



Lake morphometry moderates the relationship between water color and fish biomass in small boreal lakes

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Abstract

Lake morphometry may moderate the effects of water color on fish biomass in boreal lakes, but empirical evidence is scarce because there are a limited number of lakes for which both water color and bathymetry have been measured. We evaluated variations in catch-per-unit-effort (CPUE), an indicator of fish biomass, across orthogonal gradients of light extinction and mean depth in 16 small Swedish lakes (mean depth 1.7–4.8 m, surface area 1–10 ha). Multiple regression coefficients indicated that the effect of light extinction on CPUE was negative, and that the relationship was more negative for deeper lakes than it was for shallower lakes. The pattern was strongest for lakes with mean depths between 2.1 m and 3.5 m. We estimated that 26% of small lakes in boreal Sweden fall within this mean depth range. These results contribute to the growing understanding of how variations in water color and lake morphometry influence patterns of fish biomass across the boreal landscape.

Strong landscape-scale gradients of dissolved organic carbon (DOC) are a primary source of variation in biological, chemical, and physical properties between pristine northern lakes (Williamson et al. 1999; Sobek et al. 2007; Seekell et al. 2018). Patterns of fish biomass and production across these gradients are interesting because they relate to cultural, recreational, economic, and food security values (Youn et al. 2014; Lynch et al. 2016). Additionally, widespread increases in DOC concentration have been reported in northern lakes and analyses of fish populations across DOC gradients may contribute to predictions about future changes in fish production and biomass (Monteith et al. 2007; Solomon et al. 2015; Bartels et al. 2016). Specifically, reports of inverse correlations between fish biomass and DOC concentration suggest that populations may decline in response to increasing DOC concentrations (Karlsson et al. 2009; Craig et al. 2015; Benoit et al. 2016).

Variations in DOC concentration primarily impact fish populations by altering light environment (Stasko et al.

2012). Specifically, high DOC concentrations stain waters brown and decrease light penetration, which limits primary and secondary production in benthic habitats that are key energy pathways for fish (Persson 1988; Karlsson et al. 2009; Bartels et al. 2016). Additionally, diminished light penetration reduces the depth of the mixed layer, limiting habitat availability both for zoobenthic prey and fish by increasing the relative size of anoxic hypolimnetic zones (Stasko et al. 2012; Craig et al. 2015; Karlsson et al. 2015). The collective impact of these energetic and habitat constraints is to reduce the growth and lifetime fecundity of fish, which leads to lower production and biomass in humic lakes (Craig et al. 2017).

Analyses of the relationship between light environment and fish populations have primarily focused on DOC concentrations even though lake morphometry is also important for explaining variation in light availability among lakes (cf. Karlsson et al. 2009). Specifically, the balance between positive and negative effects of DOC on ecosystem productivity may shift depending on lake depth (Finstad et al. 2014). However, there are few empirical studies explicitly evaluating lake morphometry as moderating factor for the relationship between DOC and fish production, in part because there are a limited number of lakes for which both DOC and bathymetry have been measured (cf. Seekell et al. 2015a; Cael et al. 2017).

In this study, we evaluated patterns of fish biomass based on comparative analysis of small boreal lakes across gradients of light extinction, a proxy for DOC concentration (e.g., Pérez-Fuentetaja et al. 1999; Bukaveckas and Robbins-Forbes 2000; Seekell et al. 2015a), and mean depth. We

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identified the range of mean depths for which the relationship between light extinction and fish biomass is significant, and then applied fractal scaling relationships to estimate the proportion of small lakes that fall within this mean depth range in boreal Sweden.

Methods

Sampling

We conducted a three-tiered field sampling campaign during June–August 2014 of small lakes in boreal Sweden. This region is dominated by coniferous forest, has high lake density, and has little urban or shoreline development (Fig. 1). A multi-tiered survey was needed because bathymetric maps are unavailable for most Swedish lakes, and even the best predictive relationships for mean or maximum depths based on landscape characteristics have large uncertainties (Sobek et al. 2011; Cael et al. 2017). Therefore, we had to measure mean depth (z_{mean} , m) and light extinction (k_d , m^{-1}) for a large group of lakes during the first two tiers of sampling, and then select lakes for final sampling from this larger group.

