PROJECT SUMMARY

Overview:

Over nearly four decades, the North Temperate Lakes (NTL) LTER program has pursued a goal of understanding the long-term ecosystem dynamics of lakes and their surrounding landscapes. Lakes are charismatic landscape elements that provide a wide range of ecosystem services and are ideal study systems due to their integrative nature. Anthropogenic changes are becoming increasingly apparent in these systems, often as abrupt and substantial shifts in ecosystem structure and function that are viewed negatively by lake users. New research activities will build on a strong foundation of long-term observations and deep ecological understanding to address the overaching question: What are the causes and consequences of abrupt ecological change in lakes and their surrounding landscapes? To address this question, research activities will be organized around four central questions.

Climate variability and lake phenology: What are lake phenological responses to a warmer and more variable climate that may lead to abrupt ecological change?

Interacting drivers and abrupt change in urban aquatic ecosystems: How do interactions of land use/land cover and long-term climate change affect urban aquatic ecosystems?

Interacting drivers and water quality: How do external drivers interact with aquatic invasive species to regulate water quality?

Managing for abrupt change in whole-lake experiments: What causes intentional ecosystem manipulations to persist, revert, or lead to novel states?

We will pursue a series of interrelated research in two regions of Wisconsin, the forest- and lake-rich Northern Highlands Lake District (NHLD) and the Yahara Lakes District (YLD) where agriculture and urban land cover dominates. Our research integrates multiple approaches, including the collection and analysis of long-term data, comparative studies, experiments ranging from small-scale to whole-ecosystem, simulation and statistical modeling, and ecological synthesis. These activities combine terrestrial, aquatic, and atmospheric perspectives, and consider physical, chemical, biological processes across multiple spatial and temporal scales.

Intellectual Merit:

The set of proposed research activities organized around a central framework of abrupt ecological change provides our interdisciplinary research group with unique opportunities to elucidate mechanisms that have led to abrupt ecological changes within lakes in the past, or may lead to such shifts in the future. These efforts are facilitated by being able to draw on multiple long-term observations across a diverse set of lakes, and a strong foundation of research on ecosystems. Further, given that the potential for large and sudden ecosystem change is increasing globally as rates of environmental change accelerate, we will test, modify, and expand hypotheses regarding the causes and consequences of abrupt ecological change that are broadly relevant across diverse ecosystems.

Broader Impacts:

Ecological changes such as species invasions, disappearance of favored sport fish, or occurrences of harmful algal blooms attract substantial public attention. This provides us with an opportunity and responsibility to understand why these events are occurring, to share this understanding broadly, and increase awareness of lakes and environmental change in a rapidly changing world. NTL will continue to build bridges with lake managers, institutions, and other stakeholders concerned with the health of our lakes. In addition to training undergraduate and graduate students, NTL sponsors a host of outreach activities, ranging from K-12 programs, to building public understanding of our inland waters through science communication, to an innovative artist-in-residence program. Underpinning all of these activities are NTL efforts to promote diversity and inclusivity in science.

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RESULTS FROM PRIOR SUPPORT

Research Results: The North Temperate Lakes (NTL) LTER site began in 1981 with a goal of studying long-term dynamics in 7 lakes in Wisconsin's Northern Highlands Lake District (NHLD) and understanding how landscape position shapes these dynamics. The site expanded to include 4 lakes in the Yahara Lake District (YLD) in southern Wisconsin in 1994, adding a regional-scale approach to our long-term science. NTL research spans multiple disciplines and addresses questions relevant to basic ecological theory and policy and management challenges. Over the last 6 years, research activities were organized around 4 questions:

> **Perception of Long-Term Change**: *How and why have the lake districts changed, and how will they change in the future*?
> **Climate as a Driver of Long-Term Change**: *What are the mechanisms of physical and ecological responses of lakes to a changing climate?*
> **Dynamics of Heterogeneity**: *What are the long-term patterns, causes, and consequences of spatial heterogeneity in lakes and landscapes?*
> **Shocks, Shifts, and Compensatory Responses**: *How and when do extreme events and multiple drivers cause ecosystem transitions?*

We present brief summaries of representative results for each theme drawn from 250 NTL articles from 2014-present that have already been cited >7000 times, as well as 7 M.S. theses, 15 Ph.D. dissertations, and 136 new or updated datasets (Table S1). Bolded citations refer to Top 10 papers (Table 1).

Perception of long-term change: This first theme involved the collection, management, and analysis of long-term lake data. NTL has collected, curated, and made publicly available ca. 60 datasets that span >30 years in the 5 LTER core areas. These data are among the most complete multi-year, multi-lake, open-access datasets in the world and provide the foundation for understanding long-term change in lakes and their surrounding landscapes (Magnuson et al. 2006). Roughly 50% of NTL-related articles published since 2014 use some of these data, including several that use NTL time series exclusively (e.g., **Batt et al. 2017**; Powers et al. 2017a, b) or in cross-site analyses (e.g., **Hampton et al. 2017**; **Sharma et al. 2019**). The value of these data is also reflected in its increasing use by non-NTL researchers, and we have conservatively identified 27 publications since 2014 written by unaffiliated authors.

Climate as a driver of long-term change: Understanding effects of climate on lakes has been a long-standing NTL research theme. Over the previous 6 years, we focused on lake physical responses to warming and the ecological consequences of these changes. Pursuit of both topics share a pattern of first conducting within-lake studies to understand mechanisms followed by generation of larger data sets (e.g., Sharma et al. 2015; Winslow et al. 2017a) and development/improvement of process-based models, especially GLM-AED2 (e.g., Read et al. 2016; Winslow et al. 2016; Bruce et al. 2018) to address regional and global-scale questions. These latter activities have been collaborative cross-site efforts that involved graduate student training with NTL researchers and alumni providing leadership. We are major partners in the development of a hydrodynamic-water quality simulation model that has gained broad community acceptance (Hipsey et al. 2019), and in techniques that pair process-based model with machine learning to extract maximum information from long-term and broad-scale lake data (Read et al. 2019).

Changing lake physics- Detailed studies of NTL lakes revealed changing ice cover phenology and thermal structure, including oscillatory warming and cooling phases over the last century (Lathrop et al. 2019). Surface warming is coupled with deep layer cooling due to increased strength and duration of thermal stratification (Magee & Wu 2017b). In Lake Mendota, warming has led to stepped increases in the stratified period of ca. 1 month over the last century (Magee et al. 2016). Site-based studies have also emphasized the individuality of lake responses to warming; for example, the larger, deeper NTL study lakes Fish and Mendota experienced more thermal variability and are predicted to have more ice-free days in response to warming relative to the smaller, shallower Lake Wingra (Magee & Wu 2017a). Expanding from this site-based work to broader spatial scales via modeling and larger data sets confirmed the individuality of lakes; distinct responses of thousands of lakes to warming are modulated by interactive effects of lake surface area, depth, and water clarity (Winslow et al. 2015, 2017b; Rose et al. 2016). Regardless of among-lake differences, lakes around the world are warming (O'Reilly et al. 2015). Approximately 20% of lakes are expected to have a shift in their mixing regime (D.P. Hamilton et al. 2018; Woolway et al. 2019), ice duration may decrease by ca. 1 month over the next 50 years (Hewitt et al. 2018), and 20-200K more lakes in the northern hemisphere are likely to have intermittent ice cover in the decades to come (**Sharma et al. 2019**).

Ecological consequences- Changes in temperature, stratification, and ice duration have many ecological consequences for lakes (**Hampton et al. 2017**). For example, nitrate accumulates in direct proportion to ice duration, so spring nitrate concentrations are low following short winters (Powers et al. 2017b). For carbon, modeling metabolism using 10 years of data from 6 lakes showed most lakes shift between being C sources and C sinks, with most lakes acting as net sources during warmer summers due to an increase in respiration relative to burial of organic matter (McCullough et al. 2018). The importance of lakes in C cycling also motivated us to evaluate approaches for estimating CO_2 fluxes, including calculating pCO_2 from carbonate equilibria (Golub et al. 2017), gas transfer velocity models (Dugan et al. 2016), and techniques for quantifying whole-lake CO_2 fluxes (Baldocchi et al. in review; Reed et al. 2018).

In Wisconsin, one effect of climate change that attracts substantial public interest is the consequence of lake warming on coldwater fishes. Cisco (*Coregonus artidi*) is a coldwater sentinel species and in productive lakes, they are susceptible to a phenomenon known as 'oxythermal squeeze,' in which their habitat gets compressed from above by warming and from below by increased hypolimnetic anoxia. This process is becoming more pervasive in Wisconsin lakes as they warm (Lyons et al. 2018; Magee et al. 2018, 2019a). Warming is also one of the causes of a rapid decline in walleye (*Sander vitreum*), a highly prized gamefish, and an increase in black bass (*Micropterus spp.*) in northern Wisconsin (Hansen et al. 2015; Rypel et al. 2018). Modeled future thermal conditions for 2148 lakes suggest a loss of walleye from 33–75% of systems where recruitment is currently supported and a 27–60% increase in lakes suitable for high bass abundance over the next 50-75 years (Hansen et al. 2017).

Dynamics of heterogeneity: Describing and understanding the drivers of heterogeneity among lakes is a second long-standing NTL theme that originated with studies of lakes in the landscape (Magnuson et al. 2006). Recent questions expanded on the original landscape frame of reference to investigate (1) landscape-scale heterogeneity in temporal dynamics (i.e., synchrony); (2) the causes and consequences of heterogeneity in urban watersheds; and (3) spatial heterogeneity within individual water bodies.

Long-term patterns in lake water clarity- Water clarity reflects the biogeochemical environment of a lake, regulates photosynthesis and activities of visual predators and prey, and can be measured easily and accurately in the field or determined via remote sensing. At regional scales, synchrony in water clarity among lakes was not spatially structured (Lottig et al. 2017) but was responsive to a mixture of lake and watershed features. The significance of these drivers was modulated by precipitation or, more simply, the degree of heterogeneity in regional lake water clarity was influenced by a dynamic interaction between land cover/land use and climate (Rose et al. 2017).

Heterogeneity in urban watersheds- Through past and ongoing work, we have learned a great deal about the connections between lakes and land use/land cover in forested and agricultural settings. In the 2014 funding cycle, we broadened our scope to include urban landscapes, a theme that we will pursue further over the next 6 years. To begin to understand how lakes are affected by increasing urban land cover, we focused on heat and water movement in Madison's heterogeneous urban environment. Madison's urban heat island has been monitored via a dense network of 150 temperature sensors since 2012 (Schatz & Kucharik 2015, 2016), and recent studies examined the relationship between urban heating and trees. To maximize the daytime cooling effect of trees, at least 40% canopy cover is necessary at a scale of a typical city block (60-90m); however, reducing impervious surfaces is needed to lower nighttime temperatures (**Ziter et al. 2019**). And while patches of urban forest can create cooler zones within the city, their exposure to warmer temperatures increases the growing season length (Zipper et al. 2016) and affects urban hydrology by increasing evapotranspirational demands (Zipper et al. 2017a). Flashiness typical of urban streams is also apparent in lake water levels (Usinowicz et al. 2017) and causes increased flood risk (Zipper et al. 2018). Within Madison's residential areas, high surface runoff is driven by large areas of paved surfaces and compacted soils characteristic of both the oldest and newest neighborhoods in Madison (Ziter & Turner 2018; **Voter & Loheide 2018**), and at the scale of the whole city, differences in amount and connectivity of impervious surface features has created a complex hydrologic landscape of varying amounts of surface runoff and deep drainage (**Voter & Loheide 2018**).

<u>Heterogeneity within individual water bodies</u>- Within individual lakes, limnologists have long been aware of spatial variability in physical, chemical, and biological conditions. However, quantifying this heterogeneity is difficult, as manual sampling is labor-intensive and remotely sensed images have limits on the lake size, spatial resolution, frequency, and attributes that can be measured reliably. To address many of these challenges, we developed the Fast Limnology Automated Measurement (FLAMe) platform to generate detailed maps for multiple water quality variables (**Crawford et al. 2015**). Use of the FLAMe has allowed us to determine lake attributes associated with pronounced within-lake heterogeneity (Loken 2018), and identify CO_2 and CH_4 hotspots in streams and lakes (Crawford et al. 2017; Loken et al. 2019), areas receiving high salt inputs and with fecal coliform activity (Stadler et al. 2019), and where algal blooms may first appear. Butitta et al. (2017) used the FLAMe to illustrate changes in spatial patterning of phycocyanin (a measure of cyanobacterial abundance) in advance of bloom onset, suggesting that spatial data could be used as an advanced signal of cyanobacterial blooms. Detailed spatial data were also used to improve the accuracy and certainty of estimates of processes such as nitrogen retention, whole-lake CO_2 and CH_4 fluxes, and primary production (Loken et al. 2018, 2019; Schramm 2018).

Shocks, shifts, and compensatory responses: This thematic area was motivated by changes in some drivers (rainfall regimes, land use management) and emergence of new drivers (new water quality policies, invasive species). In the last 6 years, these changes were particularly conspicuous in YLD lakes. Here (as in most lakes), water quality is shaped by phosphorus (P) inputs, and reduction of non-point P sources continues to be a management priority. Despite major management investments, P loading has not declined (**Carpenter et al. 2018**). Causes for this lack of change include dairy intensification, shifts towards more erosive row crops, urban expansion, and increasing frequency of heavy rainfall (Gillon et al. 2016). Approximately 75% of the annual P load occurs during <30 days per year (Carpenter et al. 2015, **2018**). With continued climate change, P yields are likely to increase as a large stock of legacy P in soils erodes into surface water (**Motew et al. 2017**, 2018), and reduces ecosystem services. However, there are pathways forward to sustain future ecosystem services (Qiu et al. 2017, 2018). Finally, a key practical success of these and other allied efforts was the integration of 3 synergistic models: (1) Agro-IBIS – a dynamic model of terrestrial ecosystem processes, biogeochemistry and water balance (**Motew et al. 2017**, 2018); (2) THMB, an aquatic biogeochemistry and large-scale hydrology model (Chen et al. 2019); and (3) a Yahara Water Quality Model (YWQM; Carpenter & Lathrop 2014).

While water quality is strongly affected by P loading, grazing by zooplankton also influences water clarity and algal blooms in lakes. The spiny water flea *Bythotrephes longimanus* invasion of Lake Mendota in 2009 provided unique insights into the role of grazing on water quality. Invasion led to a 60% decline in biomass of the dominant grazer *Daphnia pulicaria*, which reversed a long-standing trophic cascade and caused a ~30% reduction in water clarity (**Walsh et al. 2016a**, 2017, 2018a). Offsetting the loss of water clarity associated with *Bythotrephes* would require a ~ 70% reduction of current P loading at an estimated cost of ~$100 million (**Walsh et al. 2016a**). The abrupt changes caused by *Bythotrephes* led to questions about the seemingly sudden arrival of this and other invaders. A paleolimnological study revealed that *Bythotrephes* existed as a low-density ‘sleeper population’ for over a decade until their 2009 outbreak when suitable environmental conditions allowed a rapid population increase (Walsh et al. 2016b). This result inspired subsequent studies, including (1) empirical and theoretical analyses on detection of low-density invasive populations (Walsh et al. 2018b, 2019b); (2) development of a conceptual framework for translating site-specific impacts to the landscape scale (Vander Zanden et al. 2017; Latzka et al. 2016); and (3) tracking new invaders to the YLD.

Additional Research Activities: The NTL Microbial Observatory maintains a DNA sequencing time series database (>18 years) in 3 core study lakes and the largest freshwater metatranscriptome dataset to date (Linz et al. 2020). These datasets have been used to study the structure, drivers of change, and biogeochemical capacities of microbial communities. This included a characterization of the core bacterial community and its inter-annual dynamics (**Linz et al. 2017**) and using long-term data to predict short-term change (Herren & McMahon 2017). Long-term metagenomics data were used to infer the physiology of major bacterial groups from 193 population genomes (Linz et al. 2018) and ecophysiological differentiation within the freshwater Actinobacteria (J.J. Hamilton et al. 2017). Several high-profile studies in collaboration with the Joint Genome Institute on freshwater viruses were also completed (Schulz et al. 2020; Chen et al. 2019; Roux et al. 2017; Paez-Espino et al. 2019).

Cross-site activities- NTL members continue to lead and be active in a range of cross-site activities within and beyond the LTER network. Gries and Hanson lead the Environmental Data Initiative (EDI) grants and provide essential IM support for many sites. Other activities include: contributing to the art-science collaboration “Ecological Reflections” (Swanson 2015) and participation in several cross-site projects on themes such as LTER-NEON synergies (Jones et al. in prep), future ecosystem trajectories (Cowles et al. in review), temporal community dynamics (Collins et al. 2018), under-ice lake ecology (**Hampton et al. 2017**; Powers et al. 2017a, b), climate change impacts in Wisconsin (Magee et al. 2019a), and a plethora of working groups associated with the Global Lake Ecological Observatory Network (GLEON) (e.g., Björnerås et al. 2017; Bruce et al. 2018; Dugan et al. 2017; Leach et al. 2018).

Table 1. Top 10 NTL Publications since 2014. Student authors underlined.

1. Batt, R.D., S.R. Carpenter, A.R. Ives. 2017. Extreme events in lake ecosystem time series. Limnology and Oceanography Letters 2: 63-69.

2. Carpenter, S.R., E.G. Booth, C.J. Kucharik. 2018. Extreme precipitation and phosphorus loads from two agricultural watersheds. Limnology and Oceanography 63: 1221-1233.

3. Crawford, J.T., L.C. Loken, N.J. Casson, C. Smith, A.G. Stone, L.A. Winslow. 2015. High-speed limnology: using advanced sensors to investigate spatial variability in biogeochemistry and hydrology. Environmental Science & Technology 49: 442-450.

4. Hampton, S.E., A.W.E. Galloway, S.M. Powers, et al. 2017. Ecology under lake ice. Ecology Letters 20: 98-111.

5. Linz, A.M., B.C. Crary, A. Shade, S. Owens, J.A. Gilbert, R. Knight, K.D. McMahon. 2017. Bacterial community composition and dynamics spanning five years in freshwater bog lakes. mSphere 2:e00296-17.

6. Motew, M., X. Chen, E.G. Booth, S.R. Carpenter, P. Pinkas, S.C. Zipper, S.P. Loheide, II, S.D. Donner, K. Tsuruta, P.A. Vadas, C.J. Kucharik. 2017. The influence of legacy P on lake water quality in a Midwestern agricultural watershed. Ecosystems 20: 1468–1482.

7. Sharma, S., K. Blagrave, J.J. Magnuson, C.M. O’Reilly, S. Oliver, R.D. Batt, M.R. Magee, D. Straile, G.A. Weyhenmeyer, L. Winslow, R.I. Woolway. 2019. Widespread loss of lake ice around the Northern Hemisphere in a warming world. Nature Climate Change 9: 227-231.

8. Voter, C.B., S.P. Loheide. 2018. Urban residential surface and subsurface hydrology: Synergistics effects of low-impact features at the parcel scale. Water Resources Research 54: 8216-8233.

9. Walsh, J.R., S.R. Carpenter, M.J. Vander Zanden. 2016a. Invasive species triggers a massive loss of ecosystem services through a trophic cascade. Proceedings of the National Academy of Sciences of the United States of America 113: 4081-4085.

10. Ziter, C., E.J. Pedersen, C.J. Kucharik, M.G. Turner. 2019. Scale-dependent interactions between tree canopy cover and impervious surfaces reduce daytime urban heat during summer. Proceedings of the National Academy of Sciences of the United States of America 116: 7575-7580.

Information Management (IM) and Data Availability: IM continues to be a priority and essential to our success in long-term ecological research. A priority is archiving and publishing and making discoverable all incoming data on a timely basis and with high quality metadata in our data repository and EDI. The demand for data publishing has increased during the last funding cycle due to journal and agency requirements. NTL IM is constantly adapting to handling new data types and larger amounts of data and pioneered archiving of modelling software and workflow scripts alongside data in EDI. We improved and upgraded our already-robust IM system in several ways over the past six years. NTL was a key contributor to upgrading the original Drupal Environmental Data Management System (DEIMS in Drupal 6) into a highly automated next version (DEIMS in Drupal 7), and now have migrated to Drupal 8 and documented the process for others to follow in our footsteps. This modularizes our already lightweight infrastructure, improving maintainability and agility in adapting to change. This latest system was built in anticipation of a major upgrade in the Ecological Metadata Language. Data flows from field to curated storage have been upgraded to mostly R workflow scripts.

Broader Impacts: The goal of our education and outreach activities has been, and continues to be, to improve awareness and understanding of the ecology of lakes, and of science in general for students at all stages of learning, resource managers, decision-makers, and the general public. To this end, we maintained a diverse portfolio of activities to reach these equally diverse audiences.

Student training and education: Since 2014, NTL has provided support for 3 post-docs and 33 graduate students in 8 different departments/programs. Graduate student development is fostered by involving these early-career scientists in multiple aspects of NTL, including monthly science meetings, interactions with visiting scholars, undergraduate hiring and mentoring. Each year, >30 undergraduates work directly on NTL-related projects, either assisting researchers or conducting their own projects. In addition to LTER REUs, the Center for Limnology supports 3-4 undergraduate summer fellows and 1 graduate student through endowment funds to form a cadre of researchers who work together and are guided by the graduate mentor. One fellow is a science communication intern who facilitates outreach activities and introduces the idea that doing and communicating science go hand in hand. The graduate mentor interacts regularly with the undergraduates and leads workshops on topics such as learning R, giving research talks, and applying to graduate school.

NTL activities also reach into classroom teaching. Several graduate seminars have been motivated by LTER activities, focusing on lake modeling; an introduction to the LTER Network; exploring and working with LTER data; building automated aquatic sensors; and science communication. Lakes also provide an effective resource for undergraduate classes, and NTL research examples are widely used by PIs, as well as by colleagues at other universities. Beyond data use, we estimate that ca. 1200 students/year take classes taught by NTL PIs in which LTER research is included in the curriculum.

K-12 activities: Our Schoolyard LTER “Winter Limnology” program provided opportunities for ~100 students/year from 5 schools in the Trout Lake Station area to learn about lakes and how we study these ecosystems. Students spend part of their day getting hands-on experience collecting data from lakes, conducting experiments, and making observations in the lab. Roughly 25% of the students are of Native American descent. In Madison, we worked with the Pre-College Enrichment Program for Learning Excellence (PEOPLE), offering limnology workshops for ca. 80 under-represented middle and high school students. We also partnered with UW Gear Learning to develop and test an ecological curriculum that integrates an iPad-based board game for learners to explore the impact of people on the environment. NTL Education representative Bohanan also organized a workshop at the 2015 LTER All Scientists Meeting on “Developing and using ecological and environmental games to improve science literacy.”

Outreach: NTL scientists gave talks and led discussions in a wide range of public fora; examples include: Science on Tap (Minocqua and Madison, WI); the Vilas County Economic Development Corporation; Wisconsin Department of Transportation; and several lake associations. NTL researchers organized a citizen-science Bioblitz in partnership with the UW-Arboretum to determine worm densities throughout the city. We led multiple trips on Lake Mendota for groups including classes from Madison East High School, the Yahara Watershed Academy (for professionals interested in management of the Yahara lakes), the Lussier Community Center (a non-profit group supporting diverse low-income families in Madison), and the Midwest chapter of NASA's Global Learning and Observations to Benefit the Environment (GLOBE), among others. We roughly estimate that NTL personnel are involved in 40 - 50 outreach events reaching well over 1,000 people each year. NTL research has been featured in a range of media outlets, ranging from local news shows, papers, and Wisconsin Public Radio to features in national and international publications including National Geographic, The Washington Post, the New York Times, and the CBC science program, "Quirks & Quarks." Through these efforts, NTL science has reached tens of millions of readers, listeners, and viewers.

Results of Supplemental Support: NTL received three supplements in 2014-2020 for information management, equipment, and an RET award. The RET supported two teachers who developed projects on dragonfly diversity in storm water retention ponds and generating curriculum for an outdoor environmental education class for high school teachers. We used the 2015 equipment supplement to replace an aging temperature assembly and data logger for a buoy and help acquire a nitrate sensor and portable greenhouse gas analyzer, for the FLAMe platform. The gas analyzer has also been used in other studies (e.g., Crawford & Stanley 2016). Finally, a 2015 supplement provided major support for planning of the new LTER data repository via a series of workshops to get input from site Information Managers. These activities led to a successful proposal for a new LTER data repository and expanded services. This supplement also supported transitioning data, websites, and documentation from the original LTER Network Office to the EDI and the new LTER Communications Office in Santa Barbara, along with several other activities. Thus, the key outcome was the establishment of EDI and providing the foundation for expanding the scope of data repository and data management services to LTER and the broader ecological research community.

RESPONSE TO PREVIOUS REVIEWS

Research: Reviewer comments from the mid-term site review emphasized opportunities to improve on integration among research activities internally and with the broader field of ecology and noted that these issues were related to the presentation of our research rather than being a structural issue. Specific suggestions related to: (1) emphasize connections and integration among themes and to the broader conceptual framework; (2) highlight research results that address broad ecological issues and contribute to ecological understanding across both aquatic and terrestrial systems; and (c) continued vigilance in placing site-based research in the context of fundamental ecological advances. We have emphasized integration among proposed research components and relate our work to ecological concepts as illustrated in our conceptual framework. We have also proposed synthesis activities near the end of the upcoming funding cycle to intentionally integrate our research with studies in other ecosystems. Finally, many of the questions we will address are inspired by terrestrial and marine research; as an example, we have drawn on the wealth of studies on phenology (a topic that is poorly developed in limnology and typically only used in the context of ice formation/loss) to consider consequences of climate change on lakes.

Information Management (IM): Suggestions from the review team for IM related to (1) maintaining Drupal DEIMS; (2) managing specialized legacy software; (3) potential for failure of automated sensors; (4) support for models and model-associated data products; and (5) continuing with integration of NTL data in the semantic web. (1) NTL's metadata have been managed in the Drupal content management system for the last 9 years. The Drupal Environmental Information Management System (DEIMS) for Drupal version 7 was unnecessarily difficult to maintain. Thus, we upgraded to version 8 and a much simpler, well-functioning DEIMS system developed by the NTL IM team. (2) We followed reviewer suggestions and upgraded one of our legacy applications and have a plan to upgrade our water sample management tool. Our application for measuring and counting zooplankton has been upgraded by a research group in Canada and we will collaborate with them to build on these developments. (3) To minimize data loss due to automated sensors failure, we now check/maintain sensors regularly during the open-water season by means of a remotely accessible website and the Campbell Scientific software that alerts us of data delivery failures. We have also developed our own low-cost sensors and have these on hand as back-ups. The backup of these rather large data files is handled on Amazon cloud storage. (4) We have begun to archive code and model outputs in the EDI repository (see example provided in the data management plan). (5) In addition to ongoing data model standardization, semantic integration will be a major focus in the next few years, as a new version of EML has recently been released providing the structure for semantic annotations.

Education Activities: The review team made two recommendations for our education and outreach initiatives: (1) broaden the diversity of participants at all levels, and (2) develop a more comprehensive assessment program. Promoting diversity is an ongoing effort at UW-Madison and for NTL. Currently, ~20% percent of our graduate students are from under-represented groups. For the upcoming funding cycle, we identified a set of opportunities intended to increase the diversity of the NTL community that includes creation of a committee on diversity, equity, and inclusion; development of workshops on these issues; and efforts to increase the diversity of our undergraduate participants by leveraging on-campus programs as detailed in the Outreach and Education section. With respect to assessment, we describe plans to develop assessment tools for our SYLTER program in partnership with the teachers involved in this program. For undergraduate training, we will expand current tracking efforts of our research fellows to better understand the impact that this experience has on students. We will embed tools and materials we develop within the NTL-IM system and share them across the LTER network.

