

Project Summary

Overview: Lakes, the iconic landscape feature of glaciated landscapes around the world, are important in hydrological and biogeochemical processes, ecological interactions, and ecosystem services. The overarching research question for the North Temperate Lakes (NTL) Long-Term Ecological Research Program is: **How do biophysical setting, climate, and land use and cover interact to shape lake dynamics and organization in the past, present and future?** Research activities are organized around four interrelated thematic questions:

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

Questions will be addressed through research in two regions in Wisconsin, the Northern Highland and Yahara Lake Districts. Physical, chemical, biological, and social patterns and interactions will be examined using a nested set of spatial scales from individual lakes and watersheds, to hydrologically-linked sets of lakes, entire lake districts, multiple lake districts within the Great Lakes region, and comparative studies of lakes and lake districts around the globe. Temporally, scales range from minutes to centuries. Research approaches include acquisition, generation, and analysis of long term observations; comparative studies; experiments; and diverse modeling and statistical tools. The interdisciplinary team includes expertise in biogeochemistry, climatology, demography, ecology (landscape, ecosystem, community, population, and paleo- ecology), economics, education and outreach, hydrodynamics, hydrology, information management, and microbiology.

Intellectual Merits: Long-term ecological research is an absolute necessity for detecting and understanding fundamental changes in ecosystems. The NTL program aims to understand change in lakes in relation to relevant abiotic, biotic, and human processes. Proposed work informs and is informed by concepts and models from research on landscape limnology, connectivity, multiple causation, and extreme events, and concepts and hypotheses will be evaluated across a span a range of scales and topics, such as responses of lake thermal regime and gas exchange to changing climate, watershed organic carbon and phosphorus dynamics, abundance-impact theory for aquatic invasive species, and many others. The multi-scale, multi-faceted NTL research program is designed to detect patterns of long-term change, evaluate and advance concepts to understand causes and consequences of these changes, and build forward-looking models and hypotheses that will be tested using future long-term observations.

Broader Impacts: Proposed research is expected to produce new synthetic understandings of ecological and social-ecological change in lake districts. It is grounded in the provision and expansion of a comprehensive, well-documented 33-year database of regional change, and it provides scientific information and understanding relevant to decisions of individuals and institutions concerned with the future of the region and the welfare of its residents. Research results are integrated in multiple K-12, undergraduate, graduate, and continuing education activities. The NTL program is committed to supporting diversity in science, and to communicating scientific results and expertise to broad academic and non-academic audiences to inform individuals, non-governmental organizations, local, and state and federal agencies.

Section 1: Results from Prior Support

Throughout the 30+ year history of the North Temperate Lakes Long-Term Ecological Research (NTL) program, we have made significant progress in understanding long-term change in two suites of lakes in the Northern Highland Lake District (NHL; northern Wisconsin) and the Yahara Lake District (YLD, southern Wisconsin) along with their surrounding landscapes (Fig. 1). We have published more than 1050 peer-reviewed articles, of which 229 were published in the last grant cycle (Fig. 2). NTL has engaged scores of graduate students and hundreds of undergraduates in research. 145 graduate theses can be attributed to the project, with 21 since 2008. Further, we have developed an efficient and robust information management system, been active contributors to LTER network-level activities, collaborated extensively with other research networks, and led significant education and outreach activities with K-12 students and teachers, the general public, natural resource managers, and policy makers. We summarize major research results over the past six years below, organized by the four themes of our prior proposal. Our ten most significant publications (Table 1) are highlighted in bold. We also describe progress in information management, cross-site activities, broader impacts, and outcomes of supplemental funding opportunities.

Perception of long-term change. NTL has collected, curated, and made publicly available over 160 datasets that include physical, chemical, biological, and socio-economic variables for eleven lakes in Wisconsin. These data are among the most complete long-term, multi-lake datasets in the world (see Table S1) and provide the foundation for understanding long-term change in lakes and their surrounding landscapes (Magnuson et al. 2006). We used these data sets in several recent ecological and limnological studies to examine decadal-scale patterns and drivers of lake dynamics. At the community level, our unprecedented decade-long time series of bacterial composition allowed us to discover unexpected seasonally-repeating patterns in community structure (**Kara et al. 2013**). We also compared long-term zooplankton assemblages from lakes that had experienced various types of disturbance to nearby reference lakes to show that disturbances result in assemblages composed of more closely related species (**Helmus et al. 2010**). This result demonstrated that a phylogenetic perspective provided new insights into disturbance effects on community composition beyond what could be learned from standard community metrics. Another significant use of our long-term data was to determine the most effective means of predicting lake conditions. Given that researchers and resource managers cannot measure all lakes at all times, **Lottig & Carpenter (2012)** asked whether information on current states of nearby lakes or historic data for a given lake was more effective for predicting the lake's current condition. Using several NTL data sets, this analysis revealed that the best models required at least 15 years of data and included both comparative and historic information.

Climate forcing of change. Understanding effects of climate forcing on lakes and their surrounding landscapes requires a long-term perspective. In northern Wisconsin, climatic forcing produce quasi-cyclical patterns of lake water levels, and in turn, these fluctuations have affected lake ecology. Over the 75-year period for which manual observations exist, water levels of seepage lakes fluctuated with a dominant period between successive low-water periods of approximately 13 years and an amplitude of approximately one meter, though the most recent low-water period was more prolonged and severe than previous cycles (Fig. 3; **Watras et al. 2014**). Downscaled climate projections for the next century suggest that water levels in some

lakes may decline by another 1-2 m in concert with increased water temperature and evaporation rates (Meyer et al. 2013). This lowering of lake levels exposes littoral zone habitat, often to the detriment of resident populations. For example, woody debris that accumulates in these areas and serves as critical fish habitat can get stranded above the water line, impairing fish foraging, recruitment, and growth (Sass et al. 2012, Gaeta et al. 2014). However, there may be unexpected benefits, as the invasive and highly destructive crayfish *Orconectes rusticus* which also occupies this shallow water area, shows declining abundances during low water periods (Hansen et al. 2013a).

In addition to quasi-cyclical drivers, we have observed changes in likelihoods of extreme climatic events, which often have more severe ecological and human consequences than changes in mean conditions. These include increased likelihood of short ice seasons across the Northern Hemisphere (**Benson et al. 2012**) and increased frequency of intense rain events in southern Wisconsin (Kucharik et al. 2010, Gillon et al. in review). Recognition of changing frequencies of extreme events and their effects on lakes motivates several studies presented later in this proposal.

Interactive drivers, scales of space and time, and regional change. In the last grant cycle, we made major progress understanding the drivers, scales, and regional dynamics of both carbon (C) and aquatic invasive species. Construction of a comprehensive regional C budget that included aquatic and terrestrial components revealed that lake sediments and wetlands account for ca. 80% of C storage within the NHLD even though forests occupy more of the landscape and are currently accruing C at far greater rates than lakes and wetlands (Fig. 4; **Buffam et al. 2011**). This result highlights the importance of small yet persistent C fluxes to lake sediments and wetland peats that lead to substantial carbon burial in aquatic systems over centuries to millennia. We will build on this previous work and examine terrestrial-aquatic C fluxes in the upcoming funding cycle. In addition to storing organic C, lakes and streams are net CO₂ sources to the atmosphere, but flux rates are controlled by a complex set of processes in each ecosystem. For example, a study of 40 lakes worldwide (including several NTL lakes) showed that gas flux to the atmosphere in small lakes (<10 ha) is controlled by convective mixing caused by nighttime cooling, whereas in larger lakes wind shear is much more important (**Read et al. 2012**). Climate fluctuations also affect CO₂ exchange, as a model of > 6,700 lakes in the NHLD indicated a 45% reduction in CO₂ efflux from lakes during dry periods, compared to a 31% increase during wet periods (Cardille et al. 2009). Interestingly, despite occupying a much smaller area of the NHLD landscape, streams may emit as much or more CO₂ as lakes (Crawford et al. 2014). Understanding stream/lake interactions and their combined influences on regional processes has been a recent area of emphasis (e.g., Hanson et al. 2011, Lottig et al. 2011, 2012, Lathrop & Carpenter 2014) that will continue in the current proposal.

Aquatic invasive species (AIS) are a major concern because of their potential impacts on the ecology, economics, and human use of lakes. We developed a framework for assessing ecosystem vulnerability to AIS that considers the potential for transport, establishment, and adverse impact to provide a basis for prioritizing invasive species prevention efforts (Vander Zanden & Olden 2008, Olden et al. 2011, Papes et al. 2011). We found that AIS typically occur at low densities, and only rarely become very abundant (Hansen et al. 2013b). However, a statewide survey also revealed that they occur in about 4X more lakes than currently reported

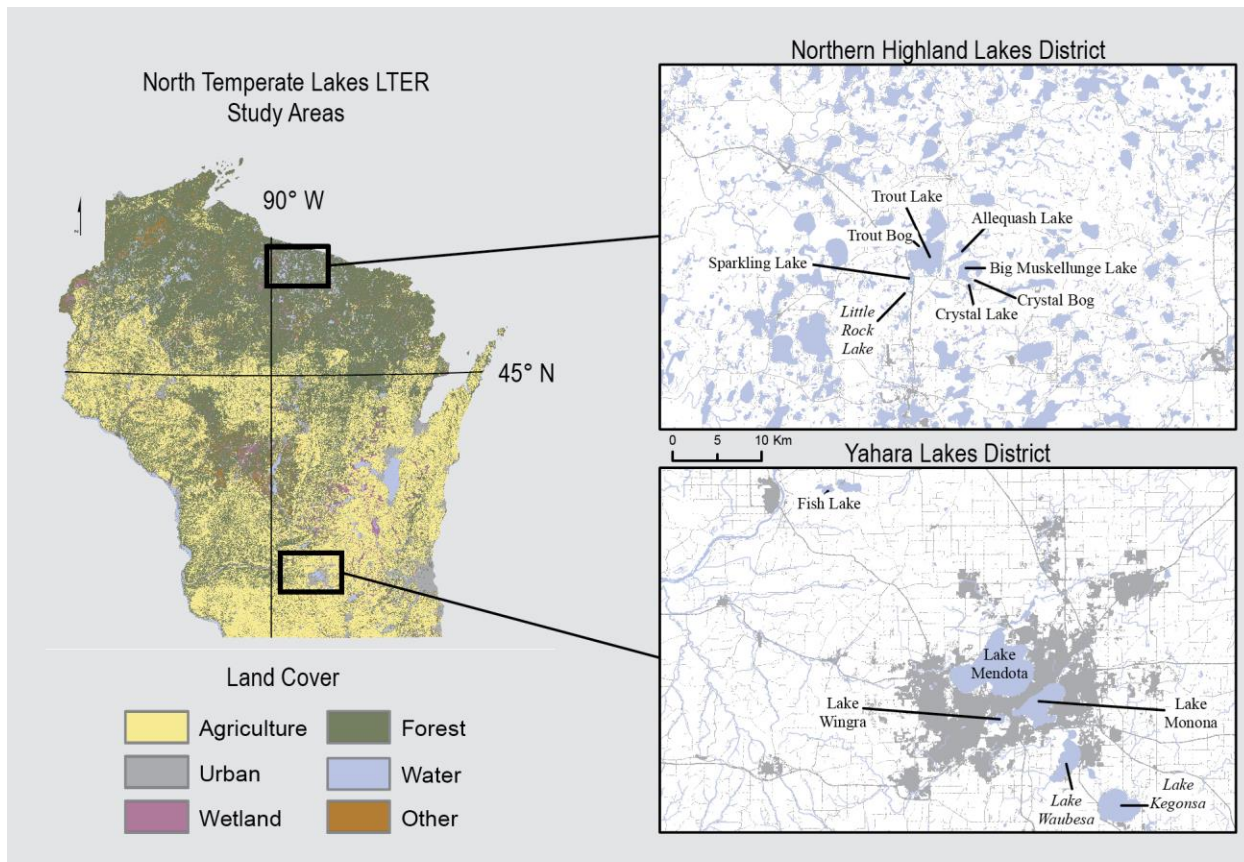


Figure 1. The North Temperate Lakes LTER study areas in the Northern Highland Lake District (NHLD) and the Yahara Lake District (YLD), Wisconsin. Locations of the 7 core NHLD and 4 core YLD lakes (standard font) along with selected secondary study lakes (italics font) are indicated in the inset maps on the right.

Table 1. Ten most significant NTL publications since 2009. Underlined names denotes lead authors who were students or post docs. Full author lists are included in the References Cited section.

Benson et al. 2012. Extreme events, trends, and variability in Northern Hemisphere lake ice phenology (1855 - 2005). *Climatic Change* 112:299-323.

Biggs et al. 2010. Preparing for the future: teaching scenario planning at the graduate level. *Frontiers in Ecology and the Environment* 8: 267-273.

Buffam et al. 2011. Integrating aquatic and terrestrial components to construct a complete carbon budget for a north temperate lake district. *Global Change Biology* 17:1193-1211.

Hansen et al. 2013c. Are rapid transitions between invasive and native species caused by alternative stable states, and does it matter? *Ecology* 94:2207-2219.

Helmus et al. 2010. Communities contain closely related species during ecosystem disturbance. *Ecology Letters* 13:162-174.

Horsch and Lewis. 2009. The effects of aquatic invasive species on property values: Evidence from a quasi-experiment. *Land Economics* 85:391-409.

Kara et al. 2013. A decade of seasonal dynamics and co-occurrences within freshwater bacterioplankton communities from eutrophic Lake Mendota, WI, USA. *The ISME Journal* 7:680-684.

Lottig and Carpenter. 2012. Interpolating and forecasting lake characteristics using long-term monitoring data. *Limnology and Oceanography* 57:1113-1125.

