Final Summary Report – Climate Change and Multiple Stressor Aquatic Research Programme

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Introduction

The Climate Change and Multiple Stressor Aquatic Research Programme at Laurentian University was created through the support of the Ontario Ministry of Environment and Climate Change (now the Ontario Ministry of Environment, Conservation and Parks). The programme commenced in 2009 and extended through 2018. The overall objective was "To promote, facilitate and conduct aquatic research in the far north of Ontario in order to advance the scientific knowledge of the effects of multiple stressors on northern aquatic ecosystems". This objective was addressed through two major elements, including:

1) Conducting collaborative, multidisciplinary studies of aquatic ecosystems in the far north of Ontario, creating northern aquatic datasets, and publishing study findings
2) Collaborating with a large network of scientists on analyzing and publishing results from ongoing studies in northeastern Ontario and internationally with relevance to aquatic ecosystems in the north.

Given the complexity of aquatic ecosystems in northern Ontario and the variety of stressors affecting these ecosystems, our overall approach was to engage scientists at many Ontario universities and resource management agencies, and international scientists, in collaborative studies. Sharing resources provided a very efficient, cost-effective way to conduct northern science, and collaborations developed the multidisciplinary approach necessary to address complex northern environmental issues. Since the far north of Ontario is primarily the home of First Nation communities we engaged a number of First Nations (especially Wasaho, Weenusk, and Eabametoong First Nations) in the planning and execution of our studies in their traditional lands. The far north work described here could not have been completed without the enthusiastic help of local First Nation peoples.

Far North of Ontario

Background:

The far north of Ontario straddles two physiographic regions, the Hudson Bay Lowlands (underlain by Paleozoic age bedrock) and the Canadian Shield (underlain by Archean age bedrock). These physiographic regions encompass two ecozones, the Hudson Plains and the Boreal Shield, respectively. Although very different in geological setting and vegetation cover, both regions contain vast numbers of freshwater lakes which are a vital component of the health of northern environments and which provide sustenance and essential services to northern peoples. A recent estimate by the Ontario Ministry of Natural Resources and Forestry (MNRF) identified ~ 708,000 lakes in the far north of Ontario with 118,000 on the Shield and 590,000 on the Lowlands. Rivers are also very important in the far north, especially for coastal communities, as travel routes and for their fisheries. The far north contains the largest rivers wholly in Ontario, including the Severn, Winisk, Albany, Attawpiskat and Moose rivers, and innumerable smaller drainages.

Aquatic ecosystems in the far north of Ontario are very vulnerable to future change Climate forecasts suggest that climate warming will be most pronounced in northern areas of the province. As well, future large-scale mining activity and associated infrastructure development is inevitable for the far north of Ontario, with the discovery of massive metal deposits in the "Ring of Fire" (ROF) area. With increasing interest in development throughout the north, and in the ROF area in particular, there is a need to improve our basic understanding of northern aquatic ecosystems so that we may understand how future impacts may affect them. Conserving the diversity, function, and provision of aquatic ecosystem services in northern Ontario in the face of climate change and future development requires sound scientific data from which to make informed management decisions. However, until very recently few data existed for lakes and rivers in the far north of Ontario, one of the least disturbed and largest (~ 452,000 km^2) ecosystems on earth. A major objective of the Climate Change and Multiple Stressor Aquatic Research Programme was to help fill the pressing need for current limnological data for this vast area, and develop our scientific understanding of the nature of northern aquatic ecosystems and their sensitivity to various stressors.

Substantial progress has been made in addressing this objective. Various collaborative surveys were completed on lakes and rivers in the far north (Figure 1), resulting in many publications in scientific journals (abstracts of journal papers produced are provided in Appendix A). Some of these papers and many others from colleagues working in northern areas of Manitoba, Ontario, and Quebec were included in a Special Issue of the journal Arctic, Antarctic, and Alpine Research on *Environmental Change in the Hudson and James Bay Region, Canada* (Appendix B). It is anticipated that publications will continue to be produced in future from the collaborations and datasets developed as part of the programme. Four progress reports (www.livingwithlakes.ca) were also completed to keep stakeholders including Government and First Nations informed and updated on our studies and to make data available (Appendix C). Data on mercury and other contaminants that were collected on fish from many northern rivers (Figure 1) were included in the current *Guide to Eating Ontario Fish* issued by the Ontario Ministry of the Environment and Climate Change. Additional contaminant data will be included in future editions of the *'Guide'*. Many graduate student projects were also supported through this programme (Appendix D). A summary of some important findings from our collaborative/multidisciplinary studies in the far north of Ontario is provided below.

Some Recent Findings:

- Lakes across the far north of Ontario exhibit widely varying water chemistry due to the very heterogeneous nature of this vast landscape. At a very broad scale, general chemistry differences between lakes on the Canadian Shield and the Hudson Bay Lowlands were apparent; however, in the transition area between these physiographic regions (notably in the 'Ring of Fire' area of northwestern Ontario) Shield and Lowlands lakes could not be differentiated based on water chemistry. In this transition area, large deposits of peat and glacial till largely decouple lakes from reactions with the underlying bedrock (MacLeod et al. 2017).

- Shield lakes in the far northwest of Ontario had calcium, magnesium, and total phosphorus concentrations higher than those of many Lowlands lakes and previously studied Shield lakes south of 50°N, related to an abundance of lacustrine and glacial end-moraine deposits in the north. Thus, the existing perception of Shield lakes in Ontario as very dilute and nutrient poor needs to be broadened to include lakes north of 50°N with relatively high ionic strength and phosphorus concentrations (MacLeod et al. 2017).

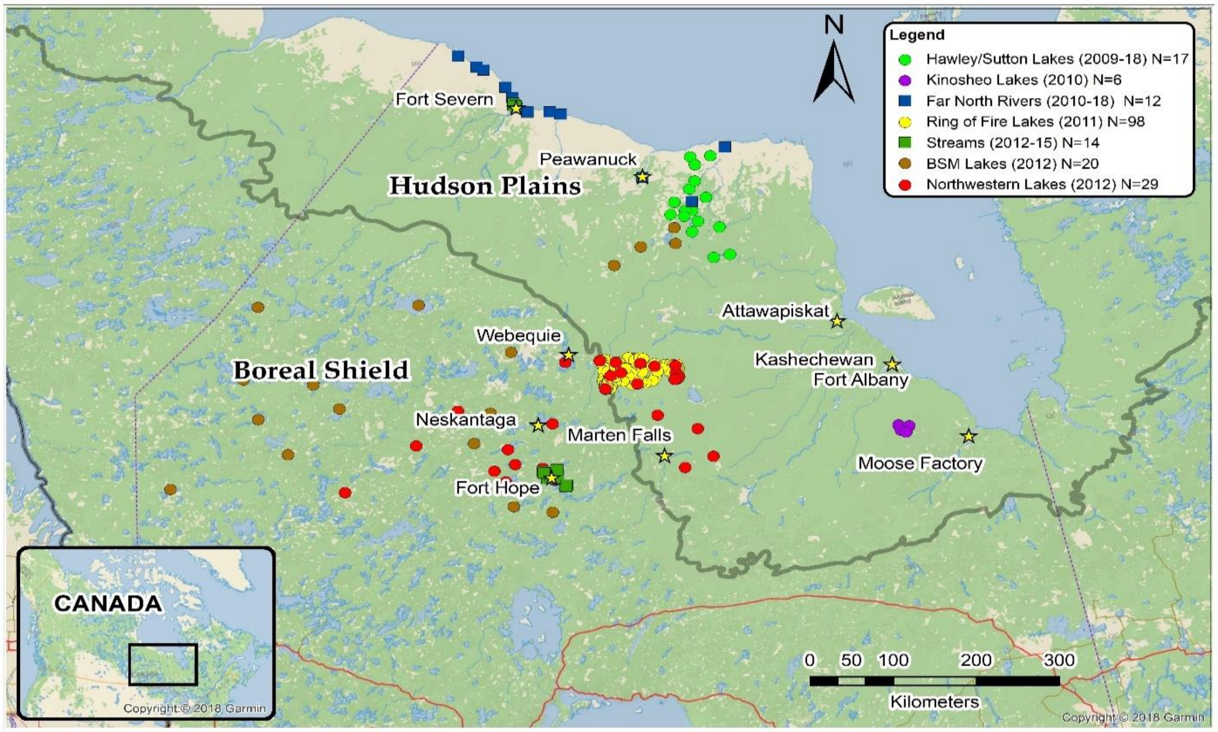

Figure 1. Climate Change and Multiple Stressor Aquatic Research Programme: Sampling Sites in the far north of Ontario.

- Crustacean zooplankton communities in lakes of the far north were generally similar to communities in more southern lakes, although some of the survey lakes appear to be at or near the northern limit for a few species (*Mesocyclops edax*, *Tropocyclops extensus*, *Daphnia mendotae*). Species richness was higher in Shield lakes than in Lowlands lakes, likely because the shallower Lowlands lakes offer less habitat space for coexistence of species than the deeper Shield lakes (Paterson et al. 2014; MacLeod et al. 2018).

- Lakes in the far north of Ontario contain diverse phytoplankton communities. Phytoplankton community composition varied widely across lakes, largely based on differences in water depth and nutrient concentrations, with non-filamentous cyanobacteria and chlorophytes more common in shallow lakes, and deeper lakes dominated by planktonic diatoms or filamentous cyanophytes (Paterson et al. 2014).

- Changes in lake plankton communities are already happening as a result of climate warming. Paleolimnological studies of diatom and cladoceran remains in dated sediment cores show clear shifts toward increased relative abundances of planktonic taxa, changes consistent with warming-induced changes in lake properties including longer ice-free periods and increased production by planktonic algae (Rühland et al. 2013, 2014; Jeziorski et al. 2015; Hargan et al. 2016).

- Warming-related changes in plankton communities have been especially pronounced in shallow lakes (Hargan et al. 2016), and community shifts occurred earlier in inland lakes (1970's) in comparison to lakes closer to the Hudson Bay coast (Rühland et al. 2013, 2014; Hargan et al. 2016; Hadley et al. 2019). In lakes near Hudson Bay (within ~150 km, clear community changes did not occur until the mid-1990's, reflecting the moderating effect of persistent sea ice on regional temperatures, an influence that declined greatly as the duration of sea-ice cover shortened, air temperatures rose, and the region reached an ecological tipping point (Rühland et al. 2013).

- Diatom assemblages recorded in the bogs and fens of northern Ontario are similar to those found in peatlands around the world, demonstrating that diatom species are very specialized to exist in these often harsh semi-aquatic environments. Diatoms from peatlands have great potential as biomonitors of environmental change in these important ecosystems (Hargan et al. 2015).

- Productivity has recently increased in northern lakes as indicated by temporal analyses of organic matter content and chlorophyll a concentrations in dated sediment cores (Brazeau et al. 2013b; Rühland et al. 2013).

- Northern lake sediments are able to produce a small amount of elemental mercury through a biogenic process which is enhanced by increasing labile carbon and ionic strength. These results suggest that under changing conditions, such as increasing temperature or alteration of water chemistry a fraction of sedimentary Hg may be remobilized and available for microbial reduction (Brazeau et al. 2013a.)

- Mercury deposition to northern lake sediments appears to be increasing although Hg deposition from the atmosphere has declined due to emission control programmes. This is likely attributable to increased algal scavenging of Hg from the water column with increased aquatic productivity resulting from climate warming (Brazeau et al. 2013b).

- The absence of a significant relationship between total Hg and methyl Hg (MeHg) in surficial sediments suggests that the inorganic Hg supply does not limit MeHg production. MeHg and organic content were highly correlated across lakes in surface and deep sediment layers, indicating that sediment organic matter explains part of the spatial variation in MeHg concentrations between lakes (Brazeau et al. 2013b).

- DNA analyses for a dated sediment core demonstrate that even in remote northern lakes microbial communities have changed in response to historical changes in mercury delivery. The effective population size of the merA gene, which is involved in Hg detoxification, increased about 200 years ago, coinciding with the industrial revolution Microbial communities may provide a useful tool for monitoring contaminant deposition to northern lakes (Poulain et al. 2015).

- Benthic invertebrate communities in five of the northernmost rivers in Ontario were correlated with water chemistry and physical habitat characteristics. Community structure was most associated with pH, nutrient concentrations, river width, current speed, and substrate size. Benthic invertebrate communities hold considerable promise as a monitoring tool to track future changes in northern rivers (Jones et al. 2014).

