treatment lakes, we have summer means for phytoplankton biomass in 1972–1974 (Hymenjaure (+P); $n = 3$), 1974 (Magnusjaure (+N)), 2012–2013 (Fisklösan, Lapptjärn, Nedre Björntjärn (all + N); $n = 6$) (i.e., in total during single fertilized conditions $n = 10$). For combined nutrient treatment lakes we have summer means in phytoplankton biomass in 1975 (Magnusjaure, Hymenjaure (+NP); $n = 2$).

2.4 | Statistical analysis

We used seasonal means for physico-chemical and phytoplankton biomass data for the different lakes and years to test the effects of DOC, light (k_d , $1:I_m$), and nutrients (TP, TN) on biological response variables (phytoplankton biomass), and the effects of DOC on physico-chemical response variables (DIN, TP, TN, k_d , $1:I_m$). Pearson's product-moment correlation, linear and nonlinear regression (Gaussian, 3 Parameter) analysis were used to test these relationships in control and non-manipulated lakes and in manipulated lakes after fertilization with non-transformed data. In each test between biological response variables (phytoplankton biomass) and physico-chemical variables (TP, TN, k_d , $1:I_m$, DOC), we made statistical comparisons between different model forms (Gaussian (3 parameter), linear, intercept only), and selected the models with the lowest corrected Akaike information criterion (AICc) as the best model (cf. Table S3). Hence, in these tests, the Gaussian models were found to have the lowest AICc with the one exception for the model analyses between phytoplankton biomass after single N and P addition (PhyBM_N_P) and DOC (Table S3). In this case, the intercept model had lowest AICs of all models, but the linear model had higher AICs than the Gaussian model (cf. Table S3). Based on the low slope (3.83) and R^2 (0.02) value in the linear model, and its lower AICs than the Gaussian model, we therefore consider the Gaussian model to be the best model also in this case.

In the models between phytoplankton biomass (response variable) and physico-chemical variables (TP, TN, k_d , $1:I_m$) during control conditions, we found one datapoint to be a possible outlier. We therefore used the standard deviation method of the sample as a cutoff (<https://machinelearningmastery.com/how-to-use-statistics-to-identify-outliers-in-data>) for identifying this datapoint as a possible outlier or not, which is a common practice for identifying outliers in Gaussian distribution of data. In this case, three standard deviations are a common cutoff practice, but sometimes for smaller samples sizes two standard deviations are used. If using the three standard deviation method, this datapoint was not cut-off as an outlier, but if instead using the two standard deviation methods, the datapoint was identified as an outlier. Thus, based on this evaluation, we do not treat this datapoint as an outlier and therefore chose to present the models with all datapoints in the main text, and present the models when excluding this potential outlier in the Supporting Information. We also made a statistical comparison between the different model forms (Gaussian (3 parameter), linear, intercept only) when including, or excluding, this possible outlier and present the results of these statistical tests in Table S3.

The Gaussian models were all assessed using automated curve fitting (Dynamic Fit Wizard) with 200 fits. Further, α values <0.05 were considered statistically significant. All t tests, Pearson's product-moment correlation, and linear and nonlinear regressions (Gaussian, 3 Parameter) were conducted using Sigma Plot 13.0 and JMP[®] version 14.01.

2.5 | Upscaling of physical-chemical properties of lakes in northern Sweden

Physical-chemical data from lakes included in the large Swedish Lake Monitoring Survey (<http://www.slu.se/vatten-miljo/datavardskap>) in 2000 were used to estimate the relative distribution of lakes at different levels of DOC (mg/L) in northern Sweden. Data from this monitoring survey are regarded to be a representative subsample of Swedish lakes (Wilander, Johnson, & Goedkoop, 2003) and we used lake data ($n = 978$) from northern Sweden (i.e., the counties of Västerbotten and Norrbotten) (Figure S4). TOC analyzed in this survey is almost equivalent to DOC (i.e., 97% of TOC in boreal lakes is dissolved carbon; cf. Kortelainen et al., 2006). The k_d was estimated from Abs_{440} data as in Seekell et al. (2015). We used the high-resolution Swedish Virtual Watercourse Network (ViVaN) to estimate the lake sizes of the 978 lakes included, which were separated into five different logarithmic size classes as in Seekell et al. (2015). The total number of lakes in northern Sweden distributed in these five different logarithmic size classes has earlier been estimated by Seekell et al. (2015). To identify numbers of lakes below and above the DOC thresholds, we estimated the percentage of lakes in each logarithmic size class in the environmental lake monitoring data with DOC below or above these thresholds. We also estimated the distribution of lakes across gradients in DOC, TN, and TP concentrations, and light availability (k_d) for the whole-monitoring dataset.