For the first-tier sampling, we selected 60 lakes that met the criteria: (1) surface area of 1–20 ha, (2) <1 km from a road, and (3) known to have fish based on a previously published database of fish distributions for Swedish lakes (Hein et al. 2011). During June 2014, we took depth profiles for photosynthetically active radiation (PAR) using a spherical quantum sensor (LI-COR LI-193). We then calculated the light extinction coefficient k_d from the slope of the linear regression of the logarithm of PAR vs. measurement depth (Wetzel and Likens 2000). We also measured lake bathymetry using an echo sounder with an integrated Global Positioning System unit (Lowrance m52i).

Based on the results of our first-tier of sampling, we revisited 32 of the lakes during July 2014 for the second-tier of sampling. The lakes were selected, to the extent possible, to represent orthogonal gradients of light extinction k_d and mean depth z_{mean} . From these second-tier lakes, we took additional light profiles to evaluate potential changes in k_d . We also conducted more intensive bathymetric surveys to improve our initial estimates of z_{mean} .

For the third-tier of sampling, we revisited 16 lakes during August for gillnetting. First, we took new depth profiles and additional depth soundings to finalize our measurements of mean depth. Then, for each lake, we set eight multi mesh gill nets (Nordic 12 nets, 30 m \times 1.5 m; Mesh sizes: 5 mm, 6.25 mm, 8 mm, 10 mm, 12.5 mm, 15.5 mm, 19.5 mm, 24 mm, 29 mm, 35 mm, 43 mm, 55 mm) overnight (approximately 12 h). Four nets were deployed in the littoral zone perpendicular to the shoreline. These nets were approximately equally spaced. Two floating nets were deployed across the deepest point of the pelagic zone, and two benthic nets were set in the hypolimnion near the deepest point of the lake. European perch (*Perca fluviatilis*) and common roach (*Rutilus rutilus*) dominated the fish communities in



Fig. 1. Photograph of a typical study lake near Ekträsk, Sweden. The study lakes were all within the boreal zone dominated by coniferous forest and with little or no shoreline development.

these lakes, but we also occasionally captured a few northern pike (*Esox lucius*) and burbot (*Lota lota*). We acknowledge that there is variation in catchability between species when using gillnets and that this can also be impacted by variations in community composition. However, gillnetting is a standard approach for environmental monitoring both in Sweden and across the European Union and is thought to give comparable estimates among lakes despite these limitations (Degerman et al. 1988; Holmgren 1999). The number and deployment of nets were set to be sufficient to identify dominant species and to make accurate estimates of catch-per-unit-effort (CPUE; Degerman et al. 1988), and is consistent with previous ecological studies in this region (e.g., Karlsson et al. 2015).

We calculated CPUE (kg/net) and used this as an indicator of fish community biomass (e.g., Persson et al. 1991). Net-specific catches were averaged with weighting based on the relative extent of the different habitat types (Lauridsen et al. 2008; Karlsson et al. 2015; Supporting Information Table S1). Specifically, the profundal nets were assumed to represent the total hypolimnetic volume and the pelagic nets were assumed to represent the volume above the hypolimnion. The volume of the littoral nets was calculated by subtracting the volume of the pelagic and profundal habitats from the total lake volume. This approach is thought to most accurately measure CPUE when using Nordic gillnets, especially when comparing lakes with very different mean to maximum depth ratios, and we used these weighted CPUE values in our statistical analyses (Degerman et al. 1988; Lauridsen et al. 2008). We evaluated the possibility that weighting created spurious patterns by also running our analyses (see below) using only catches from the dominant (in terms of catch) habitat.

