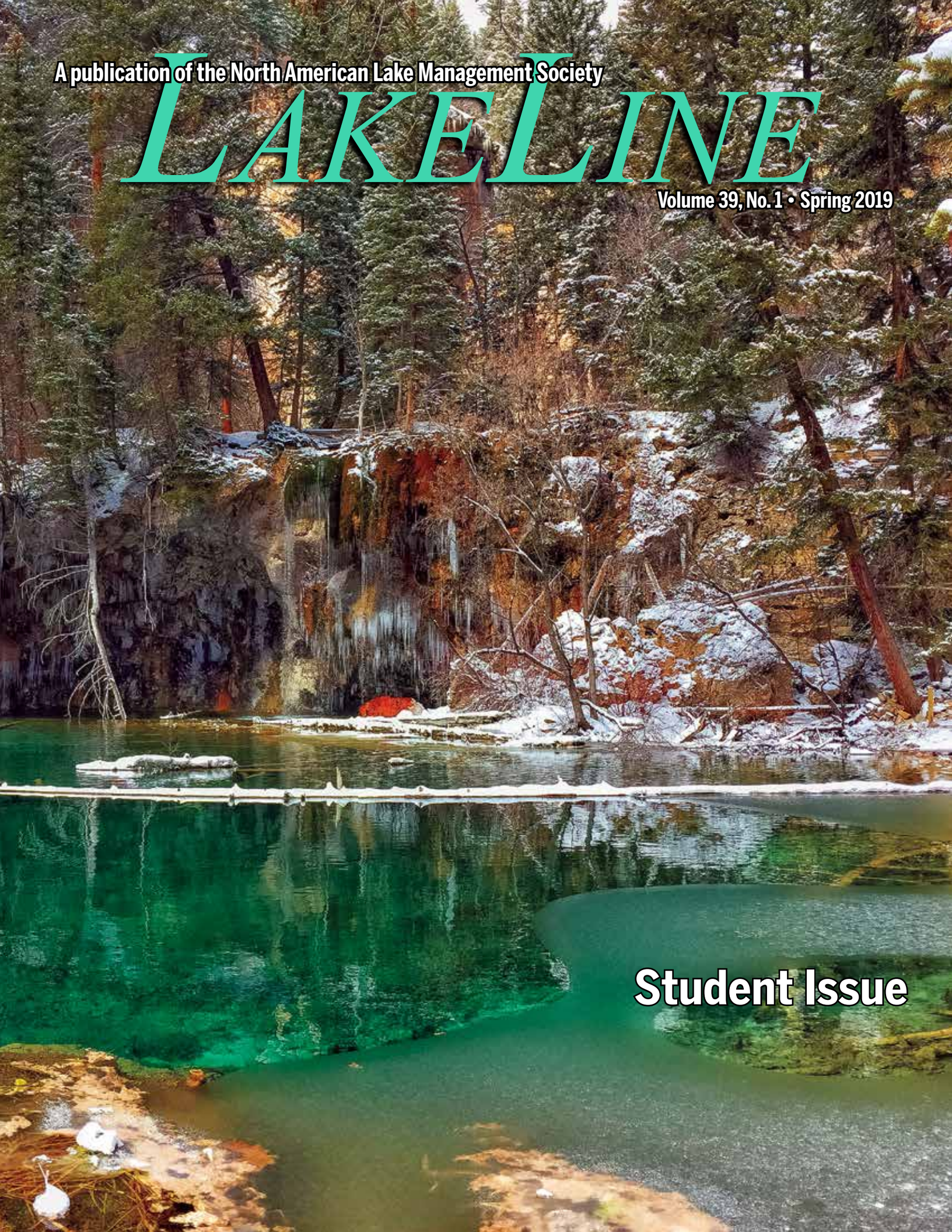


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Student Issue

Why So Bloomy? Lake Browning May Influence Algal Response to Climate Change

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The greening world, algae at large

Harmful algal blooms (HABs) in freshwater systems, resulting from an overabundance of cyanobacteria, are rapidly becoming a global concern, due to the severity of negative consequences to human health, ecological integrity, and economic stability. Warming surface waters and increased nutrients are the two most critical drivers of cyanobacteria growth in freshwater lakes (Paerl and Otten 2013). Climate change is hypothesized to accelerate lake greening by warming air temperatures and increasing storm events that deliver more nutrients to lakes, especially in the northern temperate zone (Paerl and Otten 2013). The anticipated risks to health are the impetus for government regulation of cyanobacterial toxins in drinking water and proposed regulation of toxins in recreational waters.