PROPOSED RESEARCH

Conceptual Framework: Ecological hallmarks of our entry into the Anthropocene include shifts in current drivers, emergence of new drivers of ecosystem structure and function, and accelerating change in many ecological patterns and processes. These include *abrupt ecological changes*- that is, changes that are fast in time or fast relative to their drivers (Turner et al. 2020). These rapid and often unexpected dynamics are widely reported across diverse ecosystem types, from coral reefs to grasslands to lakes, and across levels of ecological organization from populations to landscapes (Rocha et al. 2015; Botta et al. 2019). From a human perspective, abrupt ecological changes are rarely viewed as positive, and because of their speed, adapting to or managing these changes is difficult and may thus compromise ecosystem goods and services, and, more broadly, human well-being (Steffen et al. 2015; Turner et al. 2020).

As abrupt ecological changes are becoming increasingly apparent, different cause-effect relationships have been identified or hypothesized. Abrupt changes are frequently used synonymously with regime shifts, i.e., rapid, persistent ecosystem change in response to a seemingly small change in a driver. These are often situations in which a *slowly changing variable finally passes a threshold* and current ecosystem processes can no longer operate in the same fashion. But not all abrupt changes qualify as regime shifts and instead may have more obvious causes and may not necessarily persist. *Extreme events,* while difficult to define, can generally be considered as events of a magnitude that are historically rare and among ecologists, this term is synonymous with disturbance (McPhillips et al. 2018). Many well-known examples are climate-driven, particularly given the reality of increasing weather extremes. An increase in the magnitude of such events also increases the overall variability of prevailing climate conditions, as do sudden or short-term changes in weather conditions (from cold to warm, wet to dry) even if the endpoints are not themselves extreme. These “weather whiplash” occurrences have been identified as a type of extreme event that can also lead to abrupt ecological change (Loecke et al. 2017; Swain et al. 2018; Casson et al. 2019). Over longer time scales, rising climatological variability of any form- whether as extremes or as a series of

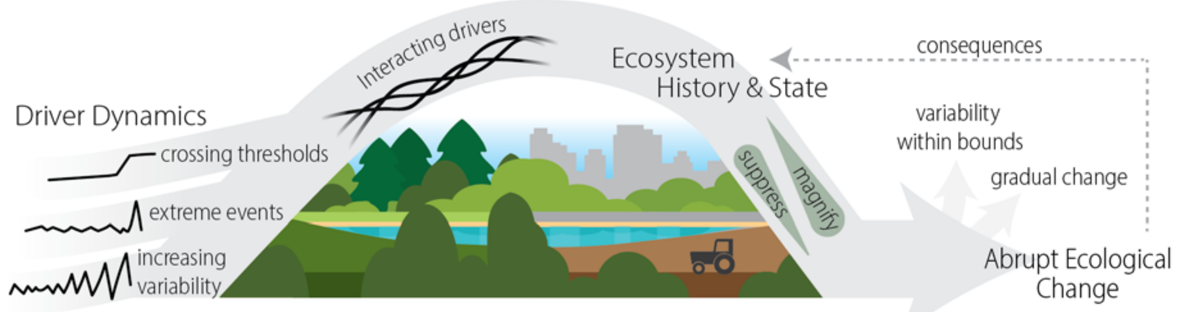


Figure 1. Conceptual illustration of driver dynamics and ecosystem conditions that shape (magnify or suppress) ecological changes over time. These changes may follow historic patterns of variability and neither increase or decrease in magnitude, may show gradual change over time, or may abruptly change (enlarged here for emphasis) and affect patterns and processes within the ecosystem.

reversals- presents sustained challenges for species with life histories that rely on regular environmental cues (Durant et al. 2007; Ohgushi et al. 2012). Thus, we expect that *rising climatological variability* may also lead to abrupt ecological change. But regardless of their form, extreme events may not cause big or abrupt ecological changes by themselves. However, when these events interact with other drivers such as changes in land use (i.e., *interacting drivers*), ecosystem consequences can be qualitatively different and produce rapid and large changes (Peters et al. 2011; Strayer 2012; Rocha et al. 2018). Similarly, a particular sequence of events in short succession, or the same event occurring at a different point in time, may produce substantial and rapid change, or the same event can have magnified effects on one lake but not another. That is, *ecosystem state or history* can modify driver-response relationships, leading to more muted or more exaggerated changes (Buma 2015). Collectively, these different causes and circumstances of abrupt change can be viewed as alternative but not mutually exclusive hypotheses that are broadly relevant across ecosystems and response variables (Fig. 1).

Within the NTL domain, we have observed shifts in driver and response variables that are both gradual and abrupt on time scales of years to decades. Examples of rapid changes in lake responses that have been particularly conspicuous to both researchers and many Wisconsin residents include the collapse of valuable walleye fisheries (Rypel et al. 2018; Embke et al. 2019); increasing fluctuations of lake levels (Watras et al. 2014; Usinowicz et al. 2017); arrival of new aquatic invaders (Wilson et al. 2004; Walsh et al. 2016b); and sudden declines in lake water clarity (Walsh et al. 2016a), among others. At the same time, we are also seeing changes in drivers that can cause abrupt change, but abrupt changes have not followed, leading us to ask why. Our research activities are inspired by these observations and are organized around the overarching question:

What are the causes and consequences of abrupt ecological change in lakes and their surrounding landscapes?

Studying abrupt ecological change is challenging specifically because of its sudden and often surprising onset; in these cases, research activities only begin after these events are well underway (e.g., as coral bleaching has become conspicuous or as an invader has already spread throughout a lake). And while sudden changes can occur over many time scales, we will emphasize ecological changes that are abrupt on timescales of years to decades that are relevant to many ecological processes as well as human perspectives. Here, long-term research programs are particularly well positioned to address questions about abrupt change by being in place all the time, understanding and studying an ecosystem prior to and during the unfolding of both sudden and gradual changes at these same timescales. Using lakes as laboratories also provides us with the opportunity to consider general concepts and hypotheses of abrupt change in ecologically distinct lakes experiencing similar regional drivers.

Over the next 6 years, our research activities will be organized around core data collection, 4 research areas, and synthesis activities that provide us with a set of opportunities to test, modify, and expand hypotheses of causes and consequences of rapid and long-term ecological change. Our approach to the overarching question is multifaceted. We will address research questions from the direction of the drivers (What are consequences of extreme events?) as well as from ecological responses (Which variables change and why? What are the consequences of these changes?) in different settings (across different lakes, in different landscapes) and from populations to ecosystems. This will involve a combination of forensic ecology (Why did a prior abrupt change occur?), opportunism: studying the ecosystem as an abrupt change occurs, and anticipation: investigating the potential for these events in the future. These different perspectives and approaches are collectively intended to illuminate underlying mechanisms of ecological changes (both sudden and gradual), and to test and develop hypotheses of abrupt ecological change that are broadly relevant across different types of ecosystems. We present a set of studies that consider abrupt changes (or lack thereof) from different angles, but we are also poised to be opportunistic in the case of the occurrence of new, surprising events. All of this proposed work begins and ends with the collection and analysis of long-term data sets across the 5 core LTER areas of primary production, population dynamics and trophic structure, organic matter accumulation and use, inputs and movements of nutrients through the ecosystem, and patterns and frequency of disturbances. Continuing these data sets is essential for documenting and understanding abrupt ecological changes in the past and future. From here, we address the following questions about abrupt ecological change:

1. **Climate variability and lake phenology**: *What are lake phenological responses to a warmer and more variable climate that may lead to abrupt ecological change?*
2. **Interacting drivers and abrupt change in urban aquatic ecosystems:** *How do interactions of land use/land cover and climate change affect urban aquatic ecosystems?*
3. **Interacting drivers and water quality:** *How do external drivers interact with aquatic invasive species to regulate water quality?*
4. **Managing for abrupt change in whole-lake experiments**: *What causes intentional ecosystem manipulations to persist, revert, or lead to novel states?*

Below, we describe our long-term data sets followed by proposed research activities for the four main questions. Each section is introduced with a tailored version of the conceptual framework that illustrates the aspects of abrupt ecological change that are emphasized within the section. Lead researchers for specific research initiatives within each of the four sections are identified on each conceptual figure. Additional information about investigators involved in these projects and project timing are detailed in Table S.3 in the Project Management Plan.

The NTL Setting and Long-Term Science: NTL activities are based in two distinct geographic, ecological, and human settings (Fig. 2). The NHLD is a water-rich forested landscape that overlies deep glacial silicate deposits. We have 7 primary study lakes that capture the range in size, groundwater influence, and trophic states (Table 2) that occur among >7500 lakes in the region. In southern Wisconsin, our 4 study lakes in the YLD lie within an agriculturally dominated, carbonate-rich landscape that is also experiencing rapid urban growth. These systems are highly enriched (eutrophic) but are still heavily used for recreation. Hence, marked differences in geology, hydrology, pre-settlement land cover, and anthropogenic influences between the NHLD and YLD provide strong contrasts in drivers and lake dynamics. We have capitalized on this distinction by pursuing studies of region-specific drivers as well as using the contrast to consider how similar or shared drivers affect pattern and process among regions.

Multi-year NTL records are complemented by pre-LTER data in both lake districts (Magnuson et al. 2006), plus secondary lakes in which a subset of information is collected. This includes Lakes Waubesa and Kegonsa in the YLD and Little Rock Lake in the NHLD. Little Rock Lake is now monitored as a secondary aquatic site for the National Ecological Observatory Network (NEON). Starting with this funding cycle, we are partnering with the Wisconsin Department of Natural Resources (WI DNR) Fisheries Research Team, who have been monitoring fish, fishing, and lake conditions since 1946 in 5 lakes located 8 km from TLS. This includes compulsory creel census of angler demographics; length, weight, sex, and age of all fish species harvested; spring and fall fish surveys; daily weather and water temperature; and annual ice off and on dates. Since 2012, standard NTL biweekly limnological and zooplankton monitoring were initiated on these lakes.

Core data collection:

Sampling program- Our sampling program allows comparisons of parameters and processes among seasons, years, lakes, and lake districts (Table S1). Sampling frequencies reflect the dynamics of individual parameters and technical/logistical capacities to make these measurements. Complete cation-anion balances are determined quarterly at spring overturn, maximum summer stratification, fall overturn, and winter stratification. Macrophyte distribution and abundance, fishes (abundance, lengths/weights, and community structure), crayfish, benthic invertebrates, and groundwater chemistry are sampled annually. We will add zebra mussels in Lake Mendota to this list in 2020. Lake attributes that are more variable over time (nutrients, pH, and inorganic and organic carbon) are sampled at multiple depths every 2 or 4 weeks, depending on the lake and variable, during the open water period, and every 5 weeks under ice as conditions permit. Temperature, dissolved oxygen (DO), chlorophyll *a*, light penetration, and abundance and composition of phytoplankton and zooplankton are similarly sampled once under ice and 5 times during the open-water season. Groundwater levels are measured monthly.

We maintain high-frequency sensing platforms (‘buoys’) on 5 of the primary NHLD lakes and 1 YLD

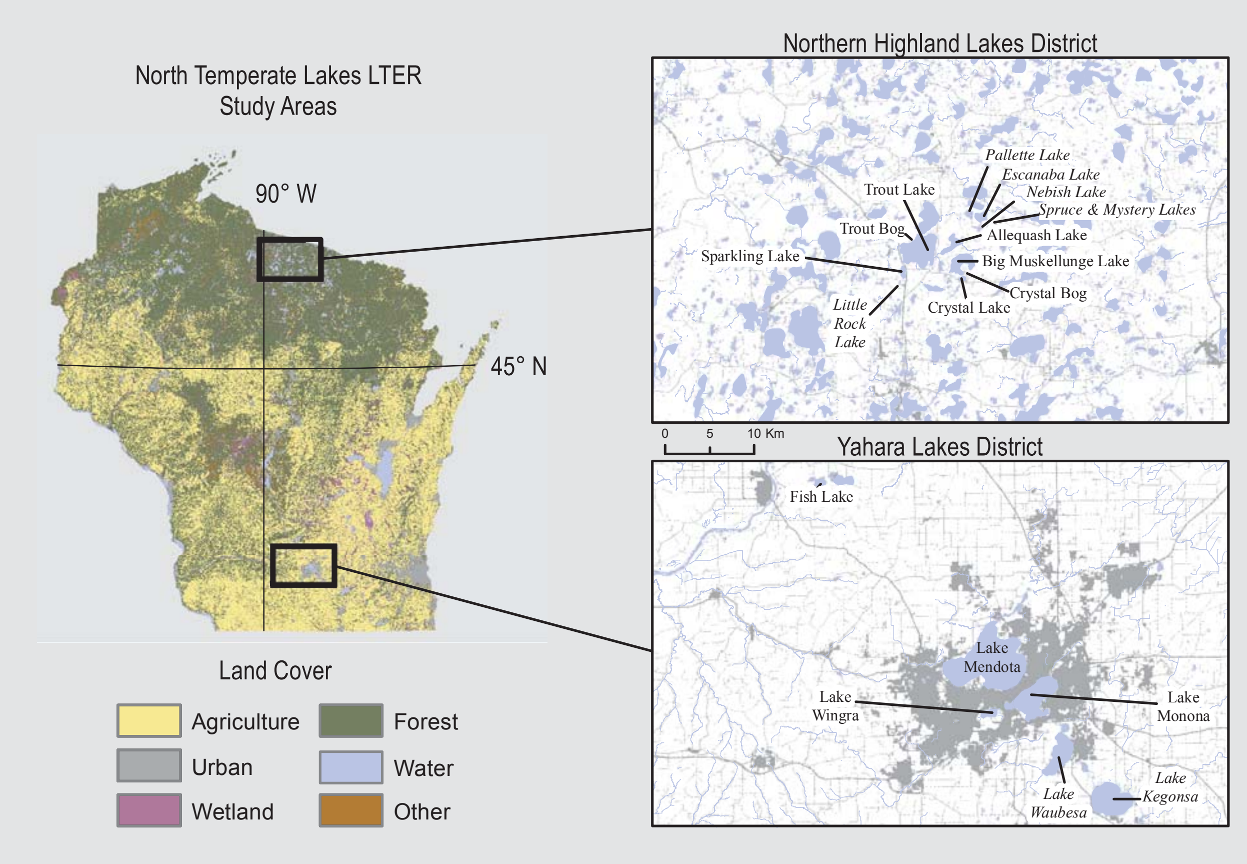


Figure 2. The North Temperate Lakes LTER study areas in the Northern Highland Lake District (NHLD) and the Yahara Lake District (YLD), Wisconsin. Locations of the 7 core NHLD and 4 core YLD lakes (standard font) along with selected secondary study lakes (italics font) are indicated in the inset maps on the right.

lake (Mendota) to monitor temperature throughout the water column and near-surface DO. Summer buoys deployed during the open-water season on Trout and Sparkling Lakes in the north also include sensors for near-surface dissolved CO_2 and conductivity, as well as meteorological variables and atmospheric CO_2 above the water surface. The Lake Mendota buoy is equipped with a weather station and sub-surface sensors for DO, dissolved CO_2, chlorophyll, phycocyanin, conductivity, pH, fDOM, turbidity, and photosynthetically active radiation. Large summer buoys are removed in the fall as they cannot withstand lake freezing and are replaced with compact under-ice sensor suites at the same location approximately 1 m below the surface. These winter installments include similar distributed temperature chains, near-surface DO and light sensors, plus 2 lakes with near-surface CO_2. Both summer and winter buoys have the capacity to support additional sensors, and we also have platforms available for deployment as needed for specific projects. All variables are measured at 1-min intervals except CO_2 in the winter when measurements are made at 2-hr intervals to conserve battery power. In addition to the lake sensing platforms, all 7 northern lakes have water level sensors that measure water levels at 30-min intervals during the open-water season. Finally, we maintain an automated weather station at the Minocqua Airport 10 km from Trout Lake and use National Weather Service data from the Dane County Regional Airport (3 km from Lake Mendota). Domain 5 NEON core and relocatable sites have been established within ~50 km of the NHLD primary study lakes and lake data sets are beginning to become available to augment our own observations. Five DOE-supported Ameriflux terrestrial forest and wetland core eddy covariance flux tower sites are also located near NHLD study lakes to provide landscape context to regional carbon and water cycling (Desai 2014).

Once each funding cycle, we conduct a survey in the NHLD to characterize long-term lake change across the region and to complement our regular sampling of the 7 core lakes. The survey includes 28 lakes that encompass a gradient of lakeshore development (houses/km) and landscape position, and that had been included in prior regional sampling efforts back to first historical studies of lakes in the region from the 1920s (e.g., Juday & Birge 1933). Variables include the same suite of water chemistry collected from our core study lakes (nutrients, cation/anions, conductivity, chlorophyll a, DO, water temperature). Shoreline conditions (presence of houses, docks, engineered structures, substrate composition, woody debris, vegetation cover) are characterized along 8 transects perpendicular to shore and a point-intercept survey is done to identify and quantify macrophytes.

Information about the landscapes surrounding our study lakes is retained in a comprehensive geographic information system (GIS; Table S1). We have detailed spatial data on land use/land cover, including statewide pre-settlement vegetation and historical land-use/land-cover files from the 1930s, 1960s, and 1990s for selected lakes. We acquire publicly available spatial datasets and remotely sensed images on an as-needed basis (e.g., from WisconsinView.org, USGS, NASA).

Table 2. Characteristics of the 11 primary NTL study lakes. For each region, lakes are ordered by their landscape position in the hydrologic flow systems. Crystal Bog (CB), Trout Bog (TB), Crystal Lake (CR), Big Muskellunge Lake (BM), Sparkling Lake (SP), Allequash Lake (AL), Trout Lake (TL), Fish Lake (FI), Lake Mendota (ME), Lake Wingra (WI), Lake Monona (MO).

	----------------Northern Highland Lake District (NHLD)----------------							------Yahara Lake District (YLD)------			
NTL Lake	**CB**	**TB**	**CR**	**BM**	**SP**	**AL**	**TR**	**FI**	**WI**	**ME**	**MO**
Area (ha)	0.5	1.1	36.7	396.3	64	168.4	1607.9	87.4	139.6	3937.7	1324
Mean Depth (m)	1.7	5.6	10.4	7.5	10.9	2.9	14.6	6.6	2.7	12.8	8.2
Landscape Position	high	high	high	int	int	low	low	high	high	low	low
pH	5.2	4.8	6.1	7.3	7.4	7.6	7.6	8.1	8.5	8.4	8.4
DOC (mg/L)	9.1	16.8	2	4	3.4	4.3	3.1	7.1	6.9	4.9	4.4
Total P (ug/L)	18	41	8	18	14	32	13	22	32	103	78
Total N (ug/L)	643	885	201	404	341	376	233	862	932	814	866
Secchi Depth (m)	1.6	1.1	7.5	6.7	6.2	3.1	4.7	2.7	1.2	3	2.7
Cholorphyll (ug/L)	8.8	16.6	1.8	2.9	2.2	7.6	3.1	6	10.3	6.7	9.2

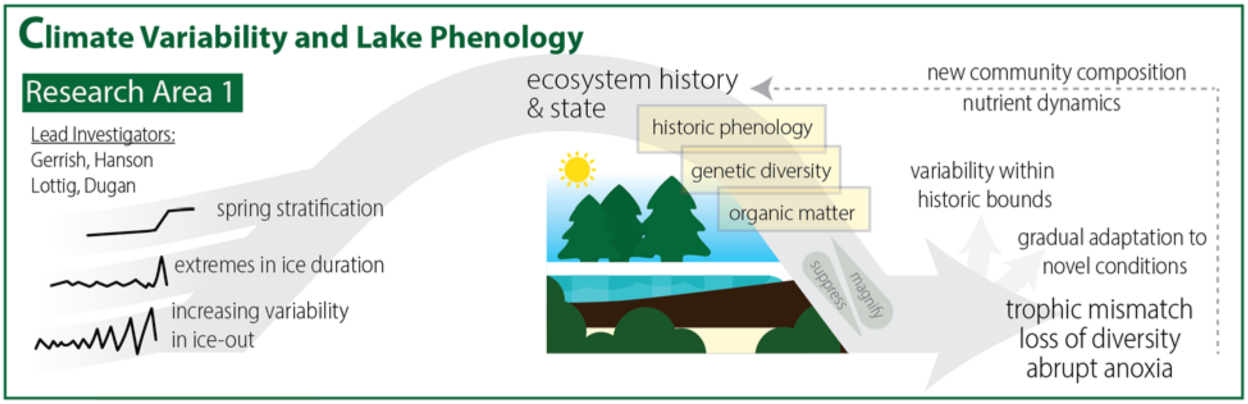
Models- NTL has a long tradition of ecological modeling that will continue in the next cycle. Central to these efforts are a suite of numerical simulation models that provide multi-dimensional representation of integrated terrestrial processes and connect with global-scale climate and land-use processes. The models have their foundations in physical and biogeochemical principles from aquatic, terrestrial, and atmospheric sciences. Each has gained broad acceptance in their respective fields and, as such, provides a basis for research, student training, and collaborations among research projects that extend beyond NTL, and a framework for integration of aquatic ecological models into larger-scale Earth system models and model-data informatics infrastructure. Here, we provide very brief overviews of these models.

GLM-AED2 (general lake model with aquatic ecodynamics) simulates in the vertical dimension lake hydrodynamics and water quality (Hipsey et al. 2019) and is suitable for a wide range of lakes and reservoirs, including shallow (well-mixed) and deep (stratified) systems. In addition to solving water and energy budgets, water quality modules enable mass balance modeling of nutrients, carbon, and dissolved gases. GLM-AED2 uses observed inflow-outflow data and meteorological data and lake-specific physical features, such as morphometry and geo-location to drive system dynamics. GLM-AED2 is a community model, with lead developers at the University of Western Australia and an oversight committee that includes NTL PIs Hanson and Dugan.

Agro-IBIS simulates plant growth, phenology, and soil-plant-atmosphere cycling of water, energy, momentum, C, N, and P in natural and managed ecosystems. It has been extensively used across the U.S. to understand impacts of changing land management and climate on ecosystem services, particularly for forests, grassland and prairie, and a variety of agroecosystems and crops (VanLoocke et al. 2010, 2012, 2017). Agro-IBIS was built on the Integrated Biosphere Simulator (IBIS) modeling framework and has been evaluated (Kucharik 2003), applied, and updated repeatedly in the past decade. Recently, three significant modifications to Agro-IBIS were made. (1) We integrated the variably saturated soil water flow model Hydrus-1D to simulate groundwater-vegetation interactions and effects of shallow groundwater on unsaturated zone processes (Soylu et al. 2014). (2) We added biogeochemical cycling of P and P loss to runoff (Motew et al. 2017, 2018) based on the SurPhos model (Vadas et al. 2004, 2005, 2007). (3) Our final modeling advance was incorporating Agro-IBIS as a module within the USGS Modular Groundwater Flow Model (MODFLOW; Harbaugh 2005) to form a complete modeling approach of critical zone processes (Zipper et al. 2017b), which are often ignored in ecosystem models.

We integrate Agro-IBIS with a physically based hydrologic routing model *THMB* (Terrestrial Hydrology Model with Biogeochemistry) to simulate temporal variability of in-channel transport of water, sediment, and nutrient (N, P) loads from the land surface and subsurface simulated by Agro-IBIS. This coupled hydrologic-biogeochemical system has been used to quantify lake level change (Chen et al. 2019) and P transport and eutrophication (Carpenter et al. 2015). The sediment module is based on a fine sediment transport model in Patil et al. (2012). The P module includes transport of dissolved and particulate P, which have different physical in-channel processes. The in-channel process functions are based on a nutrient mobilization and transport model in Viney et al. (2000), and lake-level regulation is based on equations from Chow et al. (1988).

Research Questions, Hypotheses, and Approaches



Q1. What are lake phenological responses to a warmer and more variable climate that may lead to abrupt ecological change?

Phenology, the annual timing of biological events, is consequential to nearly all biological processes, from cellular and genetic to communities and ecosystems (Forrest & Miller-Rushing 2010) and these processes are now being influenced by a warming and more variable climate. Landmark studies in terrestrial ecology have shown long-term shifts in phenology in plant flowering and fruiting (Sherry et al. 2011), leaf-out and canopy cover (Vitasse et al. 2018), and breeding (Forchhammer et al. 1998), all driven by directional climate trends. In addition to gradual change, climatic extremes, such as drought, can abruptly suppress plant phenologies and lead to loss of ecosystem resilience (Ma et al. 2015). In aquatic ecology, the responses of lakes and their biota to rapid and variable phenological perturbations caused by climate change is less understood.

The ecology of north temperate lakes is characterized by a seasonal sequence of climatically driven abiotic events that in turn regulate biological phenology. Following ice-off at the end of winter, lakes warm, become isothermal and mix, then begin to thermally stratify. These physical phenomena trigger productivity, growth, reproduction, and trophic interactions that define a historically predictable succession of communities and species interactions (Sommer et al. 2012). Warming is leading to earlier ice-off (Magnuson et al. 2000) and changing spring stratification (e.g., Magee & Wu 2017b; Moras et al. 2019), which can alter phytoplankton bloom phenology (Winder & Schindler 2004) and fish spawning (Lyons et al. 2015). As this warming trend continues, thousands of lakes at the southern extent of winter ice cover zones are now (Likens 2019) or will soon experience a rapid shift to an intermittent ice regime (Jensen et al. 2007; Sharma et al. 2019). At the same time, lakes in the Great Lakes Region are also experiencing a rapid increase in variability in the timing of ice-off (Fig. 3). We have limited understanding of the consequences for lake ecosystems, and we cannot use space-for-time substitution, because ecosystem history matters. The current ecosystem states and contingencies are the product of climate conditions that have been relatively stable for millennia. Thus, it is critical to begin developing a better understanding of how the timing and magnitude of seasonal events in lakes (i.e., lake phenology) are responding to change. What is likely to shift, what abrupt changes might we expect, and what is at risk of collapsing? Advancing understanding of phenological change requires long-term data (Kharouba et al. 2018; Thackeray et al. 2010; Stenseth & Mysterud 2002), and we are well positioned to study phenological change across multiple levels of biological organization. Ongoing climate changes present us with an opportunity to examine how phenology may shift in response to changes in variability and in the long-term mean of ice duration and consider the abrupt changes to ecosystem dynamics that may arise. To this end, we focus on: (1) Phenological mismatches that can occur when the seasonal dynamics of interacting species change independently, and (2) hypolimnetic hypoxia that threatens to cross the threshold of anoxia, abruptly reducing lake water quality and fish habitat.

Q1.1. How can year-to-year variability in ice-off (i.e., whiplash events) lead to abrupt changes in populations and communities in lakes?

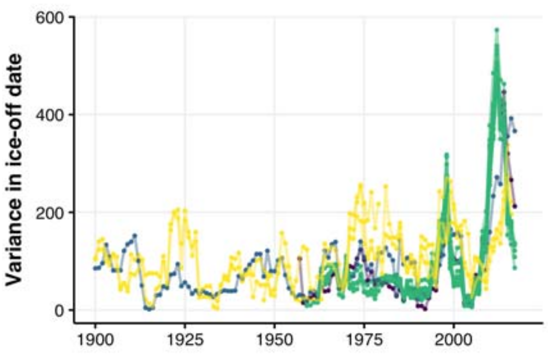


Figure 3. Long-term increases in the variability in ice-off dates for northern Wisconsin (green, n=7) and southern Wisconsin (yellow, n=4) NTL lakes, as well as two lakes in MN (Mille Lacs [purple] and Minnetonka [blue]).

