Dissolved organic matter regulates nutrient limitation and growth of benthic algae in northern lakes through interacting effects on nutrient and light availability

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Scientific Significance Statement

Long-term and widespread increases in dissolved organic matter (DOM) concentrations in northern lakes influence primary producers by simultaneously enhancing nutrient availability and decreasing light availability. Responses of pelagic primary producers to these opposing influences have been explored through field studies and models, yet we know much less about how DOM loading influences benthic autotrophs. Benthic algae can account for a large fraction of productivity in shallow northern lakes and may differentially respond to DOM inputs because they can access nutrients from lake sediments. We used in situ experiments to demonstrate a unimodal relationship in the growth of benthic algae along a regional DOM gradient, similar to that shown in pelagic communities. Direct tests of nutrient limitation revealed nitrogen as the primary limiting nutrient, with the strength of limitation decreasing with greater DOM concentration. Overall, our results demonstrate both the pattern and mechanism of benthic algal response to DOM concentration, aiding in prediction of future responses as DOM continues to rise.

Abstract

Widespread increases in dissolved organic matter (DOM) concentration across northern lakes can alter rates of primary production by increasing nutrient availability and decreasing light availability. These dual effects of DOM generate a unimodal relationship in pelagic primary production and primary producer biomass among lakes over a gradient of DOM concentration. However, the responses of benthic algae to variation in DOM loading are less clear because of their potential to access sediment nutrients. We tested algal production and nutrient limitation along a DOM gradient in northern Sweden. Without added nutrients, benthic algal production showed a unimodal relationship similar to reported pelagic responses. Nutrient addition revealed widespread nitrogen limitation, with decreasing severity in lakes with higher DOM. Because the majority of northern Swedish lakes currently fall below the inflection point in this unimodal relationship, moderate increases in DOM have the potential to increase benthic primary production, particularly for epilithic algae.

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Data Availability Statement: Data and metadata are available via the Zenodo Repository at http://doi.org/10.5281/zenodo.3736483. The code to reproduce results and figures is available on GitHub (https://github.com/meganfork/SwedenBenthicAlgae).

Additional Supporting Information may be found in the online version of this article.

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Dissolved organic matter (DOM) concentrations are increasing in many northern lakes (Monteith et al. 2007), with potentially important consequences for aquatic ecosystem processes (Solomon et al. 2015). Lake primary production is thought to be particularly sensitive to these changes because colored DOM absorbs light thereby limiting photosynthesis at high concentrations (Carpenter et al. 1998; Williamson et al. 1999; Wilkinson et al. 2013). Yet, because DOM includes, sorbs, and/or is delivered together with nitrogen (N) and phosphorus (P), it also has the potential to stimulate primary production by alleviating nutrient limitation (Klug 2002; Kissman et al. 2013). Together, the effects of DOM on nutrient supply (positive relationship) and light (negative relationship) are hypothesized to interact and generate a unimodal relationship in aquatic primary production across broad DOM gradient. Several studies have found such unimodal patterns for whole-lake or pelagic primary production or primary producer biomass vs. DOM concentration (Hanson et al. 2003; Seekell et al. 2015a; Bergström and Karlsson 2019), particularly when controlling for depth/lake morphometry. Similarly, ecosystem models reproduce the unimodal relationship observed in real lakes when the delivery of nutrients and DOM are coupled (Kelly et al. 2018).

Most studies on the effects of DOM on primary production address pelagic or whole-lake responses, but such a focus may mask or overlook the role of the benthic environment, which can be particularly important in the shallow lakes that are abundant in the north (Vadeboncoeur and Steinman 2005; Vadeboncoeur et al. 2008; Ask et al. 2009). Because of differences in nutrient availability and algal ecology between benthic and pelagic habitats, the effects of DOM on primary production may differ between these habitats. First, because of shading from phytoplankton and DOM, benthic primary production is more likely to be light-limited (Hansson 1992), they may be less likely to experience strong nutrient limitation (Jäger and Diehl 2014). By comparison, epilithic algae have less access to sediment-derived nutrients and thus may be more likely to experience limitation when concentrations in the water column are low. As such, responses of primary production to changes in DOM may be expected to differ among habitats, depths, and lakes.

