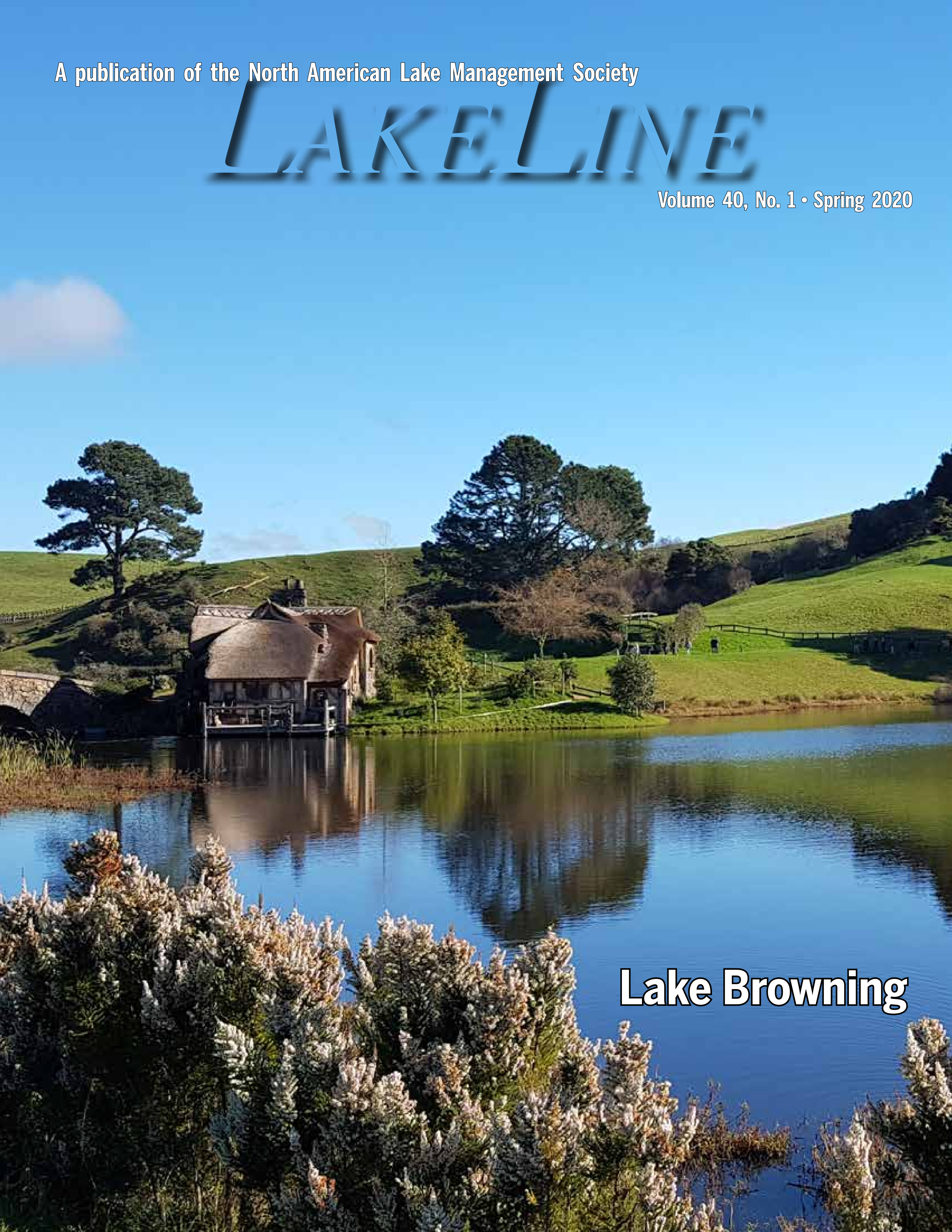
A publication of the North American Lake Management Society

LakeLine

Volume 40, No. 1 • Spring 2020



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Call for Abstracts

MINNEAPOLIS 2020

40th International Symposium of the
North American Lake Management Society

November 16–20, 2020
Minneapolis, Minnesota

NALMS at 40: Leveraging Experience to Manage Diverse Lakes, Landscapes and People

The Dakota (Sioux) homeland Mni Sóta Maķoce means "land where the waters reflect the clouds." Nicknamed "Land of 10,000 Lakes," Minnesota really has almost 12,000 inland basins covering at least 10 acres, but across the state, they are mostly rural and rather diverse. Deep, oligotrophic waters are typical in northeastern boreal forests near Superior, the world's largest areal, freshwater lake. Shallow, hypereutrophic lakes predominate in southwestern agricultural plains.

With about 30 lakes and 700,000 residents within 64 square miles, the twin cities of Minneapolis and St. Paul reflect some of the challenges of managing Minnesota's urban landscapes. Generations of Dakota (Sioux) called the area's largest and deepest lake Bdé Makhá Ská, but since the 1820s, it had been called Lake Calhoun. In 2018, the federal government officially restored the name, but the Minnesota Court of Appeals in 2019 reversed the state's official designation of the indigenous name. Positioned in this nexus between Minnesota's rural-urban diversities and past-future legacies, Minneapolis hosts the 2020 symposium that focuses on NALMS' 40 years of experience. The Program Committee hopes this symposium not only reflects with 20/20 hindsight, but also predicts with 20/20 foresight!

Prospective Program

There will be technical workshops all day Monday, November 16. Beginning Tuesday, November 17, presentations will be organized into themed tracks and sessions. We encourage oral and poster presentations on any aspect of lake and reservoir management, but especially invite valuable insights on the following:

- Lake management spanning 40 years
- Shallow lakes
- Invasive species
- Carp management
- Wild rice
- Harmful algal blooms
- Remote sensing
- Climate change
- Public engagement in planning
- Urban lakes/stormwater
- Waterfowl management
- Integrated ecologica management
- Fisheries management
- National Lakes Assessment
- Aquatic plant management
- In-lake nutrient control
- Linkage between lakes and watersheds
- Deicing salt impacts and management

Photos: Mike Krivit Photography, Courtesy of Meet Minneapolis

Important Dates

May 15, 2020
Abstracts Due

Late Spring 2020
Registration Opens

September 4, 2020
Registration for presenters of accepted abstracts due.

October 24, 2020
Last day conference hotel rate available.

Contact Us

nalms.org/nalms2020
nalms2020@nalms.org

LakeLine

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On the cover:
"Banks of the Shire, Hobbiton Lake, NZ," by Tracey Burton, winner of the 2019 NALMS Photo Contest Editor's Choice Award.

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From Amy Smagula the Editor

This issue of *LakeLine* explores topics related to lake browning. Now, most of us probably worry about our lakes turning green (or even blue-green, for that matter) from increases in algal growth over time. Most of us can recall the spectrum of lakes we've had an opportunity to visit, from very dark brown tannic (or tea-colored) waters that are hard to see into, to only slightly colored waters, to the waterbodies that appear crystal clear and colorless, where you can see far down into the depths. But there is more to lake browning than the color of the water and how far we can see into the lake. Lake browning is an actual process, with causal factors, it is happening over time, and it has some pretty complex ramifications for lakes and aquatic life. There is even evidence that brown is a natural state for many lakes, and that after decades, and more likely centuries of flux, lakes are reverting back to brown.

For those who attended the plenary session at the 38th Annual NALMS Symposium in Cincinnati, Ohio, Craig Williamson gave an excellent presentation on the topic of lake browning, and the implications that lake browning has on the physics, chemistry, biology and ecology of our lake systems. He and a network of researchers and students across the globe are working on various angles of this process, and some of that work is compiled here in this issue of *LakeLine*.

First, **Craig Williamson** shares an introduction to the process and impacts of lake browning, which uses some of the same images and content from his plenary presentation in Cincinnati, for those who may have missed it. His overview is a great introduction to lake browning, and provides a backdrop for the other articles in this issue, that explore various aspects and impacts of lake browning.

LakeLine encourages letters to the editor. Do you have a lake-related question? Or, have you read something in *LakeLine* that stimulates your interest? We'd love to hear from you via e-mail, telephone, or postal letter.

Kevin Rose and **Jonathan Stetler** from Rensselaer Polytechnic Institute in New York discuss their work with dissolved organic matter (DOM) in lakes in the Adirondacks of New York, including an overview of how lake color is measured in the laboratory, some of the drivers associated with lake browning, and implications of browning based on data from the Adirondacks of New York and the Poconos of Pennsylvania.

Chris Solomon with the Cary Institute of Ecosystem Studies and **Stuart Jones** with the University of Notre Dame co-authored an article on their work looking at implications of lake browning on food web dynamics in lakes, from the base of the food web (the algae), up through other levels of the food web, including invertebrates, zooplankton (microscopic animals), and fish. They discuss varied and unique ways in which different species are affected by consequences of lake browning, from light or nutrient levels to temperature and oxygen levels, and adaptations and evolution of these organisms to the changing conditions of lakes. They also discuss the spectrum of lake browning geographically, and provide input on what lake browning could mean for your lake.

Next, **Keiko Wilkins** shares information from her graduate work with freshwater zooplankton in lakes, where she evaluates potential impacts of DOM derived from a common native and a common invasive plant species in watersheds, and looks into the question of whether it is DOM quantity versus quality that could be a deciding factor in some food web impacts.

Our Student's Corner this month was written by **Rachel Pilla**, a Ph.D. candidate at Miami University in Ohio, whose focus is on using advanced sensors, statistics and analytics to better understand lake ecosystem structure and function, with a focus on the impacts of lake browning.

I hope you find this issue of *LakeLine* to be interesting and informative! This is the start of the second year that *LakeLine* has been electronic, and NALMS will soon be developing and sending out a survey to request your input on the format change for the magazine, as well as to invite your input for topics, content, and direction for *LakeLine* in the future.

Amy P. Smagula is a limnologist with the New Hampshire Department of Environmental Services, where she coordinates the Exotic Species Program and special studies of the state's lakes and ponds.

LAKELINE SUMMER 2020:

The summer issue of *LakeLine* will focus on the basics of lake and watershed stewardship, and will include a range of topics about the basics of limnology, watershed protection, lake and watershed associations, and more. If you have special requests for content, or would like to contribute an article, please reach out to the *LakeLine* editor.