At the community level, phenological mismatch occurs when the seasonal dynamics of interacting species change independently in a way that alters the magnitude or occurrence of their interaction (Cushing 1990; Winder & Schindler 2004). Diverse communities with robust multi-species food webs, generalist consumers, genetic diversity, and phenotypic plasticity are resilient to incidences of phenological mismatch (reviewed in Donnelly et al. 2011). However, highly variable climate conditions on annual or shorter time scales (i.e., whiplash events) may magnify the potential for trophic mismatch because demographic, evolutionary, and metacommunity dynamics have less time to compensate and thus overwhelm the 'ecological buffering' and 'evolutionary rescue' (Gienapp et al. 2014) capacities inherent in natural systems. Ultimately, decreased environmental predictability can drive species locally extinct and cause annual selective sweeps that degrade the genetic diversity of populations (Pauls et al. 2013).

Phenological mismatch is often studied as a species-species interaction but is likely to act among numerous interacting species and at multiple trophic levels (Both et al. 2009; Walther 2010). Accumulated mismatches may alter cascading trophic dynamics and cause abrupt ecosystem change. These mismatches may be more probable amid rapid shifts in the timing of key phenological events (e.g., ice-off; Fig. 3). For example, a whiplash event of >50-day difference in spring ice off occurred between 2012 and 2013 and changed demographic and growth dynamics for organisms at multiple trophic levels across NTL lakes (Fig. 4). Primary productivity (data not shown) and zooplankton diversity peaked earlier in the growing season. For fish, growth rates of yellow perch (*Perca flavescens)* correlated strongly with changes in ice-off date while extremely early or late years decreased walleye growth rates (WI DNR data), which we hypothesize is a consequence of a prey mismatch or mistiming. This preliminary analysis leads to the following hypotheses:

Hypotheses: ***H1.1a:*** *Abrupt changes in ice-off timing will increase the probability of phenological mismatches across trophic levels.* ***H1.1b:*** *Simultaneous multi-level mismatch will magnify ecosystem level impacts.* ***H1.1c:*** *Lakes with heterogeneous habitats, diverse communities and higher productivity will be more resilient/resistant to trophic mismatch.* ***H1.1d:*** *Extreme early or late ice-off years will lead to lower population genetic diversity than years with average ice-off dates.* ***H1.1e:*** *Repeated whiplashes over consecutive years will act cumulatively to reduce genetic diversity more than singular extremes.*

Approach: Using 40 years of NTL data from our 7 northern study lakes, we will examine how changes in climate variability have driven seasonal abiotic change (e.g., the timing of ice-off, lake stratification) and examine the subsequent phenological implications for biota. Biological investigations will leverage 40-70 years of historical samples (phytoplankton, zooplankton, and fish scales) that have been archived by NTL and the WI DNR Northern Highland Fishery Research Area with new high-resolution seasonal sampling of Escanaba Lake (a new NTL secondary study lake in partnership with WI DNR; see Fig. 2). Each spring, WI DNR quantifies spawning phenology and recruitment for several species of fish, emphasizing key gamefish species. Sampling includes determination of individual age, length, weight, trophic position determination, and collection of samples for genetic analysis. Individual fish are tagged and marked in order to estimate population sizes and track individual fish through time. We will supplement these efforts with weekly phytoplankton and zooplankton sampling throughout the open water period, starting immediately after ice-off. The increased frequency of sampling will provide the necessary data to identify seasonal dynamics in these communities including when and at what trophic levels phenological mismatches or mistimings are occurring. Three all-year high-frequency sensor sets will be installed in different regions of the lake (deep hole, shallow bays) that include depth-distributed temperature, DO, and light sensors to quantify temporal and spatial variability in these dynamics.

Hypotheses associated with genetic diversity will be tested by extracting and analyzing DNA from archived zooplankton samples (Wandeler et al. 2007) and fish scales (Wasko et al. 2003). For zooplankton, we will focus on *Daphnia* because they are a model evolutionary system with a fully published genome, >500 known microsatellite regions (Colbourne et al. 2004), and identified functional gene regions associated with thermal change (Jansen et al. 2017). New zooplankton and fish genetic material will be collected and preserved for ongoing analyses as part of the proposed sampling efforts described above. Changes in allele frequencies and heterozygosity of multiple gene regions (Waits & Storfer 2015) will be used to compare neutral and adaptive changes in population structure between early and late ice-off years.

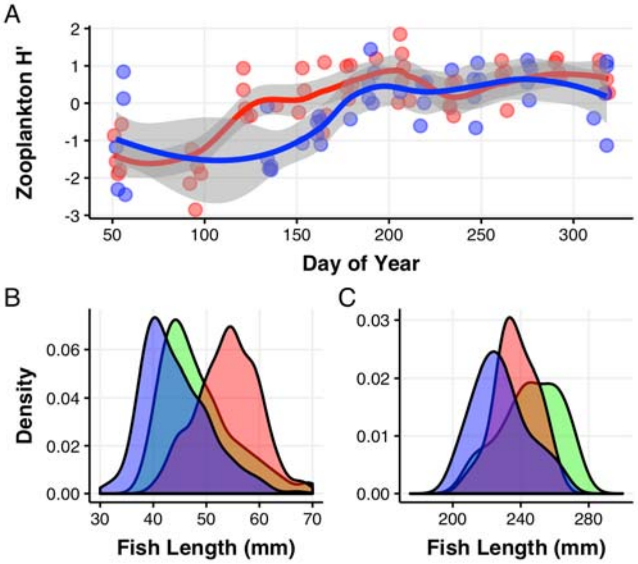


Figure 4. Scaled zooplankton diversity (Shannon's H') for northern NTL primary study lakes following consecutive late (2012; blue) and early (2013; red) ice-off years (A), and comparison of age-0 yellow perch lengths between 2011 (average ice-off year, green), 2012 (late ice-off; red), and 2013 (early ice-off; blue) for primary NTL study lakes in the NHLD (B) and age-1 walleye lengths (C) in Escanaba, a secondary NHLD study lake.

Q1.2. In what ways do warming trends, variable meteorological drivers, and OM legacies interact and lead to intermittent hypoxia or abrupt anoxia in lakes?

Thermal stratification and twice-annual mixing (dimixis) is a defining phenological characteristic of many lakes in temperate latitudes. Hypolimnetic (bottom layer) waters in stratified lakes are isolated from the atmosphere and often have negative net ecosystem production that leads to oxygen depletion. Many lakes have complete loss of oxygen (i.e., anoxia) at the sediment-water interface near the lake's maximum depth. If anoxia expands to the full extent of the hypolimnion, the lake enters an undesirable regime in which nutrient cycling accelerates and promotes harmful algal blooms (Schindler et al. 2016), release of toxic metals from sediments (Stumm & Morgan 1995), and disappearance of oxy-thermal habitat required by desirable cold-water fish species (described in Results of Prior Funding). This abrupt transition of a lake's hypolimnion to anoxia depends on organic matter (OM) availability for microbial respiration, ambient conditions governing microbial activity, and the strength and duration of thermal stratification (Müller et al. 2019). Hypolimnetic OM availability depends on a balance of allochthonous OM loads, autochthonous OM production mediated by P loads (Hanson et al. 2004; Müller et al. 2019), and the physical and biological conditions that determine the fraction of OM that remains in lake storage (Hanson et al. 2014). Stored OM (or "legacy OM") has an additional and insidious effect: it supports anoxic conditions, which slows OM mineralization (Bastviken et al. 2003) and increases water column stability by decreasing water clarity (Fee et al. 1996; Snucins & Gunn 2000), thus providing internal feedbacks that likely stabilize the anoxic regime. Climate drives anoxia through its direct effects on stratification and its indirect effects through nutrient and OM loads (Nelligan et al. 2019). In a climate with a warming trend and increased variability, lakes that experience early ice-off or years when ice does not form at all may cross the threshold into anoxia for the first time (Fig. 5).

<u>**Hypotheses**</u>: Lakes that experience earlier ice-off dates coupled with ***H1.2a*** *increases in allochthonous OM loading,* ***H1.2b*** *nutrient loading, and/or* ***H1.2c*** *enhanced OM carry-over between years are* susceptible to an abrupt change to an anoxic regime.

Approach: We will address this question through modeling studies of historical data and field campaigns. Field campaigns are needed to better quantify spring conditions and will be coupled with depth-discrete oxygen sensor deployments that provide high-frequency oxygen data throughout the water column. Currently, NTL buoys only measure epilimnetic oxygen. Hypolimnetic data are needed to understand biogeochemical conditions at the onset of stratification and for model calibration. Building off current implementation in Lake Mendota, GLM-AED2 modeling will be applied to NTL lakes (AL, BM, CR, SP, TL; see Table 2) to investigate gradients in both anoxia and its drivers (Snortheim et al. 2017). Quantification of energy budgets will enable us to determine the importance of changing ice-off dates due to warming trends and variable spring weather to onset and persistence of thermal stratification. GLM-AED2 will also be used to model time dynamics of coupled nutrient and OM cycles, leading to a better understanding of allochthony and autochthony and their contributions to the hypolimnetic OM pool. Long-term data and modeling will enable us to determine the legacy effects of nutrient and OM loads from previous seasons and years, as well as the importance of antecedent winter conditions. A detailed mechanistic understanding of lakes will untangle complex interactions that relate anoxia to lake phenology. For example, the date of onset of stratification, as well as the DO conditions at that time, have a strong influence on anoxia duration.

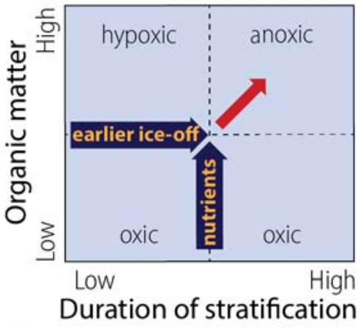
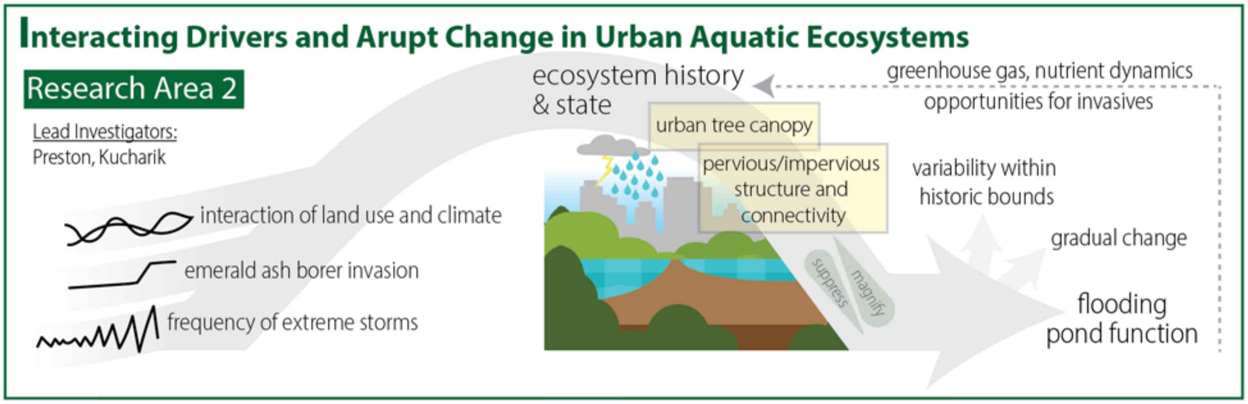


Figure 5. Conceptual model of effects of duration of stratification and organic matter (OM) influence on anoxia. Higher nutrient inputs can increase OM and therefore anoxia; similarly, anoxia increases with earlier ice-off because of longer stratification. These effects can combine in a non-linear manner to push lakes into anoxic states (red arrow).

We will use the natural gradient in summer oxic conditions among the NTL lakes to focus on systems that may switch from perennial oxic to intermittently anoxic, such as AL, and from intermittently to permanently anoxic, such as CR. We can then extend our understanding of drivers of anoxia to Midwest lakes to explore the probability of abrupt change in oxygen conditions in lakes regionally. Regional lake modeling will be implemented by building parsimonious lake oxygen models informed by NTL research, forced by thermal stratification model output distributed by USGS collaborators, and fit to regional-scale oxygen and water quality data available through the USGS/EPA Water Quality Portal (Read et al. 2017) and the LAGOS database (Soranno et al. 2017).



Q2. How do interactions of land use/land cover and climate change affect urban aquatic ecosystems? Urban landscape dynamics create hotspots of hydrologic activity (Voter & Loheide 2018) that influence the quantity, quality, and timing of water runoff, largely because of connections between pervious and impervious surfaces. Variation in the amount and spatial configuration of commercial development, residential areas, and urban greenspaces within cities is striking (Cadenasso et al. 2007), and Greater Madison is no exception. Furthermore–and with direct consequences for the lakes–urban stormwater management evolved from early reliance on informal green infrastructure (i.e., natural and semi-natural vegetation, including parks, wetlands, yards, and street trees) to dependence on gray infrastructure (e.g., storm sewers, stormwater detention ponds, infiltration basins). Greater Madison includes > 300 urban ponds, most of which were designed to manage stormwater by reducing runoff. These ponds receive inputs from local sub-catchments and ultimately drain to the Yahara lakes (Fig. 6). The lakes are also likely influenced by the energy balance of the urban heat island (UHI) and both intentional and unintentional changes in green infrastructure within the urban landscape. As annual precipitation and the frequency of extreme rainfall events increases (Fig. 7), urban LULC is expected to influence the likelihood of abrupt ecological change. Here, we propose three initiatives aimed at understanding (1) the state and function of urban ponds, (2) the interacting effects of urban LULC and climate on temperature and hydrology, and (3) how these suites of changing drivers can interact to amplify or dampen changes in lakes and ecosystem services in the Yahara basin.

Q2.1. How do interacting drivers affect urban pond states and their capacity to supply ecosystem services?

The network of >300 urban ponds (pondscape, *sensu* Hill et al. 2018) in Greater Madison was constructed primarily for flood mitigation and retention of nutrients and pollutants. Many of these waterbodies are linked to the Yahara lakes and likely play important but underappreciated roles in nutrient loading, greenhouse gas (GHG) fluxes, flood attenuation, habitat provisioning, conservation of native species, and expansion of invasive species. Shallow lakes and ponds were central to advancing understanding of alternative ecosystem states (Chase 2003; Scheffer & van Nes 2007), yet little research focuses on how urban LULC can drive (or mediate) shifts between states (Fig. 8). Pond characteristics that have potential to confer resilience to abrupt changes–including volume, depth, age, water level fluctuations, and community composition–vary due to the unique histories and water management objectives of individual ponds (Hassall 2014). Because many urban ponds are intended to slow surface runoff, they accumulate sediments, nutrients, and carbon, creating favorable conditions for biogeochemical transformations (e.g., Schroer et al. 2018; Frost et al. 2019). This hotspot character of urban ponds can be manifested as high areal emission rates of GHGs (CO_2, CH_4, N_2O) that collectively may account for a substantial but poorly quantified source of anthropogenic GHGs to the atmosphere (Grinham et al. 2018). Recognition of this hotspot behavior is recent (van Bergen et al. 2019), variability in process rates is not well explained by habitat (Blasczak et al. 2018), and temporal dynamics have yet to be considered.

As a first step toward understanding variation in the structure and function of urban ponds and their role in the Yahara basin, we surveyed 97 Madison-area ponds in 2019. From this, we identified at least four distinct states (Fig. 8) differentiated by their dominant primary producers: floating plants (mostly duckweed [*Lemna* sp.]), submerged macrophytes (e.g., nonnative Parrot Feather [*Myriophyllum aquaticum*]), emergent vegetation (nonnative cattails and reeds [*Typha* and *Phragmites*]), or phytoplankton (especially cyanobacteria). However, it is unclear if these are truly alternative states with abrupt, non-linear shifts among configurations, or if pond conditions change gradually, or simply vary over time. Changes in ecosystem services and biodiversity can stem from shifts between aquatic ecosystem states (Hilt et al. 2017), yet this linkage remains largely unexplored for urban ponds (Gómez-

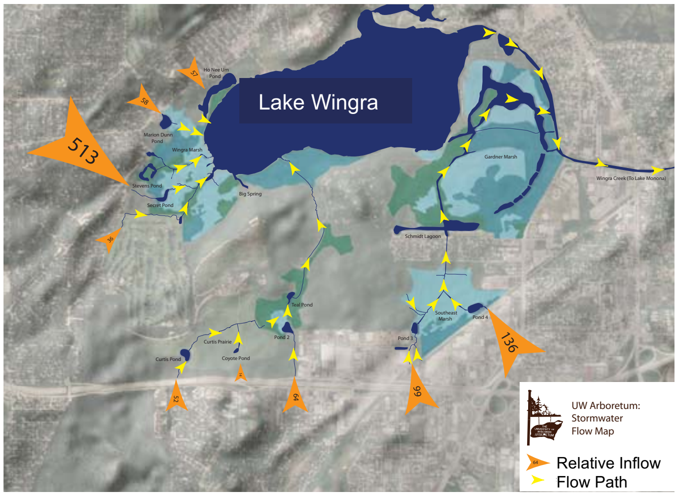


Figure 6. Map of YLD primary study lake, Lake Wingra in Madison showing 12 stormwater ponds showing flow paths in and out of the ponds (yellow arrows) and inflow volumes (orange arrows), which reflect surrounding land cover and connectivity to stormwater infrastructure. These ponds are at the interface of residential/commercial zones and a large urban greenspace, the UW-Madison Arboretum.

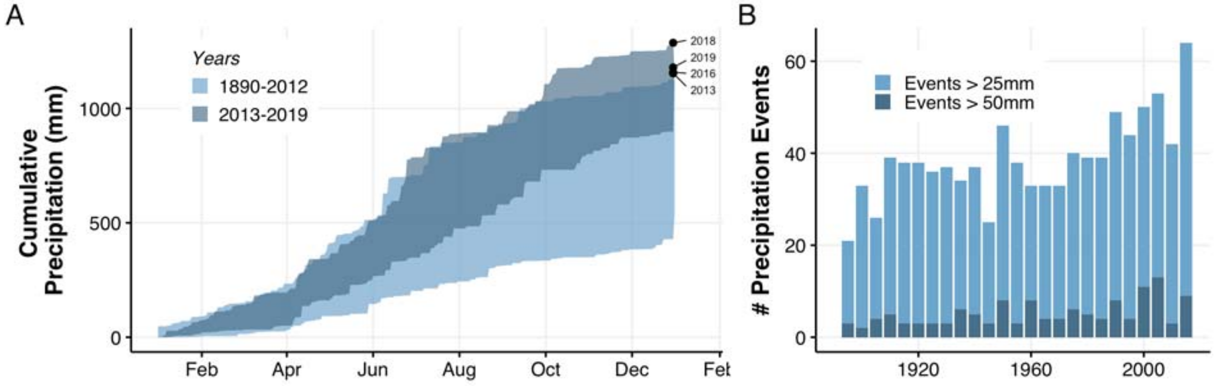


Figure 7. (A) Cumulative annual precipitation for Madison, WI. Four highest years (2018, 2019, 2016, and 2013) are shown in black. (B) Number of precipitation events > 25 and 50 mm between 1890 and 2019.

Baggethun et al. 2011; Doherty et al. 2014) despite its worldwide significance (Boyer & Polasky 2004).

Hypotheses: We expect urban LULC to affect the magnitude and frequency of extrinsic drivers of pond change, while pond characteristics mediate ecological responses to these drivers. Specifically: ***H2.1a:*** *spatial and temporal variation in pond states increase with impervious land cover via effects on stormwater inputs and dispersal barriers*, and ***H2.1b:*** *increases in pond volume, age, and community complexity (including species richness) reduce variance in pond states and resulting ecosystem services by enhancing resilience to abrupt change*. For GHG emissions, especially N_2O and CH_4. ***H2.1c:*** *GHG production/efflux only happens after ponds accumulate a store of sedimentary material to support these processes* because sediments provide the anoxic environment and OM needed to generate these gases. Alternatively, ***H2.1d:*** *GHGs emissions are high soon after pond construction in association with rapid decomposition of disturbed soil OM, then later are a function of phytoplankton abundance (Beaulieu et al. 2019) or allochthonous OM inputs (van Bergen et al. 2019) after this initial burst.*

Approach: We will initiate a long-term 'Urban Pond Observatory' by sampling ~30 ponds that vary in age and surrounding LULC. Research activities described below will be used to inform the development of a pond survey protocol that will be repeated on an annual basis in subsequent years. For hypothesis testing, we will quantify intra- and inter-annual shifts in biotic and abiotic pond parameters predicted to characterize the 4 ecosystem states described above. Communities will be tracked using standard NTL methods (focusing on phytoplankton, macrophytes, zooplankton, benthic invertebrates, and fishes), although some modification for pond sampling is expected. We will measure GHG fluxes weekly during ice-free periods for a sub-set of ponds that vary in state and age using floating chambers along with bubble traps and bubble sampling to capture ebullitive flux following methods of Crawford & Stanley (2016). As macrophytes grow, additional flux measurements will be made to capture fluxes from emergent and floating-leaved plants. Dissolved gas samples will be collected using headspace equilibration techniques and analyzed by gas chromatography. We will quantify both the means and variance of predicted drivers of change, including inflow stormwater chemistry and extreme precipitation events, and modeled carbon, water, and nutrient flows from each pondshed. After characterizing pond states (e.g., Smith 2012), the magnitude of spatial and temporal variation in pond states will be evaluated relative to extrinsic and intrinsic drivers. We will also leverage existing NTL data on a subset of Madison ponds collected over two decades ago, allowing for longer-term comparisons with specific biotic variables including zooplankton composition (Dodson 2008).

Q2.2. How do interactions of urban LULC, climate trends, and extreme rainfall events affect temperature and hydrology in the Yahara basin?

Cities differ climatologically and hydrologically from their surrounding rural areas because impervious surfaces in cities increase runoff, and the built environment absorbs and retains more heat than the natural

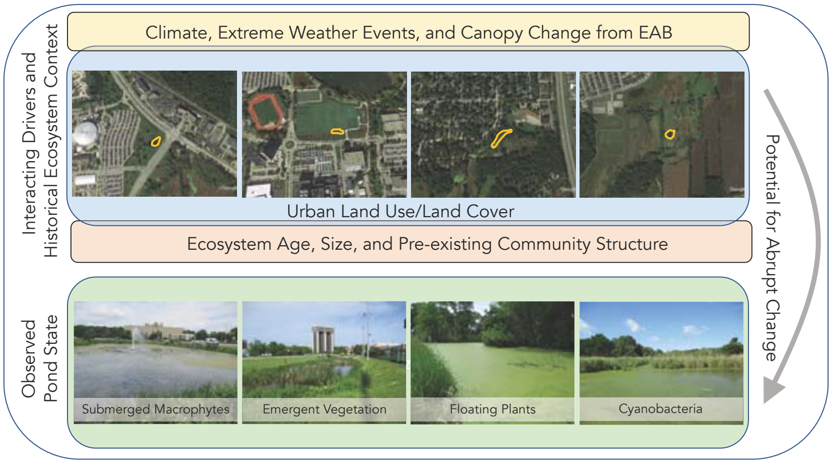


Figure 8. The network of ponds in the Madison area exists in a hetero-geneous landscape of high density commercial development, suburban neighborhoods, and greenspaces. Shifts in canopy cover, rapid urban growth, and climate are hypothesized to jointly influence urban aquatic ecosystem change. Potential for changes will be mediated by local ecosystem properties, including pond age, depth, and pre-existing community composition. Observed pond states include dominance by nonnative submerged macro-phytes, emergent vegetation, floating plants, or cyanobacteria, which in turn affect ecosystem service provisioning and inputs to the downstream Yahara Lakes. Ponds in the lower panels are outlined in orange in the upper panels.

landscape it replaced (Oke 1982). As impervious surfaces increase, air temperature, runoff, urban flooding, lake-level flashiness, and nutrient delivery to urban lakes also increase (Usinowicz et al. 2017). However, formal and informal green infrastructure can mitigate urban heat (Ziter et al. 2019), reduce water and air pollution (Nowak et al. 2014; Denman et al. 2016), and improve overall human health (Patz et al. 2005; Hartig & Kahn 2016). Contemporary urban stormwater management practices encourage more use of formal green infrastructure (e.g., green roofs, bioswales, rain gardens; Rosenzweig et al. 2018), and such features are increasing in the Yahara basin. At the same time, however, abrupt declines in the urban tree canopy are underway. As in many other regions, ash trees (*Fraxinus* spp.) were planted in green spaces and along Madison streets as the city grew. These trees are now being decimated by an invasive pest, the emerald ash borer (*Agrilus planipennis; EAB)*, and 22% (22,000) of Madison's street trees are at immediate risk (City of Madison 2019). Abrupt changes in temperature or hydrology may occur if thresholds of canopy cover are surpassed, e.g., summer air temperature declines nonlinearly with increasing tree canopy cover and increases nonlinearly with impervious surface cover (Ziter et al. 2019). However, the combinations of urban LULC, climate, and green infrastructure that are associated with gradual vs. abrupt change in temperature, hydrology and ecosystem services are not clear.

We suggest that both intentional additions and unintentional losses of urban green infrastructure mediate ecosystem vulnerability to effects of climate change and that LULC patterns developed under historical climate may lose their efficacy when confronted with novel weather (i.e., extreme events). That is, extreme events may exceed the capacity of the urban landscape to reduce flows and retain excess runoff. We expect greater hydrological connectivity to increase the likelihood of abrupt change in urban aquatic ecosystems, including the network of stormwater ponds (Goonetilleke et al. 2005; Pennino et al. 2016; Yang & Lusk 2018). Thus, we will test the following hypotheses:

Hypotheses: ***H2.2a:*** *LULC patterns that reduce connectivity of impervious surfaces and maximize green infrastructure will modulate air temperature, minimize flooding, and sustain urban water quality.* ***H2.2b:*** *There are thresholds in precipitation intensity beyond which green and gray infrastructure will fail to reduce flooding, flashiness, and nutrient delivery to downstream water bodies.* Rapid declines in the urban tree canopy may amplify climate effects, and thus we hypothesize: ***H2.2c:*** *Abrupt reductions in the urban tree canopy (due to EAB) will exacerbate the UHI effect and increase runoff due to reduced transpiration and interception*.

Approach: We will elucidate effects of variability in urbanization and green infrastructure within sub-catchments on the energy balance, hydrology, and material fluxes of pond catchments. To link precipitation events, local LULC, and urban hydrological responses, we will monitor the flashiness of stormwater inflows to the core set of 30 urban ponds (see above). Stormwater monitoring will use data loggers to record water temperature and water level to characterize differences in hydrologic responses among sub-catchments

(Doherty et al. 2014). We will characterize stormwater chemistry (total suspended solids, nutrients, chloride, and heavy metals) using automated systems that collect temporal samples over the course of precipitation events; chemical analyses will follow established NTL protocols. Local LULC within the sub-catchment of each pond will be quantified with aerial images, focusing on hypothesized links between shifting tree canopy cover (due to EAB induced losses) and air/surface temperature, urban greenspaces, and impervious surface connectivity. In conjunction with determining urban pond states, we will quantify relationships between the strength and frequency of drivers (e.g., precipitation events) and the magnitude and rate of aquatic ecosystem responses.

To quantify effects of urban LULC change and canopy declines due to EAB on air temperature, we will continue collecting air temperature data as part of our long-term UHI research. Our monitoring network of 150 temperature/humidity sensors is described in the Results of Prior Research section and has been in place since March 2012 (Schatz & Kucharik 2014). The stationary network will be augmented with mobile temperature sensor measurements at high spatial resolution (e.g., 1-m; Ziter et al. 2019) to quantify fine-scale effects of canopy loss on temperatures. We will predict how summer heat may intensify if all 22,000 ash trees are eliminated due to EAB, and how future land-use planning (e.g., "smart cities") and addition of green infrastructure might improve urban hydrology and mitigate urban heat.