- Based on food-web analyses, changes in food resources resulting from climate warming are expected to have little impact on large-bodied northern fish species because of their ability to utilize a wide variety of food types. In contrast, the direct effects of warming events may negatively affect some fish species in the shallow lakes that dominate the Hudson Bay Lowlands. While very shallow (only a few meters deep), some of these lakes do support populations of cool-water fish species (e.g. lake whitefish, *Coregonus clupeaformis*; white sucker, *Catostomus commersoni*) which may be particularly susceptible to the effects of lake warming (Persaud et al. 2015).

Far North Journal Publications:

Brazeau, M.L., J.M. Blais, A.M. Paterson, W. Keller, and A.J. Poulain. 2013a. Evidence for microbe-mediated production of elemental mercury (Hg^0) in subarctic lake sediments. Appl. Geochem. 37: 142-148.

Brazeau, M. L., A.J. Poulain, A. Paterson, W. Keller**,** H. Sanei, and J.M. Blais. 2013b. Recent Changes in Mercury deposition and primary productivity inferred from sediments of lakes from the Hudson Bay Lowlands, Ontario, Canada. Environ. Pollut. 173: 52-60**.**

Hadley, K.R., A.M. Paterson, K. Rühland, H.White, B. Wolfe, W. (Bill) Keller, and J.P. Smol. 2019. Biological and geochemical changes in shallow lakes of the Hudson Bay Lowlands: a response to recent warming. J. Paleolimnology DOI: 10.1007/s10933-018-0061-9.

Hargan, K.E., K.M. Rühland, A.M. Paterson, S.A. Finkelstein, J.R. Holmquist, G. MacDonald, W. Keller**,** and J.P. Smol. 2015. The influence of water table depth and pH on the spatial distribution of diatom species in peatlands of the Boreal Shield and Hudson Plains, Canada. Botany 93: 57-74.

Hargan, K.E., C. Nelligan, A. Jeziorski, K.M. Rühland, A.M. Paterson, W. Keller**,** and J.P. Smol. 2016. Tracking the long-term responses of diatoms and cladocerans to climate warming and human influences across lakes of the Ring of Fire in the Far North of Ontario, Canada. J. Paleolimnology 56: 153-172.

Jeziorski, A., B. Keller, R.D. Dyer, A.M. Paterson, and J.P. Smol. 2015. Differences among modern-day and historical cladoceran communities from the "Ring of Fire" lake region of northern Ontario: Identifying responses to climate warming. Fundamental and Applied Limnology 186: 203-216.

Jones, F.C., S. Sinclair, and W. Keller. 2014. Benthic macroinvertebrate communities in five rivers of the Coastal Hudson Bay Lowland. Polar Biology 37: 141-147.

Keller, W., A. Paterson, K. Rühland, and J. Blais. 2014. Introduction – environmental change in the Hudson and James Bay region. Arctic, Antarctic and Alpine Research 46: 2-5.

MacLeod, J., W. Keller, A.M. Paterson, R.D. Dyer, and J.M. Gunn. 2017. Scale and watershed features determine lake chemistry patterns across physiographic regions in the far north of Ontario, Canada. J. Limnol. 76: 211-220.

MacLeod, J., W. Keller, and A.M. Paterson. 2018. Crustacean zooplankton in lakes of the far north of Ontario, Canada. Polar Biology. doi. 10.1007/s003000018-2282-9.

Paterson, A., B.Keller**,** C. Jones, K. Rühland, and J. Winter. 2014. An exploratory survey of water chemistry and plankton communities in lakes near the Sutton River, Hudson Bay Lowlands, Ontario, Canada. Arctic, Antarctic and Alpine Research 46: 121-138.

Persaud, A., A. Luek, B. Keller, C. Jones, P. Dillon, J. Gunn, and T. Johnston. 2015. Trophic dynamics of several fish species in lakes of a climatically sensitive region, the Hudson Bay Lowlands. Polar Biology 38: 651-664. doi10.1007/s00300-014-1628-1.

Poulain, A.J., S. Aris-Brosou, J. Blais, M. Brazeau, W. Keller, and A.M. Paterson. 2015. Microbial DNA records historical delivery of anthropogenic mercury. ISME Journal 9: 2541-2550.

Rühland, K.M., A.M. Paterson, W. Keller, N. Michelutti, and J.P. Smol. 2013. Global warming triggers the loss of a key Arctic refugium. Proc. Roy. Soc. B. 280: 20131887.

Rühland, K., K. Hargan, A. Jeziorski, A. Paterson, W. Keller**,** and J. Smol. 2014. A multi-trophic exploratory survey of recent environmental change using lake sediments in the Hudson Bay Lowlands, Ontario. Arctic, Antarctic and Alpine Research 46: 139-158.

Northeastern Ontario

Background:

Thousands of lakes around Sudbury, in northeastern Ontario, Canada, were badly damaged by acid deposition and many were also metal-contaminated. Large reductions in atmospheric sulphur and metal emissions have led to widespread chemical improvements in these lakes, and recovery has been documented for various groups of aquatic biota. These findings were very important in establishing the necessity for and value of sulphur emission controls during the international debates about the effects of acid deposition and the need for cleaner air. Studies around Sudbury have provided one of the world's best examples of the environmental benefits of air pollution controls. In addition, the Wawa, Ontario area provides a further, very dramatic example of the natural recovery of aquatic systems in Ontario from severe atmospheric contaminant deposition. Acidified/metal contaminated lakes around Wawa have shown remarkable, very rapid improvements after closure of the local iron ore sintering plant in 1998; however, biological recovery is not complete.

Studies of northeastern Ontario lakes are continuing to advance our understanding of chemical and biological recovery processes; however, that knowledge is still incomplete. In some cases biological recovery has been slow to follow chemical recovery. It has become apparent that the recovery of lakes from acidification is closely linked with the responses to, and interactions with, other large-scale environmental stressors like climate change, water browning and calcium declines. Developing a better understanding of lake recovery processes and their future outcomes within such a multiple stressor context will be difficult. It will demand the merging of various approaches including monitoring, experimentation, paleolimnology and modelling, and will require effective collaboration between different research and monitoring sites and various agencies and institutions engaged in environmental science. Through the Climate Change and Multiple Stressors Aquatic Research Programme we have addressed these needs through developing extensive collaborations examining various aspects of multiple stressor interactions. The data that form the basis of these collaborations are largely from the long-term monitoring of lakes around Sudbury, a programme that was initiated in the 1970's for some lakes, and later for others. Figure 2 shows the locations of key long-term study lakes in the Sudbury area. Abstracts of journal papers resulting from our collaborations with a wide international network of researchers are provided in Appendix A. Student projects supported are listed in Appendix D.

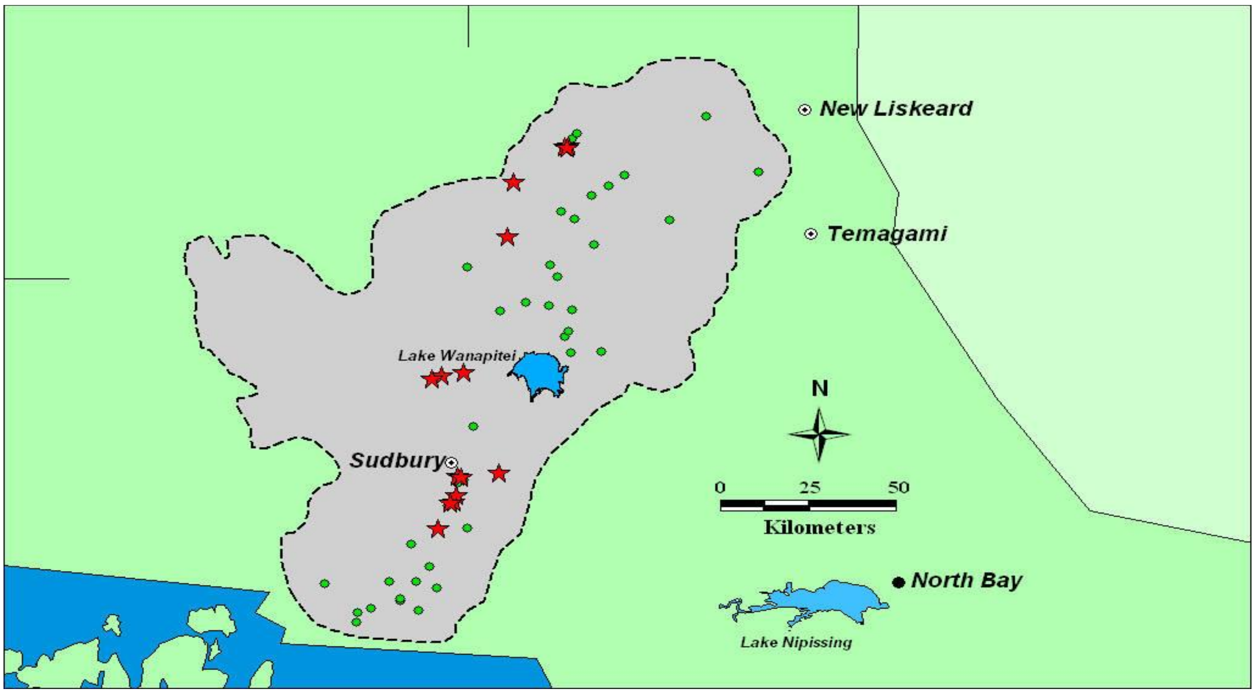

Figure 2. Key long-term monitoring lakes in northeastern Ontario. Intensive Lakes (stars) are sampled monthly during the ice-free season for chemistry, crustacean zooplankton, and phytoplankton. Extensive Lakes are sampled once annually in summer for chemistry and in some years for zooplankton.

Some Recent Findings:

- Acidification of lakes and rivers is still a major environmental concern despite reduced emissions of acidifying compounds. In 11 of 12 regions in North America and Europe, non-marine sulphate (SO4*) declined significantly between 1990 and 2008 (−15 to −59 %). From an ecological perspective, the chemical quality of surface waters in acid-sensitive areas in these regions, including northern Ontario, has clearly improved as a consequence of emission abatement strategies, paving the way for some biological recovery (Garmo et al. 2014).

- Large reductions in atmospheric sulphur and metal emissions have led to widespread chemical improvements in lakes near Sudbury, and recovery has been documented for various biota. Studies of these northeastern Ontario lakes are continuing to advance our understanding of chemical and biological recovery processes; however, that knowledge is still incomplete. It has become apparent that the recovery of lakes from acidification is closely linked with the responses to, and interactions with, other large-scale environmental stressors like climate change, water browning and calcium declines (Keller 2009; Keller et al. 2018).

- Dissolved organic carbon (DOC) concentrations and water colour are increasing in many inland waters across North America and Europe (Garmo et al. 2014). This widespread "browning" has profound implications for aquatic ecosystems including those in northern Ontario. Examination of DOC in lake sediment cores has revealed that in areas with high past acid deposition (Sudbury region) lakes have been returning to their former state although future changes to DOC levels higher than background are likely due to climate warming. In low acid deposition areas (Experimental Lakes Area) DOC concentrations already often exceed background levels, likely because of climate warming (Meyer-Jacob et al., under review).

- Calcium (Ca) concentrations are decreasing in softwater lakes across eastern North America and western Europe. Long-term contemporary and palaeo-environmental field data show that this is precipitating a dramatic change in Canadian lakes: the replacement of previously dominant pelagic herbivores (Ca-rich *Daphnia* species) by *Holopedium glacialis*, a jelly-clad, Ca-poor competitor. Greater representation by *Holopedium* within cladoceran zooplankton communities will reduce nutrient transfer through food webs, given their lower phosphorus content relative to daphniids, and greater absolute abundances may pose long-term problems to water users (Jeziorski et al. 2014).

- Recovery of acidified/metal contaminated lakes around Sudbury is affected by both biotic and abiotic processes. When these lakes were highly acidic and metal contaminated, direct toxicity was the major stressor on zooplankton, and some direct chemical effects still persist. However, as water quality improved after emission reductions, biological controls by the altered predation systems increasingly influenced zooplankton community recovery. Full recovery of zooplankton communities will require the restoration of typical aquatic food webs as well as improvements in habitat quality (Valois et al. 2010; Valois et al. 2011; Webster et al. 2013).

- *Daphnia* bioassays with Sudbury and Dorset area lake waters indicate that recovery patterns of daphniids in Sudbury lakes are affected by interactions of metals with Ca and Na concentrations, and the varying metal sensitivity of different *Daphnia* species (Celis-Salgado et al. 2016).

