ARTICLE

Trade-offs between light and nutrient availability across gradients of dissolved organic carbon concentration in Swedish lakes: implications for patterns in primary production

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Abstract: Dissolved organic carbon (DOC) limits primary production in lakes when present at high concentrations by reducing light availability, but stimulates primary production at lower concentrations by releasing nutrients through photolysis. These dual influences create the potential for threshold relationships between DOC and primary production, but empirical tests for the prevalence of thresholds are scarce. We used Box–Cox regression and environmental monitoring data from 703 subarctic and boreal lakes to assess patterns and potential threshold relationships between light and nutrient availability along gradients of DOC in northern Sweden's six major watersheds. We found consistent patterns of increasing nutrient concentration and light attenuation with DOC. Further, we identified thresholds (mean = 5.96 mg·L^{-1}) below which nutrient concentrations increased more rapidly than light extinction and above where the opposite occurred. These results suggest consistent patterns in primary production with shifts from nutrient to light limitation with increasing DOC. Accordingly, the thresholds agree with the vertex of the curvilinear relationship between lake primary production and DOC. We estimated that most lakes in Sweden are within ±3 mg·L^{-1} of the threshold, indicating high potential for changes from positive to negative influences of DOC on primary production if forecasted increases in DOC concentrations due to climate and land cover change are realized.

Résumé : À fortes concentrations, le carbone organique dissous (COD) limite la production primaire dans les lacs en réduisant la lumière disponible, mais, à plus faibles concentrations, il stimule la production primaire en libérant des nutriments par l'entremise de la photolyse. Si cette double influence se traduit par la possibilité de seuils dans les relations entre COD et production primaire, les tests empiriques permettant d'établir la prévalence de ces seuils sont rares. Nous avons utilisé la régression Box–Cox et des données de surveillance environnementale de 703 lacs subarctiques et boréaux pour évaluer les patrons et la présence pontentielle de seuils dans les relations entre la lumière et la disponibilité de nutriments le long de gradients de COD dans six grands bassins versants du nord de la Suède. Nous avons relevé des patrons consistants d'augmentation des concentrations de nutriments et de l'atténuation de la lumière parallèlement aux concentrations de COD. Nous avons en outre cerné des seuils (moyenne = 5,96 mg·L^{-1}) sous lesquels les concentrations de nutriments augmentent plus rapidement que l'atténuation de la lumière et au-dessus desquels la relation inverse est observée. Ces résultats indiqueraient des patrons répétés de production primaire d'abord limitée par les nutriments, puis par la lumière à mesure qu'augmente le COD. Ces seuils concordent avec le vertex de la relation curvilinéaire entre la production primaire des lacs et le COD. Nous avons estimé que la plupart des lacs en Suède en-deçà de ±3 mg·L^{-1} de la valeur seuil, indiquant un fort pour que le rôle du COD passe d'un efft positif à un efft négatif sur la production primaire si les augmentations prévues des concentrations de COD dues au climat et au couvert de surface devaient se concrétiser. [Traduit par la Rédaction]

Introduction

Dissolved organic carbon (DOC) concentrations are changing in lakes worldwide, with positive trends reported in most regions (Monteith et al. 2007; Larsen et al. 2011). The implications of these changes are poorly understood, in part because there are few theoretical or empirical relationships describing the influence of DOC concentration on ecosystem processes (e.g., Ask et al. 2009; Carpenter and Pace 1997; Lapierre et al. 2013; Solomon et al. 2015). DOC in lakes is mostly from terrestrial sources and is strongly colored, reducing light availability when present in high concentrations and potentially limiting primary production (Carpenter et al. 1998; Williamson et al. 1999; Ask et al. 2009; Wilkinson et al. 2013; Thrane et al. 2014). However, DOC also binds strongly to nutrients that may subsequently be released by photochemical reactions and stimulate primary production (Moran and Zepp 1997; Klug 2002; Kissman et al. 2013; Solomon et al. 2015). The rate

of such photochemical reactions is highest at low DOC concentrations where nutrient availability is the most limiting factor (Moran and Zepp 1997; Molot and Dillon 1997; Seekell et al. 2015). These dual effects have led to the hypothesis that lake primary production should have a unimodal relationship with DOC concentration, where production increases at low DOC concentrations and decreases at higher DOC concentrations (Solomon et al. 2015). This hypothesis is in contrast with prevailing understanding that primary production monotonically decreases with increasing DOC concentrations because of light attenuation (e.g., Carpenter et al. 1998; Lewis 2011). Half of Earth's lakes have DOC concentrations ≤5.7 mg·L^{-1} (Sobek et al. 2007), and the unimodal and monotonic hypotheses give opposite predictions (increase or decrease in primary production, respectively) for how many of these lakes should respond to increasing DOC concentrations (Seekell et al. 2015; Solomon et al. 2015). Hence, there is a strong need for improved understanding of the influence of DOC on lake

ecosystems to predict future changes in lake function (Williamson et al. 1999; Solomon et al. 2015).

