

The influence of dissolved organic carbon on primary production in northern lakes

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Abstract

Dissolved organic carbon (DOC) concentrations in lakes are changing globally, but little is known about potential ecosystem impacts. We evaluated the relationship between DOC and whole-lake primary production in arctic and boreal lakes. Both light extinction (inhibits primary production) and nutrient availability (stimulates primary production) are positively and nonlinearly related to DOC concentration. These nonlinearities create a threshold DOC concentration (4.8 mg L^{-1}), below which the DOC-primary production relationship is positive, and above which the relationship is negative. DOC concentration varies maximally between regions, creating a unimodal relationship between primary production and DOC that emerges at broader scales because arctic lakes largely fall below the threshold DOC concentration, but boreal lakes fall above it. Our analysis suggests that the impact of DOC trends on lake primary production will vary across lakes and regions as a result of contrasting baseline conditions relative to the DOC threshold.

Nutrients and food web structure are key controls on lake primary production in temperate zones and human-impacted regions, but most lakes are in pristine high-latitude environments where less is known about the processes constraining productivity (Carpenter et al. 1998; Karlsson et al. 2009; Verpoorter et al. 2014). These northern lakes are typically oligotrophic, but are influenced to various degrees by colored, terrestrially derived dissolved organic carbon (DOC) that is flushed into lakes from the surrounding landscape (Cole 2009; Karlsson et al. 2009; Thrane et al. 2014). DOC attenuates light due to chromophoric molecules and production in many of these lakes is light-limited due to a combination of lake morphology and DOC content (Cole 2009; Karlsson et al. 2009; Thrane et al. 2014). These findings suggest that DOC should have a key role in limiting primary production in northern lakes, such that spatial patterns (e.g., Seekell et al. 2014) and temporal trends (e.g., Monteith et al. 2007; Clark et al. 2010) in DOC concentration should be directly reflected in lake primary production.

Recently, several lines of evidence have emerged that suggest that the influences of DOC on lake primary production may be more complex than the hypothesis of monotonic decreases with increasing DOC concentration.

Specifically, nutrients tightly bind to humic compounds in terrestrial DOC inputs and these nutrients may be released by photolysis, stimulating primary production (Jones et al. 1988; Klug 2002; Kissman et al. 2013). Additionally, DOC can stimulate primary production by shielding phytoplankton from harmful ultraviolet radiation and by increasing dissolved CO_2 concentrations as a result of photochemical reactions and bacterial mineralization (Williamson et al. 1999; Jansson et al. 2012; Lapierre et al. 2013). For example, DOC additions led to increasing pelagic primary production in alpine systems with very low ambient DOC concentrations (Kissman et al. 2013). Hence, there is evidence that DOC plays an important role in influencing primary production because it is closely associated with both light limitation and nutrient availability, but the interactions between these contrasting influences of DOC on lake primary production remain poorly known (Williamson et al. 1999). This, in turn, limits the ability to generalize, extrapolate, and predict responses of lake ecosystems to changes in DOC concentrations.

Changes in DOC concentration are a dramatic manifestation of global environmental change in lakes with positive trends reported in many regions (Monteith et al. 2007; Clark et al. 2010). However, understanding of potential ecosystem impacts is mostly speculative and empirical relationships linking DOC to ecosystem processes, like primary

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production, are scarce (e.g., Sadro and Melack 2012; Brothers et al. 2014; Solomon et al. 2015). Here, we assess the role of DOC in shaping the response of lake primary production to gradients of light and nutrient availability across widely distributed arctic and boreal lakes. To do so, we evaluated light limitation and nutrient availability as potential controls on whole-lake primary production (benthic + pelagic) in boreal (lakes south of the arctic circle, but within the boreal zone) and arctic (lakes north of the Arctic circle) lakes based on a compilation of original and literature data from Sweden and Alaska. Specifically, we tested for relationships between primary production and lake light environment, a function of lake mean depth and vertical light attenuation, and primary production and total-nitrogen (TN) concentration using linear regression analyses. We then evaluate how these different factors interacted to shape the patterns in primary production across gradients in DOC.