According to the World Health Organization Guidelines for Drinking Water and Recreational Water, toxin levels at or above 1.0 µg microcystin/L (corresponding to 50 µg chlorophyll-a/L) in drinking water represent a considerable (moderate) health risk and those above 20 µg microcystin/L in recreational waters represent high health risk. Measurements above 0.3 µg microcystin/L and less than 1.0 µg microcystin/L in drinking water are considered a low health risk, but have potential to harm children and pets.

Most of the previous studies of HABs used nutrient concentrations as a predictor, because cyanotoxins are nitrogen-rich molecules and require considerable phosphorous for synthesis. Chlorophyll-a (a pigment produced by algae) has been used as a measurement for algal content.

Efforts are underway to improve predictability of HABs, given that chlorophyll-a concentrations alone are not

a good indicator of toxin presence (Paerl and Otten 2013; USEPA 2016). For example, some cyanobacteria can switch between production and non-production of toxins within a single bloom event. Furthermore, the growing body of literature on nutrient levels and HABs have not yielded consistent results regarding the predictive ability of nutrients or at what threshold toxins are produced. Toxin-producing cyanobacteria are universal (present in > 98 percent of U.S. lakes); yet, less than 1 percent of lakes contained toxins at high risk to health (USEPA 2016). The question remains – Why are algal blooms in some lakes toxic, while those in neighboring lakes are benign? To answer this question, scientists have expanded the HAB-nutrient paradigm to other factors that may indirectly influence HABs.

An alternative strategy

The traditional approach for evaluating the potential for HABs involves testing some indicator of algae or toxin concentration against key determinants, such as temperature or a spectrum of nutrients. An alternative approach would be to expand the list of predictors to those that influence the key determinants of cyanobacteria growth. For example, Leech and others (2018) reported that those lakes with the most microcystin and greater chlorophyll-a concentrations were also darker in color (≥ 20 platinum cobalt color units; PCU). The dark coloration of the water comes from the long-term increase in dissolved organic matter (DOM) from the surrounding terrestrial environment – a phenomenon termed lake browning – and from internal nutrient cycling. Preliminary analysis of the 2012 USEPA National Lakes Assessment dataset indicates a rise in chlorophyll-a with increasing DOM,

among lakes with some health risk from HABs (Figure 1); however, consideration of the role of DOM and lake browning to affect key determinants of cyanobacteria growth is largely absent in the literature.

What can brown do for you, algae?

When the phenomenon of ozone depletion was discovered, ecologists became concerned about potential consequences to aquatic life from rising exposure to damaging, ultraviolet (UV) radiation, and established a suite of lakes as long-term study sites. Over 30 years, scientists observed many northern, temperate lakes losing UV transparency and darkening in color (Williamson et al. 2015). The browning of the water and reduction in UV exposure at depth resulted from concurrent increases in precipitation and a recovery of the surrounding watershed from reduced anthropogenic acid deposition. As soils return to a more neutral state, DOM binding capacity decreases, yielding greater release of DOM in runoff, resulting in rising DOM content in some lakes.

DOM, which contains nutrients and colored carbon from decayed plant and animal material, acts as a sunblock by selectively absorbing UV. Photosynthetically active radiation is also absorbed, and in the process converts the light energy to heat. Darker waters have greater capacity for the absorption of solar radiation. As a result of this light absorption, there is accelerated warming of surface waters and a shrinking of the thickness of the warmer, well-lit surface waters. This can lead to stronger density gradients that may last longer in the summer, and trap non-motile organisms in suboptimal warmer conditions, as well as accentuate oxygen depletion in deeper, cooler waters (Knoll et al. 2018; Pilla et al. 2018).