Read et al. 2012. Lake-size dependency of wind shear and convection as controls on gas exchange. *Geophysical Research Letters* 39: doi:10.1029/2012GL051886.

Watras et al. 2014. Decadal oscillation of lakes and aquifers in the upper Great Lakes region of North America: Hydroclimatic implications. *Geophysical Research Letters* 41: doi:10.1002/2013GL058679.

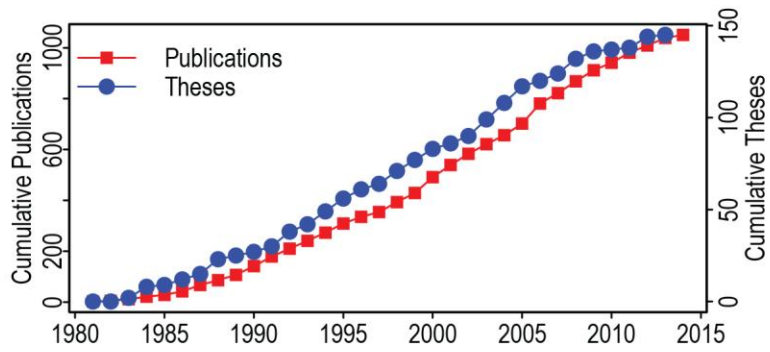


Figure 2. Cumulative publications vs. year for NTL. Publications in press are counted as 2014. All papers were either fully funded by NTL or jointly supported by NTL and other sources. Popular articles are excluded. Publication numbers are likely underestimates because we are not always made aware of every paper that uses our publicly-available data.

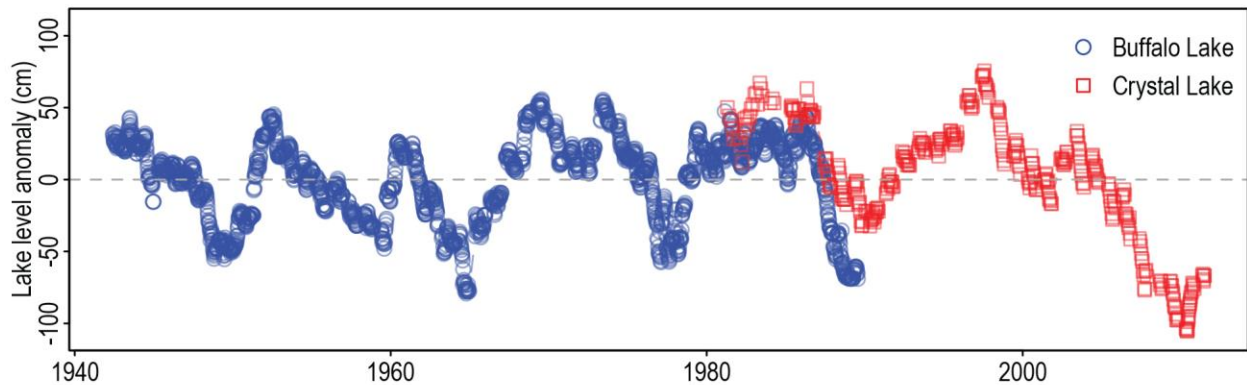


Figure 3. Near-decadal water level oscillation of Buffalo and Crystal Lakes, 1942-2011. Both are seepage lakes in the NHL, and Crystal Lake is a core NTL study lake. From Watras et al. (2014).

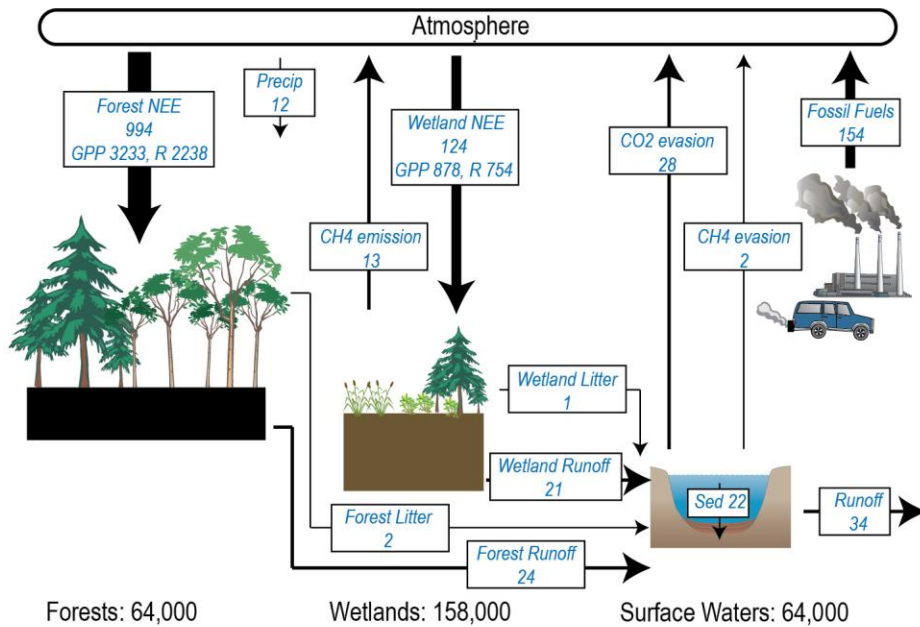


Figure 4. Summary of the regional organic carbon (C) budget for the NHL that includes forest, wetland, and lake ecosystems, along with best estimates of C flux rates (boxes) and pool sizes (bottom of figure). Forests make up 54% of the NHL area, wetlands 28%, and lakes 13%. NEE, net ecosystem exchange; GPP, gross primary production; R, respiration. Flux rates in Gg-C/yr, pool sizes in Gg-C. From Buffam et al. (2011).

(Latzka et al. unpublished data). A long-term harvest experiment (2001-2009) of invasive rusty crayfish in Sparkling Lake (Hein et al. 2006, 2007) caused a dramatic rusty crayfish decline and rapid recovery of native taxa such as sunfish, snails, native crayfish, and macrophytes (Hansen et al. 2013a). Following cessation of harvest, the lake has stayed in a native-dominated state, providing evidence for alternate stable states in this lake (Hansen et al. 2013c). In the upcoming funding cycle, we will build on these prior AIS studies by asking questions about causes of AIS spread and effects of these invaders on ecosystem state.

Ecosystem services, past present and future. NTL's work on ecosystem services covered three general areas: (1) understanding the role of scientific uncertainty in environmental decisions; (2) economic analyses of the costs of establishment of the invasive aquatic plant, Eurasian watermilfoil; and (3) phosphorus (P) budgets for the YLD watershed and lakes in relation to water quality outcomes. (1) *Uncertainty and decisions*: We showed how hierarchical statistical models can overcome some conflicts caused by observation error and environmental heterogeneity (Biggs et al. 2009) and participated in a broad literature review of methods for decision-making with scientific uncertainty in the context of global change (Polasky et al. 2011). NTL faculty taught graduate courses on scenario analysis for environmental decisions (Biggs et al. 2010) and on ecosystem services, and participated in an LTER cross-site comparison of scenario analyses (Thompson et al. 2012). (2) *Economics of invasive species*: We devised a solution to an important theoretical problem in contingent valuation (Provencher et al. 2012) and corroborated our findings using an independent method (Horsch & Lewis 2009). These new methods were used to determine that property values on lakes invaded by Eurasian watermilfoil declined by \$25,000 to \$30,000 per land parcel. (3) *Phosphorus and water quality*: A team of NTL graduate students quantified the P budget for the watershed of Lake Mendota (Kara et al. 2012). P enrichment of soils slowed over the last ~15 years, but there was still more P added to soil in fertilizers and manure than was removed in harvested crops and runoff. We synthesized 33 years of complete P budgets for four Yahara lakes and analyzed the efficacy of eutrophication mitigation plans (Carpenter & Lathrop 2013, Lathrop & Carpenter 2014). This work, along with our climate change studies, motivates proposed research on future scenarios of P management- a policy issue of increasing importance across the region.

Information Management. Information management (IM) has been and continues to be a priority and an essential ingredient of our success in long-term ecological research. We improved and upgraded our already robust IM system in several ways over the past six years. We migrated the NTL IM system from Oracle with a custom Java/JSP web portal to an entirely open source MySQL, PostGIS, Drupal Environmental Information System (DEIMS) web portal. DEIMS and a module to export EML metadata were developed in collaboration with several other LTER sites. Using these modules, all existing and new data are now integrated into the LTER Network Metacat data catalog and the new Network Information System (NIS) based on PASTA.

NTL has had efficient workflows for long-term data submission for a number of years. We developed well-annotated Kepler workflows, providing documentation for data provenance. Historic limnological data from surveys conducted in the 1920s-1930 were digitized, allowing researchers to investigate a century of change in several Wisconsin lakes. NTL also participated in the cross-site StreamChemDB project. We improved our management of sensor data and now employ a DataTurbine server in combination with two MATLAB toolboxes developed by the

Georgia Coastal Ecosystem (GCE) and NTL. The GCE MATLAB data toolbox provides quality control routines in real time, and LakeAnalyzer (Read et al. 2011a) generates real-time water temperature contour maps for the web and is now also available in R.

Finally, in collaboration with other LTER sites, several training workshops were developed, resulting in online training material with slideshows, manuals, tutorials, examples, and videos of the presentations. The latest project is a white paper on Best Practices for Environmental Sensor Management with the Earth Science Information Partners (<http://esipfed.org>).

Cross-site work. Over the past six years, NTL scientists led or contributed to many LTER network and other cross-site activities in addition to the set of IM projects discussed above. For example, Emily Stanley served on the Executive Board, Paul Hanson is the current chair of the LTER Network Information System Advisory Committee, Corinna Gries was chair of the Information Management Committee, and Tim Kratz was on the editorial committee for the LTER Ecotrends volume (Peters et al. 2013). NTL helped lead LTEArts, a successful and ongoing cross-site science/art collaboration that culminated in exhibits at NSF, ESA, and other venues. NTL scientists were involved in a number of LTER and non-LTER cross-site workshops and publications (e.g., Benson et al. 2010, **Helmus et al. 2010**, Bestelmeyer et al. 2011, Dodds et al. 2012, Knapp et al. 2012, Robertson et al. 2012, Spargo et al. 2014, Thompson et al. 2012) and have been leaders in the Global Lake Ecological Observatory Network (GLEON), a network of more than 400 scientists in over 40 countries in six continents. Kratz is one of the founders of GLEON and he and Hanson are past and present chairs, respectively. Former NTL graduate students Solomon and Read led two large, international comparative studies using high-frequency data from NTL lakes along with dozens of other lakes worldwide (Solomon et al. 2013, **Read et al. 2012**).

Broader impacts. In addition to creating new understanding of lakes and their surrounding landscapes, NTL has four main goals for its broader impact activities: providing research experience and training to K-12, undergraduate, and graduate students; engaging with the general public on the topic of long-term change in social-ecological systems; informing public policy with relevant scientific information, and encouraging multiple dimensions of diversity. We were active in all of these areas.

K-12, undergraduate and graduate students. The NTL Schoolyard LTER Program (SYLTER) provided a diverse set of resources and experiences for K-12 students and teachers throughout Wisconsin. We involved 52 elementary, middle, and high school science teachers and over 600 K-12 students and six UW undergraduates. SYLTER activities also included an annual Winter Limnology program with 130 K-8 students (including 30 Native American students), 10 teachers, and two UW undergraduates. We engaged 67 undergraduate (53 student hourlies + 14 REUs), 12 graduate students, and three post docs/trainees directly in research activities in the current grant period. Additional graduate students are affiliated indirectly with NTL and benefit from its resources. PIs incorporated NTL findings in classes ranging from non-majors biology to graduate classes in ecosystem services that annually reach over 1,000 students. NTL science also extends beyond the UW campus, as an average of ~135 distinct non-UW users downloaded ~500 distinct datasets for educational purposes each year between 2009 and 2013.

Engaging the general public. We conducted many activities to engage the public in conversations about science. As part of LTEArts (see Cross-site work, above), we led a successful local science/art collaboration, Drawing Waters, that paired local artists with NTL scientists and resulted in a travelling exhibit attended by >3,200 people throughout northern Wisconsin. We developed a public conversation series called Science on Tap-Minocqua at which NTL and other scientists led monthly discussions at the local microbrewery near Trout Lake Station. The series was attended by 70-200 people each month and discussions were often informed directly by NTL research. The Trout Lake Station and the Hasler Laboratory of Limnology held annual open houses and in the past three years >750 people toured the labs, discussed ongoing research projects, tried out limnological gear, and interacted directly with scientists. Finally, NTL scientists spoke to numerous lake associations and civic organizations, ranging from the Wisconsin Lakes Convention to the Clean Lakes Alliance, as well as to local, statewide, and national media outlets to discuss NTL research and provide expert opinions on a variety of environmental and scientific issues.

Policy relevance. NTL research is routinely done in partnership with local, state, and federal natural resource agencies and used to inform policy. For example, several NTL scientists were deeply involved in the Wisconsin Initiative on Climate Change Impacts (www.wicci.wisc.edu). This collaborative statewide network has worked to: (1) develop scientific understanding of climate impacts; (2) identify vulnerability to climate change and climatic variability; and (3) enable better planning, investment, and other adaptation activities. NTL scientists also led the aquatic invasive species Smart Prevention program which was designed to maximize efficient use of agency resources to reduce the spread and minimize AIS impacts. Results are available to managers and the general public through our invasive species mapping tool that has been accessed by more than 16,000 unique individuals (www.aissmartprevention.wisc.edu). NTL data have also been requested by USGS, EPA, and NOAA personnel to inform agency research and policy activities. Finally, we produced a synthesis of the state of the world's freshwaters, which will be of general use to policy-makers (Carpenter et al. 2011).