Methods

We compiled measurements of whole-lake (benthic + pelagic) primary production in Swedish and Alaskan lakes from published and unpublished sources (Table 1). We have previously described the methods used for determining benthic and pelagic primary production in Swedish lakes (Karlsson et al. 2002; Ask et al. 2009a). Briefly, pelagic primary production was measured at mid-day using the ^{14}C incorporation method by collecting lake water from 6 to 10 depths (depending on in situ light measurements) and incubating in transparent and dark glass bottles at the sample depth for four hours (Ask et al. 2009a). This method estimates rates somewhere between gross and net primary production and hence we refer to these rates simply as primary production (Wetzel and Likens 2000). Daily rates were estimated using the ratio of photosynthetically active irradiance during the incubation period to whole-day irradiance (Karlsson et al. 2002; Ask et al. 2009a). Benthic primary production was measured at multiple depths based on changes in dissolved inorganic carbon (DIC) over a 24-h period in closed transparent (net primary production) and dark (community respiration) plastic tubes containing a sediment core (10–15 cm) and overlying water (Ask et al. 2009a,b 2012). The tubes were incubated in situ at the depth of collection, and rates were corrected for pelagic counterparts. This methodology is thought to accurately capture gross primary production rates (by summarizing the net primary production and community respiration) if nighttime and daytime algal respiration rates are equal (Carignan et al. 2000; Williams and Lefevre 2008; Ask et al. 2012). However, because there is some uncertainty in the equality of these respiration rates, we also refer to these measurements simply as primary production. These methods were applied in both our previously published studies and in the new data included here. For two lakes (Lake A7 and Lake A9), light attenuation was high and we assumed benthic primary production was zero

because we could not record benthic production through change in DIC concentration. Methane concentrations were negligible compared to DIC. All measurements were taken during June or July. Estimates were adjusted for volume (pelagic) or area (benthic) at depth to generate average values for the whole lake. Similar methods were used to determine primary production in Alaskan lakes. A detailed description of data collection for Alaskan lakes is found elsewhere (see Whalen et al. 2006, 2008; Northington et al. 2010). In lakes where primary production was measured more than once, we used the mean of the measurements.

For each lake, we compiled ancillary information measured using standard limnological procedures (e.g., Ask et al. 2009a) including DOC concentration (mg L^{-1}), total nitrogen concentration (TN; mg L^{-1}), light attenuation coefficient (k_d ; m^{-1}), and mean depth (Z_m ; m). We calculated a standardized index of whole lake light environment based on Beer's Law (I_m) (see Sterner 1990; Karlsson et al. 2009). The index accounts for the dual influence of lake morphometry and light attenuation and ranges from 0 to 1, with 0 indicating that 0% of incident photosynthetically active radiation (PAR) reaches the mean depth, while 1 indicates that 100% of incident PAR reaches the mean depth (Karlsson et al. 2009).

$$I_m = \frac{1}{Z_m} \int_0^{Z_m} e^{-k_d z} dz = \frac{1 - e^{-k_d Z_m}}{k_d Z_m}$$

We tested for differences in mean lake characteristics between regions using two-sample *t*-tests with unequal variances. We experimented with distribution-free tests (e.g., Mann–Whitney U test), but achieved the same results. We then tested for relationships between whole-lake primary production, light environment and TN using linear regression analysis. We used TN concentration as a primary metric of nutrient availability instead of total-phosphorus (TP) concentration, the limiting nutrient in many temperate lakes, because previous analyses found that lakes in these regions are predominantly nitrogen limited (Jansson et al. 2001; Levine and Whalen 2001; Bergström et al. 2005, 2013). We also tested for the relationship between k_d , TN, and DOC using linear regression. We compared the relative impact of DOC on k_d and TN empirically by calculating the elasticity of the k_d -DOC and TN-DOC relationships. The elasticity of a relationship is the percent change in the dependent variable in response to a percent change in DOC concentration. Elasticity is calculated as $\frac{dk_d}{d\text{DOC}} \frac{\text{DOC}}{k_d}$ and $\frac{dT_N}{d\text{DOC}} \frac{\text{DOC}}{\text{TN}}$.

Results

There was no significant difference in mean lake depth between regions (overall mean = 3.68 m, $t = -1.27$, $df = 21$, $p = 0.22$). There was also no significant difference in TN concentration (overall mean = 0.316 mg L^{-1} , $t = -1.56$, $df = 14$,

Table 1. Original and literature data used in the analysis.