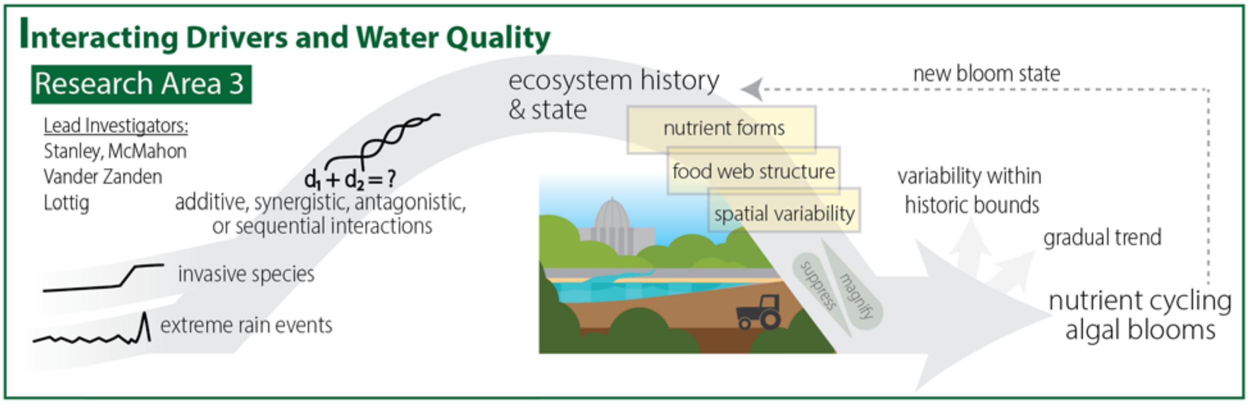
We will also develop a continuous 15-minute temporal resolution land and water surface temperature data product (at 30m x 30m spatial resolution) derived from the regression of periodic Landsat data with our observational air and pond water temperature records (Tavares et al. 2019). This temporally continuous temperature product, when combined with canopy cover and impervious surface data, will allow us to examine the combined impact of these features on pond surface water temperatures and fluxes in a variety of urban sub-catchments. This will allow us to investigate whether canopy loss due to EAB is directly affecting ponds and how the urban landscape contributes to fluctuations in land surface temperature and pond water surface temperature across seasons and years.

Q2.3. In the face of changing climate, can urban LULC sustain ecosystem services and mitigate undesirable ecological change in the Yahara lakes?

Anticipating the "perfect storm" of conditions that can lead to abrupt changes in urban aquatic ecosystems requires integration of our long-term observational data, the empirical studies described above that integrate the urban landscape with current understanding of land-water-climate interactions, and the capacity to explore the potential state-space of multiple driver interactions. Process-based models allow us to integrate climate and urban landscape characteristics (e.g., soil, ponds, and spatial arrangement of vegetation and impervious surface) and their impacts on the delivery of water and nutrients to the Yahara lakes (Fig. 6). Models also allow us to expand our understanding of ecosystem dynamics and feedbacks and identify thresholds and/or conditions that lead to abrupt change (Ratajczak et al. 2018). Integrated, process-based modeling tools can be used to explore a wide range of plausible future scenarios of LULC and climate change that may increase the likelihood of abrupt change in the Yahara lakes, and to identify patterns of LULC that increase ecosystem resilience and sustain ecosystem services (Jenerette 2018).

Hypotheses: We hypothesize ***H2.3a:*** *rising climatological variability and increasing frequency and intensity of extreme precipitation events will interact with thresholds of impervious cover to increase the flashiness of runoff and flux of nutrients to receiving water bodies, thus inducing ecosystem state change*. Furthermore, the pattern of urbanization and the extent and condition of green infrastructure can minimize the consequences of land use and climate change, but this capacity may be exceeded as climate variability continues to increase. Thus, we also hypothesize ***H2.3b:*** *green infrastructure will only succeed to a threshold of precipitation intensity beyond which flooding and nutrient loading will increase rapidly, with potential to induce abrupt ecologic change in receiving waterbodies.*

Approach: We will quantify interacting effects of LULC and climate on hydrology and hydrologic ecosystem services, including flood risk, flashiness, and nutrient flows to individual urban ponds and to the Yahara lakes, using the Agro-IBIS-THMB model suite. We will investigate interactions of climate, impervious surfaces, and variation in tree canopy cover on hydrology and nutrient flow to identify driver interactions and thresholds associated with abrupt ecological change (H3a). To assess the potential for abrupt change in urban ponds and the Yahara lakes, we will conduct factorial simulation experiments using Agro-IBIS and THMB to explore scenarios that incorporate interactions with the urban pondscape and vary the amount, type, and spatial configuration of urban LULC, including green and grey infrastructure, under alternative climate conditions (H3b). H3b intentionally parallels H2b to allow us to examine this question via different methodologies. We will use our long-term UHI spatiotemporal temperature database to modify our base climate dataset to drive model runs. We will determine LULC combinations that reduce flashiness and nutrient delivery to the lakes in response to heavy rainfall events, and combinations as well as thresholds in drivers that cause state changes in urban ponds. Natural vegetation can mitigate flooding and reduce nutrient transport following rain events, but this capacity will be exceeded at some point. We will also assess co-benefits and ecosystem services of green infrastructure, e.g., as refuges or stepping stones for native species in the face of changing climate, supporting outdoor recreation and human wellbeing (Wu 2014; Jenerette 2018).



Q3. How do external drivers interact with aquatic invasive species to regulate water quality?
There is a pervasive view that when more than one driver influences a response variable, effects will be larger than expected and the likelihood of abrupt change will increase (i.e., *synergistic interactions* among drivers) (Côté et al. 2016). However, examination of this idea reveals ambiguous outcomes. On one hand, regime shifts frequently result from interactions among multiple drivers, particularly in aquatic settings that are affected by both terrestrial and aquatic drivers (Rocha et al. 2015, 2018). On the other hand, the expectation of synergistic interactions is not well supported by experiments involving 2-3 drivers. Instead, *additive* (drivers act independently) and *antagonistic* (drivers interact to lessen the response) outcomes are more common (Jackson et al. 2016, Côté et al. 2016). And as a third outcome, or perhaps an extreme version of antagonism, Kelly et al. (2017) suggested that instead of interacting, one driver over-rides or negates the effect of another in a '*sequence of stressors*' to shape community and ecosystem dynamics. In this case, the first driver is still present but is no longer influential.

Lake Mendota is an ideal ecosystem to test these concepts of (potentially) interacting drivers and abrupt change. The lake is exposed to both external and within-lake biotic drivers and has experienced a series of abrupt changes in water clarity and algal bloom dynamics (i.e., water quality) over the past two decades. Madison has experienced 7 consecutive years of above-normal precipitation, including 4 of the 5 highest annual totals over the 130-year period of record (see Fig 7). This trend in annual precipitation is largely due to an increase in the magnitude and frequency of heavy rainfall that is occurring across the north-central

U.S. (Mallakpour & Villarini 2015). Large rain events are particularly effective at mobilizing and transporting sediments and nutrients. For Lake Mendota, these rains are falling on an increasingly urbanized watershed affecting nutrient and pollutant delivery to the lake, as will be investigated in Section 2. Extreme rain events deliver high P loads to the lake (Carpenter et al. 2015, 2018), and years with multiple events (e.g., 2007-09, 2018-19) lead to high P concentrations in the lake during spring mixing (Fig. 9); a condition that favors high phytoplankton abundance in the lake (Lathrop et al. 1998).

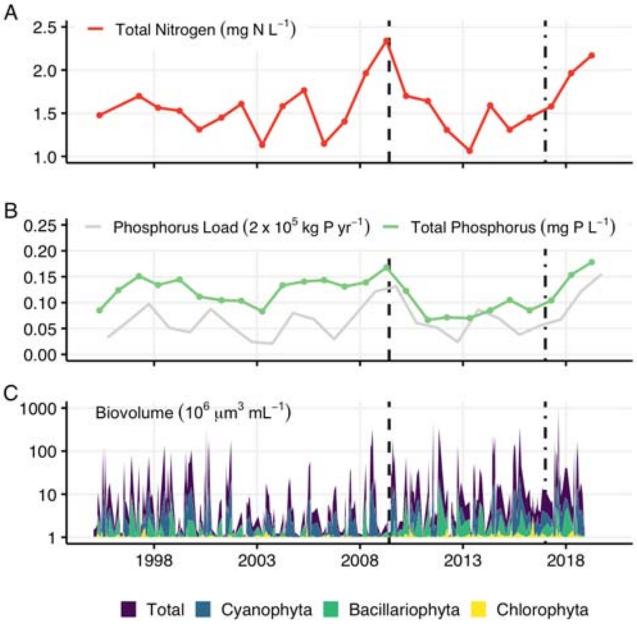


Figure 9. Total nitrogen concentration (A), Total phosphorus concentration (green line) and estimated load (gray line) into Lake Mendota (B), and phytoplankton biovolume (C) for 1995-2019. N, P concentrations are during spring mixing, an indicator of nutrient availability for the summer growing season. Vertical lines indicate spiny water flea invasion (dashed) and zebra mussel (dash-dot) establishment. Note log-scale for phytoplankton biovolume. Phosphorus loading data are preliminary estimates from USGS.

Within the lake, Mendota's food web has recently undergone two abrupt changes due to the invasion and proliferation of *Bythotrephes* in 2009 (Walsh et al. 2016a), and discovery of a small population of zebra mussels (*Dreissena polymorpha*) in 2015 that subsequently increased by 5 orders of magnitude in the next 2 years (Fig. 10). Both invasions led to food-web transitions that occurred at approximately the same time as shifts in nutrient loading to the lake, but with unexpected water quality consequences. Counterintuitively, with the *Bythotrephes* invasion, P concentrations declined dramatically but phytoplankton blooms increased, whereas N and P concentrations increased but the frequency of blooms appeared unaffected by the *Dreissena* invasion (Fig. 9). Thus, it remains unclear if and how these abrupt food web changes caused by invasive species interact with and modify the consequences of more extreme rainfall events in the watershed. To address this question, new research activities will focus on nutrient inputs and the effects of *Dreissena* and will be integrated with long-term data and prior studies on mechanisms underlying the abrupt shifts triggered by *Bythotrephes* (e.g., Walsh et al. 2016a, 2019a). We propose three initiatives to quantify: (1) nutrient inputs and nutrient patterns in the lake associated with large rain events; (2) effects of *Dreissena* and nutrients on phytoplankton composition and abundance; and (3) whether the interactions among invasive species and abiotic drivers that have led to abrupt changes in phytoplankton dynamics are independent, interactive, or sequential.

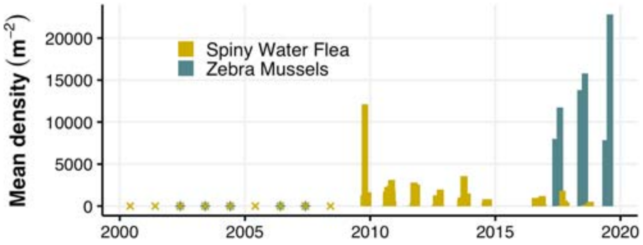


Figure 10. Mean densities of spiny water flea (SWF) from zooplankton tows and adult zebra mussels in rocky littoral sites in Lake Mendota. SWF samples were not collected in 2016, and 2019 samples are not yet reported.

Q3.1. What are effects of extreme rain events on nutrients and phytoplankton in Lake Mendota?
Extreme rain events affect lakes by rapidly delivering large amounts of water and terrestrial materials and by physically disrupting the water column. Although physical disruption can sometimes be intense, these effects are typically short-lived, and it is the input of materials from the watershed that usually has larger and longer ecological impacts on lakes (Klug et al. 2012). A notorious example is the sequence of large rain events that triggered the record-setting harmful algal blooms in Lake Erie in 2011 (Michalak et al. 2013). Here, we propose to examine storm effects within Lake Mendota. This builds on prior watershed studies

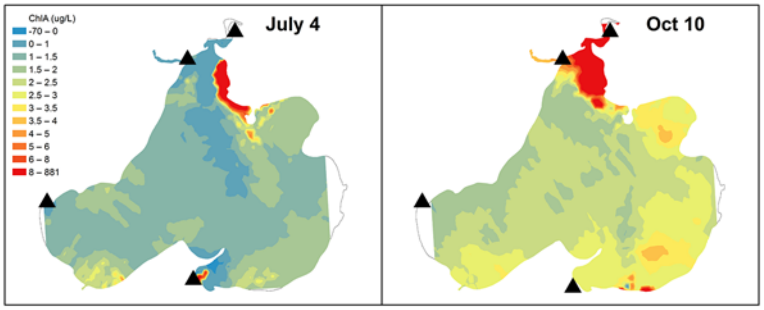


Figure 11. Spatially resolved chlorophyll a concentrations in Lake Mendota on July 4 and Oct 10 2016 quantified using the FLAMe platform. Triangles indicate location of tributaries and storm drainage. Data and maps from Loken 2018.

of P delivery by storms, especially from croplands (Lathrop 1992; Motew et al. 2017) and will dovetail with research activities in Section 2. Routine NTL sampling captures seasonal spikes in N and P during years with record-setting rains (e.g., 2009, 2018; Fig. 9), but sampling frequency is not sufficiently resolved to parse out effects of individual events. We have observed high chlorophyll concentrations near tributary confluences (Loken 2018; Fig. 11) and mapped chemically distinct plumes in the lake following storms (Stadler et al. 2019). However, we have not connected material-rich storm flows to patterns in lake chemistry, either in general or as a function of sub-watershed land cover, nor have we determined if these inputs trigger phytoplankton blooms.

Hypotheses: **H3.1a:** *Large rain events create spatial variability in Lake Mendota by delivering water that is chemically distinct from the lake, and chemically distinct among watersheds with differing land uses.* **H3.1b:** *Confluence areas receiving storm inputs become hotspots for phytoplankton blooms to take hold.*

Approach: To evaluate within-lake effects of storms and test H3.1a, we will map several physical and chemical parameters on a regular (2-4X per ice-free month) and episodic basis using the FLAMe platform (Crawford et al. 2015). In situ sensor ('buoy') data from the center of the lake and a new near-shore location will be used to examine lake responses at a finely resolved temporal scale. The near shore sensor and mapping efforts are discussed further in the Approach for Question 3.2 below. Evaluating potential land cover effects (H3.1a) will also be informed by agency data and sampling of urban runoff. Daily N, P, and sediment load estimates for 4 of Lake Mendota's 6 tributaries (including one which drains a predominantly urban basin) are available from USGS, as is water chemistry data from storm sewers from prior USGS and WI DNR studies to provide additional information about composition of inputs among a range of rain events. We will also sample storm sewers and urban streams in parallel with FLAMe mapping. Sites will include downstream outlets from pond sites in Section 2 and water chemistry analyses will match those used in the urban pond study.

Q3.2. What are mechanisms of zebra mussels and shifting nutrient influence on phytoplankton (especially cyanobacteria) composition and abundance?

Zebra mussels are powerful ecosystem engineers that can increase water clarity, favor cyanobacterial dominance, alter nutrient cycling, and shunt ecosystem productivity to benthic habitats (Strayer 2010). In Lake Mendota, however, we have not witnessed the water column clearing following *Dreissena* establishment that is often reported and had been predicted to occur in Lake Mendota (Reed-Andersen et al. 2000), nor has there been a shift toward buoyant cyanobacteria taxa such as *Microcystis* (reviewed by Higgins & Vander Zanden 2010). Nonetheless, the phytoplankton community has changed over the last 3 years. Although the annual abundance patterns have not noticeably changed (Fig. 9), diversity has unexpectedly increased (Fig. 12), and preliminary data suggest a shift in bloom timing (variability is high with only 3 years of data), and our single highest cyanotoxin measurement was collected in 2018. Further, bloom sightings in near-

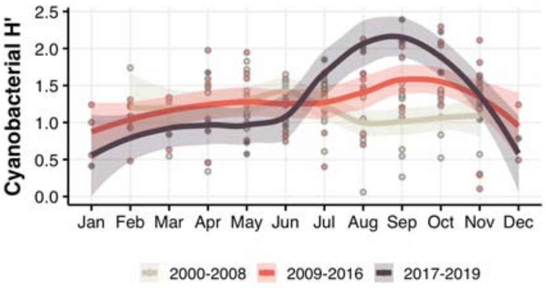


Figure 12. Cyanobacterial community diversity (Shannon's H') prior to (2000-2008), following spiny water flea invasion but before zebra mussel arrival (2009-2016), and after zebra mussel establishment.

shore areas have increased (Fig. 13), indicating a shift toward taxa capable of forming surface scums. *Dreissena* influence on phytoplankton communities often occur via two distinct mechanisms. First, these invaders are capable of selective consumption of phytoplankton (Vanderploeg et al. 2001) that can change taxonomic composition, although this effect typically reduces phytoplankton diversity and favors taxa such as *Microcystis*. Second, differential N and P excretion by *Dreissena* can change nutrient form, availability, and cycling to create conditions that may favor some phytoplankton taxa over others (Bykova et al. 2006, DeStasio et al. 2008).

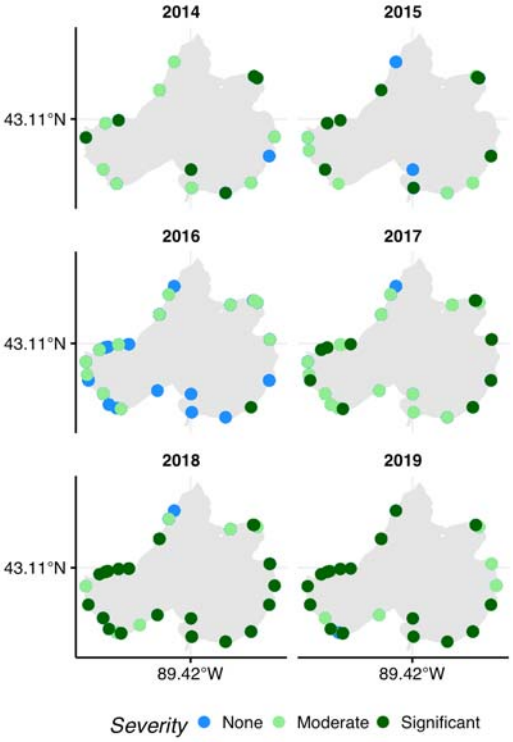


Figure 13. Severe algal blooms observed at shoreline monitoring stations on Lake Mendota. 2014-2019. Data: Clean Lakes Alliance

Cyanobacteria bloom proliferation is frequently attributed to N and or P enrichment (Huisman et al. 2018) and in Lake Mendota, as in many lakes, P limits productivity (Brock 1985; Schindler et al. 2016). Absolute concentrations of N, its form, and its abundance relative to P (N:P ratio) can also affect cyanobacterial community composition (Beversdorf et al. 2015; Weirich et al. 2019) and have been linked to toxin formation (Gobler et al. 2016; Steffen et al. 2017; Chaffin et al. 2018). As noted above, record high rainfalls over the past 4 years have driven concentrations of both nutrients up in Lake Mendota, and a swifter increase in P has lowered N:P ratios. Thus, regardless of, or in addition to, any effects *Dreissena* may have on N and P, we expect that precipitation-driven changes in N and P are also influencing phytoplankton dynamics. To understand how *Dreissena* and storm-driven nutrient loading are causing the observed changes in cyanobacteria composition and abundance, we will test the following hypotheses:

<u>Hypotheses</u>: ***H3.2a:*** *Shifts in cyanobacterial composition, timing, intensity, and toxicity bloom behavior are driven by differential consumption of phytoplankton by Dreissena,* ***H3.2b:*** *and/or indirectly via their differential retention/excretion of nutrients.* ***H3.2c:*** *Recent changes reflect changes in (a) total concentrations of N or (b) P or (c) N:P ratios.* ***H3.2d:*** *Relative amounts of ammonium (NH_4), nitrate (NO_3), and dissolved organic N (DON) control cyanobacterial communities, with DON speciation playing a major role in regulating toxin production*.

<u>Approach</u>: We will use laboratory mesocosm studies to quantify *Dreissena* feeding effects across a range of lake water nutrient concentrations and phytoplankton abundances to quantify changes in water column chlorophyll, particulate OM, and cyanobacterial assemblages (counts and DNA sequencing) (H3.2a). These experiments will also be used to estimate *Dreissena* effects on amounts and forms of N and P (H3.2b) and can be adapted to consider other factors (e.g., temperature, zooplankton composition), if needed. Results will be combined with data on lake nutrient concentrations and *Dreissena* abundances using a bioenergetic modeling approach (e.g., Reed-Andersen et al. 2000) applied at the whole-lake scale to compare changes attributable to *Dreissena* alone to those occurring in the lake (H3.2c, d).

NTL-Microbial Observatory researchers have collected microbe/cyanobacteria samples 1-2X/week (May-Oct) since 2000 and cyanotoxin samples since 2014 at the central sampling location in Lake Mendota. We will use these data to examine relationships between cyanobacterial communities and nutrient dynamics to evaluate H3.2c and H3.2d. Our metagenomic time series allows us to compare cyanobacterial taxa at strain-level resolution to ask whether some strains appear or disappear in years with extreme loading events. We will also evaluate whether the abundance and phylogenetic distribution of N-cycling genes (e.g., urea uptake, N-fixation) shift with these events. Further, we will opportunistically measure N-fixation rates as an indicator of community-level N-stress and relate this to toxin production during blooms, as there is strong evidence for a physiological link between N-stress and toxin production (Pimentel & Giani 2014; Harke & Gobler 2015). In addition to our continuing time series, we will perform short-term incubation (microcosm) experiments with lake water and nutrient additions. Our focus will be on N-species and their effects on toxin production (H3.2d), using ^{15}N-labeled N compounds (Gobler et al. 2016; Steffen et al. 2017). Finally, recent observations of shoreline blooms highlight spatial variability in cyanobacterial abundances. FLAMe mapping will emphasize coverage of the lake perimeter to quantify chlorophyll and phycocyanin as well as any influence of different sub-catchments on spatial variability in these areas. We will also add a nearshore monitoring station equipped with high-frequency measurements of temperature, phytoplankton pigments, and NO_3. Data from these sensors will be used to examine potential responses to extreme rain events (Q3.1). Instruments will be deployed at the Hasler Lab dock where we will collect manual samples for microbial community analysis and toxin measurements 1-2 times/week in the ice-free months.

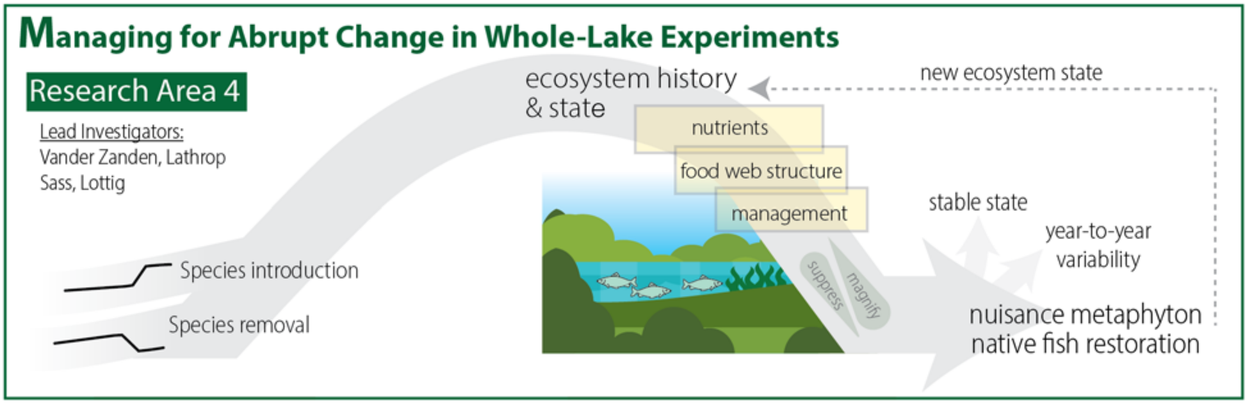
Q3.3. Do multiple drivers act independently, interactively, or sequentially?

This final question represents a synthesis of how different drivers may be influencing phytoplankton dynamics in Lake Mendota. Our goals are to identify on mechanisms involved in transitions from low to high nutrient conditions, establishment of new invaders, and changing phytoplankton dynamics, and to test the hypothesis regarding driver interactions.

Hypotheses: *Abrupt changes in phytoplankton composition and bloom timing reflect* ***H3.3a:*** *additive (independent),* ***H3.3b:*** *synergistic,* ***H3.3c:*** *antagonistic, or* ***H3.3d****: sequential effects of external drivers controlling nutrient inputs and internal drivers in the form of invasive species establishment.*

Approach: We will combine analysis of historic data with results from work described above that emphasizes mechanism and magnitude of nutrient and *Dreissena* influence. Retrospective analyses will include re-visiting prior relationships related to drivers of water quality in the 2000s and comparing these previous relationships to current conditions. These lead to a series of questions to be considered, such as, have zooplankton assemblages (especially *Bythotrephes* and *Daphnia*) changed following *Dreissena* establishment? Have relationships between *Bythotrephes* and water quality described by Walsh et al. (2016a, 2017, 2018a, 2019a) diverged in this current period of high nutrient loading and *Dreissena* abundance and, if so, how? What combination of drivers best explains changes in phytoplankton abundance over time?

NTL has a long history of leveraging statistical models to understand how ecosystems are responding to different drivers (e.g., Hansen et al. 2013; Walsh et al. 2019a; Carpenter et al. 2020). We will use this experience to develop time series models that help explain phytoplankton dynamics over the last three decades, with an emphasis on understanding how driver dynamics (i.e., effect sizes, interactions) and temporal dynamics of these drivers have changed. We will rely primarily on Multivariate autoregressive state-space models (MARSS; Holmes et al. 2012), and hierarchical general additive models (HGAMs; Pedersen et al. 2019) to better address these fundamental questions. MARSS models, for example, can integrate time-varying coefficients that will allow us to assess how the effect sizes and interactions of different drivers vary through time. The patterns in change through time can provide insights into, for example, if new drivers are overriding prior drivers (i.e., H3.3d) or have strong positive interactions (H3.3b). Hierarchical GAMs will allow us to quantify non-linear driver-response relationships and how those relationships are modified following abrupt changes in invasion dynamics (e.g., between pre-*Bythotrephes, Bythotrephes,* and *Dreissena* time periods). An additional advantage of HGAMs is that we can fit the models using appropriate error distributions and not rely on transformations of the data to accommodate normality constraints which will aid in interpretation of model results.



Q4. What causes intentional ecosystem manipulations to persist, revert, or lead to novel states?
In this final section, we propose two projects that provide another approach for studying abrupt ecological change and embrace opportunities provided by a long-term research program. Specifically, we plan a retrospective and a prospective study of two long-term ecosystem experiments. Long-term experiments are powerful tools for capturing delayed and often unexpected ecological responses and are especially appropriate when long-lived organisms and/or interacting drivers affect ecosystem dynamics (Dodds et al. 2012). Experiments also have the advantage of controlling the nature and timing of the treatment- a notable convenience for studying abrupt change. These experiments capitalize on the reality that many ecosystems are managed purposefully by humans to achieve a desired condition (Palmer et al. 2016) and management activities can be or can cause abrupt changes to an ecosystem. Pairing lake management with long-term studies allows us to test whether management-induced ecosystem shifts persist through time (i.e., are stable), whether the ecosystem returns to the original state, or if the ecosystem moves to some new configuration (Scheffer 1998). These two experiments had/have distinct motivations, but together they provide a broader opportunity to consider whether directed efforts to abruptly shift an ecosystem to an alternative state can be sustained over years to decades.

