PERSPECTIVE / PERSPECTIVE

Limnology in northeastern Ontario: from acidification to multiple stressors[1]

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Abstract: 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 among different research and monitoring sites and various agencies and institutions engaged in environmental science.

Résumé : Des milliers de lacs des environs de Sudbury, dans le nord-est de l'Ontario, Canada, ont été lourdement endommagés par les dépôts acides et plusieurs ont été aussi contaminés par des métaux. Les réductions importantes des émissions atmosphériques de soufre et de métaux ont conduit à une amélioration générale de la chimie de ces lacs et on a démontré le rétablissement de divers organismes. Ces résultats ont été de grande importance pour établir la nécessité et l'importance du contrôle des émissions de soufre lors des débats internationaux sur les effets des dépôts acides et la nécessité d'air plus pur. Les études faites sur les lacs du nord-est de l'Ontario continuent à faire progresser notre compréhension des processus de rétablissement chimique et biologique; ces connaissances demeurent cependant encore incomplètes. Il est devenu évident que la récupération des lacs de l'acidification est reliée étroitement à leurs réactions aux autres sources de stress à grande échelle dans l'environnement, tels que le changement climatique et le déclin du calcium, ainsi qu'à leurs interactions avec ces sources. Il sera difficile d'obtenir une meilleure compréhension des processus de récupération des lacs et de leur destin futur dans un tel contexte de sources multiples de stress. Cela nécessitera la conjonction de plusieurs approches dont la surveillance continue, l'expérimentation, la paléolimnologie et la modélisation; il faudra aussi une coordination effective entre les divers sites de recherche et de surveillance, ainsi qu'une collaboration des différentes agences et institutions impliquées dans les sciences de l'environnement.

[Traduit par la Rédaction]

Introduction

During the 1980s, the acidification of lakes by acid deposition emerged as a major international concern (e.g., Cowling 1982), although acid rain effects on lakes had been identified much earlier (e.g., Oden 1968). In fact, the 1980s are sometimes referred to as the acid rain decade, since that was the period when scientific, public, and political recognition of the issue came to the forefront, and large efforts were mounted to begin to understand and address the problem.

Large-scale lake liming programs were initiated to combat acidification in some areas, notably in Scandinavia (Olem et al. 1991; Henrikson and Brodin 1995). In North America, lake liming was never adopted as a widespread management tool, although experiments were conducted to examine the feasibility of liming and determine the responses of aquatic biota to the neutralization of lake acidity (Porcella 1989; Keller et al. 1990*a*). Because of the large numbers and general inaccessibility of acidified lakes in North America (an

Received 6 January 2009. Accepted 22 May 2009. Published on the NRC Research Press Web site at cjfas.nrc.ca on 3 July 2009.
20971

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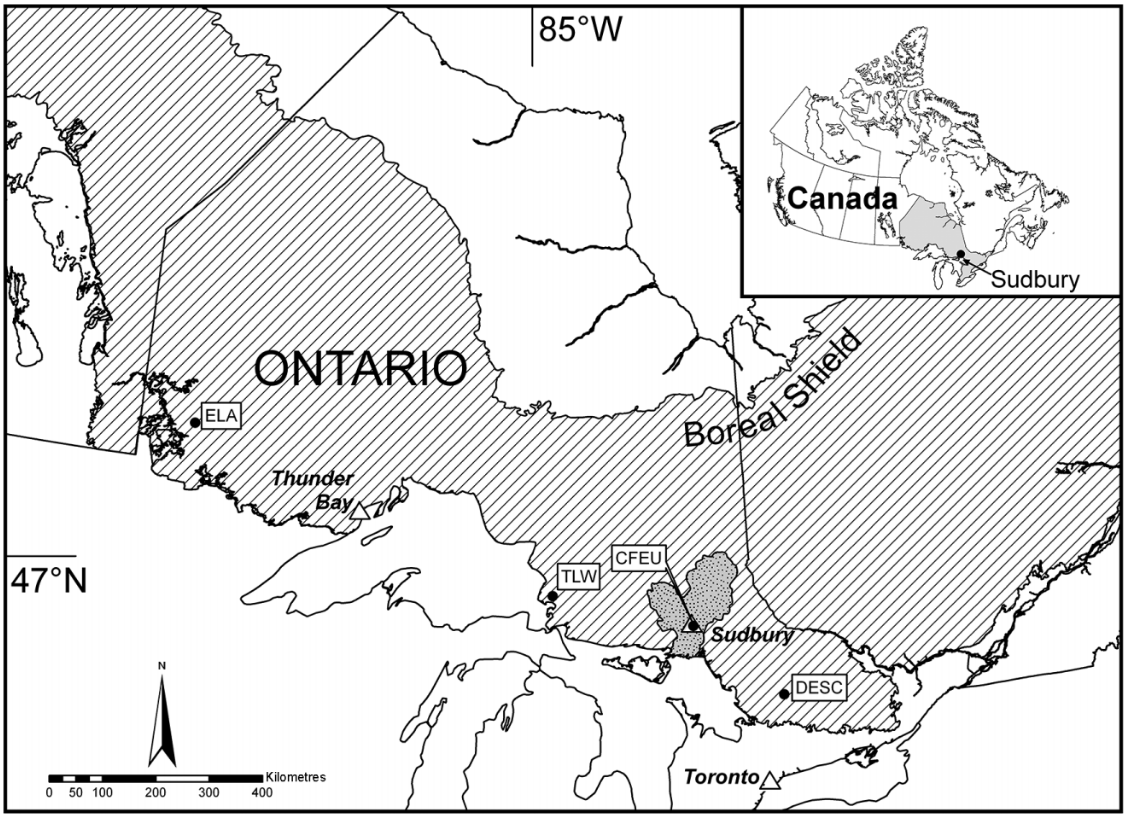
[1] This Perspective is based on the author's F.H. Rigler Lecture delivered at the annual meeting of the Society of Canadian Limnologists in Halifax, Nova Scotia, January 2008.

doi:10.1139/F09-080

Fig. 1. The location of Sudbury in the Boreal Shield Ecozone (diagonal shading), the historical lake damage zone around Sudbury (stippling), and locations of long-term aquatic research and monitoring sites in Ontario: DESC (Dorset Environmental Science Centre); CFEU (Cooperative Freshwater Ecology Unit; www.livingwithlakes.ca); TLW (Turkey Lakes Watershed; www.tlws.ca); ELA (Experimental Lakes Area; www.umanitoba.ca/institutes/fisheries/).



estimated 19 000 lakes in Ontario, Canada, alone; Neary et al. 1990) extensive liming was not considered to be logistically or economically feasible. Also, since liming only treats the symptoms and not the causes of the acid deposition problem, control programs to reduce acid emissions were given priority by government agencies in Canada and the USA.

Efforts to achieve sulphur emission controls were eventually successful. Under various agreements, both Canada and the USA substantially reduced sulphur dioxide emissions. Total North American emissions are now about 40% less than in 1980 (Jeffries et al. 2003). However, these large-scale emission reduction programs were in reality still just massive experiments, since the ultimate outcome for aquatic ecosystem recovery was far from certain.