3 | RESULTS

Lakes ranged considerably in DOC (4 to 23 mg/L) and nutrient (TP: 4 to 19 $\mu\text{g/L}$; TN: 148 to 511 $\mu\text{g/L}$; DIN: 4 to 65 $\mu\text{g/L}$) concentrations (Table S2; Figure S2b). Light (I_m , k_d^{-1}) declined ($r = -0.81$ and -0.78 , $p < 0.05$ for both) (Figure S2a), whereas TP and TN increased ($r = 0.94$ and 0.89 , $p < 0.05$ for both) with increased lake water DOC. The DIN concentrations were more variable across the lake DOC gradient (Figure S2b).

We first tested the relationship between phytoplankton biomass and main abiotic drivers; for example, nutrients and light. During unfertilized reference conditions, phytoplankton showed unimodal curved relationships with lake TP and TN concentrations (Figure 1a–b, nonlinear regressions, Peak Gaussian 3 parameter: $r^2 = 0.41$, $F_{2,15} = 4.5$, $p = 0.03$ and $r^2 = 0.52$, $F_{2,15} = 6.9$, $p = 0.01$, respectively) and with light ($1:I_m$ and k_d) (Figure 1c–d, nonlinear regression, Peak Gaussian 3 parameter: $r^2 = 0.4$, $F_{2,15} = 4.2$, $p = 0.04$ for both). In one lake, the phytoplankton biomass was considerably higher compared to in the other lakes. However, this datapoint was not considered an outlier (using the three stdev method, cf. Material and Methods), and if we would treat it as an outlier the only parameter that remained significantly related to phytoplankton biomass was TN (cf. Figure S3; Table S3) (nonlinear regressions, Peak Gaussian 3 parameter: $r^2 = 0.46$, $F_{2,14} = 5.2$, $p = 0.02$). Complete summaries of the Gaussian fitted models (with and without the outlier) are also presented in Supporting Information S1–S2 and Table S3. A stronger

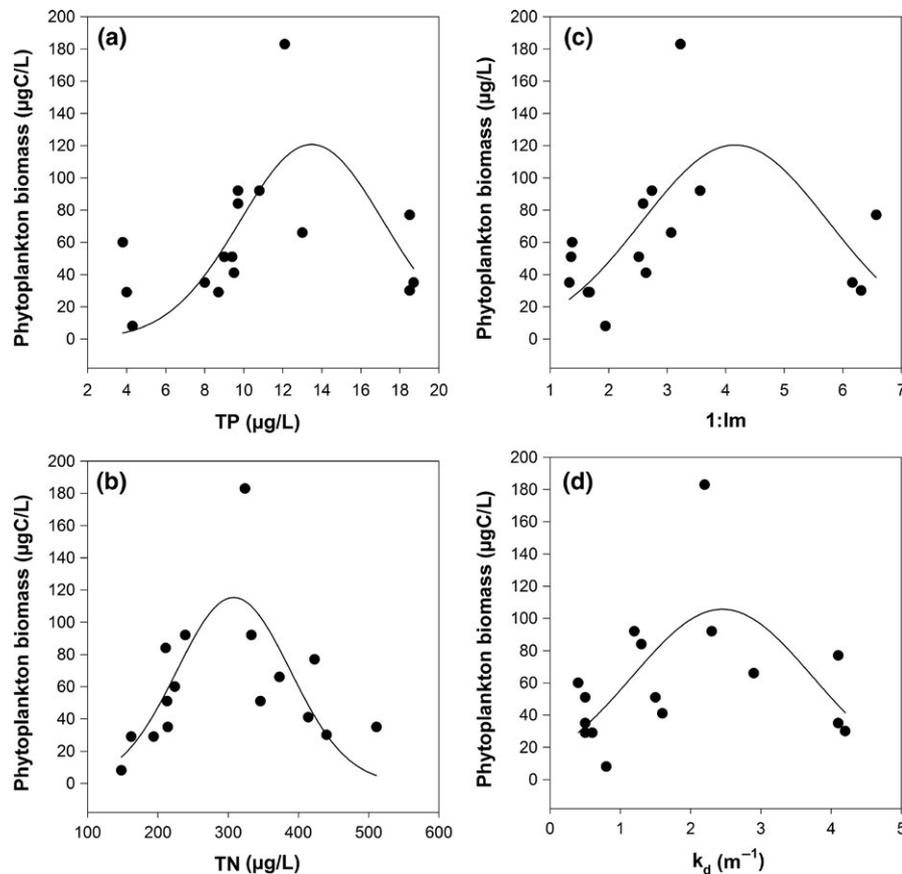


FIGURE 1 Phytoplankton biomass across gradients in (a) total phosphorus (TP), (b) total nitrogen (TN) concentrations, (c) mean light availability in the mixed layer ($1:I_m$) and (d) light extinction coefficients (k_d) in the study lakes. Data for the control lakes and the reference years for the treatment lakes. For each panel, the solid line represents the modeled nonlinear Gaussian relationship between abiotic drivers (TP, TN, $1:I_m$, k_d) and phytoplankton biomass

