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Recovery of acidified Sudbury, Ontario, Canada, lakes: a multi-decade synthesis and update

W. (Bill) Keller, Jocelyne Heneberry, and Brie A. Edwards

Abstract: 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 SO₂ and metal emissions starting in the early 1970s 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 and Ca declines. Thus, in our multiple-stressor world, recovery may not bring individual 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.

Key words: acidification, lakes, biota, recovery, Sudbury.

Résumé : La région de Sudbury au nord-est de l'Ontario, Canada, fournit un des meilleurs exemples au monde de la résistance des écosystèmes aquatiques à la suite de réductions de dépôt de contaminants atmosphériques. Des milliers de lacs autour des fonderies de Sudbury ont été sérieusement endommagés par le dépôt d'acides. Les lacs les plus proches des fonderies ont aussi été contaminés par des matières particulaires métalliques. Cependant, les grandes réductions des émissions de SO₂ et métalliques atmosphériques ayant commencé au début des années 1970 ont donné lieu à d'importantes améliorations chimiques dans ces lacs et la récupération a été observée au niveau de divers biotes aquatiques. Les études au sujet des lacs de la région de Sudbury font progresser notre compréhension de la récupération chimique et biologique des lacs; cependant, la récupération est un processus complexe et il nous reste beaucoup à apprendre. La récupération biologique a souvent tardé à suivre la récupération chimique et il est devenu apparent que la récupération des lacs à la suite des effets d'acidification soit étroitement liée aux interactions avec d'autres facteurs agressifs agissant à grande échelle comme le changement climatique et les baisses de Ca. Ainsi, en ce monde de facteurs agressifs multiples, la récupération ne peut pas rétablir exactement les lacs individuellement à leur ancien état. Cependant, avec le temps, on peut raisonnablement s'attendre à une importante récupération biologique naturelle rétablissant les communautés de lac typiques pour la plupart, mais pas nécessairement tout le biote. Pour les organismes avec un pouvoir de dispersion limité, particulièrement les poissons, l'intervention humaine peut être nécessaire afin de rétablir les communautés typiques. Dans les lacs où les réseaux alimentaires ont été sévèrement changés, le rétablissement de communautés typiques composées de différents poissons peut en fait être un élément important aidant à la récupération d'autres composants importants d'écosystèmes aquatiques y compris le zooplancton et les macroinvertébrés benthiques. Dans les lacs plus près des fonderies, où historiquement les lignes de partage des eaux aussi bien que les lacs ont été sévèrement endommagées, la récupération des systèmes aquatiques sera étroitement liée au rétablissement et à la remise en état terrestre en cours, particulièrement par les avantages des apports accrus de matière organique issue de la terre. La dramatique récupération des lacs observée dans la région de Sudbury présage un avenir plus brillant pour ces lacs. Cependant, la surveillance continue sera nécessaire afin de déterminer les changements futurs et pour aider à guider la gestion de la protection de lacs de la région de Sudbury en cette ère de facteurs agressifs multiples. [Traduit par la Rédaction]

Mots-clés : acidification, lacs, biote, récupération, Sudbury.

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Introduction

The mining and smelting of metals in the Sudbury, Ontario, Canada, area began in the late 1800s (Winterhalder 1995a), and over time the Sudbury smelters became one of the world's largest sources of sulphur dioxide (SO₂) emissions, releasing \sim 2500 kilotonnes per year in the 1960s. As well, the smelters emitted large quantities of metal (particularly Ni and Cu) particulates. The acidification of surface waters in northeastern Ontario near the Sudbury, Ontario, metal-smelting complex was first identified in the 1960s (Gorham and Gordon 1960; OWRC 1970) and by the mid-1970s it was known that lake acidification extended for a considerable distance from the Sudbury smelters (Beamish and Harvey 1972; Beamish 1974; Conroy et al. 1974, 1976; Beamish et al. 1975; Conroy and Keller 1976). By the mid-1970s, aquatic science programmes, largely led by the Ontario Ministry of the Environment (now the Ontario Ministry of Environment, Conservation and Parks), were in place to assess the extent and nature of aquatic acidification damage in northeastern Ontario (Conroy et al. 1976; Dillon et al. 1979); these programmes expanded during the 1980s.

Based on large-scale chemistry surveys conducted in the 1980s, it was estimated that over 7000 lakes in a 17 000 km² area had been acidified to pH <6.0 by the Sudbury smelter emissions (Neary et al. 1990). In the lakes closest to Sudbury, severe metal contamination (especially Cu and Ni) of lake waters (Conroy et al. 1976, 1978) and sediments (Semkin and Kramer 1976) had accompanied acidification. As studies progressed, it became apparent that widespread acidification damage had occurred to many biological components of aquatic ecosystems including fish (Keller 1978; Matuszek et al. 1992), benthic invertebrates (Conroy et al. 1976; Roff and Kwiatkowski 1977; Stephenson and Mackie 1986), zooplankton (Sprules 1975, 1977; Roff and Kwiatkowski 1977; Yan and Strus 1980; Keller and Pitblado 1984; Yan and Geiling 1985; Yan et al. 1988; MacIsaac et al. 1987), benthic filamentous algae (Keller et al. 1980; Vandermeulen et al. 1993), and phytoplankton (Conroy et al. 1976; Kwiatkowski and Roff 1976; Yan and Stokes 1978; Yan 1979; Nicholls et al. 1992). This biological damage, at various aquatic trophic levels, included the loss of acid-sensitive species and reduced community richness. However, along with the documentation of large-scale aquatic damage came the realization that lakes were already showing increases in pH and reductions in Cu and Ni concentrations in the 1980s (Hutchinson and Havas 1986; Keller and Pitblado 1986) in response to large reductions in SO₂ and metal emissions at the Sudbury smelters in the early 1970s as well as declines in overall North American sulphur emissions. The focus of aquatic studies in the Sudbury area began to change from damage assessment to investigating patterns of chemical and biological recovery. Additional emission reduction programmes in the late 1970s and early 1990s, along with the earlier cuts, achieved >90% reductions from previous peak levels of SO₂ (see for example fig. 2 in Keller 2009) and metal emissions, gave reason for guarded optimism for the future of northeastern Ontario lakes. Expectations for ecosystem recovery were positive; however, the actual knowledge of chemical and biological recovery processes was limited, and ongoing study was essential to track and understand long-term recovery patterns. Although much has been learned, many uncertainties remain.

This paper summarizes findings from Sudbury-area lake studies over the last four and a half decades. We document the current understanding of chemical and biological lake recovery in the Sudbury area. We also describe some of the complexities of assessing recovery in light of the known interactions with other important stressors, such as climate change and Ca declines.

Sudbury lakes

There is no "typical" Sudbury lake (Keller 1992). Lakes affected by the Sudbury smelter emissions fall along a continuum, from very remote, dilute, oligotrophic systems in highly acid-sensitive terrain distant from Sudbury to urban lakes close to the smelters and subjected to urban stressors such as nutrient and road salt inputs as well as atmospheric metal and acid deposition. This diversity of Sudbury lakes greatly amplifies the broad, international value of the Sudbury lake-monitoring programmes. Relatively pristine lakes distant from the smelters are similar to the dilute, acid-sensitive lakes that have typically been affected by long-range acid deposition in other areas of North America and Europe (Garmo et al. 2014) offering valuable comparisons for other regions. Because of these similarities, Norwegian scientists visited some of these lakes in the 1990s to develop and test methods of assessing lake recovery in anticipation of impending benefits from European sulphur emission controls (Gunn and Sandøy 2003). The more urbanized Sudbury lakes offer opportunities to better understand the aquatic effects of interacting multiple stressors in heavily developed landscapes (Gunn and Keller 1995; Valois et al. 2011). The lakes closest to the Subury smelters that were historically highly acidic and metal-contaminated offer valuable comparisons to other lake regions directly affected by metal smelters in other areas of Canada (Alpay et al. 2006; Jeziorski et al. 2013), the world (Moiseenko 1994), and lakes affected by other industrial sources of acid and metal contamination (Manca et al. 2016).