- There is a growing consensus that dispersal does not generally limit ecological recovery of zooplankton in most damaged Sudbury area lakes. Rather, in lake rich regions such as northeastern Ontario, the persistence of colonists, not the arrival of species is usually most important (Audet et al. 2013; Yan et al. 2016).

- Long term zooplankton data from northeastern Ontario lakes have proved very useful in developing various models for metal toxicity to organisms. These models will prove valuable in predicting the future biological impacts of freshwater acidification and metal contamination (Khan et al. 2011; Balistrierie et al. 2014; Stockdale et al. 2014).

- Zooplankton recovery was assessed by comparing 35 year trends in 4 recovering (from acidification and metal contamination) Sudbury lakes to both historical (1983–1984) and present-day (2004–2006) conditions in a set of minimally impacted reference lakes. Recovery occurred later, and improvements differed quantitatively when judged against the present-day vs. historical targets. These results show that in a changing world, the choice of reference condition can alter conclusions from recovery assessments (Palmer et al. 2013).

- The hypothesis that disturbance should result in communities of closely related species was tested with long-term crustacean zooplankton data sets from disturbed and reference lakes. Regardless of disturbance type, communities generally contained more closely related species when disturbed. This effect was independent of species richness, evenness and abundance. Communities already under stress changed the most when disturbed (Helmus et al. 2010).

- In a mesocosm experiment, surface predators (*Buenoa macrotibialis*) had no effect on zooplankton abundance, and zooplankton avoided surface predators regardless of thermal habitat structure. In contrast, *Chaoborus* had a strong predation impact and reduced total zooplankton abundance, but only in isothermal conditions. These results demonstrate that changes in lake thermal structure may result in strong, unexpected consequences for predator–prey dynamics (MacPhee et al. 2011).

- Analysis of time series data for 53 temperate zone lakes showed that zooplankton richness increased with greater temperature variation while temporal variations in chemistry tended to exclude species. Anthropogenic increases in the variability of future climates may have profound effects on biodiversity (Shurin et al. 2010).

- During acidification, *Bosmina* antennule and carapace length significantly increased in the sediments of three of five Sudbury area study lakes, while mucro length decreased in four of the five lakes. However, despite the recent return to pre-impact pH levels, the size structure of the present-day *Bosmina* community still differs from the pre-impact size distributions. The continued dominance of the food webs by small invertebrate predators (e.g., cyclopoid copepods) appears responsible for the persistent changes to *Bosmina* size structure (Labaj et al. 2016).

- Paleolimnological analyses of some Sudbury lakes recovering from acidification/metal contamination showed evidence of recovery for scaled chrysophytes but not for diatoms (Tropea et al. 2010). In non- acidified urban lakes in Sudbury the diatom composition has shifted from oligotrophic species to species that thrive in more productive conditions, likely reflecting nutrient inputs from watershed development (Tropea et al. 2011).

- A remarkable example of point-source lake acidification and metal pollution, and subsequent recovery in water quality, has occurred in lakes near the former iron sintering plant at Wawa (Ontario, Canada). Based on sedimentary records, chrysophyte, diatom and cladoceran responses to decreased emissions varied amongst the study lakes, perhaps reflecting differences in local bedrock geology and hydrological regime. Although some water chemistry variables may have recovered to near pre-industrial levels, collectively the multi proxy paleolimnological analyses of these strongly acidified lakes demonstrate delayed biological recovery across multiple trophic levels (Greenaway et al. 2012a; Greenaway et al. 2012b; Jeziorski et al. 2013).

- Lakes are effective sentinels for climate change because they are sensitive to climate, respond rapidly to change, and integrate information about changes in the catchment. The effectiveness of various indicators may however vary geographically reflecting variations in regional climate responses, catchment characteristics, and lake mixing regimes (Adrian et al. 2009).

- Two commonly used benthic macroinvertebrate sampling methods: a rapid approach, employing live, unaided sorting and a standard approach using microscope sorting of preserved samples, were compared for 61 Ontario streams. Both methods resulted in similar estimates of community composition at a site, as determined by the Bray-Curtis similarity index. However, the live sorting methodology resulted in greater family richness and higher estimates of metrics that reflect large taxa (i.e., %EPT). Despite differences in a number of metrics, both methods performed equally well at identifying impairment in the test sites, with live sorting samples being slightly more sensitive (Valois et al. 2016).

Northeastern Ontario Journal Publications:

Adrian, R., C.M. O'Reilly, H. Zagarese, S.B. Baines, D.O. Hessen, W. Keller, D.M. Livingstone, R. Sommaruga, D. Straile, E. Van Donk, G.A. Weyhenmeyer, and M. Winder. 2009. Lakes as sentinels of climate change. Limnol. Oceanogr. 54(6, part 2): 2283-2297.

Audet, C., S. MacPhee, and W. Keller. 2013. Constructed ponds colonized by crustacean zooplankton: local and regional influences. J. Limnol. 72: 524-530. DOI: 10.4081/jlimnol.2013.e43.

Balistrieri, L.S., C.A. Mebane, T.S. Schmidt, and W. Keller. 2015. Expanding a metal mixture acute toxicity models to natural stream and lake invertebrate communities. Environ. Tox. chem.doi.org/10.1002/etc.2824.

Celis-Salgado, M.P., W. Keller, and N.D. Yan. 2016. Calcium and sodium as regulators of the recovery of four *Daphnia* species along a gradient of metals and base cations in contaminated lakes in Sudbury, Ontario, Canada. J. Limnol. 75(s2): 36-49.

Garmo, Ø.A., B.L. Skjelkvale, H.E. de Wit, L. Colombo, C. Curtis, J. Folster, A. Hoffmann, T. Hogasen, D. Jeffries, W. Keller**,** V. Majer, A. Paterson, M. Rogora, D. Rzychon, A. Steingruber, J.L. Stoddard, J. Vuorenmaa, and A. Worsztynowicz. 2014. Trends in surface water chemistry in acidified areas in Europe and North America from 1990 to 2008. Water Air Soil Pollution 225:1880 DOI 10.1007/s11270-014-1880-6.

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Greenaway, C.M., A.M. Paterson, W. Keller, and J.P. Smol. 2012b. Dramatic diatom species assemblage responses in lakes recovering from acidification and metal- contamination near Wawa, Ontario, Canada: a paleolimnological perspective. Can. J. Fish. Aquat. Sci. 69: 656-669.

Helmus, M.R., W. Keller, M.J. Paterson, N.D. Yan, C.H. Cannon, and J.A. Rusak. 2010. Communities contain closely related species during ecosystem disturbance. Ecology Letters 13: 162-174.

Jeziorski, A., B. Keller, A.M. Paterson, C.M. Greenaway, and J.P. Smol. 2013. Aquatic ecosystem responses to rapid recovery from extreme acidification and metal contamination in lakes near Wawa, Ontario. Ecosystems 16: 209-223.

Jeziorski, A., A.J. Tanentzap, N.D. Yan, A.M. Paterson, M.E. Palmer, J.B. Korosi, J. Rusak, M. Arts, W. Keller, R. Ingram, and J.P. Smol. 2014. The jellification of north temperate lakes. Proc. Roy. Soc. B. 282: 20142449.

Keller**,** W. 2009. Limnology in northeastern Ontario: from acidification to multiple stressors. Can. J. Fish. Aquat. Sci. 66: 1189-1198.

Keller**,** W., J. Heneberry, and B. Edwards. 2018. Recovery of acidified Sudbury, Ontario, Canada lakes: a multi-decade synthesis and update. Environmental Reviews. Dx.doi.org/10.1139/er-2018-0018.

Khan, F.R., W. Keller, N.D. Yan, P.G. Welsh, C.M. Wood, and J,C. McGeer. 2011. Application of biotic ligand and toxic unit modeling approaches to predict improvement in species richness in smelter damaged lakes near Sudbury. Environ. Sci Technol. 46: 1641-1649.

Labaj, A.L., J.B. Korosi, J. Kurek, A. Jeziorski, W. Keller**,** and J.P. Smol. 2016. Response of *Bosmina* size structure to the acidification and recovery of lakes near Sudbury, Canada. J. Limnol. 75(s2): 22-29.

MacPhee,S., S. Arnott, and W. Keller. 2011. Lake thermal structure influences macroinvertebrate predation on crustacean zooplankton. J. Plank. Res. 33: 1586-1595.

Meyer-Jacob, C., N. Michelutti, A.M. Paterson, B.F. Cumming, W. Keller, and J.P. Smol. 201 . Are lakes browning or re-browning? Divergent trends in high and low acid deposition areas (under review, Nature Sci. Reports).

Palmer, M.E., Keller**,** W., and N.D. Yan. 2013. Reassessing the recovery of crustacean zooplankton communities in historically acidified and metal-contaminated lakes: a comparative analysis of the temporal limitations of regional restoration targets. J. Appl. Ecol. 50: 107-118.

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Stockdale, A., E. Tipping, S. Lofts, J. Fott, Ø.A. Garmo, J. Hruska, B. Keller, S. Löfgren, S.C. Maberly, V. Majer, S.A. Nierzwicki-Bauer, G. Persson, A-K. Schartau, S. J. Thackeray, A. Valois, J. Vrba, B. Walseng, and N. Yan. 2014. Metal and proton toxicity to lake zooplankton: application of a chemical speciation based modeling approach. Environ. Pollut. 186: 115-125.

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Tropea, A.E., A.M. Paterson, W. Keller, and J.P. Smol. 2011. Diatoms as indicators of long-term

nutrient enrichment in metal contaminated lakes from Sudbury, Ontario. Lake and Reserv. Mgmt. 27: 48-60.
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Valois, A.E., W. Keller, and C.W. Ramcharan. 2011. Recovery in a multiple stressor environment: using the reference condition approach to examine zooplankton community change along opposing gradients. J. Plank. Res. 33: 1417-1429.
Valois, A.E., C. Sarrazin-Delay, K. Somers, and W. Keller. 2016. Assessing stream health: do differences in sample collection and processing affect how we evaluate impairment? J. Limnol. 75: 392-402.
Webster, N.I., W. Keller and C. Ramcharan. 2013. Restoration of zooplankton communities in industrially damaged lakes: influences of residual metal contamination and the recovery of fish communities. Restoration Ecology 21: 785-792.
Yan, N.D., J. Bailey, J. McGeer, M. Manca, W. Keller, M. Celis-Salgado, and J.M. Gunn. 2016. Arrive, survive, and thrive: the essential stages of re-colonization and recovery of zooplankton in urban lakes in Sudbury, Canada. J. Limnol. 75(s2): 4-14.

Conclusions and Recommendations

Far North of Ontario:

Much progress has been made in developing an understanding of the nature and sensitivity of aquatic ecosystems in the far north of Ontario. However, we have only sampled a very small fraction of the many thousands of lakes and rivers in the far north. Additional lake, river and watershed sampling needs to be done to increase our knowledge base for northern aquatic ecosystems. Detailed, process-oriented studies examining landscape/chemistry linkages for specific lakes, rivers, and their watersheds are needed to better understand the mechanisms controlling the nature of northern aquatic systems. Given the shallow, very dynamic nature of many northern lakes, assessments of temporal chemistry variability are particularly needed. The vast, remote nature of northern Ontario creates major logistical difficulties for conventional surveys. To augment field surveys, and increase spatial and temporal data collection opportunities in a cost effective manner, the use of remote sensing and remote monitoring techniques for assessments of these northern systems needs to be explored. It is hoped that the results presented here will stimulate further research on northern lakes and rivers, help advance the basic scientific understanding of northern aquatic ecosystems, and aid in the development of comprehensive future assessment and monitoring programmes.

Northeastern Ontario:

Studies around Sudbury and Wawa have provided some of the world's best example of the environmental benefits of air pollution controls. Studies of northeastern Ontario lakes are continuing to advance our knowledge of chemical and biological recovery processes; however, that understanding is still incomplete. While remarkable lake recovery has sometimes been observed, in some cases biological recovery has been slow to follow chemical recovery and both chemical and biological recovery are incomplete in many lakes. We now understand that the recovery of lakes from acidification is closely linked with the responses to, and interactions with, other large-scale environmental stressors like climate change, water browning and calcium declines. Developing a better understanding of lake recovery processes and their future outcomes within such a multiple stressor context will be difficult. It will demand the merging of various approaches including monitoring, experimentation, and paleolimnology, and will require effective collaboration between different research and monitoring sites and various agencies and institutions engaged in environmental science. Continuation of the long-term lake monitoring programmes in the Sudbury area will be essential to further developing our understanding of lake recovery processes and likely future outcomes, within a multiple–stressor framework, and identify new stressors that may be impacting aquatic systems.