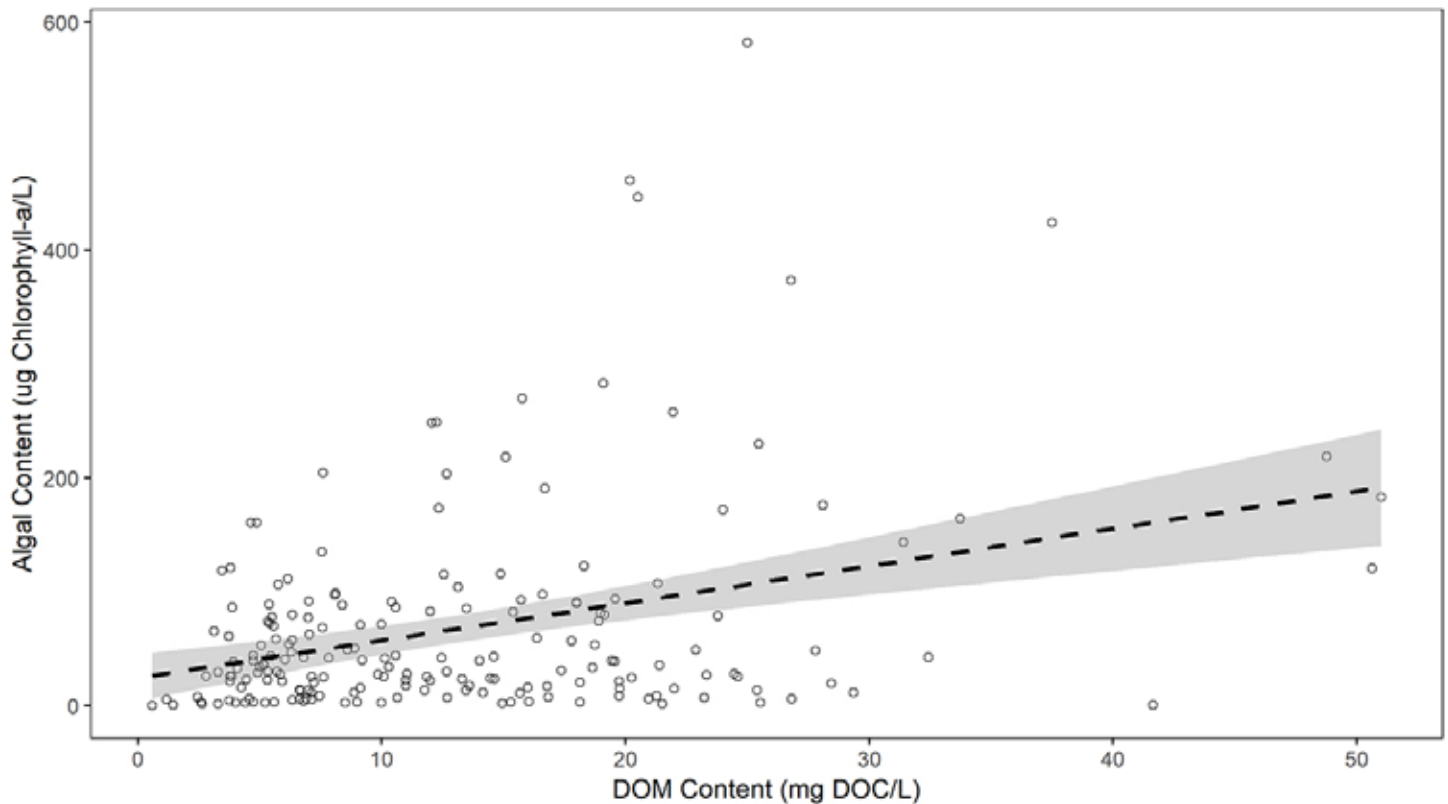


Figure 1. Algal content (in μg chlorophyll-*a*/L) by DOM content (in mg DOC/L) for samples with at least some health risk ($\geq 0.3 \mu\text{g}$ microcystin/L). Shaded (grey) area with dashed (black) line indicates regression of algal content across DOM within one standard error. Data from 2012 National Lake Assessment Survey, U.S. Environmental Protection Agency.

Persistent lack of oxygen in the deep waters can lead to the release of stored phosphorous and DOM from the sediments. This increase in nutrients combined with warmer surface waters creates ideal conditions for HABs.

Some species of cyanobacteria, including several that produce toxins, have a competitive advantage over most other algae because they can control their buoyancy in the water column to optimize light, nutrients, and temperature (Paerl and Otten 2013). Additionally, cyanobacteria can persist at warmer temperatures above which other algal competitors can survive ($>25^{\circ}\text{C}$). Cyanobacteria have a faster rate of nutrient uptake than do other algal competitors, and some cyanobacteria can fix atmospheric nitrogen when this nutrient is scarce in the water column. When a mixing event occurs, such as a large summer storm event or fall mixing, the trapped nutrients in deep waters are released to algae in the surface waters.