The long-term Sudbury lake-monitoring programmes have been conducted at two temporal scales. "Intensive" monitoring lakes were sampled for water chemistry and plankton at least monthly during the ice-free season. Regular sampling on some lakes started as early as 1973. In fact, one of the key Intensive monitoring lakes, Clearwater, has the longest continuous monitoring record of any acid lake in the world, to our knowledge. Additional Intensive lakes were added to the programme during the 1980s and 1990s to better cover the range of lake types affected by the Sudbury emissions. A few of the Intensive lakes (Fig. 1) were experimentally limed in the 1970s (Lohi, Middle, Hannah) or the 1990s (Whirligig, Little Whitepine). "Extensive" monitoring lakes were sampled only once per summer, primarily for water chemistry with periodic plankton sampling. The focus of the Extensive programme was to document the spatial extent of effects on Sudbury-area lakes, and determine temporal changes on a broad scale. The initial Extensive survey was conducted on 209 lakes during 1974-1976 (Conroy et al. 1978). During 1981-1983 these lakes were again sampled (Pitblado and Keller 1984) and additional lakes were surveyed (n = 250). Since 1981, a subset of acidic lakes, including the 42 lakes considered here, has been sampled annually (Table 1; Fig. 1). The analyses of long-term chemistry patterns presented here (Fig. 2) are based on the Extensive monitoring lakes (time series for pH, SO₄, Ca, and dissolved organic carbon (DOC) are presented in Figures A1 to A4 of Appendix A); however, changes in many of the Intensive monitoring lakes and other Sudbury-area lakes are described and discussed in the text.

Chemical and physical changes with recovery

Acidity and sulphate

Since the initial documentation of damage, there has been dramatic chemical recovery of acidified lakes near Sudbury, resulting from smelter emission reductions (e.g., Dillon et al. 1986; Hutchinson and Havas 1986; Keller and Pitblado 1986; Keller et al. 1986, 1992*a*, 1999*a*, 1999*b*, 2001*a*; Woodfine and Havas 1995). Changes included the expected declines in acidity and SO₄ concentrations (Figs. 2*a*, 2*b*). Although there are still many acidified lakes around Sudbury and elsewhere in Ontario (Jeffries et al. 2003), changes in the acidity of Sudbury lakes have been dramatic (Fig. 2*a*).

Changes in lake pH (and other chemical parameters discussed in subsequent sections) over the monitoring record were examined using linear mixed-effect models (LMM). Models were fit using the lme4 package (version 3.4.4, Bates et al. 2017) in the R statistical environment (R 3.1.3, https://www.r-project.org/), and **Fig. 1.** Locations of key Sudbury-area lakes monitored by the Ontario Ministry of the Environment, Conservation and Parks. "Extensive" monitoring lakes are sampled once annually, in summer, for chemistry and in some years for zooplankton. "Intensive" monitoring lakes are sampled at least monthly during the ice-free season for chemistry, phytoplankton, zooplankton, and oxygen and thermal structure. Long-term chemistry trend data presented in this paper are primarily from the Extensive monitoring lakes; however, chemical and biological changes in various Intensive monitoring lakes are described in the text.



Name	Abbreviation
Annie	Annie
Aurora Whitepine	Aur. Wh.
Bell	Bell
Bluesucker	Blues.
Bob	Bob
Chiniguchi	Chini.
Clearwater	Clearw.
Crooked	Crook.
David	David
Donald	Don.
Dougherty	Dough.
Florence	Flor.
Fraleck	Fral.
Frederick	Fred.
George	George
Gullrock	Gullr.
Jim Edwards	J.Ed.
Johnnie	John.
Killarney	Kill.
Klock	Klock
Landers	Land.
Laundrie	Laund.
Mahzenazing	Mahz.
Marjorie	Marj.
Matagamasi	Matag.
Nellie	Nell.
O.S.A.	O.S.A.
Pilgrim	Pilgr.
Reef	Reef
Ruth Roy	Ru.Ro.
Sans Chambre	Sa.Ch.
Seagram	Seagr.
Silvester	Silvest.
Sunnywater	Sunnyw.
Telfer	Telf.
Tillie	Till.
Tilton	Tilt.
Tyson	Tyson
Wabun	Wabun
Wavy	Wavy
White Oak	Wh.Öak
Wolf	Wolf

the structure of each LMM was identical for all parameters: with change over time (monitoring years 1–35) as a random effect and grouped by lake. The significance of lake-specific changes was assessed by deriving the 95% confidence intervals of their lake specific slope parameters. Additional details are provided in Fig. 2. Of the 42 Extensive monitoring lakes considered here, all had overall pH increases since 1981. In 1981, all these lakes had pH < 6.0 a level below which toxicity occurs to sensitive aquatic biota (Keller et al. 1990*a*; Havens et al. 1993; Holt and Yan 2003) and 26 (62%) had pH < 5.0. By 2015, none of the lakes had pH < 5.0 and 24 (57%) had pH > 6.0.

Surprisingly, some of the most dramatic declines in acidity have been observed in severely damaged urban lakes close to the Sudbury smelters, such as Clearwater and Crooked lakes (Figs. 1, 2*a*). The rapid recovery of such sulphur and metal-rich lakes is likely related to alkalinity generation from microbial reduction of the abundant sulphur and metals (White et al. 1997). Such alkalinity generation in urban lakes may be enhanced by nutrient inputs from shoreline development (Keller et al. 1999c); however, dramatic declines in acidity have also been observed in undeveloped lakes (e.g., Daisy Lake, Fig. 1). The Sudbury-area lakes that have shown the least increases in pH include headwater lakes located on weathering-resistant, soil-poor, quartzite ridges up to \sim 50 km southwest and \sim 110 km north of Sudbury, such as Nellie and Sunnywater lakes, respectively (Figs. 1, 2*a*). In addition to being located in highly acid-sensitive terrain, these deep lakes with comparatively small watersheds have water retention times of several decades. Thus, a slow response to reductions in sulphur deposition is not surprising given the important influence of flushing time on lake response (Arnott et al. 2003; Larssen et al. 2003).

While water quality issues continue, the spatial extent of the Sudbury influence on lakes is now only a fraction of what it was in the past. All Sudbury-area Extensive monitoring lakes have shown declines in SO₄ concentrations since 1981 (Fig. 2b). In the mid-1970s elevated lakewater SO₄ concentrations (>10 mg L⁻¹) were detectable to ~140 km from Sudbury (Conroy et al. 1978). Such elevated SO₄ concentrations now only occur in a few lakes very close (<10 km) to the Sudbury smelters (Fig. 3a), although concentrations over 5 mg L⁻¹ extend to ~50 km, and lakewater SO₄ concentrations out to ~90 km from Sudbury still sometimes slightly exceed concentrations in lakes 250 km to the southeast, near Dorset, Ontario (Yan et al. 2008*a*), that reflect regional background levels as affected by long range atmospheric transport (Fig. 3*a*).