Empirical tests for unimodal relationships between primary production and DOC typically provide only weak evidence in support of the unimodal hypothesis (e.g., Solomon et al. 2015). Specifically, studies typically either find (*i*) unimodal relationships, but with high magnitudes of residual variability (e.g., Solomon et al. 2015), or (*ii*) a monotonic relationship (positive or negative), but no unimodal curve (e.g., Carpenter et al. 1998; Kissman et al. 2013; Godwin et al. 2014). We previously documented a unimodal relationship between whole-lake primary production and DOC that was emergent, only appearing when comparing multiple geographic regions (Seekell et al. 2015). We identified a threshold DOC concentration, above which primary production was negatively correlated with DOC, presumably due to light absorption from chromophoric molecules, and below which primary production was positively correlated with DOC, which was attributed to nutrient availability. Because DOC concentrations vary maximally at the regional scale, geographic regions predominately fell on one side or the other of the threshold (Seekell et al. 2015). Specifically, we found that Arctic and subarctic lakes with DOC concentrations below the threshold had a positive correlation between primary production and DOC. Boreal lakes with DOC concentrations above the threshold had a negative correlation between primary production and DOC. There was no unimodal relationship within each individual region, and this potentially explains why most studies find weak unimodal or monotonic relationships, because most previous studies were based on one or a few lakes within the same region (e.g., Carpenter et al. 1998; Kissman et al. 2013; Godwin et al. 2014). This emphasizes the need to examine lake characteristics at broad spatial scales to understand their response to this type of large-scale environmental change (e.g., Monteith et al. 2007).
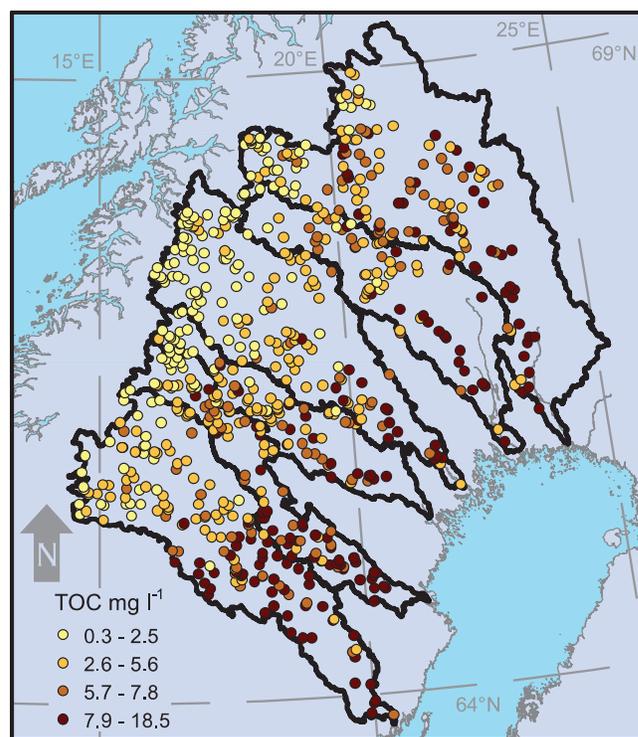
How pervasive are DOC thresholds for primary production? Our previous study was unable to evaluate this question because it was based on a small number ($n = 28$) of lakes (Seekell et al. 2015). We identified, however, a mechanism that appeared to explain the changing role of DOC on lake primary production across regions. Specifically, we evaluated patterns and elasticity in total nitrogen–DOC and light attenuation – DOC relationships. Elasticity is the percent change in either light extinction or nutrient concentration with a percent change in DOC concentration (Haque 2005). With estimates of elasticity, we identify ranges of DOC concentration where nutrient concentration increases proportionally more rapidly than light extinction and identify DOC concentrations where this pattern reverses (i.e., the threshold value). Such data are routinely available via lake surveys, and this trade-off can be used as a surrogate to understand the potential role of DOC as either a promoter or a limiter of lake primary production (Seekell et al. 2015). Here, we apply this methodology to evaluate the light attenuation – DOC and nutrient concentration – DOC relationships in 703 Swedish lakes to explore the geographic patterns in thresholds in light–nutrient trade-offs related to landscape characteristics. We then use a high-resolution lake census to estimate the number of lakes near the thresholds as an indicator of the likelihood that lakes will transition across DOC thresholds in the coming decades.

Methods

Study area

Our study focuses on boreal and subarctic lakes in northern Sweden. Specifically, we examine lakes in six large watersheds within Västerbotten and Norrbotten counties (Fig. 1). We limit our analysis to this region because it is above the atmospheric nitrogen deposition zone, reducing nutrient deposition as a potential confounding factor in nutrient–DOC relationships (Bergström et al. 2005). Primary production in this region's lakes is predomi-

Fig. 1. The study region in northern Sweden comprises six large watersheds. Heavy black lines denote the watershed boundaries. Circles denote study lakes. Portions of some watersheds fall in Norway or Finland, but lakes in these countries are not included in our analysis. From north to south, the watersheds are as follows: Torneälven, Kalixälven, Luleälven, Piteälven, Skellefteälven, and Umeälven. Each watershed drains from alpine and subarctic landscapes in the northwest, through boreal lowlands, into the Baltic Sea.

nantly limited by light and nitrogen availability (Jansson et al. 2001; Bergström et al. 2005; Ask et al. 2009; Karlsson et al. 2009). Hence, we focus on these factors in our analysis instead of other factors such as phosphorus availability. Portions of some watersheds fall within Finnish or Norwegian territory. Lakes from these countries are not included in our analysis.

