Rachel Pilla

Student Corner

Dark Waters: Structural Changes to Lake Ecosystems Due to Browning

Introduction to lake browning

In recent decades, many lakes throughout northeastern North America and northern Europe have experienced long-term decreases in water clarity caused by rising concentrations of brown-colored terrestrial materials entering lakes from the watershed. This phenomenon has been called lake "browning" (Roulet and Moore 2006), and is a driven by increasing concentrations of dissolved organic matter (DOM) due to recovery from acidification, increased precipitation, severe storm events, and other factors. In the Pocono Plateau region of northeastern Pennsylvania, Lake Giles, a well-protected, pristine lake has experienced browning since sampling began in the late 1980s, where DOM concentrations have more than doubled in the past three decades. The pH has rebounded due to recovery from acidification following the Clean Air Act amendments in the 1990s, and precipitation has increased by 40 percent, which together have driven increases in DOM in the lake. The reduction in water clarity due to browning has changed the vertical light and heat distribution in Lake Giles, which have in turn affected its chemical and biological properties. I have been researching this and other lakes in the region for both my Master's and PhD graduate programs starting in 2013, and have worked to understand the implications of lake browning and changes in water clarity on the physical, chemical, and biological properties of lakes.

Lake physical responses to browning

My first research project in the Pocono lakes focused on the long-term changes in water temperature and thermal structure as it linked to browning (Pilla et al. 2018). Over the past three decades, surface waters in Lake Giles have warmed by 3°C, which is about three times faster than the global average for lake surface water temperature warming. However, the air temperatures have not warmed in northeastern Pennsylvania during this period, so this typical driver of warming lake surface temperatures implicated in many other studies was not, in fact, a primary driver in Lake Giles during this study period. Instead, the higher concentration of DOM that has darkened the waters absorbs more light and heat at the surface, leading to this rapid warming of the surface waters. The deep waters of this lake are responding to browning in the opposite manner: they have cooled by nearly 4°C over the same three decades. We attribute this cooling of deeper waters to the fact that light and heat no longer reach as deep due to higher absorption in the darker surface waters. The differential responses in the warming surface waters vs. cooling deep waters have led to very strong increases in thermal stratification and thus stability that in turn reduce vertical mixing. These changes in temperature and density also influence deep water dissolved oxygen concentrations – a lake response to browning that our lab has been studying more recently with high-frequency automated sensors deployed at multiple depths.

Lake Giles historically had well-oxygenated deep waters, rarely reaching critically low concentrations of dissolved oxygen. However, in recent years, the frequency and duration of low oxygen conditions in deep waters have increased (Knoll et al. 2018). Lake browning, rather than eutrophication or warming air temperatures, is the most likely driver of these changes. The mechanisms involve increased thermal stability in the lake that reduces vertical mixing of dissolved oxygen from well-oxygenated surface waters to the deeper waters. In addition, decreased light availability limits the depths that algae can photosynthesize enough to replenish oxygen. Finally, greater DOM concentrations provide a substrate for microbial decomposers in deep waters, which increases oxygen consumption. Combined, these effects of browning on deep water oxygen depletion could be critically important for lake organisms that require ample oxygen to survive, grow, and reproduce. If the low oxygen conditions become more prevalent in this lake, or the volume of low oxygen waters increase, suitable habitat for aerobic plankton and fish will be reduced.

Biological consequences of browning

Browning has consequences for aquatic biota due to changes in suitable habitat as temperature and oxygen in the lake are altered (Figure 1). My research is examining these changes using high-frequency data combined with ecological modelling for projecting past and future lake conditions. A common and ecologically important genus of zooplankton, *Daphnia*, serves as a grazer of algae and a food source for larger zooplankton and fish. In Lake Giles, *Daphnia* abundance during summertime has decreased dramatically over the past three decades as the lake has browned (Williamson et al. 2015). *Daphnia* thrive best in temperatures around 13°C-18°C, but reach their lethal tolerance near 28°C-30°C. Daphnia also require oxygen, generally at level of at least ~2 mg/L. With warming surface waters and increasingly prevalent low oxygen conditions in deep waters, the suitable habitat for *Daphnia* is being compressed