The Sudbury area of northeastern Ontario, Canada, provides one of the best examples in the world of the ecological effects of sulphur emissions and their control and is the case study I focus on here. Sudbury (Fig. 1) is located roughly at the centre of the Boreal Shield, Canada's largest ecozone, which contains 22% of Canada's freshwater surface area (Urquizo et al. 2000). Typical of the Boreal Shield, lakes in northeastern Ontario are generally low in ionic strength, nutrient poor, and very sensitive to anthropogenic influences, including acid deposition. Over a century of sulphur and metal particulate emissions from metal smelters led to widespread terrestrial and aquatic damage near Sudbury (Gunn 1995). It is estimated that over 7000 lakes in a 17 000 km^2 area around Sudbury were acidified to the point that biological damage occurred (Neary et al. 1990; Fig. 1). Many of the lakes closest to the Sudbury smelters were also highly metal-contaminated (Keller and Pitblado 1986). However, large-scale emission reduction programs were implemented at the Sudbury smelters in the 1970s and 1990s, achieving overall reductions of ~90% in sulphur (Fig. 2*a*) and metal emissions in comparison with the peak emission levels in the 1960s (Potvin and Negusanti 1995; Keller et al. 2007).

Lake recovery

Have sulphur emission reduction programs worked? The answer is clearly yes, or perhaps more accurately, yes, they are working. The acid rain story is still far from over in Canada and in other areas of the world affected by excessive acid deposition. However, very encouraging evidence of chemical and biological recovery of lakes following reductions in acid deposition is emerging, particularly in the Sudbury area, where emission controls were implemented earlier than in most other acid-affected regions and where emission reductions were very large (Keller et al. 1999*a*).

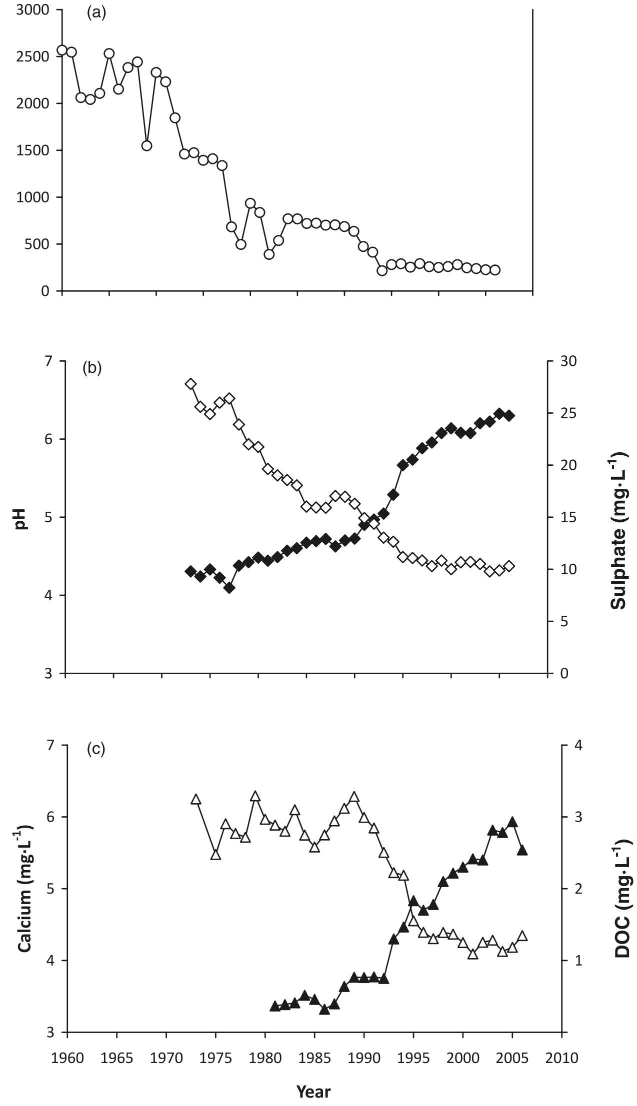
In northeastern Ontario, changes in lake chemistry, including increased pH and reduced sulphate and metal concentrations, followed the major reductions in emissions from the Sudbury area smelters in the 1970s and 1990s (Keller and Pitblado 1986; Keller et al. 1992*a*; Keller et al. 2007). While many of the thousands of historically damaged lakes are still acidic, the pH of some formerly acidified lakes has increased to >6.0 (Keller et al. 2007), a widely accepted threshold for effects on many acid-sensitive aquatic species (Keller et al. 1990*b*; Havens et al. 1993; Holt and Yan 2003). Changes in the sulphate concentrations and pH of Clearwater Lake near Sudbury over the last several decades provide a dramatic example of this chemical recovery from acidification (Fig. 2*b*), which has been accompanied by increases in dissolved organic carbon (DOC) concentrations and decreases in calcium concentrations (Fig. 2*c*). The metal concentrations in many lakes have declined greatly with time, including metals related to acid leaching of watersheds (e.g., aluminum, manganese) and smelter-related metals (e.g., copper, nickel). However, despite dramatic declines, concentrations of some smelter-related metals, including copper and nickel, remain elevated in lakes close (within ~30 km) to Sudbury (Keller et al. 1999*b*).

Following water quality improvements, evidence of biological recovery has emerged for many groups of aquatic organisms, including phytoplankton (Nicholls et al. 1992; Graham et al. 2007; Winter et al. 2008), zooplankton (Keller and Yan 1991; Locke et al. 1994; Keller et al. 2002), benthic invertebrates (Griffiths and Keller 1992; Snucins 2003), and fish (Gunn and Keller 1990) in Sudbury area lakes. However, it has also become apparent that biological recovery can be a very complex process that we cannot yet predict with confidence.

Improvements in biological communities may not simply follow improvements in chemical habitat quality. Altered food webs resulting from previous chemical damage can continue to control community structure even after suitable chemistry is restored. In lakes where planktivorous fish were eliminated by acidification, abundant populations of invertebrate predators usually controlled by fish predation, like *Chaoborus*, may control zooplankton communities (Yan et al. 1991; Keller et al. 2002). In cases where some fish have persisted or are becoming reestablished in recovering lakes, unusually simple fish communities such as abundant populations of the acid-tolerant yellow perch (*Perca flavescens*) may also retard zooplankton recovery (Yan et al. 2004). Such “biological resistance” (Keller and Yan 1998) can be a major factor affecting recovery patterns in lakes after the removal of chemical stress. As well, many other poorly understood factors can be expected to influence biological recovery processes, including various physical and biological constraints on the ability of different organisms to disperse and effectively colonize lakes (Keller and Yan 1998; Yan et al. 2003). Examples of complicating factors include possible suppression of colonists by established acid-tolerant zooplankton (Binks et al. 2005) and within-species adaptations in acid tolerance (Derry and Arnott 2007). The relative influence of different factors may be very lake specific.

Various conceptual models have been proposed as frameworks for the study of lake recovery processes (Keller and Yan 1998; Yan et al. 2003; Keller et al. 2007). However, we are far from being to able to realistically model biological recovery in a quantitative sense. Attempts to model biological recovery to date have had to rely only on direct relationships observed between species distributions and lake chemistry (e.g., Doka et al. 2003) without the ability to incorporate the many biological and physical factors affecting recovery processes. Our incomplete understanding of the roles of various physical and biological factors in affecting recovery processes in lakes of different types will need to be much improved to enhance predictive abilities for future biological recovery.

Fig. 2. (*a*) Annual sulphur dioxide emissions (kilotonnes (kt)) from Sudbury area smelters, (*b*) average annual pH (◆) and sulphate concentrations (◇), and (*c*) calcium (Δ) and dissolved organic carbon (DOC, ▲) concentrations for Clearwater Lake. Clearwater Lake, 13 km from Sudbury, has the longest continuous monitoring record of any acidified lake in the world.