Metals

Although lake water metal (Cu, Ni) concentrations have also declined greatly in Sudbury-area lakes, residual metal contamination in water and sediments persists in the lakes closest to Sudbury, and will likely continue for many years (Nriagu et al. 1998; Keller et al. 1999a). Some of the lakes close to Sudbury are also affected by urban stresses such as road salting and nutrient inputs from shoreline development (Gunn and Keller 1995; Pearson et al. 2002; Tropea et al. 2011), affecting metal toxicity and complicating patterns of recovery (Celis-Salgado et al. 2016). In the 1970s, metal (Ni, Cu) concentrations in lake waters exceeding 30 μ g L⁻¹ for Ni and 25 μ g L⁻¹ for Cu were detected to \sim 40 and 80 km, respectively, from Sudbury (Conroy et al. 1976). As of 2015, elevated concentrations of these metals, exceeding Ontario Guidelines (MOEE 1994) for surface waters (Ni 25 µg L⁻¹, Cu 5 µg L⁻¹), were restricted to lakes within \sim 20 km of Sudbury. However, slightly elevated Ni and Cu concentrations are still detectable in some lakes up to \sim 50 km from Sudbury (Figs. 3b, 3c), a legacy of past widespread metal deposition on the landscape.

In contrast to Cu and Ni, concentrations of total Al (Fig. 3d) do not show a relationship to distance from the smelters, since acidleaching of soils and increased lake acidity, not direct atmospheric deposition, were the major factors causing elevated Al concentrations (Keller et al. 2003) in acidified lakes. Although Al concentrations have greatly declined through time, they are still (2015) highly correlated with pH ($r_s - 0.78$, p < 0.05). The Extensive monitoring lakes with the highest recent Al concentrations (140 – 258 µg L⁻¹) all still have pH < 5.6.

Calcium

Unexpectedly, large declines in Ca concentrations (Fig. 2*c*) were also observed in Sudbury lakes as acidity decreased (Keller et al. 2001*b*), a pattern that was soon after documented broadly in Precambrian Shield lakes across central and northern Ontario (Jeziorski et al. 2008; Edwards et al. 2009). Ca concentrations in many formerly acidified lakes near Sudbury are now much lower than diatom-inferred background conditions determined from paleolimnological analyses of sediment cores (Keller et al. 2001*b*, 2003). Declines in lake water Ca concentrations averaging 55% (49%–67%) have occurred in all Extensive monitoring lakes since annual sampling commenced in 1981 (Fig. 2*c*). Declines in Ca (1981 vs. 2015) were significantly correlated ($r_s = 0.84$, p < 0.05) with declines in SO₄. Considering charge balances (μ eq L⁻¹) the declines in Ca on average balance 46% of the declines in SO₄ (27%–72% in





individual lakes). Almost all (40) of the 42 Sudbury-area Extensive monitoring lakes considered here (Fig. 1) now have Ca < 2 mg L⁻¹ (Fig. 2c), and most (33) of these lakes now have Ca concentrations below 1.5 mg L⁻¹, an approximate threshold for damage to the most sensitive *Daphnia* species and chronic stress in native crayfish in Precambrian Shield lakes (Ashforth and Yan 2008; Jeziorski et al. 2008; Cairns and Yan 2009; Edwards et al. 2015). However, the effect of Ca declines on aquatic species is a complex issue, involving differing species sensitivities, lethal and sub-lethal toxicity, and altered predatory interactions (Cairns and Yan 2009; Riessen et al. 2012; Azan and Arnott 2017; Jeziorski and Smol 2017). The only two Extensive monitoring lakes with Ca still above 2 mg L⁻¹ are urban lakes (Clearwater, Tilton; Fig. 1). Ca concentrations in these lakes may have been affected by urban influences such as local watershed development and dust control applications of CaCl₂ to gravel roads.

Declining Ca concentrations are already having effects on lake zooplankton communities in Ontario (Jeziorski et al. 2014) induc**Fig. 3.** Relationships of lakewater SO_4 (*a*), Ni (*b*) Cu (*c*), and Al (*d*) (total concentrations for metals) with distance from the Sudbury smelters, in 2015, for the Extensive and Intensive monitoring lakes (based on single summer samples). Three additional lakes not shown in Fig. 1 (Bowland, Silver, Whitson) were added to the dataset. Provincial Water Quality Objectives (PWQO, MOEE 1994) for total Ni and Cu are shown. The PWQO for Al in such dilute lakes is based on inorganic Al, which has not been measured. For comparison to the Sudbury lakes, the range in SO_4 concentrations in eight Dorset, Ontario, lakes in July 2015 is also shown in panel a (horizontal dashed lines).



ing a shift from Ca-rich daphnids to Ca-poor *Holopedium* and are likely also affecting other biota. Because of its moderating role on the sensitivity of biota to other stressors like acidity, metals, UV-B irradiance, and temperature (Skeffington and Brown 1992; Hessen and Alstad Rukke 2000; Ashforth and Yan 2008), declines in Ca concentrations are of major concern (Jeziorski and Smol 2017) and need to be closely monitored (Keller 2009). Based on estimated weathering rates, further declines in the Ca concentrations of northern Ontario lakes are likely (Watmough and Aherne 2008).

Dissolved organic carbon

Similar to observations in many areas of Europe and North America (Garmo et al. 2014), dissolved organic carbon (DOC) concentrations have increased in many Ontario lakes (Keller et al. 2008; Yan et al. 2008b) including those around Sudbury (Fig. 2d). Such "browning" can have dramatic ecological effects (Williamson et al. 2015). Although changes in atmospheric deposition chemistry after sulphur emission reductions explain much of the widely observed DOC increase in surface waters in many areas of the world (Monteith et al. 2007), recent DOC increases in Ontario lakes, including lakes near Sudbury, also appear to be related to a warming climate (Keller et al. 2008). Dramatic increases in lake DOC have generally accompanied recovery from acidification (Dixit et al. 2001; Keller et al. 2003, 2005); however, DOC increases have also been observed in northeastern Ontario lakes that never acidified (Keller 2007), pointing to changes in soil solution chemistry rather than in-lake processes as a dominant factor affecting lake DOC.

Increased UV-B penetration resulting from acidification-related DOC declines likely contributed to the biological damage observed in very clear, low DOC lakes (Yan et al. 1996a; Keller et al. 2003; Persaud and Yan 2003). DOC increases in recovering lakes have substantially reduced DOC-inferred UV-B penetration (Dixit et al. 2001). Since 1981, DOC has increased in all but the five clearest (DOC < 1.5 mg L⁻¹) Extensive monitoring lakes (Sunnywater, Nellie, Ruth Roy, OSA, Marjorie; Fig. 2d). Considering the overall DOC changes between 1981 and 2015, summer lake waters now contain 1.2–326 (average 51) tonnes more DOC (n = 38, lake volume not available for 4 lakes) than they did several decades ago. Temporal changes (1981 vs. 2015) in DOC concentrations were significantly correlated with changes in SO₄ ($r_s = -0.60$, p < 0.05), again suggesting that declines in sulphur deposition were a major factor affecting DOC increases. Ontario lakes are generally not at great risk of damage by UV-B irradiance (Molot et al. 2004), although some very clear Sudbury-area lakes may be exceptions. However, in 2015, only six of the 42 Extensive monitoring lakes had $DOC < 2 \text{ mg } L^{-1}$, a level below which UV attenuation is greatly reduced (Williamson et al. 1996).

In the relatively small (<500 ha) lakes that cover the northerm Ontario landscape, lake clarity or DOC has a dominant influence on determining lake thermal structure (Snucins and Gunn 2000) including the amount of cold-water habitat (Keller et al. 2005) and epilimnion thickness (Keller et al. 2006). Even with a generally warming climate, the amount of cold-water habitat in some Sudbury-area lakes has been observed to increase with increased DOC (Keller et al. 2005; Tanentzap et al. 2008).