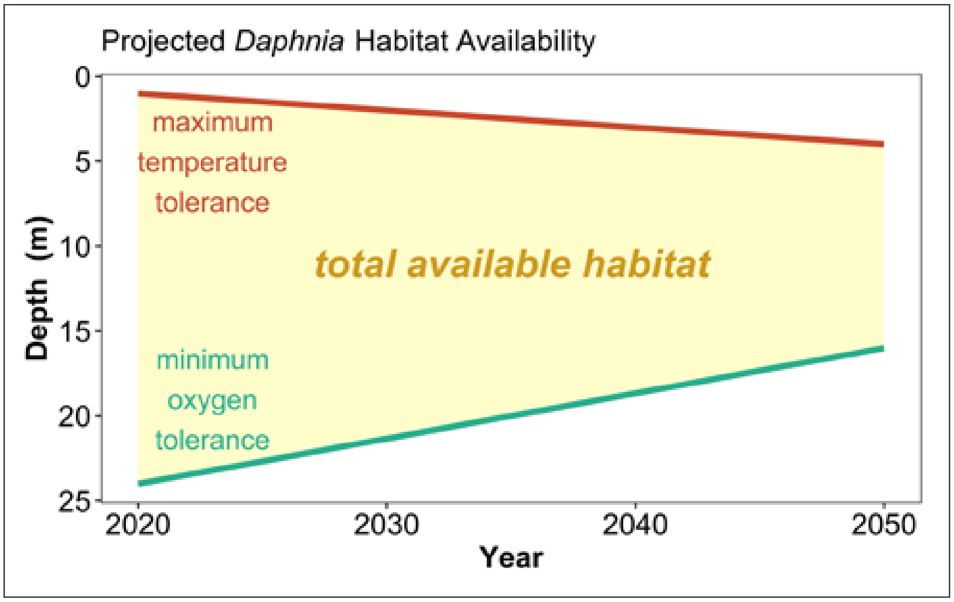

Figure 1. Projected vertical habitat availability for Daphnia *under continued lake browning (yellow), where maximum thermal tolerance (red) will limit the upper habitat range, and minimum oxygen tolerance (green) will limit the lower habitat range.*

(Figure 1). This may influence their interaction with their food source or their predators, or force them into less optimal habitats. I hypothesize that this "habitat squeeze" of *Daphnia* may be partly responsible for their decline in the lake during the summer.

Changes to lake characteristics during wintertime

Most of the research on lakes has focused on the ice-free summer season, but climate change is acting to decrease ice cover in many lakes throughout the world. Reduced or intermittent ice cover can influence water temperature and oxygen conditions during the winter, where sampling efforts have been notably less focused.

In 2016, I deployed a suite of sensors in Lake Giles to monitor the changes in temperature and oxygen throughout the lake during the entire year (Figure 2). These high-frequency automated sensors measure temperature and oxygen every 10 minutes for all 12 months of the year, and have proven very reliable and robust, even under ice during wintertime. Paired with these in-lake sensors are time-lapse trail cameras in place since late 2018 that take photos of the lake four times each day to visualize ice freeze and ice break-up (Figure 3).

Using these sensors, I have been able to couple periods of oxygen depletion during wintertime with periods of ice cover. For example, the two most recent winters show strongly contrasting patterns of ice cover on Lake Giles. In the winter of 2017-2018 there was consistent ice cover for three months, whereas in the milder winter of 2018-2019, there were multiple short, intermittent periods of ice cover.

Paired with the high-frequency sensor data, responses of deep water oxygen between these two winters also showed strongly contrasting patterns. In the winter of 2017-2018, there was a fairly consistent decline in oxygen throughout the ice cover period, which reached near-critical levels towards the end of the winter. In contrast, oxygen declines during the milder winter of 2018-2019 only occurred during the intermittent periods of ice cover, and recovered during the ice-free periods of mixing (Figure 4). There were no critically low oxygen conditions during this entire winter period due to the intermittent mixing associated with the ice-free periods. This suggests that the shorter or intermittent periods of ice cover that are occurring with climate change are simultaneously alleviating low oxygen conditions during winter. However, shorter periods of winter ice cover have been associated with longer periods of thermal stratification during the summer, which may lead to more severe oxygen depletion during warmer seasons and will only increase with climate warming.

Implications for lake management

This research highlights the importance of lake browning on lake physical, chemical, and biological changes, in addition to the more traditional consideration and management of eutrophication. These ecosystem responses to lake browning alter water clarity and water quality, and ultimately may influence the ecosystem function and services of lakes experiencing browning. Further, the less studied changes that lakes