Data

Our analysis is based on water chemistry data from a national water quality survey conducted every 5 years. Lake surface water (0.5 m) was sampled from above the deepest part of the lake during early autumn when the water column is mixed. The lakes were randomly sampled with stratification by logarithmic size class. Water quality analyses were performed using standard limnological techniques (detailed methods available on the internet: http://www.slu.se/en/departments/aquatic-sciences-assessment/laboratories/geochemical-laboratory/water-chemical-analyses/) by a certified water analysis laboratory at the Swedish University of Agricultural Sciences. The data are freely available on the Internet at http://www.slu.se/vatten-miljo. In our analysis, we consider total nitrogen concentration (TN, $\mu g \cdot L^{-1}$), absorbance at 420 nm (*D*), which is a metric of water color, and total organic carbon concentration (TOC, $mg \cdot L^{-1}$). We calculated absorption coefficients (*a*, m^{-1}) from the absorbance values *D*:

$$(1) \qquad a = (D \times 2.303)/L$$

where *L* is the optical path length in metres, 0.05 m in the case of the monitoring data (Hu et al. 2002). TOC comprises almost exclu-

sively (97%) dissolved carbon in boreal lakes (Kortelainen et al. 2006; von Wachenfeldt et al. 2008). Hence, in our study we use TOC (mg·L⁻¹) measurements from the lake survey interchangeably with DOC in testing the unimodal and monotonic hypotheses described in the Introduction. We used TN as an indicator of nutrient availability because previous analyses found that lakes in this region are predominantly nitrogen-limited (Jansson et al. 2001; Bergström et al. 2005). If a lake was sampled more than once during the lake-monitoring program, we used the mean of the sample values in our analysis.

Light attenuation coefficients (k_d, m⁻¹) are measures of light availability in lakes, which is a key constraint to lake ecosystem processes in northern Sweden (e.g., Ask et al. 2009; Karlsson et al. 2009). Light attenuation coefficients are not measured as part of the Swedish lake-monitoring program, but these coefficients are tightly correlated with absorbance measurements in these low-nutrient boreal and subarctic lakes (Ask et al. 2009). To establish a k_d–a relationship for this region, we sampled 55 lakes in northern Sweden (27 near the town of Arvidsjaur, 65.5833°N, 19.1667°E; and 28 near the town of Ekträsk, 64.5°N, 19.48°E) during June 2014. We measured photosynthetically active radiation (PAR) in depth profiles over the deepest point of each lake using a spherical quantum sensor (LI-193, LI-COR Biosciences). We calculated k_d as the slope of a linear regression of the logarithm of PAR versus depth (Ask et al. 2009). We took surface water samples from the same location and measured absorbance at 420 nm in filtered (0.45 μm) subsamples using a Shimadzu UV-160A spectrophotometer with 1 cm cuvettes. We converted these values into absorption coefficients (a) using eq. 1 prior to analysis (here, $L = 0.01$) and used the relationship between a and k_d to estimate k_d for all 703 lakes in the environmental monitoring dataset. The relationship between k_d and a for the 55 lakes was

$$(2) \qquad k_d = 0.3121 + 0.1327a$$

where the parameters are the maximum likelihood fits (see online Supplemental Fig. 1[1]). We use this relationship ($r^2 = 0.91$) to convert absorbance values to light extinction coefficients for all 703 lakes from the monitoring data for use in our statistical analysis.

Statistical analysis

Estimates of elasticity depend strongly on the shape of the relationship between two variables (Haque 2005). Common shapes (functional forms) in limnological analyses include linear, exponential, and power-law relationships. In our case, there was no a priori reason to assume any particular shape, and in preliminary analyses we found that common functional forms often appeared to fit equally as well. Consequently, we used Box–Cox regression models, which identify optimal power transformations when a theoretical transformation is unknown (Zarembka 1968; Heckman and Polachek 1974; Kim and Hill 1993; Haque 2005). This model includes all regressions commonly found in limnological studies (e.g., linear, power-law, exponential) as special cases, but is more general and also identifies other functional forms. The Box–Cox regression model is

$$(3) \qquad \frac{Y^\theta - 1}{\theta} = c + \beta\frac{X^\lambda - 1}{\lambda}$$

The parameters θ, λ, c, and β are solved for simultaneously by maximizing the likelihood function (log L)

$$(4) \qquad \log L = \left(\frac{-N}{2}\right)[\log(2\pi) + \log(\sigma^2)] + (\theta - 1)\sum_{i=1}^{N}\log(y_i) \\ - \left(\frac{1}{2\sigma^2}\right)\text{SSR}$$

where SSR is the sum of squares due to the regression, N is the sample size, and σ^2 is the error variance. When θ or $\lambda = 0$, it is equivalent to taking the log transformation of Y or X, respectively, owing to L'Hospital's Rule. We fit the Box–Cox regression model for each of the six watersheds in northern Sweden. During the analysis, we checked for and removed any outlying values that may have had a disproportionate influence on the model-fitting procedure.

We used the Box–Cox regression parameters to calculate elasticity according to Haque (2005):

$$(5) \qquad \frac{d\log Y}{d\log X} = \beta\frac{X^\lambda}{Y^\theta}$$

Here, Y is the predicted value from the Box–Cox regression. In retransforming Y into the original scale, we account for the error term in the conditional expectation function using the smearing approach described by Duan (1983). We identified thresholds by plotting the elasticity (eq. 5) across a range of the range of TOC concentrations observed in each watershed. If one elasticity curve is higher than the other, it indicates that one dependent variable (i.e., TN or k_d) is more responsive to changes in TOC than the other. The pattern reverses if the lines intersect. We consider the intersection point to be a threshold point (Seekell et al. 2015). All statistical analyses were conducted using Stata/IC, version 13 (www.stata.com).

Comparison with watershed characteristics

We conducted correlation analyses between the calculated thresholds and previously reported watershed characteristics to explain variability in the thresholds. We specifically tested for a relationship between thresholds and water residence time (years), terrestrial carbon (C) export (g C·m⁻²·year⁻¹), and lake density (percent catchment area) based on values for these watershed reported by Algesten et al. (2004).