Complexing by organic compounds is an important factor moderating the toxicity of metals, especially copper (Park et al. 2009; Cloran et al. 2010; Cuss et al. 2010; Taylor et al. 2016*a*) to aquatic organisms. Thus, it is likely that DOC increases are helping reduce metal toxicity in Sudbury-area lakes and that such benefits will increase as terrestrial systems recover further, rebuilding organic soils and contributing increased organic matter inputs to lakes.

Total phosphorus and nitrate

Only six of the Extensive monitoring lakes showed any evidence of temporal changes in total phosphorus (TP) concentrations based on analyses of slopes over the 1981-2015 period. This conclusion is not surprising perhaps, since shoreline development is not heavy on any of the Extensive lakes and most have none, although many lakes in south-central Ontario have declined in TP even with increases in human activity (Eimers et al. 2009) from causes that are not clear. More heavily urbanized lakes in Sudbury have shown evidence of cultural eutrophication based on comparisons with background conditions estimated by hindcasts from watershed TP models (Gunn and Keller 1995) and inferred from paleolimnological analyses of diatoms in sediment cores (Tropea et al. 2011). Lake and watershed characteristics do not point to any obvious explanation for the apparent decreases (Sans Chambre, Telfer) or increases (Bob, Klock, Tillie, Crooked) in a few of the Extensive lakes. It is recognized, however, that the use of singlesummer samples for TP analyses may limit the ability to detect trends since substantial biological TP (and nitrogen) utilization may already have occurred at the time of sampling. Future, more

rigourous assessment of trends in nutrients, considering lakes with more frequently collected seasonal data such as the Intensive lakes might be more revealing.

Atmospheric deposition of N in the Sudbury area is primarily from long-range sources since the Sudbury smelters have never been a large N source (Keller et al. 2003). Although nitrate (NO₃) can sometimes be an important factor in lake acidification, the main driver of widespread recovery from aquatic acidification in Europe and North America has been declines in sulphur deposition, although the relative importance of NO₃ to acidification may change with reduced sulphur deposition (Garmo et al. 2014). The dominant trend in the Extensive lakes has been a decline in NO₃ concentrations (28 lakes) with no trend observed in 14 lakes. This generally agrees with other North American and European observations indicating either declines or no change in surface water NO₃ concentrations in recent decades (Garmo et al. 2014; Vuorenmaa et al. 2018).

Biological changes with recovery

Algae

The richness and community composition of phytoplankton communities in the Sudbury area have generally changed relatively rapidly (within decades) after chemical recovery. During recovery, phytoplankton communities have typically increased in species richness and shifted from dominance by acid-tolerant dinoflagellates and chlorophytes to increased abundance of chrysophytes, diatoms, and cyanobacteria (Nicholls et al. 1992; Havas et al. 1995; Findlay 2003; Graham et al. 2007; Winter et al. 2008; Bergeron 2012).

Paleolimnological studies utilizing diatoms and scaled chrysophytes have been instrumental in revealing both the patterns of acidification of Sudbury lakes and their recovery (Dixit et al. 1988, 1989, 1992*a*, 1992*b*, 1993, 1995, 1996; Smol et al. 1998). While evidence of recovery was widely observed, changes were not always towards inferred background conditions. In Sudbury-area lakes with residual metal contamination, communities of diatoms have not begun to recover (Tropea et al. 2010). As well, even in lakes that were not heavily metal contaminated, recovery trajectories do not necessarily track towards pre-industrial diatom assemblages (Sivarajah et al. 2016, 2017), likely because of climate warming effects.

The benthic filamentous algae *Zygogonium* that often proliferated along shorelines of very clear, acid lakes was observed to decline dramatically with pH increases in Swan Lake (Fig. 1), giving way to more diverse benthic algal communities (Vandermeulen et al. 1993).

Zooplankton

Recovery of zooplankton communities has been particularly well studied in Sudbury-area lakes and elsewhere. There have been two reviews examining patterns of zooplankton community recovery from acidification (Keller and Yan 1998; Gray and Arnott 2009). Substantial zooplankton community recovery has often been observed within decades of water quality improvements. Typically, recovery included re-establishment of acid-sensitive crustacean species including *Daphnia mendotae*, *Epischura lacustris*, *Skistodiaptomus oregonensis*, *Eubosmina longispina*, and others, leading to increased species richness (Keller and Yan 1991; Keller et al. 1992b, 2002, 2007; Locke et al. 1994; Holt and Yan 2003). Among rotifers, with increased pH the acid-tolerant *Keratella taurocephela* typically declined and acid-sensitive species including *Keratella cochlearis*, *Polyarthra* sp., and *Conochilus* sp. increased in importance (MacIsaac et al. 1986; Keller et al. 1992c).

Dispersal does not seem to greatly constrain recovery in lakerich regions where there are many colonist sources (Watson et al. 1999; Pollard et al. 2003; Keller et al. 2007; Audet et al. 2013; Yan et al. 2016). Dispersal may, however, be a more important factor affecting recovery in lakes that are isolated from colonist sources by distance and (or) elevation (Keller and Yan 1998; Gray and Arnott 2009, 2011). Although most zooplankton species (both rotifers and crustaceans) seem to re-establish comparatively quickly (MacIsaac et al. 1986; Keller et al. 1992c, 2002; Havas et al. 1995), some species including hypolimnetic forms (*Daphnia longiremis*, *Cyclops scutifer*), and the so called "glacial opportunists" including *Senecella calanoides*, *Limnocalanus macrurus*, *Leptodiaptomus sicilis*, and *Diaptomus ashlandi* appear to be much less able to disperse between waterbodies (Keller and Yan 1998; Gray and Arnott 2009).

Improved water quality does not guarantee zooplankton community recovery even if dispersal is not limiting, since "biological resistance" (sensu Keller and Yan 1998) as well as chemical factors can be important in recovery processes (Keller and Yan 1998; Yan et al. 2003; Gray et al. 2012). Established acid-tolerant zooplankton communities may resist invasions by acid-sensitive species, delaying community recovery (Binks et al. 2005; Derry and Arnott 2007). In lakes where planktivorous fish were eliminated by acidification, zooplankton community structure can be controlled by invertebrate predators such as Chaoborus (Yan et al. 1991; Keller et al. 2002; MacPhee et al. 2011) and water beetles (Arnott et al. 2006) that expand in the absence of fish. In such cases the reintroduction of planktivorous fish is required to re-establish a more typical vertebrate-based predation system. However, in the absence of piscivores, predation by abundant planktivorous fish such as small yellow perch (Perca flavescens) can itself be a constraint to zooplankton recovery (Keller and Yan 1998; Yan et al. 2004; Webster et al. 2013). Ultimately the development of typical zooplankton communities will likely depend on the re-establishment of diverse fish communities containing both planktivores and piscivores (Valois et al. 2010, 2011; Webster et al. 2013).

In the lakes closest to Sudbury, residual metal contamination is also still a factor negatively affecting zooplankton communities (Yan et al 2004; Valois et al. 2011; Labaj et al. 2015; Taylor et al. 2016*b*) as it has been for many decades (Yan et al. 1996*b*). Interestingly, in urban Sudbury lakes with Ca and Na levels elevated because of anthropogenic activities, the sensitivity of *Daphnia* to metals is considerably reduced (Celis-Salgado et al. 2016) in comparison with lake waters without elevated Ca and Na.