Statistical analysis

To evaluate overall relationships, we fit a multiple regression where CPUE was predicted by z_{mean} , k_d , and a multiplicative interaction term. We mean centered the data prior to our analysis to improve the quality of the statistical tests by reducing multicollinearity. We evaluated the statistical

Table 1. Lake locations and data used in the analysis. Geographic coordinates (northing and easting) are based on the Swedish grid (<http://www.lantmateriet.se>). Fish species are abbreviated: P for European perch (*Perca fluviatilis*), R for common roach (*Rutilus rutilus*), N for northern pike (*Esox lucius*), B for burbot (*Lota lota*).

| Lake | Northing | Easting | Surface area (ha) | z_{mean} (m) | k_d (m^{-1}) | CPUE (kg/net) | Species |
|------|----------|---------|-------------------|-----------------------|---------------------------|---------------|---------|
| A1 | 7248150 | 1666940 | 7.5 | 2.6 | 0.64 | 1.49 | P |
| A6 | 7250830 | 1668510 | 4.5 | 4.2 | 1.06 | 0.24 | P, R |
| A10 | 7260900 | 1662850 | 8.6 | 2.5 | 0.49 | 2.70 | P |
| A11 | 7261550 | 1664440 | 8.7 | 4.8 | 0.66 | 1.22 | P, N, B |
| A12 | 7261870 | 1666790 | 2.3 | 3.2 | 1.19 | 1.20 | P, R |
| A13 | 7262370 | 1666640 | 4.7 | 2.1 | 1.35 | 3.49 | P, R |
| A15 | 7263140 | 1668770 | 5.5 | 2.7 | 0.56 | 1.86 | P |
| A311 | 7299180 | 1668430 | 8.6 | 1.7 | 0.97 | 2.12 | P, N |
| E12 | 7155540 | 1667740 | 9.4 | 3.1 | 1.22 | 0.61 | P, N |
| E16 | 7160760 | 1674400 | 10.0 | 1.9 | 1.42 | 1.52 | P, R, N |
| E17 | 7160880 | 1697250 | 2.4 | 3.3 | 2.64 | 0.49 | P, R, N |
| E18 | 7162640 | 1697890 | 5.3 | 2.6 | 2.08 | 1.60 | P, R, N |
| E19 | 7162760 | 1696400 | 3.2 | 1.7 | 3.19 | 1.13 | P, R, N |
| E24 | 7173190 | 1678430 | 8.8 | 2.9 | 0.40 | 1.59 | P, N |
| E25 | 7173810 | 1685170 | 4.5 | 3.2 | 1.49 | 0.10 | N |
| E29 | 7177110 | 1681780 | 7.1 | 3.1 | 0.83 | 1.42 | P, R, N |

significance at the $\alpha=0.05$ threshold which we selected by convention. We used one-tailed probability values because, for the ecological reasons described in the introduction, the alternate hypothesis for each factor is an inverse relationship.

We calculated the range of mean depths for which CPUE– k_d relationship was significant using the simple slopes technique (Bauer and Curran 2005; Preacher et al. 2006). The simple slope is the linear composite of the main, additive effect of k_d on CPUE, and the interactive effect of light extinction conditional on mean depth. It allows for the graphical evaluation of the CPUE– k_d relationship and its 95% confidence interval across mean depths. The simple slope and its confidence interval are calculated from the multiple regression coefficients and covariance matrix. We used the Johnson–Neyman technique, modified for continuous variables in a multiple regression framework, to calculate the range of mean depths over which the CPUE– k_d relationship is significant (Bauer and Curran 2005; Preacher et al. 2006). This is a quantitative approach to identifying the two mean depths where the 95% confidence interval for the CPUE– k_d relationship equals zero. Within this mean depth range, the CPUE– k_d relationship is statistically significant (one-tailed $p \leq 0.05$); outside this mean depth range, the relationship is not statistically significant (one-tailed $p > 0.05$).

We conducted the regression and simple slopes analyses using the “stats” and “jtools” packages in R version 3.4.3 (Long 2017; R Core Team 2017). The data used in the analysis are archived online (doi:10.5281/zenodo.1194496) and the R code used in the statistical analysis is provided the Supporting Information.