Comparison with whole-lake primary production estimates

We evaluated the thresholds identified in the elasticity analysis by testing for a curvilinear relationship between previously published measurements of whole-lake (benthic + pelagic) primary production and DOC concentration. Specifically, we first evaluated the relationship between primary production and mean depth for 20 lakes in boreal and subarctic Sweden reported by Seekell et al. (2015). This accounts for the influence of depth on productivity. We then fit a quadratic curve to the residuals of the depth–productivity relationship and DOC concentration. The hypothesis that DOC stimulates production over low ranges of DOC concentration and inhibits production across high ranges of DOC concentration suggests that this quadratic curve should be inverted and that the vertex should be equivalent to the threshold marking the transition from nutrient to light limitation (Solomon et al. 2015).

Upscaling analysis

After identifying thresholds with the Box–Cox analysis, we used the high-resolution Swedish Virtual Watercourse Network (ViVaN) lake census dataset to estimate the total number of lakes and total surface area of lakes above and below thresholds in the study

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catchments (Nisell et al. 2007). To identify the number of lakes above and below the TOC thresholds, we calculated the percentage of lakes in each logarithmic size class in the environmental monitoring data with TOC above and below the threshold and multiplied this by the number of lakes in the same size class in the ViVaN dataset. We estimated the total area of lakes above and below the threshold by multiplying the total number of lakes above and below the threshold in each size class from the ViVaN dataset by the mean surface area of lakes within the size class (cf. Downing et al. 2006).

Results

Mean TOC concentrations by watershed varied between 3.81 and 6.67 mg·L^{-1} (Table 1). These values are similar to the global median (5.71 mg·L^{-1}) DOC concentration reported by Sobek et al. (2007). TOC concentrations were lowest in the mountainous west and highest in the low-lying south and east (Fig. 1). Variation in TN concentration and k_d was lower than variation in TOC concentration. Overall there were no substantial differences between watersheds in terms of mean values or variability (Table 1).

Both TN and k_d increased with TOC concentration across all lakes in the study area (Fig. 2). However, the Box–Cox regression procedure did not identify any of the functional forms (e.g., linear, power-law, exponential) that are commonly used in limnological studies as the optimal regressions for k_d–TOC or TN–TOC relationships (Table 2). This emphasizes the uncertainty in selecting the functional form of limnological regressions. For instance, in Fig. 3 we display linear (Fig. 3A) and exponential (Fig. 3B) fits for the k_d–DOC relationship in the Torneälven watershed. The r^2 values are very similar, and the AIC values calculated for each regression using the typical approaches cannot be compared because exponential regression is based on a log-transformed k_d value, while linear regression is not (Anderson and Burnham 2002). The regressions have similar fit, but patterns of elasticity are very different and this would impact the identification or location of thresholds (Fig. 3C). The Box–Cox procedure implemented here overcomes this limitation. In Fig. 4A, we show the Box–Cox transformed data for the Torneälven watershed, which fits substantially better than the linear and exponential functional forms. Additionally, the predictive power of the Box–Cox function remains high when the data are back-transformed into their original units (Fig. 4B).

The mean threshold TOC concentration was 5.96 mg·L^{-1} but the values ranged from 4.0 to 7.1 mg·L^{-1} (Fig. 5). There was no clear geographic pattern in these values, and we did not find any significant correlations between threshold DOC concentrations and watershed characteristics. This suggests that the variability we observed may be random variability around the mean threshold or that the watersheds in the study area do not provide strong enough contrasts to identify correlates of DOC thresholds. Despite this variability, the overall results are consistent between watersheds in that TN increased proportionally more rapidly than light extinction at low TOC concentrations and light extinction increased more rapidly than TN at medium and high TOC concentrations. This is illustrated in Fig. 5 where the solid TN lines are higher than the dashed k_d lines. Here the slope should not be interpreted in terms of ecological units. Rather, a higher slope indicates a higher relative rate of change. At medium and high TOC concentrations, the dashed k_d line is higher than the solid TN line, indicating that the light attenuation coefficient increases proportionally more rapidly than TN. Figure 5 shows that the asymmetric relationship among TOC, TN, and light extinction across the range of observed TOC values that had previously only been described for small numbers of lakes (Seekell et al. 2015) is a common characteristic of northern lakes.

There was an inverse relationship between mean depth and whole-lake primary production in the measurements reported by Seekell et al. (2015) for Swedish lakes. However, there was consid-

Table 1. Mean values and coefficients of variation (CV) of total organic carbon (TOC), total nitrogen (TN), and the light attenuation coefficient (k_d) for lakes in the study watersheds.

| Watershed	N	Mean			CV		
		TOC (mg·L^{-1})	TN (ug·L^{-1})	k_d (m^{-1})	TOC	TN	k_d
Torneälven	151	5.54	311.0	0.53	0.63	0.60	0.37
Kalixälven	68[a]	6.07	251.1	0.57	0.52	0.39	0.4
Luleälven	138[b]	3.81	218.2	0.46	0.84	0.68	0.36
Piteälven	83[c]	4.81	218.5	0.48	0.67	0.49	0.35
Skellefteälven	102[d]	6.67	260.0	0.56	0.59	0.46	0.37
Umeälven	161[d]	6.06	221.2	0.55	0.72	0.44	0.42

Note: N is the sample size.
[a]Total sample size; four outliers were excluded during the statistical analyses.
[b]Total sample size; one outlier was excluded during the statistical analyses.
[c]Total sample size; two outliers were excluded during the statistical analyses.
[d]Total sample size; three outliers were excluded during the statistical analyses.