Appendices

Appendix A. Abstracts of Far North and Northeastern Ontario journal papers

Appendix B. Cover and contents of AAAR Special Issue

Appendix C. List of Far North Study progress reports

Appendix D. List of student projects supported

Appendix A. Abstracts of Far North and Northeastern Ontario journal papers

Far North of Ontario:

Brazeau, M.L., J.M. Blais, A.M. Paterson, W. Keller, and A.J. Poulain. 2013a. Evidence for microbe-mediated production of elemental mercury (Hg0) in subarctic lake sediments. Appl. Geochem. 37: 142-148. The production and fate of Hg0 in lake sediments remains poorly characterized, although it can potentially influence Hg toxicity and mobility. Using slurry incubations, we assessed the effect of nutrients, pH, ionic strength, and tested the role of microbes, on Hg0 production from pristine lake sediments of the Hudson Bay Lowlands in Ontario, Canada. We showed that Hg0 production from oxygenated sediments was low (<1% of the Hg flux to sediments), biogenic, and did not appear to be dependent on the predicted HgII speciation in the slurry. The addition of biologically labile carbon sources and ionic strength, particularly [Na+], had the greatest impact on Hg0 production, increasing it by over 10-fold.These results suggest that under changing conditions, such as increasing temperature or alteration of water chemistry as observed in numerous locations throughout Arctic and subarctic environments, a fraction of sedimentary Hg may be remobilized and available for microbial reduction.

Brazeau, Michelle L., Alexandre J. Poulain, Andrew Paterson, Wendel Keller, Hamed Sanei, and Jules M. Blais. 2013b. Recent Changes in Mercury deposition and primary productivity inferred from sediments of lakes from the Hudson Bay Lowlands, Ontario, Canada. Environ. Pollut. 173: 52-60. Spatial and temporal changes in mercury (Hg) concentrations and organic carbon in lake sediments were examined from the Hudson Bay Lowlands to investigate whether Hg deposition to sediments is related to indicators of autochthonous production. Total organic carbon, "S2" carbon (mainly algal derived OC), C:N and v13C indicators suggest an increase in autochthonous productivity in recent decades. Up-core profiles of S2 concentrations and fluxes were significantly correlated with Hg suggesting that varying algal matter scavenging of Hg from the water column may play an important role in the temporal profiles of Hg throughout the sediment cores. Absence of a significant relationship between total Hg and methyl Hg (MeHg) in surficial sediments suggested that inorganic Hg supply does not limit MeHg production. MeHg and OC were highly correlated across lakes in surface and deep sediment layers, indicating that sediment organic matter content explains part of the spatial variation in MeHg concentrations between lakes.

Hadley, K.R., A.M. Paterson, K. Rühland, H.White, B. Wolfe, W. (Bill) Keller, and J.P. Smol. 2019. Biological and geochemical changes in shallow lakes of the Hudson Bay Lowlands: a response to recent warming. J. Paleolimnology DOI: 10.1007/s10933-018-0061-9. The Hudson Bay Lowlands (HBL) region of the far north of Ontario (Canada) is expected to undergo considerable physical, chemical and biological change as a result of ongoing climatic change. Previous research in the region has shown marked limnological changes during the past ~20 years in relatively deep lakes that have been attributed to increased air temperatures and changes in sea ice phenology in Hudson Bay since the mid-1990s. Here, we present diatom assemblage, primary production and geochemical data from lake sediments documenting recent limnological change in two shallow sub-arctic lakes in the Sutton River region of the HBL. Both lakes recorded increased whole-lake production and diatom diversity changes that are consistent with a longer ice-free period and growing season. Changes in diatom composition at Wolfgang Lake were characterized by a response amongst benthic/periphytic taxa whereas a modest increase in planktonic diatoms was observed at Sam Lake. Geochemical changes ($\delta^{15}N$, C/N and %N) were temporally coherent with diatom assemblage changes, but showed different responses in the two study lakes. Thus, although the biological and geochemical changes were consistent with recent warming, differences in the nature and timing of these shifts illustrate the heterogeneous nature of shallow lakes, and suggest that local (catchment-specific) factors are important determinants of the trajectory of limnological change in these sensitive systems.

Hargan, K.E., K.M. Rühland, A.M. Paterson, S.A. Finkelstein, J.R. Holmquist, G. MacDonald, W. Keller, and J.P. Smol. 2015. The influence of water table depth and pH on the spatial distribution of diatom species in peatlands of the Boreal Shield and Hudson Plains, Canada. Botany 93: 57-74. Diatoms collected from 113 surface peat samples from the Boreal Shield and Hudson Plains show taxonomic distributions that are associated with macro-vegetation type, pH, and position relative to the water table, the main environmental variables measured in this study. The overall goal of our research was to determine the ecological distribution and response of diatoms to microhabitat conditions, and to assess the potential for diatoms to be applied as indicators of long-term environmental change in northern peatlands. Our results indicate that diatom assemblage composition was determined by both the broader peatland type (i.e., bog, rich and poor fens) and microhabitats within peatland formations (e.g., hummock, hollow). The diatom assemblages were primarily influenced by pH with the sites divided at a critical pH of 5.5, and secondarily by the depth to the water table. Acidic bog hollow and hummock microhabitats were species-poor and dominated almost exclusively by *Eunotia paludosa* A.Grunow and (or) *Eunotia mucophila* (H.Lange-Bertalot, M.Norpel-Schempp & E.Alles) H.Lange-Bertalot. These acidophilic and aerophilic diatom species were associated with the narrow pH optima of the dominant *Sphagnum* L. species (e.g., *Sphagnum fuscum* (Schimp.) Klinggr., *Sphagnum angustifolium* (C.E.O. Jensen ex Russow) C.E.O.Jensen) found in these bog habitats. Rich and poor fen samples, which were less acidic, supported a more diverse diatom assemblage (>30 species) with greater variability in both diatom and bryophyte pH tolerances. The diatom assemblages recorded in the bogs and fens of our study are similar to those found in peatlands around the world, demonstrating that diatom species are very specialized to exist in these often harsh semi-aquatic environments. Diatoms from peatlands have great potential as biomonitors of environmental change in these important ecosystems.

Hargan, K.E., C. Nelligan, A, Jeziorski, K.M. Rühland, A.M. Paterson, W. Keller, and J.P. Smol. 2016. Tracking the long-term response of diatoms and Cladocera to climate warming across lakes of the Far North of Ontario, Canada. J. Paleolimnology 56: 153-172. The extensive peatlands and lakes of the Far North of Ontario warrant committed scientific attention given their status as a significant carbon sink. Economic interest in this region has recently increased due to the discovery of vast mineral deposits (mainly chromite and nickel) known as the ‘‘Ring of Fire’’. Mineral exploration and infrastructure planning are underway, but environmental monitoring is only beginning. Detailed baseline ecological information is required to assess the impacts of future resource extraction within the context of multiple environmental stressors (including recent regional climate warming). Here we use sediment cores from two relatively deep lakes (Zmax ~10 m) and two shallow lakes (Zmax ~2 m), all located in the vicinity of the Ring of Fire, to examine biotic responses to warming prior to the commencement of mining activities. Our data show that, over the past ~150 years, diatom and cladoceran sedimentary assemblages have transitioned from dominance by littoral/benthic forms to greater abundances of planktonic cladoceran (an increase of~3 to 34 %) and diatom taxa (an increase of ~3 to 22 %). Increased relative abundances of planktonic taxa are consistent with warming-induced changes in lake properties including longer ice-free periods and increased production by planktonic algae. The response of diatom assemblages in shallow lakes to warming preceded the deeper lakes by ~45 to 60 years, and substantial increases in aquatic production (~4 to 15 times higher than in sediments deposited prior to 1900) were observed in the shallow lakes, in agreement with previous analyses demonstrating the heightened sensitivity of shallow systems to climate warming. These data provide important information necessary to distinguish potential ecological impacts related to resource extraction from natural variation and the ongoing responses to regional climate warming.

Jeziorski, A., B. Keller, R.D. Dyer, A.M. Paterson, and J.P. Smol. 2015. Differences among modern-day and historical cladoceran communities from the "Ring of Fire" lake region of northern Ontario: Identifying responses to climate warming. Fundamental and Applied Limnology 186: 203-216. The "Ring of Fire" in the Far North of Ontario (50 – 57° N, 79 – 94° W) is a region of growing economic and environmental interest due to recent mineral discoveries and the potential for resource development. Due to the remote location of the region, little baseline ecological information is available to distinguish any environmental impacts of mine development from ongoing regional warming. Here, we compare modern and pre-industrial sedimentary cladoceran assemblages from 60 lakes centered on McFaulds Lake in the "Ring of Fire" to identify directional changes through time and compare the assemblages with prior paleolimnological cladoceran studies of Ontario lakes closer to the Hudson Bay coast, and further south in the Muskoka-Haliburton region. The cladoceran assemblages from the "Ring of Fire" contain diverse littoral assemblages relative to the other two regions; however, despite the shallow depth of these lakes, there have been significant increases in the relative abundances of pelagic taxa (e.g. *Bosmina* spp. and *Daphnia* spp.) since pre-industrial times; taxonomic shifts consistent with warming induced changes in lake properties including a longer ice-free period and increased algal plankton production. This evidence of widespread changes within the cladoceran assemblages in the "Ring of Fire" prior to the onset of resource extraction provides lake managers and stewards with information to better monitor and evaluate future development projects.

Jones, F.C., S. Sinclair and W. Keller. 2014. Benthic macroinvertebrate communities in five rivers of the Coastal Hudson Bay Lowland. Polar Biology 37: 141-147. As a precursor to developing a biomonitoring programme for rivers of the Coastal Hudson Bay Lowland, this study characterized and compared the benthic macroinvertebrate communities and water chemistry in 5 remote, previously undescribed rivers near Fort Severn, Ontario, Canada. The pH of river water ranged from 8.1 to 8.7, total phosphorus from 11 to 26 ug/L, dissolved organic carbon from 8 to 12 mg/L, and chloride from 56 to 153 mg/L. A total of 57 benthic macroinvertebrate taxa were represented, and the 10 most numerically dominant were the Chironominae (26% of collected individuals), Orthocladiinae (16%), oligochaetous clitellata

(9%), Hyalellidae (7%), Hydropsychidae (6%), Gammaridae (5%), Elmidae (5%), Sphaeriidae/Pisidiidae (4%), Nemata (3%), and Tanypodinae (3%). Rivers' positions in ordinations of chemical and biological datasets were similar suggesting that water chemistry has a role in structuring riverine benthic communities in the study region. Correlations between water chemistry or habitat predictors and site scores in the ordination of benthic macroinvertebrate taxa counts suggested that biological community structure was most associated with river-water pH, nutrient concentrations (i.e. the concentrations of chloride and various other dissolved ions) and several geomorphological variables (e.g. bank-full river width, current speed, and the size of the dominant inorganic particles in the pavement layer of the streambed). Interest in mineral extraction and other resource based exploration in Ontario's Far North is increasing. This study represents a start on baseline characterization for ecological monitoring and cumulative effects assessment that should proceed along with northern development.

Keller, W., A. Paterson, K. Rühland, and J. Blais. 2014. Introduction – environmental change in the Hudson and James Bay region. Arctic, Antarctic and Alpine Research 46: 2-5. Introductory overview article, with no Abstract.

MacLeod, J. W. (Bill) Keller, A. Paterson, J. Gunn and R. Dyer. 2017. Scale and watershed features determine lake chemistry patterns across physiographic regions in the far north of Ontario, Canada. J. Limnol. 76:211-220. Changes in the far north of Ontario (>50°N latitude), like climate warming and increased industrial development, will have direct effects on watershed characteristics and lakes. To better understand the nature of remote northern lakes that span the Canadian Shield and Hudson Bay Lowlands, and to address the pressing need for limnological data for this vast, little-studied area of Ontario, lake chemistry surveys were conducted during 2011-2012. Lakes at the transition between these physiographic regions displayed highly variable water chemistry, reflecting the peatland landscape with a mix of bog and fen watersheds, and variations in the extent of permafrost. In the transition area, Shield and Lowlands lakes could not be clearly differentiated based on water chemistry; peat cover decouples, to varying degrees, the lakes from the influences of bedrock and surficial deposits. Regional chemistry differences were apparent across a much broader area of northern Ontario, due to large-scale spatial changes in geology and in the extent of peatlands and permafrost. Shield lakes in the far northwest of Ontario had Ca, Mg, and TP concentrations markedly higher than those of many Lowlands lakes and previously studied Shield lakes south of 50°N, related to an abundance of lacustrine and glacial end-moraine deposits in the north.