Here, we used nutrient diffusing substrates (NDS) to assess how the growth and nutrient limitation of benthic algae vary among lakes with different DOM content. We hypothesized that benthic algae are light limited in lakes with high DOM concentrations, and explored two alternative hypotheses for the pattern in their growth at low DOM. First, benthic algae may be nutrient limited at low DOM, and thus respond to DOM-associated nutrients up to an inflection point where light limitation becomes more important, similar to patterns observed in pelagic and whole-lake studies. In this case, we would predict a unimodal relationship in treatments without added nutrients, and stronger responses to nutrient addition under low vs. high DOM conditions. Alternatively, the proximity of benthic algae to nutrients remineralized from sediments may preclude nutrient limitation across the whole DOM gradient. If benthic algae are not nutrient limited, we would predict a monotonic relationship in algal growth of un-amended treatments with increasing DOM as the result of light limitation. In this case, we would not expect large responses to added nutrients.

**Methods**

**Study sites**

We conducted experimental deployments during summer 2018 in 10 lakes in Boreal and Arctic Sweden (Fig. S1). For the boreal region, mean annual temperature, precipitation, and sunlight hours (2008–2018) were approximately 3.1°C, 653 mm, and 1877 h, respectively. For Arctic lakes, these were ~0.4°C, 344–821 mm (precipitation increases from east to west), and 1410 h (Swedish Meteorological and Hydrological Institute 2018). Total atmospheric N deposition is low in both regions (< 200 kg km−2 yr−1) and pelagic primary production is often limited by N availability (Bergström et al. 2008, 2013). Lakes included in this study were small (1.8–9.1 ha) and their altitude ranged from 238 to 490 m.a.s.l. The benthic substrate in the littoral zone consisted of cobble-boulder or organic-rich soft sediments.

**Water chemistry and environmental variables**

We visited each lake three times, with approximately 3 weeks between each visit, and collected water from approximately 10 cm depth in littoral zone for analysis of (1) pH, (2) absorbance, (3) dissolved nutrients (nitrate [NO3−], ammonium [NH4+], total dissolve nitrogen [TDN], soluble reactive phosphorus [SRP], and total dissolved phosphorus [TDP]), and (4) dissolved organic carbon (DOC). Samples for pH were unfiltered with no headspace and measured immediately on return to the laboratory (within 8 h of collection) using a benchtop pH meter (Mettler Toledo SevenCompact for Arctic and SevenEasy for Boreal samples). Absorbance, nutrients, and DOC samples were filtered in the field using 0.45 μm syringe filters flushed with sample. All samples were stored on ice in the dark during transport to the lab. Absorbance samples were stored dark at 4°C until measurement on a benchtop spectrometer (Aqualog, Horiba Scientific). Dissolved nutrient samples were frozen at −20°C and then analyzed colorimetrically on a continuous segmented flow analyzer (QuAAtro39 AutoAnalyzer, SEAL Analytical). Total dissolved nutrients were analyzed in the same manner following in-line digestion by the alkaline acidic persulfate method. DOC samples were...
Table 1. Physical and chemical characteristics and benthic algal nutrient limitation status of lakes used in this study (ordered by DOC concentration).

| Site name | Lat | Long | Substrate | Estimated | DOC* (μmol L⁻¹) | NO₃⁻ (μmol L⁻¹) | NH₄⁺ (μmol L⁻¹) | TDN* (μmol L⁻¹) | SRP* (μmol L⁻¹) | TDP* (μmol L⁻¹) | Nutrient limitation status |
|-----------|-----|------|-----------|-----------|----------------|----------------|----------------|----------------|----------------|----------------|--------------------------|
| BD06      | 68.44 | 18.15 | 0.0226 | 0.44 | 6.27 | 2.03 |
| Abbottnet | 64.48 | 19.43 | 0.0018 | Organic | 0.39 | 6.12 | 3.37 |
| Ambergnet | 68.35 | 19.04 | 0.0065 | Mixed | 0.50 | 7.14 | 4.73 |
| BD03      | 68.36 | 18.60 | 0.0107 | Organic | 0.43 | 6.33 | 5.27 |

Sites indicated (†) had three NDS deployments at approximately 1, 0.5, and 0.1 m depth whereas all other sites had one deployment at approximately 1 m depth. Reported values of starred (*) parameters are the means of samples collected during three visits to each lake during summer 2018. Substrate column describes the type of substrate at the deployment location. "N" denotes single-nutrient limitation by N, "NP" denotes colimitation by N and P, and "N+P" denotes serial limitation by N then P (i.e., further stimulation by P only in the presence of N, sensu Harpole et al. 2011), while "None" indicates that nutrient addition of any kind did not stimulate benthic algal growth.