Region	Lake	Area (ha)	TN (mg L ⁻¹)	DOC (mg L ⁻¹)	k_d (m ⁻¹)	Z_m (m)	Primary production (g C m ⁻² d ⁻¹)	Source
Arctic Sweden	Tjabrak	6.23	0.131	3.12	0.46	4.7	0.097	Ask et al. (2009a)
Arctic Sweden	Almberga	5.48	0.178	4.02	0.51	3.2	0.121	Ask et al. (2009a)
Arctic Sweden	Vuorejaure	4.28	0.135	2.81	0.44	2.8	0.109	Ask et al. (2009a)
Arctic Sweden	Ruozutjaure	3.5	0.116	2.4	0.44	2.8	0.114	Ask et al. (2009a)
Arctic Sweden	Erkkijärvi	10.99	0.431	7.07	0.65	2.3	0.211	Ask et al. (2009a)
Arctic Sweden	Estvåjärvi	2.47	0.406	13.11	1.62	1.5	0.190	Ask et al. (2009a)
Arctic Sweden	Sourra	17.42	0.080	1.8	0.32	4.7	0.093	Ask et al. (2009a)
Arctic Sweden	Knivsjön	10.85	0.089	2.43	0.41	4.5	0.131	Ask et al. (2009a)
Arctic Sweden	Solbacka	—	0.365	9.4	0.18	1.8	0.343	This study
Arctic Alaska	GTH-99	0.7	—	4.48* [†]	1.1	2.1	0.119	Northington et al. (2010) and Whalen et al. (2008)
Arctic Alaska	NE-8	5	—	—	0.5	1.3	0.251	Northington et al. (2010) and Whalen et al. (2008)
Arctic Alaska	GTH-112	2.8	0.700	6.11*	2.5	2.2	0.103	Northington et al. (2010) and Whalen et al. (2006)
Arctic Alaska	GTH-114	3.9	0.280	8.07* [†]	1.3	2.2	0.148	Northington et al. (2010) and Whalen et al. (2006)
Arctic Alaska	I-4	8.2	—	8.53*	0.8	3.2	0.113	Northington et al. (2010) and Whalen et al. (2008)
Arctic Alaska	I-8	18.3	—	—	0.9	3.5	0.107	Northington et al. (2010) and Whalen et al. (2008)
Arctic Alaska	GTH-100	5.4	—	6.43* [†]	0.7	6.4	0.073	Northington et al. (2010) and Whalen et al. (2008)
Arctic Alaska	NE-12	7.5	—	4.42* [†]	0.5	7.6	0.079	Northington et al. (2010) and Whalen et al. (2008)
Boreal Sweden	Övre Björntjärn	4.84	0.476	16.8	3.77	4.0	0.005	Ask et al. (2009a)
Boreal Sweden	Nedre Björntjärn	3.37	0.427	15.1	3.2	6.0	0.006	Ask et al. (2009a)
Boreal Sweden	Lilla Björntjärn	1.54	0.483	15.91	2.97	4.6	0.031	Ask et al. (2009a)
Boreal Sweden	Holmtjärn	3.72	0.354	9.5	1.89	3.1	0.064	Ask et al. (2009a)
Boreal Sweden	Snottertjärn	2.48	0.336	10.12	1.14	2.0	0.201	Ask et al. (2009a)
Boreal Sweden	Abborrtjärn	5.82	0.262	11.11	1.9	4.6	0.052	Ask et al. (2009a)
Boreal Sweden	Rengårdstjärnen	4.86	0.277	7.99	1.08	2.6	0.192	Ask et al. (2009a)
Boreal Sweden	AT3	9.3	0.230	3.81	0.42	6.4	0.070	This study
Boreal Sweden	AT4	2.4	0.262	4.05	0.56	7.5	0.076	This study
Boreal Sweden	A7	—	0.492	17	3.2	2.8	0.018 [†]	This study
Boreal Sweden	A9	—	0.446	21	4.2	2.7	0.020 [†]	This study

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[†]Mean value.

$p = 0.14$) between regions, but this is in part because concentrations for two unstratified Alaskan lakes were very high due to wind mixing (Whalen et al. 2008). Excluding these lakes, TN concentration was significantly greater in boreal compared to in arctic lakes ($t = 2.707$, $df = 13$, $p = 0.018$). Lake water DOC concentrations were significantly higher in the boreal (mean = 12.0 mg L⁻¹) than in the arctic region (mean = 5.6 mg L⁻¹) ($t = -3.43$, $df = 14$, $p = 0.004$). As a consequence, vertical light extinction coefficients (k_d , m⁻¹) were

significantly higher in the boreal (mean = 2.21 m⁻¹) than in the arctic (mean = 0.78 m⁻¹) ($t = -3.38$, $df = 12$, $p = 0.005$). Whole-lake (benthic + pelagic) primary production ranged between 0.005 g C m⁻² d⁻¹ and 0.343 g C m⁻² d⁻¹, with production in arctic lakes ($n = 17$, mean = 0.141 g C m⁻² d⁻¹) being significantly greater than production in boreal lakes ($n = 11$, mean = 0.067 g C m⁻² d⁻¹) ($t = 2.77$, $df = 21$, $p = 0.011$). Primary production in both regions is substantially lower than for temperate lakes. For instance,