Fig. 2. The light attenuation coefficient (k_d; A) and total nitrogen concentration (TN; B) in lakes increase consistently, but nonlinearly, with total organic carbon (TOC) concentration. Measurements are from 703 lakes in northern Sweden's six major watersheds.
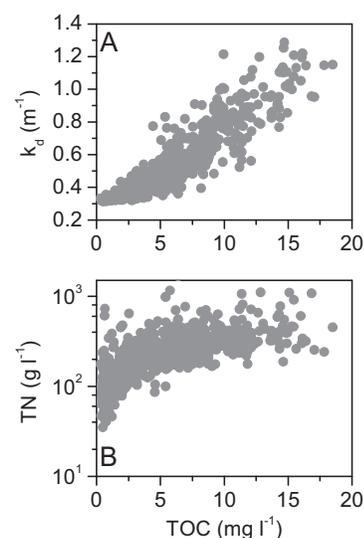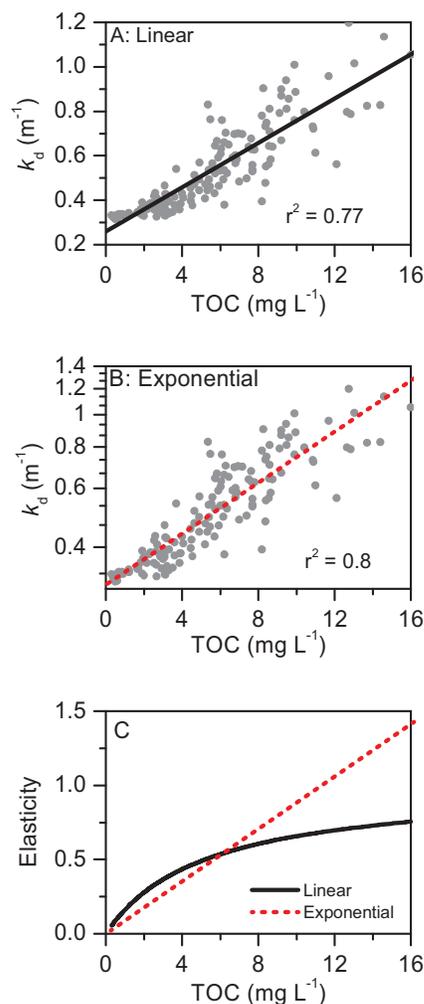

Table 2. Maximum likelihood parameter fits for the Box–Cox models.

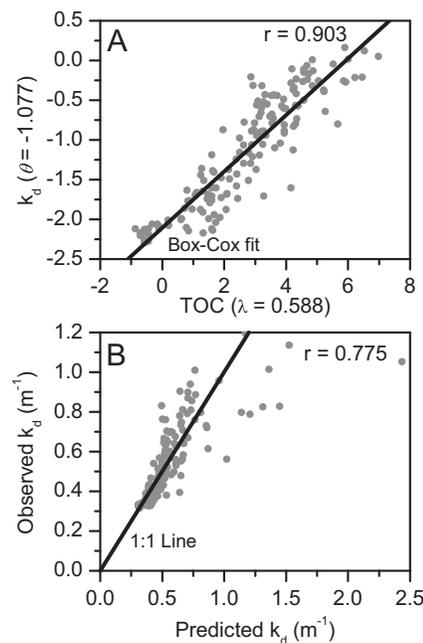| Watershed	TN–TOC				k_d–TOC			
	c	β	λ	θ	c	β	λ	θ
Torneälven	4.710	0.386	0.211	−0.011	−2.107	0.355	0.588	−1.077
Kalixälven	2.725	0.306	−0.322	−0.229	−1.671	0.223	0.769	−0.617
Luleälven	5.483	0.700	0.137	0.069	−4.219	1.058	0.364	−2.100
Piteälven	6.010	1.024	0.053	0.122	−2.037	0.267	0.744	−0.980
Skellefteälven	5.205	0.160	0.679	0.021	−1.707	0.216	0.708	−0.718
Umeälven	8.81	1.777	−0.042	0.256	−1.754	0.258	0.615	−0.798

erable unexplained variability in this relationship (Fig. 6A) where the residual variability in primary production could largely be explained by an inverse quadratic relationship with DOC (Fig. 6B). This indicates a positive correlation between primary production and DOC over the range of DOC concentrations 0–6 mg·L^{-1} and a negative correlation over 6 mg·L^{-1}, consistent with our previous analyses based on combined measurements from Alaskan and Swedish lakes (Seekell et al. 2015). The vertex of the curvilinear relationship is almost exactly the same as the mean (of the six watersheds) DOC threshold identified in the elasticity analysis (Fig. 6B).

Fig. 3. Linear (A) and exponential (B) regression fits for the k_d–dissolved organic carbon (DOC) relationship in the Torneälven watershed. The fits are almost identical but have different implications for relative rates of change (C).

Fig. 4. (A) The Box–Cox regression fits for the k_d–TOC relationships for lakes in the Torneälven watershed. (B) The observed and predicted values of k_d after back-transformation from the Box–Cox fit.