relationship with TN, than with TP, can also be expected since phytoplankton primarily is N-limited in these lakes (Bergström et al., 2008; Bergström et al., 2013, and Figure S1). Combining these relationships indicate a positive effect of nutrients, especially of nitrogen, on phytoplankton biomass development up to TN, $1:I_m$ and k_d levels (i.e., the peaks in the regression analyses of these parameters in Figure 1) of 308 $\mu\text{g/L}$, 3.4 and 2.2 m^{-1} , respectively. Above the peak, and with continuously lower-light conditions (i.e., at $1:I_m$ and k_d values >3.4 and 2.4), phytoplankton biomass declines despite the higher-nutrient concentrations (i.e., TN).

We then tested the relationship between phytoplankton biomass and DOC. During unfertilized reference conditions, phytoplankton biomass showed an unimodal curved relationship across the DOC gradient, with a modeled peak in biomass (155 $\mu\text{gC/L}$) at DOC of 12.3 mg/L (nonlinear regression, Peak Gaussian 3 parameter: $r^2 = 0.62$, $F_{2,21} = 15.3$, $p = 0.0001$) (Figure 2). Fertilization with limiting inorganic nutrients (i.e., with N or P alone at DOC around 5 mg/L; with N alone at DOC of ca 8, 15 and 19 mg/L) enhanced phytoplankton biomass at all DOC levels, with strongest effects in the lake Fisklösan with DOC concentration of ~ 7 –8 mg/L (Figure 2). Similar to un-fertilized controls, the model between phytoplankton biomass and DOC following single limiting nutrient enrichment also expressed an unimodal curved relationship with a model peak in

phytoplankton biomass (451 $\mu\text{gC/L}$) at DOC of 10.6 mg/L (nonlinear regression, Peak Gaussian 3 parameter: $r^2 = 0.62$, $F_{2,9} = 5.7$, $p = 0.03$) (Figure 2) (complete summaries of the Gaussian fitted models are presented in Supporting Information S3). Fertilization with N and P combined to lakes Magnusjaure and Hymenjaure increased phytoplankton biomass 20 to 40 times relative to control years and unfertilized lakes, hence, significantly more compared to the biomass increase from single fertilization with N or P (Figure 2).

The data from the Swedish Lake Monitoring Survey revealed that a majority of lakes in each logarithmic size class had DOC concentrations <10.6 mg/L (72 to 97%) and <12.3 (76 to 100%) (Table 1). Of the 978 lakes included in the lake survey, 54% had DOC concentrations ≤ 6 mg/L, with a majority situated in the Swedish mountain areas to the west (Figure S4b). As a whole for northern Sweden, the most common lake is small (Table 1) relatively clear (DOC ~ 5 mg/L; $k_d \sim 1/\text{m}$) and nutrient poor (TN ~ 300 $\mu\text{g/L}$; TP ~ 3 –7 $\mu\text{g/L}$) (Figure S5).

4 | DISCUSSION

This study shows that phytoplankton biomass in unproductive northern lakes is controlled by both nutrients and colored DOC. We found

unimodal curved relationships between phytoplankton biomass and lake DOC, but with consistently higher biomass after nutrient enrichment. These results imply that changes in DOC and nutrient input, individually and combined, affect phytoplankton biomass in northern lakes and that the magnitude and direction of impact can be highly variable across systems. Our study is the first in using empirical data on a whole-lake scale to identify these patterns for phytoplankton biomass and these results are consistent and support model estimates for small lakes in how pelagic primary production will respond to changes in DOC and nutrient loadings (Kelly et al., 2018).