Upscaling results to the Swedish boreal zone

We wanted to estimate the number of lakes with mean depths in the Johnson–Neyman interval to provide context for our analysis, but mean depth has only been measured for a small number of lakes in boreal Sweden, and existing measurements are biased to specific lake types (Cael et al. 2017). To overcome this, we estimated lake volumes based on the fractal scaling technique described in detail by Cael et al. (2017), and summarized here. First we extracted lakes 1–10 ha from the Swedish Lake Registry based on the extent of the Swedish boreal zone as delineated by Olson et al. (2001). We then estimated the volume of each lake based on surface area, a scaling coefficient, and previously characterized uncertainty (Cael et al. 2017). We calculated the mean depth of each lake by dividing volume by area and counted the percentage of lakes falling in the Johnson–Neyman interval. Because our volume estimates are based in part on a random term, we repeated this process 200 times to calculate an average and 95% confidence interval for the percentage of lakes falling in the Johnson–Neyman interval. This approach is robust for developing population level statistics for large numbers of lakes, but we note that it is not suitable for making predictions about individual lakes and we do not pursue such predictions in our analysis.

Results

The sixteen study lakes were typical of small lakes in boreal Sweden (Table 1). The lakes had surface areas between 1 ha and 10 ha, which is the most common size class in boreal Sweden; 74% ($n = 38,843$) of all lakes ≥ 1 ha fall

within this range. The average mean depth of the study lakes was 2.85 m, was similar to our estimated mean depth (2.35 m) of 1–10 ha lakes in boreal Sweden. The range of light extinction coefficients ($0.4\text{--}3.2\text{ m}^{-1}$) measured in the study lakes includes 90.5% of light extinction coefficients estimated for small lakes across boreal Sweden (Supporting Information Text 1). The mean k_d for our lakes (1.26 m^{-1}) was similar to both the mean (1.53 m^{-1}) and median (1.30 m^{-1}) for small boreal lakes (Supporting Information Text 1). Light extinction (k_d) and mean depth (z_{mean}) were not significantly correlated among the study lakes ($r = -0.28$, $p = 0.3$). This does not imply independence, but does indicate that the factors are not redundant when evaluating relationships with fish biomass.

Overall, light extinction, mean depth, and the interaction term explained half of the variation in CPUE between study lakes (multiple R-squared = 0.50) and this was statistically significant ($F_{3,12} = 4.03$, $p = 0.034$; Supporting Information Table S2). The additive effects of k_d and z_{mean} were both significantly and inversely related to CPUE (Supporting Information Table S3). The interaction term was negative, meaning that CPUE declines more rapidly with increasing k_d in deeper lakes than it does in shallower lakes. The interaction term was not significant. While this lack of significance suggests that z_{mean} does not moderate the CPUE- k_d relationship for all lakes, it does not preclude significance within a narrower range of mean depths (Rogosa 1981).

The Johnson–Neyman technique identified the mean depth range 2.1–3.5 m as containing a significant (one-tailed $p < 0.05$) inverse relationship between CPUE and k_d (Fig. 2). This is within the range of mean depths of the study lakes (range = 1.7–4.8 m). Based on scaling relationships, we estimated that 25.9% (95% CI = 25.5–26.4%) of small (1–10 ha) lakes in boreal Sweden have mean depths within the Johnson–Neyman interval. These lakes comprise 29% of small lake volume (95% CI = 28.1–29.4%) and 28% of small lake surface area (95% CI = 27.1–28.2%) in the region.

The Johnson–Neyman technique indicates that the CPUE- k_d relationship is not statistically significant for lakes with mean depths less than 2.1 m, or for lakes with mean depths greater than 3.5 m. Because of the nature of null hypothesis testing, this result does not conclude no CPUE- k_d relationship for these lakes, but rather should be interpreted as indicating that our sampling does not provide evidence to generalize to lakes outside of the 2.07–3.5 m range. 56.3% (95% CI = 55.9–56.8%) of small lakes have mean depths less than 2.07 m, and these lakes account for approximately half of small lake surface area but only a quarter of small lake volume. Lakes with mean depths deeper than 3.5 m account for 46% of small lake volume and 21.6% of small lake surface area.