MacLeod, J., W. Keller, and A.M. Paterson. 2018.Crustacean zooplankton in the far north of Ontario, Canada. Polar Biology 41: 1257-1267 DOI 10.1007/s00300-018-2282-9. The far north of Ontario, Canada, is a region that is very vulnerable to future change due to climate warming and resource extraction. Despite its vast size (~ 450,000 km^2) and large numbers of lakes (> 700,000) there has been very little study of aquatic ecosystems in this remote area. To address this lack of limnological data, forty-one northern Ontario lakes spanning two physiographic regions, the Hudson Bay Lowlands and the Canadian Shield, were sampled during 2012 for crustacean zooplankton and water chemistry. These sub-Arctic lakes supported diverse crustacean plankton communities with species richness similar to the richness of lakes in central and northeastern Ontario. While some of the species collected appear to be at the northern limit of their distributions, most relatively common Ontario species occurred throughout the 2012 study area. The physico-chemical characteristics showing relationships with species richness and relative abundances were variables associated with lake morphometry, ionic strength and nutrient status. There were differences in community richness and composition between Lowlands and Shield lakes; however, these differences do not seem attributable to biogeographical influences on species occurrences. Rather, the lower species richness and differences in community composition in Lowlands lakes relative to Shield lakes appear to be largely related to lake morphometry. The shallower and generally smaller Lowlands lakes provide much less habitat diversity, i.e. niche space, than the larger, deeper Shield lakes, leading to simpler communities.

Paterson, A., B. Keller, C. Jones, K. Rühland, and J. Winter. 2014. An exploratory survey of water chemistry and plankton communities in lakes near the Sutton River, Hudson Bay Lowlands, Ontario, Canada. Arctic, Antarctic and Alpine Research 46: 121-138. We provide the first assessment of regional water chemistry and plankton (phytoplankton and crustacean zooplankton) for a suite of lakes near the Sutton River region of the northcentral Hudson Bay Lowlands (HBL). We use ordination analyses to examine the spatial variation in water chemistry and plankton across lakes, and to explore the factors that may explain this variation. Based on data collected during summer from 2009 to 2011, we found that in addition to geology, water chemistry was strongly influenced by a lake's proximity to salt water and the degree of permafrost development within its catchment. Phytoplankton composition varied across lakes based on differences in water depth and nutrient concentrations, with non-filamentous cyanobacteria and chlorophytes more common in shallow lakes, and deeper lakes dominated by planktonic diatoms or filamentous cyanophytes. Crustacean zooplankton community composition and richness in the HBL lakes was similar to communities found in Ontario lakes in more temperate regions within the Precambrian Shield. These baseline data provide a foundation upon which future surveys in this climatically sensitive region may be compared.

Persaud, A., A. Luek, B. Keller, C. Jones, P. Dillon, J. Gunn, and T. Johnston. 2014. Trophic dynamics of several fish species in lakes of a climatically sensitive region, the Hudson Bay Lowlands. Polar Biology 38: 651-664, doi10.1007/s00300-014-1628-1. Freshwater lakes in the Hudson Bay Lowlands (HBL) area of Ontario are expected to undergo considerable physical, chemical and biological changes related to climatic change; however, the nature of those changes is still very uncertain. As a first step to improve our understanding of fish communities within these subarctic lakes, we aimed to: (a) characterize trophic dynamics of several large-bodied species within three HBL lakes and (b) determine whether trophic dynamics of selected species in the HBL lakes differed from the same species in Southern Ontario lakes. We found that species-specific trophic position and littoral resource reliance varied significantly within and among the HBL lakes of differing biological communities, chemistry and morphometry. Although several significant differences were evident among lakes in the northern and southern regions, we did not find striking consistent differences in trophic dynamics. Based on observations of high variation in trophic position and/or littoral reliance, we can hypothesize that changes in food resources resulting from climatic change would have little impact on most of the large-bodied species.

Poulain, A.J., S. Aris-Brosou, J. Blais, M. Brazeau, W. Keller, and A.M. Paterson. 2015. Microbial DNA records historical delivery of anthropogenic mercury. ISME Journal 9: 2541-2550. Mercury (Hg) is an anthropogenic pollutant that is toxic to wildlife and humans, but the response of remote ecosystems to globally distributed Hg is elusive. Here, we use DNA extracted from a dated sediment core to infer the response of microbes to historical Hg delivery. We observe a significant association between the mercuric reductase gene (merA) phylogeny and the timing of Hg deposition. Using relaxed molecular clock models, we show a significant increase in the scaled effective population size of the merA gene beginning ~ 200 years ago, coinciding with the Industrial Revolution and a coincident strong signal for positive selection acting on residues in the terminal region of the mercuric reductase. This rapid evolutionary response of microbes to changes in the delivery of anthropogenic Hg indicates that microbial genomes record ecosystem response to pollutant deposition in remote regions.

Rühland, K.M., A.M. Paterson, W. Keller, N. Michelutti, and J.P. Smol. 2013. Global warming triggers the loss of a key Arctic refugium. Proc. Roy. Soc. B. 280: 20131887. We document the rapid transformation of one of the Earth's last remaining Arctic refugia, a change that is being driven by global warming. In stark contrast to the amplified warming observed throughout much of the Arctic, the Hudson Bay Lowlands (HBL) of subarctic Canada has maintained cool temperatures, largely due to the counteracting effects of persistent sea ice. However, since the mid-1990s, climate of the HBL has passed a tipping point, the pace and magnitude of which is exceptional even by Arctic standards, exceeding the range of regional long-term variability. Using high-resolution, palaeolimnological records of algal remains in dated lake sediment cores, we report that, within this short period of intense warming, striking biological changes have occurred in the region's freshwater ecosystems. The delayed and intense warming in this remote region provides a natural observatory for testing ecosystem resilience under a rapidly changing climate, in the absence of direct anthropogenic influences. The environmental repercussions of this climate change are of global significance, influencing the huge store of carbon in the region's extensive peatlands, the world's southern-most polar bear population that depends upon Hudson Bay sea ice and permafrost for survival, and native communities who rely on this landscape for sustenance.

Rühland, K., K. Hargan, A. Jeziorski, A. Paterson, W. Keller, and J. Smol. 2014 . A multi-trophic exploratory survey of recent environmental change using lake sediments in the Hudson Bay Lowlands, Ontario. Arctic, Antarctic and Alpine Research 46: 139-158. A multi-proxy paleolimnological survey was performed in the Hudson Bay Lowlands (HBL) of northern Ontario in order to provide an exploratory regional analysis of recent environmental change in this poorly understood sub-Arctic region. In contrast to the amplified warming experienced throughout the circum-Arctic since the mid-1800s, the climate of the Hudson Bay (HB) region has remained relatively cool and stable for hundreds of years. However, since the ~1990s, the HBL has experienced rapid, high magnitude increases in air temperature and declines in sea ice concentration. Diatom, cladoceran and chironomid remains preserved in the sediments of 13 lakes were used to examine whether this new climate regime has resulted in species compositional changes across multiple trophic levels. Our results suggest early signs of a response to warming among the freshwater biota of HBL lakes; however, the magnitude of this change varied among both biological indicators and sites. The diatoms exhibited the greatest degree of change, closely followed by chironomids, and relatively little change was observed among cladoceran assemblages. Modern assemblages contained planktonic diatom taxa that were previously not present and all indicator groups recorded a change in benthic/littoral taxa in the recent sediments indicative of warming-induced increases in habitat availability.

Northeastern Ontario

Adrian, R., C.M. O'Reilly, H. Zagarese, S.B. Baines, D.O. Hessen, W. Keller, D.M. Livingstone, R. Sommaruga, D. Straile, E. Van Donk, G.A. Weyhenmeyer, and M. Winder. 2009. Lakes as sentinels of climate change. Limnol. Oceanogr. 54(6, part 2): 2283-2297. While there is a general sense that lakes can act as sentinels of climate change, their efficacy has not been thoroughly analyzed. We identified the key response variables within a lake that act as indicators of the effects of climate change on both the lake and the catchment. These variables reflect a wide range of physical, chemical, and biological responses to climate. However, the efficacy of the different indicators is affected by regional response to climate change, characteristics of the catchment, and lake mixing regimes. Thus, particular indicators or combinations of indicators are more effective for different lake types and geographic regions. The extraction of climate signals can be further complicated by the influence of other environmental changes, such as eutrophication or acidification, and the equivalent reverse phenomena, in addition to other land-use influences. In many cases, however, confounding factors can be addressed through analytical tools such as detrending or filtering. Lakes are effective sentinels for climate change because they are sensitive to climate, respond rapidly to change, and integrate information about changes in the catchment.

Audet, C., S. MacPhee, and W. Keller. 2013. Constructed ponds colonized by crustacean zooplankton: local and regional influences. J. Limnol. 72: 524-530. DOI: 10.4081/jlimnol. 2013.e43. We examined monthly changes in crustacean zooplankton community composition during the initial colonisation period of a newly constructed pond (LWL pond), and in the littoral zone of an adjacent lake (Ramsey lake). In addition, four unconnected constructed ponds aged ≥20 years with established zooplankton communities were sampled and compared to the LWL pond. The species richness of both LWL pond and Ramsey Lake increased over the ice-free season, although Ramsey lake always had more species. Almost half of all species sampled occurred in both pond and lake. None of the zooplankton communities in the ponds used in the spatial analysis resembled communities of the LWL pond or one another. Taken together, these results indicate a lack of dispersal limitation, which suggests that differing local habitat factors had a strong influence in structuring the zooplankton communities.

Balistrieri, L.S., C.A. Mebane, T.S. Schmidt, and W. Keller. 2014. Expanding a metal mixture acute toxicity models to natural stream and lake invertebrate communities. Environ. Tox. chem.doi.org/10.1002/etc.2824. A modeling approach that was used to predict the toxicity of dissolved single and multiple metals to trout is extended to stream benthic macroinvertebrates, freshwater zooplankton, and *Daphnia magna*. The approach predicts the accumulation of toxicants (H, Al, Cd, Cu, Ni, Pb, and Zn) in organisms using 3 equilibrium accumulation models that define interactions between dissolved cations and biological receptors (biotic ligands). These models differ in the structure of the receptors and include a 2-site biotic ligand model, a bidentate biotic ligand or 2-pKa model, and a humic acid model. The predicted accumulation of toxicants is weighted using toxicant specific coefficients and incorporated into a toxicity function called Tox, which is then related to observed mortality or invertebrate community richness using a logistic equation. All accumulation models provide reasonable fits to metal concentrations in tissue samples of stream invertebrates. Despite the good fits, distinct differences in the magnitude of toxicant accumulation and biotic ligand speciation exist among the models for a given solution composition. However, predicted biological responses are similar among the models because there are interdependencies among model parameters in the accumulation–Tox models. To illustrate potential applications of the approaches, the 3 accumulation–Tox models for natural stream invertebrates are used in Monte Carlo simulations to predict the probability of adverse impacts in catchments of differing geology in central Colorado (USA); to link geology, water chemistry, and biological response; and to demonstrate how this approach can be used to screen for potential risks associated with resource development.