Upscaling the results to the whole catchments based on TOC concentration alone show that 61% of lakes comprising 71% of lake surface area fall below the TOC threshold. Accordingly, TOC concentrations are above the threshold in 39% of lakes comprising 29% of total lake surface (Table 3). The patterns in TOC, TN, and k_d found here may translate differently to patterns of primary production in small versus large lakes. For instance, benthic contributions to whole-lake primary production in small lakes are substantial (>50% in many reports) and most likely to be influenced by changes in TOC concentration (e.g., Hansson 1992; Ask et al. 2009). In large lakes, benthic production may be lower than in small lakes because greater depths preclude high light availability in the benthic zone, regardless of DOC concentration (Vadeboncoeur and Steinman 2002; Seekell et al. 2015). Because of this, we repeated our upscaling analysis with small lakes only (0.001–0.1 km²). More than half (62%) of lakes in these small size classes would fall below the TOC threshold. Small lakes that are below the TOC threshold account for 57% of all lakes in the study area, but because of the asymmetry in the lake abundance – size relationship, these lakes would only comprise 8.7% of the total lake surface area in the region (Seekell and Pace 2011; Seekell et al. 2013; Verpoorter et al. 2012). Small lakes that fall above the DOC threshold account for 36% of the total number of lakes and comprise 5% of the total lake area. Hence, a majority of lakes in this

region likely have TOC concentrations below the mean threshold identified in our study, but the percentage of total lake surface area impacted depends strongly on how lake depth mediates the light–nutrient trade-off.

What percentage of lakes are near the threshold and thus susceptible to transition across the threshold? For small lakes (0.001–0.1 km²), 16% of lakes are within ±1 mg·L⁻¹ of the DOC threshold and 34% and 50% of lakes are within ±2 and 3 mg·L⁻¹, respectively. The magnitude of trends in DOC concentration varies geographically and exceeds +1.5 mg·L⁻¹ per decade in some regions, including parts of Scandinavia (Monteith et al. 2007; Skjelkvåle et al. 2007). Significant trends in DOC concentration have not been reported in northern Sweden (Skjelkvåle et al. 2007). However, concentrations are forecasted to increase owing to increased terrestrial vegetation cover related to climate changes (Larsen et al. 2011). If these forecasts are realized at the rates of 1.5 mg·L⁻¹ per decade, 12% of small lakes below the DOC threshold would pass the threshold within 10 years and 45% within 30 years. Whether or not past trends in DOC concentration will continue changing at the rate of past observation is unknown and likely depends on the factors driving DOC change (e.g., climate warming versus recovery from acid rain) and the consistency of these patterns geographically. Regardless, it is clear that a large proportion of lakes have DOC concentrations near the threshold identified in our analysis.

Discussion

Our results demonstrate consistent patterns of increasing nutrient concentrations and light attenuation with DOC and that thresholds in trade-offs between nutrient and light availability across DOC gradients are likely a general feature of boreal and subarctic lakes. Based on the interpretation developed in our previous analysis of Swedish and Alaskan lakes (Seekell et al. 2015), our results indicate that DOC may have a stimulating influence on primary production in more than half (57%) of lakes in northern Sweden and an inhibiting influence in a large minority (36%) of the lakes. Hence, our results support the hypothesis that DOC has a unimodal relationship with lake primary production, at least

Fig. 5. Elasticity curves for k_d (dashed lines) and TN (solid lines) based on Box–Cox regression. The higher curve responds proportionally more strongly than the lower curve to changes in TOC concentration. Elasticity curves were only plotted to TOC < 10 mg·L^{-1} to emphasize the location of the thresholds.
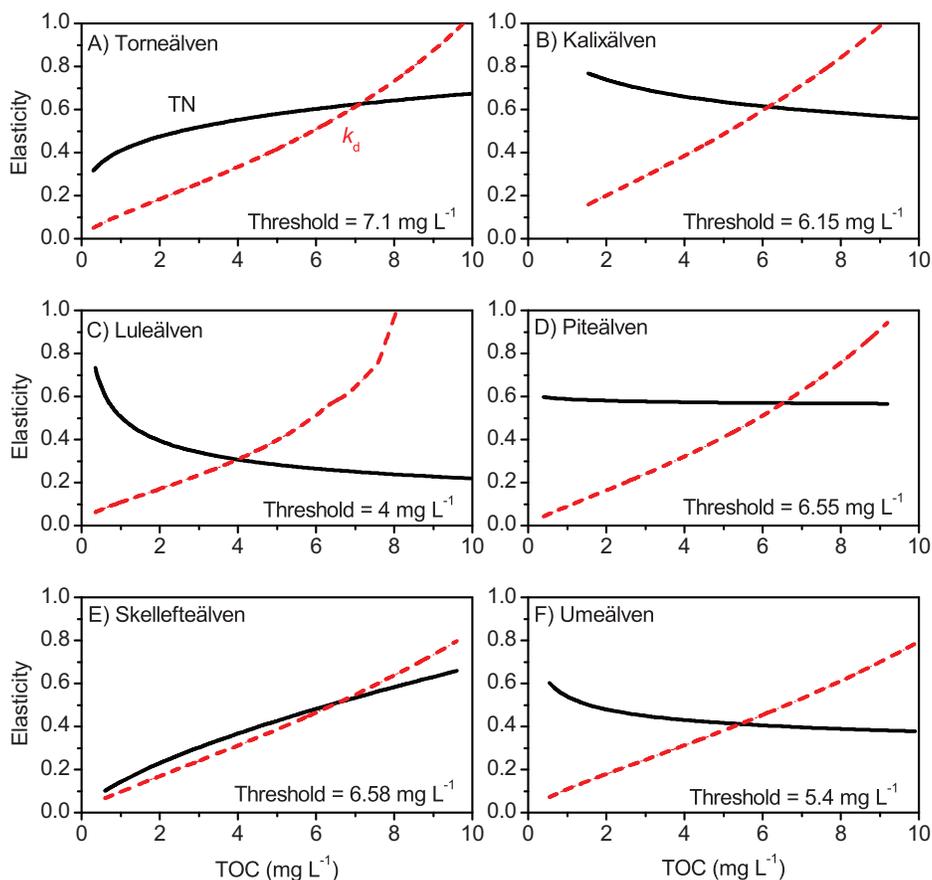
when comparing lakes in regions with contrasting baseline DOC concentrations (Solomon et al. 2015). Further, the intersections in the elasticity curves for nutrients and light provide a general explanation for the origin of this relationship (Seekell et al. 2015). This extends our previous findings (Seekell et al. 2015) for a small number of lakes ($n = 28$) by showing that similar patterns in thresholds for light–nutrient tradeoffs exist over wide geographic areas when examining large datasets. The main implications of our present results are that substantial numbers of lakes could respond oppositely (i.e., primary production may increase with increasing DOC concentration) to changes in DOC concentration relative to predictions based on the hypothesis of monotonic decreases in primary production with increasing DOC concentration. Our results thus emphasize a complex response of boreal and subarctic lakes to changes in DOC, with potential implications for food webs and biogeochemical processes.