Benthic macroinvertebrates

There are many examples of at least partial recovery of benthic macroinvertebrate communities in Sudbury-area lakes after reductions in acidity, including soft sediment littoral and profundal areas (Gunn and Keller 1990; Griffiths and Keller 1992; Reasbeck 1997; Babin-Fenske et al. 2012) and rocky near-shore habitats (Gunn and Keller 1990; Snucins 2003). Relatively rapid recovery of benthic macroinvertebrate communities is not surprising given the relative mobility of many species, especially the winged stages of insects. However, there are some macroinvertebrates (e.g., snails, clams, amphipods, crayfish) with more limited dispersal abilities. Natural re-establishment of such species may be a very slow process unless there are residual populations persisting in refuges within a lake or its watershed. Dispersal, if slow, does however occur for nonmobile species by passive means including transport by humans and wildlife (Kappes and Haase 2012). Snails (Gastropoda: Fossaria exigua, Heliosoma anceps, and Physella sp.) and amphipods (Hyalella azteca) were observed to colonize a small, newly created Sudbury-area lake within 2 years, with waterfowl being the suspected vector of introductions (Watson et al. 1999). Little is known about aquatic macrophytes in Sudbury lakes; however, if macrophyte abundance increases in recovering lakes then positive responses in benthic macroinvertebrate communities will likely follow. The abundance of the amphipod, H. azteca, is positively associated with the extent of littoral macrophyte cover in a number of Sudbury lakes (Kielstra et al. 2017).

The continuing low species richness of benthic macroinvertebrate communities in some lakes near Sudbury is related to residual metal contamination of waters and sediments, which continues to affect biological communities in the lakes closest to Sudbury where metal deposition was highest (Reasbeck 1997; Borgmann et al. 1998; Borgmann 2003; Wesolek et al. 2010; Szkokan-Emilson et al. 2010; Luek et al. 2013, 2015). Benthic macroinvertebrate communities in these lakes are characterized by absence or scarcity of taxa such as decapoda, mollusca, ephemeroptera, and amphipoda, and an abundance of Chironomidae. The scarcity of large grazers such as amphipods and crayfish may lead to extensive periphyton accumulations (Heneberry 1997) that can affect the recovery of other invertebrates.

In the mid-1990s sediment concentrations of Ni and Cu still exceeded, often greatly, Ontario Sediment Quality Guidelines for the protection of aquatic life (75 and 110 μ g g⁻¹ for Ni and Cu, respectively (MOEE 1993)) out to ~50 km from Sudbury (Keller et al. 2004). Although metal concentrations in surface sediments are generally declining (Borgmann et al. 1998; Tropea et al. 2010), very high levels persist in some Sudbury lakes, with concentrations of Ni and Cu exceeding, sometimes far exceeding, 1000 μ g g⁻¹ (Tropea et al. 2010). Burial of contaminated sediment with clean sediment may be a very slow process (Belzile and Morris 1995).

Additionally, even after reductions in chemical stress from contaminated water and sediments, in lakes with scarce or absent piscivores intensive predation by fish species such as yellow perch (*P. flavescens*) can negatively affect the recovery of macroinvertebrate communities (Wesolek et al. 2010; Luek et al. 2010, 2013, 2015). In lakes where food webs have been badly altered by acidification, the re-establishment of typical fish communities may be required to achieve recovery of benthic macroinvertebrate populations.

Fish

In a few cases such as Whitepine (Fig. 1) and Nelson lakes, small remnant populations of lake trout (*Salvelinus namaycush*) have increased dramatically in response to decreased lake acidity (Gunn and Keller 1990; Casselman and Gunn 1992). However, when fish have been extirpated, re-colonization is not likely unless there are direct connections between affected lakes and other lakes that contain fish source populations. Intentional or unintentional introductions by humans are a major cause of fish species expansions.

Intentional stocking of sport fish including lake trout, aurora trout (*Salvelinus fontinalis*), and smallmouth bass (*Micropterus dolomieu*) for experimental or fisheries management purposes has been successful in formerly acidified lakes (Gunn et al. 1988; Gunn and Keller 1990; Snucins and Gunn 2003; Luek et al. 2010). Reestablishment of acid-sensitive piscivores (lake trout, smallmouth bass) in formerly acidified lakes has resulted in rapid and substantial declines in very abundant acid-tolerant yellow perch populations (Gunn et al 1988, 1990; Gunn and Keller 1990; Casselman and Gunn 1992; Luek et al. 2010) and likely contributed to changes in populations of zooplankton and benthic macroinvertebrates through relaxed fish predation (Gunn and Keller 1990; Keller et al. 1990b, 1992c; Griffiths and Keller 1992).

Lake and watershed liming

In contrast to other acid-affected areas of the world, particularly Scandinavia (Olem et al. 1991; Henrikson and Brodin 1995), largescale lake liming programmes were not implemented in Ontario because with an estimated 19 000 acidified lakes (Neary et al. 1990) liming as a lake management strategy was not considered to be economically or logistically feasible. As well, since liming is only a temporary interim step, not a solution, for the lake acidification problem, the focus in Ontario was on achieving effective controls on acid-causing emissions (Keller 2009). A small number of wholelake liming activities were, however, conducted in Ontario to experimentally determine the responses of lake communities to reduced acidity (Dillon et al. 1979; Dodge et al. 1988; Keller et al. 1990c; Yan et al. 1995) or to assist with the restoration of a unique strain of brook trout, the aurora trout, which had been eliminated from its natural lakes by acidification (Snucins et al. 1995*a*, 1995*b*).

In total, eight lakes were limed in Ontario, with seven in the Sudbury area. Lake liming activities were successful in increasing lake pH (Dillon et al 1979; Molot et al. 1990*a*; Yan et al. 1995) and in also substantially reducing lake water metal concentrations in the highly metal-contaminated lakes closest to Sudbury, although metal concentrations remained high (Dillon et al. 1979). Positive responses to liming were observed in many groups of organisms, including stocked lake trout (Gunn et al. 1990), phytoplankton (Molot et al. 1990*b*), littoral algae (Jackson et al. 1990), zooplankton (Keller et al. 1990*b*; Carbone et al. 1998). However, in most of the limed lakes re-acidification occurred relatively quickly, providing only limited opportunities to examine biological responses to neutralization.

In the limed lakes within the City of Greater Sudbury (Middle, Hannah, Lohi; Fig. 1) long-term re-acidification did not occur because of terrestrial reclamation programmes that included liming of their watersheds (Lautenbach et al. 1995; Winterhalder 1996), an unplanned, but very positive outcome. Watershed liming as an aquatic remediation measure has had limited application in Ontario, although it has been widely applied to assist terrestrial reclamation efforts on the metal-contaminated soils of the Sudbury area. Watershed liming experiments demonstrate that it is a useful practice to improve drainage water quality (Gunn et al. 2001) with benefits for littoral lake biota (Gunn et al. 2016).

Watershed effects on recovery

Lakes and rivers are intimately linked to their watersheds and their chemistry can largely be viewed as a watershed effect. Thus, Sudbury-area watersheds affected by atmospheric deposition of sulphur and metals may negatively affect downstream chemistry, potentially for very long periods, when there has been substantial contaminant storage in watershed soils and wetlands (Nriagu et al. 1998; Keller et al. 1992a; Yan et al. 1996a; Szkokan-Emilson et al. 2013, 2014, 2017). Wet-dry cycles effectively oxidize and liberate quantities of acid and metals from storage under anoxic conditions in wetlands, saturated soils, and lake sediments. Drought-induced increases in the acidity and metal concentrations of streams and lakes can negatively affect biota including zooplankton (Arnott et al. 2001; Arnott and Yan 2002) and littoral macroinvertebrates (Szkokan-Emilson et al. 2013, 2017). We do not know how long such events may continue as an unfortunate legacy of the historically high contaminant deposition near Sudbury, although it has been suggested that effects from metal-contaminated watersheds may persist for over a thousand years (Nriagu et al. 1998). Watershed-scale loss of soil ions, including Ca, also occurred as a result of acid deposition. Naturally thin and ion poor catchment soils in Precambrian Shield regions, along with slow mineral weathering rates and further loss of ions through vegetation removal with land-use changes combine to result in ongoing loss of Ca and reduced inputs to lakes, that likely will continue for decades to come (Watmough and Aherne 2008). Time and continuing monitoring will tell.