Lakes with greater DOM tend to have extended periods of oxygen depletion and little to no oxygen in the deep waters for most of the summer, which may explain

the expanding HAB season observed among northern, temperate lakes.

Measuring algal response across the color spectrum from brown to green

Given the potential for lake browning to influence temperature, light and nutrient conditions, my work tests the importance of lake browning within the greening framework. I hypothesized that the release of nutrients from the sediment and their subsequent upwelling to warmer surface waters, accelerated by lake browning, predisposes lakes to greater algal blooms. I predicted that the algal response (i.e., higher chlorophyll-*a* levels) would be greater in darker lakes than less dark lakes.

In the summer of 2018, I tested this hypothesis using an in-lake experiment that simulated a mixing event within three lakes of different DOM and nutrient content. The experiment was implemented in a blue (low nutrient, low DOM) lake, a green (high nutrient, moderate DOM) lake, and a brown (moderate nutrient, moderate DOM) lake in the first half of August. All three lakes are relatively small (< 50 hectares), glacial lakes located

within forested watersheds of northeast Pennsylvania.

I collected unfiltered surface water containing algae and deep water (one meter above the bottom) from each lake, using a sampling bottle, and placed the water in gas-permeable, Bitran bags. Five replicate bags, containing either unmixed surface or bottom water or a 50:50 mixture of the two, were incubated below the surface of each lake for seven days and analyzed for changes in algal concentration. No artificial nutrients were added, and water was incubated within its respective lake. Samples were averaged for pre- and post-incubation measurements of DOM (as DOC concentration), chlorophyll-*a* concentration, and nutrient content (total and dissolved nitrogen and phosphorous) (Table 1).

Chlorophyll-*a* concentrations increased significantly (pre to post, $p < 0.05$) when bottom water was mixed with surface water for all three lakes but didn't change when surface water was left alone (Figure 2). The greatest change occurred in the green lake, followed by the brown lake, then the blue lake (Figure 2). Interestingly, the greatest increase in

chlorophyll-a for all three lakes occurred where bottom water was incubated alone (Figure 2). This was unexpected for these two lakes, considering samples were collected in deep (> 9m), dark (0% UV/PAR), low oxygen (< 0.4mg DO/L, except in the blue lake) waters, which would have challenged the survival of autotrophs. Even though the brown lake and green lake had similar DOM content, bottom water from the green lake, which also had the greatest nutrient content, had the greatest increase in algae when brought to the surface.

This experiment has yet to uncover which algae benefitted the most from DOM-mediated changes in temperature and nutrient conditions and whether changes in algal content would translate to changes in toxin concentrations. Further investigation is needed to determine the cause of chlorophyll generation, such as the sudden warming stimulated growth of dormant spores or there was a shift in metabolic pathways in mixotrophic species (i.e., from heterotrophy to autotrophy). Thus, efforts are underway to identify and enumerate the algal species and toxin concentrations among the samples.

Conclusion

These findings support the continued investigation of how DOM may play a role in the hypothesized climate change-driven increases in HABs. Higher DOM

and nutrient content, especially near the bottom of the lake, appears to predispose lakes to greater algal blooms. Further comparisons of algal response between lakes that are greening and browning versus only greening is needed. Additionally, this study speaks to the importance of sampling design, such that samples from the deep waters may be more predictive for mid- to late-summer HABs.

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Table 1. Initial conditions for the three study lakes, including temperature and oxygen, algae, DOM, and nutrient content (i.e., mean pre-incubation values).

Lake	Blue Lake	Brown Lake	Green Lake
Surface area (hectares)	47.3	21.0	27.5
Maximum depth (m) where sampled	22.0	10.0	12.5
Surface Oxygen (mg DO/L)	8.86	7.72	8.55
Surface Temperature (°C)	22.3	25.0	17.3
Surface DOM Content (mg DOC/L)	1.82	5.20	5.28
Surface Total Phosphorous (µg P/L)	13.27	22.23	N.A.
Surface Total Nitrogen (mg N/L)	0.29	0.36	1.64
Surface Algae Content (µg chlorophyll-a/L)	0.97	2.83	28.55
Bottom Oxygen (mg DO/L)	3.25	0.33	0.21
Bottom Temperature (°C)	5.5	6.4	6.1
Bottom DOM Content (mg DOC/L)	2.11	4.56	5.74
Bottom Total Phosphorous (µg P/L)	36.47	23.53	N.A.
Bottom Total Nitrogen (mg N/L)	0.52	0.45	3.02
Bottom Algae Content (µg chlorophyll-a/L)	0.27	0.00	6.14