Almost all fish (average 84% by weight) were caught in the littoral nets. We ran the regression and simple slopes analysis based only on littoral-CPUE and the results were

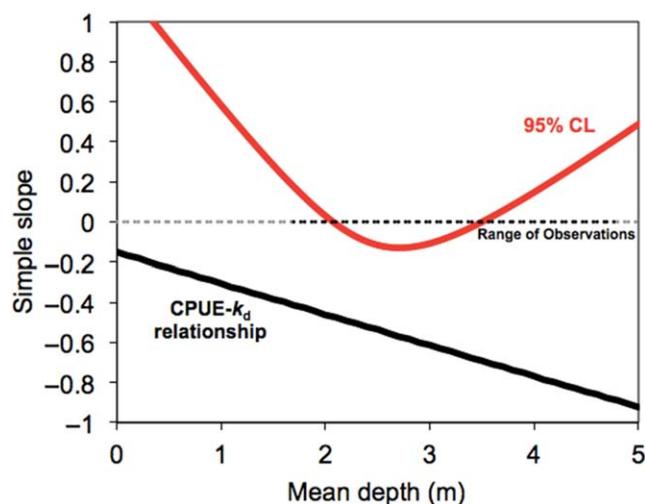


Fig. 2. The slope of the CPUE- k_d relationship is moderated by mean depth. The slope of the black line indicates that changes in k_d have a stronger impact on CPUE in deeper lakes than in shallower lakes. The black line would be horizontal if mean depth did not moderate the CPUE- k_d relationship. However, CPUE- k_d relationship is only statistically significant for lakes with mean depths between 2.07 m and 3.5 m, which is the range of depths where the 95% confidence limit (red line) is less than 0 (dotted line). The dotted line is black over the range of mean depths of the study lakes.

almost exactly the same as with whole-lake CPUE. Specifically, k_d , z_{mean} , and the interaction term all had inverse relationships with littoral-CPUE. Additionally, the relationship between littoral-CPUE and k_d was more negative for deeper lakes. Finally, the Johnson–Neyman interval was 1.91–4.07, which is very similar to the interval for whole-lake CPUE. Collectively, these results indicate that our weighting scheme is not responsible for the patterns we report above.

Discussion

Within the boreal region, patterns of fish biomass relate to light climate which, for lakes at similar latitude, primarily reflect concentrations of terrestrially derived DOC and depth (Schindler and Gunn 2004; Karlsson et al. 2009; Stasko et al. 2012; Karlsson et al. 2015). Our results extend understanding of these patterns by demonstrating that lake depth moderates the relationship between water color and biomass. Specifically, we show that the relationship between CPUE and k_d is more negative in deeper lakes than in shallower lakes. In our analysis, the CPUE- k_d relationship was statistically significant for lakes with mean depths between 2.07 m and 3.5 m. Hence, our results can be generalized to the 26% of small boreal lakes that fall into this depth range.

The relationship between CPUE and k_d being more negative in deeper lakes than shallower lakes likely reflects the combination of several patterns reported among lakes of different depths. For example, light limitation of primary production sets in at lower levels of light extinction in

deeper lakes than in shallower lakes (Finstad et al. 2014). Whole-lake energy mobilization (benthic + pelagic, autotrophic + heterotrophic) into the food web declines with increasing mean depth and increasing light extinction, and the impact of higher light extinction is larger (in relative terms) in deeper lakes than in shallower lakes (Ask et al. 2009). Additionally, the relative contribution of benthic energy pathways is lower in deeper lakes than in shallower lakes (Ask et al. 2009). Finally, the relative size of the littoral zone in our lakes, where most fish were caught (mean = 84% by weight), declined with increasing mean depth ($r = -0.64$). Hence, both the habitat and energy pathways most used by fish are smaller and more sensitive to variation in light environment in deeper lakes than in shallower lakes (Karlsson and Byström 2005).