Surprises

Many of the chemical changes in Sudbury area lakes that followed emission reductions, such as increased pH and reduced sulphate concentrations, were anticipated. Other important changes came as surprises, revealed by the monitoring programs implemented to study acidification.

Long-term monitoring data for northeastern Ontario lakes clearly demonstrated that the declines in lake water sulphate due to reductions in sulphur deposition were not simply balanced by declines in lake acidity, but also by substantial declines in base cation concentrations. Declines in calcium concentrations (Keller et al. 2001*a*) were of particular concern because of the implications for biota. Many important organisms have relatively high calcium requirements that can affect their distributions (Tessier and Horwitz 1990; Hessen et al. 1995), and calcium modifies the effects on biota of many other stressors, such as acidity and metals (Brown 1983), ultraviolet (UV) radiation (Hessen and Alstad Rukke 2000), and temperature (Ashforth and Yan 2008). Recent investigations have shown that calcium declines throughout much of Ontario are in fact a major threat to the biota of soft-water Precambrian Shield lakes, with effects already evident on *Daphnia*, a calcium-rich taxon very important in aquatic food webs (Jeziorski et al. 2008). Declines in base cations, including calcium, are widespread in regions recovering from acidification (Stoddard et al. 1999). These declines likely are a result of reduced current acid leaching rates and depletion of exchangeable base cation pools in lake watersheds by many years of elevated cation export. However, other factors, including base cation removal through forest harvesting and regrowth, may be very important regionally (Watmough and Dillon 2003)

Monitoring has also revealed other important surprises. Swan Lake, near Sudbury, like many other area lakes, was increasing in pH during the early to mid-1980s, when abruptly the pH declined from ~5.7 to ~4.5 in 1988. Acid deposition did not change during that time; the change that caused the re-acidification of Swan Lake was a change in the weather. During a prolonged drought (1986–1987), watershed soils and littoral sediments dried, and stored sulphur and metals were oxidized and later mobilized into the lake water when wet conditions resumed (Keller et al. 1992*a*). The re-acidification profoundly changed the nature of the lake in many ways, including increasing metal concentrations, transparency, UV-B penetration, and bottom temperatures (Yan et al. 1996*a*), with dramatic effects on phytoplankton and zooplankton communities (Arnott et al. 2001). Two decades ago, Swan Lake provided a very strong signal of some of the dramatic changes that might result from climate change in the future and helped reveal the potential importance of interactions between different large-scale stressors, including acidification, climate change, and ozone depletion.

Clearly, the usefulness of long-term studies extends far beyond the direct assessment of changes related to specific environmental control measures. The surprises revealed by monitoring can be crucial to identifying new threats that need to be addressed.

Land–water linkages

The above examples (widespread calcium decline and the re-acidification of Swan Lake) also illustrate very well something that we all know; lakes are intimately linked to their watersheds. Watershed processes, not just lake processes, will strongly affect lakes and lake recovery. If we remove important ecosystem components like calcium from the landscape through anthropogenic activities, we will have to wait a long time for weathering to replace them. Contaminants like sulphur and metals stored in saturated watershed soils, lake sediments, and wetlands are not gone, but can be mobilized, particularly through the effects of droughts, as has been observed near Sudbury (Keller et al. 1992*a*) and in south-central Ontario (Dillon et al. 1997; Adkinson et al. 2008). When we store contaminants on the landscape, we create a legacy that will persist for an unknown time period. It has been estimated that the effects of metals deposited in the watersheds of some of the most severely affected Sudbury lakes may continue for centuries (Nriagu et al. 1998).

Furthermore, watersheds around Sudbury that were denuded by very harsh historical logging and smelting processes do not provide the woody debris for nearshore cover or the typical amounts and types of organic material (Rasmussen et al. 2008) important to the functioning of littoral lake habitats (Roth et al. 2007; Helmus and Sass 2008). Forest regrowth on formerly denuded watersheds around Sudbury has already reduced wind speeds, which in turn has affected lake thermal structure by reducing wind-induced mixing (Tanentzap et al. 2008); however, reestablishment of healthy forests in such badly damaged landscapes is a very slow process that may sometimes require human intervention (Courtin 1995). As well, many of the major impacts of climate change on small Boreal Shield lakes will likely be through effects on watershed processes such as organic matter production and decomposition, with resultant effects on lake clarity and thermal structure (Keller et al. 2008) underscoring the need for a better understanding of key land–water linkages.

Additional process-oriented research is needed on the important linkages between lakes and their watersheds. Effective management of recovering lakes near Sudbury and elsewhere clearly needs to consider watershed management strategies, not simply lake management techniques.

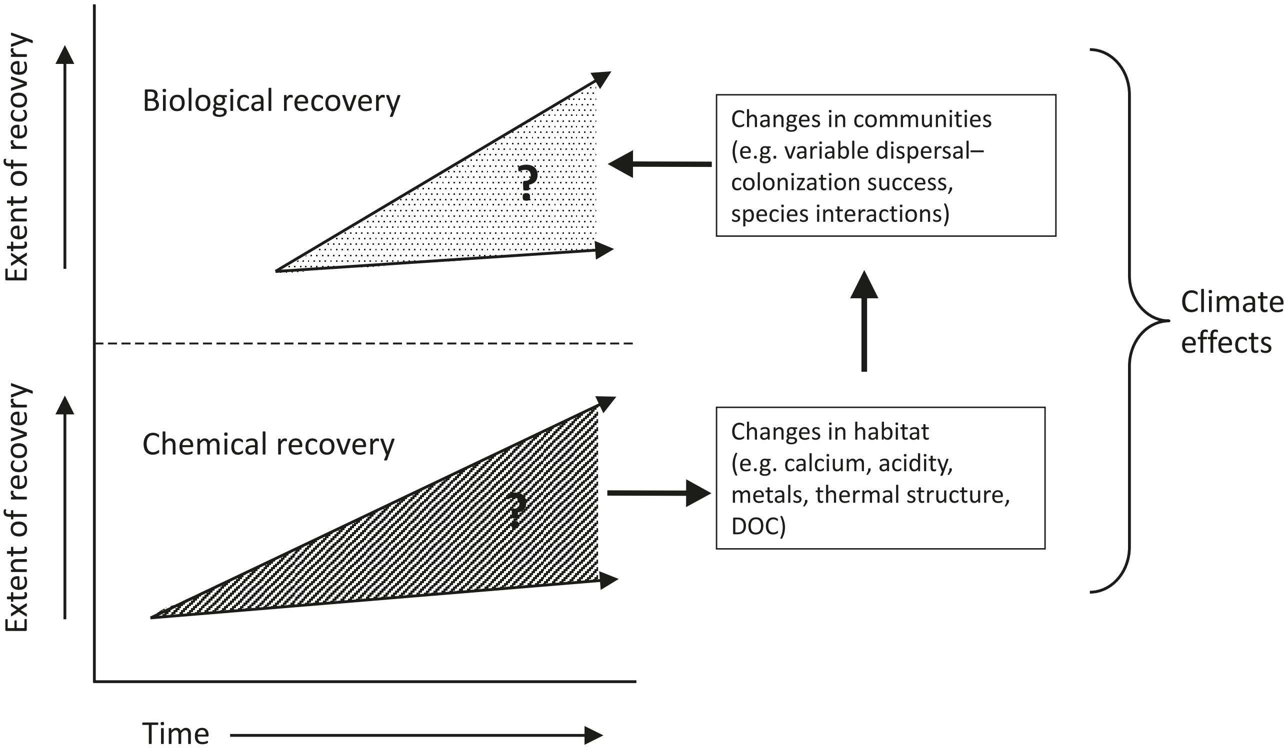
Multiple stressors, multiple approaches

We cannot address major environmental issues like acidification, or understand processes like recovery from acidification, in isolation from other large-scale stressors affecting aquatic ecosystems. Multiple interacting stressors are the reality in many of today's aquatic environments (Sala et al. 2000). Stressors such as acidification, base cation depletion, and invasive species — all under the overarching influence of a changing climate (Fig. 3) — will interact and affect lakes in ways we cannot yet predict with confidence (Schindler 2001; Keller 2007; Yan et al. 2008).