Celis-Salgado, M.P., W. Keller, and N.D. Yan. 2016. Calcium and sodium as regulators of the recovery of four Daphnia species along a gradient of metals and base cations in contaminated lakes in Sudbury, Ontario, Canada. J. Limnol. 75(s2): 36-49. Smelting of sulphur-rich metallic ores in Sudbury, Ontario, Canada, has caused acidification and metal contamination of thousands of lakes in the region. Recent reductions in smelter emissions have resulted in much ecological recovery, but the recovery of *Daphnia* species has been poor. To determine if Cu and Ni toxicity could explain differences in daphniid recovery among lakes, we compared results of 14 d static with renewal bioassays in waters from Blue Chalk Lake, an uncontaminated reference lake 200 km from Sudbury, and from five Sudbury lakes ranging in distance from the smelters and varying in metal and cation concentrations. We spiked Blue Chalk Lake water with Cu and Ni to levels resembling those of the Sudbury lakes and also tested the lake waters for toxicity. Survival of *Daphnia pulex*, *D. pulicaria* and *D. mendotae* decreased monotonically with increasing metal concentrations in the spiked Blue Chalk Lake treatments, falling from 90% in the controls to 0% at the two highest Cu and Ni levels, reflecting levels of Middle and Hannah lakes. In contrast, survival in waters collected from the actual Sudbury lakes did not monotonically track their total metal concentrations. Rather, survival fell to 0% in Clearwater Lake water, a lake with intermediate metal contamination (8.9 and 79.9 μg L–1 of Cu and Ni, respectively) vs 70-100% in the other lakes. We performed an additional assay with Clearwater Lake waters increasing its Ca and Na concentrations, singly and in combination to levels that reflected the levels in Middle Lake. The survival of the four daphniid species increased from 0% up to 80-100% with added Ca and from 0% to 60-90% with added Na. Lipid-ovarian indices had a similar trend to survival for *D. mendotae* and *D. pulicaria* in Bioassay 1, varying with the cation concentrations in the lakes for the daphniids in Bioassay 2. The bioassays results imply that regional recovery patterns of daphniids in Sudbury lakes cannot be understood without as a minimum considering both metal and base cation concentration differences among lakes, and give an indication of differences among *Daphnia* species to cope with metal stress.

Garmo, Ø.A., B.L. Skjelkvale, H.E. de Wit, L. Colombo, C. Curtis, J. Folster, A. Hoffmann, T. Hogasen, D. Jeffries, W. Keller, V. Majer, A. Paterson, M. Rogora, D. Rzychon, A. Steingruber, J.L. Stoddard, J. Vuorenmaa, and A. Worsztynowicz. 2014. Trends in surface water chemistry in acidified areas in Europe and North America from 1990 to 2008. Water Air Soil Pollution 225:1880 DOI 10.1007/s11270-014-1880-6. Acidification of lakes and rivers is still an environmental concern despite reduced emissions of acidifying compounds. We analysed trends in surface water chemistry of 173 acid-sensitive sites from 12 regions in Europe and North America. In 11 of 12 regions, non-marine sulphate (SO4*) declined significantly between 1990 and 2008 (−15 to −59 %). In contrast, regional and temporal trends in nitrate were smaller and less uniform. In 11 of 12 regions, chemical recovery was demonstrated in the form of positive trends in pH and/or alkalinity and/or acid neutralising capacity (ANC). The positive trends in these indicators of chemical recovery were regionally and temporally less distinct than the decline in SO4* and tended to flatten after 1999. From an ecological perspective, the chemical quality of surface waters in acid-sensitive areas in these regions has clearly improved as a consequence of emission abatement strategies, paving the way for some biological recovery.

Greenaway, C.M., AM. Paterson, W. Keller, and J.P. Smol. 2012. Scaled-chrysophyte assemblage changes in the sediment records of lakes recovering from marked acidification and metal-contamination near Wawa, Ontario, Canada. J. Limnol. 71: 267-278. A remarkable example of point-source lake acidification and metal pollution, and subsequent recovery in water quality, has occurred in lakes near the former iron sintering plant at Wawa (Ontario, Canada). Surface water pH levels in some of these lakes have increased from three to seven following local sulphur emission reductions and eventual closure of the sintering plant. Previous paleolimnological work documented striking successional changes in diatom species assemblages within dated sediment cores that could be related to past industrial activities. To gain additional insights into the chemical and biological recovery trajectories of the Wawa lakes, we used paleolimnological techniques to track euplanktonic scaled-chrysophyte (classes Chrysophyceae and Synurophyceae) species assemblage responses to historical water quality changes in five lakes. Coincident with the period of iron sintering from 1939 to 1998, striking successional changes were noted in the sedimentary profiles, with marked increases in the relative abundances of the acid- and metal-tolerant taxon synura echinulata. The scaled chrysophyte changes pre-dated diatom responses, confirming the former's status as reliable early warning indicators of lake acidification. Following closure of the sintering plant, species-specific chrysophyte responses to decreased emissions varied amongst the study lakes, perhaps reflecting differences in local bedrock geology and hydrological regime. Although some water chemistry variables may have recovered to near pre-industrial levels, similar to the diatom study, our data show that chrysophyte assemblages in the most recent sediments are now significantly different from pre-industrial assemblages.

Greenaway, C.M., A.M. Paterson, W. Keller, and J.P. Smol. 2012. Dramatic diatom species assemblage responses in lakes recovering from acidification and metal- contamination near Wawa, Ontario, Canada: a paleolimnological perspective. Can. J. Fish. Aquat. Sci. 69: 656-669. Several lakes near Wawa (Ontario, Canada) present a rare opportunity for studying rapid chemical and biological recovery from acidification and metal contamination. Surface water pH levels in some of these lakes have increased from 3 to 7 following local sulphur emission reductions and closure of an iron ore sintering plant. We used paleolimnological techniques to track diatom community responses to historical water quality changes in five lakes. Pre-industrial diatom assemblages recorded in lake sediments were dominated by species typical of circumneutral pH levels and were characterized by minimal species compositional change. Following the onset of sintering in 1939, there was a striking shift towards acid- and metal-tolerant Eunotia-dominated species assemblages, sometimes consisting of high quantities of teratological Eunotia valves. Recent dramatic water quality improvements, following first reductions in and then cessation of emissions, were accompanied by decreases in the relative abundance of benthic acid- and metal-tolerant species in the sediment record. However, diatom recovery trajectories did not entirely progress towards predisturbance communities, as the contemporaneous increase in relative abundance of other species was restricted to a few groups. Moreover, diatom responses were not synchronous among cores, with recovery rates influenced by local bedrock and the hydrological regime of each lake.

Helmus, M.R., W. Keller, M.J. Paterson, N.D. Yan, C.H. Cannon, and J.A. Rusak. 2010. Communities contain closely related species during ecosystem disturbance. Ecology Letters 13: 162-174. Predicting community and species responses to disturbance is complicated by incomplete knowledge about species traits. A phylogenetic framework should partially solve this problem, as trait similarity is generally correlated with species relatedness, closely related species should have similar sensitivities to disturbance. Disturbance should thus result in community assemblages of closely related species. We tested this hypothesis with 18 disturbed and 16 reference whole-lake, long-term zooplankton data sets. Regardless of disturbance type, communities generally contained more closely related species when disturbed. This effect was independent of species richness, evenness, and abundance. Communities already under stress (i.e., those in acidic lakes) changed most when disturbed. Species sensitivities to specific disturbances were phylogenetically conserved, were independent of body size, and could be predicted by the sensitivities of close relatives within the same community. Phylogenetic relatedness can effectively act as a proxy for missing trait information when predicting community and species responses to disturbance.

Jeziorski, A., B. Keller, A.M. Paterson, C.M. Greenaway, and J.P. Smol. 2013. Aquatic ecosystem responses to rapid recovery from extreme acidification and metal contamination in lakes near Wawa, Ontario. Ecosystems 16: 209-223. In the region northeast of Wawa, Ontario (Canada), many circumneutral lakes downwind of a nearby iron-sintering plant were strongly acidified (pH 3–4) in response to the emissions of large amounts of sulfur dioxide from 1939–1998. Following closure of the plant in 1998, lakewater pH has returned to circumneutral conditions due to the high buffering capacity of the local geological substrate. Prior paleolimnological analyses of dated sediment cores have detected some biological recovery among algal communities (diatoms and chrysophytes), although they have not returned to their pre-impact assemblages. Here we take a broader ecosystem approach, and build upon the algal analyses by examining cladoceran sedimentary assemblages, and spectrally-inferred chlorophyll a and dissolved organic carbon (DOC) from the same dated sediment cores. Similar to the algal communities, recent cladoceran sedimentary assemblages from three impacted lakes remain in an altered state relative to the pre-impact period (for example, increased relative abundances of *Chydorus brevilabris* and reduced cladoceran density in sediments). However, trends in the spectrally-inferred chlorophyll a and DOC were mixed, with long-term decreases in the study lake closest to the plant and long-term increases within the other lakes. Collectively, the multi-proxy paleolimnological analyses of these markedly acidified lakes demonstrate the delayed biological recovery from acidification (and differences in timing) across multiple trophic levels, despite the near-elimination of acid deposition almost a decade previously, which led to a striking recovery in lakewater pH and increased food availability.

Jeziorski, A., A.J. Tanentzap, N.D. Yan, A.M. Paterson, M.E. Palmer, J.B. Korosi, J. Rusak, M. Arts, W. Keller, R. Ingram, and J.P. Smol. 2014. The jellification of north temperate lakes. Proc. Roy. Soc. B. 282: 20142449. Calcium (Ca) concentrations are decreasing in softwater lakes across eastern North America and western Europe. Using long-term contemporary and palaeo-environmental field data, we show that this is precipitating a dramatic change in Canadian lakes: the replacement of previously dominant pelagic herbivores (Ca-rich *Daphnia* species) by *Holopedium glacialis*, a jelly-clad, Ca-poor competitor. In some lakes, this transformation is being facilitated by increases in macro-invertebrate predation, both from native (*Chaoborus* spp.) and introduced (*Bythotrephes longimanus*) zooplanktivores, to which *Holopedium*, with its jelly coat, is relatively invulnerable. Greater representation by *Holopedium* within cladoceran zooplankton communitieswill reduce nutrient transfer through food webs, given their lower phosphorus content relative to daphniids, and greater absolute abundances may pose long-term problems to water users. The dominance of jelly-clad zooplankton will likely persist while lakewater Ca levels remain low.

Keller, W. 2009. Limnology in northeastern Ontario: from acidification to multiple stressors Can.J.Fish. Aquat. Sci. 66: 1189-1198. Thousands of lakes around Sudbury, in northeastern Ontario, Canada, were badly damaged by acid deposition and many were also metal-contaminated. Large reductions in atmospheric sulphur and metal emissions have led to widespread chemical improvements in these lakes, and recovery has been documented for various biota. These findings were very important in establishing the necessity and value of sulphur emission controls during the international debates about the effects of acid deposition and the need for cleaner air. Studies of northeastern Ontario lakes are continuing to advance our understanding of chemical and biological recovery processes; however, that knowledge is still incomplete. It has become apparent that the recovery of lakes from acidification is closely linked with the responses to, and interactions with, other large-scale environmental stressors like climate change and calcium declines. Developing a better understanding of lake recovery processes and their future outcomes within such a multiple stressor context will be difficult. It will demand the merging of various approaches including monitoring, experimentation, paleolimnology and modelling, and will require effective collaboration between different research and monitoring sites and various agencies and institutions engaged in environmental science.

Keller, W., J. Heneberry, and B.A. Edwards. 2018. Recovery of acidified Sudbury, Ontario, Canada, lakes: a multi-decade synthesis and update. Environmental Reviews. Dx.doi.org/10.1139/er-2018-0018. The Sudbury region of northeastern Ontario, Canada, provides one of the world's best examples of the resilience of aquatic ecosystems after reductions in atmospheric contaminant deposition. Thousands of lakes around the Sudbury metal smelters were badly damaged by acid deposition. Lakes closest to the smelters were also contaminated by metal-particulates. However, large reductions in atmospheric SO_2 and metal emissions starting in the early 1970's have led to widespread chemical improvements in these lakes, and recovery has been observed for various aquatic biota. Studies of Sudbury area lakes are advancing our understanding of chemical and biological lake recovery; however, recovery is a complicated process and much remains to be learned. Biological recovery has often been slow to follow chemical recovery, and it has become apparent that the recovery of lakes from acidification is closely linked to interactions with other large-scale environmental stressors like climate change,

water browning, and Ca declines. Thus, in our multiple stressor world, recovery may not bring lakes back to their exact former state. However, with time, substantial natural biological recovery toward typical lake communities can be reasonably expected for most but not necessarily all biota. For organisms with limited dispersal ability, particularly fish, human assistance may be necessary to re-establish typical communities. In lakes where food webs have been severely altered, re-establishment of typical diverse fish communities may in fact be an important element aiding the recovery of other important components of aquatic ecosystems including zooplankton and benthic macroinvertebrates. In the lakes closest to the smelters, where historically watersheds as well as lakes were severely damaged, the recovery of aquatic systems will be closely linked to ongoing terrestrial recovery and rehabilitation, particularly through the benefits of increased inputs of terrestrially-derived organic matter. The dramatic lake recovery observed in the Sudbury area points to a brighter future for these lakes. However, continued monitoring will be needed to determine future changes and help guide the management and protection of Sudbury area lakes in this multiple-stressor age.