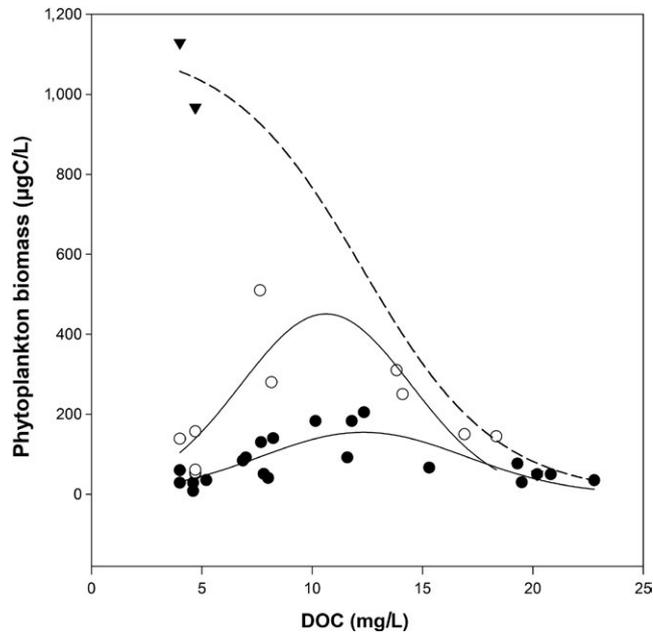


FIGURE 2 Phytoplankton biomass across gradients in dissolved organic carbon (DOC) concentration during reference conditions (black circles) and after whole-lake fertilization with nitrogen- (N) or phosphorus (P) alone (open white circles), and with N and P combined (black triangles). Solid lines represents the modeled nonlinear Gaussian relationships between DOC and phytoplankton biomass during reference and single-nutrient enrichment with N or P. Dotted line for responses in phytoplankton biomass following fertilization with N and P combined is hypothesized based on the low response in phytoplankton biomass to single N-addition at high-DOC concentrations

We interpret the unimodal curved relationships between phytoplankton biomass and DOC (Figure 2) to be mainly an effect of the dual influence that DOC has on light and nutrient availability (Jones, 1992; Seekell et al., 2015). Hence, phytoplankton biomass increase with DOC because of increasing supply of limiting nutrients (in this case especially of N; cf. Figure 1 and Figure S3; Table S3) as long as light availability is sufficient for photosynthetic growth (Figure 1). Above the threshold enhanced DOC increasingly attenuates light, and light starts constraining photosynthetic growth despite the continuously higher-nutrient concentrations (Figure 1 and Figure S3; Table S3).

The strength of this study is that we use lakes of similar sizes and mean depths, thereby decreasing the influence of lake depth on light availability (cf. Kelly et al., 2018), that are located in regions where phytoplankton biomass development has not been affected by enhanced lake water N:P stoichiometry from N deposition (Bergström, Blomqvist, & Jansson, 2005; Elser et al., 2009). Yet, since our data are from relatively shallow lakes, we do not know if a similar unimodal curved relationship between phytoplankton biomass and DOC also exists for deeper and larger lakes, where depths of the mixed layers often exceeds the depths of the photic zones and, thus, potentially promotes greater light limitation at a given DOC concentration compared to the situation for smaller lakes (cf. Jones, 1998; Kelly et al., 2018). Thrane et al. (2014) assessed how DOC influences light and nutrient availability for pelagic primary production in a set of large northern lakes (>1 km²) and found a negative correlation of light and a positive effect of nutrients, but never detected a unimodal curved relationship with increased lake DOC. However, since their lake DOC gradient ranged between 0.3 and 12.3 mg/L, it is likely that the highest DOC lake occurred close to the DOC threshold (i.e., at the peak in primary production, cf. Thrane et al., 2014). Although the unimodal curved relationship between phytoplankton biomass (or pelagic primary production) and DOC has been modeled for large lakes (Kelly et al., 2018), it may be hard to find in reality due to the fact that large lakes rarely reach high-DOC concentrations (Table 1) with deep enough mixed layers for creating the trade-offs between light and nutrient availability affecting phytoplankton development as seen in smaller lakes.

A consistent unimodal curved relationship between phytoplankton biomass and DOC was also found following whole-lake nutrient enrichments, when ratios between DOC and single limiting nutrients were reduced, consistent with model results (Kelly

TABLE 1 Number and area of lakes in northern Sweden by logarithmic size class and number and area of these lakes with dissolved organic carbon (DOC) concentrations <10.6 and <12.3 mg/L, respectively

Overall				Below threshold	
Area class (km ²)	Abundance	Mean area (km ²)	Total area (km ²)	Percentage of lakes	
				DOC < 10.6 mg/L	DOC < 12.3 mg/L
0.001-0.01	50,186	0.004	214.6	81	83
0.01-0.1	24,175	0.03	728.4	76	78
0.1-1	4,919	0.285	1,401.2	72	76
1-10	834	2.627	2,190.8	76	81
10-100	95	24.61	2,338	97	100

et al., 2018). This relationship was not caused because lakes with higher responses in phytoplankton biomass after N enrichment were fertilized more compared to lakes with lower responses (i.e., the low- and high-DOC lakes had the highest artificial N loadings, cf. Material and methods). Further, and in line with results from short-term bioassay experiments (Figure S1; Bergström et al., 2013, 2008), phytoplankton responded to single additions of both N and P at low DOC (Figure 2), and to single addition of N at higher DOC (≥ 8 mg/L) (Figure 2; Deining et al., 2017). Hence, at the low-DOC end, where both N and P concentrations are low (and light is high), single additions of N or P promote the limited response in phytoplankton biomass since phytoplankton becomes rapidly limited by the other element after enrichment (i.e., N-addition induces P-limitation; P addition induces N-limitation) (cf. Elser et al., 2009). Response to single nutrient addition (in this case N) then increases with higher DOC (lower light) and higher P concentrations up to the thresholds in DOC (Figure 2). Part of this stimulating effect following nutrient enrichment might also be attributed to enhanced CO_2 (Hamdan et al., 2018; Jansson et al., 2012).