We are unaware of long-term fish biomass records from small boreal lakes with increasing DOC concentrations that we can compare to our results. However, long-term studies evaluating the impact of liming on fisheries may provide some useful insight. In naturally humic lakes, liming causes DOC to precipitate from the water column, increasing water clarity (Hasler et al. 1951; Degerman et al. 1992). In lakes subject to anthropogenic acidification, liming increases DOC concentrations and reduces water clarity (Bukaveckas and Driscoll 1991; Degerman et al. 1992). Recovery from acidification is thought to be the primary cause of increasing DOC concentrations in many regions (Monteith et al. 2007). Hence, liming experiments may provide temporally resolved information on the relationship between of water clarity on fish biomass or production, which can be evaluated relative to our comparative analysis.

Shallow lakes are often un-stratified and a synthesis of whole-lake liming experiments indicates that increases in DOC concentration and color in shallow (mean depth $< \sim 2.25$ m, see below) acidic lakes do not alter patterns of stratification in ways that strongly impact fish populations (Schofield et al. 1993). This result is consistent with the lower significance boundary (2.07 m) from our comparative analysis. While our analysis cannot conclude (in the statistical sense) that there is no CPUE- k_d relationship in shallow lakes, there are additional reasons to believe that the lower bound of the Johnson-Neyman interval is ecologically meaningful. Specifically, shallow lakes may freeze to the bottom. Even if there is sufficient habitat, low oxygen conditions are likely to cause winterkills (Danylchuk and Tonn 2003). Small lakes are also less likely to have surface water connections with other lakes to buffer these changes through migration (Mark 1983). Finally, light may penetrate to the bottom over a wide range of water colors in shallow lakes but not in deep lakes. For example, the compensation depth will change in response to variations in k_d , but for shallow lakes the compensation depth may always exceed the maximum depth despite this variation. In this case, mechanisms for CPUE- k_d relationship related to primary production may not be active

in shallow lakes. Hence there are several reasons to believe that light extinction may not be a primary regulator of fish biomass in very shallow lakes and this is consistent with a lack of significant CPUE- k_d relationship for shallow lakes in our study.

Both whole-ecosystem experiments and comparative analysis have shown that changes in water color impact thermocline depths and hypolimnetic oxygenation in deeper lakes including those with mean depths within and above the Johnson-Neyman range of our analysis (Bukaveckas and Driscoll 1991; Mazumder and Taylor 1994; Christensen et al. 1996). However, a synthesis of whole-lake liming experiments that were interpreted in the context of stratification influences on fish energetics indicated that increases in DOC concentration and color in acidic lakes only impacted fish populations in lakes with maximum depths in the range 5–10 m (Schofield et al. 1993). This corresponds to a mean depth range of 2.25–4.5 m when assuming a mean to maximum depth ratio of 0.45, which is the average depth ratio for small lakes in their study region (ALSC 1990). This mean depth range is very similar to the Johnson-Neyman interval (2.05–3.5 m) from our study (Schofield et al. 1993). Additionally, comparative analyses have reported an inverse correlation between CPUE and DOC in pristine Michigan (U.S.A.) lakes not impacted by acidification (Craig et al. 2015), but in one relatively clear lake where DOC concentrations were experimentally increased, no substantial changes were observed in fish abundance or growth (Koizumi et al. 2018). In two nearby dystrophic lakes, water clarity improved substantially after lime addition. Habitat availability increased in terms of oxygenated volume, but no increase in fish production or biomass was observed (Johnson and Hasler 1954). The mean depths of lakes in both of these studies exceeded the range of mean depths for significant relationships observed in our study and two of three lakes exceeded the range of maximum depths reported by Schofield et al. (1993). We cannot rule out that the Johnson-Neyman range identified in our analysis might change with additional data (higher statistical power could result in a wider range of mean depths with a significant CPUE- k_d relationship). However, the results of these whole-ecosystem experiments suggest that there is an ecologically meaningful limit for depth beyond with there is no significant relationship between water color and fish populations and this is consistent with the result of our analysis.