Khan, F.R., W. Keller, N.D. Yan, P.G. Welsh, C.M. Wood, and J.C. McGeer. 2011. Application of biotic ligand and toxic unit modeling approaches to predict improvement in species richness in smelter damaged lakes near Sudbury. Environ. Sci Technol. 46: 1641-1649. Using a 30-year record of biological and water chemistry data collected from seven lakes near smelters in Sudbury (Ontario, Canada) we examined the link between reductions of Cu, Ni, and Zn concentrations and zooplankton species richness. The toxicity of the metal mixtures was assessed using an additive Toxic Unit (TU) approach. Four TU models were developed based on total metal concentrations (TM-TU); free ion concentrations (FI-TU); acute LC50s calculated from the Biotic Ligand Model (BLM-TU); and chronic LC50s (acute LC50s adjusted by metal specific acute-to-chronic ratios, cBLM-TU). All models significantly correlated reductions in metal concentrations to increased zooplankton species richness over time ($p < 0.01$) with a rank based on r2 values of cBLM-TU > BLM-TU = FI-TU > TM-TU. Lake-wise comparisons within each model showed that the BLM-TU and cBLM-TU models provided the best description of recovery across all seven lakes. These two models were used to calculate thresholds for chemical and biological recovery using data from reference lakes in the same region. A threshold value of TU = 1 derived from the cBLM-TU provided the most accurate description of recovery. Overall, BLM-based TU models that integrate site-specific water chemistry-derived estimates of toxicity offer a useful predictor of biological recovery.

Labaj, A.L., J.B. Korosi, J. Kurek, A. Jeziorski, W. Keller, and J.P. Smol. 2016. Response of *Bosmina* size structure to the acidification and recovery of lakes near Sudbury, Canada. J. Limnol. 75(s2): 22-29. In response to biotic and abiotic cues, the cladoceran genus *Bosmina* can undergo changes in body size and appendage length and shape over successive generations. To improve our understanding of the environmental controls on *Bosmina* size structure, we used paleolimnological techniques to examine Bosmina size responses to the extreme acidification and metal contamination, and then subsequent chemical recovery, of lakes in the vicinity of mining and smelting operations near Sudbury, Canada. During the acidification period, *Bosmina* antennule and carapace length significantly increased in three of the five study lakes, while mucro length significantly decreased in four of the five lakes. However, despite the recent return to pre-impact pH levels, the size structure of the present-day *Bosmina* community still differs from the pre-impact size distributions. We suggest that the continued dominance of the food webs by small invertebrate predators (e.g., cyclopoid copepods) is responsible for the persistent changes to *Bosmina* size structure.

MacPhee, S., S. Arnott, and W. Keller. 2011. Lake thermal structure influences macroinvertebrate predation on crustacean zooplankton. J. Plank. Res. 33: 1586-1595. Changes in lake thermal structure, which are predicted with future climate warming, may alter predator–prey interactions if foraging rates or the spatial overlap of predators and prey depend on thermal conditions. Small Boreal Shield lakes are particularly responsive to weather-induced changes in thermal structure. They are often fishless, with macroinvertebrate predators regulating crustacean zooplankton communities. We performed a mesocosm experiment to examine how thermal structure (stratified and isothermal) influences the predation impact of surface-orienting *Buenoa macrotibialis* and vertically migrating *Chaoborus punctipennis* on crustacean zooplankton. We expected predation from surface-orienting predators to be greatest in stratified conditions when food resources are concentrated near the surface in proximity with predators. Surprisingly, surface predators had no effect on zooplankton abundance, and zooplankton avoided surface predators regardless of thermal habitat structure. In contrast, *Chaoborus* had a strong predation impact and reduced total zooplankton abundance, but only in isothermal conditions. We hypothesize that this predation effect was due to increased predator metabolism, foraging and ingestion rates when migrating through a thermally homogenous warm water column without access to cool bottom waters. These results demonstrate that changes in lake thermal structure may result in strong, unexpected consequences for predator–prey dynamics.

Palmer, M.E., Keller, W., and N.D. Yan. 2013. Gauging recovery of zooplankton from historical acid and metal contamination: the influence of temporal changes in restoration targets. J. Appl. Ecol. 50: 107-118. 1. Clearly defined restoration targets are necessary to judge the effectiveness of management actions in restoring damaged ecosystems. However, the identification of appropriate targets is difficult in a rapidly changing world. Historical reference conditions commonly provide recovery targets, but they may not be appropriate if present-day environments have shifted in response to regional or global drivers. Such shifts may need to be incorporated into restoration targets to avoid erroneous conclusions about the recovery of ecosystems damaged by localized stressors. No previous study has examined whether the selection of historical vs. present-day reference conditions alters judgments of the recovery of historically damaged ecosystems. 2. We examined 35-year trends in the zooplankton communities of four lakes polluted by smelter emissions in Sudbury, Ontario, Canada. Recovery was assessed by comparing the Sudbury lakes to both historical (1983–1984) and present-day (2004–2006) conditions in a set of minimally impacted reference lakes in south-central Ontario. 3. Sudbury zooplankton communities improved substantially over time when compared with both the historical and present-day recovery targets. However, recovery occurred later, and improvements differed quantitatively when judged against the present-day vs. historical targets. These differences were attributable to regional shifts in zooplankton communities that happened after the historical sampling period but were reflected in the present-day data. 4. Species richness in two Sudbury lakes met recovery targets and communities in all four lakes became more similar to those in the reference lakes. However, the continued absence of many daphniids, cyclopoids and large calanoids indicated that the lakes had not fully recovered and further monitoring is needed. 5. Synthesis and applications. Our results show that the choice of reference condition can alter recovery assessments. This finding emphasizes the importance of establishing

clearly defined restoration goals to ensure appropriate choice of reference conditions. Restoration is unlikely to be judged as successful if an historical reference point is used to guide management actions meant to restore an ecosystem to present-day regional conditions.

Shurin, J.B., M. Winder, R. Adrian, W. Keller, B. Matthews, A.M. Paterson, M. Paterson, B. Pinel-Alloul, J.A. Rusak, and N.D. Yan. 2010. Environmental stability and lake zooplankton diversity – contrasting effects of chemical and thermal variability. Ecology Letters 13: 453-463. Environmental variability in space and time is a primary mechanism allowing species that share resources to coexist. Fluctuating conditions are a double edged sword for diversity, either promoting coexistence through temporal niche partitioning or excluding species by stochastic extinctions. The net effect of environmental variation on diversity is largely unknown. We examined the association between zooplankton species richness in lakes and environmental variability on interannual, seasonal and shorter time scales, as well as long-term average conditions. We analyzed data on physical, chemical and biological limnology in 53 temperate zone lakes in North America and Europe sampled over a combined 1042 years. Large fluctuations in pH, phosphorus and dissolved organic carbon concentration on different time scales were associated with reduced zooplankton species richness. More species were found in lakes that showed greater temperature variation on all time scales. Environmental variability on different time scales showed similar or, in some cases, stronger associations with zooplankton species richness compared with long-term average conditions. Our results suggest that temporal fluctuations in the chemical environment tend to exclude zooplankton species while temperature variability promotes greater richness. The results indicate that anthropogenic increases in temporal variability of future climates may have profound effects on biodiversity.

Stockdale, A., E. Tipping, S. Lofts, J. Fott, Ø.A. Garmo, J. Hruska, B. Keller, S. Löfgren, S.C. Maberly, V. Majer, S.A. Nierzwicki-Bauer, G. Persson, A-K. Schartau, S. J. Thackeray, A. Valois, J. Vrba, B. Walseng and N. Yan. 2014. Metal and proton toxicity to lake zooplankton: application of a chemical speciation based modeling approach. Environ. Pollut. 186: 115-125. The WHAM-FTOX model quantifies the combined toxic effects of protons and metal cations towards aquatic organisms through the toxicity function (FTOX), a linear combination of the products of organism bound cation and a toxic potency coefficient for each cation. We describe the application of the model to predict an observable ecological field variable, species richness of pelagic lake crustacean zooplankton, studied with respect to either acidification or the impacts of metals from smelters. The fitted results give toxic potencies increasing in the order Hþ < Al < Cu < Zn < Ni. In general, observed species richness is lower than predicted, but in some instances agreement is close, and is rarely higher than predictions. The model predicts recovery in agreement with observations for three regions, namely Sudbury (Canada), Bohemian Forest (Czech Republic) and a subset of lakes across Norway, but fails to predict observed recovery from acidification in Adirondack lakes (USA).

Tropea, A.E., A.M. Paterson, W. Keller, and J.P. Smol. 2010. Sudbury sediments revisited: evaluating limnological recovery in a multiple stressor environment. Water Air Soil Pollut. 210: 317-333. Paleolimnological techniques were utilized to determine whether diatom and scaled chrysophyte assemblages in Daisy, Swan, and Tilton lakes (Sudbury, Ontario) have recovered toward their preimpact conditions as a result of reduced inputs of anthropogenic pollutants (SO_4^{2-} and metals) or whether other environmental stressors have affected recovery trajectories. In addition, geochemical analysis was used to track trends in sedimentary nickel and

copper concentrations through time. Preindustrial algal assemblages were primarily dominated by circumneutral to alkaline and pH-indifferent taxa. However, with the onset of open-pit roasting and smelting operations, there was a stratigraphic shift toward acid-tolerant species. With wide-scale smelter emission reductions commencing in the 1970s, scaled chrysophyte assemblages in Swan and Daisy lakes have started to show signs of biological recovery in ~1984 and ~1991, respectively. Although the scaled chrysophyte assemblage in Tilton Lake has not recovered toward the predisturbance assemblage, the decline in acidophilic taxa and increase in circumneutral taxa in recently deposited lake sediments indicate that the community is responding to increased lake water pH. Conversely, diatom assemblages within each of the study lakes have not begun to recover, despite well-documented chemical recovery. It is suspected that biological recovery in Sudbury area lakes may be impeded by other environmental stressors such as climate warming. Copper and nickel concentrations in lake sediments increased with the onset of mining activities and subsequently declined with emission controls. However, metal concentrations in lake sediments remain elevated compared to preindustrial concentrations. Together, biological and geochemical evidence demonstrates the clear environmental benefits associated with smelter emission controls.

Tropea, A.E., A.M. Paterson, W. Keller, and J.P. Smol. 2011. Diatoms as indicators of long-term nutrient enrichment in metal contaminated lakes from Sudbury, Ontario. Lake and Reserv. Mgmt. 27: 48-60. The majority of the limnological research in Sudbury, Ontario, has focused on the anthropogenic impacts of industrialemissions (SO_2 and metals), with the potential effects of cultural eutrophication largely being overlooked. However, the population of the City of Sudbury has grown with the prosperity of the mining sector, which poses a risk to the quality of freshwater resources. As with many environmental issues, there is often a lack of predisturbance data that can assist in gauging the full extent of environmental change. Therefore, paleolimnological approaches were used to track long-term biological changes in sedimentary diatom assemblages related to cultural eutrophication in 4 lakes from Sudbury. Diatom assemblages were primarily dominated by oligotrophic taxa prior to watershed development; however, with the onset of urban environmental stressors (e.g., septic systems, the application of lawn fertilizers and watershed development), there was a shift toward taxa that thrive in more productive systems. Diatom assemblages also seem to track an increase in lakewater pH through time, which is likely related to increased acid neutralizing capacity as a result of watershed disturbances, algal assimilation and bacterial reduction of NO_3, and increased base cation export from the watershed due to acidic deposition. Insight into predisturbance conditions of the lakes should help lake managers set realistic biological targets for restoration and may be used to help gauge the response of these systems to future mitigation efforts.