Q4.1: What are the interacting drivers that lead to different macrophyte states in a shallow lake?
Shallow lakes have provided an early example of abrupt ecosystem change and a case study for development of alternative state theory (e.g., Scheffer 1998; Scheffer & Carpenter 2003). These systems can shift from a turbid state (high phytoplankton abundance, low water clarity) to a clear water state (abundant macrophytes, high water clarity). Each state is maintained by several well-described feedback mechanisms and shifts between the two states are abrupt and non-linear. This theory is now used to manage lakes in the turbid state. For example, removal of fish such as common carp (*Cyprinus carpio*), whose feeding activities re-enforce the turbid state, has been used to push shallow lakes to the more desirable macrophyte-dominated clear water state (Jeppesen et al. 1990; Hansson et al. 1998; Scheffer 1998). This first retrospective project will examine such a management experiment in which most carp were removed from Lake Wingra in 2008. The intervention was successful in producing an abrupt shift from the turbid state to a clear water state (Lathrop et al. 2013) and water clarity has generally remained high, but variable among years (Fig. 14). However, an unexpected response to the clear water state was a significant expansion of invasive Eurasian watermilfoil (*Myriophyllum spicatum*; EWM) into deeper areas that previously lacked macrophytes (Fig. 15). EWM can grow in dense stands and reach the

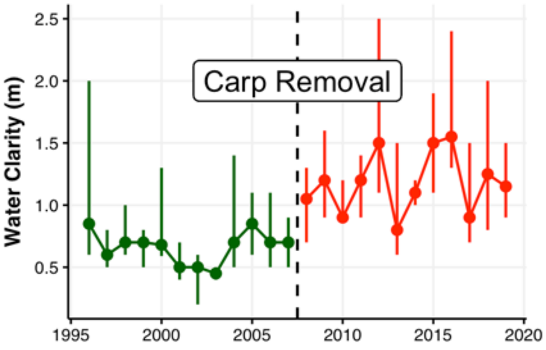


Figure 14. Median summer water clarity (measured as Secchi disc depth) in Lake Wingra 1995-2019. Vertical lines represent minimum and maximum values. Dashed line denotes when carp removal manipulation occured.

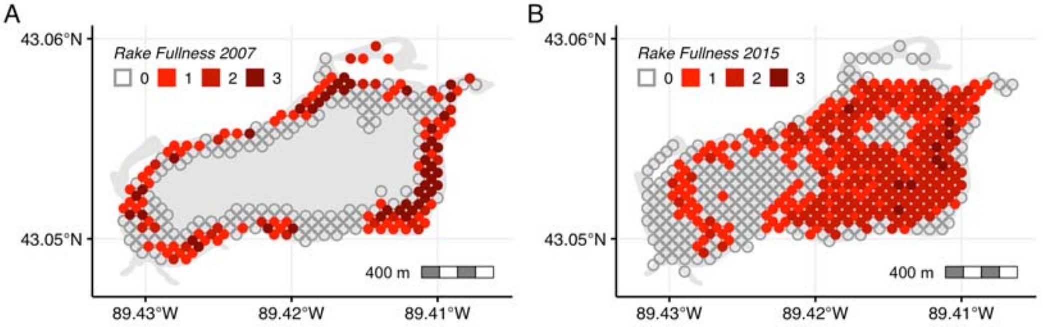


Figure 15. Eurasian water milfoil during turbid lake state conditions in 2007 prior to carp removal (A) and in 2015 illustrating the macrophyte spread throughout the lake.

water surface, and in some years, these plants became overgrown with filamentous algae (metaphyton; Fig. 16A). Presence of metaphyton has varied among years; when it occurs, EWM and metaphyton severely degrade lake aesthetics and recreational activities. These conditions represent an unintended consequence of shifting the lake to the macrophyte state and suggest a modification to the conventional model of two alternative states in shallow lakes. Our proposed modification was hinted at by Irfanullah & Moss (2005) and recognizes the potential for a desirable (moderate macrophyte biomass) and undesirable (high macrophyte biomass and metaphyton overgrowth) version of the macrophyte-dominated state (Fig. 16B), the latter of which can be thought of as the 'third state.' The question is: what conditions lead to one macrophyte state or another? The ecosystem state in a given year is expected to result from interactions between light, nutrients, and grazing, and we will test these specific hypotheses:

Hypotheses: ***H4.1a:*** *High water clarity during spring gives macrophyte growth a jump start, allowing them to reach the lake surface and provide substrate for metaphyton, and* ***H4.1b*** *the metaphyton state is favored by high water column nutrient concentrations during summer combined with high zooplankton grazing on phytoplankton.*

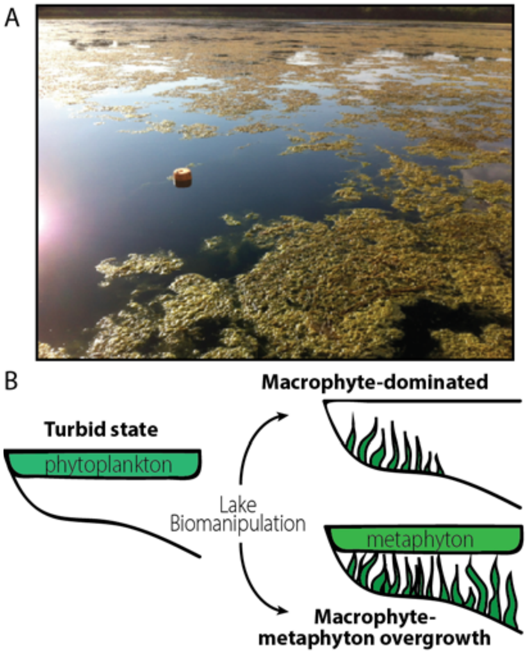


Figure 16. (A) Lake Wingra in July 2012 showing excessive macrophtye and metaphyton overgrowth. (B) Two potential outcomes of a biomanipulation of a turbid (phytoplankton-dominated) lake. The moderate macrophyte-dominated state (top) is the desirable outcome. The macrophyte-metaphyton overgrowth state (bottom) is characterized by excessive macrophyte and filamentous metaphyton biomass reaching the surface, and the less desirable outcome.

Approach: We will use NTL core data for a retrospective analysis of nutrient, water clarity, chlorophyll, macrophytes, and metaphyton in Lake Wingra over the past two decades complemented with occasional lake-wide macrophyte surveys from WI DNR and air photos and satellite imagery for macrophyte coverage (Silva et al. 2008; Villa et al. 2018) to quantify shifts between the two macrophyte states. We will test whether years of metaphyton dominance are associated with high spring water clarity, high summer water column nutrients, and/or abundant zooplankton grazers. We will also develop a seasonally-dynamic lake model designed for evaluating interactions among metaphyton, macrophytes, and phytoplankton to explore the drivers and interactions among these groups and perhaps reveal other hidden factors which may regulate metaphyton overgrowth.

Q4.2. Does food web structure influence restoration of native biota and control of invasive species?

Invasive species are a leading cause of biodiversity decline, particularly in aquatic ecosystems where species losses have been particularly acute (Reid et al. 2019). In many Wisconsin lakes, threats posed by invasive species can co-occur with climate change effects. Lake warming can jeopardize native coldwater fishes by limiting available habitat (Sharma et al. 2007; Magee et al. 2019b). Cisco, a pelagic forage fish that can strongly influence zooplankton dynamics (Rudstam et al. 1993), is emblematic of coldwater fishes facing these dual threats in many Midwestern lakes. Climate models predict 25-70% of cisco populations will be extirpated by 2100 due to loss of deep water oxythermal habitat (Sharma et al. 2011). Extirpations have already been observed in the southern portion of their range (Honsey et al. 2016), including several lakes in Wisconsin (Rypel et al. in prep). At the same time, another pelagic forage fish, rainbow smelt (*Osmerus mordax*) presents a challenge for cisco. Rainbow smelt are native to the north Atlantic coast and have invaded many lakes in the Upper Midwest and Canada and are expected to continue to spread (Mercado-Silva et al. 2006). Smelt feed on juvenile cisco and compete with adult cisco, and thus can be a direct cause of cisco extirpation (Evans & Loftus 1987; Hrabik et al. 1998). Yet most studies of the viability of native cisco populations have focused on habitat availability (Jacobson et al. 2008, 2010; Honsey et al. 2016) and have not considered biotic interactions (Roth et al. 2010).

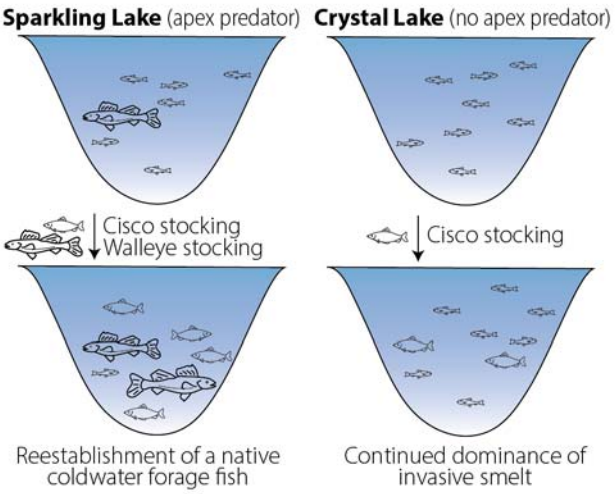


Figure 17. Experimental reintroduction of the native coldwater forage fish, cisco, into Sparkling and Crystal Lakes, WI. Both lakes have been invaded by rainbow smelt. Sparkling contains the apex predator walleye, and will continue to be stocked with walleye. Crystal lacks apex predators. We will also monitor two reference lakes, Big Muskellunge (cisco only) and Anderson (rainbow smelt only).

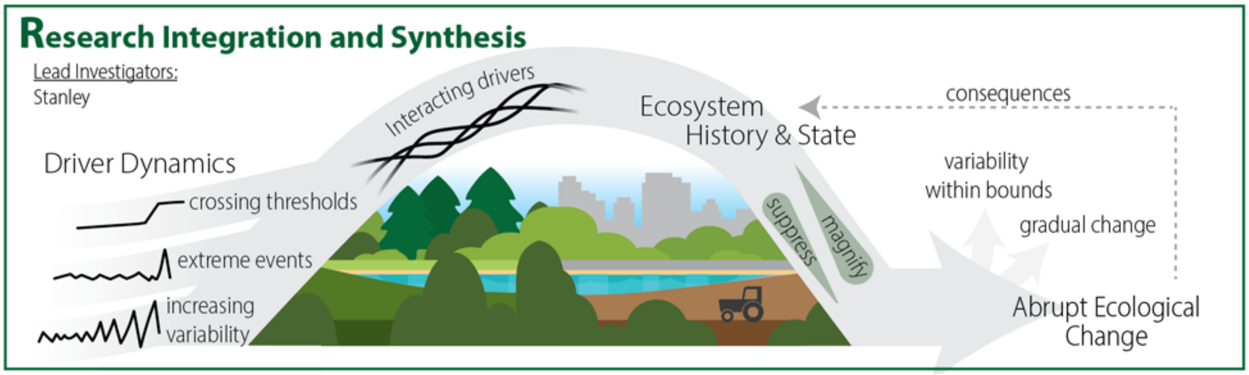
We propose an ecosystem experiment intended to test the role of apex predators (piscivorous fishes) in mediating the interaction between cisco and rainbow smelt in a species reintroduction context (Fig. 17). Apex predators can regulate community structure and have profound ecological effects that extend to the base of the food web (Pace et al. 1999; Terborgh & Estes 2010). This can include mediating interactions among its prey species (Abrams 1987), and this effect has been reported for smelt-cisco interactions. For example, heavy stocking of the apex predator, walleye into two different lakes reduced the abundance of smelt via selective predation, which shifted the competitive advantage from smelt to cisco and allowed small resident cisco populations to recover (Krueger & Hrabik 2005). This idea that interactions between native and invasive forage fishes is mediated by the presence of a predator is the foundation for our proposed question.

Hypothesis: ***H4.2a*** *The presence of an apex predator mediates the interactions between native and invasive coldwater forage fishes, and this interaction can determine the outcome of native species restoration and invasive species control.*

Approach- We will introduce native cisco into two core NTL lakes, Sparkling and Crystal, both of which have suitable oxythermal habitat for this species. Both lakes have been invaded by smelt and lost their historic populations of cisco (Hrabik et al. 1998). Sparkling Lake has apex predators (muskellunge and walleye) and will receive additional walleye stocking. Crystal Lake has no apex predator. By reintroducing native cisco into two lakes with distinctly different food web configurations (no apex predator in Crystal, abundant apex predator in Sparkling), we will test the hypothesis that presence of a native apex predator (walleye) facilitates the reestablishment of cisco by affecting the nature and/or magnitude of interactions between smelt and cisco. We will take a long-term approach to this experiment, as interactions among these species may vary over time in response to differences in generation times or inter-annual variabil in recruitment success among these three species. These circumstances are conducive to delayed effects or surprises, and thus merit more than 2-3 years of examination.

Fish population and lake monitoring will begin a year prior to walleye and/or cisco reintroduction and will continue throughout the duration of this funding cycle, with the aim of generating a decadal or longer time series. Cisco will be transferred from a nearby lake by WI DNR personnel who have done this procedure before. Walleye will come from a second neighboring lake. We will also sample two reference lakes to account for any climate-driven changes (Carpenter 1998). Big Muskellunge Lake is a core NTL lake and contains cisco but no smelt. Anderson Lake is 25 miles northeast of the core NTL lakes, and contains smelt but no cisco. Smelt and cisco populations will be quantified by hydroacoustic surveys using standard NTL methods 4 times/year along with diet and growth studies (smelt, cisco, walleye) to provide a basis for understanding predation and competitive interactions. Routine NTL limnological sampling will be expanded to Anderson Lake during this period. At the end of this grant cycle, we will revisit our results to assess whether sampling frequencies can be maintained or reduced for subsequent longer-term monitoring.

INTEGRATION AND SYNTHESIS



The four research sections address questions from different angles and focus on different settings and response variables. Although all are linked by the common interest in causes and consequences of abrupt change, different questions, approaches, and study systems will inevitably lead investigators down different paths. However, we are motivated to consider our results in a larger context and extract generalities from these findings. Thus, we propose two final activities to assure synthesis across the different facets and scales of our research. First, we will co-teach a graduate seminar designed to assess the current state-of-the-science regarding empirical observations of abrupt vs. gradual ecological change. The seminar will be led jointly by NTL-affiliated faculty, as we have done successfully with other current topics in ecology. Indeed, the 2015 report on re-envisioning environmental research and education at NSF states, "*Preparing for and responding to future rapid environmental change, including extreme events, requires a different perspective and skillset than planning and designing for common or average conditions"* (Advisory Committee for Environmental Research and Education 2015). We will develop a structured review of case studies to understand common themes among examples of abrupt ecological change as well as identify gaps in understanding and opportunities for future research.

Second, we will convene a working group to synthesize our insights about abrupt ecological change in NTL lakes and their surrounding landscapes and consider these insights relative to other similar long-term ecological studies. Informed by current ecological examples and theory, our goal is to extend understanding from the individual questions presented above to broader generalities about ecosystem change. Questions to be addressed include: Are there common circumstances that lead to abrupt changes across lakes? Are these circumstances distinct for ecosystem-wide abrupt changes vs. abrupt changes in, for example, individual populations or specific ecosystem attributes? Do we see consistent evidence for interactions among drivers, or do drivers tend to act in an additive or sequential fashion? In short, what have we learned from these diverse tests and examinations of potential agents of abrupt change, and of abrupt changes themselves? Additional high-priority questions are listed by Turner et al. (2020), providing us with a useful guide for these synthesis activities. We anticipate that these working group activities will generate papers emerging from cross-project comparisons, insights and additions to current theory, as well as identifying critical future research needs and opportunities.

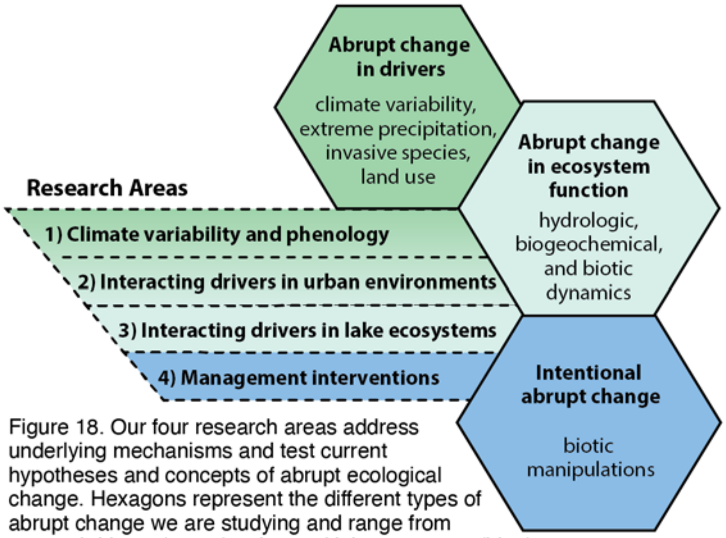


Figure 18. Our four research areas address underlying mechanisms and test current hypotheses and concepts of abrupt ecological change. Hexagons represent the different types of abrupt change we are studying and range from external drivers (green) to internal lake responses(blue).

Collectively, research activities presented in this proposal are motivated both by our increasing awareness of changes in climate, land use, and species gains and losses that are impinging on the NTL study region, and by a growing number of examples of rapid changes that are occurring in and around our study lakes. This reality is by no means unique to NTL, providing a clear incentive to place observations and mechanisms underlying abrupt change into a broader framework to advance ecological understanding. As we have described, our approach to for studying abrupt ecological change is one of multiple approaches (Fig. 18). We consider both single and multiple drivers that include an increasingly unpredictable climate, growing urban land use, new species, and human efforts to push ecosystems in a particular direction; response variables range from population genetics to whole ecosystems. We expect this diversity of views to lead to novel insights. Regardless of the specific research area, driver, or response being considered, all research activities are built on the foundation of long-term data and understanding. We are keenly aware that ecological changes such as species invasions, disappearance of favored sport fish, or increasingly frequent harmful algal blooms attract wide attention in Wisconsin. This attention presents us with an opportunity and responsibility to understand why these events are occurring, to share this understanding broadly, and increase awareness of lakes and environmental change in a rapidly changing world. To this end, education at all levels, outreach and communication, and partnerships with agencies will continue to be points of emphasis for us over the next six years and beyond.

Education and Outreach Activities

Expanding and strengthening education and outreach activities have been a priority for NTL and in this proposal, we continue our commitment to successful long-term activities and include a set of new initiatives. As we described in the Result of Prior Research section, the long-standing goal of our education and outreach activities has been, and continues to be, to improve awareness and understanding of the ecology of lakes, and of science in general for students at all stages of learning, resource managers, decision-makers, and the general public. These broad and ambitious goals are addressed through multiple activities that involve education at all levels, outreach and education, and promoting a diverse and inclusive environment for learning about lakes and the environment.

Graduate Students: Graduate student training is a cornerstone of NTL educational activities, and these early-career scientists are active participants and significant contributors to our research (e.g., see list of Top 10 publications in Results of Prior Funding), education, and outreach accomplishments. NTL faculty and staff will continue to provide workshops and seminars for graduate students, prioritizing information management, data analysis, sensors use and construction, science communication, and the science of abrupt ecological change. Capitalizing on our experience with lake sensing platforms, we held a workshop led by NTL staff in 2019 for graduate students and Ph.D.-level researchers from other universities and state and federal agencies on the use of these sensors. We now plan to offer the workshop every other year starting in 2020 for any interested scientist, with top priority given to graduate students, and will advertise this opportunity through the LTER Network. The week-long program provides an introduction to electronics and sensors that measure physical and chemical variables in freshwater, and attendees create their own sensor systems during the workshop. Finally, to ensure that new graduate students are familiar with NTL opportunities, we will hold graduate student workshops each fall to provide an overview of NTL and the broader LTER network, ongoing and planned research activities, data availability, and ways for students to get more involved. This will be oriented toward new graduate students working on lake-related science, but all interested graduate students will be welcomed. There are currently 15 NTL graduate students and we expect similar participation over the next 6 years.

Undergraduates: NTL personnel engage in several undergraduate educational activities, from use of NTL research and data in classrooms to providing hands-on experiences through independent research projects, assistantships, and REU fellowships. Further, we have support for 2 additional summer undergraduate fellowships/year supported by endowment funds. These awards are identical to REU awards and allow us to have a critical mass of undergraduate researchers who can work together and support each other. Fellows work in partnership with graduate students, providing an additional graduate training opportunity to develop mentoring skills. We have had good success with fellows presenting their findings at scientific meetings and being authors on publications, and most of these undergraduates have gone on to graduate school and scientific careers. We will continue to promote this level of achievement, and to improve the quality of the experience, we will conduct end-of-summer interviews with fellows and formalize our tracking of career trajectories of these students to better understand student outcomes and the impact of these opportunities on their professional lives.

K-12 Activities: NTL Schoolyard program (SYLTER) is a foundation of our K-12 activities and involves students from four schools near Trout Lake Station. Approximately 100 students/year participate in a “Winter Limnology” program where students spend part of their day getting hands-on experience in the field then conducting experiments and making observations in the lab. Trout Lake Station and the Lac du Flambeau Band of Lake Superior Chippewa are co-located in the same community and >25% of our participants are of Native American descent. A goal of our SYLTER is to engage this community and SYLTER provides an early opportunity for interactions between students from the tribal and non-tribal schools. Activities are designed to create collaborative learning groups and have students from different schools work together. Following site review recommendations, we initiated an effort with the K-12 teachers associated with our SYLTER program, many of whom we have long-standing relationships with, to develop our “draw a lake” assessment efforts and generate additional assessment tools to address how SYLTER activities are meeting and contributing to Next Generation Science Standards. The results and protocols of the assessments will be integrated into our NTL-IM system and shared with other LTER sites at PI meetings and LTER All Scientist meetings.

Promoting Diversity and Inclusivity: As mentioned briefly in our responses to prior reviews, expanding the diversity of students involved in NTL and supporting an inclusive workplace environment are ongoing goals. We have had recent successes in recruiting graduate students from under-represented groups assisted by offering RA and other support from NTL packaged with 2-year Advanced Opportunity Fellowships from UW-Madison and will continue these efforts and build on our growing informal network of contacts to recruit students. We also see an opportunity to increase the involvement of underrepresented undergraduate students via our summer research fellowship program described above. We will pursue partnerships with the Center for Education Opportunity and the STEM Diversity Network here on-campus for guidance and assistance in recruiting undergraduates, and these efforts will be augmented by promoting/advertising fellowship opportunities through the UW-Madison SACNAS chapter, ESA-SEEDS, and the Diversity Joint Venture for Conservation Careers.

A second set of activities that have already been initiated include creation of a standing committee on Diversity, Equity, and Inclusion and development of a workshop that addresses diversity, inclusion, and workplace climate, especially as they relate to national concerns about negative experiences during field study and at field stations (Clancy et al. 2014). We are taking steps internally to improve our operations, codes of conduct, and student and staff training to create an informed and more inclusive climate. This will include a "Wellness in the Northwoods" workshop early in the next funding cycle that will include TransAlly, bullying and intimidating behavior, and suicide prevention training for NTL PIs and students. PI Gerrish is also collaborating with LTER field site leaders to build a network of workshop facilitators who can provide training and resources to field stations, LTER sites, and professional organizations.

Outreach and Communication: Outreach and communications activities intended to raise awareness and translate NTL science to policymakers, resource managers, and the general public will continue to be an emphasis for us. This includes providing support for science communications and outreach specialist Adam Hinterthuer to facilitate media interactions, promote NTL research, and assist with and coordinate activities. We plan to continue supporting activities such as 'Science on Tap' events in both southern and northern Wisconsin, Open House events at Trout Lake Station and the Hasler Lab of Limnology, leading graduate seminars in science communication, and coordinating boat trips on Lake Mendota for a wide range of groups. Innovative art/science collaborations have also been an integral part of the NTL outreach and communication efforts since 2006 and have helped motivate discussions about developing informed visions for the future. We will support 1-3 artists in residence at Trout Lake Station each summer, which provides a unique opportunity for both artists and scientists to collaborate on art-science communication projects. We now look to expand this residence program to include scientist and artist co-mentorship of college students. This expansion is intended to 1) grow regional community connections around art and science; 2) cultivate student interests in communication of science (a much-needed specialty); 3) disseminate science findings/ NTL research to a broader regional audience; 4) develop communication outlets and user-bases that sustain the network; and 5) strive to include first-generation, Native American and underrepresented participants as mentors and students.

RELATED RESEARCH PROJECTS

NTL has a long history of leveraging other funding sources, projects, and data to enhance our research, education, and outreach activities. We will continue to pursue these opportunities in the upcoming funding cycle. However, with three exceptions, activities described in this proposal do not rely on existence or acquisition of such funds. The three exceptions involve partnerships with the WI DNR. WI DNR is responsible for fish collections that are part of proposed research in (1) Q1.1 and (2) fish additions in Q4.2. Both efforts are spearheaded by WI DNR scientist and NTL senior personnel Greg Sass. Third, most water chemistry for YLD lakes has been analyzed at the Wisconsin State Laboratory of Hygiene through support provided by WI DNR. This arrangement has been in place since 1994 when YLD lakes were brought into NTL. All commitments have been approved by UW and WI DNR for the upcoming funding cycle.

REFERENCES CITED

Abrams, P.A. 1987. Indirect interactions between species that share a predator: Varieties of indirect effects. Pages 38–54 *in* W. C. Kerfoot and A. Sih, editors. Predation: direct and indirect impacts on aquatic communities. University Press of New England, Dartmouth, N.H.