N.A. = data not available at this time

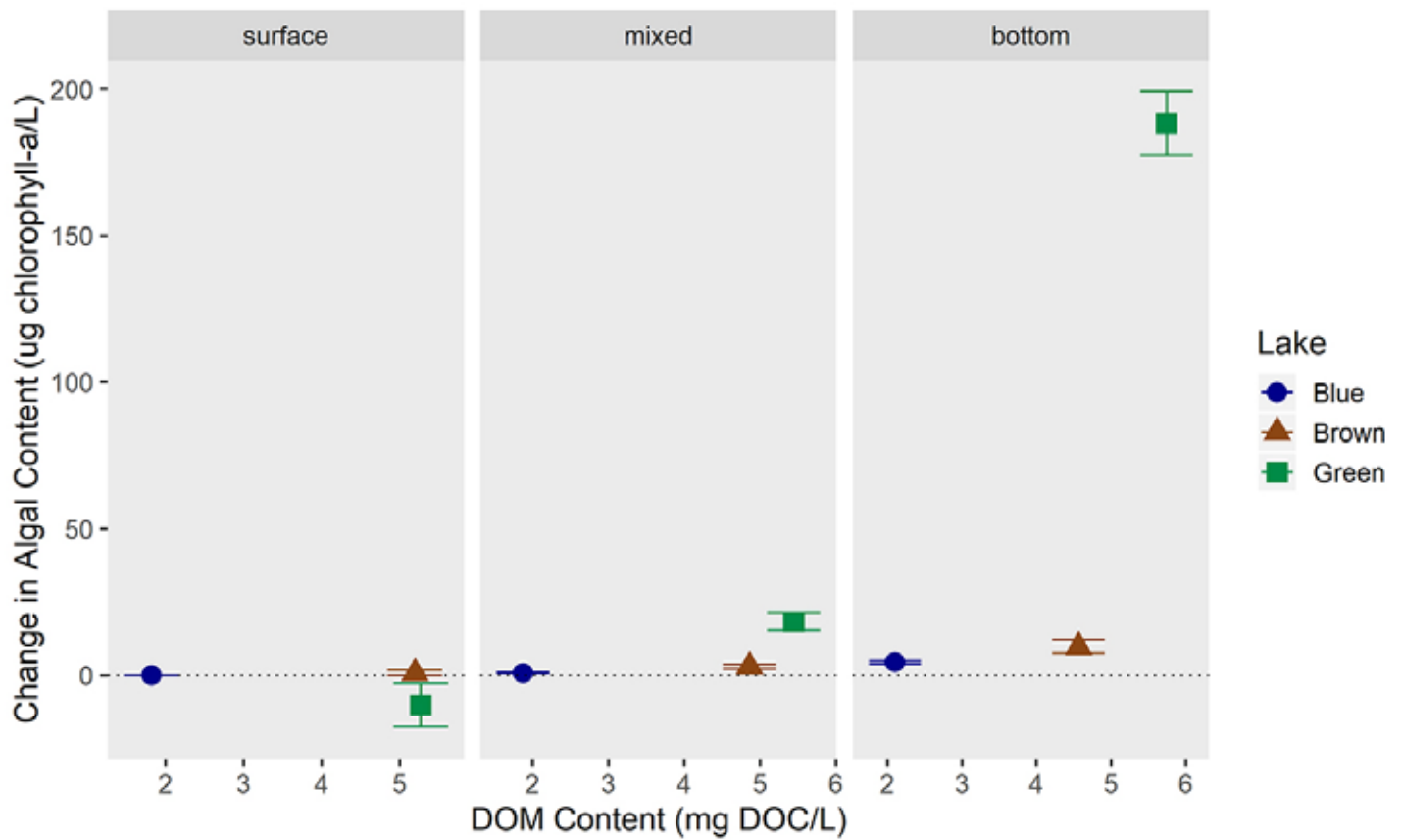


Figure 2. Average change in algal content (in μg chlorophyll-a/L) by DOM content (in mg DOC/L) for each treatment group among the three lakes. Error bars represent one standard error from the mean. Data from August 2018 in-lake experiment.



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