From Perry Thomas

the President

Greetings to all from my home in Kentucky, where cardinals visit the feeder outside our kitchen window,

redbud blooms pop among fresh green leaves of hedgerow shrubs, and a pair of snapping turtles perform their spring dance in the pond next door. As the number of COVID-19 cases increases daily across North America, natural rhythms of springtime bring hope that current uncertainty will lead to positive change. While we wait to learn how the need to protect our health will affect plans for 2020 conferences, NALMS leadership continues conversations with partners about new and ongoing initiatives.

Discussions with leaders of the Society of Lake Management Professionals (SLMP) during their 2020 Summit in January revealed common needs among SLMP and NALMS members, as SLMP focuses on management of small private lakes while NALMS focuses on management of larger public waters. For example, how can SLMP and NALMS members use online marketing tools to increase awareness of lake ecology and the importance of protecting lake watersheds? We encourage *LakeLine* readers to visit the SLMP website (lakeprofessionals.org) and consider attending the 2021 SLMP Summit scheduled for January in Savannah, Georgia, with the theme of "Building Bridges to Profit from Change."

Meanwhile, the evolving partnership between NALMS and the Aquatic Plant Management Society (apms.org) has brought fresh perspectives to each organization. As we explore the question of how to frame a joint technical session for upcoming conferences, we focus on the integration of in-lake management approaches with lake-watershed management measures to address Harmful Algal Blooms (HABs). Important questions surface during our conversations, such as "When does the need to protect public health require communities to take simultaneous actions in lakes and in their watersheds?" We look forward to addressing this question and others through a combination of expert presentations and robust discussions, whether face-to-face or online during 2020.

Looking further into the future, members of the Consortium for Aquatic Science Societies (CASS, aquaticsocieties.org) consider how to strengthen collaboration while planning for the Joint Aquatic Sciences Meeting (JASM) scheduled for May 16-20, 2022 in Grand Rapids, Michigan. In preparation for JASM, NALMS anticipates finding new ways to highlight and expand the work of our Inland Harmful Algal Blooms (HABs) Program, in collaboration with other CASS members.

As we consult with partners during these days of social distancing, we consider innovative approaches not only to lake and watershed management but also to the ways we connect with one another. This issue of *LakeLine* highlights the importance of NALMS' role in bringing updates from the research community to inform the work of lake managers and community leaders. How can we broaden the audience that receives these important updates? Are we using online marketing tools effectively? If our members do not have opportunities to meet in person during the coming year, are there other ways we can support the kinds of inspiring and information-rich interactions that happen during our annual Symposium? We hope to answer these kinds of questions as we continue conversations with partners over the coming months.

Perry Thomas holds a Ph.D. in biology with a focus on aquatic ecology. She taught ecology and worked as a college administrator until 2015 when her career path took a turn into state government. After working with the Lakes Program of the Vermont Watershed Management Division, she now collaborates with environmental scientists in the Kentucky Watershed Management Branch. She feels fortunate to collaborate with thoughtful, dedicated colleagues – many of whom share her passion for paddling.

Lake Management in a Browning World: **Beyond the Holy Grail of Nutrients**

Craig E. Williamson

Water clarity is a primary determinant of water quality in lakes across the continent. The economic, recreational, and aesthetic value of lakes, and, in particular, their value as drinking water resources, is directly related to their clarity. Even in the clearest of lakes, water resource managers and the public shout slogans like "Keep Tahoe Blue!" The good news is that scientists have found the holy grail of lake management – excess nutrients, most often from human activity, are a primary contributor to algae blooms and green lakes. But why then, has there been so little change in the relationship between nutrients and algae in lakes across much of the continent in spite of the many success stories of controlling nutrients and decreasing algae blooms in individual lakes? The largest study to date of changes in water quality in over 2,900 lakes in the northeastern and Midwestern USA has shown that in spite of this awareness of the importance of nutrients and extensive management efforts, there has been little change in nutrients or algae in lakes since 1990; rather, we have seen an "unexpected stasis in a changing world" (Oliver et al. 2017).

At the same time that an unexpected stasis has been observed in nutrients and algae, many lakes across northeastern USA, northern Europe, and beyond, have seen up to a doubling or more in their dissolved organic matter (DOM) (Monteith et al. 2007), a phenomenon often referred to as "browning." Thus we need to think beyond the holy grail of nutrients, and consider how DOM and browning influence lake ecosystems (Figure 1). DOM is a major regulator of the clarity of inland waters around the world, often more important than chlorophyll. Our most pristine, oligotrophic, blue lakes are threatened not only by nutrients turning them green with algae, but also by DOM that can turn them into dystrophic brown lakes. When both chlorophyll and DOM are high, lakes can become mixotrophic, with a brownish-green color (Figure 1).

This special issue of *LakeLine* includes articles that examine the multiple effects of lake browning on many aspects of lakes ranging from the thermal structure and dissolved oxygen in water to zooplankton, fish, and human health and wellbeing. This lead article provides an overview and answers to key questions about the causes and consequences of browning and their implications that will enable more effective lake management in a browning world.

What is DOM and why is it increasing and turning lakes browner?

Anyone who has walked on a sidewalk after a fresh leaf-fall followed

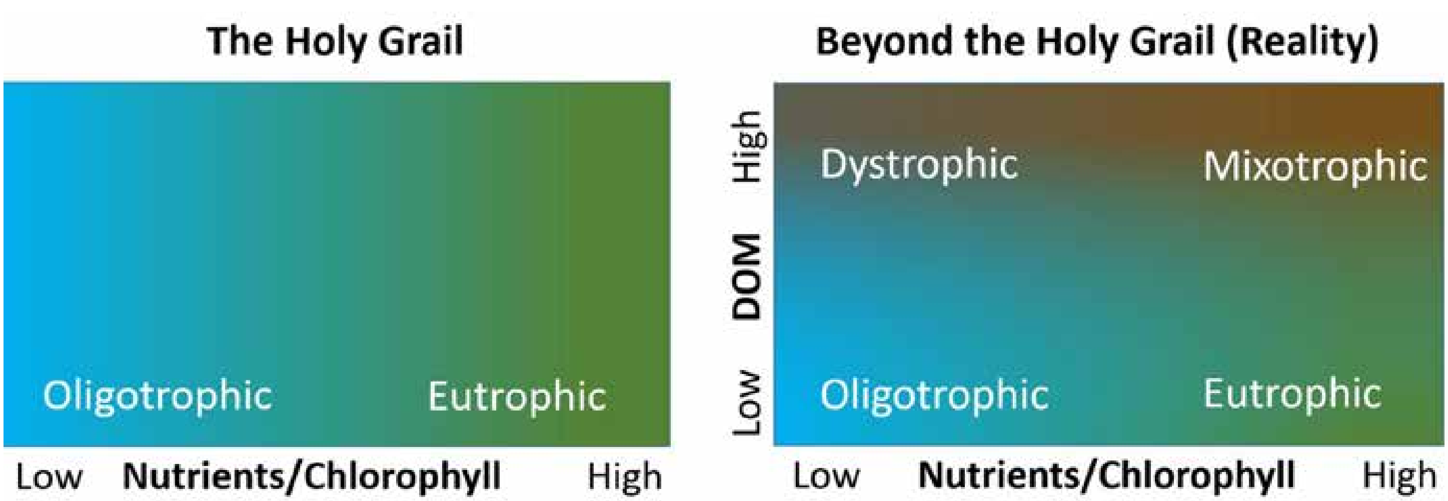

Figure 1. Conceptual diagrams showing the holy grail of nutrients and chlorophyll from the conventional, single-dimensional perspective (left), and a more complete paradigm that includes dissolved organic matter (DOM) and browning (right). Lakes do not vary only along a single gradient of nutrients and chlorophyll from oligotrophic blue lakes to eutrophic green lakes. DOM is a major regulator of water transparency, and in many regions around the world it is leading to more dystrophic (brown) lakes, or mixotrophic lakes in which both chlorophyll and DOM reduce water clarity.

by an autumn rain has seen DOM staining the sidewalks (Figure 2). The DOM that is turning lakes brown is largely derived from terrestrial sources, has a dark yellow-brown to black color, and is thus often referred to as colored, or chromophoric DOM, CDOM. The extent of the color of this DOM is a function of the plants from which it is derived, with some plants producing more highly colored DOM than others (Figure 2). This DOM is in turn processed by microbial degradation in the soils and receiving waters (biodegradation) and by the short wavelength visible and ultraviolet (UV) radiation in sunlight (photodegradation), which alter both its color and its quality.

Figure 2. Dissolved organic matter in lakes, reservoirs, and other inland and coastal waters is derived primarily from terrestrial plants, as can be seen from freshly fallen leaves leaching DOM on a sidewalk (left). Different types of trees and other plants leach different types of DOM, which vary in their color, and thus potential contribution to changes in inland water quality. Soil microbes and photodegradation by sunlight can further alter the composition and thus color and quality of the DOM, with important consequences for aquatic ecosystems.

There are multiple causes of the observed increases in DOM and browning in lakes and other inland waters. The two primary causes tell contrasting good news and bad news stories. The good news story is that acid deposition has decreased substantially since the 1990 Clean Air Act legislation was passed to limit industrial emissions of sulfur and nitrogen-based compounds that were acidifying the soils (Figure 3). Less acidic soils have increased the mobilization of DOM to downstream waters. The bad news story is that climate change is leading to strong increases in precipitation, and extreme precipitation events in particular (Figure 3). These increases in precipitation saturate the soils with water, creating anoxic conditions that increase DOM production. Heavy precipitation also increases the flow of water from terrestrial ecosystems, washing increasing quantities of DOM into inland waters (Strock et al. 2016). Climate change is causing an acceleration of the hydrologic cycle that is expected to continue to increase browning of inland waters far into the future. The associated increases in extreme events will also cause more severe droughts, which will offset browning, and depending on the hydrology of the lake basin, may even increase water clarity in lakes (Williamson et al. 2016).