Advisory Committee for Environmental Research and Education. 2015. America's Future: Environmental Research and Education for a Thriving Century. A Report by the NSF Advisory Committee for Environmental Research and Education. 48 pp. https://www.nsf.gov/news/news_images.jsp?cntn_id=136041&org=NSF

Baldocchi, A.K., D.E. Reed, L.C. Loken, E.H. Stanley, H. Huerd, and A.R. Desai. in review. Resolving space and time variation of lake-atmosphere carbon dioxide fluxes using multiple methods. Biology. doi:10.1002/essoar.10501554.1

Bastviken, D., M. Olsson, and L. Tranvik. 2003. Simultaneous measurements of organic carbon mineralization and bacterial production in oxic and anoxic lake sediments. Microbial Ecology 46:73–82. doi:10.1007/s00248-002-1061-9

Batt, R.D., S.R. Carpenter, and A.R. Ives. 2017. Extreme events in lake ecosystem time series. Limnology and Oceanography Letters 2:63–69. doi:10.1002/lol2.10037

Beaulieu, J.J., T. DelSontro, and J.A. Downing. 2019. Eutrophication will increase methane emissions from lakes and impoundments during the 21st century. Nature Communications 10:1375. doi:10.1038/s41467-019-09100-5

van Bergen, T.J.H.M., N. Barros, R. Mendonça, R.C.H. Aben, I.H.J. Althuizen, V. Huszar, L.P.M. Lamers, M. Lürling, F. Roland, and S. Kosten. 2019. Seasonal and diel variation in greenhouse gas emissions from an urban pond and its major drivers. Limnology and Oceanography 64:2129–2139. doi:10.1002/lno.11173

Beversdorf, L.J., S.D. Chaston, T.R. Miller, and K.D. McMahon. 2015. Microcystin mcyA and mcyE gene abundances are not appropriate indicators of microcystin concentrations in lakes. PLOS ONE 10:e0125353. doi:10.1371/journal.pone.0125353

Björnerås, C., G.A. Weyhenmeyer, C.D. Evans, M.O. Gessner, H.-P. Grossart, K. Kangur, I. Kokorite, P. Kortelainen, H. Laudon, J. Lehtoranta, N. Lottig, D.T. Monteith, P. Nõges, T. Nõges, F. Oulehle, G. Riise, J.A. Rusak, A. Räike, J. Sire, S. Sterling, and E.S. Kritzberg. 2017. Widespread increases in iron concentration in European and North American freshwaters. Global Biogeochemical Cycles 31:1488–1500. doi:10.1002/2017GB005749

Blaszczak, J.R., M.K. Steele, B.D. Badgley, J.B. Heffernan, S.E. Hobbie, J.L. Morse, E.N. Rivers, S.J. Hall, C. Neill, D.E. Pataki, P.M. Groffman, and E.S. Bernhardt. 2018. Sediment chemistry of urban stormwater ponds and controls on denitrification. Ecosphere 9:e02318. doi:10.1002/ecs2.2318

Both, C., M. van Asch, R.G. Bijlsma, A.B. van den Burg, and M.E. Visser. 2009. Climate change and unequal phenological changes across four trophic levels: Constraints or adaptations? Journal of Animal Ecology 78:73–83. doi:10.1111/j.1365-2656.2008.01458.x

Botta, F., D. Dahl-Jensen, C. Rahbek, A. Svensson, and D. Nogués-Bravo. 2019. Abrupt change in climate and biotic systems. Current Biology 29:R1045–R1054. doi:10.1016/j.cub.2019.08.066

Boyer, T., and S. Polasky. 2004. Valuing urban wetlands: A review of non-market valuation studies. Wetlands 24:744–755. doi:10.1672/0277-5212(2004)024[0744:VUWARO]2.0.CO;2

Brock, T.D. 1985. A eutrophic lake: Lake Mendota, Wisconsin. Springer-Verlag, New York

Bruce, L.C., M.A. Frassl, G.B. Arhonditsis, G. Gal, D.P. Hamilton, P.C. Hanson, A.L. Hetherington, J.M. Melack, J.S. Read, K. Rinke, A. Rigosi, D. Trolle, L. Winslow, R. Adrian, A.I. Ayala, S.A. Bocaniov, B. Boehrer, C. Boon, J.D. Brookes, T. Bueche, B.D. Busch, D. Copetti, A. Cortés, E. de Eyto, J.A. Elliott, N. Gallina, Y. Gilboa, N. Guyennon, L. Huang, O. Kerimoglu, J.D. Lenters, S. MacIntyre, V. Makler-Pick, C.G. McBride, S. Moreira, D. Özkundakci, M. Pilotti, F.J. Rueda, J.A. Rusak, N.R. Samal, M. Schmid, T. Shatwell, C. Snorthheim, F. Soulignac, G. Valerio, L. van der Linden, M. Vetter, B. Vinçon-Leite, J. Wang, M. Weber, C. Wickramaratne, R.I. Woolway, H. Yao, and M.R. Hipsey. 2018. A multi-lake comparative analysis of the General Lake Model (GLM): Stress-testing across a global observatory network. Environmental Modelling & Software 102:274–291. doi:10.1016/j.envsoft.2017.11.016

Buma, B. 2015. Disturbance interactions: Characterization, prediction, and the potential for cascading effects. Ecosphere 6:1–15. doi:10.1890/ES15-00058.1

Butitta, V.L., S.R. Carpenter, L.C. Loken, M.L. Pace, and E.H. Stanley. 2017. Spatial early warning signals in a lake manipulation. Ecosphere 8:e01941. doi:10.1002/ecs2.1941

Bykova, O., A. Laursen, V. Bostan, J. Bautista, and L. McCarthy. 2006. Do zebra mussels (Dreissena polymorpha) alter lake water chemistry in a way that favours Microcystis growth? Science of The Total Environment 371:362–372. doi:10.1016/j.scitotenv.2006.08.022

Cadenasso, M.L., S.T.A. Pickett, and K. Schwarz. 2007. Spatial heterogeneity in urban ecosystems: Reconceptualizing land cover and a framework for classification. Frontiers in Ecology and the Environment 5:80–88. doi:10.1890/1540-9295(2007)5[80:SHIUER]2.0.CO;2

Carpenter, S.R. 1998. The need for large-scale experiments to ssess and predict the response of ecosystems to perturbation. Pages 287–312 *in* M. L. Pace and P. M. Groffmann, editors. Successes, Limitations, and Frontiers in Ecosystem Science. Springer New York, New York, NY. doi:10.1007/978-1-4612-1724-4_12

Carpenter, S.R., B.M.S. Arani, P.C. Hanson, M. Scheffer, E.H. Stanley, and E. Van Nes. 2020. Stochastic dynamics of Cyanobacteria in long-term high-frequency observations of a eutrophic lake. Limnology and Oceanography Letters:6. doi:10.1002/lol2.10152

Carpenter, S.R., E.G. Booth, and C.J. Kucharik. 2018. Extreme precipitation and phosphorus loads from two agricultural watersheds. Limnology and Oceanography 63:1221–1233. doi:10.1002/lno.10767

Carpenter, S.R., E.G. Booth, C.J. Kucharik, and R.C. Lathrop. 2015. Extreme daily loads: Role in annual phosphorus input to a north temperate lake. Aquatic Sciences 77:71–79. doi:10.1007/s00027-014-0364-5

Carpenter, S.R., and R.C. Lathrop. 2014. Phosphorus loading, transport and concentrations in a lake chain: A probabilistic model to compare management options. Aquatic Sciences 76:145–154. doi:10.1007/s00027-013-0324-5

Casson, N.J., A.R. Contosta, E.A. Burakowski, J.L. Campbell, M.S. Crandall, I.F. Creed, M.C. Eimers, S. Garlick, D.A. Lutz, M.Q. Morison, A.T. Morzillo, and S.J. Nelson. 2019. Winter weather whiplash: Impacts of meteorological events misaligned with natural and human systems in seasonally snow-covered regions. Earth's Future 7:1434 –1450. doi:10.1029/2019EF001224

Chaffin, J.D., T.W. Davis, D.J. Smith, M.M. Baer, and G.J. Dick. 2018. Interactions between nitrogen form, loading rate, and light intensity on Microcystis and Planktothrix growth and microcystin production. Harmful Algae 73:84–97. doi:10.1016/j.hal.2018.02.001

Chase, J.M. 2003. Experimental evidence for alternative stable equilibria in a benthic pond food web. Ecology Letters 6:733–741. doi:10.1046/j.1461-0248.2003.00482.x

Chen, X., M.M. Motew, E.G. Booth, S.C. Zipper, S.P. Loheide, and C.J. Kucharik. 2019. Management of minimum lake levels and impacts on flood mitigation: A case study of the Yahara Watershed, Wisconsin, USA. Journal of Hydrology 577:123920. doi:10.1016/j.jhydrol.2019.123920

Chow, V.T., D.R. Maidment, and L.W. Mays. 1988. Applied Hydrology. McGraw-Hill, New York, NY

Clancy, K.B.H., R.G. Nelson, J.N. Rutherford, and K. Hinde. 2014. Survey of Academic Field Experiences (SAFE): trainees report harassment and assault. PLoS ONE 9:e102172. doi:10.1371/journal.pone.0102172

Colbourne, J.K., B. Robison, K. Bogart, and M. Lynch. 2004. Five hundred and twenty-eight microsatellite markers for ecological genomic investigations using Daphnia. Molecular Ecology Notes 4:485–490. doi:10.1111/j.1471-8286.2004.00721.x

Collins, S.L., M.L. Avolio, C. Gries, L.M. Hallett, S.E. Koerner, K.J. La Pierre, A.L. Rypel, E.R. Sokol, S.B. Fey, D.F.B. Flynn, S.K. Jones, L.M. Ladwig, J. Ripplinger, and M.B. Jones. 2018. Temporal heterogeneity increases with spatial heterogeneity in ecological communities. Ecology 99:858–865. doi:10.1002/ecy.2154

Côté, I.M., E.S. Darling, and C.J. Brown. 2016. Interactions among ecosystem stressors and their importance in conservation. Proceedings of the Royal Society B: Biological Sciences 283:20152592. doi:10.1098/rspb.2015.2592

Cowles, J., L. Templeton, J.J. Battles, P.J. Edmunds, R.C. Carpenter, S.R. Carpenter, M.P. Nelson, N.L. Cleavitt, P.M. Groffman, J.H. Sullivan, M.C. Neel, G.J.A. Hansen, S. Hobbie, S.J. Holbrook, C.E. Kazanski, E.W. Seabloom, R.J. Schmitt, E.H. Stanley, N.S. van Doorn, and M.J. Vander Zanden. in review. Ecosystem trajectories, resilience, and the state of our future earth: Insight from the U.S. LTER Network

Crawford, J.T., L.C. Loken, N.J. Casson, C. Smith, A.G. Stone, and L.A. Winslow. 2015. High-speed limnology: Using advanced sensors to investigate spatial variability in biogeochemistry and hydrology. Environmental Science & Technology 49:442–450. doi:10.1021/es504773x

Crawford, J.T., L.C. Loken, W.E. West, B. Crary, S.A. Spawn, N. Gubbins, S.E. Jones, R.G. Striegl, and E.H. Stanley. 2017. Spatial heterogeneity of within-stream methane concentrations. Journal of Geophysical Research: Biogeosciences 122:1036–1048. doi:10.1002/2016JG003698

Crawford, J.T., and E.H. Stanley. 2016. Controls on methane concentrations and fluxes in streams draining human-dominated landscapes. Ecological Applications 26:1581–1591. doi:10.1890/15-1330

Cushing, D.H. 1990. Plankton production and year-class strength in fish populations: An update of the match/mismatch hypothesis. Pages 249–293 Advances in Marine Biology. Elsevier. doi:10.1016/S0065-2881(08)60202-3

De Stasio, B., M. Schrimpf, A. Beranek, and W. Daniels. 2008. Increased Chlorophyll a, phytoplankton abundance, and cyanobacteria occurrence following invasion of Green Bay, Lake Michigan by dreissenid mussels. Aquatic Invasions 3:21–27. doi:10.3391/ai.2008.3.1.5

Denman, E.C., P.B. May, and G.M. Moore. 2016. The potential role of urban forests in removing nutrients from stormwater. Journal of Environmental Quality 45:207–214. doi:10.2134/jeq2015.01.0047

Desai, A.R. 2014. Influence and predictive capacity of climate anomalies on daily to decadal extremes in canopy photosynthesis. Photosynthesis Research 119:31–47. doi:10.1007/s11120-013-9925-z

Dodds, W.K., C.T. Robinson, E.E. Gaiser, G.J.A. Hansen, H. Powell, J.M. Smith, N.B. Morse, S.L. Johnson, S.V. Gregory, T. Bell, T.K. Kratz, and W.H. McDowell. 2012. Surprises and insights from long-term aquatic data sets and experiments. BioScience 62:709–721. doi:10.1525/bio.2012.62.8.4

Dodson, S.I. 2008. Biodiversity in southern Wisconsin storm-water retention ponds: Correlations with watershed cover and productivity. Lake and Reservoir Management 24:370–380. doi:10.1080/07438140809354847

Doherty, J.M., J.F. Miller, S.G. Prellwitz, A.M. Thompson, S.P. Loheide, and J.B. Zedler. 2014. Hydrologic regimes revealed bundles and tradeoffs among six wetland services. Ecosystems 17:1026–1039. doi:10.1007/s10021-014-9775-3

Donnelly, A., A. Caffarra, and B.F. O'Neill. 2011. A review of climate-driven mismatches between interdependent phenophases in terrestrial and aquatic ecosystems. International Journal of Biometeorology 55:805–817. doi:10.1007/s00484-011-0426-5

Dornelas, M., L.H. Antão, F. Moyes, A.E. Bates, A.E. Magurran, D. Adam, A.A. Akhmetzhanova, W. Appeltans, J.M. Arcos, H. Arnold, N. Ayyappan, G. Badihi, A.H. Baird, M. Barbosa, T.E. Barreto, C. Bässler, A. Bellgrove, J. Belmaker, L. Benedetti-Cecchi, B.J. Bett, A.D. Bjorkman, M. Błażewicz, S.A. Blowes, C.P. Bloch, T.C. Bonebrake, S. Boyd, M. Bradford, A.J. Brooks, J.H. Brown, H. Bruelheide, P. Budy, F. Carvalho, E. Castañeda-Moya, C.A. Chen, J.F. Chamblee, T.J. Chase, L. Siegwart Collier, S.K. Collinge, R. Condit, E.J. Cooper, J.H.C.

Cornelissen, U. Cotano, S. Kyle Crow, G. Damasceno, C.H. Davies, R.A. Davis, F.P. Day, S. Degraer, T.S. Doherty, T.E. Dunn, G. Durigan, J.E. Duffy, D. Edelist, G.J. Edgar, R. Elahi, S.C. Elmendorf, A. Enemar, S.K.M. Ernest, R. Escribano, M. Estiarte, B.S. Evans, T.-Y. Fan, F. Turini Farah, L. Loureiro Fernandes, F.Z. Farneda, A. Fidelis, R. Fitt, A.M. Fosaa, G.A. Daher Correa Franco, G.E. Frank, W.R. Fraser, H. García, R. Cazzolla Gatti, O. Givan, E. Gorgone-Barbosa, W.A. Gould, C. Gries, G.D. Grossman, J.R. Gutierréz, S. Hale, M.E. Harmon, J. Harte, G. Haskins, D.L. Henshaw, L. Hermanutz, P. Hidalgo, P. Higuchi, A. Hoey, G. Van Hoey, A. Hofgaard, K. Holeck, R.D. Hollister, R. Holmes, M. Hoogenboom, C. Hsieh, S.P. Hubbell, F. Huettmann, C.L. Huffard, A.H. Hurlbert, N. Macedo Ivanauskas, D. Janík, U. Jandt, A. Jażdżewska, T. Johannessen, J. Johnstone, J. Jones, F.A.M. Jones, J. Kang, T. Kartawijaya, E.C. Keeley, D.A. Kelt, R. Kinnear, K. Klanderud, H. Knutsen, C.C. Koenig, A.R. Kortz, K. Král, L.A. Kuhnz, C.-Y. Kuo, D.J. Kushner, C. Laguionie-Marchais, L.T. Lancaster, C. Min Lee, J.S. Lefcheck, E. Lévesque, D. Lightfoot, F. Lloret, J.D. Lloyd, A. López-Baucells, M. Louzao, J.S. Madin, B. Magnússon, S. Malamud, I. Matthews, K.P. McFarland, B. McGill, D. McKnight, W.O. McLarney, J. Meador, P.L. Meserve, D.J. Metcalfe, C.F.J. Meyer, A. Michelsen, N. Milchakova, T. Moens, E. Moland, J. Moore, C. Mathias Moreira, J. Müller, G. Murphy, I.H. Myers-Smith, R.W. Myster, A. Naumov, F. Neat, J.A. Nelson, M. Paul Nelson, S.F. Newton, N. Norden, J.C. Oliver, E.M. Olsen, V.G. Onipchenko, K. Pabis, R.J. Pabst, A. Paquette, S. Pardede, D.M. Paterson, R. Pélissier, J. Peñuelas, A. Pérez-Matus, O. Pizarro, F. Pomati, E. Post, H.H.T. Prins, J.C. Priscu, P. Provoost, K.L. Prudic, E. Pulliainen, B.R. Ramesh, O. Mendivil Ramos, A. Rassweiler, J.E. Rebelo, D.C. Reed, P.B. Reich, S.M. Remillard, A.J. Richardson, J.P. Richardson, I. van Rijn, R. Rocha, V.H. Rivera-Monroy, C. Rixen, K.P. Robinson, R. Ribeiro Rodrigues, D. de Cerqueira Rossa-Feres, L. Rudstam, H. Ruhl, C.S. Ruz, E.M. Sampaio, N. Rybicki, A. Rypel, S. Sal, B. Salgado, F.A.M. Santos, A.P. Savassi-Coutinho, S. Scanga, J. Schmidt, R. Schooley, F. Setiawan, K.-T. Shao, G.R. Shaver, S. Sherman, T.W. Sherry, J. Siciński, C. Sievers, A.C. da Silva, F. Rodrigues da Silva, F.L. Silveira, J. Slingsby, T. Smart, S.J. Snell, N.A. Soudzilovskaia, G.B.G. Souza, F. Maluf Souza, V. Castro Souza, C.D. Stallings, R. Stanforth, E.H. Stanley, J. Mauro Sterza, M. Stevens, R. Stuart-Smith, Y. Rondon Suarez, S. Supp, J. Yoshio Tamashiro, S. Tarigan, G.P. Thiede, S. Thorn, A. Tolvanen, M. Teresa Zugliani Toniato, Ø. Totland, R.R. Twilley, G. Vaitkus, N. Valdivia, M.I. Vallejo, T.J. Valone, C. Van Colen, J. Vanaverbeke, F. Venturoli, H.M. Verheye, M. Vianna, R.P. Vieira, T. Vrška, C. Quang Vu, L. Van Vu, R.B. Waide, C. Waldock, D. Watts, S. Webb, T. Wesołowski, E.P. White, C.E. Widdicombe, D. Wilgers, R. Williams, S.B. Williams, M. Williamson, M.R. Willig, T.J. Willis, S. Wipf, K.D. Woods, E.J. Woehler, K. Zawada, and M.L. Zettler. 2018. BioTIME: A database of biodiversity time series for the Anthropocene. Global Ecology and Biogeography 27:760–786. doi:10.1111/geb.12729

Dornelas, M., N.J. Gotelli, B. McGill, H. Shimadzu, F. Moyes, C. Sievers, and A.E. Magurran. 2014. Assemblage time series reveal biodiversity change but not systematic loss. Science 344:296–299. doi:10.1126/science.1248484

Dugan, H.A., S.L. Bartlett, S.M. Burke, J.P. Doubek, F.E. Krivak-Tetley, N.K. Skaff, J.C. Summers, K.J. Farrell, I.M. McCullough, A.M. Morales-Williams, D.C. Roberts, Z. Ouyang, F. Scordo, P.C. Hanson, and K.C. Weathers. 2017. Salting our freshwater lakes. Proceedings of the National Academy of Sciences 114:4453–4458. doi:10.1073/pnas.1620211114

Dugan, H.A., R.I. Woolway, A.B. Santoso, J.R. Corman, A. Jaimes, E.R. Nodine, V.P. Patil, J.A. Zwart, J.A. Brentrup, A.L. Hetherington, S.K. Oliver, J.S. Read, K.M. Winters, P.C. Hanson, E.K. Read, L.A. Winslow, and K.C. Weathers. 2016. Consequences of gas flux model choice on the interpretation of metabolic balance across 15 lakes. Inland Waters 6:581–592. doi:10.1080/IW-6.4.836

Durant, J., D. Hjermann, G. Ottersen, and N. Stenseth. 2007. Climate and the match or mismatch between predator requirements and resource availability. Climate Research 33:271–283.

doi:10.3354/cr033271

Embke, H.S., A.L. Rypel, S.R. Carpenter, G.G. Sass, D. Ogle, T. Cichosz, J. Hennessy, T.E. Essington, and M.J. Vander Zanden. 2019. Production dynamics reveal hidden overharvest of inland recreational fisheries. Proceedings of the National Academy of Sciences 116:24676–24681. doi:10.1073/pnas.1913196116

Evans, D.O., and D.H. Loftus. 1987. Colonization of inland lakes in the Great Lakes region by rainbow smelt, Osmerus mordax: Their freshwater niche and effects on indigenous fishes. Canadian Journal of Fisheries and Aquatic Sciences 44:s249–s266. doi:10.1139/f87-327

Fee, E.J., R.E. Hecky, S.E.M. Kasian, and D.R. Cruikshank. 1996. Effects of lake size, water clarity, and climatic variability on mixing depths in Canadian Shield lakes. Limnology and Oceanography 41:912–920. doi:10.4319/lo.1996.41.5.0912

Forchhammer, M.C., E. Post, and N.Chr. Stenseth. 1998. Breeding phenology and climate. Nature 391:29–30. doi:10.1038/34070

Forrest, J., and A.J. Miller-Rushing. 2010. Toward a synthetic understanding of the role of phenology in ecology and evolution. Philosophical Transactions of the Royal Society B: Biological Sciences 365:3101–3112. doi:10.1098/rstb.2010.0145

Frost, P.C., C. Prater, A.B. Scott, K. Song, and M.A. Xenopoulos. 2019. Mobility and bioavailability of sediment phosphorus in urban stormwater ponds. Water Resources Research:2018WR023419. doi:10.1029/2018WR023419

Gienapp, P., T.E. Reed, and M.E. Visser. 2014. Why climate change will invariably alter selection pressures on phenology. Proceedings of the Royal Society B: Biological Sciences 281:20141611. doi:10.1098/rspb.2014.1611

Gillon, S., E.G. Booth, and A.R. Rissman. 2016. Shifting drivers and static baselines in environmental governance: Challenges for improving and proving water quality outcomes. Regional Environmental Change 16:759–775. doi:10.1007/s10113-015-0787-0

Gobler, C.J., J.M. Burkholder, T.W. Davis, M.J. Harke, T. Johengen, C.A. Stow, and D.B. Van de Waal. 2016. The dual role of nitrogen supply in controlling the growth and toxicity of cyanobacterial blooms. Harmful Algae 54:87–97. doi:10.1016/j.hal.2016.01.010

Golub, M., A.R. Desai, G.A. McKinley, C.K. Remucal, and E.H. Stanley. 2017. Large uncertainty in estimating *p* CO_2 from carbonate equilibria in lakes. Journal of Geophysical Research: Biogeosciences 122:2909–2924. doi:10.1002/2017JG003794

Gómez-Baggethun, E., P. Alcorlo, and C. Montes. 2011. Ecosystem services associated with a mosaic of alternative states in a Mediterranean wetland: case study of the Doñana marsh (southwestern Spain). Hydrological Sciences Journal 56:1374–1387. doi:10.1080/02626667.2011.631495

Goonetilleke, A., E. Thomas, S. Ginn, and D. Gilbert. 2005. Understanding the role of land use in urban stormwater quality management. Journal of Environmental Management 74:31–42. doi:10.1016/j.jenvman.2004.08.006

Grinham, A., S. Albert, N. Deering, M. Dunbabin, D. Bastviken, B. Sherman, C.E. Lovelock, and C.D. Evans. 2018. The importance of small artificial water bodies as sources of methane emissions in Queensland, Australia. Hydrology and Earth System Sciences 22:5281–5298. doi:10.5194/hess-22-5281-2018

Hamilton, D.P., M.R. Magee, C.H. Wu, and T.K. Kratz. 2018. Ice cover and thermal regime in a dimictic seepage lake under climate change. Inland Waters 8:381–398. doi:10.1080/20442041.2018.1505372

Hamilton, J.J., S.L. Garcia, B.S. Brown, B.O. Oyserman, F. Moya-Flores, S. Bertilsson, R.R. Malmstrom, K.T. Forest, and K.D. McMahon. 2017. Metabolic network analysis and metatranscriptomics reveal auxotrophies and nutrient sources of the cosmopolitan freshwater microbial lineage acI. mSystems 2:e00091-17. doi:10.1128/mSystems.00091-17

Hampton, S.E., A.W.E. Galloway, S.M. Powers, T. Ozersky, K.H. Woo, R.D. Batt, S.G. Labou, C.M. O'Reilly, S. Sharma, N.R. Lottig, E.H. Stanley, R.L. North, J.D. Stockwell, R. Adrian, G.A.