Understanding the effects of multiple stressors will be a complex undertaking and will demand assessment approaches that will also be complex and multidisciplinary. Using studies on lakes in northeastern Ontario as examples, it can be seen that much of the success of the acidification science programs that ultimately led to the widespread implementation of sulphur emission controls was due to the effective merging of results from different scientific approaches. These included temporal and spatial surveys, paleolimnological reconstructions, laboratory and field toxicity tests, and lake-scale experimental liming studies.

Keller et al. (1990*b*) combined results from large spatial surveys, laboratory toxicity studies, and a whole-lake neutralization experiment to demonstrate that widespread losses of the important, widely distributed crustacean zooplankter, *Daphnia mendotae*, had resulted from acidification and that these losses had occurred in lakes below a pH threshold of ~6.0. Such studies were instrumental in making the case for

Fig. 3. Conceptual diagram of some of the biotic and abiotic factors potentially affecting the extent of lake recovery from acidification.



the occurrence of extensive biological damage even at what were then considered comparatively moderate levels of lake acidity. This was a case that needed to be made internationally, not just to scientists but also to policy makers, to demonstrate the critical need for sulphur emission controls.

Paleolimnological reconstructions of lake acidity histories in many northeastern Ontario lakes (Dixit et al. 1992; Vinebrooke et al. 2002) revealed widespread acidification and showed that natural acidity could not account for the extensive occurrence of acid lakes observed in contemporary large-scale field surveys (Keller and Pitblado 1986). This effectively countered early arguments that lake acidification was predominantly a natural process (Krug et al. 1985). Temporal comparisons of monitoring data (Keller and Pitblado 1986; Keller et al. 1992*a*) demonstrated that chemical recovery would follow reductions in acid deposition, and paleoecological reconstructions (Dixit et al. 1989), observations from naturally recovering lakes (Gunn and Keller 1990; Keller and Yan 1991), and liming experiments (Keller et al. 1992*b*; Yan et al. 1996*b*) showed that biological recovery could be expected to follow chemical improvements in aquatic habitats. In combination, findings from these studies provided a compelling case for the ecological benefits of sulphur emission controls.

The examples given above show how findings from multiple approaches were combined to make a strong scientific case for acid rain damage and demonstrate the clear need for, and benefits of, sulphur emission controls. Knowledge generated through a variety of scientific strategies came together to clearly show that widespread lake acidification was directly due to excessive acid deposition, that lake acidification had caused extensive damage to lake communities, and that removal of acid stress would stimulate the chemical and biological recovery of aquatic ecosystems. The successful combination and dissemination of knowledge from investigations using different approaches and conducted at a variety of scales was essential in helping raise the scientific and public concern and ultimately stimulate the political will to address the acidification issue, although there were many concerns about the difficulty of effectively linking acid rain science and policy (e.g., Alm 2003). This scientific knowledge, based on many publications in the primary literature, was summarized in a number of comprehensive synthesis reports (e.g., RMCC 1990; NAPAP 1991) for communication to stakeholders and decision makers.

Multiple supporting lines of evidence make a very strong case, an important lesson learned from the acid rain issue, and something to remember as we confront other large-scale threats like climate change in a multiple-stressor world. We need to take on these environmental challenges together, not from individual research silos.

Reference conditions

Assessment of lake damage or recovery depends on having a measure of “normal” for comparison. Normal, however, may be difficult to define. Since predisturbance conditions are often not precisely known, normal must generally be defined by what is considered typical for regional lakes or lake types that are undisturbed or minimally disturbed. Lakes of interest for damage and recovery assessments are compared either visually or statistically with temporal (monitored through time) or spatial (synoptic surveys) reference lakes or better yet with both types of reference lakes (e.g., Keller et al. 1992*b*; Yan et al. 1996*b*). The dilemma of course lies in the availability and selection of appropriate reference lakes, similar in attributes to the test lake but not affected by the particular stressor(s) under investigation. Of necessity, groups of reference lakes are often used to define the normal range of variability (Kilgour et al. 1998) for minimally disturbed systems against which test systems can be compared. While this approach has proved to be very useful for recovery assessments, the true appropriateness of statistical definitions of normal for comparisons with specific test lakes is difficult to judge.

Paleolimnological reconstructions can tell us much about the actual prestress conditions for many chemical and biological attributes of lakes (Smol 2008). However, historical conditions in a given lake may not necessarily represent the appropriate reference condition for contemporary assessments. It was recognized decades ago that given changes to other parts of disturbed ecosystems, a return to predisturbance communities within a reasonable time frame may not always be possible even after a stress is removed (Cairns 1990).

Studies in Ontario over the last three decades have demonstrated broadscale temporal changes in many key attributes of lake habitats, including concentrations of calcium, DOC, and phosphorus (Jeziorski et al. 2008; Keller et al. 2008; Yan et al. 2008). Recovery targets determined from reference lakes that are affected by multiple large-scale regional or global influences will be moving targets, underscoring the need for maintaining up-to-date, appropriate, reference data sets as part of long-term lake monitoring programs, to allow accurate assessments of the effects of environmental stressors.

A better understanding of the specific linkages between important aquatic habitat attributes and aquatic communities under reference conditions and the development of improved methods for reference condition definition based on habitat characteristics (Bowman and Somers 2005; Linke et al. 2005; Whittier et al. 2007) would greatly help with the assessment of stressor effects and recovery from them. More standardized definitions of what we actually mean by reference conditions for particular situations would also aid in the effective application of reference condition approaches to aquatic assessments (Stoddard et al. 2006).

The value of monitoring

Monitoring programs have sometimes been unfairly criticized as being unnecessary and expensive. In reality, monitoring is essential, for among many other purposes, determining what has been accomplished through environmental management programs and what further actions are required. The costs of environmental monitoring programs in fact are usually a very small fraction, much less than 1%, of the implementation costs or expected benefits of pollution control programs (Lovett et al. 2007).

Wise lake management depends on understanding the aquatic resources we are trying to manage. Long-term monitoring is an essential element in developing and maintaining that knowledge. As outlined in the previous examples, long-term lake monitoring studies in northeastern Ontario have played an essential role in documenting the responses of acidified lakes to sulphur emission controls, findings that were important not just regionally, but nationally and internationally in the debates for cleaner air. These studies have also played an important role in identifying and raising awareness of new stressors like calcium depletion (Keller et al. 2001*a*) and drought effects (Yan et al. 1996*a*) that may fundamentally change the nature of many aquatic ecosystems in the future.