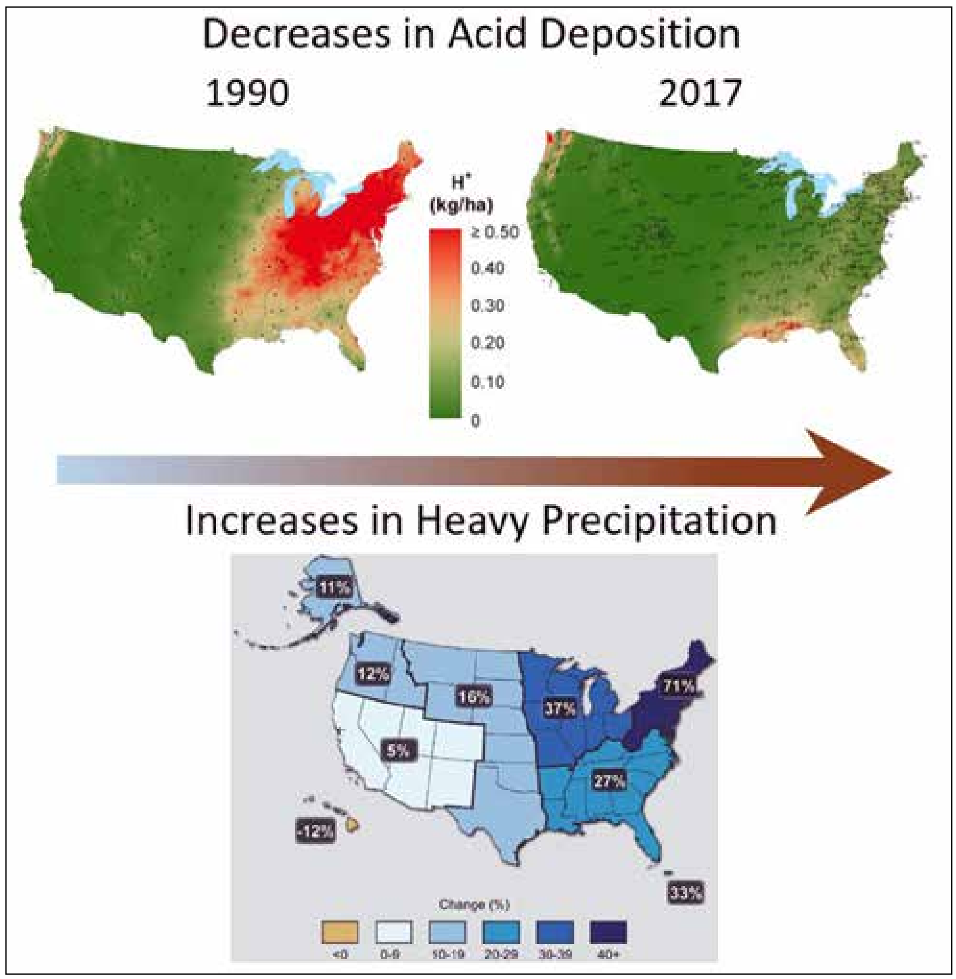

Figure 3. Two major causes of lake browning (horizontal middle arrow) include decreases in acid deposition related to the 1990 Clean Air Act Amendments (top), and increases in precipitation, particularly heavy precipitation events (top 1% of events) which have shown stronger increases in the north and east than in the western USA over the period from 1958 to 2012 (bottom). Sources (top): http://nadp.slh.wisc.edu/maplib/pdf/2017/h_dep_2017.pdf; (bottom): https://nca2014.globalchange.gov/report/our-changing-climate/heavy-downpours-increasing.

How does browning influence light, temperature, and oxygen in lake ecosystems?

The primary mechanism through which DOM alters lake ecosystems is through absorption of sunlight, which reduces light for photosynthesis, the primary source of energy that supports aquatic food webs. Thus, both photosynthetically active radiation (PAR) and UV do not penetrate as deep in brown lakes as they do in blue lakes (Figure 4). DOM strongly and selectively absorbs the shorter wavelength UV radiation (Figure 4), with important implications for the multiple effects of UV radiation on aquatic ecosystem services ranging from disinfection of parasites and pathogens, to photodegradation and nutrient cycling, to zooplankton vertical migration and invasion of warm-water fish into cool, clear-water lakes (Williamson et al. 2016). The absorption of sunlight in the surface waters of brown-water lakes also has multiple effects on the vertical habitat gradients in the water column. These effects include stronger thermal gradients (steeper thermoclines), and greater depletion of dissolved oxygen in deeper waters (Figure 4). The depth to which one percent (1%) of PAR penetrates approximates the compensation depth (see the intersection of the solid PAR line with the vertical axis in Figure 4). Below the compensation depth there is net consumption of oxygen and thus the threat of hypoxia and even "dead zones" in the cooler deeper waters that are anoxic, totally depleted of dissolved oxygen (Figure 4). Thus, the light-absorbing DOM in brown lakes creates vertical habitat gradients in light, temperature, and oxygen that are very similar to those observed in green lakes that have high concentrations of light-absorbing phytoplankton.

Why should water resource managers care that lakes are browning?

In addition to making lakes darker and aesthetically less desirable for some, browning has many effects on a wide variety of critical ecosystem services provided by lakes from drinking water to public health to fisheries. When drinking water is chlorinated, DOM combines with chlorine to produce carcinogenic disinfection byproducts such as trihalomethanes. The UV radiation in sunlight is also the most potent natural mechanism to disinfect the surface waters of lakes. By strongly and selectively absorbing UV radiation, DOM can reduce the effectiveness of solar disinfection of parasites and pathogens of humans and wildlife, leading to increases in parasitism and infectious diseases. Aquatic vectors of disease such as mosquitoes are also killed in their early larval stages by exposure to high levels of solar UV radiation. Increases in DOM associated with browning may thus provide a refuge from damaging UV that increases the breeding success of mosquitoes (Figure 5).

Increases in DOM during either long-term browning, or during extreme precipitation events that result in DOM-rich river plumes such as observed in Western Lake Erie (Figure 6) may also favor the development of cyanobacteria and harmful algal blooms. These blooms have been on the rise nationwide as illustrated by an animation from the Environmental Working Group at https://www.ewg.org/key-issues/water/toxicalgae. There are several mechanisms through which DOM can favor cyanobacteria blooms. First, cyanobacteria are better at regulating their buoyancy than other algae, and they can thus remain in the more well-lit surface waters when DOM darkens the water. Second, the increased absorption of sunlight in surface waters can lead to shallower, warmer surface waters that favor cyanobacteria due to their higher temperature optima compared to other types of algae. Third, DOM can increase nutrient availability through transport

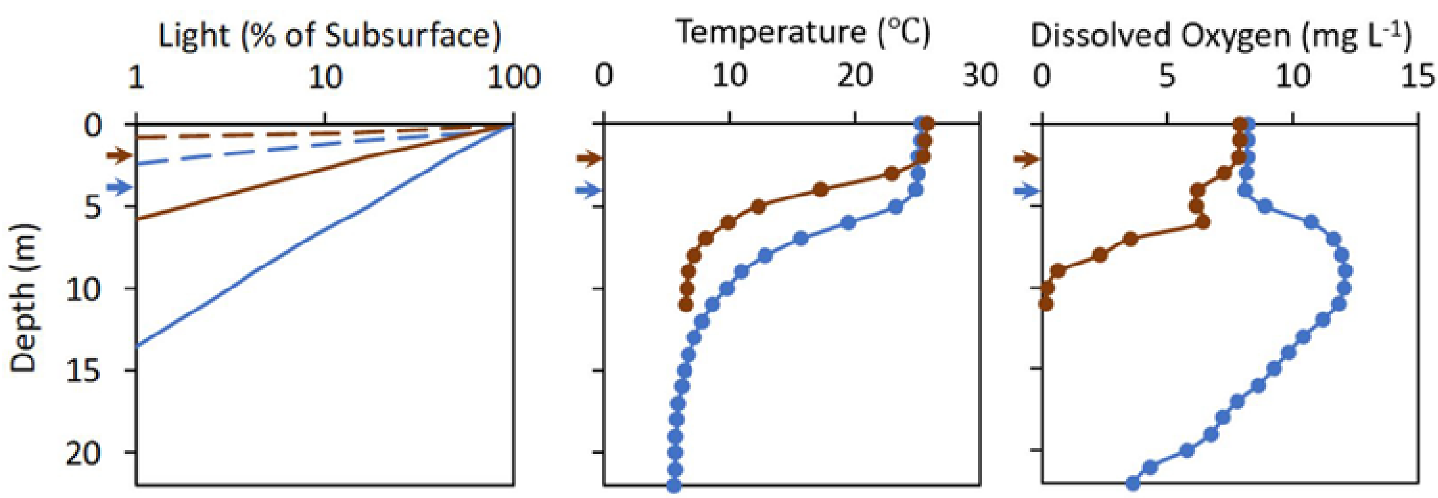

Figure 4. Vertical profiles in a dystrophic brown and an oligotrophic blue lake in northeastern Pennsylvania showing attenuation of light, including photosynthetically active radiation (PAR, solid line), and ultraviolet radiation (320 nm UV, dashed line), temperature, and dissolved oxygen in the water column (averages for 2016-2019). Arrows indicate the average depth of the mixed layer. Note the more rapid attenuation of light, steeper thermocline, and total depletion of dissolved oxygen in the deep waters of the dystrophic brown lake, all characteristic of what is found in eutrophic green lakes as well. The midwater peak in dissolved oxygen in the oligotrophic blue lake is due to a combination of the higher solubility of oxygen in colder water, and a deep-water peak in oxygen-producing phytoplankton that have plenty of light for net photosynthesis at depths shallower than the compensation depth (1% PAR depth).

Figure 5. Aedes aegypti*, the yellow fever mosquito, is one of several species that are expanding their range northward from subtropical environments with climate change. Browning of inland waters where mosquitoes breed provides a refuge from damaging solar UV radiation that may contribute to the expansion of these vectors of infectious diseases that include zika, dengue, chikungunya, and other viruses.* Photo from Center for Disease Control (https://www.cdc.gov/zika/vector/range.html).

Figure 6. Dark brown plume of dissolved organic matter (red arrow) entering Western Lake Erie where toxic cyanobacteria blooms have been an ongoing problem. In 2014 high levels of microcystin closed down the water supply to over 400,000 people in the Toledo, Ohio, area. Integrating DOM into our understanding of toxic algae blooms is essential for more effective management of such blooms. NASA MODIS image May 16, 2016.

from terrestrial ecosystems followed by bio- or photodegradation and release of the nutrients. The selective binding of nutrients by DOM may also alter nutrient ratios and potentially stimulate toxin production. In spite of these many ways that DOM may enhance harmful cyanobacteria blooms, there has been inadequate integration of DOM into the models used by management agencies to predict and control these blooms.