Encouraging diversity. We are proactive in enhancing multiple facets of diversity within the NTL project. In addition to having a female lead PI, we have three co-PIs from underrepresented groups and one Native American graduate student. Our Schoolyard LTER program routinely engages students from the Native American-dominated K-8 school on the reservation closest to the Trout Lake Station. More information on our efforts to increase diversity is given the Project Management section in the Supplementary Documents section of this proposal.

Results from supplemental funding. Many activities described in the Information Management and Education sections above were supported by supplemental funds. We also received supplements for social science and “other” research opportunities. Social science supplements were used to support the cross-site “Maps and Locals” (MALS) project, develop a GIS data layer of parcel-level land use over time for the YLD, and initiate a study of relationships between climate, land use, and demography. The latter two efforts brought Katherine Curtis into the NTL group and provided the foundation for proposed work on urban ecology and demography. The “other” category funds contributed to the purchase of an ion chromatograph, replacing a 10+ year old unit, and a nitrate sensor. The sensor was deployed in Lake Mendota and will generate data for proposed research on nitrogen biogeochemistry.

Section 2: Proposed Research

Conceptual framework

Lakes, iconic features of glaciated landscapes around the world, are important in hydrological and biogeochemical processes, ecological interactions, and ecosystem services. Changes in climate, land use and cover, nutrient mobilization, species invasions, and direct human use of water resources have altered lake-rich landscapes in fundamental ways (Carpenter et al. 2011). Now and into the future, human livelihoods and well-being are intertwined with freshwater resources. The NTL program aims to understand long-term changes in freshwater ecosystems and their interactions with terrestrial, atmospheric, and human processes.

Our conceptual framework uses a nested set of spatial scales, from individual lakes and their watersheds, to hydrologically-linked sets of lakes, entire lake districts, multiple lake districts within the Great Lakes region, and comparative studies of lakes and lake districts around the globe. Our core study areas are the NHL and YLD, respectively in Wisconsin (Fig. 1) and our temporal perspective spans thousands of years, including paleolimnological studies, ecological studies since 1875, NTL data since 1981, a variety of shorter comparative and experimental studies, and scenarios and models that project into the future. Our overarching question is:

How do biophysical setting, climate, and land use and cover interact to shape lake dynamics and organization in the past, present and future?

Developing and evaluating ecological theory is a hallmark of NTL research, and our proposed science operates within several guiding conceptual contexts (Fig. 5). Our research will contribute to development of *landscape limnology*, which explains and predicts regional-scale variability in freshwater ecosystems by considering drivers and processes at multiple scales (Magnuson et al. 2006, Soranno et al. 2010, Cheruvilil et al. 2013). Understanding *connectivity* is a current goal in terrestrial and aquatic ecology (e.g., Van Nieuwenhuysse et al. 2011, Tschardt et al. 2012, Mitchell et al. 2013). We will consider functional connectivity for flows of water, nutrients, and organisms and evaluate consequences of enhancing or reducing connectivity. Ecologists have increasingly embraced the need to understand how patterns and processes emerge from *multiple causes* that may interact in unexpected ways to influence species and ecosystems (e.g., Rahel & Olden 2008, Hof et al. 2011, Callaghan et al. 2013). We will assess the relative contributions and interactions of multiple natural and anthropogenic drivers that affect lakes. Given the increasing frequency and magnitude of climate extremes and disturbances, the need to understand how *extreme events* shape ecological systems is paramount (e.g., Reid & Ogden 2006, Turner 2010) and demands long-term study. Our research will evaluate effects of extreme events on freshwater ecosystems. In the context of this conceptual framework, we have organized our research for the next six years under four interrelated themes, each with a guiding question (Fig. 6).

Perception of Long-Term Change: *How and why have the lake districts changed, and how will they change in the future?* Long-term observations, comparisons, and experiments, together with concepts and models are necessary to perceive and understand the causes and consequences of change. The NTL program is committed to collecting, maintaining, analyzing, and synthesizing a long-term, comprehensive set of physical, chemical, biological, and socioeconomic data. All of

the predictions, hypotheses, and questions to be evaluated in our proposed research build upon the sustained growth of these databases.

Climate as a driver of long-term change: *What are the mechanisms of physical and ecological responses of lakes to a changing climate?* Climatic forcing affects lakes in multiple ways. We will focus on improved models and data assimilation for lake thermal regimes, effects of climate on carbon exchange between lakes and the atmosphere, causes of changing dominance of cyanobacteria in eutrophic lakes, and changing geographic distributions of species.

Dynamics of heterogeneity: *What are the long-term patterns, causes, and consequences of spatial heterogeneity in lakes and landscapes?* Because the spatial structure of ecosystems and landscapes responds to changing drivers and can also drive ecological dynamics, understanding heterogeneity is critical for studying long-term change. We will use emerging remote sensing tools to analyze patterns and drivers of change in lake clarity across multiple lake districts; evaluate effects of species invasions and lakeshore development on biotic heterogeneity; analyze changes in nutrient cycling through a chain of lakes; and examine hydrologic and chemical responses to changing patterns in urban landscapes.

Shocks, shifts, and multiple causation: *How and when do extreme events and multiple drivers cause ecosystem transitions?* Frequency and magnitude of extreme precipitation and species invasions are changing in the NHLD and YLD. These events interact with other drivers to shape lake dynamics and may potentially trigger ecosystem regime shift, depending on compensatory responses. We will focus on organic carbon and phosphorus responses to precipitation extremes and other concurrent drivers; ecosystem responses to invasive species; and the uses of scientific knowledge by organizations that manage environmental responses.

These four thematic questions consider a range of ecological drivers and response variables. Our research approaches blend long-term study with process-based experiments, comparisons, and modeling to provide the multi-pronged approach needed for understanding ecosystem responses to global change (Luo et al. 2011). Modeling plays an important role in our efforts as a means of synthesizing, exploring, and forecasting long-term dynamics and testing hypotheses. NTL has a long history of model innovation as well as development of computational and data assimilation approaches to understand long term dynamics of lakes and landscape. This tradition will continue over the next six years and beyond.

Interdisciplinary aspects of our conceptual framework date back to the start of the NTL program in its integration of biology, chemistry, geology, and physics (Magnuson et al. 2006). Lakes and their landscapes are shaped by humans, and human activities must be considered to understand lakes. We added a social science dimension to NTL in 1994. Our interdisciplinary approach has matured, and human activities are now seamlessly integrated into questions and are an integral emphasis of NTL. Engaging with the arts has expanded our scope from its solid core in natural sciences to include key linkages with social sciences and humanities.

Our research focus on lakes as integrators of regional change benefits from a strong interdisciplinary team that embraces a long-term perspective and conducts research at multiple spatial scales in common study regions. We next describe the research proposed in each of the

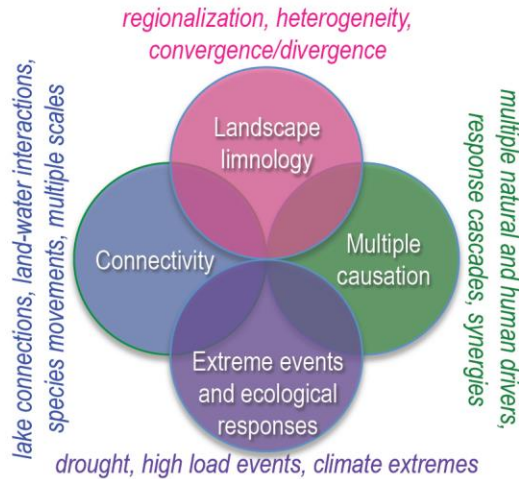


Figure 5. NTL research continues to test and develop current theories and concepts in ecology. Proposed study topics (vertical and horizontal titles) fall within four primary conceptual domains (circles), and many lines of inquiry touch multiple themes.

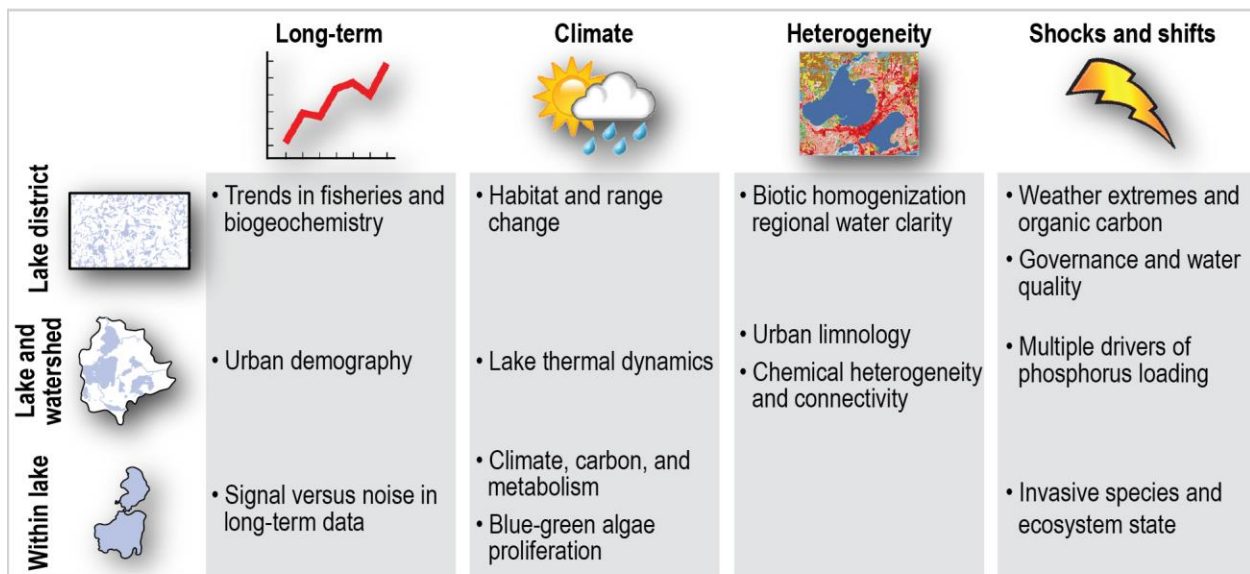


Figure 6. Schematic of four proposed research themes (columns), major scale of study (rows) and the corresponding research topics for each theme-scale combination.

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-----						-----Yahara Lake District-----				
NTL Lake	CB	TB	CR	BM	SP	AL	TL	FI	WI	ME	MO
Area (ha)	0.5	1.1	37	396	64	168	1608	80	136	3961	1360
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	8.5
ANC (µeq/L)	14	11	23	390	631	831	846	2921	3745	3665	3547
DOC (mg/l)	9.1	16.8	2.0	4.0	3.4	4.3	3.1	7.1	6.9	4.9	4.4
Total P (µg/l)	18.2	46.6	8.3	17.5	15	29.3	13.5	22.4	40.3	109.5	73.5
Total N (µg/l)	722	961	210	441	371	379	247	835	933	860	845
Secchi Depth (m)	1.5	1.1	7.5	6.6	6.2	3.2	4.7	2.4	0.7	3	2.4
Chlorophyll (µg/l)	9.9	16.2	1.8	2.9	2.2	7.8	3.1	5.1	10.5	4.8	8.1

four themes, summarize the significance of the research, describe interactions with ongoing projects, and propose a set of outreach and education activities for the next six years.

Theme 1. Perception of Long Term Change: *How and why have the lake districts changed and how will they change in the future?*

One of the foundations of the NTL program is the ability to perceive and understand causes of long-term change in the coupled human-natural systems of the NHLD and the YLD. The collection and management of ecologically relevant data that allow investigators to observe and analyze long-term changes are crucial to understanding our study regions (Carpenter et al. 2007, Liu et al. 2007). Natural and human-induced phenomena such as change in population sizes of long-lived predators, a series of dry or wet years, residential development on lake shorelines, nutrient enrichment, or establishment of non-native species can cause multi-year to decadal effects in lakes, often with substantial time lags between cause and effect (Magnuson 1990, Webster et al. 2000, Kratz et al. 2003). Hence, these and other drivers can cause changes that are difficult to understand without a long-term context (Magnuson et al. 2006, Carpenter et al. 2007). We will continue to maintain and develop core, associated, and reference datasets (see Table S1 and Data Management Plan). As described in Section 1, this comprehensive collection of physical, chemical, biological, and socioeconomic data is unparalleled, and maintenance and expansion of these data are essential for addressing the questions that follow and strengthening the empirical foundation of landscape limnology.

Background: Since 1981, we have conducted a balanced, integrated data collection program (Kratz et al. 1986, Magnuson et al. 2006; see Table S1). We selected lakes and measurements to address important interdisciplinary questions regarding the ecology and management of lakes from a long-term perspective at individual lake, lake chain, lake-district, and regional scales.

Study regions. NTL activities focus on two sets of lakes and their surrounding landscapes (Table 2, Fig. 1). Both regions have a substantial history of ecological research dating back as far as the 1870s (Frey 1963). From 1981 onwards, we have focused on seven primary lakes and their surrounding terrestrial areas in the NHLD. These lakes are linked by a common groundwater and surface water flow system and share common climatic, edaphic, and biogeographic regimes. The lake set includes oligotrophic, dystrophic, and mesotrophic lakes chosen to represent marked differences in size, morphometry, habitat diversity, thermal and chemical regimes, species richness and composition, and position in the groundwater flow system. In 1994, we expanded our regional and disciplinary scope by adding four primary study lakes in the YLD (Table 2, Fig. 1). These four eutrophic lakes were chosen in a 2x2 design of urban vs. agricultural setting and headwater vs. lower in the landscape. Substantial historical data are available on YLD lakes (Watson & Loucks 1979, Brock 1985, Kitchell 1992, Lathrop et al. 2002, Lathrop 2007). In addition to these 11 primary lakes we have a set of secondary lakes for which less-complete information is collected on an *ad hoc* basis to address specific research questions or increase sample size for cross-lake studies. This has included Little Rock Lake in the NHLD and Lakes Waubesa and Kegonsa at the end of the Yahara River chain in the YLD.