Lake monitoring studies in northeastern Ontario have, in their own right, made large contributions to understanding the effects of multiple stressors on Boreal Shield lakes. However, one of the greatest values of such regional studies comes when they are merged with the results of studies from other long-term research and monitoring sites to address environmental issues on much broader geographical scales: for example, the extent of calcium declines in Ontario (Jeziorski et al. 2008), chemical recovery from acidification in eastern Canada (Clair et al. 2007), future risk from UV-B penetration across Canada (Molot et al. 2004), or recent changes in DOC concentrations in the Northern Hemisphere (Monteith et al. 2007).

Each of the major long-term limnological research and monitoring sites in Ontario, for example (Fig. 1), including the lakes studied at the Dorset Environmental Science Centre (south-central Ontario), the Cooperative Freshwater Ecology Unit (northeastern Ontario), the Turkey Lakes Watershed (Algoma Region), and the Experimental Lakes Area (northwestern Ontario), captures a unique set of characteristics and differing ecological histories, reflecting different regions of the Boreal Shield. Collectively these sites span large gradients in various stressors such as acid deposition, climate, and extent of shoreline development (Keller et al. 2001*b*). Interagency cooperation in effect links these sites into a network, where through collaborations the ability of the whole to answer science questions becomes much greater than the sum of the parts. Such collaborations need to be encouraged and strengthened.

As already demonstrated, data from long-term monitoring sites are valuable for many purposes beyond simply allowing us to track how aquatic ecosystems have responded to stressors or the removal of stressors. Monitoring data form the baseline from which important ecological hypotheses can be constructed and from which realistic experiments can be designed to test them. For example, the previously mentioned drought-induced acidification event observed in the Swan Lake monitoring record stimulated in-lake experimentation investigating the role of drought and re-acidification on zooplankton emergence from sediments (Arnott and Yan 2002). Long-term monitoring data also allow determination of the direct and indirect relationships between important lake attributes and stressors, information that can help us use the past to forecast the future of our lakes through the construction of empirical and conceptual models.

Lakes, as low points in the local landscape, integrate the effects of changes in processes within their watersheds as well as changes in internal processes. Lakes and specific lake attributes can be extremely important indicators of environmental change, notably in a climate change context (Williamson et al. 2009), but also for changes related to many other environmental stressors. The usefulness of lakes and lake attributes for tracking and understanding environmental changes is, however, only as good as the quality and security of the monitoring programs that employ them. The maintenance of well designed and carefully operated long-term aquatic research and monitoring studies needs to be an integral part of environmental protection and management systems.

What now?

A decade ago, four research questions were identified for recovering lakes in the Sudbury area (Keller et al. 1999*b*). If we revisit these questions with a view to what has changed, it is evident that while our knowledge has advanced over the last decade (e.g., Keller et al. 2007), much more needs to be learned, and these questions still remain valuable as general guides for future research.

What are the interactive effects of lake acidification and other large-scale stressors such as climate change and UV-B irradiance?

While our understanding of multiple stressor effects is improving, it is still very incomplete. The potentially very severe implications of new stressors such as calcium depletion and invasive species introductions are now recognized, but how these and other large-scale stressors like climate change will interact to structure future lake environments is still poorly understood (Christensen et al. 2006). We do know that the indirect effects of stressors and stressor interactions, manifested through altered species interactions, will likely play a major role in structuring aquatic communities in the future. To advance our scientific understanding of lake recovery against an increasingly complex background, future studies will need to be conducted within a multiple stressor, multidisciplinary framework.

What will be the legacy of atmospheric contaminants such as sulphur and metals stored in the environment?

We have known for many years that the large amounts of pollutants, such as sulphur, stored in wetlands, lake sediments, and saturated watershed soils, can be mobilized with severe consequences for aquatic ecosystems. However, we still do not know the magnitude of these contaminant pools, the realistic time frames over which periodic mobilization might continue, and the probable long-term effects on aquatic communities. Such legacy issues will of course be closely tied to the overarching effects of changes in climate, again arguing strongly for future study in a multiple stressor context. Our recognition of important legacy issues in the Sudbury area and elsewhere now also includes not just the storage of contaminants but the removal of important elements like calcium from watersheds and the continuing effects of severe historical watershed disturbances (forest damage, soil erosion) on the physical and chemical characteristics of some recovering lakes.

Which organisms are capable of unassisted recovery and which are not?

Over the last decade, our understanding of biological recovery processes has advanced substantially, but we are still not in a position to clearly address this question for more than a few species. There are contrasting results showing widely varying patterns of recovery of aquatic communities in different studies. For example, crustacean zooplankton showed stronger evidence of recovery in species richness than in community composition in Whitepine Lake after pH 6.0 was reached (Keller et al. 2002), while in contrast, in a group of chemically recovered (pH > 6.0) Killarney area lakes, community composition but not species richness showed evidence of recovery (Holt and Yan 2003). Considering phytoplankton, while limited recovery has been observed in many Sudbury area lakes (Graham et al. 2007), complete community recovery appears to have occurred in Clearwater Lake (Winter et al. 2008), which is recovering from very severe acidification and metal contamination (Fig. 2*b*). Our understanding of the relative roles of different chemical, physical, and biological factors in controlling the recovery of lakes of different types is still very incomplete. In particular, the effects of biological interactions within the altered food webs in disturbed lakes and the effects of the various biological and physical factors controlling species dispersal and colonization success are very poorly known. Substantial additional research is required to develop more refined models to permit prediction of future biological recovery and identify additional management actions that may be needed to promote ecosystem recovery.

What are reasonable recovery targets?

There is recognition that the predisturbance condition may not necessarily be an appropriate target for aquatic ecosystem recovery. It is also apparent that the future reference conditions appropriate to gauge the recovery of acidified lakes may be a moving target because of changes in other large-scale stressors. This emphasizes the continuing need for developing and applying better methods for selecting and using aquatic reference data for assessments of both recovery and effects. It also argues strongly for the incorporation of reference data collection as an integral part of long-term monitoring programs designed to track the effects of various environmental stressors.

The future of recovering lakes in northeastern Ontario and in other regions of the world affected by excessive acid deposition is far from clear. Additional knowledge in the above research areas would contribute substantially to our ability to understand recovery processes and realistically forecast future lake recovery in a multiple stressor environment. The recovery story is becoming more complex as our understanding develops. Unravelling it further will demand effective collaboration between various agencies and institutions engaged in environmental science and management and will require the continuing synthesis of findings from various complementary scientific approaches.

Acknowledgements

This paper is dedicated to all my past and current colleagues in limnology, but especially those at the Cooperative Freshwater Ecology Unit. Through almost four fascinating decades of struggling to understand the complexities of lakes and streams, they have been my friends and extended family, my sampling companions in boats and bush planes, and my critics and advisors about all things scientific. Rolf Vinebrooke and Gary Sprules provided very helpful comments on the paper.

References

Adkinson, A., Watmough, S.A., and Dillon, P.J. 2008. Drought-induced metal release from a wetland at Plastic Lake, central Ontario. Can. J. Fish. Aquat. Sci. **65**: 834–845. doi:10.1139/F07-195.

Alm, L. 2003. Science and policy: the view from the world of scientists. J. Environ. Syst. **29**: 299–310. doi:10.2190/9VWL-UGD4-RJEN-8361.

Arnott, S.E., and Yan, N.D. 2002. The influence of drought and re-acidification on zooplankton emergence from resting stages. Ecol. Appl. **12**: 138–153. doi:10.1890/1051-0761(2002)012[0138:TIODAR]2.0.CO;2.