Valois, A., W. Keller, and C. Ramcharan. 2010. Abiotic and biotic processes in recovering lakes: the role of metal toxicity and fish predation as barriers to zooplankton recovery. Freshwat. Biol. 55: 2585-2597. 1. Recovery of acidified aquatic systems may be affected by both abiotic and biotic processes. However, the relative roles of these factors in regulating recovery may be difficult to determine. Lakes around the smelting complexes near Sudbury, Ontario, Canada, formerly affected by acidification and metal exploration, provide an excellent opportunity to examine the factors regulating the recovery of aquatic communities. 2. Substantial recovery of zooplankton communities has occurred in these lakes following declines in acidity and metal concentrations, although toxicity by residual metals still appears to limit survival for

many species. Metal bioavailability, not simply total metal concentrations, was very important in determining effects on zooplankton and was associated with a decrease in the relative abundance of cyclopoids and *Daphnia* spp., resulting in communities dominated by *Holopedium gibberum*.
3. As chemical habitat quality has improved and fish, initially yellow perch and later piscivores (e.g. smallmouth bass, walleye), have invaded, biotic effects on the zooplankton are also becoming apparent. Simple fish assemblages dominated by perch appear to limit the survival of some zooplankton species, particularly *Daphnia mendotae*.4. Both abiotic (residual metal contamination) and biotic (predation from planktivorous fish) processes have very important effects on zooplankton recovery. The re-establishment of the zooplankton in lakes recovering from stress will require both improvements in habitat quality and the restoration of aquatic food webs.

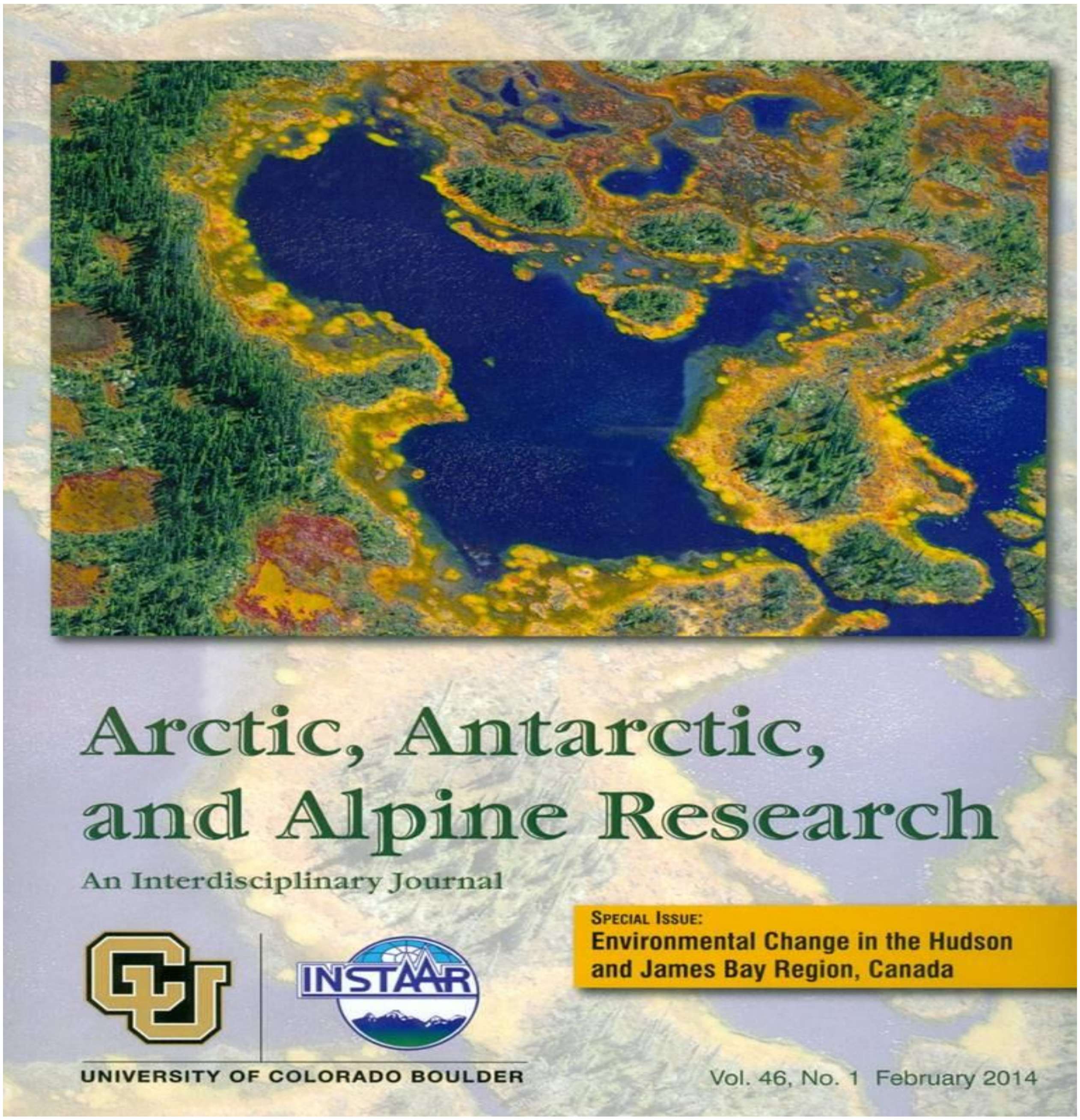
Valois, A.E., W. Keller, and C.W. Ramcharan. 2011. Recovery in a multiple stressor environment: using the reference condition approach to examine zooplankton community change along opposing gradients. J. Plank. Res. 33: 1417-1429. Lakes around the metal smelters of Sudbury, Ontario, Canada offer a unique opportunity to study recovery processes in stressed aquatic ecosystems. Following major reductions in the atmospheric deposition of sulphur and metal particulates, chemical and biological recovery have been observed in many lakes; however, the magnitudes and trajectories of biological recovery are variable. Crustacean zooplankton communities have proven to be particularly valuable in tracking the biological recovery patterns in Sudbury lakes. In a survey of 87 lakes, zooplankton community structure revealed strong gradients related to acidification, metal contamination, trophic status and depth. The study lakes could be divided into four groups related to these gradients: acidified, recovered, urban and reference lakes. Community composition in recovered (to $pH > 6.0$) lakes did not differ from reference lakes for copepods and cladocerans. In contrast, urban lakes subjected to the effects of watershed development as well as atmospheric metal contamination had either copepod or cladoceran communities that differed from reference conditions. Among the acidified lakes, most lakes with $pH < 5.5$ contained species poor copepod communities; however, substantial community recovery was evident in lakes with $pH < 5.5$. Our study illustrates the complexity of biological recovery processes in lakes subjected to multiple environmental stressors. Although substantial zooplankton community recovery clearly occurs as lakes recover from acidification, other stressors including metal contamination and eutrophication in urban environments may greatly affect recovery processes and outcomes.

Valois, A.E., C. Sarrazin-Delay, K. Somers, and W. Keller. 2016. Are bioassessments based on the reference condition approach affected by rapid approaches to sample collection and processing? J. Limnol. 75(2):392-402. Benthic invertebrates are used by a number of agencies worldwide as indicators for assessing stream health, which has resulted in the development of a variety of protocols for collecting and processing benthic samples. The large number of methods used means that calibration of data collection is not always possible, but if different methods produce similar estimates of community composition and metric values, then sharing of data can make bioassessments more efficient. This study explored the effect of two approaches to subsampling and sorting of benthic invertebrates on community composition, calculation of metrics, and assessment of stream health. We compared two commonly used sampling methods: a rapid approach, employing live, unaided sorting and a standard approach using microscope sorting of preserved samples, through a comparison of replicate samples collected from 61 streams. This study found that both methods resulted in similar estimates of community composition at a site, as determined by the Bray-Curtis similarity index. However, the live sorting methodology resulted in greater family richness and higher estimates of metrics that reflect large taxa (i.e., %EPT). Despite differences in a number of metrics, both methods performed equally well at identifying impairment in the test sites, with livesorting samples slightly more sensitive.

Webster, N.I., W. Keller, and C. Ramcharan. 2013. Restoration of zooplankton communities in industrially damaged lakes: influences of residual metal contamination and the recovery of fish communities. Restoration Ecology 21: 785-792. The Sudbury, Ontario, Canada area offers a unique opportunity to develop our understanding of biotic and abiotic lake recovery processes in industrially damaged natural systems. In recent decades, lakes in the Sudbury area have shown improvements in water quality due to decreases in sulfur (S) and metal emissions from area smelters, and reduced acid deposition from more distant sources. However, biological recovery is lagging and mechanisms controlling the lag are not yet clear. Our study examines the roles of two factors, residual metal contamination and altered fish predation, on zooplankton community recovery. Data collected over three decades on six study lakes were analyzed using redundancy analysis (RDA) and partial RDA's to assess historical and present relationships of water chemistry and fish abundance with zooplankton community recovery. Continuing metal toxicity appears to be the primary cause of the absence of some zooplankton species, particularly *Daphnia* spp. from metal-contaminated lakes. Conversely, once water quality is suitable and abundant planktivores reestablish, fish planktivory becomes a factor affecting *Daphnia* spp. establishment. The introduction of piscivores into these lakes may be necessary to facilitate the return of many *Daphnia* species. Further reductions in metal toxicity will also assist with the complete recovery of zooplankton communities. Studying natural systems over several decades allows us to better understand the intricate steps involved with recovery of industrially damaged lakes, and this knowledge will greatly benefit future restoration efforts in other industrially damaged systems.

Yan, N.D., J. Bailey, J. McGeer, M. Manca, W. Keller, M. Celis-Salgado, and J.M. Gunn. 2016. Arrive, survive, and thrive: essential stages in the re-colonization and recovery of zooplankton in urban lakes in Sudbury, Canada. J. Limnol. 75(s2): 4-14. The recovery of lakes from severe, historical acid and metal pollution requires that colonists of extirpated species arrive, survive and subsequently thrive. We employed 40 year records from weekly to monthly crustacean zooplankton samples from Middle and Clearwater lakes near Sudbury, Canada, to identify the main mechanistic bottlenecks in this recovery process. While both lakes now have circum-neutral pH, acidity decreased more rapidly in Middle Lake because of past liming interventions, while Clearwater Lake, being larger and supporting more housing, likely receives more zooplankton colonists than Middle Lake. Community richness increased much faster in Middle Lake than in Clearwater Lake, at 1.6 vs 0.9 species decade^{-1}, respectively. Richness has recovered in Middle Lake, when assessed against a target of 9-16 species collection^{-1} determined from regional reference lakes, but it has not yet recovered in Clearwater Lake. Species accumulation curves and a metric of annual persistence show that this difference is a product not of greater rates of species introduction into Middle Lake, but rather to their greater annual persistence once introduced. Greater annual persistence was associated with better habitat quality (i.e., lower acid and metal toxicity) in Middle Lake, particularly early in the record, and lower planktivore abundance, more recently. These results support a growing consensus that ecological recovery of zooplankton from acidification and metal pollution does not depend strongly on propagule introduction rates which are adequate, but rather on propagule persistence, in lake-rich, suburban landscapes such as those near Sudbury.

Appendix B. Cover and contents of AAAR Special issue.



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Special Issue on Environmental Change in the Hudson and James Bay Region, Canada
Edited by Wendel (Bill) Keller, Andrew M. Paterson, Kathleen M. Rühland, and Jules M. Blais

Appendix C. List of Far North Study Progress Reports.

Progress Report – Aquatic Ecosystem Studies in the Hawley Lake/Sutton River Area of the Hudson Bay Lowlands, 2009 – 2010. Cooperative Freshwater Ecology Unit, Laurentian University.

Second Progress Report – Aquatic Ecosystem Studies in the Hawley Lake / Sutton River Area of the Hudson Bay Lowlands, 2009 – 2012. Cooperative Freshwater Ecology Unit, Laurentian University.

Progress Report: River Studies in the Fort Severn Area, 2011-2013. Cooperative Freshwater Ecology Unit, Laurentian University.

Progress Report - Lake and Stream Surveys in Northwestern Ontario, 2012 and 2013. Cooperative Freshwater Ecology Unit, Laurentian University.

Reports are available on the Cooperative Freshwater Ecology (Laurentian University) Website
www.livingwithlakes.ca

Appendix D. List of graduate student projects supported

Bergeron, J.M. 2012. Urban and industrial drivers of phytoplankton communities in Sudbury, Ontario urban lakes. M. Sc. Laurentian University.

Brazeau, M. 2012. Historical deposition and microbial redox cycling of mercury in lake sediments from the Hudson Bay Lowlands, Ontario, Canada. M. Sc. University of Ottawa.

Dejong, R. 2017. Life history characteristics of lake whitefish (*Coregonus clupeaformis*), cisco (*Coregonus artedi*), and northern pike (*Esox lucius*) in rivers of the Hudson Bay Lowlands. M. Sc. University of Waterloo.

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