Above the DOC thresholds, phytoplankton biomass declines with N enrichment despite the higher P concentrations that follow with increased lake DOC, and we interpret this as being mainly caused by subsequent poorer light conditions (Figures 1,2; Deining et al., 2017). It is possible that the response in phytoplankton to colored DOC and nutrients to some extent was subdued due to competitive interactions with bacteria for limiting nutrients (Jansson et al., 2007). However, the fact that bacteria and phytoplankton communities are generally not limited by the same nutrient in these lakes (i.e., phytoplankton are N- and bacteria are P-limited, Jansson, Blomqvist, Jonsson, & Bergström, 1996; Faithfull, Bergström, & Vrede, 2011), and that the unimodal curved relationships occurs both during reference- and single-nutrient enrichment conditions, implies that competition for nutrients cannot be the underlying reason promoting these patterns. Studies in boreal lakes have also shown that bacteria gradually become less nutrient limited with increased lake DOC concentrations (i.e., shifting from P-limitation at DOC around 10 mg/L to C-limitation at DOC > 15 mg/L) (Jansson et al., 2001). In addition, if bacteria would be responsible for the decline above the DOC thresholds, phytoplankton biomass would increase following N fertilization at high DOC where P concentrations are highest. This was not the case and we instead attribute the moderate phytoplankton response to N enrichment in high-DOC lakes as mainly a result of low-light conditions (Figures 1 and 2; Deining et al., 2017), constraining phytoplankton growth and overriding any positive effect that might come from CO_2 supersaturated water (Jansson et al., 2012).

Responses to addition of N and P combined (which relieve nutrient limitation) contributed to a much higher phytoplankton biomass development compared to single addition of N or P in the low-DOC lakes (Figure 2). Based on the low response to single-limiting nutrient enrichment found in the high-DOC lake, light therefore seems to set the limit and determine the extent to in which phytoplankton will respond to addition of N and P across lake DOC gradients, which should follow the hypothesized dotted line in Figure 2. Thus, the lack of strong

response in phytoplankton biomass to nutrient enrichment, and the decrease in biomass with increasing DOC concentration following N-addition, is likely not due to lack of other essential nutrients (P or CO_2), or by competition for nutrient with bacteria, suggesting strong light control of phytoplankton carrying capacity in northern lakes.

Our lakes had different food web structures, some with fish and some without (Table S1), which potentially could have affected phytoplankton biomass development by reducing zooplankton predation (Hanson et al., 2003). However, in our study lakes with lowest responses in phytoplankton biomass following single nutrient enrichment had both absence (lowest DOC lake) and presence of fish (highest DOC lake). In addition, we found a unimodal curved relationship between phytoplankton biomass and DOC during reference controlled conditions despite differences in presence/absence of fish among lakes (cf. Tables S1–S2). Thus, our data suggest control by nutrient and light, rather than by food web structure, on phytoplankton biomass development in unproductive northern lakes.

Our results can be used to identify potential trajectories in phytoplankton biomass development of northern lakes following global change (Figure 3). First, lake browning will have a positive impact on phytoplankton biomass development in lakes situated below the DOC threshold, mainly via associated increase in limiting nutrients, and a negative effect on biomass development above the DOC threshold, mainly by colored DOC constraining light availability. The DOC threshold is likely to be modified by the impact of lake depth and aromaticity of DOC on the light climate. That is, deeper lakes will be more light limited at a given DOC

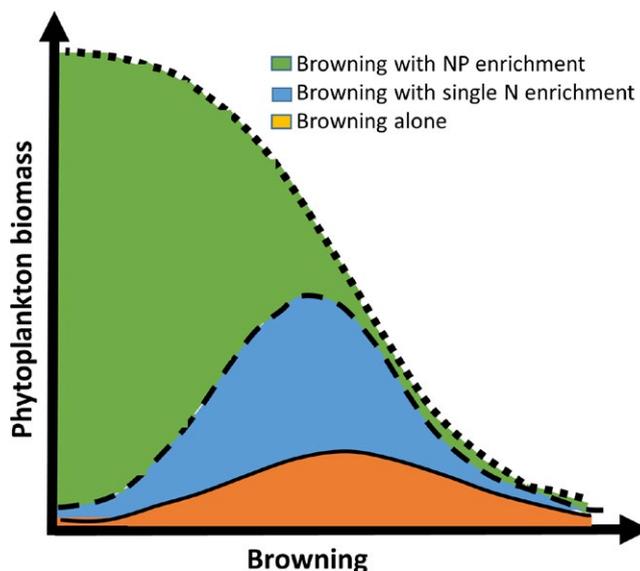


FIGURE 3 Conceptual model illustrating trajectories in phytoplankton biomass development with global change; that is, with browning alone (brown areas), and combined with single nitrogen (N) enrichment from deposition (blue areas), and nitrogen and phosphorus (NP) enrichment with eutrophication (green area). The dotted top-line illustrates the carrying capacity in phytoplankton set by light