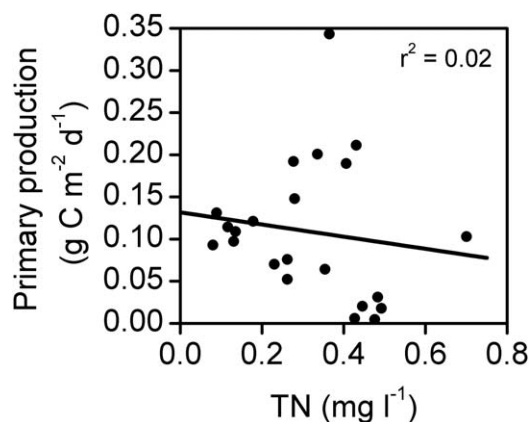


Fig. 1. Primary production is not related to total nitrogen concentration in the study lakes.

Vadeboncoeur and Steinman (2002) report that whole-lake primary production averaged $1.21 \text{ g C m}^{-2} \text{ d}^{-1}$ for four temperate lakes (annual primary production values divided by five month growing season).

There was a substantial range among lakes in benthic contribution to overall primary production (0–97%), but no significant difference in mean values between regions. This lack of difference is likely due to wind driven mixing in two unstratified Alaskan lakes with low mean depth which increases rates of pelagic primary production by increasing nutrient availability through sediment resuspension (Whalen et al. 2008; overall mean = 59%; $t = 1.14$, $df = 15$, $p = 0.273$). In several lakes where primary production measurements were repeated over the growing season, production was low and without strong trends (Ask et al. 2009b). In sum, the principal difference between lakes in these regions is that the arctic lakes are clearer than the boreal lakes due to lower DOC concentrations and this difference is reflected in higher whole-system productivity of the arctic lakes.

TN concentration was inversely, but not significantly, related to whole-lake primary production (Fig. 1) ($r^2 = 0.02$; $F_{1,20} = 0.400$, $p = 0.534$). This indicates that the lakes are not primarily nutrient limited (e.g., Karlsson et al. 2009). Rather, whole-lake primary production is strongly related to the light environment (Fig. 2A) ($r^2 = 0.7$, $F_{1,26} = 59.7$, $p < 0.001$); whole-lake primary production is high when lakes are shallow or have relatively clear water, and low when lakes are deep or have relatively dark water. Benthic contributions to whole-lake primary production were significantly correlated with light environment ($r = 0.705$, $p < 0.001$); high-light lakes have higher relative contributions of benthic primary production than low-light lakes. TN explains some residual variation around the primary production-light relationship (overall model adj. $r^2 = 0.81$), indicating that nitrogen stimulates primary production, but this influence is secondary to light limitation (Fig. 2B). The effect of TN on residual primary production is nonlinear and saturating, indicating that

there is more residual variability in clearer lakes and that increased nutrient availability mainly stimulates whole-lake primary production in these clearer, nutrient replete systems. This is confirmed by refitting the regression separately for boreal and arctic lakes. In the darker boreal lakes, whole-lake primary production is related (adjusted $r^2 = 0.73$) to light environment (partial relationship $t = 4.32$, $p = 0.003$), but not to TN (partial relationship $t = 0.69$, $p = 0.511$). In the clearer arctic lakes, whole-lake primary production is positively related (adjusted $r^2 = 0.81$) to both light environment (partial relationship $t = 5.65$, $p < 0.001$) and TN (partial relationship $t = 4.85$, $p < 0.001$). We experimented with including TP concentration in the regression, but there was not a substantial improvement in explanatory power relative to simpler models. Further, the partial relationship is negative which is inconsistent with phosphorus limitation (Karlsson et al. 2009). We also evaluated the univariate relationships between primary production and TP. The relationship was negative and not statistically significant ($r^2 = 0.181$; $F_{1,19} = 4.19$; $p = 0.055$).