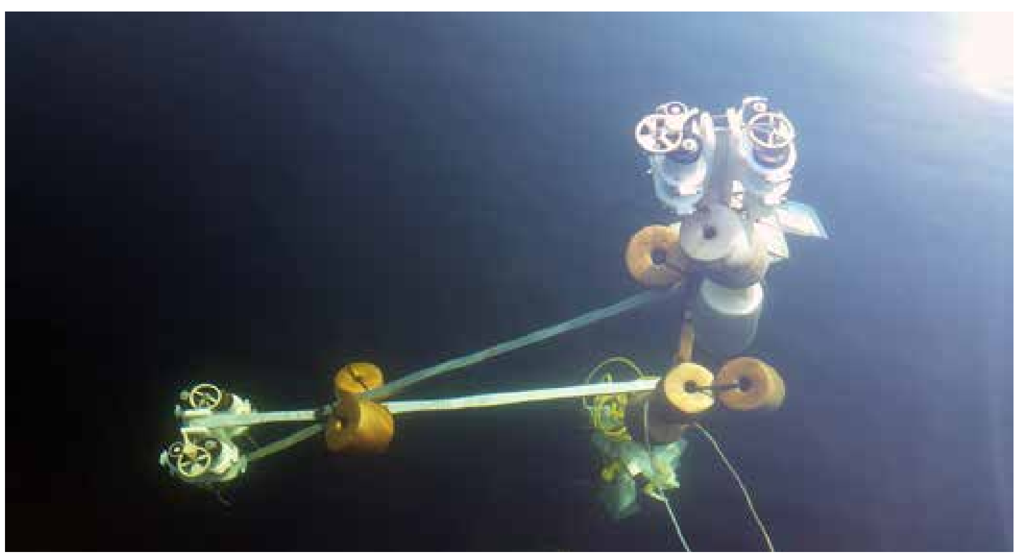

Figure 2. Photo of the underwater sensor set-up that includes high-frequency sensors measuring temperature, dissolved oxygen, and, more recently, visible light and dissolved organic matter.