concentration as the mixed water layer will be deeper compared to smaller lakes, and aromatic rich DOC will increased light extinction more compared to aromatic poor DOC (cf. Kelly et al., 2018). The peak in phytoplankton biomass may also be modified by changes in terrestrial DOC:nutrient export ratios, with lower ratios promoting higher peaks at a given DOC concentration and light condition (cf. Kelly et al., 2018). Secondly, increased N loadings from atmospheric deposition will have a positive effect on phytoplankton biomass across all lake DOC levels. The response will be highest around the DOC threshold where both P and light availability are sufficiently high for phytoplankton to respond to enhanced N availability. Thirdly, the effect on phytoplankton biomass will be especially pronounced following cultural eutrophication elevating both N and P, where the phytoplankton biomass carrying capacity will be mainly controlled by light.

For northern Sweden, we found that a majority of the lake population have DOC concentrations below the thresholds (Table 1). Thus, assuming space-for time substitution, enhanced DOC loadings may promote and contribute to increased phytoplankton biomass in a majority of lakes in northern Sweden, and if enhanced DOC loadings would be accompanied by enhanced limiting nutrient inputs the biomass increase would become even higher. However, more research is clearly needed to assess how global change will affect not only terrestrial DOC loadings, but also its character (DOC:nutrient stoichiometry, aromaticity) since these factors, combined with changes in nutrient pollution by humans, will determine future productivity of phytoplankton in northern lakes. Despite many unknowns requiring attention, our results are consistent with model predictions of phytoplankton development following browning and nutrient enrichment and important for our understanding how these ecosystems may response to future environmental changes.

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REFERENCES

- Ask, J., Karlsson, J., Persson, L., Ask, P., Byström, P., & Jansson, M. (2009). Terrestrial organic matter and light penetration effects on bacterial and primary production in lakes. *Limnology and Oceanography*, 54, 2034–2040. <https://doi.org/10.4319/lo.2009.54.6.2034>
- Bergström, A.-K., Blomqvist, P., & Jansson, M. (2005). Effects of atmospheric nitrogen deposition on nutrient limitation and phytoplankton biomass in unproductive Swedish lakes. *Limnology and Oceanography*, 50, 987–994. <https://doi.org/10.4319/lo.2005.50.3.0987>
- Bergström, A.-K., Faithfull, C. L., Karlsson, D., & Karlsson, J. (2013). Nitrogen deposition and warming – Effects on phytoplankton nutrient limitation in subarctic lakes. *Global Change Biology*, 19, 2557–2568. <https://doi.org/10.1111/gcb.12234>
- Bergström, A.-K., Jonsson, A., & Jansson, M. (2008). Phytoplankton response to nitrogen and phosphorus along a gradient in atmospheric nitrogen deposition. *Aquatic Biology*, 4, 55–64.
- Bergström, A.-K., Karlsson, D., Karlsson, J., & Vrede, T. (2015). N-limited consumer growth and low nutrient regeneration N: P ratios in lakes with low N deposition. *Ecosphere*, 6, 9. <https://doi.org/10.1890/ES14-00333.1>
- Blomqvist, P., Bell, R. T., Olofsson, H., Stensdotter, U., & Vrede, K. (1995). Plankton and water chemistry in lake Njupfatet before and after liming. *Canadian Journal of Fisheries and Aquatic Sciences*, 52, 551–565. <https://doi.org/10.1139/f95-056>
- Carpenter, S. R., Cole, J. J., Kitchell, J. F., & Pace, M. L. (1998). Impact of dissolved organic carbon, phosphorus, and grazing on phytoplankton biomass and production in lakes. *Limnology and Oceanography*, 43, 73–80.
- Creed, I. F., Bergström, A.-K., Trick, C. G., Grimm, N. B., Hessen, D. O., Karlsson, J., ... Weyhenmeyer, G. A. (2018). Global change-driven effects on dissolved organic matter composition: Implications for food webs of northern lakes. *Global Change Biology*, 24, 3692–3714. <https://doi.org/10.1111/gcb.14129>
- de Wit, H. A., Valinia, S., Weyhenmeyer, G. A., Futter, M. N., Kortelainen, P., Austnes, K., ... Vuorenmaa, J. (2016). Current browning of surface waters will be further promoted by wetter climate. *Environmental Science and Technology Letters*, 3, 430–435. <https://doi.org/10.1021/acs.estlett.6b00396>
- Deininger, A., Faithfull, C. L., & Bergström, A.-K. (2017). Phytoplankton response to whole lake inorganic N fertilization along a gradient in dissolved organic carbon. *Ecology*, 98, 982–994. <https://doi.org/10.1002/ecy.1758>
- Downing, J. A., Prairie, Y. T., Cole, J. J., Duarte, C. M., Tranvik, L. J., Striegl, R. G., ... Middelburg, J. J. (2006). The global abundance and size distribution of lakes, ponds and impoundments. *Limnology and Oceanography*, 51, 2388–2397. <https://doi.org/10.4319/lo.2006.51.5.2388>
- Elser, J. J., Andersen, T., Baron, J. S., Bergström, A.-K., Jansson, M., Kyle, M., ... Hessen, D. O. (2009). Shifts in lake N: P stoichiometry and nutrient limitation driven by atmospheric nitrogen deposition. *Science*, 326, 835–837. <https://doi.org/10.1126/science.1176199>
- Faithfull, C. L., Bergström, A.-K., & Vrede, T. (2011). Effects of nutrients and physical lake characteristics on bacterial and phytoplankton production: A meta-analysis. *Limnology and Oceanography*, 56, 1703–1713. <https://doi.org/10.4319/lo.2011.56.5.1703>
- Finstad, A. G., Andersen, T., Larsen, S., Tominaga, K., Blumentrath, S., de Wit, H. A., & Hessen, D. O. (2006). From greening to browning: Catchment vegetation development and reduced S-deposition promote organic carbon load on decadal time scale in Nordic lakes. *Scientific Reports*, 6, 31944.
- Hamdan, H., Byström, P., Hotchkiss, E. R., Al-Haidarey, M., Ask, J., & Karlsson, J. (2018). Carbon dioxide stimulates lake primary production. *Scientific Reports*, 8, 10878. <https://doi.org/10.1038/s41598-018-29166-3>
- Hanson, P. C., Bade, D. L., Carpenter, S. R., & Kratz, T. K. (2003). Lake metabolism: Relationships with dissolved organic carbon and