Core data collection. Our study systems exhibit important dynamics at time scales ranging from minutes to decades and beyond. To capture the full complexity of these dynamics, we designed

our core data collection program to allow inference across multiple time scales. Sampling frequencies are tuned to the dynamics of individual variables and processes and allow us to answer questions spanning all five core LTER topics (primary production, population studies, movement of inorganic materials, organic matter accumulation, and disturbance). We have evaluated the ability of our sampling program to detect differences among lakes and years for a diverse set of physical, chemical, and biotic variables. This analysis demonstrated that our sampling strategies do indeed allow detection of long-term trends such as changes in planktonic assemblage structure (Rusak & Montz 2009) or shifts in water chemistry (Hanson et al. 2006).

Slow-changing variables are sampled at frequencies ranging from quarterly to annually to once per grant cycle. 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), benthic invertebrate abundance, and groundwater chemistry are sampled once per year, while property ownership patterns are determined once per grant cycle.

Variables that change at intermediate frequencies, including nutrients, pH, and inorganic and organic carbon, are sampled every two or four weeks, depending on the lake and the variable. Temperature, dissolved oxygen, chlorophyll *a*, light penetration, and zooplankton abundance are sampled every two weeks during the open-water season and every five weeks under ice cover. Primary production rates are measured every two weeks in selected lakes, and samples for phytoplankton community composition are collected six times throughout the year. Groundwater levels are measured monthly.

We make increasing use of high-frequency measurements from instrumented buoys. We operate buoys on six of the primary lakes in the NHLD and YLD to measure water temperature profiles, surface layer dissolved oxygen, and relevant meteorological variables at 1-10 minute frequencies. Some of the buoys measure additional variables, such as nitrate and algal biomass via fluorescence. In the NHLD, we maintain an automated weather station at the Minocqua Airport 10 km from Trout Lake. In the YLD we use National Weather Service data from the Dane County Regional Airport near Lake Mendota. Finally, Domain 5 NEON core and relocatable sites will be established within ~50 km of the NHLD primary study lakes; we anticipate using NEON data to augment our NTL observations and make inferences both locally and at a regional scale.

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

Socioeconomic datasets have been developed for NTL research. We created GIS layers for historical parcel subdivisions in Vilas County in the NHLD (1974-2011) and Dane County in the YLD (1962-2005). We maintain a dataset of market prices for shoreline parcels in Vilas County that is matched to the GIS layer of parcel boundaries. This dataset is derived from market sales

records provided each year by the Wisconsin Department of Revenue. Survey data that provide a long-term perspective on human attitudes and behavior are also part of our long-term data set. In the last grant cycle, we initiated two surveys in the NHLD that targeted property owners and lake users, respectively; we will repeat these surveys once per funding cycle. These long-term data on social-ecological interactions around NHLD lakes allow us to address questions such as how the value of ecosystem services varies temporally and spatially, how social and ecological factors influence these patterns, and how institutions, zoning practices, or property values affect lake dynamics (e.g., Butsic et al. 2010, 2012, Gaeta et al. 2013).

Our long-term measurements are complemented by whole-lake experiments designed to test our understanding of causal relationships. In 2001, we commenced intensive trapping of invasive rusty crayfish in Sparkling Lake, reducing their abundance by 30-fold over an 8-year removal period and causing dramatic ecosystem-level changes in response to the manipulation (Hansen et al. 2013a). Although the removal phase is complete, we continue to sample key food web components in order to determine if the current, native-species dominated food web configuration is stable. A second removal experiment in 2008-09 involved extraction of 26,100 kg of carp from Lake Wingra. Water clarity increased rapidly, and the aquatic macrophyte community composition began to shift the following summer (Lathrop et al. 2013). As with the crayfish removal, post-removal assessment is ongoing. Finally, in 2012 and 2013, we used a novel technology (Read et al. 2011b) to destratify Crystal Lake. We expected the destratification to eliminate the cold-water habitat needed by the invasive fish, rainbow smelt (Gaeta et al. 2012). To determine physical, chemical, and biological response to thermal manipulation, assessment of lake state will continue until at least 2020, encapsulating the lifespan of smelt born the year after the manipulation. Each experiment builds on long-term data collected by the NTL program and each contributes to invasive species ecology while informing lake management.

Proposed New Initiatives: We will continue to collect and maintain our core data and propose four new initiatives for perceiving and understanding change that include new analyses, development and incorporation of existing data, and a new sampling effort.

NI.1. Comprehensive analysis of long-term change in lakes. We now have 28 multi-variable datasets for the NTL primary study lakes that have at least 30 years of data – a sufficient time span to identify trends, abrupt changes, episodes of high variability, or cycles with frequencies of up to 10 years. Thus, we propose an initiative to understand the temporal scales of variation of interdependent physical, chemical, and biological characteristics of lakes. What are the dominant time scales of variation represented by these variables? Which drivers of long-term lake dynamics vary at the same temporal scales as the responses? Under what circumstances and for which variables do lags, thresholds, and other types of responses appear? To our knowledge, this will be the first systematic and comprehensive analysis of patterns of long-term dynamics using a three-decade long dataset spanning multiple lakes and a diverse set of variables.

NI.2. Capturing data on fish life histories. Fisheries are culturally and ecologically significant natural resources of lakes worldwide. Anglers are attracted to lakes and purchase lakefront properties where quality fishing opportunities exist (Peterson et al. 2003), and angling and fisheries regulations can have cascading and counterintuitive effects on ecosystem dynamics (Arlinghaus et al. 2008, Pine et al. 2009). Yet long-term studies of lake fisheries are surprisingly

rare, giving us little understanding of how fisheries change over time, and how target species respond to regulatory shifts or external drivers. Historical fisheries data exist for many of our core lakes, some of which date back to the mid-20th century. Available examples suggest long-term changes in life history variables (Fig. 7). Currently, much of this high-value information is dispersed across multiple sources such as agency reports, theses, and local resource management databases. We will assemble historical data on fisheries production potential (length, weight, size-frequency distributions, length-at-age) for our NTL study lakes to complement existing NTL data and ask how widespread these shifts in basic life history variables are, and why they may have changed over several decades. We will incorporate these newly collated data sets as part of our core data, and NTL researchers employed by the Wisconsin Department of Natural Resources (WDNR) will collate and add survey data in future years.

NI.3. Human demography and urbanization data in the YLD. The ecology of lakes and their surrounding landscapes are inextricably linked with human population dynamics and human activities. Human demography of our lake districts shows trends of urban expansion, population aging, and increasing racial/ethnic diversity. Within the YLD, population size has increased over 25% and developed areas expanded by roughly 66% (>7,800 ha) since the inclusion of these study lakes into the NTL program in 1994 (Fig. 8). Urbanization produces wide-ranging effects on terrestrial and aquatic ecosystems, and the distribution, type, and intensity of environmental change depends on socio-demographic dynamics (Grimm et al. 2008a, Pickett et al. 2011). We propose new collection and analyses of data on human population dynamics related to ecosystem changes. This includes information on basic demographic features (e.g., age, race/ethnicity) in addition to markers of socioeconomic well-being (e.g., education, employment, industry, income) and urbanization (population and housing density). Results will inform questions pertaining to environmental change and social-environmental feedbacks, and will directly contribute to new research on urban limnology (described later). Demographic, socioeconomic, and urban data will be extracted from existing databases available from UW's Applied Population Lab and Center for Demography and Ecology, and customized to the YLD. These data will be served through the NTL web page and augmented in future years as new data become available.

NI.4. Regional water chemistry surveys to understand long term change over a large spatial scale.

The NHLD is one of the few regions in the world with periodic comprehensive water chemistry data from hundreds of lakes spanning almost a century. Birge and Juday directed the first comprehensive assessment of water chemistry in the NHLD, sampling more than 600 lakes in the 1920s and 30s (Eilers et al. 1989). These surveys have been repeated by various agencies and we now have data from the 1920s (UW), 1960s (WDNR), 1970s (EPA), 1980s (EPA), 1990s (EPA), and 2000s (NTL). Seventy-eight lakes have been sampled by at least four of these regional surveys. We propose to institute a once/funding cycle survey of 50 of these lakes, emphasizing fundamental limnological measurements and water chemistry, including water clarity (Secchi disk depth), chlorophyll *a*, pH, conductivity, major cations and anions, nutrients, and dissolved inorganic and organic carbon. The subset of 50 lakes will be selected to represent a gradient of landscape position and shoreline development, both of which are important factors influencing social and ecological dynamics of lakes in the NHLD. This long-term regional dataset will lead to a greater understanding of whether and how large-scale drivers such as

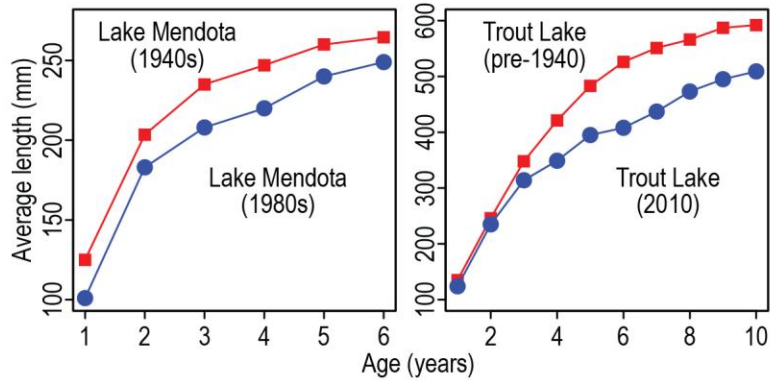


Figure 7. Examples of shifts in length-at-age relationships for fish populations in two NTL study lakes. Both yellow perch in Lake Mendota (left) and walleye in Trout Lake (right) show a shift toward smaller individuals across all age classes over a 40-50-year period. This shift may reflect decreased growth rates or changes in fishing pressure or regulations.

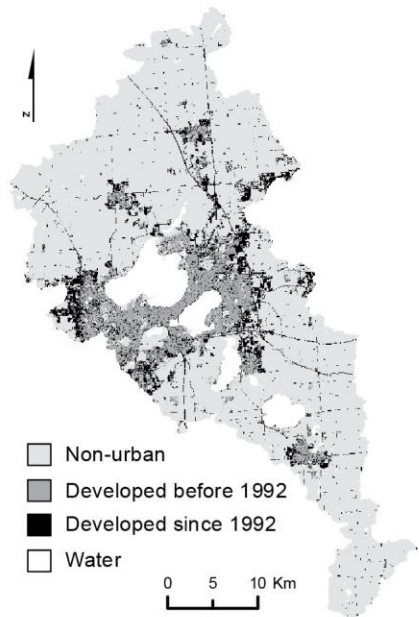


Figure 8. Expansion of urban cover in the Yahara Lakes Watershed between 1992 and 2006. Non-urban lands are primarily agricultural; black areas denote the extent of urbanization since 1992. Urban settlement in the 1840s began in the strip of land between Lakes Mendota and Monona (lakes in white) and now almost completely encircles these lakes as well as Lake Wingra.

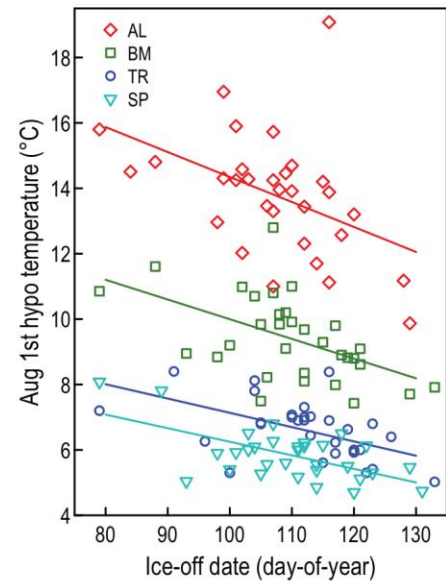


Figure 9. Relationship between ice-off date and August 1st hypolimnion temperature. All lakes showed a significant ($p < 0.05$) negative correlation between ice-off date and hypolimnion temperature. Allequash Lake (AL), Big Muskellunge Lake (BM), Trout Lake (TL), Sparkling Lake (SP).

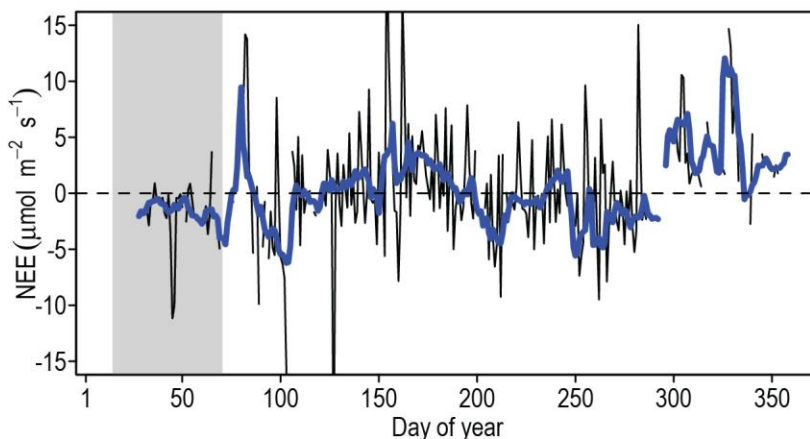


Figure 10. Daily (thin black line) and weekly (thick blue line) averaged CO_2 flux for 2012 from a shoreline flux tower on Lake Mendota. Positive values occur when the lake is a CO_2 source to the atmosphere; negative values indicate net CO_2 uptake by the lake. Ice covered period denoted by grey shading. NEE- net ecosystem exchange.

climate change and variability, lakeshore residential development, introductions of invasive species, or forest management have altered regional water chemistry.