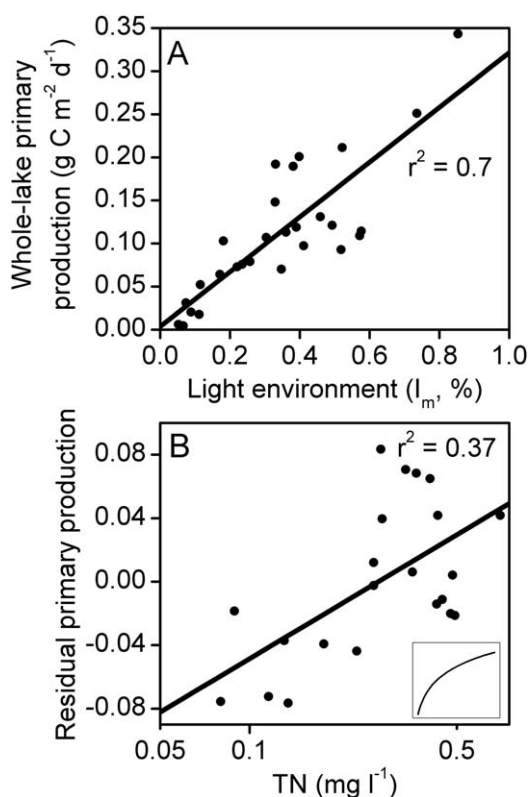


Fig. 2. Panel (A) Light environment (proportion of surface light at mean depth) explains a majority share of variation of gross primary production in northern lakes. Panel (B) TN explains residual variability in the primary production-light relationship. The inset shows the shape of the untransformed curve. Without first controlling for light environment, there is no statistically significant relationship between primary production and TN (Fig. 1).

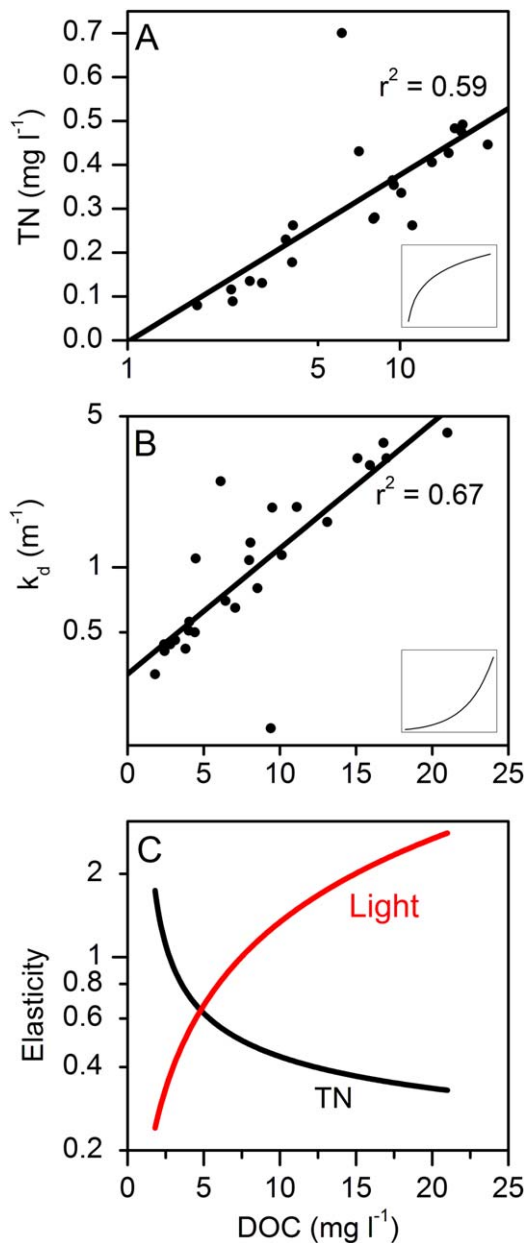


Fig. 3. DOC is related to both TN concentration (Panel A) and vertical light extinction (Panel B). Note differences in the scale between panels; insets show the shapes of untransformed curves. Panel (C) Elasticity is greater for TN than light extinction at low DOC concentrations (i.e., the TN curve is higher than the DOC curve), indicating a greater relative impact on increased nutrient availability than increased light extinction. At moderate and high DOC concentrations, increasing light extinction has a greater relative impact than increased nutrient availability (i.e., the DOC curve is higher than the TN curve).

The light extinction coefficient ($r^2 = 0.67$; $F_{1,24} = 49.23$, $p < 0.001$) and TN concentration ($r^2 = 0.59$, $F_{1,20} = 28.75$, $p < 0.001$) are both strongly, nonlinearly related to DOC concentration (Fig. 3A,B). However, the function form of the relationships is dissimilar. Specifically, light extinction

changes little across low DOC concentrations, and increases exponentially at moderate and high concentrations (Ask et al. 2009a). TN concentration changes rapidly at low DOC concentrations, but little at moderate and high concentrations. The elasticity curves intersect at 4.8 mg L^{-1} , creating a threshold above which (i.e., at moderate and high DOC concentrations) light limitation increases more rapidly than nutrient availability (i.e., the DOC curve is higher than the TN curve), and below which (i.e., at low DOC concentrations) nutrient availability increases more rapidly than light extinction (i.e., the TN curve is higher than the DOC curve) (Fig. 3C).