- phosphorus. *Limnology and Oceanography*, 48, 1112–1119. <https://doi.org/10.4319/lo.2003.48.3.1112>
- Hessen, D. O. (1985). The relation between bacterial carbon and humic compounds in oligotrophic lakes. *FEMS Microbial Ecology*, 31, 215–223.
- Hessen, D. O., Andersen, T., Larsen, S., Skjelvåle, B. L., & de Wit, H. (2009). Nitrogen deposition, catchment productivity, and climate determinants of lake stoichiometry. *Limnology and Oceanography*, 54, 2520–2528.
- Holmgren, S. (1983). *Phytoplankton biomass and algal composition in natural, fertilized and polluted subarctic lakes*. Uppsala: Acta Universitatis Upsaliensis 674, Uppsala University.
- Isles, P. D. F., Creed, I. F., & Bergström, A.-K. (2018). Recent synchronous declines in DIN:TP in Swedish lakes. *Global Biogeochemical Cycles*, 32, 208–225. <https://doi.org/10.1002/2017GB005722>
- Jansson, M., Bergström, A.-K., Drakare, S., & Blomqvist, P. (2001). Nutrient limitation of bacterioplankton and phytoplankton in humic lakes northern Sweden. *Freshwater Biology*, 46, 653–666.
- Jansson, M., Blomqvist, P., Jonsson, A., & Bergström, A.-K. (1996). Nutrient limitation of bacterioplankton, autotrophic and mixotrophic phytoplankton, and heterotrophic nanoflagellates in Lake Örträsket. *Limnology and Oceanography*, 41, 1552–1559. <https://doi.org/10.4319/lo.1996.41.7.1552>
- Jansson, M., Jonsson, A., Andersson, A., & Karlsson, J. (2010). Biomass and structure of planktonic communities along an air temperature gradient in subarctic Sweden. *Freshwater Biology*, 55, 691–700. <https://doi.org/10.1111/j.1365-2427.2009.02310.x>
- Jansson, M., Karlsson, J., & Jonsson, A. (2012). Carbon dioxide supersaturation promotes primary production in lakes. *Ecology Letters*, 15, 527–532. <https://doi.org/10.1111/j.1461-0248.2012.01762.x>
- Jansson, M., Persson, L., DeRoos, A., Jones, R. I., & Tranvik, L. J. (2007). Terrestrial carbon and intraspecific size-variation shape lake ecosystems. *Trends in Ecology and Evolution*, 22, 316–322. <https://doi.org/10.1016/j.tree.2007.02.015>
- Jones, R. I. (1992). The influence of humic substances on lacustrine planktonic food webs. *Hydrobiologia*, 229, 73–91.
- Jones, R. I. (1998). Phytoplankton, primary production and nutrient cycling. In D. O. Hessen, & L. J. Tranvik (Eds.), *Aquatic Humic Substances* (pp. 145–175). Ecology and Biogeochemistry. Ecological Studies 133. Heidelberg, New York: Springer-Verlag, Berlin.
- Karlsson, J., Byström, P., Ask, J., Ask, P., Persson, L., & Jansson, M. (2009). Light limitation of nutrient-poor lake ecosystems. *Nature*, 460, 506–509. <https://doi.org/10.1038/nature08179>
- Karlsson, J., Jonsson, A., & Jansson, M. (2001). Bacterioplankton production in lakes along an altitude gradient in the subarctic north of Sweden. *Microbial Ecology*, 42, 372–383. <https://doi.org/10.1007/s00248-001-0009-9>
- Kelly, P. T., Solomon, C. T., Zwart, J. A., & Jones, S. E. (2018). A framework for understanding variation in pelagic gross primary production of lake ecosystems. *Ecosystems*, <https://doi.org/10.1007/s10021-018-0226-4>