Theme 2. Climate as a driver of long-term change: *What are the mechanisms of physical and ecological responses of lakes to a changing climate?*

The upper Great Lakes region has experienced substantial climate variability superimposed on gradual warming (Kucharik et al. 2010, WICCI 2011). In recent decades, Wisconsin has seen increased average annual temperatures, shorter winters, and more heat waves. In the YLD, the frequency of high-intensity storms has increased while the NHLD has experienced prolonged drought (WICCI 2011). Observed consequences for lakes include warming surface waters (Schneider & Hook 2010), reduced duration of ice cover (Sharma et al. 2013), increased hydrologic flashiness in the YLD (Gillon et al. in review), and record low lake levels in the NHLD (Fig. 3; Watras et al. 2014). Because climate trends and ecosystem responses are increasingly evident in our long-term records, we build upon this thematic research area from our 2008 proposal. Over the next six years, we will focus on mechanisms of past and possible future within-lake physical and ecological responses to climate change.

Climate change motivates our focus on concepts and hypotheses about multiple causation of ecosystem change (Fig. 5). Climate change is not a single directional force on ecosystems but instead involves a multiplicity of changes in timing, duration, magnitude and variability of temperature and precipitation regimes (Grimm et al. 2013). Nonetheless, ecosystem responses to climate forcing start with physical changes that then lead to complex ecological outcomes. Thus, our approach for addressing Theme 2 is to first develop an understanding of lake physical responses to climate drivers (Q2.1), and then to ask how these physical changes affect key ecosystem (Q2.2), community (Q2.3), and population (Q2.4) dynamics. This examination will inform our understanding of how multiple drivers affect these ecosystems, and the mechanisms by which drivers initiate different responses that cascade from physical to chemical and biological consequences.

Q2.1. Lake thermal dynamics: How do climate change and variability alter physical conditions in a diverse set of lakes?

Stratification is a major feature of lake structure, controlling linkages between the benthos and surface waters, water chemistry, processing of nutrients and organic matter, and availability of thermal and chemical habitat for biota (Wetzel 2001). Recent studies suggest that warming trends will lead to increased strength and duration of stratification in temperate lakes (Sahoo et al. 2011, Foley et al. 2012, Posch et al. 2012). Yet two long-term patterns in NTL lakes run counter to this expectation: decreased ice cover and flashier hydrographs. Earlier ice-off dates are associated with warmer hypolimnia (Fig. 9) and reduced thermal differences between lake layers. This in turn reduces, rather than strengthens stratification. Hydrologic inputs during larger and/or more frequent floods can decrease water residence times and further weaken stratification (Klug et al. 2012). These contradictions highlight our current uncertainty about how temperature and stratification will respond to regional climate trends and suggest that not all lakes will respond the same way.

To understand how lake thermal conditions respond to climate changes, we will combine hydrodynamic lake modeling with multi-decadal limnological and meteorological observations and downscaled climate scenarios (WICCI 2011) for the 11 NTL lakes. This approach will allow us to determine how climate-driven physical changes vary among a range of lake sizes, landscape positions, and trophic states; what physical attributes of lakes are most responsive to climate drivers; and whether continued warming may strengthen or weaken stratification. This modeling work forms the foundation for investigating ecological responses to climate that result from physical changes to the lake environment. We will use the “General Lake Model” (GLM; Table 3). GLM was developed from a partnership between GLEON and the Aquatic Ecosystem MOdelling Network (AEMON), is open source, and can be coupled to an R package for calculating metrics of lake physical state (LakeAnalyzer; Read et al. 2011a), as well as a biogeochemical model that will be used to address subsequent questions (described below). NTL is one of 20 different research programs involved in the GLEON-AEMON partnership, providing us with an opportunity for cross-site research in developing these models and collaborating to study lake responses to climate change in disparate regions around the globe.

Q2.2. Climate, carbon, and metabolism: How does climate affect CO₂ and CH₄ exchange between lakes and the atmosphere?

Lakes are capable of storing and processing large quantities of organic C and venting CO₂ to the atmosphere (Raymond et al. 2013). CH₄ released from freshwaters is equivalent to roughly 25% of the estimated terrestrial C sink (Bastviken et al. 2011), and efflux of this potent greenhouse gas may increase rapidly in response to warming (Yvon-Durocher et al. 2011). As such, lake-atmosphere gas exchange affects, and is affected by climate (Tranvik et al. 2009). Unfortunately, current understanding of lake CO₂ and CH₄ fluxes is fraught with uncertainties, reflecting critical data gaps that result from logistical challenges in measuring these fluxes, as well as conceptual gaps in understanding how underlying processes such as primary production and respiration will respond to climate changes (Kosten et al. 2010, Kritzberg et al. 2014). We propose new gas exchange measurements and modeling to address both of these sources of uncertainty.

Global lake CO₂ and CH₄ emissions estimates are based on site-specific measurements mostly made during summer months (Bastviken et al. 2011, Raymond et al. 2013) despite evidence of active under-ice metabolism (Striegl et al. 2001, Karlsson et al. 2008). Up to half of a lake’s annual gas efflux can occur during ice break-up in some lakes (Michmerhuizen et al. 1996, Karlsson et al. 2013), while in others, ice-off is a time of high CO₂ uptake (Fig. 10). Missing these critical transition periods can thus lead to an erroneous perception of a lake as a source or a sink (Karlsson et al. 2013). Automated sensors can be used to capture *p*CO₂ dynamics during these critical periods, but subsequent flux calculations are challenged by high uncertainty in estimating air-water exchange rates (Read et al. 2012, Raymond et al. 2013). Fortunately, this hurdle can be overcome by measuring CO₂ flux directly with eddy covariance (EC) approaches (Regnier et al. 2013), and we began measuring CO₂ fluxes using EC for Lake Mendota in 2012 to determine the feasibility of this technique (Fig. 10). In this funding cycle, we will extend these observations to establish the long-term record necessary for evaluating climate effects, and couple flux estimates with in situ *p*CO₂ measurements to determine annual in-lake patterns and the relationship between water column *p*CO₂ and CO₂ exchange. To broaden the scope of this work, NTL investigators will lead a synthesis project bringing together researchers using EC

approaches to investigate how climate-CO₂ flux relationships vary in vastly different lakes and locations around the world.

Quantifying concentrations and fluxes of CH₄ with automated sensors is not yet tractable. Thus, we will undertake a 2-year field campaign focusing on NTL lakes to determine CO₂ and CH₄ concentrations and fluxes throughout the entire year- not just during the warm summer months. Floating chambers will be used to quantify CH₄ fluxes (a reliable method for this gas; Schilder et al. 2013). Finally, to investigate the linkage between climate-driven physical lake changes and gas fluxes, we return to GLM (Q2.1) and will use FABM (Framework for Aquatic Biogeochemical Model; Table 3) to couple GLM with carbon cycling models based on libraries available in Aquatic Ecodynamics Model (AED; Table 3). The coupled models will be used in an experimental fashion to investigate how production and respiration respond to different climate conditions that occurred historically or are expected based on downscaled projections. Collectively, this combination of measurements and modeling will allow us to assess how C gas production and efflux vary over time and in response to shifting climate and physical conditions, to calibrate and validate new models, and to improve uncertainty estimates of these processes.

Q2.3. Blue-green proliferation: How are cyanobacterial dominance and toxin production in eutrophic lakes linked to climate dynamics?

Cyanobacteria blooms can cause toxicity, odor, and fish kill problems in eutrophic lakes, and the frequency and intensity of these events are now increasing around the world (Paerl & Paul 2012). Climate drivers are thought to cause these shifts, perhaps in concert with multiple factors such as shifting availability of N and P or reduced grazing pressure (O'Neil et al. 2012, Paerl & Otten 2013). Multiple interpretations have been published, perhaps reflecting the fact that most investigations have either relied on long-term dynamics from a single lake (Jöhnk et al. 2008, Posch et al. 2012) or on one-time surveys of multiple lakes (Orihel et al. 2012, Rigosi et al. 2014). Species composition, including the abundance of toxin-producing forms, is connected to lake physics and biogeochemistry through a complex web of interactions, and bloom formation is triggered by multiple simultaneous causes (O'Neil et al. 2012). Hence, disentangling climate effects from other possible influences will be facilitated by evaluation of long-term limnological records from contrasting lakes and weather-years coupled with detailed information about cyanobacterial assemblages and toxin dynamics (Beverdors et al. 2013, Pitois et al. 2014).

We will analyze long-term observations of physics, nutrients, and cyanobacteria to identify conditions associated with bloom formation, and whether blooms are dominated by toxigenic taxa. Analyses will focus on the four YLD eutrophic lakes studied intensively by NTL (Fish, Mendota, Monona, Wingra). These lakes differ in landscape setting, morphology, water residence time, grazer composition, nutrient availability, and seasonal variability of cyanobacterial taxa (see Table 2; Kasprzak et al. 1999, Hoffman et al. 2013, Lathrop & Carpenter 2014). Our time series includes wet and dry years with a wide range of water and nutrient input rates (Lathrop & Carpenter 2014), and information on historic lake thermal and hydraulic conditions will be known from modeling activities described above. We will also conduct two studies to quantify the physical and biogeochemical conditions that lead to toxic versus non-toxic blooms in these lakes. First, long-term patterns in the four lakes will be fitted to linear and nonlinear mixed-effects models to determine associations among drivers and cyanobacterial dominance (Gelman & Hill 2007, Taranu et al. 2012). Next, we will conduct a

two-year field campaign in all four lakes to obtain more detailed data on prevailing biogeochemical conditions, toxin (microcystin) concentrations, and cyanobacterial composition using microscopic and genomic determinations (described in Beversdorf et al. 2013). Collectively, the long-term and intensive two-year studies will allow us to characterize physical and biogeochemical correlates of toxic bloom formation.

Q2.4. Habitat and range change: How does a shifting climate affect species distribution?

Climate is a fundamental determinant of species ranges, and multiple examples now exist of expanding, contracting, and shifting range distributions in response to changing climate conditions (Staudinger et al. 2013). Marine studies have revealed surprisingly rapid range shifts despite ocean warming rates that are slower than terrestrial settings (Burrows et al. 2011, Pinsky et al. 2013). Lakes may be warming at a faster rate than terrestrial ecosystems (Schneider & Hook 2010), suggesting the potential for particularly swift responses by freshwater biota. However, range adjustments are often idiosyncratic and difficult to predict because they are rarely driven by temperature alone. Improved predictions of species range responses must include consideration of species requirements, habitat changes, and dispersal abilities (Staudinger et al. 2013). Here, we take on this challenge, focusing on a sentinel coldwater species of the Great Lakes region. Cisco (*Coregonus artedii*) is a planktivorous fish that reaches its southern range limit in the YLD. Its sensitivity to environmental conditions has resulted in its listing as species of special concern in Wisconsin (Lyons et al. 2000).

Coldwater fish and invertebrates require cold temperatures and high oxygen concentrations, and during summer stratification, these conditions only exist in deeper lake layers. Climate-driven warming coupled with nutrient loading can impinge on this critical ‘oxythermal niche,’ as warmer waters hold less oxygen and nutrient enrichment increases oxygen consumption. The net result is a squeezing, and in some cases elimination, of appropriate habitat for coldwater taxa (Rudstam & Magnuson 1985, Jacobson et al. 2008, 2010). A recent NTL study predicted extirpation of cisco from 25-70% of the 184 Wisconsin lakes known to support this species during the next century due to climate warming (Sharma et al. 2011). However, the authors pointed out the need for mechanistic analyses of climate effects on thermal regimes and oxygen availability in the context of cisco persistence. We will use the hydrodynamic-biogeochemical models presented above (GLM-FABM, Q2.1, Q2.2) to estimate how the oxythermal niche of cisco has changed over the past three decades in NTL lakes that have supported cisco, and to assess whether modern cisco declines and major die-off events (e.g., 1987 in Lake Mendota; Magnuson & Lathrop 1992) can be predicted. These models will then be used to forecast future oxythermal regimes given a range of climate change scenarios. Our approach will provide a basis for understanding how projected climate changes will affect coldwater fish habitat and perhaps, eventually, the extirpation of sensitive coldwater biota from individual lakes.

Theme 3. Dynamics of heterogeneity: What are the long-term patterns, causes, and consequences of spatial heterogeneity in lakes and landscapes?

Heterogeneity is a key characteristic of social-ecological systems and both a response to changing drivers and a driver of other responses (Turner 2005), and thus is an essential ingredient of landscape limnology. Patterns and scales of lake heterogeneity are shaped by

interactions of physical, chemical, and biological processes as well as land-use change, climate change, and/or the spread of invasive species. Determining the relative importance of these drivers, how they interact with one another, whether they enhance or reduce connectivity, and whether they promote convergence (homogenization) or divergence (heterogeneity) in ecosystem structure and function are central to understanding patterns and trajectories of lakes in the landscape.

To better understand causes and consequences of changing heterogeneity among lakes, we will address four research questions that consider heterogeneity at different scales and in distinct ways: regional patterns of changing water clarity (Q3.1); lakeshore development as a driver of physical habitat and biotic homogenization (Q3.2); changing nutrient dynamics along a lake chain (Q3.3); and urban land use/land cover patterns and their implications for hydrology and water chemistry (Q3.4). The broader goal is to evaluate and expand upon concepts of landscape limnology (Soranno et al. 2010) beyond its original application to water chemistry, and to consider how different vectors of connectivity (hydrologic, organismal, anthropogenic) may affect heterogeneity among lakes.