The effects of browning on fisheries depends largely on the initial transparency of the lake. Many fish species spawn in shallow waters where exposure to UV radiation can kill often highly transparent eggs and larvae (Figure 7). The UV damage potential is likely important only in lakes of high water clarity such as Crater Lake in Oregon, Lake Tahoe, and the Upper Laurentian Great Lakes (Superior, Huron, and Michigan), and the many other highly transparent lakes across the continent such as alpine lakes as well as in shallow lakes. In cool-water, highly transparent lakes, native fish and other aquatic biota may possess UV protective mechanisms that enable them to survive under high UV exposures. At the same time, embayments with high DOM concentrations can provide refugia for less UV-tolerant invasive warm-water fish to spawn successfully, as has been demonstrated in Lake Tahoe. In contrast to these very clear-water lakes, the growth and reproduction of fish tends to decrease with increasing DOM in browner lakes with higher DOM concentrations.

Browning-related reduction in the value of the ecosystem services provided by lakes have obvious economic consequences that include increased costs ranging from water purification for drinking to the effective management of fisheries. Lake-front property values also decline with decreases in water clarity. A study of property values for lake-front cottages in Ontario showed a 10 percent reduction in Secchi depth (a crude measure of transparency) decreases property values by 2.2 percent (Clapper and Caudill 2014). Similar results have been obtained in New Hampshire and Maine. While these and other studies have assumed that changes in water transparency are due primarily to eutrophication, browning is now also having a strong effect on water clarity across much of North America and needs to be folded into the current nutrient-algae paradigm for more effective lake management.

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Figure 7. Photographs of the transparent larvae of three species of fish from Lake Tahoe. The two warmwater invasive species bluegill (top) and largemouth bass (middle), have little photoprotective melanin, and are correspondingly highly susceptible to UV damage in the shallow, clear waters of Lake Tahoe where they need to spawn to get warm enough temperatures for reproduction. In contrast, the native Lahontan Redside (bottom) contains higher levels of melanin (black granules) and correspondingly can tolerate higher levels of UV exposure. Photo credits: Andrew J. Tucker.

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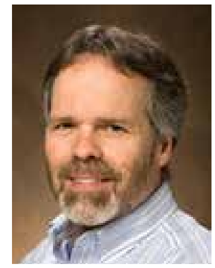

Craig Williamson is the Eminent Scholar of Ecosystem Ecology at Miami University in Ohio where he leads the Global Change Limnology Laboratory. He is passionate about lakes, and protecting their water quality. His expertise is in the ecology of ultraviolet (UV) radiation and climate change, with a current focus on the effects of changing water clarity on lakes. His research ranges from the effects of UV on the ecology of zooplankton, larval fish, and infectious diseases, to deploying advanced sensors to decipher the sentinel responses of lakes to climate change. He is the Chief Scientific Adviser of the Pocono Lake Ecological Observatory Network (PLEON), an outreach program on public education and monitoring of Pocono lakes. He is active in the Global Lake Ecological Observatory Network (GLEON) where he leads the Climate Sentinels Working Group, and he serves on the United Nations Environment Programme Environmental Effects Assessment Panel (UNEP EEAP).

UPCOMING IN *LAKELINE* – FALL 2020

NALMS at **40**

The fall issue will include some articles related to the evolution of NALMS and lake management over the last 40 years. We would like to include an array of personal stories from members of NALMS (both long-time and new) about what NALMS means to them. Articles on the evolution of lake management, and in particular some articles on how federal Section 314 funding was useful in the past, and the gaps it left behind when funding for that program was terminated. How did you adapt, or not adapt to that loss of funding on the state level? Case studies, data driven information, and/or anecdotal information is all useful. Also, it would be nice to have some short articles on how NALMS could and should grow and evolve for the next 40 years (what do we do well, what do we need to tweak or add).

The Causes & Food Web Consequences of Lake Browning: How are They Linked?

Kevin C. Rose and Jonathan T. Stetler

If one were to take snapshots of lakes and their watersheds in places such as throughout the northeastern U.S. or Northern Europe over the past few decades, it would be easy to tell that many things have changed. Looking underwater, one of the most dramatic would be a color change. Many lakes are substantially darker today than they were in recent past decades.

Many lakes are undergoing what is referred to as "browning." Browning is often described as a measure of increases in dissolved organic carbon (DOC) content. DOC is what gives many lakes a brown, "tea-like" hue to them, and browning is, first and foremost, a measure of water color change. Color often closely correlates with DOC content, but color is also sensitive to DOC quality. In turn, DOC quality refers to characteristics such as the sensitivity to photochemical or biological degradation (Jane and Rose 2018).

Quantifying lake color and DOC

Lake color can be measured in several different ways. Traditionally, water color was measured in Platinum Cobalt units (and still is measured this way regularly, for example in the US EPA National Lakes Assessment program). Another, more contemporary method, is measuring water color by spectrophotometry. Using this method, lake color is typically characterized by absorbance at 440 nm. Other optical indices, such as the change in absorbance per wavelength (called "spectral slope") can provide additional information on DOC quality such as information on the source and past light exposure of the organic matter (Williamson et al. 2014).

Meanwhile, DOC content is typically measured using a total organic carbon analyzer after filtration to remove particulates. Often, color and DOC content closely correlate, but there are some reasons why they do not always correlate. For example, iron absorbs light and can contribute to dissolved absorbance without contributing to DOC content, thereby affecting the DOC:color ratio.

What causes lake browning?

It has convincingly been demonstrated that browning occurs as inland water bodies recover from previous decades of acidification. While other drivers are also plausible, lakes in regions that are historically downwind of large sources of atmospheric pollution (e.g., coal power plants) such as in the northeastern U.S. and Northern Europe were sensitive to acidification and many waterbodies in these regions are undergoing contemporary browning (Monteith et al. 2007) widespread increases in concentrations of dissolved organic carbon. Since the 1990s, policies such as the Clean Air Act Amendments in the U.S. have led to cleaner air, soil, and water.

Contemporary increases in pH and decreases in ionic strength closely correlate with observed trends in both color and DOC content in regions such as the Poconos in Pennsylvania and the Adirondacks in New York, U.S. In these regions, acidification was pervasive in part due to poorly buffered soils. These regions are now recovering. In the Adirondacks, for example, DOC has increased by about 0.5 mg per liter per decade over the period 1994-2012 (Figure 1; Leach et al. 2019). However, other anthropogenic changes may also contribute to browning in some regions. For example, climate-change induced increases in precipitation may facilitate increases in DOC loading from the terrestrial landscape, and recovery of forests in some regions may stimulate browning (Kritzberg 2017). In the longer-term, climate-changed induced increases in growing-season length may increase the amount of vegetation and thus carbon available for export to aquatic ecosystems. Thus, it is plausible that browning may continue for decades to come even after lakes fully recover from acidification, but perhaps at slower rates than have been observed.

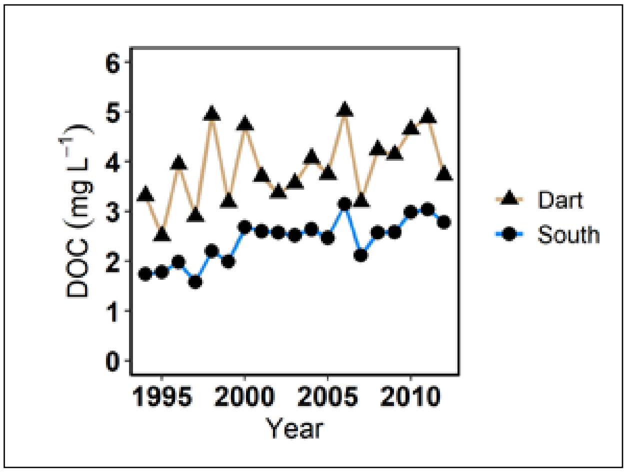

Figure 1. Mean annual summer (July, August, September) dissolved organic carbon (DOC) concentration for two lakes in the Adirondacks region. South Lake is denoted by a blue line and circles while Dart Lake is denoted by a tan line and triangles. South and Dart DOC increased at rates of 0.62 and 0.69 mg per liter per decade, respectively.

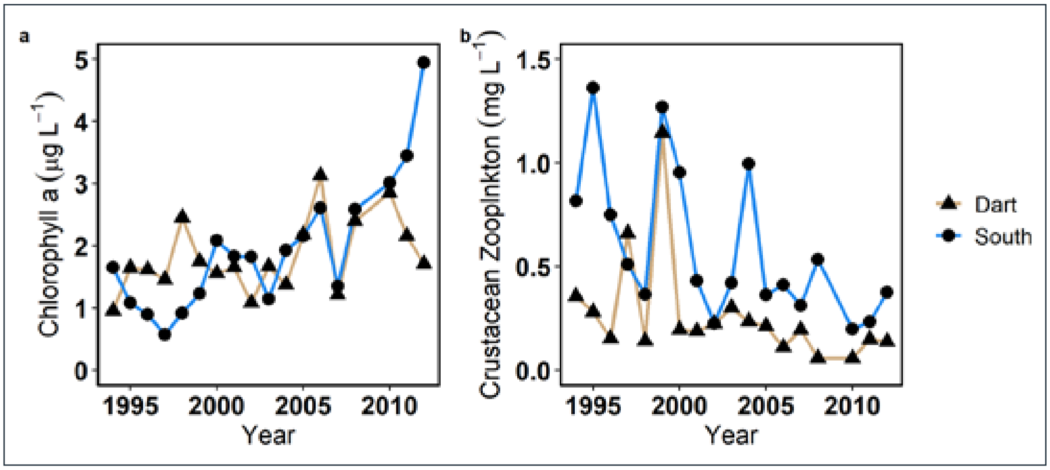

Figure 2. Mean annual summer (July, August, September) chlorophyll-a concentration (a) and crustacean zooplankton biomass (b) for two lakes in the Adirondacks. South Lake is denoted by a blue line and circles while Dart Lake is denoted by a tan line and triangles. South and Dart chlorophyll-a increased at rates of 1.56 and 0.48 µg per liter per decade, respectively. Zooplankton biomass declined at rates of -0.38 and -0.20 mg per liter per decade, respectively.

Concomitant with acidification-associated browning, many aquatic ecosystems are undergoing many other changes in water chemistry. For example, in the Adirondacks lakes have increased in pH and acid neutralizing capacity, and decreased in nitrogen, sulfate, calcium, and aluminum concentrations in recent decades. Most, if not all, of these water chemistry changes are driven by a decline in acid deposition, indicating that, at least chemically speaking, the lakes are recovering and browning is but one of many changes occurring. Some characteristics, such as declines in lake water clarity (as measured by Secchi disk depth) are directly attributable to lake browning.