Geographically, DOC concentrations vary maximally at the regional scale (i.e., between arctic and boreal regions) (Seekell et al. 2014). This means that there are regional baseline concentrations of DOC and lake-to-lake variability in concentrations is typically lower than the variability in regional baselines (Seekell et al. 2014). This broad-scale variability structures primary production in the sense that regions with low baseline DOC concentrations will be below the threshold identified in our regression analysis and regions with moderate to high DOC concentrations will be above the threshold. Hence, nonlinear relationships may interact with the broader scale variability in DOC concentrations to create spatial heterogeneity in the primary production-DOC relationship. We tested for spatial heterogeneity by testing for a DOC-primary production relationship separately for the boreal and arctic regions. Whole-lake primary production increased significantly across the range of DOC for arctic lakes ($r^2 = 0.33$, $F_{1,13} = 6.44$, $p = 0.025$) but decreased significantly for boreal lakes ($r^2 = 0.47$, $F_{1,9} = 8.26$, $p = 0.018$) (Fig. 4). Hence, DOC influences primary production in individual lakes through light attenuation and associated nutrient availability, and also structures region-to-region patterns of lake primary production. These patterns are mainly driven by differences in the

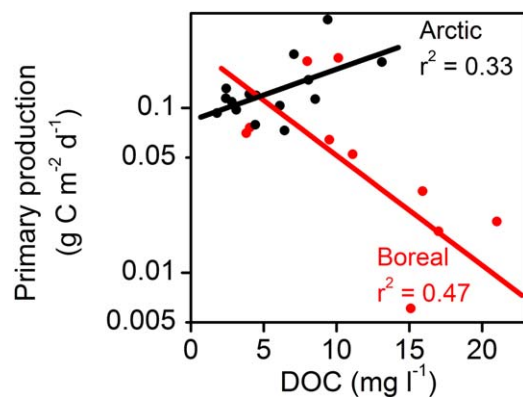


Fig. 4. There is a positive relationship between primary production and DOC for arctic lakes, and a negative relationship for boreal lakes. A unimodal-like relationship emerges when assessing the regions together. This would not necessarily be observed by comparative studies within a single lake (i.e., the within-region relationships are monotonic).

benthic primary production-DOC relationship between regions (boreal benthic primary production-DOC Spearman's $\rho = -0.843$, $p = 0.001$; boreal pelagic primary production-DOC Spearman's $\rho = 0.645$, $p = 0.032$; arctic benthic primary production-DOC Spearman's $\rho = 0.071$, $p = 0.800$; arctic pelagic primary production Spearman's $\rho = 0.539$, $p = 0.038$).

Discussion

Our analysis shows that light environment explains the majority share of variation in whole-lake primary production in northern lakes. DOC concentration is the main determinant of light extinction in these lakes, and hence DOC has a key role in limiting whole-lake primary production in these systems (Ask et al. 2009a; Cole 2009). These results complement our previous findings that secondary production increases with light availability (Karlsson et al. 2009). The shift to benthic dominance of whole-lake primary production in clearer lakes identified here plays an important role in shaping this previously described relationship because benthic primary production is more efficiently transferred to the upper food web than other basal energy sources (Karlsson and Byström 2005; Vander Zanden et al. 2011). Our results differ substantially from prevailing knowledge that light limitation of lake primary production is rare (Lewis 2011). This difference derives at least in part because most broad-scale analyses only consider pelagic production (e.g., Håkanson and Boulion 2001; Lewis 2011). Benthic primary production contributes substantially to overall primary production (59% in our analysis) and this production is more sensitive to variation in lake depth or water color than planktonic production (Hansson 1992; Vadaboncoeur et al. 2001, 2008). This contrast emphasizes that understanding variations in benthic primary production is a key to improving understanding of the ecology of lakes at broad spatial scales.