Arnott, S.E., Yan, N., Keller, W., and Nicholls, K. 2001. The influence of drought-induced acidification on the recovery of plankton in Swan Lake. Ecol. Appl. **11**: 747–763. doi:10.1890/1051-0761(2001)011[0747:TIODIA]2.0.CO;2.

Ashforth, D., and Yan, N.D. 2008. The interactive effects of Ca concentration and temperature on the survival of *Daphnia pulex* at high and low food concentration. Limnol. Oceanogr. **53**: 420–432.

Binks, J.A., Arnott, S.E., and Sprules, W.G. 2005. Local factors and colonist dispersal influence crustacean zooplankton recovery from cultural acidification. Ecol. Appl. **15**: 2025–2036. doi:10.1890/04-1726.

Bowman, M.F., and Somers, K.M. 2005. Considerations when using the reference condition approach for bioassessment of freshwater ecosystems. Water Qual. Res. J. Canada, **40**: 347–360.

Brown, D.J.A. 1983. Effect of calcium and aluminum concentration on the survival of brown trout (*Salmo trutta*) at low pH. Bull. Environ. Contam. Toxicol. **30**: 582–587. doi:10.1007/BF01610178. PMID:6860811.

Cairns, J., Jr., 1990. Lack of theoretical basis for predicting rate and pathways of recovery. Environ. Manage. **14**: 517–526. doi:10.1007/BF02394707.

Christensen, M.R., Graham, M.D., Vinebrooke, R.D., Findlay, D.L., Paterson, M.J., and Turner, M.A. 2006. Multiple anthropogenic stressors cause ecological surprises in boreal lakes. Glob. Change Biol. **12**: 2316–2322. doi:10.1111/j.1365-2486.2006.01257.x.

Clair, T.A., Aherne, J., Dennis, I.F., Gilliss, M., Couture, S., McNicol, D., Weeber, R., Dillon, P.J., Keller, W., Jeffries, D.S., Page, S., Timoffee, K., and Cosby, B.J. 2007. Past and future changes to acidified eastern Canadian lakes: a geochemical modeling approach. Appl. Geochem. **22**: 1189–1195. doi:10.1016/j.apgeochem.2007.03.010.

Courtin, G.M. 1995. Birch coppice woodland near the Sudbury smelters: dynamics of a forest monoculture. *In* Restoration and recovery of an industrial region. *Edited by* J.M. Gunn. Springer–Verlag, New York, Berlin, Heidelberg. pp. 233–245.

Cowling, E.B. 1982. An historical perspective on acid precipitation. *In* Acidic precipitation and fisheries impacts in eastern North America. *Edited by* R.E. Johnson. American Fisheries Society, Bethesda, Md. pp. 15–31.

Derry, A.M., and Arnott, S.E. 2007. Adaptive reversals in acid tolerance in copepods from lakes recovering from historical stress. Ecol. Appl. **17**: 1116–1126. doi:10.1890/06-1382. PMID:17555222.

Dillon, P.J., Molot, L.A., and Futter, M. 1997. The effect of El Niño-related drought on the recovery of acidified lakes. Environ. Monit. Assess. **46**: 105–111. doi:10.1023/A:1005740002952.

Dixit, S.S., Dixit, A.S., and Smol, J.P. 1989. Lake acidification recovery can be monitored using chrysophycean microfossils. Can. J. Fish. Aquat. Sci. **46**: 1309–1312. doi:10.1139/f89-168.

Dixit, S.S., Dixit, A.S., and Smol, J.P. 1992. Assessment of changes in lake water chemistry in Sudbury area lakes since pre-industrial times. Can. J. Fish. Aquat. Sci. **49**(Suppl. 1): 8–16. doi:10.1139/f92-295.

Doka, S.E., McNicol, D.K., Mallory, M.L., Wong, I., Minns, C.K., and Yan, N.D. 2003. Assessing potential for recovery of biotic richness and indicator species due to changes in acidic deposition and lake pH in five areas of southeastern Canada. Environ. Monit. Assess. **88**: 53–101. doi:10.1023/A:1025548518991. PMID:14570411.

Graham, M.D., Vinebrooke, R.D., Keller, W., Heneberry, J., Nicholls, K.H., and Findlay, D.L. 2007. Comparative responses of phytoplankton during chemical recovery in atmospherically and experimentally acidified lakes. J. Phycol. **43**: 908–923. doi:10.1111/j.1529-8817.2007.00398.x.

Griffiths, R.W., and Keller, W. 1992. Benthic macroinvertebrate changes in lakes near Sudbury, Ontario, following a reduction in acid emissions. Can. J. Fish. Aquat. Sci. **49**(Suppl. 1): 63–75.

Gunn, J.M. (*Editor*). 1995. Restoration and recovery of an industrial region. Springer–Verlag, New York, Berlin, Heidelberg.

Gunn, J.M., and Keller, W. 1990. Biological recovery of an acid lake after reductions in industrial emissions of sulphur. Nature (London), **345**: 431–433. doi:10.1038/345431a0.

Havens, K.E., Yan, N.D., and Keller, W. 1993. Lake acidification: effects on crustacean zooplankton populations. Environ. Sci. Technol. **27**: 1621–1624. doi:10.1021/es00045a019.

Helmus, M.R., and Sass, G.G. 2008. The rapid effects of a whole-lake reduction of coarse woody debris on fish and benthic macroinvertebrates. Freshw. Biol. **53**: 1423–1433. doi:10.1111/j.1365-2427.2008.01974.x.

Henrikson, L., and Brodin, Y.W. (*Editors*). 1995. Liming of acidified surface waters a Swedish synthesis. Springer–Verlag, New York, Berlin, Heidelberg.

Hessen, D.O., and Alstad Rukke, N. 2000. UV radiation and low calcium as mutual stressors for *Daphnia*. Limnol. Oceanogr. **45**: 1834–1838.

Hessen, D.O., Faafeng, B.A., and Andersen, T. 1995. Competition or niche segregation between *Holopedium* and *Daphnia*; empirical light on abiotic key parameters. Hydrobiologia, **307**: 253–261. doi:10.1007/BF00032019.

Holt, C., and Yan, N.D. 2003. Recovery of crustacean zooplankton communities from acidification: pH 6 as a recovery goal. Ambio, **32**: 203–207. PMID:12839196.

Jeffries, D.S., Brydges, T.G., Dillon, P.J., and Keller, W. 2003. Monitoring the results of Canada/U.S.A. acid rain control programs: some lake responses. Environ. Monit. Assess. **88**: 3–19. doi:10.1023/A:1025563400336. PMID:14570408.

Jeziorski, A., Yan, N., Paterson, A., DeSellas, A., Turner, M., Jeffries, D., Keller, W., Weeber, R., McNicol, D., Palmer, M., McIver, K., Arseneau, K., Ginn, B., Cumming, B., and Smol, J. 2008. The widespread threat of calcium decline in freshwaters. Science (Washington, D.C.), **322**: 1374–1377. doi:10.1126/science.1164949. PMID:19039134.

Keller, W. 2007. Implications of climate warming for Boreal Shield lakes: a review and synthesis. Environ. Rev. **15**: 99–112. doi:10.1139/A07-002.

Keller, W., and Pitblado, J.R. 1986. Water quality changes in Sudbury area lakes: a comparison of synoptic surveys in 1974–76 and 1981–83. Water Air Soil Pollut. **29**: 285–296. doi:10.1007/BF00158760.