Implications of browning for aquatic food webs

What are the implications of browning for lakes and the organisms that inhabit them? Short-term and cross-sectional surveys have been conducted to understand browning, but long-term changes may not be well-predicted from spatial surveys if the drivers of long-term change are not also important drivers of spatial variability. For example, spatial surveys show that limiting nutrient concentrations (e.g., nitrogen and phosphorus) are closely correlated with DOC content, but they are not through time. Unfortunately, there are few datasets to examine the long-term impacts of browning and other associated water chemistry changes on aquatic food webs.

One of the few such datasets that has monitored lake browning, phytoplankton, zooplankton, and many other water chemistry characteristics was collected 1994-2012 in the Adirondacks (Leach et al. 2018). In those lakes, chlorophyll concentrations were slowly increasing (Figure 2a) and there were no changes in phytoplankton biovolume. Meanwhile, zooplankton populations were in substantial decline (Figure 2b; median biomass decline >50 percent across 28 lakes). Similar zooplankton declines have also been observed in Pennsylvania, U.S. in lakes undergoing browning and acidification recovery (Williamson et al. 2016) multi-decadal studies that document the net ecological consequences of long-term browning are lacking. Here we show that browning over a 27-year period in two lakes of differing transparency resulted in fundamental changes in vertical habitat gradients and food web structure and that these responses were stronger in the more transparent lake. Surface water temperatures increased by 2-3 °C in both lakes in the absence of any changes in air temperature. Water transparency to ultraviolet (UV). Water chemistry changes other than lake browning regulated these food web changes. For example, calcium appears to be the primary regulator of zooplankton, as recovery from acidification has been associated with substantial declines in calcium and many lakes are now at levels below which many zooplankton taxa can survive. Additionally, aluminum is declining; in past decades high aluminum concentrations were toxic to fish, but fish recovery has been uneven, perhaps due to limited dispersal pathways.

Overall, many of the observed long-term food web changes that have occurred in Adirondack lakes are concomitant with browning, but likely not driven by browning itself. However, recovery from acidification, which stimulates lake browning as well as many other water chemistry changes observed, appears to be the single overarching driver of observed food web changes. The ultimate driver of browning – whether it be recovery from acidification, climate change, land use change, or something else – may ultimately regulate the overall magnitude and diversity of food web changes that are observed. In Adirondack lakes (e.g., Polliwog Pond, Figure 3), recovery from acidification is associated with a whole suite of water chemistry changes. In regions where climate or land-use change are responsible for browning lakes, it is likely that food web changes will be markedly different from those observed in Adirondack lakes. Only through further research and monitoring, including documenting long-term biological changes and concomitant water chemistry and quality changes, can we disentangle the complexities of browning to fully understand the linkages between the causes and food web consequences of lake browning.

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Figure 3. Author Dr. Rose and his son canoeing on Polliwog Pond in the Adirondacks (New York, U.S.). Pollywog Pond, like many lakes in the Adirondack region, has undergone browning in recent decades. The lake's brown color is visible in the lower foreground.

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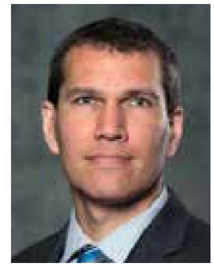

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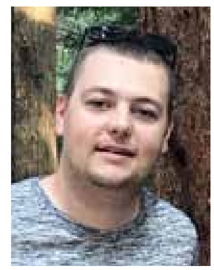

Jonathan Stetler is a Ph.D. student working with Dr. Rose at RPI. For his dissertation, Jonathan is studying the effects of increasing dissolved organic matter and climate on lakes.

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Terrestrially Derived Dissolved Organic Matter – Its Influence on Lake Food Webs

Christopher T. Solomon and Stuart E. Jones

Terrestrially derived dissolved organic matter (DOM) can profoundly influence life in lakes, from the primary producers at the base of the food web all the way up to the fishes. In this article we provide an overview of these influences, based on completed and ongoing research conducted by scientists across the lake-rich regions of the northern hemisphere. We find it to be a fascinating research area, because it incorporates many fundamental principles of lake ecology and because we are learning more about it all the time.

The effects of DOM on lake food webs are diverse and interconnected. The most visually apparent effect is on the penetration of sunlight through the water. Complex molecules common in terrestrially derived DOM absorb solar radiation at particular wavelengths. This gives the water a characteristic brownish tinge, just the way that tea leaves do to a cup of tea (Figure 1). A higher DOM concentration means more light absorption, and less light available at any depth in the water column of the lake. Absorption of sunlight by DOM also warms up the water, increasing surface water temperature and altering stratification patterns. DOM also has chemical and biological effects. For instance, it includes weak organic acids that can reduce pH, nutrients like nitrogen and phosphorus that benefit algae, and organic carbon compounds that can provide a source of energy to bacteria.

The base of the food web

When DOM reduces light penetration, the effects on algae – the primary producers at the base of the food web – can be profound. Consider first what reduced light penetration means for the benthic algae that live on the mud, rocks, and other surfaces at the bottom of the lake. While a tree in a forest might grow from the shade to reach the sun, these benthic algae are stuck in place, doing the best they can with the light they can capture. A reduction in light availability limits their ability to photosynthesize, reducing their productivity. If light levels are low enough, benthic algae may not be able to capture enough energy to keep ahead of their maintenance costs. Thus their total productivity across the lake as a whole decreases as both their productivity at any depth, and the range of depths over which they can persist, decrease.

For the pelagic (open water) algae that float in the water, the effects of DOM on productivity are more complex. These pelagic algae (also known as phytoplankton) experience the same reduction in light availability at a given depth that the benthic algae do. But they are also subjected to two counterbalancing effects of DOM that are unique to the pelagic habitat.

Figure 1. Samples from lakes spanning a gradient of terrestrial dissolved organic matter (DOM) concentrations.

The first of these counterbalancing effects is an increase in nutrient availability: Higher DOM concentrations are generally associated with higher concentrations of the nutrients that algae need for growth, like phosphorus and nitrogen. This matters for phytoplankton living in the water column, but is less important for benthic algae that can access nutrients oozing upward from rich lake sediments.

The second counterbalancing effect is a little harder to understand, but boils down to an interaction between light, heat, and mixing. Recall that higher DOM concentrations mean lower light availability at any depth, because DOM molecules absorb solar radiation. Like a black shirt on a sunny day, darker water not only absorbs light, but heats up in the process. In a high-DOM lake, therefore, the vertical distribution of heat tends to be weighted towards the surface – the epilimnion (upper water layer) is warm and thin, the thermocline (zone of temperature transition) is fairly shallow and sharp, and the hypolimnion (bottom layer) is cold and thick. For phytoplankton circulating throughout the epilimnion, the shallow extent of this layer can actually be good news: even though they experience less light at any given depth, the range of depths they are circulating over has been reduced. Under the right conditions, this may even mean that the average amount of light that they "see" in a day may not be much different than it would be in a lower-DOM lake (Figure 2).

What does this all mean for pelagic primary productivity? Recent research

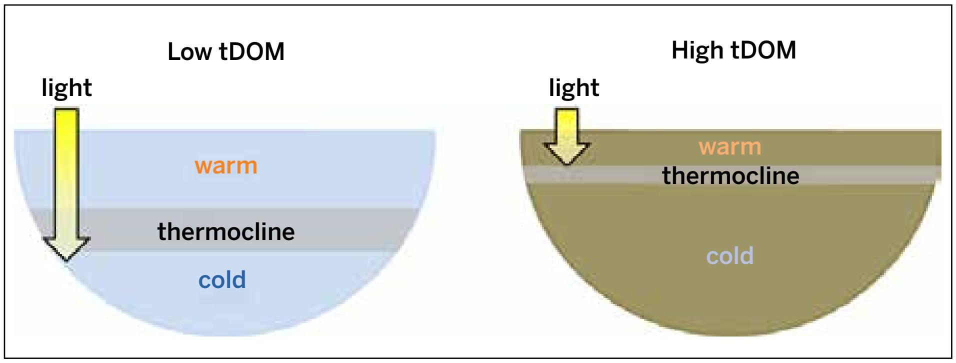

Figure 2. Contrasting depths of stratification in a clear (low tDOM) and brown (high tDOM) lake.

suggests that it follows a hump-shaped relationship with DOM concentration (Kelly et al. 2018; Figure 3). When DOM concentrations are very low there's plenty of light available in the water column, but nutrients are limiting and so primary productivity is low. At the other extreme, when DOM concentrations are very high there's very little light available, so primary productivity is low even though nutrients are plentiful. Somewhere in the middle there's a switch point where primary productivity is maximized. The DOM concentration at which this switch occurs is predicted to depend on the molecular characteristics of the DOM, which influence how much light it absorbs and how nutrient-rich it is. Lake size is also important, because in a large lake the depth of the thermocline is driven primarily by the wind, rather than by the effects of DOM on heat absorption.

Moving up the food web

The effects of DOM on light, heat, and the productivity at the base of the food web also influence organisms at higher trophic levels, like benthic invertebrates, zooplankton, and fishes. Several studies have documented relationships between DOM concentrations and the productivity, biomass, or individual growth of these groups.

These patterns presumably arise in large part from bottom-up limitation: control of primary productivity by DOM in turn limits the potential productivity of the organisms further up the food web that depend on that primary productivity. The bottom-up effects are strong enough to overwhelm the modest positive effects of DOM on food web productivity which occur when bacteria consume DOM and are in turn consumed by animals like zooplankton. There is even some evidence that the hump-shaped relationship between DOM concentration and pelagic primary production can be mirrored by the organisms that rely on that primary production. For instance, in one whole-lake experiment where a modest increase in DOM concentration led to an increase in pelagic primary productivity, the productivity of zooplankton increased as well (Kelly et al. 2016).