Q3.1. Regional water clarity: What are the patterns and drivers of changing lake water clarity at the regional scale?

Water clarity is perhaps the oldest and most widespread measure of lake water quality. The value of this parameter results from its integrated nature, ease of measurement, and easily understood significance (Carlson 1977). Because it is a function of lake productivity, sediment input, and presence of light-absorbing dissolved organic matter (CDOM; Wetzel 2001), water clarity can indicate land-use effects such as erosion or eutrophication. It is easily, inexpensively, and reliably measured for individual lakes using a Secchi disk (Canfield et al. 2002) and can be quantified for virtually all lakes across a large area using satellite imagery. NTL scientists were among the first to develop methods for estimating water clarity from Landsat images that were ground-truthed using citizen science Secchi disk data (Chipman et al. 2004). Changes in water clarity have also been quantified at large spatial scales using historic satellite images, but these studies have yielded contradictory trends. For example, across adjacent regions of the upper Midwest, lake water clarity has increased, decreased, and remained stable over the past 15-30 years (Peckham & Lillesand 2006, Olmanson et al. 2008). Possible drivers of these long-term trends include land use practices, climate-driven increases in productivity, and ‘browning’ of lakes due to increased inputs of CDOM (Olmanson et al. 2008, McCullough et al. 2013, Montieth et al. 2007).

We propose to expand upon earlier NTL studies and generate and analyze a complete time-series of water clarity for >8,000 Wisconsin lakes to determine regional patterns of heterogeneity, and understand how and why it may have changed over the past 1-2 decades. The length of the Landsat imagery archive combined with NTL data and extensive Secchi disc records from a long-term citizen-science program run by the WDNR provide us with the information needed to determine how water clarity varies over time and space; what landscape, lake, and climatic factors predict water clarity and its inter-annual variation; and whether the relative influence of in-lake and landscape characteristics varies with climate. Field measurements of Secchi depth will be related to Landsat 5 and 7 data (per Olmanson et al. 2001, Kloiber et al. 2002a,b) and lake water clarity will be mapped annually for lakes > 2 ha (e.g., Fig. 11). We will also evaluate

Table 3. Model names, descriptions, and sources for additional information and/or download. All models are numerical, have been calibrated and validated in other locations and/or at various spatial scales, and will undergo calibration and validation in addition to parameter sensitivity analyses as part of the modeling activities proposed here.

Description	Source/additional information
General Lake Model (GLM) Lake hydrodynamics and stratification	aed.see.uwa.edu.au/research/models/GLM/
Framework for Aquatic Biogeochemical Models (FABM) A framework that links GLM to AED	fabm.sourceforge.net/
Aquatic EcoDynamics Model (AED) Aquatic ecosystem process models	aed.see.uwa.edu.au/research/models/GLM/
ParFlow Watershed model to simulate surface and subsurface flow	computation.llnl.gov/casc/parflow/parflow_home.html
Community Land Model (CLM) Climate-vegetation model	http://www.cgd.ucar.edu/tss/clm/
Agro-IBIS Terrestrial ecosystem model	lter.limnology.wisc.edu/project/agro-ibis
Terrestrial Hydrology Model with Biogeochemistry (THMB) Hydrologic routing model for surface and sub-surface drainage	www.sage.wisc.edu/download/HYDRA/hydra.html
MODFLOW Groundwater flow simulation	water.usgs.gov/ogw/modflow/

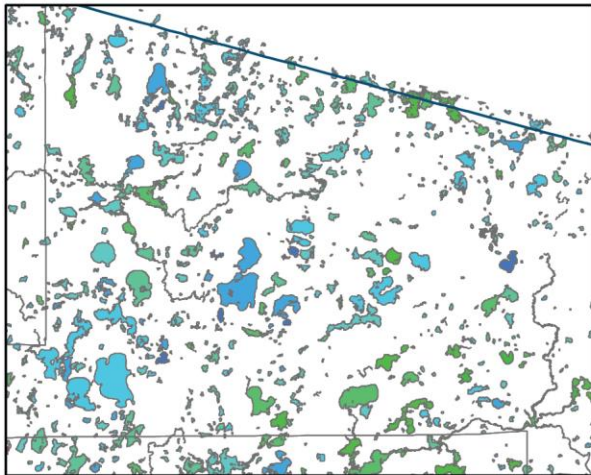


Figure 11. Lake water clarity estimates generated from Landsat satellite imagery from 10 Sept. 2010. Blue to green shading represents a gradient of high to low Secchi disk depth (high to low water clarity) derived from satellite data.

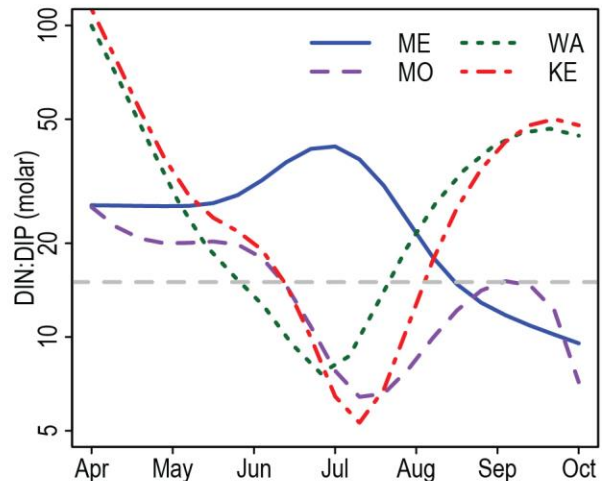


Figure 12. Mean monthly molar ratios of inorganic N to inorganic P from 1995-2012 for the YLD lake chain during open water period. The dashed horizontal line represents the Redfield ratio (15), an approximate indicator of the shift between potential N and P limitation of primary productivity. (ME) Mendota, (MO) Monona, (WA) Waubesa, and (KE) Kegonsa.

whether the enhanced water quality monitoring capability of Landsat 8, launched in December 2012, allows accurate estimation of chlorophyll *a*, total suspended solids, and CDOM (Pahlevan & Schott 2013), and thus the partitioning of the constituents contributing to water clarity. After completing analyses of spatial and temporal patterns, we will develop scenarios to explore implications of future climate and land-use change for lake water clarity.

Q3.2. Biotic homogenization: How do lakeshore development and species introductions interact to homogenize lakeshore biota?

For some ecological characteristics, lakes can be viewed as isolated aquatic patches with distinct biotic composition, leading to a high degree of beta-diversity across the landscape. However, two human-driven processes, residential development of lakeshores and the spread of aquatic invasive species, may homogenize the habitat and biota in lakes. Lakeshore development reduces riparian vegetation and littoral coarse woody habitat (Christensen et al. 1996, Marburg et al. 2006) which in turn can reduce fish growth rates (Schindler et al. 2000, Gaeta et al. 2011) and destabilize predator-prey interactions (Sass et al. 2006). Further, developed lakes may be more likely to have aquatic invasive species (Capelli & Magnuson 1983). Our hypothesis is that lakeshore development leads to physical habitat homogenization, native species loss, and species introductions, all of which interact to promote biotic homogenization.

Information from both local and regional scales is needed to determine diversity responses to environmental change (Angeler & Drakare 2013). Thus, two types of data will be used to test our hypothesis. First, data from core NTL lakes provide over 30 years of information on fish and littoral zoobenthos assemblages that will be used to test for convergence or divergence at the local scale. Second, several large cross-lake studies assessed shoreline habitat, fish, and littoral zoobenthos communities in the NHLD, including a 60-lake survey in the early-2000s. Resampling these lakes 15 years later will allow us to quantify changes in, and linkages between habitat and biotic structure at the regional scale. The resampling will be coordinated with the regional water chemistry survey (Theme 1) to maximize available information for these lakes. We predict that: (1) habitat diversity will be reduced and structurally similar among developed lakes compared to undeveloped lakes; (2) communities in developed lakes will be significantly more similar to each other relative to undeveloped lakes and that this pattern is driven by the occurrence of non-native species; and (3) both biotic community and habitat patterns correlate strongly with shoreline development. These predictions can be evaluated among lakes from our survey data, as well as by examining changes in habitat and assemblage composition for lakes that have become more developed over the 15 years since the initial survey, providing us with a robust test of our hypothesis of lakeshore development and biotic homogenization.

Q3.3. Chemical heterogeneity and connectivity: What creates chemical heterogeneity among well-connected lakes?

Connectivity among patches is often a homogenizing influence that limits the degree to which individual patch attributes can diverge (Rahel 2007, Thomaz et al. 2007). For lakes, connectivity exists in the conspicuous form of streams and rivers that link one lake to the next, and these flows often homogenize water chemistry across lakes in a connected chain (Einola et al. 2011, Sadro & Melack 2012). Yet even in well-connected systems, chemistry can differ among lakes (Soranno et al. 1999, Sadro et al. 2012). We hypothesize that if this divergence occurs, it reflects a shift in the balance between connectivity-driven convergence and process-based divergence.

That is, differences in water chemistry among lakes develop when the homogenizing effect of river flow is overwhelmed by biogeochemical processes that alter forms or amounts of chemicals within individual lakes. This dynamic is analogous to strong biotic interactions within a patch reducing the size of a local population even in the presence of sustained immigration (Pulliam 1988). If heterogeneity develops for nutrients among lakes, then lake-to-lake differences could potentially cause among-lake heterogeneity in phytoplankton species composition, rates of production, and even occurrence of nuisance algal blooms (Beverly et al. 2013).

The four lakes in the YLD chain (Mendota, Monona, Waubesa, Kegonsa) are in close proximity to each other and connected by the Yahara River, which provides ~60-100% of hydrologic inputs to each individual lake (Carpenter & Lathrop 2013). Nutrient concentrations are elevated in early summer across all of the lakes, and then decrease to annual minima as summer progresses. Yet rates of decline differ among lakes, causing inorganic nutrient ratios to diverge (Fig. 12). We focus on this among-lake heterogeneity to test our hypothesis regarding the shifting balance of converging and diverging processes, and the more specific expectation that low N:P ratios at the end of the lake chain are driven by in-lake N transformations. Current central-station nutrient measurements will be augmented with sediment assays and water column sampling at lake inflow and outflow stations to quantify inputs, outputs, and N transformations (fixation, uptake, denitrification) through the chain. These data will be combined with existing hydrologic and biological data to examine the conditions in which within-lake processes overcome the homogenizing effects of river flow, and if the balance is shifted because connectivity weakens or internal processing becomes amplified.

Q3.4. Urban limnology: How does arrangement of landscape elements in urban areas affect fluxes of water and chemicals?

Urbanization can either increase or decrease landscape heterogeneity, depending on the spatial scale considered. At a broad spatial scale, urbanization is a homogenizing process (Groffman et al. 2014). However, at finer scales, urban land cover resolves into a mixture of roads, houses, lawns, trees, sidewalks, and gardens, and the composition and arrangement of these patches can vary from place to place within a city (Cadenasso et al. 2007). This phenomenon also seems to apply to aquatic systems embedded within urban environments. At a continental scale, size, shape, and abundance of water bodies are highly similar across disparate cities (Steele et al. 2014, Steele & Heffernan 2014), and urban land cover is strongly correlated with invertebrate community composition and water quality indicators (King et al. 2011, Miserendino et al. 2011). But within cities, multiple types of aquatic habitats exist (Kaushal & Belt 2012) and there can be substantial variability in aquatic communities from site to site due to differences in urban landscape structure (Brabec et al. 2002, Alberti 2005). We hypothesize that variability in composition, arrangement, and size of urban elements (i.e., differences in fine scale heterogeneity) creates differences in hydrologic fluxes to, and water chemistry of recipient streams and lakes. But at a large spatial scale, like water body morphology, water chemistry among cities is relatively homogeneous. To test this hypothesis, we will examine several ecosystem services that are important in urban settings: flood risk reduction, water infiltration, and distribution of nutrients and contaminants.

Within the YLD, the hydrologic effects of long-term change have been recorded since the mid-1970s in three gauged catchments of Lake Mendota that have undergone sharply contrasting

development trajectories (Spring Harbor, urban residential; Pheasant Branch, commercial; Yahara, low density suburban). We will use the physically-based hydrological model ParFlow (Ashby & Falgout 1996, Jones & Woodward 2001, Kollet & Maxwell 2006) linked with the climate-vegetation Community Land Model (CLM) (Maxwell & Miller 2005, Kollet & Maxwell 2008; Table 3) to evaluate water balance dynamics by running factorial simulation experiments to test the extent to which degree of urbanization, amount and arrangement of impervious features, and connectivity of urban landscape elements impact the above ecosystems services. The relationship between water chemistry and urban structure will be investigated at both fine and broad spatial scales. At the within-city scale, we will conduct an extensive summertime survey that includes a range of surface water features in the City of Madison. Differences in composition and concentration of nutrients, salts, and contaminants (e.g., heavy metals, petroleum hydrocarbons and perfluoroalkyl acids) will be evaluated in the context of fine-scale landscape structure. To determine if larger scale chemical patterns are relatively homogeneous, or if factors such as city history, geographic context, or differences in infrastructure maintain distinct conditions among cities as hypothesized by Grimm et al. (2008b), we will undertake a cross-site comparative study with researchers from BES, CAP, and other interested urban aquatic researchers. The goal will be to determine if common chemical profiles emerge across very different urban centers, or if water chemistry remains city- or region-specific.