Acidified (1% v : v 8 M HCl) and stored dark at 4°C until analysis by high-temperature catalytic combustion on a TOC analyzer (Formac™ HT-I, Skalar).

Experiment set up, deployment, and processing

We prepared NDS using the method described by Tank et al. (2006), with four treatments: control (C; 2% agar only), N addition (N: 0.5 M NaNO₃ in 2% agar), P addition (P: 0.1 M PO₄³⁻ as 0.05 M KH₂PO₄ + 0.05 M K₂HPO₄ in 2% agar), and combined N and P addition (N+P: combination of the N and P treatments in 3% agar). Treatment solutions were poured into 30 mL plastic cups (Polycon) modified with 25 mm holes in the lids and fritted ceramic discs (Leco) fitted snugly between the cooled agar solution and lid. We secured the cups onto metal racks with at least 4 cm (one cup diameter) between each, using a stratified random placement. Each rack was then placed on the lake bottom in the littoral zone at approximately 1 m (all lakes), 0.5 m, or 0.1 m (shallow waters in a subset of 4 lakes, Table 1), with discs approximately 3.8 cm above the benthic surface. After placement, the depth of each of the four corners of the rack was measured and these were averaged to determine the actual depth of each deployment (n = 18).

 Deployments were left to incubate for 3 weeks, the time during which nutrient diffusion enriches the overlying disc (Tank et al. 2006). To extend our experiment to 6 weeks, we replaced the agar solution by placing each disc onto a fresh cup of agar with the same treatment and replacing the racks in the same position for an additional 3 weeks. After a total of 6 weeks, discs were transferred to 50 mL centrifuge tubes filled with lake water and stored on ice in the dark until return to the laboratory. We recovered 3–4 replicates per treatment for chlorophyll a (Chl a) analysis.

After return to the lab, discs were transferred to plastic zip bags and stored dark at –80°C until spectrophotometric analysis of Chl a. We extracted Chl a from frozen discs in 90% acetone solution in the dark at room temperature for 24 h with occasional shaking. Absorbance spectra of the resulting solutions were measured (JASCO V-560 or Horiba Aqualog) and used to calculate pheophytin-corrected Chl a concentration according to Steinman et al. (2007), but corrected by absorbance at 700 nm rather than 750 nm (these two correction wavelengths produce nearly identical values for Chl a, Fig. S2). We converted these concentrations to areal Chl a using the area of disc exposed during incubation.

Light calculations

While epilimnetic water chemistry parameters vary among individual lakes, light penetration to NDS surfaces is a function of optical properties of the water as well as depth. As such, the percent of incident light transmitted varies among deployments within and among lakes. For each deployment, we determined light transmitted by using mean of absorbance at 440 nm to estimate light extinction (kd) per the relationship between these values for 55 lakes across Boreal and Arctic
Sweden described by Seekell et al. (2015b). Then, we used the calculated value of $k_d$ for each lake combined with the measured depth of each experimental deployment to determine the proportion of incident light that reached each NDS deployment.

Statistical methods
Within each of the four lakes that had multiple deployments, we used ANOVA to examine how incubation depth affected algal growth, followed by Tukey’s Honest Significant Difference test to identify which depths differed from others. We compare outcomes among lakes to assess how depth effects differed among lakes with different DOC concentrations.

To differentiate among predicted relationships for benthic algal growth over the gradient among lakes (unimodal or monotonic decline with higher DOC/lower light), we fit multiple models and used the Bayesian information criterion (BIC) to select the best. Specifically, we fit three types of monotonic models (simple linear, logarithmic, and exponential to encompass a range of possible behaviors) and one unimodal (second-order polynomial) to Chl $a$ vs. DOC, light, and TDN. For each independent variable, we chose the model with the lowest BIC as the best model for describing the relationship of Chl $a$ along the gradient of interest.

We assessed nutrient limitation by first using ANOVA to distinguish differences among treatment effects within individual deployments and then assessed differences among treatments with Tukey’s Honest Significant Difference test. We then calculated the transformed response ratio for each treatment by dividing the Chl $a$ measured in each treatment replicate by the mean Chl $a$ in controls of the same deployment and taking the natural log. We investigated the relationship between nutrient response ratios and light using simple linear regression. We checked assumptions of models and by visually examining Q-Q and residual plots. All statistics were carried out in the R environment (R Development Core Team 2012).