Are the threshold values identified here universally applicable? The mean threshold of 5.96 mg·L^{-1} (range 4.0–7.1 mg·L^{-1}) identified in the elasticity analysis in this study is similar to the one previously identified in a study for boreal and arctic lakes in Sweden and Alaska (4.8 mg·L^{-1}; Seekell et al. 2015), and this suggests consistency between two datasets. However, it is possible that differences in the light-absorbing properties of DOC between regions are not visible at the geographic scale of our analysis, and hence there could be geographic patterning in threshold values at spatial scales broader than the boundaries of the current study. Specifically, the color of DOC is strongly influenced by photobleaching, a process that is closely related to the acid-neutralizing capacity (ANC) of water (Reche et al. 1999). ANC varies both between lakes and between regions, and this suggests that there

should be detectable differences in color between regions, which would in turn influence the relationship between light availability and DOC (Landers et al. 1988). Additionally, phosphorus is considered the primary limiting nutrient in most lakes south of our study area, and thresholds in these regions would have to be evaluated based on phosphorus–DOC relationships instead of the TN–DOC relationships presented here (e.g., Carpenter et al. 1998; Bergström et al 2005). It is possible that thresholds in these systems are substantially different than the ones identified here. For example, pelagic primary production in phosphorus-limited temperate lakes is positively correlated with DOC concentration below approximately 12 mg·L^{-1} but negatively correlated with DOC about this value (Solomon et al. 2015). This suggests a higher threshold than the ones identified in our study, and this difference may be due in part to the between-region differences in identity of limiting nutrients.

The mechanism we propose for creating thresholds is general, relying only on the existence of nonlinear relationships and regional-scale variation. In principle, between-region heterogeneity in relationships could be found for any lake characteristics that exhibit these patterns. Relative to DOC specifically, most of Earth's lakes are located in northern latitudes where DOC is a master variable influencing many biological, chemical, and physical processes (Prairie 2008; Verpoorter et al. 2014; Seekell et al. 2014; Lapierre et al. 2015). We thus speculate that the concept of a threshold DOC concentration may be a common feature of lakes, which are typically unproductive and are characterized by strong relationships between DOC and nutrient concentration. For lakes outside these types of pristine northern environments, DOC thresholds for primary production may not exist if there is not a

Table 3. Number and area of lakes in the study region by logarithmic size class and number and area of lakes with TOC concentrations <5.96 mg·L⁻¹.

Area class (km²)	Overall			Below threshold		
	Abundance	Mean area (km²)	Total area (km²)	Percentage of lakes	Abundance	Total area (km²)
0.001–0.01	50 186	0.004	214.6	60%	30 112	128.76
0.01–0.1	24 175	0.030	728.4	65%	15 714	473.46
0.1–1	4 919	0.285	1 401.2	53%	2 607	742.62
1–10	834	2.627	2 190.8	60%	500	1 314.5
10–100	95	24.61	2 338	95%	90	2 221.1

Fig. 6. (A) There is an inverse relationship between whole-lake primary production (PP) and mean depth in Swedish lakes. (B) There is a curvilinear relationship between the residuals of the depth–production relationship and DOC concentration. The vertex of the curve is almost exactly the mean threshold identified in the elasticity analysis. For both panels, the solid line is the fit relationship and the dashed lines are the upper and lower 95% prediction intervals.
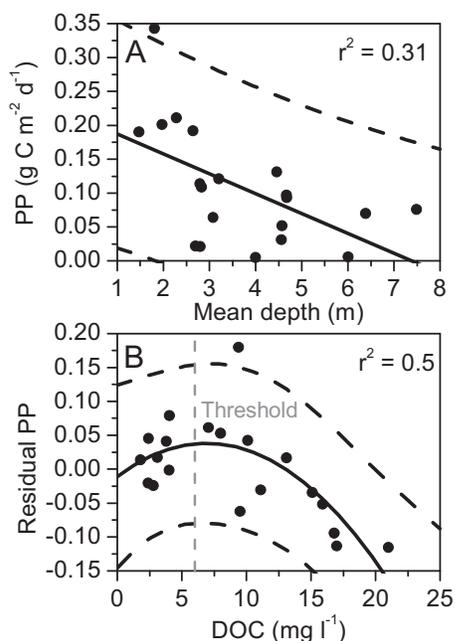
strong relationship among DOC, nutrients, and light attenuation. Such lakes may be especially prevalent in heavily agricultural regions where human influence on nutrient concentrations over-rides natural processes (Dodds et al. 2006). However, this does not rule out the potential existence of thresholds in other key lake characteristics (e.g., Lapierre and del Giorgio 2012). Future evaluations in other biomes would be especially useful in testing for these differences at broader scales, and the methodology applied in our analysis would be suitable for application to the measurements commonly taken in lake surveys (e.g., water color, nutrient concentrations, DOC concentration) in different biomes (Landers et al. 1988; Pace and Cole 2002; Rantakari and Kortelainen 2008; Lapierre et al. 2015).