Historically, clear-cut logging and SO_2 fumigations from early metal smelting activities damaged vegetation in a large area surrounding Sudbury, leading to large-scale erosion (Winterhalder 1995*a*). Terrestrial damage left a large (17 000 ha) area barren of vegetation with severely eroded soils, within a 72 000 ha semibarren area, around the Sudbury smelters (Winterhalder 1995*a*). However, with time, some natural revegetation has occurred (Winterhalder 1995*b*,1995*c*) with reduced smelter emissions (Potvin and Negusanti 1995), and large-scale land restoration programmes including soil liming and tree planting have dramatically regreened the Sudbury-area landscape (Lautenbach et al. 1995; Winterhalder 1996). In areas where watershed soils and vegetation were historically disturbed, terrestrial recovery may be a very important element assisting aquatic recovery. Increased organic matter export by streams from reforested areas is expected to have direct benefits to benthic invertebrates and ultimately to fish growth (Wesolek et al. 2010; Szkokan-Emilson et al. 2011; Tanentzap et al. 2014). Watershed re-forestation can have physical as well as chemical effects on downstream lakes. Reductions in wind speed related to a growing forest around Sudbury (Tanentzap et al. 2007) have been related to reduced lake mixing and increased cold water habitat (Tanentzap et al. 2008).

Shifting reference conditions

The fundamental nature of aquatic ecosystems in Ontario is changing in the face of multiple anthropogenic stressors including climate warming, Ca decline, and invasive species. Even in nonacidified Ontario lakes, chemistry and populations of zooplankton (Jeziorski et al. 2008; Yan et al. 2008; Palmer et al. 2011, 2013; Palmer and Yan 2013) and phytoplankton (Paterson et al. 2008) have changed in recent decades. Variability in observed temporal changes in lake plankton communities suggests that there can be strong heterogeneity in lake responses within and across regions due to influences such as climate change (Arnott et al. 2003b). Paleolimnological studies suggest that cladoceran and diatom communities in some recovering lakes are not moving back to their historical conditions, but rather they are moving to new states, likely because of climate warming (Labaj et al. 2016; Sivarajah et al. 2016, 2017).

Exotic invasive species are not yet widely distributed in inland lakes in Ontario; however, when present the exotic invader Bythotrephes has had dramatic effects on resident zooplankton populations (Yan et al. 2008). Future expansions of this invader, likely with severe consequences for resident zooplankton, including reduced species richness and altered community structure (Strecker and Arnott 2005: Strecker et al. 2006), appear to be inevitable (Pagnucco et al. 2015). Range expansion of native species as well as exotic species can have dramatic effects on aquatic ecosystems. The northward expansion of bass (M. dolomieu, Micropterus salmoides, Ambloplites rupestris) with a warming climate has the potential to significantly alter food webs in northern Ontario lakes through heavy predation by bass on littoral food resources (Vander Zanden et al. 2004; Alofs and Jackson 2015). Recovering lakes without established fish communities and lacking top predators may be particularly at risk of invasion (Alofs and Jackson 2014). Climate change is also predicted to threaten the reestablishment and persistence of many native cool- and coldwater fish species, further increasing the invasibility of northern lakes (Edwards et al. 2016; Van Zuiden et al. 2016).

Assessments of recovery must therefore consider this changing baseline, since the use of outdated reference data sets can substantially alter conclusions (Palmer et al. 2013). The choice of recovery metrics, and the use of multiple metrics is also important since different metrics vary in their detection sensitivity (Yan et al. 1996c) and can also lead to different conclusions (Keller et al. 2002; Gray and Arnott 2009). While much biological recovery has been observed in lakes near Sudbury, current assessments of the degree of recovery for various groups of biota are needed to gauge the actual extent and completeness of community recovery to date. Such assessments will need to be done against a background of changing reference conditions.

Summary

Once viewed as an international icon of environmental devastation, the Sudbury area now provides one of the best examples in the world of successful environmental restoration and recovery. Sudbury-area studies have given a powerful demonstration of the environmental benefits of air pollution controls. Long-term monitoring of lakes in the region has shown remarkable chemical improvements after very large reductions of sulphur and metal emissions from area smelters and reduced acid deposition from long-range sources. Because of the large, relatively early regional sulphur emission reductions, lakes in the Sudbury area allowed documentation of the lake recovery process before the implementation of substantial emission controls in other areas. This evidence of aquatic ecosystem recovery was crucial in establishing the necessity of sulphur emission controls during the international debates about the effects of acid deposition and the need for action. Results from Sudbury-area lakes have also led to the development of a number of conceptual models of chemical and biological recovery processes (Keller and Yan 1998; Yan et al. 2003; Keller et al. 2007) that continue to guide international lake recovery studies. Although the major contribution of Sudbury lake studies has been to acidification research, these long-term data series, especially for zooplankton, have also had substantial additional value for limnology in general. For example, Sudbury lakemonitoring data have helped advance the understanding of broad ecological issues related to relationships of aquatic community change with environmental change (Helmus et al. 2010; Shurin et al. 2010; Lamothe et al. 2018) and have allowed real-world validation of metal toxicity models for aquatic invertebrates (Khan et al. 2012; Stockdale et al. 2014; Balistrieri et al. 2015).

The future of Sudbury lakes looks promising. Biological recovery, including many groups of organisms, has followed chemical recovery. However, in some lakes recovery from acidification and metal contamination is not yet complete, and recovery processes are complicated by interactions with other large-scale environmental stressors like climate change and Ca decline. Lake communities may not return exactly to their pre-acidification state because of the influence of such large-scale stressors. In severely damaged lakes where food webs were greatly altered, reintroduction of key fish species may be necessary to achieve recovery of invertebrates to more normal communities. In the most severely affected lakes, with watersheds that were also badly damaged, aquatic recovery will likely be closely linked to terrestrial recovery.

Future directions

Foremost, continued monitoring of Sudbury-area lakes will be essential to track future changes and further develop our understanding of aquatic recovery processes amidst a variety of concurrent local and regional environmental changes. Only by looking will we be able to see and understand the changes that are happening in lakes. Studies in the Sudbury area have provided a very clear demonstration of the necessity of comprehensive lakemonitoring programmes to evaluate the effectiveness of pollution control measures and also to reveal the effects of other new environmental stressors affecting aquatic ecosystems.

Monitoring programmes only have their greatest value when the necessary resources are committed toward timely interpretation and reporting. To improve our current understanding of biological recovery, increased effort needs to be devoted to updating analyses of temporal patterns in the long-term zooplankton and phytoplankton data sets collected by the Sudbury lake-monitoring programmes. Long-term temporal patterns in thermal and oxygen regimes in these lakes also need to be examined given the likely influence on thermal habitats and oxygen distribution of large-scale changes such as climate warming and browning. As well, various past studies of fish benthic macroinvertebrates, aquatic macrophytes and planktonic *Chaoborus* in Sudbury-area lakes can now provide a baseline from which the extent of recent community change can be assessed. Future work should include repeat sampling of lakes with previous data and assessments of temporal changes and current status.