Results
Nutrient concentrations and absorbance were positively correlated with DOC (Table 1; Figs. S3, S4). Across all lakes, DOC concentration explained 55% and 68% of the variation in TDN ($p < 0.0001$; $F_{1,28} = 35.9$) and TDP ($p < 0.0001$; $F_{1,28} = 62.9$), respectively. Relationships between DOC and inorganic nutrients were weaker than with total dissolved nutrients. For example, DOC concentration explained 39% of the variation in NO$_3^-$ ($p = 0.0002$; $F_{1,27} = 18.9$), 55% in NH$_4^+$ ($p < 0.0001$; $F_{1,28} = 36.0$), and 42% in SRP ($p < 0.0001$; $F_{1,28} = 22.3$).

Depth of incubation affected algal growth in control treatments in two of the four lakes that received multiple deployments (Fig. S5). In the lake with the lowest DOC (BD06), Chl $a$ in controls was higher in the 1 m incubation compared to the other depths ($p = 0.01$; $F_{2,7} = 8.194$). In contrast, the lake with the highest DOC (Övre Björntjärn) had lower Chl $a$ at 1 m than at 0.1 m ($p = 0.02$; $F_{2,9} = 5.696$). In the other lakes with incubations at multiple depths, Chl $a$ in controls did not differ among depths ($p > 0.05$ for all pairwise comparisons; $F_{2,8} = 4.268$ for Almberga and $F_{2,9} = 4.528$ for Nästtjärn).

Chl $a$ on control discs showed unimodal relationships with DOC, light, and TDN among lakes (Fig. 1; Table S1). In each case, the second-order polynomial had the lowest BIC and explained the greatest proportion of the variation in Chl $a$, as compared to the monotonic models. A second-order polynomial with mean DOC concentration as the independent variable described 28% of the variation among Chl $a$ on discs incubated at ~1 m depth (Fig. 1A; Table S2). Similarly, a second-order polynomial between Chl $a$ vs. DOC, light, and TDN. For each independent variable, we chose the model with the lowest BIC as the best model for describing the relationship of Chl $a$ along the gradient of interest.
and TDN described 32% of the variation in Chl $a$ (Fig. 1B; Table S2). Finally, using data from all depths, the unimodal relationship between Chl $a$ and the proportion of light transmitted to discs was also described by a second-order polynomial ($R^2 = 27\%$, Fig. 1C; Table S2).

The effects of added nutrients on Chl $a$ production differed along the DOC gradient (Fig. 2). The addition of P alone never stimulated Chl $a$ accumulation relative to controls ($p > 0.05$ for P vs. C treatments in 16 of 18 deployments; Table S3) and Chl $a$ was lower on P than C treatments for two deployments. In contrast, there was widespread evidence for primary or colimitation by N (Table 1; Table S3). In 11 of 18 deployments, we found single-nutrient N limitation, in two we found serial limitation by N then P (sensu Harpole et al. 2011), and four deployments were colimited by N and P. Only one deployment showed no evidence of nutrient limitation (Övre Björntjärn 1 m; $p = 0.305$; $F_{4,15} = 1.33$). Furthermore, the strength of nutrient limitation was positively correlated with light absorption in the water column: both N and NP response ratios increased with the proportion of incident light reaching the deployment (Fig. 2; Table S4).

Discussion

Given their importance to primary productivity (Ask et al. 2009), the responses of benthic algae to changing environmental drivers have key consequences for northern lakes. We demonstrate a unimodal relationship between benthic algal growth and DOC concentration across Arctic and Boreal lakes in northern Sweden, as reported elsewhere for pelagic and whole-lake primary production and primary producer biomass (Hanson et al. 2003; Seekell et al. 2015a; Kelly et al. 2018; Bergström and Karlsson 2019). Because DOM regulates the light environment and correlates with terrestrial nutrient supply, we observe similar unimodal relationships for benthic algal growth vs. light and TDN (Fig. 1). Overall, this pattern suggests that when DOM is low, light is abundant but nutrients are limiting to benthic algae; conversely, when DOM is high, nutrients are replete and primary production is
increasingly light-limited. Indeed, our results suggest that increases in DOM input to clear lakes may stimulate benthic autotrophs by supplying limiting nutrients, up to a point where the negative effects of light limitation take over.