Our interpretation of the light–nutrient availability trade-offs are based on relationships between whole-lake primary production and DOC that have been previously described for small boreal and arctic lakes (Seekell et al. 2015). These relationships could be different in large lakes where greater depth can reduce light availability, but we are unable to evaluate this because our empirical analysis of the production–depth relationship (i.e., Fig. 6) only extends to small lakes. Hence, in our upscaling analysis we specif-

ically limited our results to small lakes where the whole-lake primary production – DOC relationship has been previously verified (Seekell et al. 2015). Orthogonal gradients of color and depth would be useful for better understanding how depth may moderate primary production – DOC relationships, but are not possible based on environmental monitoring data, which often do not reflect lake morphometry (Sobek et al. 2011; Heathcote et al. 2015). Future studies could focus on collecting data in this manner.

Our elasticity analysis is meant to emphasize patterns of nutrient and light availability based on measurements commonly taken during broad-scale lake surveys. However, more mechanistic models (e.g., Jäger and Diehl 2014) of algal primary production not based on elasticity analyses may produce similar broad-scale patterns if they form a unimodal relationship between primary production and DOC, such that DOC concentrations in different regions fall on different sides of the vertex of the relationship (cf. Seekell et al. 2014, 2015). Such models would be a welcome advancement in connecting individual ecosystem processes to broad-scale patterns like those we have focused on in this study. In the end, whole-ecosystem experiments are needed to understand how these spatial patterns translate into temporal changes in individual lakes in response to changing environmental conditions (Solomon et al. 2015). Such analyses could provide strong contrasts while maintaining constant lake morphometry and food web structure. Dual experiments in contrasting geographic settings (i.e., Arctic and boreal) would be ideal as the environmental context is key in this analysis (cf. Rustad et al. 2001).

A key feature of our analysis is application of the Box–Cox regression model that does not assume a particular relationship (functional form) a priori beyond that the shape can be formed based on power transformations (Heckman and Polachek 1974; Kim and Hill 1993). This approach is particularly useful in cases like ours where there is no theoretically derived functional form and it is difficult to determine the optimal fit because common functional forms appear to fit equally as well (cf. Heckman and Polachek 1974). Other approaches are possible. For instance, chlorophyll–phosphorus relationships are well studied by limnologists, and potential functional forms have been described based on decades of research (Wagner et al. 2011; Filstrup et al. 2014). In this case Bayesian methods can be used to identify likely functional forms based on prior descriptions of the relationship (Filstrup et al. 2014). Lack of a large number of previously published relationships precluded us from adopting this approach in the present study. Additionally, theoretical functional forms could be derived, but this is currently difficult because theoretical analyses of broad-scale limnological processes are rare (cf. Seekell et al. 2013). Regardless of the approach, quantifying and minimizing this uncertainty for critical scaling relationships (e.g., light extinction – DOC) is a major challenge for limnologists that must be addressed to ensure reliable predictions of lake response to broad-scale environmental change.

We previously reported that Sweden comprises two distinct biogeochemical regions where DOC concentrations and landscape correlates were similar within region and dissimilar between regions (Seekell et al. 2014). These two DOC regions roughly

correspond to the mountainous subarctic and boreal lowlands and cut across the watersheds used as the geographic boundaries in the present analysis. We did not apply these previously delineated regions here because the identification of thresholds requires the comparison of systems across a range of conditions, and these previously identified regions emphasize similarity. In other words, applying regions with similar DOC concentrations does not allow for the contrasting conditions necessary to identify thresholds. Because each watershed comprises a portion of each of the two DOC regions, the major watersheds allowed for the necessary contrasts. This observation emphasizes that DOC thresholds are emergent characteristics that are observed when comparing multiple regions (Seekell et al. 2015). In this sense, our analysis contributes to the emerging view that the regional scale is key to understanding patterns and dynamics in lakes (e.g., Lapierre and del Giorgio 2012; Cheruvelil et al. 2013; Filstrup et al. 2014; Seekell et al. 2014, 2015). Further development of understanding of mechanisms creating variability in relationships between regions, such as the nutrient–light availability trade-off examined here, will be critical in making accurate predictions about lake ecosystem response to global environmental change.

Acknowledgements

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Supplemental Material
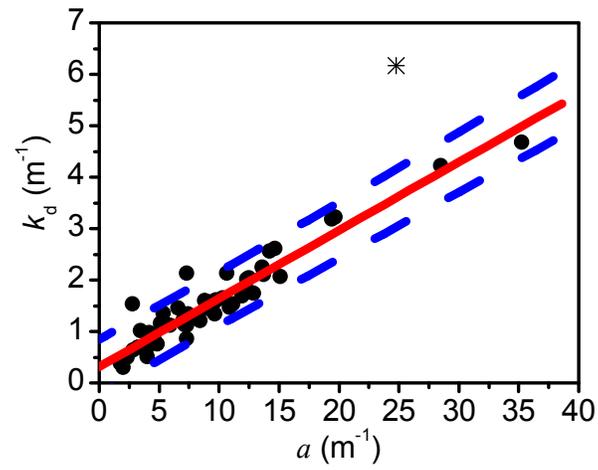
Figure S1. The relationship ($r^2 = 0.91$) between k_d and a from 55 lakes in northern Sweden. Dashed blue lines are the upper and lower 95% prediction limits. The starred point is an outlier and was excluded when fitting the regression.