Theme 4. Shocks, shifts, and multiple causation: *How and when do extreme events and multiple drivers cause ecosystem transitions?*

The NTL study regions, like other regions around the globe, are subject to changing frequency and intensity of disturbance, occasional massive shifts in drivers or ecosystem processes, and compensatory responses in ecological or social organization. Responses to extreme events often depend on previous events or current conditions, and thereby suggest multiple causal pathways (Turner 2010). For example, a drought in the late 1980s was associated with multi-year changes in hydrology and biogeochemistry of the NHLD (Magnuson et al. 2006). In the YLD, the 1988-89 drought caused the lowest P load observed in decades (Lathrop & Carpenter 2014). This brief decrease in nutrient supply coincided with a massive food web manipulation that increased water clarity (Lathrop et al. 2002, Lathrop & Carpenter 2014), and subsequently triggered a rapid ecosystem transition.

In this new grant cycle, we expand our view of sharp ecosystem change to consider the impacts of extreme precipitation events and floods, as well as drought, invasive species, and adaptive responses of people and institutions to ecosystem change. This new research brings in a landscape perspective of organic carbon (OC) movement (Q4.1); a long-term view of P flows (Q4.2); ecosystem state changes associated with species invasions (Q4.3); and examination of the role of scientific evidence in water quality governance (Q4.4). In all of these cases, we will examine transitions in, and feedbacks among multiple ecosystem processes.

Q4.1. Moving carbon from land to water: How do precipitation, temperature, and soil type, interact to affect dissolved organic carbon loading to lakes?

Dissolved organic carbon (DOC) plays a central role in aquatic ecosystems, affecting processes such as metabolism, the balance between autotrophy and heterotrophy, acidity, nutrient uptake,

and bioavailability of toxic compounds (Prairie 2008). DOC composition and concentrations are undergoing long-term changes across a range of aquatic environments in response to multiple human and natural drivers (Stanley et al. 2012). In non-eutrophic lakes, the DOC pool is typically dominated by material with a terrestrial origin (Wilkinson et al. 2013). Yet patterns and controls of inputs of this allochthonous C are surprisingly poorly understood (Aufdenkampe et al. 2011). A salient example is the recent widespread increase in terrestrial DOC inputs to many freshwater systems in north temperate and boreal regions referred to as ‘browning’ (Roulet and Moore 2006). Discussion about causality has been lively, and explanations include climate warming, land management effects, and changes in sulfate deposition due to air quality legislation (Clark et al. 2010). Interestingly, some of the NTL study lakes are experiencing this DOC enrichment while others -even adjacent lakes- are not (Fig. 13). DOC fluxes to aquatic systems have multiple drivers and can vary spatially due to differences in flow paths, soil type, or land cover, and temporally in response to temperature, precipitation regime, or precipitation chemistry (Stanley et al. 2012). We will investigate how DOC moves from land to water, how controls on these fluxes vary over space and time, and what may explain apparent increased loading (browning) to some lakes and not others.

Inputs of allochthonous DOC to surface waters reflect the combination of OC sources in the landscape and subsequent OC transformation and transport along flow paths. We will build on our partnership with the USGS WEBB program (e.g., Dripps et al. 2006, Lowry et al. 2009, Crawford et al. 2014) to evaluate variation in source, transport, and transformation of DOC among different sites in the NHLD. Hydrology in the watersheds of the NHLD primary study lakes is well known (e.g., Pint et al. 2003, Hunt et al. 2006, Lowry et al. 2007), allowing us to link changes in DOC with hydrologic fluxes. Current USGS WEBB research is investigating variations in the DOC pool as water moves from the soil surface, through the soil profile, and into the groundwater system following snowmelt and rain events. We will complement this event-based sampling with a series of laboratory experiments in which we will evaluate effects of different drivers both by themselves and in combination, on DOC composition and concentration. Wet and dry precipitation regimes will be imposed on forest (mineral) and wetland (peaty) soils to assess how precipitation fluctuations affect C composition and fluxes among contrasting sites. Subsequent experiments will include sulfate amendments to test effects of altered atmospheric deposition, additions of organic material from different vegetation sources, and temperature manipulations to consider possible warming effects. These short-term measurements and experiments along with long-term data on amount and composition of precipitation, air temperature, and other aspects of lake water chemistry will inform our interpretation of long-term lake DOC dynamics (Fig. 13).

Q4.2. Multiple drivers of phosphorus: How do changing precipitation, land cover, and landscape management affect the timing and magnitude of P loading?

Lake levels and water quality reflect the bulk movements of water and nutrients from the surrounding watershed. In the YLD, these fluxes are affected by climate, land-use change, and management of nonpoint pollution (Carpenter et al. 2006, Gillon et al. in review). At the same time, P-rich farmland is gradually being converted to suburban land use, with potentially high short-term P losses from the landscape due to construction and long-term increases resulting from the expansion of impervious surfaces (Gillon et al. in review). The combination of increased frequency of high-intensity rainfall and land-cover change has led to more frequent

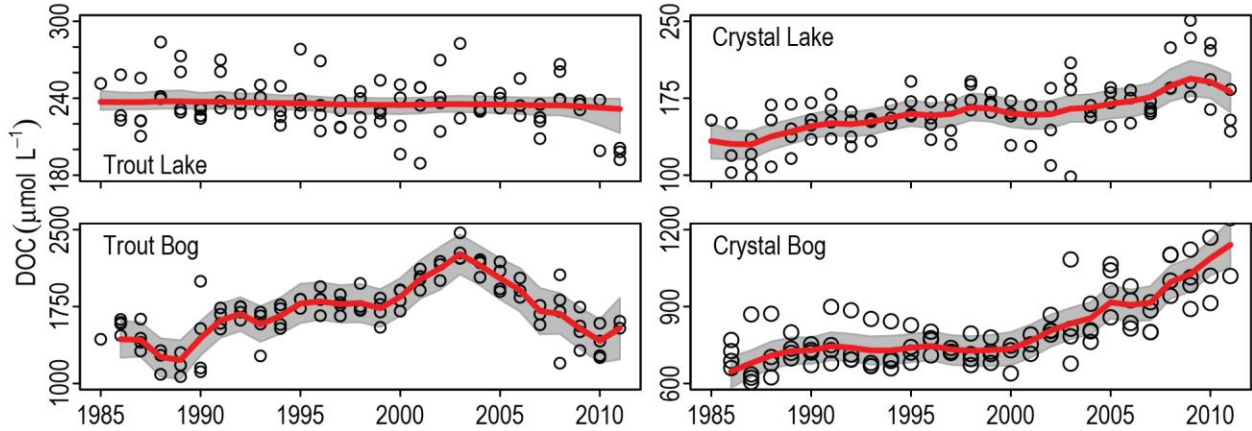


Figure 13. Long-term dissolved organic carbon (DOC) trends in four NHLD lakes, illustrating diverse temporal dynamics for these adjacent systems (see Fig. 1). While Crystal Bog and Crystal Lake show DOC increases consistent with widespread observations of ‘browning,’ Trout Lake shows a minor decrease and Trout Bog is variable over time. Trend (red line) estimated using first-order dynamic linear model. Grey shading represents 95% credible interval of the trend.



Figure 14. Drivers of P load to Yahara lakes have intensified as management efforts have increased, perhaps explaining the lack of change in P loads. The frequency of large (> 50 mm) and very large (> 75 mm) precipitation events has increased (A), manure production has increased (B), and impervious surface is more extensive (not shown), all of which promote increased P inputs to lakes. Management interventions to control P runoff have increased (C). Nonetheless, no trend is evident in P loads or other components of the P budget for Lake Mendota (D).

large-runoff events (Fig.14a) and greater public concern about lake water levels, water quality, and flooding- trends that are likely to continue in the future (Vavrus & Van Dorn 2010).

To analyze these complex changes in the Yahara watershed, we will expand our watershed modeling capacity to address erosion, P runoff, and the influence of groundwater on soil-plant-atmosphere water cycling. Using downscaled climate and land use-land cover change scenarios at high spatial (100-400m) resolution, we will quantify the plausible magnitude and frequency distribution of P load events for the next 60 years. Further, we will evaluate potential future frequency distributions of extremely high or low water levels and their implications for public perception and management of the lakes. Historical management shifts will be investigated to determine impacts if different historical decisions and policies had been implemented. Regional decision-makers have emphasized the value of such an approach in illustrating the connections between governance decisions and water outcomes. To support this work, a process-based agroecosystem model (Agro-IBIS; Kucharik et al. 2000) will be modified to have expanded capabilities to handle soil erosion and P cycling, and then will be coupled to a 3-D groundwater flow model (MODFLOW; Harbaugh 2005) and hydrologic routing model (THMB – the Terrestrial Hydrology Model with Biogeochemistry; Coe 2000; Table 3). This will provide the best-integrated modeling of ecohydrology and biogeochemistry in the Yahara watershed to date and allow us to better understand the effects of multiple factors on P-loading to YLD lakes.

Q4.3. Invasive species and ecosystem state: Can species invasions cause large, persistent changes in ecosystems?

Individual species often play important roles in ecosystems and can be part of complex feedbacks and rapid transitions among ecosystem states (Scheffer 1998, Scheffer & Carpenter 2003, Suding & Hobbs 2009). The role of species in such transitions is often revealed through species introductions and deletions (Sax et al. 2007). Studies to date reveal that some species invasions show signs of alternate stable states, while others do not (Hansen et al. 2013c). Long-term records at multiple sites, including NTL, provide a unique opportunity to test current ideas about the role of introduced species presence and abundance in causing shifts in ecosystem state.

How invasive species occurrence and abundance relate to impact, and specifically large impacts such as shifts in ecosystem state, are poorly known (Gaertner et al. 2014). Therefore, it is vital to understand the nature of the relationship between ecosystem state and invasive species abundance. Non-linear relationships may indicate the potential for critical transitions in ecosystem state (Scheffer & Carpenter 2003). Using the NTL time series of invasive species (rusty crayfish in Sparkling and Trout, rainbow smelt in Crystal and Sparkling, common carp and Eurasian watermilfoil in Wingra), we will use multivariate autoregressive models with time-varying coefficients (Ives & Dakos 2012) to quantify ecosystem changes across the observed range of invasive species abundance. The result is analogous to abundance-impact relationships from the biological invasions literature (Yokomizo et al. 2009). We will select response variables that are well-established indicators of ecosystem state (native macrophyte cover for rusty crayfish, native coldwater fish abundance for rainbow smelt, Secchi depth for common carp). We will also apply this analysis to predict the impact of an unfolding invasion: spiny water fleas were first observed in Lake Mendota in 2009 and have now reached the highest densities ever recorded anywhere (up to 1000 per m³). Finally, we will lead a cross-site synthesis and apply this approach to time series of invasive species from other LTER sites to seek broad generalities

regarding how ecosystem state responds across a gradient of invasive species abundance. Seven LTER sites and three non-LTER sites have appropriate data and will participate in this collaboration, allowing us to include multiple invaders in both aquatic and terrestrial ecosystems.

Q4.4. Water quality and governance: How do decision-makers use scientific knowledge about environmental conditions and changes as evidence in environmental management?

Ecosystem regime shifts may be either facilitated or prevented by management, and management can be influenced by availability of scientific knowledge (Gunderson & Holling 2001).

Knowledge about environmental drivers and thresholds should help frame discussions of environmental problems, evaluate prior management actions, and forecast the effects of different management options (Mitchell et al. 2006, Ostrom 2007, Pahl-Wostl 2009). However, the role of scientific knowledge in decision-making is challenging to predict (Prewitt et al. 2012) and its use may even worsen political disagreement (Sarewitz 2004). As an epicenter of water policy innovation in the Midwest, the Yahara watershed serves as an excellent site for examining the use of science as evidence in management, policy, and governance.

Water quality is not improving in YLD lakes despite substantial investment in mitigation of nonpoint pollution (Lathrop & Carpenter 2014; Fig. 14). Competing interpretations of these trends have emerged in current debates about the future of the lakes, and the role of scientific information in these interpretations varies substantially. These debates will shape decisions about management options that will affect water quality. Our goal is to identify institutional factors that may facilitate the use of science in policy argumentation and management planning and evaluation. To this end, we will adapt the framework of Ostrom (1990) and examine policy documents and public meeting transcripts for the use of scientific knowledge as evidence. We will interview resource managers, scientists, elected officials, agricultural advisors, farmers, and other resource users to compare their perspectives on science, belief in model estimates, value orientations, and engagement in policy and management. Collectively, this analysis will improve our understanding of the feedbacks between scientific efforts to monitor and model environmental conditions and shocks, water resource management, and policy argumentation (Jacobs et al. 2010).

Synthesis and Significance

Long-term ecological research is an absolute necessity for discerning fundamental changes in ecosystems. Ecosystem responses to shifting drivers are governed, in part, by slowly changing variables, such as organic carbon pools, population sizes of long-lived species, or watershed land cover. Long-term studies involving cross-system comparisons at multiple scales, focused experiments on key processes, and innovative models are required to detect and understand long-term change (Luo et al. 2011). In addition, future trajectories of climate, land use and cover, species invasions, and their combined ecosystem consequences are uncertain (Polasky et al. 2011). Today's models and scenarios of future projections derived from long-term studies become tomorrow's hypotheses to test with continued long-term research (Carpenter 2002).