Perhaps a less intuitive result of our study is the between-region variability in the whole-lake primary production-DOC relationship; although DOC had a negative effect on whole-lake primary production in boreal lakes, a positive effect was observed in arctic lakes where DOC concentrations were typically low. This positive influence of DOC on primary production has previously been hypothesized and tested on pelagic primary production with bag experiments, but ecosystem-scale evidence has been lacking (Kissman et al. 2013). Here we are able to explain this heterogeneity as arising due to between-regional variation in DOC structuring lakes geographically relative to a threshold DOC concentration. Higher DOC concentrations increase light attenuation in both regions, but nutrient availability increases more rapidly (proportionally) than light attenuation if baseline DOC concentrations are low. This spatial heterogeneity is particularly important for understanding how lakes in different regions may respond to the increasing DOC concentrations

forecasted due to climate warming and shifting precipitation patterns (Monteith et al. 2007; Skjelkvåle et al. 2007; Weyhenmeyer and Karlsson 2009). For example, analyses of long-term DOC records in Sweden report no significant trends in the northern Sweden (arctic lakes), but significant increases of at least $0.1 \text{ mg L}^{-1} \text{ yr}^{-1}$ in southern Sweden (boreal lakes) (Skjelkvåle et al. 2007). These contrasting trends suggest that there should be no change in primary production in northern Sweden, but that primary production should decrease in southern Sweden, which is in the boreal zone where primary production is inversely related to DOC. Assuming that past trends in DOC concentration continue in the future and that relationship between primary production and DOC reported here across many boreal lakes holds for individual lakes, we estimate an 8.7% decrease in whole-lake primary production per decade in the boreal lakes of southern Sweden. Whole-ecosystem experiments would be the ultimate test of these predictions for regional differences in ecosystem response.

Why has the DOC threshold reported here not been observed before? One reason may be that most studies evaluating the influence of DOC on primary production have been in temperate and boreal regions where DOC concentrations are relatively high and thus over the threshold that we have calculated here. For example, a recent study of pelagic primary production in Norwegian lakes found decreased production due to increased DOC concentration (Thrane et al. 2014). The median DOC concentration in this study was 5.9 mg L^{-1} , i.e., above the 4.8 mg L^{-1} threshold identified in our analysis. Likewise, in a study of temperate lakes where benthic primary production declined due to increasing DOC concentration, the median DOC concentration was 8.2 mg L^{-1} (Godwin et al. 2014), and high DOC concentrations were also observed in whole-lake experiments that documented negative effects of DOC on pelagic primary production (Carpenter et al. 1998). In alpine lakes, however, dissolved organic matter additions have led to increases in phytoplankton production in a small-bag experiment, where ambient water had DOC concentrations well below ($< 1 \text{ mg L}^{-1}$) the threshold identified in our analysis (Kissman et al. 2013); this was explained by DOC providing nutrients while having negligible effect on light limitation in the experimental systems. Our present results from arctic and boreal regions are consistent with these previous findings, which are based on lakes from a variety of biophysical regions. In our analysis, the arctic lakes had a median DOC concentration (4.5 mg L^{-1}) below the calculated threshold (Fig. 3C), and these lakes had a positive correlation between primary production and DOC. The boreal lakes, in contrast, had a median DOC concentration of 11.1 mg L^{-1} , above the threshold concentration, and an inverse correlation between primary production and DOC was observed. These comparisons between habitat specific and whole-lake primary production estimates are imperfect, but nonetheless, these

differences in conclusions are reconciled by taking the perspective of nutrient limitation at low DOC concentrations and light limitation at high concentrations.

Why do arctic lakes with DOC concentrations above 4.8 mg L^{-1} not exhibit decreased primary production relative to arctic lakes with lower DOC concentrations? A potential explanation is because the two arctic lakes with the highest DOC concentrations were also two of the shallowest. Their shallow mean depths partly offset increased light extinction due to DOC concentrations above the threshold value. Examining primary production and DOC values for two boreal lakes with similar DOC concentrations and shallow mean depths supports this explanation (see Fig. 4, upper two red dots). In these cases primary production is similar to the arctic lakes despite no strong deviation from the k_d -DOC relationship (i.e., the color of DOC is consistent). This emphasizes the potential importance of lake depth in modulating the primary production relative to the light-nutrient threshold identified in our analysis. This threshold would potentially be variable if measured across a wider range of lake sizes, but such an analysis is not possible in the present study, which is based on small lakes (Table 1). Another potential explanation is that relatively high rates of benthic primary production in these shallow lakes could result in the release of uncolored DOC to the water column by benthic algae, implying lower light limiting properties compared to a system dominated by highly colored terrestrially derived DOC (Rodríguez et al. 2013). This is a contributing factor for at least one lake (Solbacka), which has a very low light extinction coefficient relative to what is expected based on DOC concentration alone (Fig. 3B). Developing analyses based on orthogonal gradients of depth and lake color will be important in future studies for determining how these factors contribute to constraining ecosystem processes in northern lakes. However, this was not possible in our present analysis, which is mostly based on a compilation of literature data. These limitations emphasize the need to collect data on lake ecosystem processes at broader scales to more adequately account for these morphometric and environmental gradients.