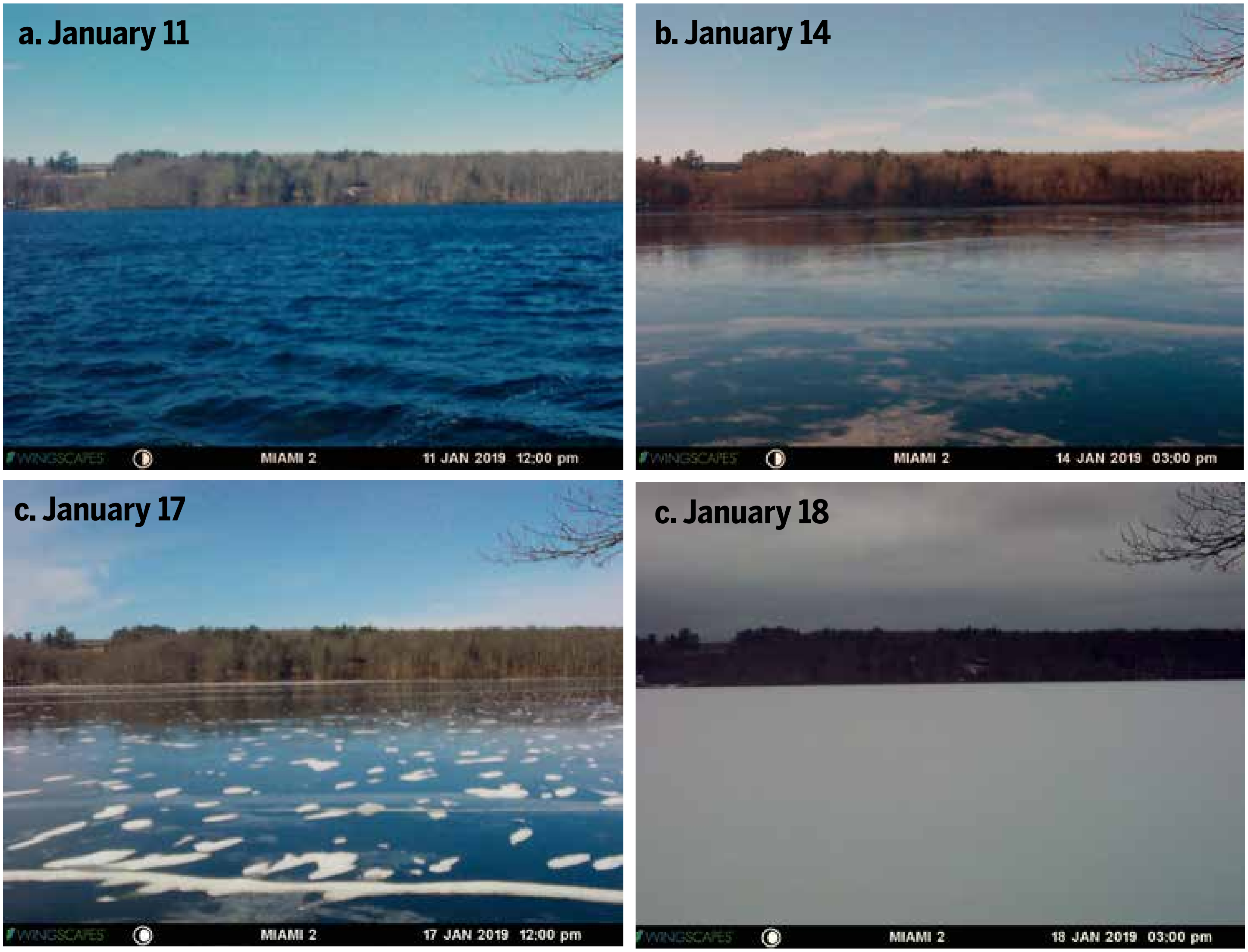

Figure 3. Time-lapse photos during winter 2018-2019 showing the formation of ice cover over the course of one week (January 11 through January 18). Deep water oxygen depletion tends to begin shortly after ice freezes (b).

are experiencing during winter are critical to research with more sampling efforts and attention, as the responses during winter may contrast strongly with the patterns observed during the summer. The biological changes during winter are critical to understanding future population dynamics across a range of trophic levels in lakes (Hampton et al. 2017).

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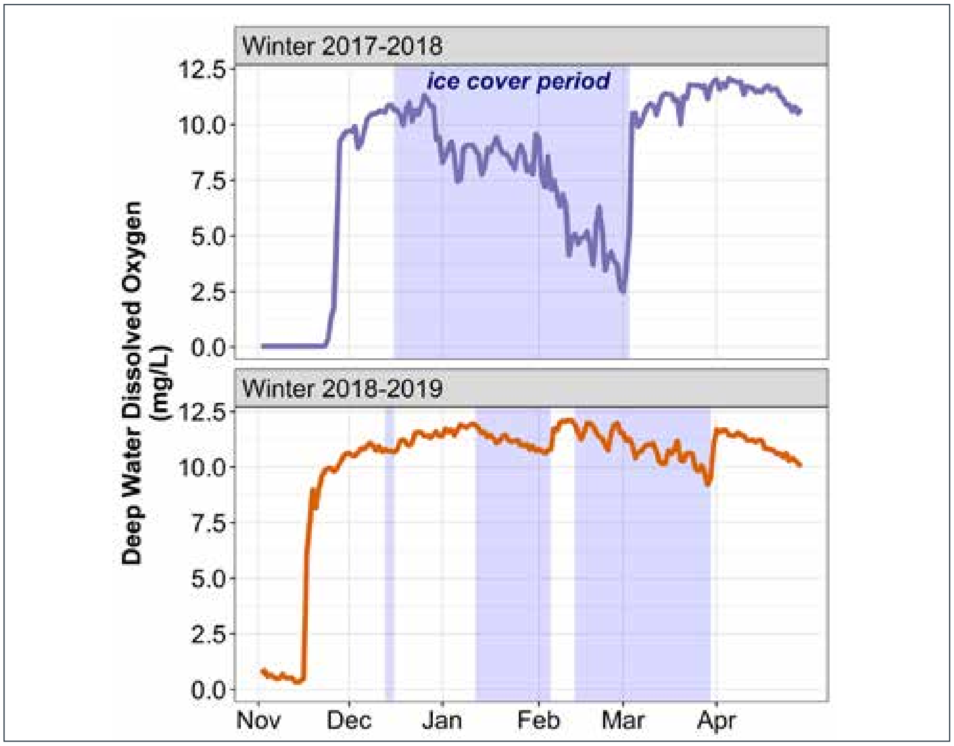

Figure 4. Comparison of deep water dissolved oxygen data between two contrasting winters. Top panel shows the winter of 2017-2018 that had one long period of ice cover from mid-December through early March (highlighted in blue). Bottom panel shows the milder winter of 2018-2019 that had several periods of ice cover with alternating periods ice cover that had oxygen depletion and periods of no ice cover that had vertical mixing and replenishment of oxygen.

Rachell Pilla is a Ph.D. candidate at Miami University in Ohio. She completed her master's of science and certification in applied statistics at Miami University as well, following her undergraduate degree in environmental science at the University of Notre Dame, where she first was introduced to limnological research and data analytics. Her research focuses on understanding the changes in lake ecosystems as a result of climate change, environmental stressors, and human influences. She is particularly interested in using advanced sensors, statistics, and analytics to understand these patterns and their importance in lake ecosystem structure, function, and services.