Over the past 33 years, NTL researchers have established a firm benchmark against which further change of our landscapes and lakes can be assessed and understood (Fig. 15). NTL

databases provide a strong foundation for developing models, testing mechanisms, and evaluating uncertainties. We will continue to detect emerging patterns, evaluate and advance concepts of change, and build forward-looking models and hypotheses that will be tested using future long-term observations. Concepts, models and hypotheses from four areas of ecological research – landscape limnology, connectivity, multiple causation and ecological responses to extreme events – are intertwined in the research that we propose here (Fig. 5). Our studies address important trends in drivers in the Great Lakes region as large rainfall events grow more frequent (Peterson et al. 2008, Villarini et al. 2013), urban land uses expand (Pijanowski & Robinson 2011), agricultural practices evolve (Shortle et al. 2012), species invasions become more common (Strayer 2010) and ecosystem change escalates in pace, magnitude and variability (Grimm et al. 2013).

Proposed research addresses important ecological questions that derive from general concepts and theories, are grounded in our long-term databases, and require further long-term data collection to be answered. During the next six years, we will conduct new empirical and modeling studies of ecological change at regional, lake district, lake watershed, and in-lake scales (Fig. 16). Regional studies include cross-site comparisons (e.g., synthesis of lake-atmosphere gas exchange, urban water chemistry, and invasive species effects on ecosystems), in addition to Great Lakes region-scale studies of water clarity. Projects to evaluate concepts, theories, models, and mechanisms span a range of scales and topics, such as responses of lake thermal regime and gas exchange to changing climate, organic carbon and phosphorus dynamics of watersheds and lakes, abundance-impact theory for aquatic invasive species, and many others.

Just as drivers and ecosystems change, the topography of how we do science is evolving. Emerging opportunities include observation networks such as GLEON and NEON (Hanson 2007, Keller et al. 2008, Weathers et al. 2013), big data and macrosystems science (Heffernan et al. 2014), advances in interdisciplinary team building (Cheruvilil et al. 2014), and expanding scales of integration of knowledge. NTL continues to originate and embrace new approaches for expanding the intellectual scope of our research (Fig. 15).

Education at all levels will continue to be a focus at NTL over the next six years. Undergraduate and graduate research and postdoctoral training are central to our program, and students and postdocs will contribute to most of the research proposal here. NTL public outreach activities are accessed by hundreds of citizens each year and integrate with our contributions to public policy.

NTL research will continue to be directly relevant to management and policy from global to local scales. Many of the science-policy connections in the current funding cycle (see Section 1) will continue over the next six years via research on aquatic invasive species and climate change, as the ecological consequences of these large-scale drivers become increasingly conspicuous. We also expect that proposed work on conditions favoring toxic cyanobacterial blooms, effects of urbanization on flood risk and pollutants, and models of overland P flows will be used by resource managers. Finally, while our long-standing partnerships with agencies and inclusion of agency scientists in NTL facilitates the informing of policy, we expect that proposed work on how scientific information is used in policy debates to be of substantial value to us as researchers as well as to policy makers aspiring to make informed, scientifically-based decisions.

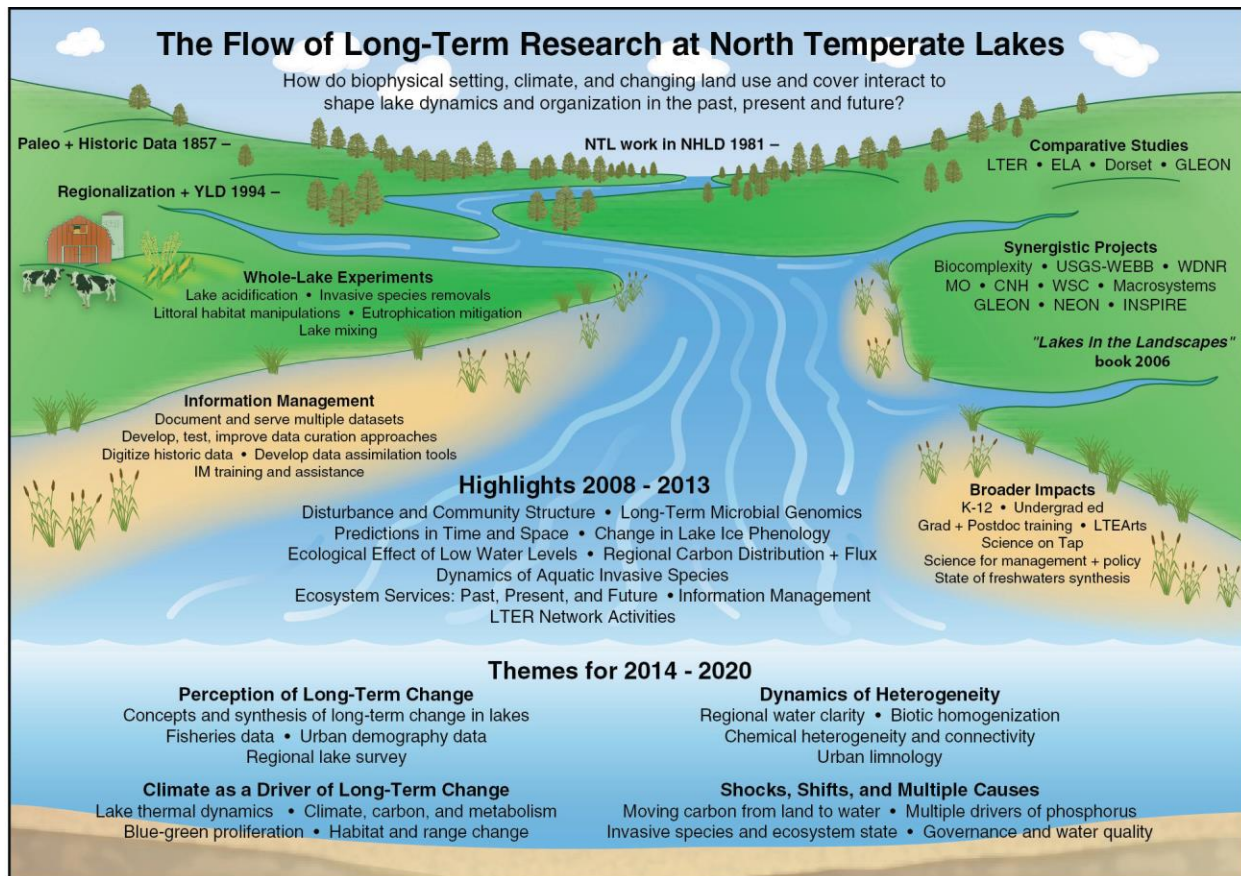


Figure 15. The flow of long-term research at NTL, illustrating project origins, major activities, experiments, allied projects, accomplishments in the current funding cycle, and themes for the next six years.

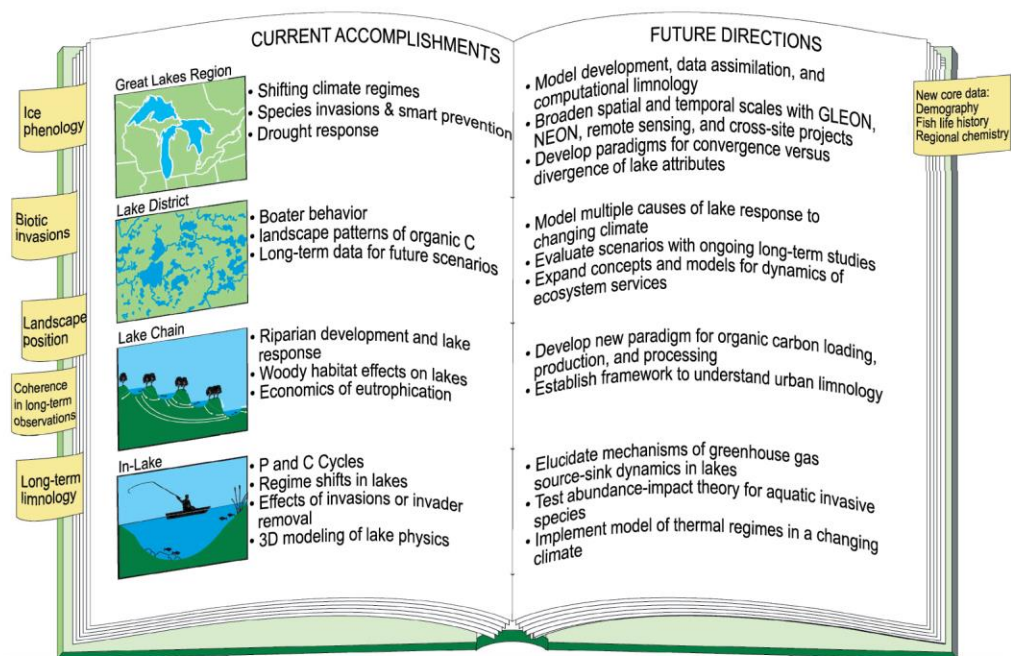


Figure 16. Current and future chapters of the NTL program summarized for regional, lake chain, and in-lake spatial scales, with tabs denoting a few key accomplishments and data sets.

NTL research has produced new insights and fundamental knowledge of long-term ecology of lakes and their interactions with landscape, atmospheric, and human processes. As we begin a new chapter of LTER research (Fig. 16), we will develop and evaluate concepts and theories using ongoing long-term data, advance understanding of lake district dynamics, integrate our findings across multiple scales, collaborate with other researchers in long-term and cross-site comparisons, and use modeling as a tool to develop forward-looking hypotheses to be evaluated with future long-term research.

Section 3. 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 two exceptions, activities described in this proposal do not rely on existence or acquisition of such funds. The two exceptions involve partnerships with the WDNR. First, NTL and WDNR will jointly fund a post-doctoral scientist for the regional water clarity study (Q3.1). Second, most water chemistry for YLD lakes has been analyzed at the Wisconsin State Laboratory of Hygiene through support provided by WDNR. This arrangement has been in place since 1994 when YLD lakes were brought into NTL. Both commitments have been approved by UW and WDNR for the upcoming funding cycle.

Section 4. Education and Outreach Activities

Expanding and strengthening education and outreach activities have been a priority for NTL in recent funding cycles, and in this proposal we continue our commitment to highly successful long-term activities and include a set of new initiatives.

Education- Graduate student training is a cornerstone of NTL educational activities, and these early-career scientists make fundamental contributions to research (e.g., see Table 1), education, and outreach accomplishments. Their involvement and mentorship will continue to be central to our activities and our success. Graduate students are welcome under the broad tent of NTL research and encouraged to contribute and collaborate on an equal level with PIs and post docs to foster a collaborative community of scholars. Adding to these opportunities, we will also formalize ecological information management training for NTL graduate and interested undergraduate students through various venues over the next six years (see section 4 for details). We currently involve 20 graduate students in NTL research either with direct support or indirectly through collaborative interactions, and we expect these numbers to be maintained each year over the next six years.

NTL is involved 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 are guaranteed more than 15 summer undergraduate fellowships from private sources during the upcoming grant cycle, and these opportunities will be coordinated with 12 requested LTER-supported REUs to create a critical mass for a community of undergraduate researchers. REUs are highly valued opportunities for us

on several levels. Fellows often work in partnership with graduate students and postdocs, providing an additional training opportunity to develop mentoring skills. REU science often results in presentations at scientific meetings, contribution to or leadership of publications, and most REUs go on to graduate school and scientific careers. We look forward to engaging students through these high-value fellowship opportunities over the next six years and beyond.

Our K-12 activities are led by Dr. Robert Bohanan through a partnership with UW's Institute for Biology Education, and are grounded in long-term relationships that have been established between NTL and schools and school districts throughout the state. The NTL Schoolyard program provides a diverse set of resources and experiences for K-12 students and teachers and includes UW undergraduate and graduate students, staff, and faculty. We plan to: (1) continue our successful Winter Limnology program in Madison and at Trout Lake; (2) develop and pilot a school/citizen science project including hydrology and adult dragonfly surveys and (3) adapt the ecological game "Trails Forward" (www.gameslearningsociety.org/games.php) for exploring connections of landscapes, land use, policy, stakeholders, water quality and quantity in an urban-exurban landscape. Because of their focus on urban areas, activities (2) and (3) will be coordinated with new proposed research on urban limnology (Q3.4). An emergent principle of these activities has been to engage people in the neighborhoods around the ponds as observers and data collectors. In addition to student- and classroom-collected data on water clarity, dissolved oxygen, conductivity, and aquatic biodiversity, neighbors will routinely measure water levels, water clarity, and riparian predators, chiefly birds and adult dragonflies. To support the accuracy and reliability of the data related to bird and dragonfly identification, we will: (1) provide web- and kiosk-based field guides; (2) facilitate training opportunities for the public led by local schools, including printed material, web-based resources such as webinars; and (3) coordinate a Spring Bird Count Day and a mid-summer Great Dragonfly Count Day. Collectively, these will support the development of a new catalog of citizen science data with data visualization tools and tutorials to promote their use in community decision-making. Water level monitoring in urban areas is inspired by a citizen-science project piloted in 2013 (see below) that we hope to expand across the state in the next five years. Partners involved in these education activities include the WDNR, The WI Odonata Survey and WI USGS.

Outreach and Communication- An area of substantial activity over the past three years has been development of new outreach and communications activities intended to raise awareness and translate NTL science to policy makers, resource managers, and the general public. These efforts include partial support of a science communications specialist to facilitate media interactions, promote NTL research and researchers, and assist/coordinate new activities. We are requesting funds to continue to support this individual and activities that have proven to be highly successful, as well as to develop new initiatives. Efforts to be continued include Science on Tap, our Art-Science collaborations- including a new effort to host an artist in residence during the summer at Trout Lake Station- and open houses at Trout Lake Station and the Hasler Lab of Limnology (see Section 1 for more information). We also plan to formalize and expand a citizen science project on lake water levels in coordination with partners at USGS. Citizens submit data on lake levels via text message, and can access near-real time information on lake levels and connect to the NTL web page for more information about lake levels across the state and about NTL and long-term ecological research.

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