When we formulated our analysis, we hypothesized that mean depth moderates the relationship between CPUE and k_d . We used this formulation because light extinction can change rapidly due to numerous abiotic and biotic factors and is an immediate management concern, whereas lake depths are typically constant or changing slowly on the order of hundreds to thousands of years or longer (Downing 2010; Solomon et al. 2015). Additionally, other researchers had previously identified depth as a potential moderating factor for biomass-DOC relationships (Finstad et al. 2014).

Hence, it makes sense to identify lakes based on relatively static mean depths where changing light extinction may impact fish biomass. However, we also experimented with reversing the analysis to evaluate light extinction moderation of the biomass–mean depth relationship. We found that mean depth was significantly inversely related to CPUE for lakes with k_d 0.38–2.74 m^{-1} . This range includes 87% of small lakes in boreal Sweden (Supporting Information Text 1). The significance of mean depth in predicting fish biomass for the vast majority of small boreal lakes emphasizes the fundamental importance of lake morphometry to ecosystem patterns and processes, and highlights the challenge that the widespread lack of bathymetric maps poses to the field of limnology. Our theory driven upscaling is robust and useful for defining the percentages of small lakes where increasing k_d is likely to reduce fish biomass, but it cannot make predictions of mean depth and potential changes in fish biomass for individual lakes (Cael et al. 2017). This is not easily overcome in a cost-effective way. Application of geostatistical models to estimate depth has low cost, but also low accuracy and little theoretical support (Cael et al. 2017). Depth sounding produces accurate measurements, but is expensive on a per-lake basis due to personnel costs (Håkanson 1978). New airborne lidar can create high-resolution bathymetric maps for large number of lakes in a short period of time, but with a high total cost related to airplane operations (Paine et al. 2013). This is a major limitation to predicting change in lake ecosystems at the regional and global scales.

We observed an inverse correlation between CPUE and light availability in boreal Sweden and this is consistent with previous reports from our region (e.g., Karlsson et al. 2015), but other patterns have been hypothesized. For example, Finstad et al. (2014) has suggests a unimodal relationship where there is a positive CPUE–DOC relationship at low DOC concentrations, and an inverse CPUE–DOC relationship at high DOC concentrations. This pattern is not very likely in the boreal zone where DOC concentrations are relatively high. Finstad et al. (2014) give DOC concentrations of 0.32–2.21 mg^{-1} as examples of the transition between positive and negative relationships, depending on lake morphometry and landscape characteristics. This corresponds with 2.5–22.3% of lakes in the range of positive CPUE–DOC relationships based on the global distribution of DOC concentrations reported by Sobek et al. (2007). These estimates are imprecise because the joint distribution of DOC and depth is poorly characterized, but it is clear that a minority share of lakes, probably clustered in mountainous regions, have low enough DOC concentrations to potentially exhibit a positive CPUE–DOC relationship (Sobek et al. 2007; Seekell et al. 2014, 2015a,b). We cannot rule out that a nonlinear relationship might exist for lakes outside the range of water colors included in our analysis, but only 9.5% of small lakes fall outside of this range which means that the inverse relationship described in our study is probably widespread in

higher DOC regions like the Swedish boreal zone (Sobek et al. 2007; Seekell et al. 2014).

Conclusion

The primary contribution of our study is the empirical finding that the relationship between fish biomass and water color is more negative in deeper lakes than shallower lakes. A secondary contribution is the application of fractal scaling relationships that allow us to generalize this result to 26% of small lakes and provide regional context. This fills an important gap created by a global paucity of bathymetric maps. Finally, our study has highlighted how monitoring and experimental studies in lakes with different morphometry are likely to generate different outcomes in response to similar environmental changes. Our study thus provides context for integrating future experiments and potentially explaining divergent results to help form the basis for predictions about ecosystem change.

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Conflict of Interest

None declared.

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