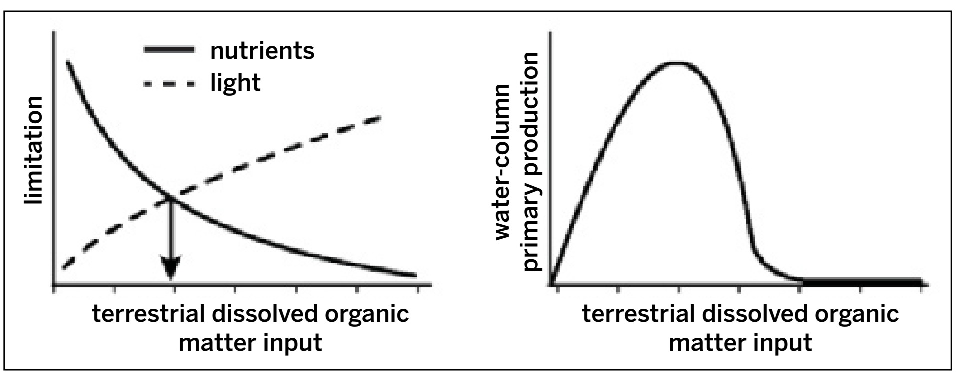

Figure 3. With low DOM input nutrient availability can be limiting and therefore productivity is low. At high DOM input levels light is severely limiting and productivity is also low. We expect the highest productivity at intermediate DOM input levels because neither nutrients nor light are extremely limiting. (Figure after Kelly et al. 2018.)

Other forces beside bottom-up limitation are also clearly at work in the relationship between DOM and animal populations in lakes. One study of benthic invertebrates from ten lakes that spanned a wide range of DOM concentrations showed that it was the effects of DOM on heat, rather than on primary production, that seemed to be most important for controlling productivity of this important group of lake organisms (Craig et al. 2015). Lakes with high DOM concentrations had shallower thermoclines and thus less of the warm, well-oxygenated bottom habitat that supports fast growth of benthic invertebrates. Other studies have demonstrated the ways in which DOM alters predation rates of fish on their prey via changes in the visible light environment (Jönsson et al. 2013), and the ways in which it alters rates of cellular damage in zooplankton via changes in the ultraviolet light environment (Wolf et al. 2016).

As these examples make clear, differences in DOM concentrations can impose strong differences on the environment and ecological interactions that organisms experience in lakes – the kinds of differences that might be expected to impose selective pressure on the traits of those organisms. One interesting new thread of research has begun to explore the potential for these sorts of eco-evolutionary dynamics. Reductions in the availability of benthic prey for fishes in high DOM lakes has been shown in several studies to drive a shift to higher use of pelagic prey. One such study documented systematic changes in the body shape of Eurasian perch inhabiting high DOM lakes when compared to those from low DOM lakes, including increased eye size and loss of habitat-specific morphologies (Bartels et al. 2016). Another study revealed that the time to maturity and investment in reproduction by bluegill sunfish changed dramatically across a set of lakes spanning a DOM concentration gradient, such that lifetime reproductive output of fish residing in high DOM lakes was significantly less than fish in low DOM lakes (Craig et al. 2017).

What does this mean for my lake?

Watershed inputs of DOM vary significantly from lake to lake and on a regional basis as a result of differences in land cover and climate. Depending on the amount of forest and wetlands surrounding a lake, as well as the size of a lake's watershed relative to its volume, the DOM concentration of lakes can vary over more than a factor of ten. However, most lakes, especially those that tend to have shoreline residential development, are low in DOM concentration and have relatively high water clarity unless excess nutrient inputs have resulted in eutrophication. Low DOM concentrations and high water clarity mean that supply of non-DOM-associated nutrients from a lake's watershed, often from human sources like fertilizer, dictate algal growth and growth of consumers, including fish. In contrast, lakes that have high DOM concentrations and low light availability are expected to have low food web productivity regardless of the level of nutrient supply.

Inputs of DOM can also vary across time. Inter-annual differences in precipitation can cause year-to-year differences in lake DOM concentrations, but many lakes across the northern hemisphere have shown long-term increases in DOM concentrations over the past four decades, a process referred to as lake browning (Monteith et al. 2007). Lake browning is thought to be driven by recovery of lake watersheds from acidification and because of changes in climate and land use. As a result, in regions historically impacted by acidification essentially all lakes are gradually increasing in their DOM concentrations, but regions with limited past effects of acidification have shown more heterogeneous long-term trends in lake DOM concentrations (Meyer-Jacob et al. 2019).

Although the diverse and important effects of DOM on lakes have been recognized for over a century, our current, synthetic understanding of how physical, chemical, and biological responses combine to impact lake food webs has only emerged recently as a result of a renewed focus on DOM in lakes driven by observations of global lake browning. The most important implication of recent work is that how a lake food web responds to increased DOM concentrations will depend on its current DOM concentration, as well as its size and shape. Lakes low in DOM are expected to see moderate increases in growth of phytoplankton and consumers that are able to make use of pelagic prey with increased DOM inputs. These increases will result from fertilization effects of nutrients associated with DOM. In contrast, lakes that are already high in DOM are more likely to see reductions in food web productivity both in the water column and benthic habitat because these systems are predominantly light-limited, rather than limited by nutrients, and more DOM means even less light availability.

Like many ongoing global changes, the causes of browning are diffuse and non-local. As a result, discrete, local actions are unlikely to alter long-term trends in inputs of DOM to lakes. Further, increases in DOM input to lakes in areas recovering from acidification actually represent a return to a less human-impacted state. This clouds the judgement of browning as a good or bad environmental change. Rather aquatic scientists and managers should focus on the implications of a new, browner world for the future use and management of aquatic resources, such as drinking water and fisheries.

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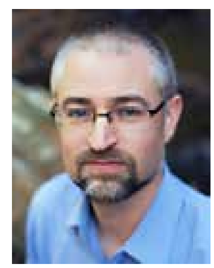

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Different Types **of Tea**

Keiko Wilkins

Importance of dissolved organic matter from a native and an invasive plant species in determining freshwater zooplankton success

The effects of increasing dissolved organic matter

Materials from terrestrial plants can have important impacts on organisms living within lakes. Lakes have been experiencing increases in dissolved organic matter (DOM) in the northeastern United States and western Europe. This DOM is often composed of brown, tea-colored substances (Figure 1) that can strongly impact a lakes' suitability as a habitat for organisms. DOM can alter both temperature and light due to its tea-colored materials that absorb light leading to warmer surface waters, stable thermal stratification, and alteration of the vertical gradients of dissolved oxygen and other chemicals (Solomon et al. 2015). These changes in habitat availability could have significant effects for freshwater zooplankton species that have specific temperature optima and tolerances to hypoxia (low oxygen) or anoxia (no oxygen). The complex roles of DOM in freshwater systems makes it difficult to determine the continued effects that it may have on aquatic organisms.

The effects of DOM on freshwater organisms has been widely debated with both beneficial and harmful effects suggested. It is thought that a unimodal relationship between DOM concentration and primary production (phytoplankton) helps to explain these contrasting results (Figure 2). At low DOM concentrations, positive effects are seen on primary production through the addition of nutrients to systems that are often nutrient-limited. However, at high DOM concentrations, negative effects are seen on primary production through the shading of visible light that is needed for photosynthesis. The concentration where DOM switches from the positive to negative effects appears to vary among systems. These effects are also thought to transfer to higher trophic levels such as zooplankton, an important consumer of planktonic algae and important prey for fish, and fish through effects on their food resources. However, DOM concentration does not appear to directly affect zooplankton, as they have been found to tolerate DOM at concentrations far above the proposed threshold concentrations (Nova et al. 2019). This raises questions about the potential importance of DOM quality that might be related to the origin of the DOM. Is DOM quality perhaps more important than DOM concentration?

Inputs of DOM into lakes include a diverse group of materials that originate from different types of terrestrial plants which are then partially broken down in the soils by microbes and sunlight before entering aquatic ecosystems (Solomon et al. 2015). The specific plant species from which the DOM is derived could have a strong influence on its possible effects on freshwater zooplankton. It has been found that not all terrestrial plant species have the same effects on algal or zooplankton abundance in wetlands (Stoler and Rylea 2011), suggesting that this may also be true in lakes. For my thesis research, I tested the hypothesis that the effects of DOM on zooplankton varies with the

Figure 1. Dissolved Organic Matter (DOM) derived from a variety of plant sources with different colors of tea seen from the different plant species compared to distilled water. Photo: Craig Williamson.

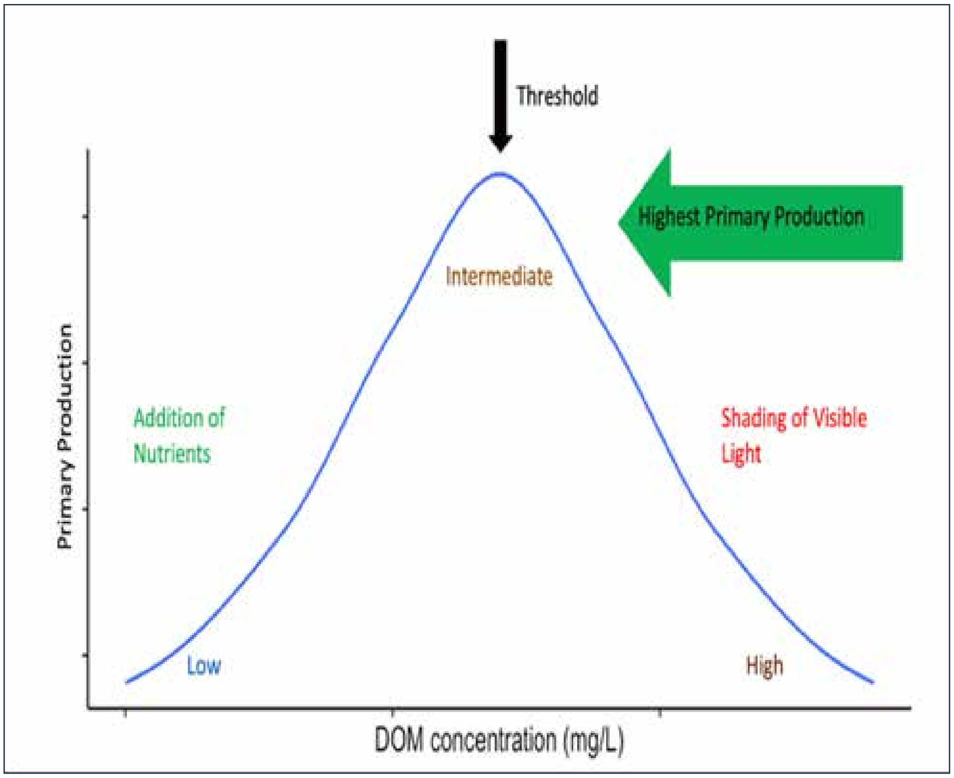

Figure 2. Unimodal relationship between DOM concentration and primary production where the relationship between DOM concentration and primary production is positive (green) at low DOM concentration below a threshold DOM concentration and negative (red) at high DOM concentrations above the threshold.

source of the plants from which it is derived.