Weyhenmeyer, L. Arvola, H.M. Baulch, I. Bertani, L.L. Bowman, C.C. Carey, J. Catalan, W. Colom-Montero, L.M. Domine, M. Felip, I. Granados, C. Gries, H.-P. Grossart, J. Haberman, M. Haldna, B. Hayden, S.N. Higgins, J.C. Jolley, K.K. Kahilainen, E. Kaup, M.J. Kehoe, S. MacIntyre, A.W. Mackay, H.L. Mariash, R.M. McKay, B. Nixdorf, P. Nõges, T. Nõges, M. Palmer, D.C. Pierson, D.M. Post, M.J. Pruett, M. Rautio, J.S. Read, S.L. Roberts, J. Rücker, S. Sadro, E.A. Silow, D.E. Smith, R.W. Sterner, G.E.A. Swann, M.A. Timofeyev, M. Toro, M.R. Twiss, R.J. Vogt, S.B. Watson, E.J. Whiteford, and M.A. Xenopoulos. 2017. Ecology under lake ice. Ecology Letters 20:98–111. doi:10.1111/ele.12699

Hansen, G.J.A., S.R. Carpenter, J.W. Gaeta, J.M. Hennessy, and M.J. Vander Zanden. 2015. Predicting walleye recruitment as a tool for prioritizing management actions. Canadian Journal of Fisheries and Aquatic Sciences 72:661–672. doi:10.1139/cjfas-2014-0513

Hansen, G.J.A., A.R. Ives, M.J. Vander Zanden, and S.R. Carpenter. 2013. Are rapid transitions between invasive and native species caused by alternative stable states, and does it matter? Ecology 94:2207–2219. doi:10.1890/13-0093.1

Hansen, G.J.A., J.S. Read, J.F. Hansen, and L.A. Winslow. 2017. Projected shifts in fish species dominance in Wisconsin lakes under climate change. Global Change Biology 23:1463–1476. doi:10.1111/gcb.13462

Hanson, P.C., I. Buffam, J.A. Rusak, E.H. Stanley, and C. Watras. 2014. Quantifying lake allochthonous organic carbon budgets using a simple equilibrium model. Limnology and Oceanography 59:167–181. doi:10.4319/lo.2014.59.1.0167

Hanson, P.C., A.I. Pollard, D.L. Bade, K. Predick, S.R. Carpenter, and J.A. Foley. 2004. A model of carbon evasion and sedimentation in temperate lakes. Global Change Biology 10:1285–1298. doi:10.1111/j.1529-8817.2003.00805.x

Hansson, L.-A., H. Annadotter, E. Bergman, S.F. Hamrin, E. Jeppesen, T. Kairesalo, E. Luokkanen, P.-Å. Nilsson, M. Søndergaard, and J. Strand. 1998. Biomanipulation as an application of food-chain theory: Constraints, synthesis, and recommendations for remperate lakes. Ecosystems 1:558–574. doi:10.1007/s100219900051

Harbaugh, A.W. 2005. MODFLOW-2005: The U.S. Geological Survey modular ground-water model--the ground-water flow process. U.S. Geological Survey, Reston, VA

Harke, M.J., and C.J. Gobler. 2015. Daily transcriptome changes reveal the role of nitrogen in controlling microcystin synthesis and nutrient transport in the toxic cyanobacterium, Microcystis aeruginosa. BMC Genomics 16:1068. doi:10.1186/s12864-015-2275-9

Hartig, T., and P.H. Kahn. 2016. Living in cities, naturally. Science 352:938–940. doi:10.1126/science.aaf3759

Hassall, C. 2014. The ecology and biodiversity of urban ponds: Ecology and biodiversity of urban ponds. Wiley Interdisciplinary Reviews: Water 1:187–206. doi:10.1002/wat2.1014

Herren, C.M., and K.D. McMahon. 2017. Cohesion: A method for quantifying the connectivity of microbial communities. The ISME Journal 11:2426–2438. doi:10.1038/ismej.2017.91

Hewitt, B., L. Lopez, K. Gaibisels, A. Murdoch, S. Higgins, J. Magnuson, A. Paterson, J. Rusak, H. Yao, and S. Sharma. 2018. Historical trends, drivers, and future projections of ice phenology in small north temperate lakes in the Laurentian Great Lakes region. Water 10:70. doi:10.3390/w10010070

Higgins, S.N., and M.J.V. Zanden. 2010. What a difference a species makes: a meta–analysis of dreissenid mussel impacts on freshwater ecosystems. Ecological Monographs 80:179–196. doi:10.1890/09-1249.1

Hill, M.J., C. Hassall, B. Oertli, L. Fahrig, B.J. Robson, J. Biggs, M.J. Samways, N. Usio, N. Takamura, J. Krishnaswamy, and P.J. Wood. 2018. New policy directions for global pond conservation. Conservation Letters 11:e12447. doi:10.1111/conl.12447

Hilt, S., S. Brothers, E. Jeppesen, A.J. Veraart, and S. Kosten. 2017. Translating Regime Shifts in Shallow Lakes into Changes in Ecosystem Functions and Services. BioScience 67:928–936.

doi:10.1093/biosci/bix106

Hipsey, M.R., L.C. Bruce, C. Boon, B. Busch, C.C. Carey, D.P. Hamilton, P.C. Hanson, J.S. Read, E. de Sousa, M. Weber, and L.A. Winslow. 2019. A General Lake Model (GLM 3.0) for linking with high-frequency sensor data from the Global Lake Ecological Observatory Network (GLEON). Geoscientific Model Development 12:473–523. doi:10.5194/gmd-12-473-2019

Holmes, E., E., E. Ward J., and K. Wills. 2012. MARSS: Multivariate autoregressive state-space models for analyzing time-series data. The R Journal 4:11. doi:10.32614/RJ-2012-002

Honsey, A.E., S.B. Donabauer, and T.O. Höök. 2016. An analysis of lake morphometric and land-use characteristics that promote persistence of cisco in Indiana. Transactions of the American Fisheries Society 145:363–373. doi:10.1080/00028487.2015.1125949

Hrabik, T.R., J.J. Magnuson, and A.S. McLain. 1998. Predicting the effects of rainbow smelt on native fishes in small lakes: Evidence from long-term research on two lakes. Canadian Journal of Fisheries and Aquatic Sciences 55:1364–1371. doi:10.1139/f98-032

Huisman, J., G.A. Codd, H.W. Paerl, B.W. Ibelings, J.M.H. Verspagen, and P.M. Visser. 2018. Cyanobacterial blooms. Nature Reviews Microbiology 16:471–483. doi:10.1038/s41579-018-0040-1

Irfanullah, H.M., and B. Moss. 2005. A filamentous green algae-dominated temperate shallow lake: Variations on the theme of clear-water stable states? Archiv für Hydrobiologie 163:25–47. doi:10.1127/0003-9136/2005/0163-0025

Jackson, M.C., C.J.G. Loewen, R.D. Vinebrooke, and C.T. Chimimba. 2016. Net effects of multiple stressors in freshwater ecosystems: A meta-analysis. Global Change Biology 22:180–189. doi:10.1111/gcb.13028

Jacobson, P.C., T.S. Jones, P. Rivers, and D.L. Pereira. 2008. Field estimation of a lethal oxythermal niche boundary for adult ciscoes in Minnesota lakes. Transactions of the American Fisheries Society 137:1464–1474. doi:10.1577/T07-148.1

Jacobson, P.C., H.G. Stefan, and D.L. Pereira. 2010. Coldwater fish oxythermal habitat in Minnesota lakes: Influence of total phosphorus, July air temperature, and relative depth. Canadian Journal of Fisheries and Aquatic Sciences 67:2002–2013. doi:10.1139/F10-115

Jansen, M., A.N. Geerts, A. Rago, K.I. Spanier, C. Denis, L. De Meester, and L. Orsini. 2017. Thermal tolerance in the keystone species *Daphnia magna* -a candidate gene and an outlier analysis approach. Molecular Ecology 26:2291–2305. doi:10.1111/mec.14040

Jenerette, G.D. 2018. Ecological contributions to human health in cities. Landscape Ecology 33:1655–1668. doi:10.1007/s10980-018-0708-y

Jensen, O.P., B.J. Benson, J.J. Magnuson, V.M. Card, M.N. Futter, P.A. Soranno, and K.M. Stewart. 2007. Spatial analysis of ice phenology trends across the Laurentian Great Lakes region during a recent warming period. Limnology and Oceanography 52:2013–2026. doi:10.4319/lo.2007.52.5.2013

Jeppesen, E., J.P. Jensen, P. Kristensen, M. Søndergaard, E. Mortensen, O. Sortkjær, and K. Olrik. 1990. Fish manipulation as a lake restoration tool in shallow, eutrophic, temperate lakes 2: Threshold levels, long-term stability and conclusions. Pages 219–227 *in* R. D. Gulati, E. H. R. R. Lammens, M.-L. Meijer, and E. van Donk, editors. Biomanipulation Tool for Water Management. Springer Netherlands, Dordrecht. doi:10.1007/978-94-017-0924-8_18

Jones, J.J., P.M. Groffman, J. Blair, F.W. Davis, H.A. Dugan, E.S. Eukirchen, S.D. Frey, T. Harms, E.L. Hinckley, M. Kosmala, S. Loberg, S. Malone, K. Novick, S. Record, A.V. Rocha, B. Ruddell, E.H. Stanley, C. Sturtevant, A. Thorpe, T. White, W.R. Wieder, L. Zhai, and K. Zhu. in prep. The age of network science: Emerging synergies between NEON and the US LTER networks

Juday, C., and E.A. Birge. 1933. The transparency, the color and the specific conductance of the lake waters of northeastern Wisconsin 28:205–259

Kardan, O., P. Gozdyra, B. Misic, F. Moola, L.J. Palmer, T. Paus, and M.G. Berman. 2015. Neighborhood greenspace and health in a large urban center. Scientific Reports 5:11610.

doi:10.1038/srep11610

Kelly, N.E., J.D. Young, J.G. Winter, M.E. Palmer, E.A. Stainsby, and L.A. Molot. 2017. Sequential rather than interactive effects of multiple stressors as drivers of phytoplankton community change in a large lake. Freshwater Biology 62:1288–1302. doi:10.1111/fwb.12945

Kharouba, H.M., J. Ehrlén, A. Gelman, K. Bolmgren, J.M. Allen, S.E. Travers, and E.M. Wolkovich. 2018. Global shifts in the phenological synchrony of species interactions over recent decades. Proceedings of the National Academy of Sciences 115:5211–5216. doi:10.1073/pnas.1714511115

Klug, J.L., D.C. Richardson, H.A. Ewing, B.R. Hargreaves, N.R. Samal, D. Vachon, D.C. Pierson, A.M. Lindsey, D.M. O'Donnell, S.W. Effler, and K.C. Weathers. 2012. Ecosystem effects of a tropical cyclone on a network of lakes in northeastern North America. Environmental Science & Technology 46:11693–11701. doi:10.1021/es302063v

Krueger, D.M., and T.R. Hrabik. 2005. Food web alterations that promote native species: The recovery of cisco (*Coregonus artedi*) populations through management of native piscivores. Canadian Journal of Fisheries and Aquatic Sciences 62:2177–2188. doi:https://doi.org/10.1139/f05-132

Kucharik, C.J. 2003. Evaluation of a process-based agro-ecosystem model (Agro-IBIS) across the U.S. cornbelt: Simulations of the inter-annual variability in maize yield. Earth Interactions 7:1–33. doi:10.1175/1087-3562(2003)007<0001:EOAPAM>2.0.CO;2

Lathrop, C., Richard, P. Kasprzak, M. Tarvainen, A.-M. Ventelä, T. Keskinen, R. Koschel, and D.M. Robertson. 2019. Seasonal epilimnetic temperature patterns and trends in a suite of lakes from Wisconsin (USA), Germany, and Finland. Inland Waters 9:471–488. doi:0.1080/20442041.2019.1637682

Lathrop, R.C. 1992. Nutrient loadings, lake nutrients, and water clarity. Pages 69–96 *in* J. F. Kitchell, editor. Food Web Management. Springer New York, New York, NY. doi:10.1007/978-1-4612-4410-3_6

Lathrop, R.C., S.R. Carpenter, C.A. Stow, P.A. Soranno, and J.C. Panuska. 1998. Phosphorus loading reductions needed to control blue-green algal blooms in Lake Mendota. Canadian Journal of Fisheries and Aquatic Sciences 55:1169–78. doi:10.1139/f97-317#.WMxGSGf9m70

Lathrop, R.C., D.S. Liebl, and K. Welke. 2013. Carp removal to increase water clarity in shallow eutrophic Lake Wingra. Lakeline:23–30

Latzka, A.W., G.J.A. Hansen, M. Kornis, and M.J. Vander Zanden. 2016. Spatial heterogeneity in invasive species impacts at the landscape scale. Ecosphere 7:e01311. doi:10.1002/ecs2.1311

Leach, T.H., B.E. Beisner, C.C. Carey, P. Pernica, K.C. Rose, Y. Huot, J.A. Brentrup, I. Domaizon, H.-P. Grossart, B.W. Ibelings, S. Jacquet, P.T. Kelly, J.A. Rusak, J.D. Stockwell, D. Straile, and P. Verburg. 2018. Patterns and drivers of deep chlorophyll maxima structure in 100 lakes: The relative importance of light and thermal stratification. Limnology and Oceanography 63:628–646. doi:10.1002/lno.10656

Likens, G.E. 2019. Unusual sequence of ice cover formation on Mirror Lake, New Hampshire, USA. Inland Waters 9:408–410. doi:10.1080/20442041.2019.1629216

Linz, A.M., F.O. Aylward, S. Bertilsson, and K.D. McMahon. 2020. Time-series metatranscriptomes reveal conserved patterns between phototrophic and heterotrophic microbes in diverse freshwater systems. Limnology and Oceanography 65:S101–S112. doi:10.1002/lno.11306

Linz, A.M., B.C. Crary, A. Shade, S. Owens, J.A. Gilbert, R. Knight, and K.D. McMahon. 2017. Bacterial community composition and dynamics spanning five years in freshwater bog lakes. mSphere 2:e00169-17, /msph/2/3/e00169-17.atom. doi:10.1128/mSphere.00169-17

Linz, A.M., S. He, S.L.R. Stevens, K. Anantharaman, R.R. Rohwer, R.R. Malmstrom, S. Bertilsson, and K.D. McMahon. 2018. Freshwater carbon and nutrient cycles revealed through reconstructed population genomes. PeerJ 6:e6075. doi:10.7717/peerj.6075

Loecke, T.D., A.J. Burgin, D.A. Riveros-Iregui, A.S. Ward, S.A. Thomas, C.A. Davis, and M.A.St. Clair. 2017. Weather whiplash in agricultural regions drives deterioration of water quality. Biogeochemistry 133:7–15. doi:10.1007/s10533-017-0315-z

Loken, L.C. 2018. Spatial heterogeneity of water chemistry within lakes and rivers. Ph.D., University of Wisconsin, Madison, WI

Loken, L.C., J.T. Crawford, M.M. Dornblaser, R.G. Striegl, J.N. Houser, P.A. Turner, and E.H. Stanley. 2018. Limited nitrate retention capacity in the Upper Mississippi River. Environmental Research Letters 13:13. doi:10.1088/1748-9326/aacd51

Loken, L.C., J.T. Crawford, P.J. Schramm, P. Stadler, A.R. Desai, and E.H. Stanley. 2019. Large spatial and temporal variability of carbon dioxide and methane in a eutrophic lake. Journal of Geophysical Research – Biogeosciences, 124:2248–2266. doi:10.1029/2019JG005186

Lottig, N.R., P.N. Tan, T. Wagner, K.S. Cheruvelil, P.A. Soranno, E.H. Stanley, C.E. Scott, C.A. Stow, and S. Yuan. 2017. Macroscale patterns of synchrony identify complex relationships among spatial and temporal ecosystem drivers. Ecosphere 8. doi:10.1002/ecs2.2024

Lyons, J., T.P. Parks, K.L. Minahan, and A.S. Ruesch. 2018. Evaluation of oxythermal metrics and benchmarks for the protection of cisco (*Coregonus artedi*) habitat quality and quantity in Wisconsin lakes. Canadian Journal of Fisheries and Aquatic Sciences 75:600–608. doi:10.1139/cjfas-2017-0043

Lyons, J., A.L. Rypel, P.W. Rasmussen, T.E. Burzynski, B.T. Eggold, J.T. Myers, T.J. Paoli, and P.B. McIntyre. 2015. Trends in the Reproductive Phenology of two Great Lakes Fishes. Transactions of the American Fisheries Society 144:1263–1274. doi:10.1080/00028487.2015.1082502

Ma, X., A. Huete, S. Moran, G. Ponce-Campos, and D. Eamus. 2015. Abrupt shifts in phenology and vegetation productivity under climate extremes. Journal of Geophysical Research: Biogeosciences 120:2036–2052. doi:10.1002/2015JG003144

Madison, City of. 2019. Emerald ash borer plan. Page 1. City of Madison, Madison, WI

Magee, M.R., C.L. Hein, J.R. Walsh, P.D. Shannon, M.J. Vander Zanden, T.B. Campbell, G.J.A. Hansen, J. Hauxwell, G.D. LaLiberte, T.P. Parks, G.G. Sass, C.W. Swanston, and M.K. Janowiak. 2019a. Scientific advances and adaptation strategies for Wisconsin lakes facing climate change. Lake and Reservoir Management 35:364–381. doi:10.1080/10402381.2019.1622612

Magee, M.R., P.B. McIntyre, P.C. Hanson, and C.H. Wu. 2019b. Drivers and management implications of long-term cisco oxythermal habitat decline in Lake Mendota, WI. Environmental Management 63:396–407. doi:10.1007/s00267-018-01134-7

Magee, M.R., P.B. McIntyre, and C.H. Wu. 2018. Modeling oxythermal stress for cool-water fishes in lakes using a cumulative dosage approach. Canadian Journal of Fisheries and Aquatic Sciences 75:1303–1312. doi:10.1139/cjfas-2017-0260

Magee, M.R., and C.H. Wu. 2017a. Effects of changing climate on ice cover in three morphometrically different lakes. Hydrological Processes 31:308–323. doi:10.1002/hyp.10996

Magee, M.R., and C.H. Wu. 2017b. Response of water temperatures and stratification to changing climate in three lakes with different morphometry. Hydrology and Earth System Sciences 21:6253–6274. doi:10.5194/hess-21-6253-2017

Magee, M.R., C.H. Wu, D.M. Robertson, R.C. Lathrop, and D.P. Hamilton. 2016. Trends and abrupt changes in 104 years of ice cover and water temperature in a dimictic lake in response to air temperature, wind speed, and water clarity drivers. Hydrology and Earth System Sciences 20:1681–1702. doi:10.5194/hess-20-1681-2016

Magnuson, J.J., B.J. Benson, T.K. Kratz, D.E. Armstrong, C.J. Bowser, A.C.C. Colby, T.W. Meinke, P.K. Montz, and K.E. Webster. 2006. Origin, operation, evolution and challenges. Pages 280–322 *in* J. J. Magnuson, T. K. Kratz, and B. J. Benson, editors. Long-Term Dynamics of Lakes in the Landscape: Long-Term Ecological Research on North Temperate Lakes. Oxford University Press

Magnuson, J.J., D.M. Robertson, B.J. Benson, R.H. Wynne, D.M. Livingstone, T. Arai, R.A. Assel, R.G. Barry, V. Card, E. Kuusisto, N.G. Granin, T.D. Prowse, K.M. Stewart, and V.S. Vuglinski. 2000. Historical trends in lake and river ice cover in the Northern Hemisphere. Science 289:1743–1746. doi:10.1126/science.289.5485.1743

Mallakpour, I., and G. Villarini. 2015. The changing nature of flooding across the central United States.

Nature Climate Change 5:250–254. doi:10.1038/nclimate2516

McCullough, I.M., H.A. Dugan, K.J. Farrell, A.M. Morales-Williams, Z. Ouyang, D. Roberts, F. Scordo, S.L. Bartlett, S.M. Burke, J.P. Doubek, F.E. Krivak-Tetley, N.K. Skaff, J.C. Summers, K.C. Weathers, and P.C. Hanson. 2018. Dynamic modeling of organic carbon fates in lake ecosystems. Ecological Modelling 386:71–82. doi:10.1016/j.ecolmodel.2018.08.009

McPhillips, L.E., H. Chang, M.V. Chester, Y. Depietri, E. Friedman, N.B. Grimm, J.S. Kominoski, T. McPhearson, P. Méndez-Lázaro, E.J. Rosi, and J. Shafiei Shi va. 2018. Defining extreme events: A cross-disciplinary review. Earth's Future 6:441 –455. doi:10.1002/2017EF000686

Mercado-Silva, N., J.D. Olden, J.T. Maxted, T.R. Hrabik, and M.J.V. Zanden. 2006. Forecasting the spread of invasive rainbow smelt in the Laurentian Great Lakes region of North America. Conservation Biology 20:1740–1749. doi:10.1111/j.1523-1739.2006.00508.x

Michalak, A.M., E.J. Anderson, D. Beletsky, S. Boland, N.S. Bosch, T.B. Bridgeman, J.D. Chaffin, K. Cho, R. Confesor, I. Daloglu, J.V. DePinto, M.A. Evans, G.L. Fahnenstiel, L. He, J.C. Ho, L. Jenkins, T.H. Johengen, K.C. Kuo, E. LaPorte, X. Liu, M.R. McWilliams, M.R. Moore, D.J. Posselt, R.P. Richards, D. Scavia, A.L. Steiner, E. Verhamme, D.M. Wright, and M.A. Zagorski. 2013. Record-setting algal bloom in Lake Erie caused by agricultural and meteorological trends consistent with expected future conditions. Proceedings of the National Academy of Sciences 110:6448–6452. doi:10.1073/pnas.1216006110

Moras, S., A.I. Ayala, and D.C. Pierson. 2019. Historical modelling of changes in Lake Erken thermal conditions. Hydrology and Earth System Sciences 23:5001–5016. doi:10.5194/hess-23-5001-2019

Motew, M., E.G. Booth, S.R. Carpenter, X. Chen, and C.J. Kucharik. 2018. The synergistic effect of manure supply and extreme precipitation on surface water quality. Environmental Research Letters 13:044016. doi:10.1088/1748-9326/aaade6

Motew, M., X. Chen, E.G. Booth, S.R. Carpenter, P. Pinkas, S.C. Zipper, S.P. Loheide, S.D. Donner, K. Tsuruta, P.A. Vadas, and C.J. Kucharik. 2017. The Influence of legacy P on lake water quality in a midwestern agricultural watershed. Ecosystems 20:1468–1482. doi:10.1007/s10021-017-0125-0

Müller, B., T. Steinsberger, R. Schwefel, R. Gächter, M. Sturm, and A. Wüest. 2019. Oxygen consumption in seasonally stratified lakes decreases only below a marginal phosphorus threshold. Scientific Reports 9:18054. doi:10.1038/s41598-019-54486-3

Nelligan, C., A. Jeziorski, K.M. Rühland, A.M. Paterson, and J.P. Smol. 2019. Long-term trends in hypolimnetic volumes and dissolved oxygen concentrations in Boreal Shield lakes of south-central Ontario, Canada. Canadian Journal of Fisheries and Aquatic Sciences 76:2315–2325. doi:10.1139/cjfas-2018-0278

Nowak, D.J., S. Hirabayashi, A. Bodine, and E. Greenfield. 2014. Tree and forest effects on air quality and human health in the United States. Environmental Pollution 193:119–129. doi:10.1016/j.envpol.2014.05.028

Ohgushi, T., O.J. Schmitz, and R.D. Holt, editors. 2012. Trait-Mediated Indirect Interactions: Ecological and Evolutionary Perspectives. Cambridge University Press

Oke, T.R. 1982. The energetic basis of the urban heat island. Quarterly Journal of the Royal Meteorological Society 108:1–24. doi:10.1002/qj.49710845502

O'Reilly, C.M., S. Sharma, D.K. Gray, S.E. Hampton, J.S. Read, R.J. Rowley, P. Schneider, J.D. Lenters, P.B. McIntyre, B.M. Kraemer, G.A. Weyhenmeyer, D. Straile, B. Dong, R. Adrian, M.G. Allan, O. Anneville, L. Arvola, J. Austin, J.L. Bailey, J.S. Baron, J.D. Brookes, E. de Eyto, M.T. Dokulil, D.P. Hamilton, K.E. Havens, A.L. Hetherington, S.N. Higgins, S.J. Hook, L.R. Izmest'eva, K.D. Joehnk, K. Kangur, P.H. Kasprzak, M. Kumagai, E. Kuusisto, G.A. Leshkevich, D.M. Livingstone, S. MacIntyre, L. May, J.M. Melack, D.C. Mueller-Navarra, M.A. Naumenko, P. Noges, T. Noges, R.P. North, P. Plisnier, A. Rigosi, A. Rimmer, M. Rogora, L.G. Rudstam, J.A. Rusak, N. Salmaso, N.R. Samal, D.E. Schindler, S.G. Schladow, M. Schmid, S.R. Schmidt, E.A. Silow, M.E. Soylu, K. Teubner, P. Verburg, A. Voutilainen, A. Watkinson, C.E.

Williamson, and G. Zhang. 2015. Rapid and highly variable warming of lake surface waters around the globe. Geophysical Research Letters 42:10773–10781

Pace, M.L., J.J. Cole, S.R. Carpenter, and J.F. Kitchell. 1999. Trophic cascades revealed in diverse ecosystems. Trends in Ecology & Evolution 14:483–488. doi:10.1016/S0169-5347(99)01723-1

Paez-Espino, D., J. Zhou, S. Roux, S. Nayfach, G.A. Pavlopoulos, F. Schulz, K.D. McMahon, D. Walsh, T. Woyke, N.N. Ivanova, E.A. Eloe-Fadrosh, S.G. Tringe, and N.C. Kyrpides. 2019. Diversity, evolution, and classification of virophages uncovered through global metagenomics. Microbiome 7:157. doi:10.1186/s40168-019-0768-5

Palmer, M.A., J.B. Zedler, and Falk, Donald A., editors. 2016. Foundations of Restoration Ecology. Second edition. Island Press, Washington, D. C.

Patil, S., M. Sivapalan, M.A. Hassan, S. Ye, C.J. Harman, and X. Xu. 2012. A network model for prediction and diagnosis of sediment dynamics at the watershed scale. Journal of Geophysical Research: Earth Surface 117:n/a-n/a. doi:10.1029/2012JF002400

Patz, J.A., D. Campbell-Lendrum, T. Holloway, and J.A. Foley. 2005. Impact of regional climate change on human health. Nature 438:310–317. doi:10.1038/nature04188

Pauls, S.U., C. Nowak, M. Bálint, and M. Pfenninger. 2013. The impact of global climate change on genetic diversity within populations and species. Molecular Ecology 22:925–946. doi:10.1111/mec.12152

Pedersen, E.J., D.L. Miller, G.L. Simpson, and N. Ross. 2019. Hierarchical generalized additive models in ecology: An introduction with mgcv. PeerJ 7:e6876. doi:10.7717/peerj.6876

Pennino, M.J., R.I. McDonald, and P.R. Jaffe. 2016. Watershed-scale impacts of stormwater green infrastructure on hydrology, nutrient fluxes, and combined sewer overflows in the mid-Atlantic region. Science of The Total Environment 565:1044–1053. doi:10.1016/j.scitotenv.2016.05.101

Peters, D.P.C., A.E. Lugo, F.S. Chapin, S.T.A. Pickett, M. Duniway, A.V. Rocha, F.J. Swanson, C. Laney, and J. Jones. 2011. Cross-system comparisons elucidate disturbance complexities and generalities. Ecosphere 2:art81. doi:10.1890/ES11-00115.1

Pimentel, J.S.M., and A. Giani. 2014. Microcystin production and regulation under nutrient stress conditions in toxic microcystis strains. Applied and Environmental Microbiology 80:5836–5843. doi:10.1128/AEM.01009-14

Powers, S.M., H.M. Baulch, S.E. Hampton, S.G. Labou, N.R. Lottig, and E.H. Stanley. 2017a. Nitrification contributes to winter oxygen depletion in seasonally frozen forested lakes. Biogeochemistry 136:119–129. doi:10.1007/s10533-017-0382-1

Powers, S.M., S.G. Labou, H.M. Baulch, R.J. Hunt, N.R. Lottig, S.E. Hampton, and E.H. Stanley. 2017b. Ice duration drives winter nitrate accumulation in north temperate lakes. Limnology and Oceanography Letters 2:177–186. doi:10.1002/lol2.10048

Qiu, J., S.R. Carpenter, E.G. Booth, M. Motew, S.C. Zipper, C.J. Kucharik, X. Chen, S.P. Loheide, J. Seifert, and M.G. Turner. 2018. Scenarios reveal pathways to sustain future ecosystem services in an agricultural landscape. Ecological Applications 28:119–134. doi:10.1002/eap.1633

Qiu, J., C.B. Wardropper, A.R. Rissman, and M.G. Turner. 2017. Spatial fit between water quality policies and hydrologic ecosystem services in an urbanizing agricultural landscape. Landscape Ecology 32:59–75. doi:10.1007/s10980-016-0428-0

Ratajczak, Z., S.R. Carpenter, A.R. Ives, C.J. Kucharik, T. Ramiadantsoa, M.A. Stegner, J.W. Williams, J. Zhang, and M.G. Turner. 2018. Abrupt change in ecological systems: inference and diagnosis. Trends in Ecology & Evolution 33:513–526. doi:10.1016/j.tree.2018.04.013

Read, E.K., L. Carr, L. De Cicco, H.A. Dugan, P.C. Hanson, J.A. Hart, J. Kreft, J.S. Read, and L.A. Winslow. 2017. Water quality data for national-scale aquatic research: The Water Quality Portal. Water Resources Research 53:1735–1745. doi:10.1002/2016WR019993

Read, J.S., C. Gries, E.K. Read, J. Klug, P. Hanson, M.R. Hipsey, E. Jennings, C.M. O'Reilly, L.A. Winslow, D. Pierson, C. McBride, and D. Hamilton. 2016. Generating community-built tools for data sharing and analysis in environmental networks. Inland Waters 6:637–644. doi:10.1080/IW-

6.4.889

Read, J.S., X. Jia, J. Willard, A.P. Appling, J.A. Zwart, S.K. Oliver, A. Karpatne, G.J.A. Hansen, P.C. Hanson, W. Watkins, M. Steinbach, and V. Kumar. 2019. Process-guided deep learning predictions of lake water temperature. Water Resources Research. doi:10.1029/2019WR024922

Reed, D.E., H.A. Dugan, A.L. Flannery, and A.R. Desai. 2018. Carbon sink and source dynamics of a eutrophic deep lake using multiple flux observations over multiple years: Carbon sink and source dynamics. Limnology and Oceanography Letters 3:285–292. doi:10.1002/lol2.10075

Reed-Andersen, T., S.R. Carpenter, D.K. Padilla, and R.C. Lathrop. 2000. Predicted impact of zebra mussel (*Dreissena polymorpha*) invasion on water clarity in Lake Mendota. Canadian Journal of Fisheries and Aquatic Sciences 57:1617–1626. doi:10.1139/f00-094