Many questions remain about the future of Sudbury-area lakes that need to be addressed through ongoing research. We need to better understand the linkages between land and water since these interactions will affect future lake recovery. Key aspects that need to be further examined include determining the current magnitude of sulphur and metal storage in watersheds and estimation of the timeframes that significant metal and acid inputs (long-term and episodic) to lakes are likely to continue. Estimation of current sediment recovery rates from metal contamination would also be valuable since severe sediment metal contamination persists in some lakes, affecting benthic macroinvertebrates. The extent to which increasing organic matter from recovering terrestrial landscapes affects lake recovery also needs to be further investigated. The above studies would ideally include detailed process-oriented investigations, including field surveys, paleolimnological studies, and experiments on key lakes and larger-scale empirical assessments of relationships between lake recovery patterns and catchment characteristics across a broad lake set using remote sensing and GIS tools. The above studies would greatly enhance the ongoing Sudbury lakemonitoring programmes and lead to a much better understanding of the patterns and processes of lake recovery in our multiple stressor world. This knowledge would have great benefits, informing future lake management efforts in the Sudbury area and other areas of the world affected by acid deposition.

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References

- Alofs, K.M., and Jackson, D.A. 2014. Meta-analysis suggests biotic resistance in freshwater environments is driven by consumption rather than competition. Ecology, 95: 3259–3270. doi:10.1890/14-0060.1.
- Alofs, K.M., and Jackson, D.A. 2015. The vulnerability of species to range expansions by predators can be predicted using historical species associations and body size. Proc. R. Soc. B-Biol. Sci. 282: 20151211. doi:10.1098/rspb.2015.1211.
- Alpay, S., Veillette, J.J., Dixit, A.S., and Dixit, S.S. 2006. Regional and historical distributions of lake-water pH within a 100-km radius of the Horne smelter in Rouyn-Noranda, Quebec, Canada. Geochem. Explor. Environ. Anal. 6: 179– 186. doi:10.1144/1467-7873/05-097.
- 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.D., Keller, W., and Nicholls, K. 2001. The influence of droughtinduced acidification on the recovery of plankton in Swan Lake (Canada). Ecol. Appl. **11**: 747–763. doi:10.1890/1051-0761(2001)011[0747:TIODIA]2.0.CO;2.
- Arnott, S.E., Dillon, P.J., Somers, K.M., and Keller, B. 2003a. Inter- and intraannual chemical variability during the ice-free season in lakes with different flushing rates and acid deposition histories. Environ. Monit. Assess. 88: 21– 37. doi:10.1023/A:1025540217174. PMID:14570409.
- Arnott, S.E., Keller, B., Dillon, P.J., Yan, N.D., Paterson, M., and Findlay, D. 2003b. Using temporal coherence to determine the response to climate change in

Boreal Shield lakes. Environ. Monit. Assess. 88: 365–388. doi:10.1023/A: 1025537628078. PMID:14570423.

- Arnott, S.E., Jackson, A.B., and Alarie, Y. 2006. Distribution and potential effects of water beetles in lakes recovering from acidification. J. N. Am. Benthol. Soc. 25: 811–824. doi:10.1899/0887-3593(2006)025[0811:DAPEOW]2.0.CO;2.
- Ashforth, D., and Yan, N.D. 2008. The interactive effects of calcium concentration and temperature on the survival and reproduction of *Daphnia pulex* at high and low food concentrations. Limnol. Oceanogr. 53(2): 420–432. doi:10. 4319/lo.2008.53.2.0420.
- Audet, C., MacPhee, S., and Keller, W. 2013. Constructed ponds colonized by crustacean zooplankton: local and regional influences. J. Limnol. 72: 524– 530. doi:10.4081/jlimnol. 2013.e43.
- Azan, S.S.E., and Arnott, S.E. 2017. The impact of calcium decline on population growth rates of crustacean zooplankton in Canadian Shield lakes. Limnol. Oceanogr. 63: 602–616. doi:10.1002/lno.10653.
- Babin-Fenske, J.J., Merritt, T.J.S., Gunn, J.M., Walsh, T., and Lesbarrère, D. 2012. Phylogenetic analysis of *Hyalella* colonization in lakes recovering from acidification and metal contamination. Can. J. Zool. **90**: 624–629. doi:10.1139/ z2012-028.
- Balistrieri, L.S., Mebane, C.A., Schmidt, T.S., and Keller, W. 2015. Expanding metal mixture acute toxicity models to natural stream and lake invertebrate communities. Environ. Toxicol. Chem. 34: 761–776. doi:10.1002/etc. 2824. PMID:25477294.
- Bates, R., Maechler, M., Bolker, B., and Walker, S. 2017. Package 'lme4': Linear Mixed-Effects. Available from https://cran.r-project.org/web/packages.lme/ lme1/lme4.pdf
- Beamish, R.J. 1974. Loss of fish populations from unexploited remote lakes in Ontario, Canada, as a consequence of atmospheric fallout of acid. Water Res.
 8: 85–95. doi:10.1016/0043-1354(74)90012-8.
- Beamish, R.J., and Harvey, H.H. 1972. Acidification of the La Cloche Mountain lakes, Ontario, and resulting fish mortalities. J. Fish. Res. Board Can. 29: 1131–1143. doi:10.1139/f72-169.
- Beamish, R.J., Lockhart, W.L., van Loon, J.C., and Harvey, H.H. 1975. Long term acidification of a lake and resulting effects on fishes. Ambio, 4: 98–102.
- Belzile, N., and Morris, J.R. 1995. Lake sediments: sources or sinks of industrially mobilized elements. *In* Restoration and recovery of an industrial region. *Edited by* J.M. Gunn. Springer Verlag. pp. 183–193.
- Bergeron, J.M. 2012. Urban and industrial drivers of phytoplankton communities in Sudbury, Ontario, urban lakes. M.Sc. thesis, Laurentian University, Sudbury, Ontario, Canada, 197 p.
- 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.
- Borgmann, U. 2003. Derivation of cause-effect based sediment quality guidelines. Can. J. Fish. Aquat. Sci. 60: 352–360. doi:10.1139/f03-026.
- Borgmann, U., Jackson, T.A., Reynoldson, T.B., and Rosa, F. 1998. Interim report on the effects of atmospheric deposition of metals from the Sudbury smelters on aquatic benthic ecosystems. National Water Research Institute Rep. 98-230. Burlington, Ontario, 148 p.
- Cairns, A., and Yan, N.D. 2009. A review of the influence of low ambient calcium concentrations on freshwater daphniids, gammarids, and crayfish. Environ. Rev. 17: 67–79. doi:10.1139/A09-005.
- Carbone, J., Keller, W., and Griffiths, R.W. 1998. Effects of changes in acidity on aquatic insects in rocky littoral habitats of lakes near Sudbury, Ontario. Restor. Ecol. 6: 376–389. doi:10.1046/j.1526-100X.1998.06408.x.
- Casselman, J.M., and Gunn, J.M. 1992. Dynamics in year-class strength, growth, and calcified–structure size of native lake trout (*Salvelinus namaycush*) exposed to moderate acidification and whole-lake neutralization. Can. J. Fish. Aquat. Sci. 49(Suppl. 1): 102–113. doi:10.1139/f92-305.
- Celis-Salgado, M.P., Keller, W., and Yan, N.D. 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. doi:10.4081/jlimnol.2016.1271.
- Cloran, C.E., Burton, G.A., Hammerschmidt, C.R., Taulbee, W.K., Custer, K.W., and Bowman, K.L. 2010. Effects of suspended solids and dissolved organic carbon on nickel toxicity. Environ. Toxicol. Chem. 29: 1781–1787. PMID: 20821632.
- Conroy, N.I., and Keller, W. 1976. Geological factors affecting biological activity in Precambrian Shield lakes. Can. Mineral. 14: 62–72.
- Conroy, N.I., Jeffries, D.S., and Kramer, J.R. 1974. Acid shield lakes in the Sudbury, Ontario, region. Proc. Water Pollut. Res. Can. 9: 45–61.
- Conroy, N.I., Hawley, K., Keller, W., and Lafrance, C. 1976. Influences of the atmosphere on lakes in the Sudbury area. J. Great Lakes Res. 2(Suppl. 1): 146–165. doi:10.1016/S0380-1330(76)72324-4.
- Conroy, N.I., Hawley, K., and Keller, W. 1978. Extensive monitoring of lakes in the greater Sudbury area, 1974–76. Ontario Ministry of the Environment Rept., Sudbury Ontario. 40 p, plus appendices.
- Cuss, C.W., Guéguen, C., Hill, E., and Dillon, P.J. 2010. Spatio-temporal variation in the characteristics of dissolved organic matter in streams of boreal forests: impacts on modelled copper speciation. Chemosphere, 80: 764–770. doi:10. 1016/j.chemosphere.2010.05.012. PMID:20653075.
- Derry, A.M., and Arnott, S.E. 2007. Zooplankton community response to exper-