Experimental nutrient additions support these interacting mechanisms, while also identifying N as the primary limiting nutrient. At low DOM, N limitation of benthic primary production was widespread, whereas addition of P alone had no measurable stimulation in any lake. These responses are consistent with N or N+P limitation observed from whole lake nutrient additions (Deininger et al. 2017; Bergström and Karlsson 2019) and bioassays of pelagic primary production in northern Sweden (Bergström et al. 2008, 2013). The dominance of N-fixing cyanobacteria in epilithic communities of lakes provides additional support for the importance of N as a constraint to aquatic primary production in this region (Diehl et al. 2018). However, the response of algal growth to added N decreased across lakes with greater DOM concentration (Fig. 2), even under conditions when light should not have been limiting. If we focus below the inflection point (i.e., on the rising limb of the unimodal relationship), this declining response ratio, together with the positive correlation between Chl a and DOM on controls (Fig. 1), supports the idea that terrestrial nutrient inputs are a key resource that reduces limitation. Yet, algal growth on nutrient-amended discs was still much greater than on controls, indicating that these external inputs never completely satisfy benthic algal N demand.

Strong N limitation of benthic algae also suggests nutrient supply from underlying sediments was insufficient to fully support high rates of benthic productivity, as has been observed in strongly oligotrophic lakes elsewhere (Hansson 1992). This observation contrasts with other findings that suggest benthic algae are less subject to nutrient limitation than pelagic counterparts because they take advantage of nutrients in both water column and sediment pools (Hansson 1988; Jäger and Diehl 2014). For example, Daniels et al. (2015) and Björk-Ramberg (1983) found that benthic algae did not increase in response to water column fertilization in northern lakes, and thus concluded that benthic algal production was likely not nutrient-limited. However, fertilizing the water column is not an independent test of nutrient limitation of benthic algae since it not only modifies nutrient supply, but also potentially decreases light availability by stimulating phytoplankton growth (Hansson 1988). By comparison, our approach tested responses to nutrient addition without modifying the light environment and thus provides a more direct assessment of nutrient limitation. Overall, despite their potential to be better competitors than phytoplankton for nutrients (Hansson 1988), our results show benthic algae can be subject to strong nutrient limitation in DOM- and nutrient-poor lakes.

Reconciling these different perspectives on nutrient limitation of benthic algae requires that we consider how the type of benthic substrate influences the extent to which algal growth is coupled to internal vs. external nutrient supplies. Specifically, epipelic algae may be able to more easily access remineralized nutrients in sediments, whereas epilithic algae are more strongly linked to nutrients in the water column. Higher rates of N-fixation in epilithic vs. epipelic communities provide evidence for such differences in nutrient availability between these habitat types (Lundgren 1978). Thus, while our results show the response of epilithic algae to differences in water column chemistry, they may not capture that of epipelagic algae if they indeed have more direct access to limiting nutrients. Comparing rates of algal growth between unamended and nutrient-enriched samples provides a glimpse into the potential response of benthic algae that may arise from nutrients supplied by external inputs as opposed to underlying sediments (Fig. 3). Potential differences in response between epilithic and epipelic algae are likely to be most pronounced in lakes with low concentrations of DOM and nutrients in the water column, where epipelic algae could have a major advantage provided adequate nutrient availability in the sediments. Further, if epipelagic algae have access to sediment nutrients, their growth may not be stimulated by DOM-associated nutrients in the way we observed over the rising limb of the relationship among unamended discs (Fig. 1). Indeed, under nutrient-replete conditions (N and NP treatments in our experiment), this rising limb of the unimodal relationship disappears, while the effect of light limitation is still apparent in the darkest lake (Fig. 3; Fig. S6). Overall, as DOM concentrations in northern lakes continue to increase over time, differences between epilithic and epipelic algal responses to DOM loading may have important implications for future ecosystem function in northern lakes.

Our findings have implications for multiple environmental changes in northern Fennoscandia. In this region, ongoing browning trends (De Wit et al. 2016) are concurrent with declines in N deposition, soil N export, and DIN concentrations in surface waters (Lucas et al. 2016, Isles et al. 2018). These opposing trends make future lake productivity difficult to predict. First, the nonlinear relationship between primary production and DOM means that future primary production in a lake depends on its current DOM concentration and the magnitude of increase. A majority of northern Swedish lakes are less than 10 ha in area (~ 93%), like the lakes studied here, and have DOC concentrations below the inflection point indicated in this study (Seekell et al. 2015b; Bergström and Karlsson 2019). This suggests that benthic algal production in most lakes ought to show positive responses to increasing DOM. However, the simultaneous trend of oligotrophication (Huser et al. 2018) could push algal communities toward more severe nutrient limitation.

The ultimate outcome for benthic algal production under simultaneous trends of increasing DOM and decreasing nutrient inputs will depend on the mechanisms that couple DOC and DIN supply. For example, if the N that supports algal production is derived from mineralization of DOM within lakes.
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