Keller, W., and Yan, N.D. 1991. Recovery of crustacean zooplankton species richness in Sudbury area lakes following water quality improvements. Can. J. Fish. Aquat. Sci. **48**: 1635–1644. doi:10.1139/f91-194.

Keller, W., and Yan, N.D. 1998. Biological recovery from lake acidification: zooplankton communities as a model of patterns and processes. Restor. Ecol. **6**: 364–375. doi:10.1046/j.1526-100X.1998.06407.x.

Keller, W., Dodge, D.P., and Booth, G.M. 1990*a*. Experimental lake neutralization program: overview of neutralization studies in Ontario. Can. J. Fish. Aquat. Sci. **47**: 410–411. doi:10.1139/f90-043.

Keller, W., Yan, N.D., Holtze, K., and Pitblado, J.R. 1990*b*. Inferred effects of lake acidification on *Daphnia galeata mendotae*. Environ. Sci. Technol. **24**: 1259–1261. doi:10.1021/es00078a015.

Keller, W., Pitblado, J.R., and Carbone, J. 1992*a*. Chemical responses of acidic lakes in the Sudbury, Ontario, area to reduced smelter emissions, 1981–89. Can. J. Fish. Aquat. Sci. **49**(Suppl. 1): 25–32. doi:10.1139/f92-297.

Keller, W., Yan, N.D., Howell, T., Molot, L.A., and Taylor, W.D. 1992*b*. Changes in zooplankton during the experimental neutralization and early reacidification of Bowland Lake near Sudbury, Ontario. Can. J. Fish. Aquat. Sci. **49**(Suppl. 1): 52–62. doi:10.1139/f92-300.

Keller, W., Gunn, J., and Yan, N. 1999*a*. Acid rain: perspectives on lake recovery. J. Aquat. Ecosyst. Stress Recovery, **6**: 207–216. doi:10.1023/A:1009983318502.

Keller, W., Heneberry, J., and Gunn, J. 1999*b*. Effects of emission reductions from the Sudbury smelters on the recovery of acid- and metal-damaged lakes. J. Aquat. Ecosyst. Stress Recovery, **6**: 189–198. doi:10.1023/A:1009975116685.

Keller, W., Dixit, S.S., and Heneberry, J. 2001*a*. Calcium declines in northeastern Ontario lakes. Can. J. Fish. Aquat. Sci. **58**: 2011–2020. doi:10.1139/cjfas-58-10-2011.

Keller, W., Gunn, J.M., and Arnott, S.E. 2001*b*. Developing a framework for assessing the effects of climate change and other stressors on the waters of Ontario's Boreal Shield. Cooperative Freshwater Ecology Unit Report. Laurentian University, Sudbury, Ont.

Keller, W., Yan, N.D., Somers, K.M., and Heneberry, J.H. 2002. Crustacean zooplankton communities in lakes recovering from acidification. Can. J. Fish. Aquat. Sci. **59**: 726–735. doi:10.1139/f02-042.

Keller, W., Yan, N.D., Gunn, J.M., and Heneberry, J. 2007. Recovery of acidified lakes: lessons from Sudbury, Ontario, Canada. Water Air Soil Pollut. Focus, **7**: 317–322. doi:10.1007/s11267-006-9061-2.

Keller, W., Paterson, A., Somers, K., Dillon, P., Heneberry, J., and Ford, A. 2008. Relationships between dissolved organic carbon concentrations, weather, and acidification in small Boreal Shield lakes. Can. J. Fish. Aquat. Sci. **65**: 786–795. doi:10.1139/F07-193.

Kilgour, B.W., Somers, K.M., and Matthews, D.E. 1998. Using the normal range as a criterion for ecological significance in environmental monitoring and assessment. Ecoscience, **5**: 542–550.

Krug, E.C., Isaacson, P.J., and Frink, C.R. 1985. Appraisal of some current hypotheses describing acidification of watersheds. J. Air Pollut. Control Assoc. **35**: 109–114.

Linke, S., Norris, R.H., Faith, D.P., and Stockwell, D. 2005. ANNA: a new prediction method for bioassessment programs. Freshw. Biol. **50**: 147–158. doi:10.1111/j.1365-2427.2004.01286.x.

Locke, A., Sprules, W.G., Keller, W., and Pitblado, J.R. 1994. Zooplankton communities and water chemistry of Sudbury area lakes: changes related to pH recovery. Can. J. Fish. Aquat. Sci. **51**: 151–160. doi:10.1139/f94-017.

Lovett, G.M., Burns, D.A., Driscoll, C.T., Jenkins, J.C., Mitchell, M.J., Rustad, L., Shanley, J.B., Likens, G.E., and Hauber, R. 2007. Who needs environmental monitoring? Front. Ecol. Environ, **5**: 253–260. doi:10.1890/1540-9295(2007)5[253:WNEM]2.0.CO;2.

Molot, L.A., Keller, W., Leavitt, P.R., Robarts, R.D., Waiser, M.J., Arts, M., Clair, T.A., Pienitz, R., Yan, N.D., McNicol, D.K., Prairie, Y., Dillon, P.J., Macrae, M., Bello, R., Nordin, R., Curtis, P.J., Smol, J.P., and Douglas, M. 2004. Risk analysis of dissolved organic matter-mediated ultraviolet B exposure in Canadian inland waters. Can. J. Fish. Aquat. Sci. **61**: 2511–2521. doi:10.1139/f04-165.

Monteith, D.T., Stoddard, J.L., Evans, C.D., de Wit, H.A., Forsius, M., Hogasen, T., Wilander, A., Skjelkvale, B.L., Jeffries, D.S., Vuorenmaa, J., Keller, B., Kopacek, J., and Vesely, J. 2007. Dissolved organic carbon trends resulting from changes in atmospheric deposition chemistry. Nature (London), **450**: 537–541. doi:10.1038/nature06316. PMID:18033294.

NAPAP. 1991. Acidic deposition: state of science and technology — summary report of the U.S. National Acid Precipitation Assessment Program (NAPAP), Washington, D.C. ISBN 0-16-035925-2.

Neary, B.P., Dillon, P.J., Munro, J.R., and Clark, B.J. 1990. The acidification of Ontario lakes: an assessment of their sensitivity and current status with respect to biological damage. Ontario Ministry of the Environment, Dorset, Ont., Canada. Tech. Rep.

Nicholls, K.H., Nakamoto, L., and Keller, W. 1992. Phytoplankton of Sudbury area lakes (Ontario) and relationships with acidification status. Can. J. Fish. Aquat. Sci. **49**(Suppl. 1): 40–51. doi:10.1139/f92-299.

Nriagu, J.O., Wong, H.K.T., Lawson, G., and Daniel, P. 1998. Saturation of ecosystems with toxic metals in Sudbury basin, Ontario, Canada. Sci. Total Environ. **223**: 99–117. doi:10.1016/S0048-9697(98)00284-8. PMID:9861730.

Oden, S. 1968. The acidification of air and precipitation and its consequences in the natural environment. Swedish National Science Research Council, Stockholm, Sweden. Ecol. Committ. Bull. No. 1. [Translation Consultants Ltd., Arlington, Va.]

Olem, H., Schreiber, R.K., Brocksen, R.W., and Porcella, D.B. (*Editors*). 1991. International lake and watershed liming practices. The Terrene Institute, Washington, D.C. ISBN 1-880686-00-7.

Porcella, D.B. 1989. Lake acidification mitigation project (LAMP): an overview of an ecosystem perturbation experiment. Can. J. Fish. Aquat. Sci. **46**: 246–248. doi:10.1139/f89-034.