The importance of DOM source

Both red maple (*Acer rubrum*), a native plant species and Amur honeysuckle (*Lonicera maackii*), an invasive plant species are common in forests in the eastern United States and contribute DOM inputs into aquatic systems. Amur honeysuckle is known to have only a few herbivore predators (McNeish and McEwan 2016). In addition, negative effects of Amur honeysuckle have been found on both terrestrial and aquatic organisms. In the terrestrial environment, Amur honeysuckle contains important plant secondary compounds used for plant defenses to deter herbivores and suppress germination of native plant species and aide in its invasion. Due to the highly successful invasion of Amur honeysuckle, the riparian zone of streams can become near monocultures with potentially significant negative effects on aquatic biota. In streams, DOM derived from Amur honeysuckle has been found to reduce amphibian larvae survival likely due to harmful compounds in the Amur honeysuckle leaves (McNeish and McEwan 2016). In contrast, red maple did not have any negative effects on algal or zooplankton abundance in wetlands (Stoler and Rylea 2011). This suggests that Amur honeysuckle may have more direct negative effects on freshwater zooplankton than red maple.

For my research I used juvenile *Daphnia* (Figure 3), an important zooplankton grazer, in a series of bioassays to explore the importance of the source of the DOM in determining the survival and growth of zooplankton. Juvenile *Daphnia* were exposed to DOM derived from either red maple or Amur honeysuckle leaves in the presence or absence of algae for five days. I hypothesized that DOM derived from Amur honeysuckle would have a more negative effect on *Daphnia* survival and growth than DOM derived from red maple. In contrast with expectations, I found that DOM derived from Amur honeysuckle had only indirect negative effects on growth through decreasing *Daphnia*'s food source (phytoplankton), while red maple had direct negative effects on *Daphnia* survival and even greater indirect negative effects than Amur honeysuckle on growth. Plant secondary compounds used to defend plants from herbivores could explain the direct negative effects of red maple on *Daphnia* survival. Both Amur honeysuckle and red maple likely decreased growth rates due to phytotoxicity reducing their phytoplankton resources. Phytotoxicity occurs in DOM when the derived plant species have high DOM concentrations, and high C:N ratios which are associated with plant secondary compounds. These secondary compounds include phenols, quinones, and lignin phenols which can act as natural biocides (Nielen et al. 2017).

Implications for management

My research stresses the importance of considering the composition of the terrestrial plant community surrounding a freshwater system when considering lake management. The terrestrial environment can play a key role in determining what is happening in aquatic systems. DOM derived from terrestrial plants can have negative effects on *Daphnia*, which are important consumers of phytoplankton that can help control algae blooms. In addition, invasive plant species in terrestrial environments have the potential to strongly impact aquatic systems. The plant source and chemical composition of DOM is an important determinant of the effects DOM will have on freshwater biota.

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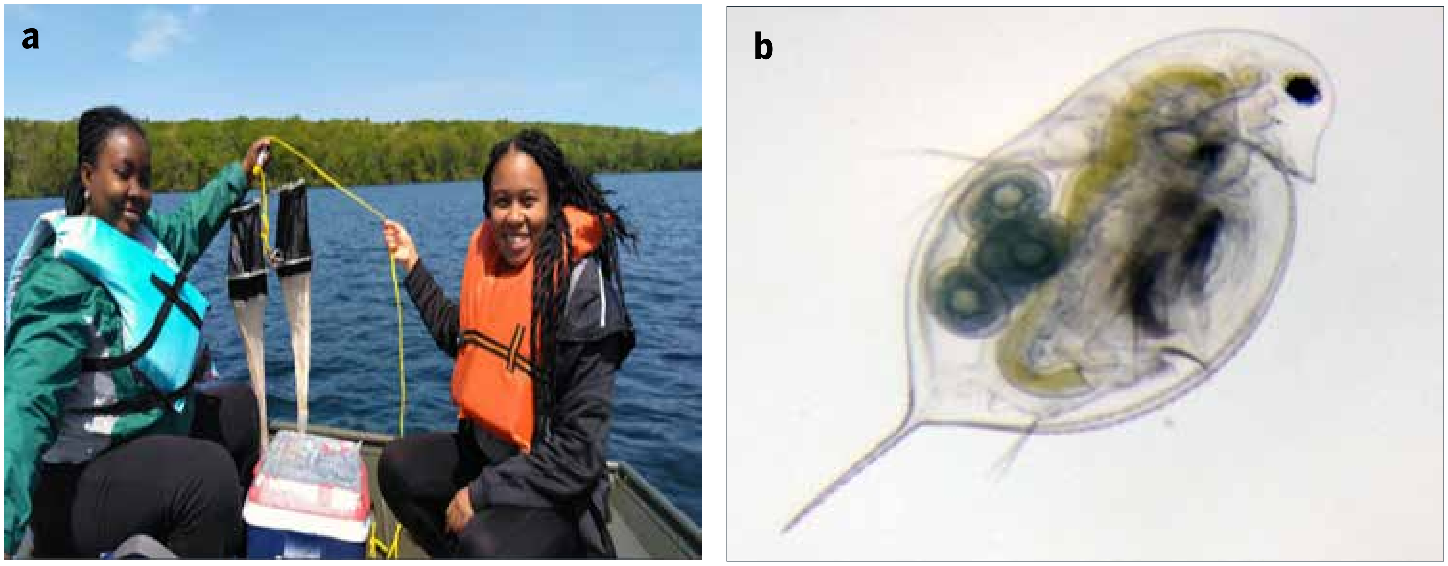

Figure 3. (a) Miami University graduate students Oluwaseun Olubodun (left) and Keiko Wilkins (right) collecting zooplankton from Lake Lacawac, Pennsylvania, USA (b) Daphnia an important zooplankton grazer of primary production and prey for fish.

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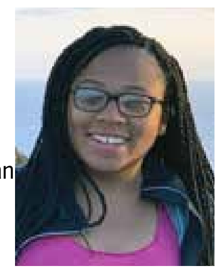

Keiko Wilkins is a recent graduate of Miami University (Oxford, Ohio). She completed both her bachelor's of science and master's of science with an applied statistics certificate from Miami University. Since completing her master's thesis research project looking at the effects of dissolved organic matter on freshwater zooplankton, she has transitioned to Southern Cross University (Lismore, Australia), where she is taking part in the Association for the Sciences of Limnology and Oceanography: Limnology and Oceanography Research Exchange. Her research there will focus on the effects of climate change on coral reef feeding rates.

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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

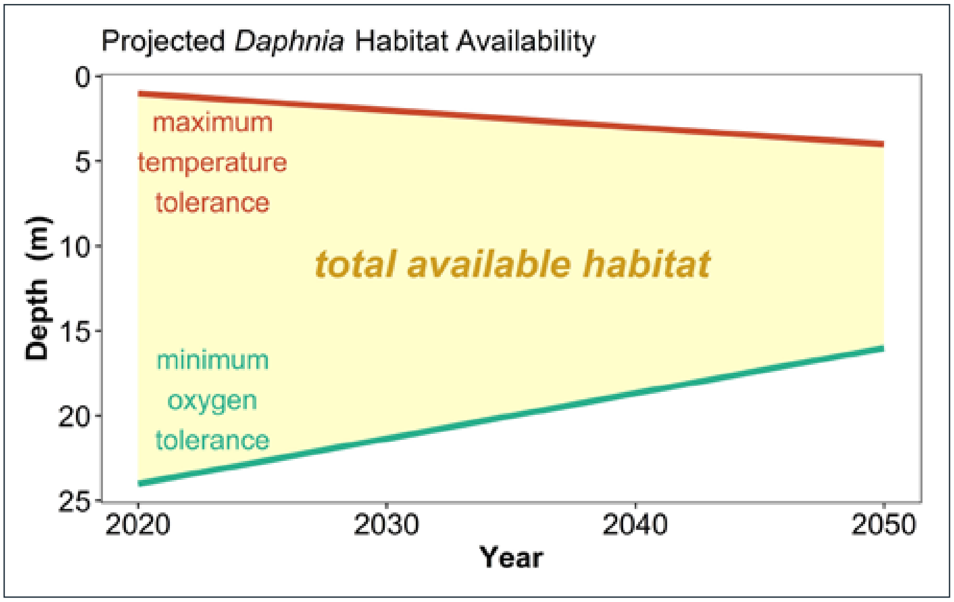

Figure 1. Projected vertical habitat availability for Daphnia *under continued lake browning (yellow), where maximum thermal tolerance (red) will limit the upper habitat range, and minimum oxygen tolerance (green) will limit the lower habitat range.*

(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

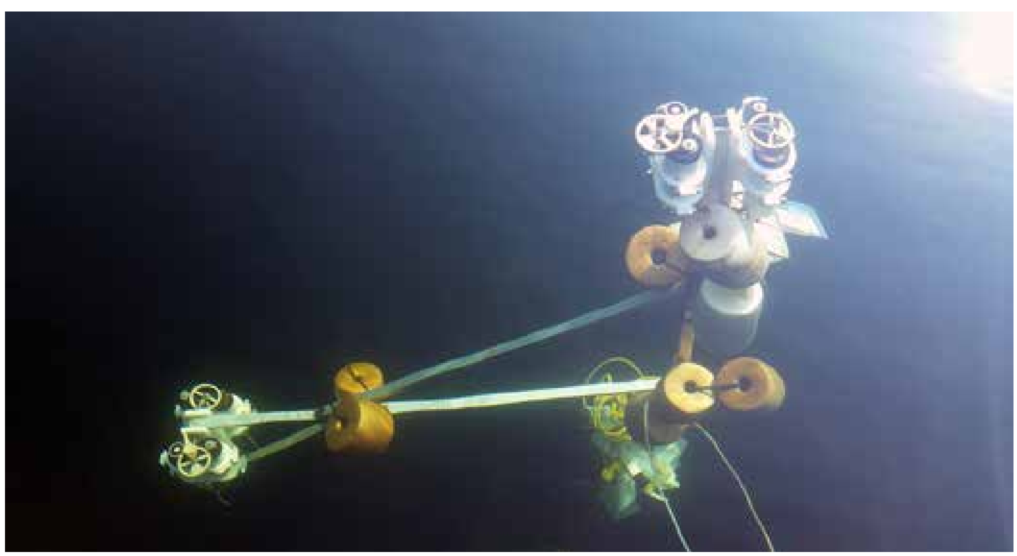

Figure 2. Photo of the underwater sensor set-up that includes high-frequency sensors measuring temperature, dissolved oxygen, and, more recently, visible light and dissolved organic matter.