- Klaus, M., Bergström, A.-K., Jonsson, A., Deininger, A., Geibrink, E., & Karlsson, J. (2018). Weak response of greenhouse gas emissions to whole lake N enrichment. *Limnology and Oceanography*, 63, S340–S353. <https://doi.org/10.1002/lno.10743>
- Kortelainen, P., Mattsson, T., Finer, L., Ahtiainen, M., Saukkonen, S., & Sallantausta, T. (2006). Controls on the export of C, N, P and Fe from undisturbed boreal catchments, Finland. *Aquatic Sciences*, 68, 453–468.
- Kreutzweiser, D. P., Hazlett, P. W., & Gunn, J. M. (2008). Logging impacts on the biogeochemistry of boreal forest foils and nutrient export to aquatic systems: A review. *Environmental Review*, 16, 157–179.
- Kritzberg, E. S. (2017). Centennial-long trends of lake browning show major effect of afforestation. *Limnology and Oceanography Letters*, 2, 105–112. <https://doi.org/10.1002/lol2.10041>
- Larsen, S., Andersen, T., & Hessen, D. O. (2011). Climate change predicted to cause severe increase of organic carbon in lakes. *Global Change Biology*, 17, 1186–1192. <https://doi.org/10.1111/j.1365-2486.2010.02257.x>
- Lewis, W. M. (2011). Global primary production of lakes: 19th Baldi Memorial Lecture. *Inland Waters*, 1, 1–28.
- Monteith, D. T., Stoddard, J. L., Evans, C. D., de Wit, H. A., Forsius, M., Høgåsen, T., ... Vesely, J. (2007). Dissolved organic carbon trends resulting from changes in atmospheric deposition chemistry. *Nature*, 450, 537–540. <https://doi.org/10.1038/nature06316>
- Schindler, D. W. (1977). Evolution of phosphorus limitation in lakes. *Science*, 195, 260–262. <https://doi.org/10.1126/science.195.4275.260>
- Schindler, D. W. (1998). Replication versus realism: The need for ecosystem-scale experiments. *Ecosystems*, 1, 323–334.
- Seekell, D., Lapiere, J.-F., & Karlsson, J. (2015). Trade-offs between light and nutrient availability across gradients of dissolved organic carbon concentrations in Swedish lakes: Implications for patterns in primary production. *Canadian Journal of Fisheries and Aquatic Sciences*, 72, 1663–1671.
- Solomon, C. T., Jones, S. E., Weidel, B. C., Buffam, I., Fork, M. L., Karlsson, J., ... Saros, J. E. (2015). Ecosystem consequences of changing inputs of terrestrial dissolved organic carbon to lakes: Current knowledge and future challenges. *Ecosystems*, 18, 376–389.
- Sterner, R. W., & Hessen, D. O. (1994). Algal nutrient limitation and the nutrition of aquatic herbivores. *Annual Review of Ecology and Systematics*, 25, 1–29. <https://doi.org/10.1146/annurev.es.25.110194.000245>
- Thrane, J.-E., Hessen, D. O., & Andersen, T. (2014). The absorption of light in lakes: Negative impact of dissolved organic carbon on primary production. *Ecosystems*, 17, 1040–1052.
- Vitousek, P. (1997). Human domination of Earth's ecosystems. *Science*, 278, 21–22. <https://doi.org/10.1126/science.277.5325.494>
- Wilander, A., Johnson, R. K., & Goedkoop, W. (2003). *Riksinventering 2000 - En synoptisk studie av vattenkemi och bottenfauna i svenska sjöar och vattendrag*. Rapport 2003:1. Institutionen för miljöanalys, Uppsala, Sweden: SLU (in Swedish).

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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