Potvin, R., and Negusanti, J. 1995. Declining industrial emissions, improving air quality, and reduced damage to vegetation. *In* Restoration and recovery of an industrial region. *Edited by* J.M. Gunn. Springer–Verlag, New York, Berlin, Heidelberg. pp. 51–62.

Rasmussen, J.B., Gunn, J.M., Sherwood, G.D., Iles, A., Gagnon, A., Campbell, P.G.C., and Hontela, A. 2008. Direct and indirect (foodweb mediated) effects of metal exposure on the growth of yellow perch (*Perca flavescens*): implications for ecological risk assessment. Hum. Ecol. Risk Assess. **14**: 317–350. doi:10.1080/10807030801935017.

RMCC. 1990. The 1990 Canadian long-range transport of air pollutants and acid deposition assessment report. Part 4. Aquatic effects. RMCC (Federal/Provincial Research and Monitoring Coordinating Committee), Ottawa, Ont.

Roth, B.M., Kaplan, I.C., Sass, G.G., Johnson, P.T., Marburg, A.E., Yannarell, A.C., Havlicek, T.D., Willis, T.V., Turner, M.G., and Carpenter, S.R. 2007. Linking terrestrial and aquatic systems: the role of woody habitat in lake food webs. Ecol. Model. **203**: 439–452. doi:10.1016/j.ecolmodel.2006.12.005.

Sala, O.E., Chapin, F.S., III, Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., and Wall, D.H. 2000. Global biodiversity scenarios for the year 2100. Science (Washington, D.C.), **287**: 1770–1774. doi:10.1126/science.287.5459.1770. PMID:10710299.

Schindler, D.W. 2001. The cumulative effects of climate warming and other human stresses on Canadian freshwaters in the new millennium. Can. J. Fish. Aquat. Sci. **58**: 18–29. doi:10.1139/cjfas-58-1-18.

Smol, J.P. 2008. Pollution of lakes and rivers: a paleoenvironmental perspective. 2nd edition. Blackwell Publishing, Malden, Mass., Oxford, UK, Victoria, Australia.

Snucins, E. 2003. Recolonization of acid-damaged lakes by the benthic invertebrates *Stenacron interpunctatum, Stenonema femoratum* and *Hyalella azteca.* Ambio, **32**: 225–229. PMID:12839200.

Stoddard, J.L., Jeffries, D.S., Lukewille, A., Clair, T.A., Dillon, P.J., Driscoll, C.T., Forsius, M., Johannessen, M., Kahl, J.S., Kellogg, J.H., Kemp, A., Mannio, J., Monteith, D.T., Murdoch, P.S., Patrick, S., Rebsdorf, A., Skjelkvale, B.L., Stainton, M.P., Traen, T., van Dam, H., Webster, K.E., Wieting, J., and Wilander, A. 1999. Regional trends in aquatic recovery from acidification in North America and Europe. Nature (London), **401**: 575–578. doi:10.1038/44114.

Stoddard, J.L., Larsen, D.P., Hawkins, C.P., Johnson, R.K., and Norris, R.H. 2006. Setting expectations for the ecological condition of streams: the concept of reference condition. Ecol. Appl. **16**: 1267–1276. doi:10.1890/1051-0761(2006)016[1267:SEFTEC]2.0.CO;2. PMID:16937796.

Tanentzap, A.J., Yan, N.D., Keller, W., Girard, R., Heneberry, J., Gunn, J.M., Hamilton, D.P., and Taylor, P.A. 2008. Cooling lakes while the world warms: effects of forest re-growth and increased dissolved organic matter on the thermal regime of a temperate urban lake. Limnol. Oceanogr. **53**: 404–410.

Tessier, A.J., and Horwitz, R.J. 1990. Influence of water chemistry on size structure of zooplankton assemblages. Can. J. Fish. Aquat. Sci. **47**: 1937–1943. doi:10.1139/f90-218.

Urquizo, N., Bastedo, J., Brydges, T., and Shear, H. 2000. Ecological assessment of the Boreal Shield ecozone. Environment Canada, Ottawa, Ont. ISBN-662-28679-0.

Vinebrooke, R.D., Dixit, S.S., Graham, M.D., Gunn, J.M., Chen, Y.-W., and Belzile, N. 2002. Whole-lake algal responses to a century of acidic industrial deposition on the Canadian Shield. Can. J. Fish. Aquat. Sci. **59**: 483–493. doi:10.1139/f02-025.

Watmough, S.A., and Dillon, P.J. 2003. Calcium losses from a forested catchment in south-central Ontario, Canada. Environ. Sci. Technol. **37**: 3085–3089. doi:10.1021/es034034t. PMID:12901654.

Whittier, T.R., Stoddard, J.L., Larsen, D.P., and Herlihy, A.T. 2007. Selecting reference sites for stream biological assessments: best professional judgement or objective criteria. J. N. Am. Benthol. Soc. **26**: 349–360. doi:10.1899/0887-3593(2007)26[349:SRSFSB]2.0.CO;2.

Williamson, C.E., Saros, J.E., and Schindler, D.W. 2009. Sentinels of change. Science (Washington, D.C.), **323**: 887–888. doi:10.1126/science.1169443. PMID:19213905.

Winter, J.G., Keller, W., Paterson, A.M., and Yan, N.D. 2008. Three decades of recovery of the phytoplankton community in Clearwater Lake (Sudbury, Canada) from acid and metal contamination. Verh. Internat. Verein. Limnol. **30**(Part 2): 247–252.

Yan, N.D., Keller, W., MacIsaac, H.J., and McEachern, L.J. 1991. Regulation of zooplankton community structure of an acidified lake by *Chaoborus.* Ecol. Appl. **1**: 52–65. doi:10.2307/1941847.

Yan, N.D., Keller, W., Scully, N.M., Lean, D.R.S., and Dillon, P.J. 1996*a*. Increased UV-B penetration in a lake owing to drought-induced acidification. Nature (London), **381**: 141–143. doi:10.1038/381141a0.

Yan, N.D., Keller, W., Somers, K.M., Pawson, T.W., and Girard, R. 1996*b*. Recovery of crustacean zooplankton communities from acid and metal contamination: comparing manipulated and reference lakes. Can. J. Fish. Aquat. Sci. **53**: 1301–1327. doi:10.1139/cjfas-53-6-1301.

Yan, N.D., Leung, B., Keller, W., Arnott, S.E., Gunn, J.M., and Raddum, G. 2003. Developing conceptual ecological frameworks for the recovery of aquatic biota from acidification. Ambio, **32**: 165–169. PMID:12839190.

Yan, N.D., Girard, R., Heneberry, J., Keller, W., Gunn, J., and Dillon, P.J. 2004. Recovery of copepod, but not cladoceran, zooplankton from severe and chronic effects of multiple stressors. Ecol. Lett. **7**: 452–460. doi:10.1111/j.1461-0248.2004.00599.x.

Yan, N.D., Somers, K.M., Girard, R.E., Paterson, A.M., Keller, B., Ramcharan, C.W., Rusak, J.R., Ingram, R., Morgan, G.E., and Gunn, J.M. 2008. Long-term trends in zooplankton of Dorset, Ontario, lakes: the probable interactive effects of changes in pH, total phosphorus, dissolved organic carbon, and predators. Can. J. Fish. Aquat. Sci. **65**: 862–877. doi:10.1139/F07-197.