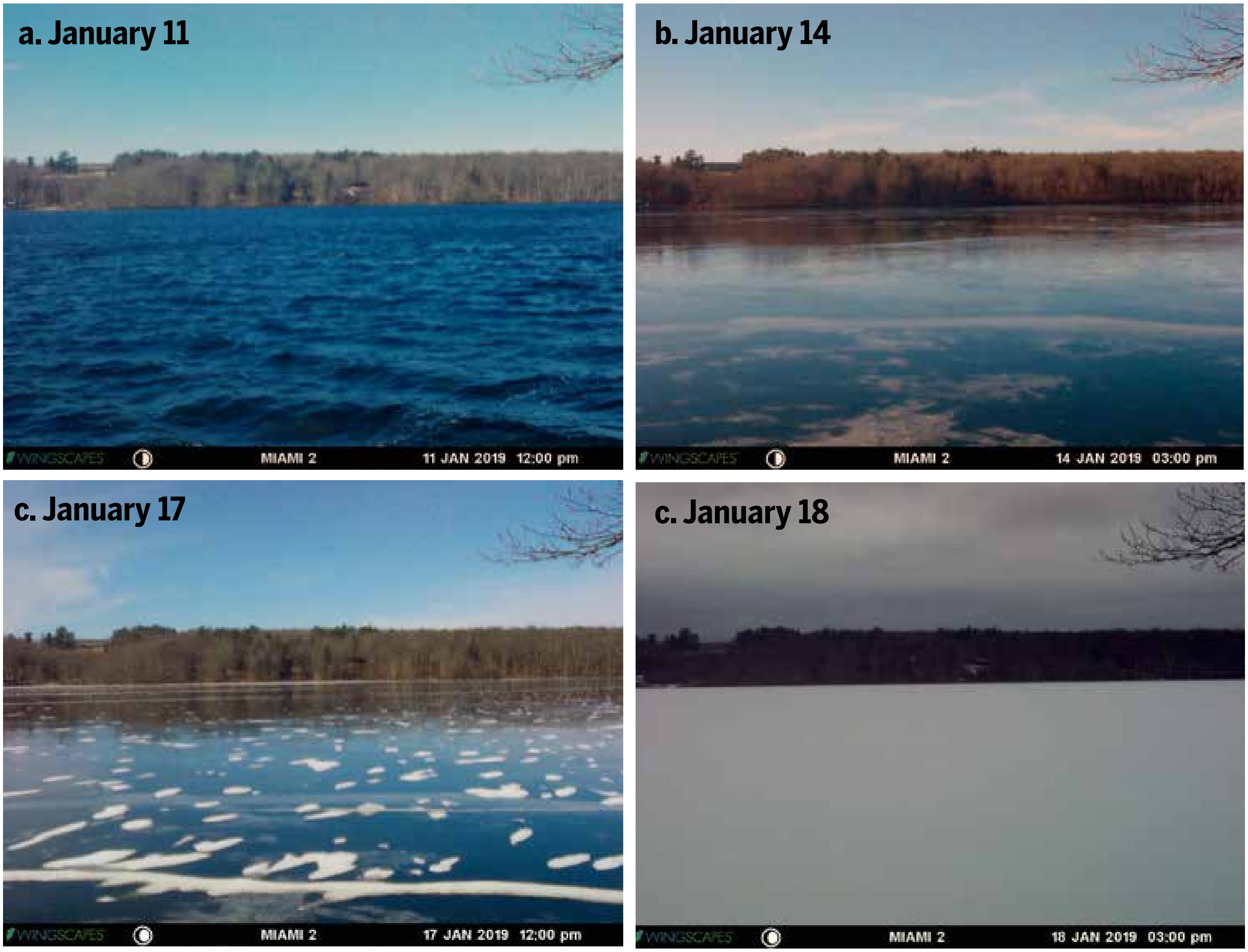

Figure 3. Time-lapse photos during winter 2018-2019 showing the formation of ice cover over the course of one week (January 11 through January 18). Deep water oxygen depletion tends to begin shortly after ice freezes (b).

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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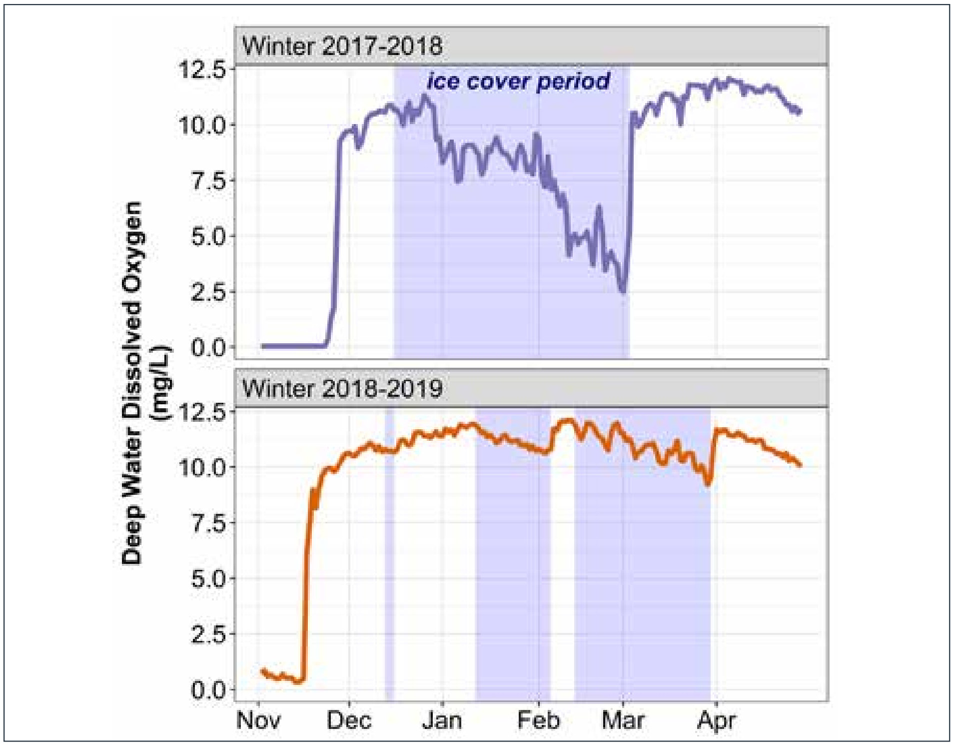

Figure 4. Comparison of deep water dissolved oxygen data between two contrasting winters. Top panel shows the winter of 2017-2018 that had one long period of ice cover from mid-December through early March (highlighted in blue). Bottom panel shows the milder winter of 2018-2019 that had several periods 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.

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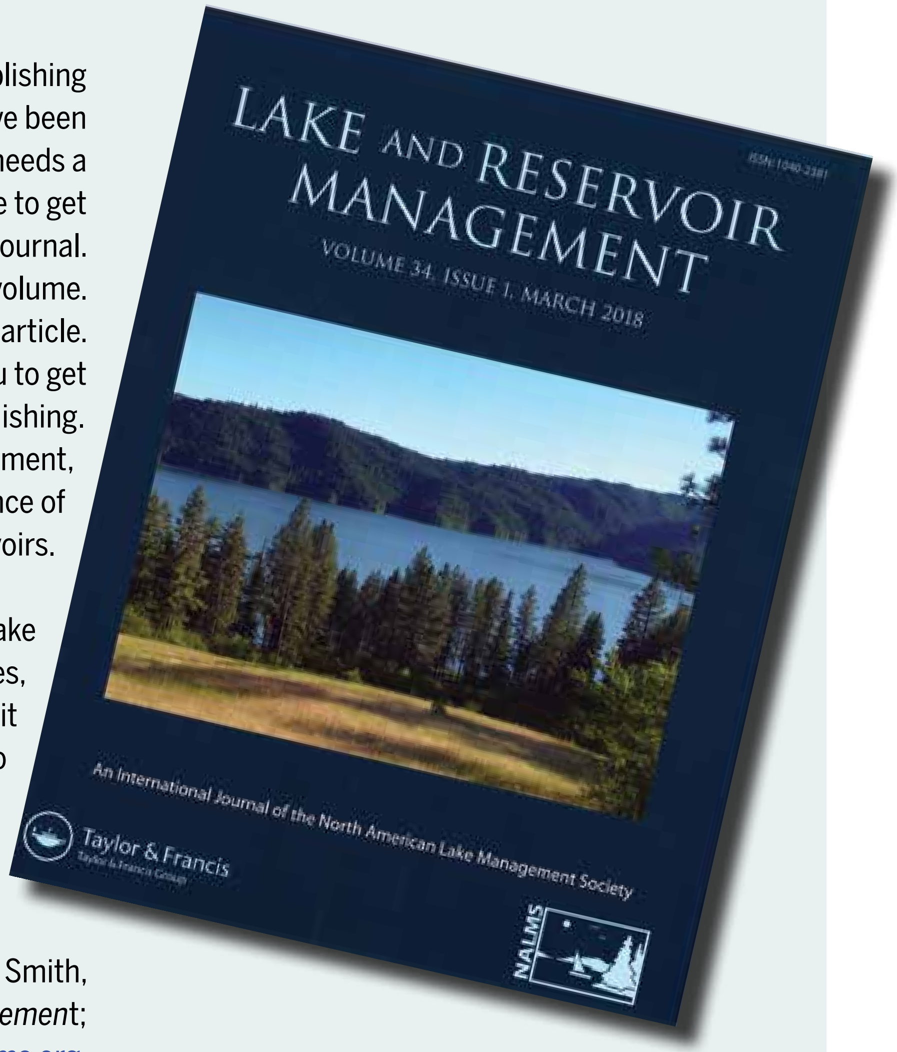

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