Reid, A.J., A.K. Carlson, I.F. Creed, E.J. Eliason, P.A. Gell, P.T.J. Johnson, K.A. Kidd, T.J. MacCormack, J.D. Olden, S.J. Ormerod, J.P. Smol, W.W. Taylor, K. Tockner, J.C. Vermaire, D. Dudgeon, and S.J. Cooke. 2019. Emerging threats and persistent conservation challenges for freshwater biodiversity. Biological Reviews 94:849–873. doi:10.1111/brv.12480

Rocha, J.C., G. Peterson, Ö. Bodin, and S. Levin. 2018. Cascading regime shifts within and across scales. Science 362:1379–1383. doi:10.1126/science.aat7850

Rocha, J.C., G.D. Peterson, and R. Biggs. 2015. Regime shifts in the Anthropocene: Drivers, risks, and resilience. PLOS ONE 10:e0134639. doi:10.1371/journal.pone.0134639

Rose, K.C., S.R. Greb, M. Diebel, and M.G. Turner. 2017. Annual precipitation regulates spatial and temporal drivers of lake water clarity. Ecological Applications 27:632–643. doi:10.1002/eap.1471

Rose, K.C., L.A. Winslow, J.S. Read, and G.J.A. Hansen. 2016. Climate-induced warming of lakes can be either amplified or suppressed by trends in water clarity: Clarity-climate warming of lakes. Limnology and Oceanography Letters 1:44–53. doi:10.1002/lol2.10027

Rosenzweig, B.R., L. McPhillips, H. Chang, C. Cheng, C. Welty, M. Matsler, D. Iwaniec, and C.I. Davidson. 2018. Pluvial flood risk and opportunities for resilience. Wiley Interdisciplinary Reviews: Water 5:e1302. doi:10.1002/wat2.1302

Roth, B.M., T.R. Hrabik, C.T. Solomon, N. Mercado-Silva, and J.F. Kitchell. 2010. A simulation of food-web interactions leading to rainbow smelt Osmerus mordax dominance in Sparkling Lake, Wisconsin. Journal of Fish Biology 77:1379–1405. doi:10.1111/j.1095-8649.2010.02764.x

Roux, S., L.-K. Chan, R. Egan, R.R. Malmstrom, K.D. McMahon, and M.B. Sullivan. 2017. Ecogenomics of virophages and their giant virus hosts assessed through time series metagenomics. Nature Communications 8:858. doi:10.1038/s41467-017-01086-2

Rudstam, L.G., R.C. Lathrop, and S.R. Carpenter. 1993. The rise and fall of a dominant planktivore: Direct and indirect effects on zooplankton. Ecology 74:301–19. doi:10.2307/1939294

Rypel, A.L., D. Goto, G.G. Sass, and M.J. Vander Zanden. 2018. Eroding productivity of walleye populations in northern Wisconsin lakes. Canadian Journal of Fisheries and Aquatic Sciences 75:2291–2301. doi:10.1139/cjfas-2017-0311

Rypel, A.L., T.P. Parks, G.J.A. Hansen, D.L. Oele, K.S. Cheruvelil, P.C. Jacobson, M.R. Magee, J. Lyons, G.G. Sass, K.E. Wehrly, J.E. Breck, S.B. Donabauer, M.J. Jennings, J.M. Kampa, A.E. Honsey, J. Nohner, and M.J. Vander Zanden. in prep. Land use confers climate change resilience for cold water fish populations

Schatz, J., and C.J. Kucharik. 2014. Seasonality of the urban heat island effect in Madison, Wisconsin. Journal of Applied Meteorology and Climatology 53:2371–2386. doi:10.1175/JAMC-D-14-0107.1

Schatz, J., and C.J. Kucharik. 2015. Urban climate effects on extreme temperatures in Madison, Wisconsin, USA. Environmental Research Letters 10:094024. doi:10.1088/1748-9326/10/9/094024

Schatz, J., and C.J. Kucharik. 2016. Urban heat island effects on growing seasons and heating and cooling degree days in Madison, Wisconsin USA: Heat island effects on growing seasons and degree days in Madison, Wisconsin USA. International Journal of Climatology 36:4873–4884.

doi:10.1002/joc.4675

Scheffer, M. 1998. Ecology of Shallow Lakes. Springer, Netherlands

Scheffer, M., and S.R. Carpenter. 2003. Catastrophic regime shifts in ecosystems: Linking theory to observation. Trends in Ecology & Evolution 18:648–656. doi:10.1016/j.tree.2003.09.002

Scheffer, M., and E.H. van Nes. 2007. Shallow lakes theory revisited: various alternative regimes driven by climate, nutrients, depth and lake size. Pages 455–466 *in* R. D. Gulati, E. Lammens, N. De Pauw, and E. Van Donk, editors. Shallow Lakes in a Changing World. Springer Netherlands, Dordrecht. doi:10.1007/978-1-4020-6399-2_41

Schindler, D.W., S.R. Carpenter, S.C. Chapra, R.E. Hecky, and D.M. Orihel. 2016. Reducing phosphorus to curb lake eutrophication is a success. Environmental Science & Technology 50:8923–8929. doi:10.1021/acs.est.6b02204

Schramm, P.J. 2018. Modeling spatial variability of light extinction in north temperate lakes. M.S., University of Wisconsin, Madison, WI

Schroer, W.F., C.R. Benitez-Nelson, E.M. Smith, and L.A. Ziolkowski. 2018. Drivers of sediment accumulation and nutrient burial in coastal stormwater detention ponds, South Carolina, USA. Ecosystems 21:1118–1138. doi:10.1007/s10021-017-0207-z

Schulz, F., S. Roux, D. Paez-Espino, S. Jungbluth, D.A. Walsh, V.J. Denef, K.D. McMahon, K.T. Konstantinidis, E.A. Eloe-Fadrosh, N.C. Kyrpides, and T. Woyke. 2020. Giant virus diversity and host interactions through global metagenomics. Nature 578:432–436. doi:10.1038/s41586-020-1957-x

Sharma, S., K. Blagrave, J.J. Magnuson, C.M. O'Reilly, S. Oliver, R.D. Batt, M.R. Magee, D. Straile, G.A. Weyhenmeyer, L. Winslow, and R.I. Woolway. 2019. Widespread loss of lake ice around the Northern Hemisphere in a warming world. Nature Climate Change 9:227–231. doi:10.1038/s41558-018-0393-5

Sharma, S., D.K. Gray, J.S. Read, C.M. O'Reilly, P. Schneider, A. Qudrat, C. Gries, S. Stefanoff, S.E. Hampton, S. Hook, J.D. Lenters, D.M. Livingstone, P.B. McIntyre, R. Adrian, M.G. Allan, O. Anneville, L. Arvola, J. Austin, J. Bailey, J.S. Baron, J. Brookes, Y. Chen, R. Daly, M. Dokulil, B. Dong, K. Ewing, E. de Eyto, D. Hamilton, K. Havens, S. Haydon, H. Hetzenauer, J. Heneberry, A.L. Hetherington, S.N. Higgins, E. Hixson, L.R. Izmest'eva, B.M. Jones, K. Kangur, P. Kasprzak, O. Köster, B.M. Kraemer, M. Kumagai, E. Kuusisto, G. Leshkevich, L. May, S. MacIntyre, D. Müller-Navarra, M. Naumenko, P. Noges, T. Noges, P. Niederhauser, R.P. North, A.M. Paterson, P.-D. Plisnier, A. Rigosi, A. Rimmer, M. Rogora, L. Rudstam, J.A. Rusak, N. Salmaso, N.R. Samal, D.E. Schindler, G. Schladow, S.R. Schmidt, T. Schultz, E.A. Silow, D. Straile, K. Teubner, P. Verburg, A. Voutilainen, A. Watkinson, G.A. Weyhenmeyer, C.E. Williamson, and K.H. Woo. 2015. A global database of lake surface temperatures collected by in situ and satellite methods from 1985–2009. Scientific Data 2:150008. doi:10.1038/sdata.2015.8

Sharma, S., D.A. Jackson, C.K. Minns, and B.J. Shuter. 2007. Will northern fish populations be in hot water because of climate change? Global Change Biology 13:2052–2064. doi:10.1111/j.1365-2486.2007.01426.x

Sharma, S., M.J. Vander Zanden, J.J. Magnuson, and J. Lyons. 2011. Comparing climate change and species invasions as drivers of coldwater fish population extirpations. PLoS ONE 6:e22906. doi:10.1371/journal.pone.0022906

Sherry, R.A., X. Zhou, S. Gu, J.A. Arnone, D.W. Johnson, D.S. Schimel, P.S.J. Verburg, L.L. Wallace, and Y. Luo. 2011. Changes in duration of reproductive phases and lagged phenological response to experimental climate warming. Plant Ecology & Diversity 4:23–35. doi:10.1080/17550874.2011.557669

Silva, T.S.F., M.P.F. Costa, J.M. Melack, and E.M.L.M. Novo. 2008. Remote sensing of aquatic vegetation: theory and applications. Environmental Monitoring and Assessment 140:131–145. doi:10.1007/s10661-007-9855-3

Smith, S.D.P. 2012. Identifying and evaluating causes of alternative community states in wetland plant communities. Oikos 121:675–686. doi:10.1111/j.1600-0706.2011.19790.x

Snortheim, C.A., P.C. Hanson, K.D. McMahon, J.S. Read, C.C. Carey, and H.A. Dugan. 2017. Meteorological drivers of hypolimnetic anoxia in a eutrophic, north temperate lake. Ecological Modelling 343:39–53. doi:10.1016/j.ecolmodel.2016.10.014

Snucins, E., and J. Gunn. 2000. Interannual variation in the thermal structure of clear and colored lakes. Limnology and Oceanography 45:1639–1646. doi:10.4319/lo.2000.45.7.1639

Sommer, U., R. Adrian, L. De Senerpont Domis, J.J. Elser, U. Gaedke, B. Ibelings, E. Jeppesen, M. Lürling, J.C. Molinero, W.M. Mooij, E. van Donk, and M. Winder. 2012. Beyond the Plankton Ecology Group (PEG) model: Mechanisms driving plankton succession. Annual Review of Ecology, Evolution, and Systematics 43:429–448. doi:10.1146/annurev-ecolsys-110411-160251

Soranno, P.A., L.C. Bacon, M. Beauchene, K.E. Bednar, E.G. Bissell, C.K. Boudreau, M.G. Boyer, M.T. Bremigan, S.R. Carpenter, J.W. Carr, K.S. Cheruvelil, S.T. Christel, M. Claucherty, S.M. Collins, J.D. Conroy, J.A. Downing, J. Dukett, C.E. Fergus, C.T. Filstrup, C. Funk, M.J. Gonzalez, L.T. Green, C. Gries, J.D. Halfman, S.K. Hamilton, P.C. Hanson, E.N. Henry, E.M. Herron, C. Hockings, J.R. Jackson, K. Jacobson-Hedin, L.L. Janus, W.W. Jones, J.R. Jones, C.M. Keson, K.B.S. King, S.A. Kishbaugh, J.-F. Lapierre, B. Lathrop, J.A. Latimore, Y. Lee, N.R. Lottig, J.A. Lynch, L.J. Matthews, W.H. McDowell, K.E.B. Moore, B.P. Neff, S.J. Nelson, S.K. Oliver, M.L. Pace, D.C. Pierson, A.C. Poisson, A.I. Pollard, D.M. Post, P.O. Reyes, D.O. Rosenberry, K.M. Roy, L.G. Rudstam, O. Sarnelle, N.J. Schuldt, C.E. Scott, N.K. Skaff, N.J. Smith, N.R. Spinelli, J.J. Stachelek, E.H. Stanley, J.L. Stoddard, S.B. Stopyak, C.A. Stow, J.M. Tallant, P.-N. Tan, A.P. Thorpe, M.J. Vanni, T. Wagner, G. Watkins, K.C. Weathers, K.E. Webster, J.D. White, M.K. Wilmes, and S. Yuan. 2017. LAGOS-NE: a multi-scaled geospatial and temporal database of lake ecological context and water quality for thousands of US lakes. GigaScience 6. doi:10.1093/gigascience/gix101

Soylu, M.E., C.J. Kucharik, and S.P. Loheide. 2014. Influence of groundwater on plant water use and productivity: Development of an integrated ecosystem – Variably saturated soil water flow model. Agricultural and Forest Meteorology 189–190:198–210. doi:10.1016/j.agrformet.2014.01.019

Stadler, P., L.C. Loken J.T. Crawford, P.J. Schramm, K. Sorsa, C. Kuhn, D. Savio, R.G. Striegl, D. Butman, E.H. Stanley, A.H. Farnleitner, and M. Zessner. 2019. Spatial patterns of enzymatic activity in large water bodies: Ship-borne measurements of beta-D-glucuronidase activity as a rapid indicator of microbial water quality. Science of The Total Environment 651:1742–1752. doi:10.1016/j.scitotenv.2018.10.084

Steffen, M.M., T.W. Davis, R.M.L. McKay, G.S. Bullerjahn, L.E. Krausfeldt, J.M.A. Stough, M.L. Neitzey, N.E. Gilbert, G.L. Boyer, T.H. Johengen, D.C. Gossiaux, A.M. Burtner, D. Palladino, M.D. Rowe, G.J. Dick, K.A. Meyer, S. Levy, B.E. Boone, R.P. Stumpf, T.T. Wynne, P.V. Zimba, D. Gutierrez, and S.W. Wilhelm. 2017. Ecophysiological examination of the Lake Erie *Microcystis* bloom in 2014: Linkages between biology and the water supply shutdown of Toledo, OH. Environmental Science & Technology 51:6745–6755. doi:10.1021/acs.est.7b00856

Steffen, W., W. Broadgate, L. Deutsch, O. Gaffney, and C. Ludwig. 2015. The trajectory of the Anthropocene: The great acceleration. The Anthropocene Review 2:81–98. doi:10.1177/2053019614564785

Stenseth, N.C., and A. Mysterud. 2002. Climate, changing phenology, and other life history traits: Nonlinearity and match-mismatch to the environment. Proceedings of the National Academy of Sciences 99:13379–13381. doi:10.1073/pnas.212519399

Strayer, D.L. 2010. Alien species in fresh waters: ecological effects, interactions with other stressors, and prospects for the future. Freshwater Biology 55:152–174. doi:10.1111/j.1365-2427.2009.02380.x

Strayer, D.L. 2012. Eight questions about invasions and ecosystem functioning. Ecology Letters 15:1199–1210. doi:10.1111/j.1461-0248.2012.01817.x

Stumm, W., and J.J. Morgan. 1995. Aquatic Chemistry: Chemical Equilibria and Rates in Natural Waters.

3rd edition. Wiley

Swain, D.L., B. Langenbrunner, J.D. Neelin, and A. Hall. 2018. Increasing precipitation volatility in twenty-first-century California. Nature Climate Change 8:427–433. doi:10.1038/s41558-018-0140-y

Swanson, F.J. 2015. Confluence of arts, humanities, and science at sites of long-term ecological inquiry. Ecosphere 6:art132. doi:10.1890/ES15-00139.1

Tavares, M., A. Cunha, D. Motta-Marques, A. Ruhoff, J. Cavalcanti, C. Fragoso, J. Martín Bravo, A. Munar, F. Fan, and L. Rodrigues. 2019. Comparison of methods to estimate lake-surface-water temperature using landsat 7 ETM+ and MODIS imagery: Case study of a large shallow subtropical lake in southern Brazil. Water 11:168. doi:10.3390/w11010168

Terborgh, J., and J.A. Estes, editors. 2010. Trophic Cascades. Island Press, Washington, D. C.

Thackeray, S.J., T.H. Sparks, M. Frederiksen, S. Burthe, P.J. Bacon, J.R. Bell, M.S. Botham, T.M. Brereton, P.W. Bright, L. Carvalho, T. Clutton-Brock, A. Dawson, M. Edwards, J.M. Elliott, R. Harrington, D. Johns, I.D. Jones, J.T. Jones, D.I. Leech, D.B. Roy, W.A. Scott, M. Smith, R.J. Smithers, I.J. Winfield, and S. Wanless. 2010. Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. Global Change Biology 16:3304–3313. doi:10.1111/j.1365-2486.2010.02165.x

Turner, M.G., W.J. Calder, G.S. Cumming, T.P. Hughes, A. Jentsch, S.L. LaDeau, T.M. Lenton, B.N. Shuman, M.R. Turetsky, Z. Ratajczak, J.W. Williams, A.P. Williams, and S.R. Carpenter. 2020. Climate change, ecosystems and abrupt change: Science priorities. Philosophical Transactions of the Royal Society B: Biological Sciences 375:20190105. doi:10.1098/rstb.2019.0105

Usinowicz, J., J. Qiu, and A. Kamarainen. 2017. Flashiness and flooding of two lakes in the Upper Midwest during a century of urbanization and climate change. Ecosystems 20:601–615. doi:10.1007/s10021-016-0042-7

Vadas, P.A., W.J. Gburek, A.N. Sharpley, P.J.A. Kleinman, P.A. Moore, M.L. Cabrera, and R.D. Harmel. 2007. A model for phosphorus transformation and runoff loss for surface-applied manures. Journal of Environmental Quality 36:324–332. doi:10.2134/jeq2006.0213

Vadas, P.A., B.E. Haggard, and W.J. Gburek. 2005. Predicting dissolved phosphorus in runoff from manured field plots. Journal of Environmental Quality 34:1347–1353. doi:10.2134/jeq2004.0424

Vadas, P.A., P.J.A. Kleinman, and A.N. Sharpley. 2004. A simple method to predict dissolved phosphorus in runoff from surface-applied manures. Journal of Environmental Quality 33:749–756. doi:10.2134/jeq2004.7490

Vander Zanden, M.J., G.J.A. Hansen, and A.W. Latzka. 2017. A framework for evaluating heterogeneity and landscape-level impacts of non-native aquatic species. Ecosystems 20:477–491. doi:10.1007/s10021-016-0102-z

Vanderploeg, H.A., J.R. Liebig, W.W. Carmichael, M.A. Agy, T.H. Johengen, G.L. Fahnenstiel, and T.F. Nalepa. 2001. Zebra mussel (*Dreissena polymorpha*) selective filtration promoted toxic *Microcystis* blooms in Saginaw Bay (Lake Huron) and Lake Erie. Canadian Journal of Fisheries and Aquatic Sciences 58:1208–1221. doi:10.1139/f01-066

VanLoocke, A., C.J. Bernacchi, and T.E. Twine. 2010. The impacts of Miscanthus×giganteus production on the Midwest US hydrologic cycle. GCB Bioenergy:180–191. doi:10.1111/j.1757-1707.2010.01053.x

VanLoocke, A., T.E. Twine, C.J. Kucharik, and C.J. Bernacchi. 2017. Assessing the potential to decrease the Gulf of Mexico hypoxic zone with Midwest US perennial cellulosic feedstock production. GCB Bioenergy 9:858–875. doi:10.1111/gcbb.12385

VanLoocke, A., T.E. Twine, M. Zeri, and C.J. Bernacchi. 2012. A regional comparison of water use efficiency for miscanthus, switchgrass and maize. Agricultural and Forest Meteorology 164:82–95. doi:10.1016/j.agrformet.2012.05.016

Villa, P., M. Pinardi, R. Bolpagni, J.-M. Gillier, P. Zinke, F. Nedelcuţ, and M. Bresciani. 2018. Assessing macrophyte seasonal dynamics using dense time series of medium resolution satellite data.

Remote Sensing of Environment 216:230–244. doi:10.1016/j.rse.2018.06.048

Viney, N.R., M. Sivapalan, and D. Deeley. 2000. A conceptual model of nutrient mobilisation and transport applicable at large catchment scales. Journal of Hydrology 240:23–44. doi:10.1016/S0022-1694(00)00320-6

Vitasse, Y., C. Signarbieux, and Y.H. Fu. 2018. Global warming leads to more uniform spring phenology across elevations. Proceedings of the National Academy of Sciences 115:1004–1008. doi:10.1073/pnas.1717342115

Voter, C.B., and S.P. Loheide. 2018. Urban residential surface and subsurface hydrology: Synergistic effects of low-impact features at the parcel scale. Water Resources Research 54:8216–8233. doi:10.1029/2018WR022534

Waits, L.P., and A. Storfer. 2015. Basics of population genetics: Quantifying neutral and adaptive genetic variation for landscape genetic studies. Pages 35–57 *in* N. Balkenhol, S. A. Cushman, A. T. Storfer, and L. P. Waits, editors. Landscape Genetics. John Wiley & Sons, Ltd, Chichester, UK. doi:10.1002/9781118525258.ch03

Walsh, J.R., S.R. Carpenter, and M.J. Vander Zanden. 2016a. Invasive species triggers a massive loss of ecosystem services through a trophic cascade. Proceedings of the National Academy of Sciences 113:4081–4085. doi:10.1073/pnas.1600366113

Walsh, J.R., J.R. Corman, and S.E. Munoz. 2019a. Coupled long-term limnological data and sedimentary records reveal new control on water quality in a eutrophic lake. Limnology and Oceanography:lno.11083. doi:10.1002/lno.11083

Walsh, J.R., R.C. Lathrop, and M.J. Vander Zanden. 2017. Invasive invertebrate predator, *Bythotrephes longimanus* , reverses trophic cascade in a north-temperate lake: Invasive invertebrate reverses cascade. Limnology and Oceanography 62:2498–2509. doi:10.1002/lno.10582

Walsh, J.R., R.C. Lathrop, and M.J. Vander Zanden. 2018a. Uncoupling indicators of water quality due to the invasive zooplankter, *Bythotrephes longimanus*: Water quality indicators uncoupled by invasion. Limnology and Oceanography 63:1313–1327. doi:10.1002/lno.10773

Walsh, J.R., S.E. Munoz, and M.J. Vander Zanden. 2016b. Outbreak of an undetected invasive species triggered by a climate anomaly. Ecosphere 7:e01628. doi:10.1002/ecs2.1628

Walsh, J.R., E.J. Pedersen, and M.J. Vander Zanden. 2018b. Detecting species at low densities: A new theoretical framework and an empirical test on an invasive zooplankton. Ecosphere 9:e02475. doi:10.1002/ecs2.2475

Walsh, J.R., M.J. Spear, T.P. Shannon, P.J. Krysan, and M.J. Vander Zanden. 2019b. Using eDNA, sediment subfossils, and zooplankton nets to detect invasive spiny water flea (Bythotrephes longimanus). Biological Invasions 21:377–389. doi:10.1007/s10530-018-1862-5

Walther, G.-R. 2010. Community and ecosystem responses to recent climate change. Philosophical Transactions of the Royal Society B: Biological Sciences 365:2019–2024. doi:10.1098/rstb.2010.0021

Wandeler, P., P.E.A. Hoeck, and L.F. Keller. 2007. Back to the future: museum specimens in population genetics. Trends in Ecology & Evolution 22:634–642. doi:10.1016/j.tree.2007.08.017

Wasko, A.P., C. Martins, C. Oliveira, and F. Foresti. 2003. Non-destructive genetic sampling in fish. An improved method for DNA extraction from fish fins and scales. Hereditas 138:161–165. doi:10.1034/j.1601-5223.2003.01503.x

Watras, C.J., J.S. Read, K.D. Holman, Z. Liu, Y.-Y. Song, A.J. Watras, S. Morgan, and E.H. Stanley. 2014. Decadal oscillation of lakes and aquifers in the upper Great Lakes region of North America: Hydroclimatic implications. Geophysical Research Letters 41:456–462. doi:10.1002/2013GL058679

Weirich, C.A., D.M. Robertson, and T.R. Miller. 2019. Physical, biogeochemical, and meteorological factors responsible for interannual changes in cyanobacterial community composition and biovolume over two decades in a eutrophic lake. Hydrobiologia 828:165–182. doi:10.1007/s10750-018-3810-x

Wilson, K.A., J.J. Magnuson, D.M. Lodge, A.M. Hill, T.K. Kratz, W.L. Perry, and T.V. Willis. 2004. A long-term rusty crayfish (Orconectes rusticus) invasion: Dispersal patterns and community change in a north temperate lake. Canadian Journal of Fisheries and Aquatic Sciences 61:2255–2266. doi:10.1139/f04-170

Winder, M., and D.E. Schindler. 2004. Climatic effects on the phenology of lake processes. Global Change Biology 10:1844–1856. doi:10.1111/j.1365-2486.2004.00849.x

Winslow, L.A., G.J.A. Hansen, J.S. Read, and M. Notaro. 2017a. Large-scale modeled contemporary and future water temperature estimates for 10774 Midwestern U.S. Lakes. Scientific Data 4:170053. doi:10.1038/sdata.2017.53

Winslow, L.A., J.S. Read, G.J.A. Hansen, and P.C. Hanson. 2015. Small lakes show muted climate change signal in deepwater temperatures. Geophysical Research Letters 42:355–361. doi:10.1002/2014GL062325

Winslow, L.A., J.S. Read, G.J.A. Hansen, K.C. Rose, and D.M. Robertson. 2017b. Seasonality of change: Summer warming rates do not fully represent effects of climate change on lake temperatures. Limnology and Oceanography 62:2168–2178. doi:10.1002/lno.10557

Winslow, L.A., J.A. Zwart, R.D. Batt, H.A. Dugan, R.I. Woolway, J.R. Corman, P.C. Hanson, and J.S. Read. 2016. LakeMetabolizer: an R package for estimating lake metabolism from free-water oxygen using diverse statistical models. Inland Waters 6:622–636. doi:10.1080/IW-6.4.883

Woolway, R.I., C.J. Merchant, J.V.D. Hoek, C.A. Molina, P. Nõges, A. Laas, E.. B. Mackay, and I.D. Jone. 2019. Northern Hemisphere atmospheric stilling accelerates lake thermal responses to a warming world. Geophysical Research Letters. doi:10.1029/2019GL082752

Wu, J. 2014. Urban ecology and sustainability: The state-of-the-science and future directions. Landscape and Urban Planning 125:209–221. doi:10.1016/j.landurbplan.2014.01.018

Yang, Y.-Y., and M.G. Lusk. 2018. Nutrients in urban stormwater runoff: Current state of the science and potential mitigation options. Current Pollution Reports 4:112–127. doi:10.1007/s40726-018-0087-7

Zipper, S.C., M. Motew, E.G. Booth, X. Chen, J. Qiu, C.J. Kucharik, S.R. Carpenter, and S.P. Loheide. 2018. Continuous separation of land use and climate effects on the past and future water balance. Journal of Hydrology 565:106–122. doi:10.1016/j.jhydrol.2018.08.022

Zipper, S.C., J. Schatz, C.J. Kucharik, and S.P. Loheide. 2017a. Urban heat island-induced increases in evapotranspirative demand. Geophysical Research Letters 44:873–881. doi:10.1002/2016GL072190

Zipper, S.C., J. Schatz, A. Singh, C.J. Kucharik, P.A. Townsend, and S.P. Loheide. 2016. Urban heat island impacts on plant phenology: Intra-urban variability and response to land cover. Environmental Research Letters 11:054023. doi:10.1088/1748-9326/11/5/054023

Zipper, S.C., M.E. Soylu, C.J. Kucharik, and S.P. Loheide. 2017b. Quantifying indirect groundwater-mediated effects of urbanization on agroecosystem productivity using MODFLOW-AgroIBIS (MAGI), a complete critical zone model. Ecological Modelling 359:201–219. doi:10.1016/j.ecolmodel.2017.06.002

Ziter, C., and M.G. Turner. 2018. Current and historical land use influence soil-based ecosystem services in an urban landscape. Ecological Applications 28:643–654. doi:10.1002/eap.1689

Ziter, C.D., E.J. Pedersen, C.J. Kucharik, and M.G. Turner. 2019. Scale-dependent interactions between tree canopy cover and impervious surfaces reduce daytime urban heat during summer. Proceedings of the National Academy of Sciences 116:7575–7580. doi:10.1073/pnas.1817561116