The threshold we present here could vary at scales beyond those presented in the present analysis. For instance, DOC composition is a function of landscape characteristics including type of vegetative cover and water residence times (e.g., Kothawala et al. 2014). The implication of this is that the slopes or shapes of the k_d -DOC and nutrient-DOC relationships may be geographically variable and hence the threshold DOC concentration could be location specific. The existing literature provides several hints that this may be the case. For instance, the relationship between k_d and DOC in the present study is positive exponential which is consistent with previous studies in this region (e.g., Ask et al. 2009a). However, reports from temperate regions have identified linear or power-law relationships between k_d and DOC and this difference suggests variability in the colored fraction of DOC

that could impact the value of observed thresholds (Bukaveckas and Robbins-Forbes 2000). Variability in the nutrient composition could also impact the value of the thresholds. Specifically, the relative abundance of inorganic vs. organic nitrogen in the total nitrogen pool could vary geographically due to variability in anthropogenic nitrogen loading and nitrogen retention in the catchment (Bergström 2010). At broader spatial scales, phosphorus rather than nitrogen may be a limiting factor to primary production and this could also cause variability in the location of the DOC threshold (Bergström et al. 2005). We cannot resolve this potential variability in the present study, which is based on data from only two regions, however future studies on this topic would provide both important insights into how lakes in different regions may respond to environmental change.

DOC has a controlling influence on thermocline depth and this could be a source of variability not accounted for in our analysis (Jones 1998; Houser 2006). Specifically, we used areal measures of primary production because these are most relevant to ecosystem-scale questions, but patterns in pelagic primary production measurements could be confounded if the mixed layer depth changes across gradients of DOC (Carpenter et al. 1999). If differences in thermocline depth were a confounding factor there would be a negative correlation between pelagic primary production and DOC concentration. In our analysis, there was a positive correlation between pelagic primary production and DOC concentration and this indicates that the patterns described here, which are mostly driven by variability in benthic primary production, are not confounded by differences in thermocline depth. We would further not expect any signal of variability in thermocline depth on volumetric pelagic primary production because differences in thermocline depth are offset by changes light extinction such that there is no difference in the light environment experienced by phytoplankton across DOC gradients (Jones 1998). There are several other factors that may have contributed to the residual variability around the relationships described here which we have not explicitly accounted for. For instance, observation error, top-down control in the food web, and differences in the availability of substrate for benthic algae growth could all cause lake-to-lake variation in the primary production-DOC relationship (Hansson 1992). However, light and nitrogen availability accounted for 81% of variance in whole-lake primary production and this indicates that these other factors are not critical to influencing overall patterns at the broad scales analyzed here. Another factor we have not accounted for is patterns at extremely high DOC concentrations. For example, a positive relationship between primary production and DOC over time has been reported for a temperate lake with extremely high DOC concentrations (e.g., $50 + \text{mg L}^{-1}$) due to promotion of an anoxic hypolimnion and subsequent nutrient release from sediments (Brothers et al. 2014). This high primary production at high DOC concentrations is in

contrast to the patterns reported in our study. We cannot rule out that we would observe such a pattern if our data extended into this range, but we note that such high concentrations are extremely rare at the global scale, and the patterns the types of changes in feedback cycles reported by Brothers et al. (2014) appear unlikely to occur within these normal ranges of DOC concentration (Carpenter and Pace 1997; Sobek et al. 2007). The threshold described here, which is not associated with changes in feedback cycles, is based on data that cover a range of DOC concentrations similar to what has been reported for the vast majority of Earth's lakes (Sobek et al. 2007).

Our results contribute to a growing understanding of the influence of DOC on lake ecosystems (e.g., Carpenter et al. 1998; Kissman et al. 2013; Godwin et al. 2014), in particular how impacts vary at broad spatial scales. Specifically, we show that the influence of DOC on whole-lake primary production depends on regional environmental characteristics, and that relationships in one region do not necessarily extrapolate to other regions. Thus, our results contribute to understanding broad-scale variability in primary production by showing that nonlinear relationships and regional scale variability interact to form emergent relationships, and that these interactions are critical to connecting landscape characteristics to ecosystem processes of individual lakes.

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