imental acidification in Boreal Shield lakes with different ecological histories. Can. J. Fish. Aquat. Sci. **64**: 887–898. doi:10.1139/f07-061.

- Dillon, P.J., Yan, N.D., Scheider, W.A., and Conroy, N. 1979. Acidic lakes in Ontario, Canada: characterization, extent, and responses to base and nutrient additions. Arch. Hydrobiol. Beih. 13: 317–336.
- Dillon, P.J., Reid, R.A., and Girard, R. 1986. Changes in the chemistry of lakes near Sudbury, Ontario, following reductions of SO₂ emissions. Water Air Soil Pollut. **31**: 59–65. doi:10.1007/BF00630819.
- Dixit, S.S., Dixit, A.S., and Evans, R.D. 1988. Scaled chrysophytes (Chrysophyceae) as indicators of pH in Sudbury, Ontario, lakes. Can. J. Fish. Aquat. Sci. 45: 1411–1421. doi:10.1139/f88-165.
- 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. 1992a. Assessment of changes in lakewater chemistry in Sudbury area lakes since preindustrial times. Can. J. Fish. Aquat. Sci. **49**(Suppl. 1): 8–16. doi:10.1139/f92-295.
- Dixit, S.S., Dixit, A.S., and Smol, J.P. 1992b. Long term trends in lake water pH and metal concentrations inferred from diatoms and chrysophytes in three lakes near Sudbury, Ontario. Can. J. Fish. Aquat. Sci. 49(Suppl. 1): 17–24. doi:10.1139/f92-296.
- Dixit, A.S., Dixit, S.S., and Smol, J.P. 1993. Acidification and metal contamination in Whitepine Lake (Sudbury, Canada): a paleolimnological perspective. J. Paleolimnol. 9: 141–146. doi:10.1007/BF00677515.
- Dixit, S.S., Dixit, A.S., Smol, J.P., and Keller, W. 1995. Reading the records stored in the lake sediments: a method of examining the history and extent of industrial damage to lakes. *In Restoration and recovery of an industrial region. Edited by J.M. Gunn. Springer Verlag. pp. 33–44. doi:10.1007/978-1-4612-2520-1 3.*
- Dixit, A.S., Dixit, S.S., and Smol, J.P. 1996. Long-term trends in limnological characteristics in the aurora trout lakes, Sudbury, Canada. Hydrobiologia, 335: 171–181. doi:10.1007/BF00018984.
- Dixit, S.S., Keller, W., Dixit, A.S., and Smol, J. 2001. Diatom-inferred dissolved organic carbon reconstructions provide assessments of past UV-B penetration in Canadian Shield lakes. Can. J. Fish. Aquat. Sci. 58: 543–550. doi:10. 1139/f01-013.
- Dodge, D.P., Booth, G.M., Richman, L.A., Keller, W., and Tomassini, F.D. 1988. An overview of lake neutralization experiments in Ontario, 1981–1987. Water Air Soil Pollut. 41(1–4): 75–84.
- Edwards, B.A., Jackson, D.A., and Somers, K.M. 2009. Multispecies crayfish declines in lakes: implications for species distributions and richness. J. N. Am. Benthol. Soc. 28: 719–732. doi:10.1899/08-148.1.
- Edwards, B.A., Jackson, D.A., and Somers, K.M. 2015. Evaluating the effect of lake calcium concentration on the acquisition of carapace calcium by freshwater crayfish. Hydrobiologia, **744**: 91–100. doi:10.1007/s10750-014-2059-2.
- Edwards, B.A., Southee, F.M., and McDermid, J.L. 2016. Using climate and a minimum set of local characteristics to predict the future distributions of freshwater fish in Ontario, Canada, at the lake-scale. Glob. Ecol. Conserv. 8: 71–84. doi:10.1016/j.gecco.2016.08.006.
- Eimers, C., Watmough, S.A., Paterson, A.M., Dillon, P.J., and Yao, H. 2009. Longterm declines in phosphorus export from forested catchments in southcentral Ontario. Can. J. Fish. Aquat. Sci. 66: 1682–1692. doi:10.1139/F09-101.
- Findlay, D.L. 2003. Response of phytoplankton communities to acidification and recovery in Killarney Park and the Experimental lakes area, Ontario. Ambio, 32(3): 190–195. doi:10.1579/0044-7447-32.3.190, PMID:12839194.
- Garmo, Ø.A., Skjelkvåle, B.L., de Wit, H.E., Colombo, L., Curtis, C., Fölster, J., et al. 2014. Trends in surface water chemistry in acidified areas in Europe and North America from 1990 to 2008. Water Air Soil Pollut. 225: 1880. doi:10. 1007/s11270-014-1880-6.
- Gorham, E., and Gordon, A.G. 1960. The influence of smelter fumes upon the chemical composition of lake waters near Sudbury, Ontario, and upon the surrounding vegetation. Can. J. Bot. 38: 477–487. doi:10.1139/b60-044.
- Graham, M.D., Vinebrooke, R.D., Keller, B., 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.
- Gray, D.K., and Arnott, S.E. 2009. Recovery of acid damaged zooplankton communities: measurement, extent and limiting factors. Environ. Rev. 17: 81–99. doi:10.1139/A09-006.
- Gray, D.K., and Arnott, S.E. 2011. Does dispersal limitation impact the recovery of zooplankton communities damaged by a regional stressor? Ecol. Appl. 21(4): 1241–1256. doi:10.1890/10-0364.1. PMID:21774427.
- Gray, D.K., Arnott, S.E., Shead, J.A., and Derry, A.M. 2012. The recovery of acid damaged zooplankton communities in Canadian lakes: the relative importance of abiotic, biotic and spatial variables. Freshwater Biol. 57: 741–758. doi:10.1111/j.1365-2427.2012.02739.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. doi:0.1139/f92-301.
- Gunn, J.M., and Keller, W. 1990. Biological recovery of an acid lake after reductions in industrial emissions of sulphur. Nature, 345: 431–433. doi:10.1038/ 345431a0.

- Gunn, J.M., and Keller, W. 1995. Urban lakes: integrators of environmental damage and recovery. *In* Restoration and recovery of an industrial region. *Edited by* J.M. Gunn. Springer Verlag. pp. 257-269.
 Gunn, J.M., and Sandøy, S. 2003. Introduction to the Ambio special issue on bio-
- Gunn, J.M., and Sandøy, S. 2003. Introduction to the Ambio special issue on biological recovery from acidification: Northern Lakes recovery study. Ambio, 32: 162–164. doi:10.1579/0044-7447-32.3.162.
- Gunn, J.M., McMurty, M.J., Casselman, J.M., Keller, W., and Powell, M.J. 1988. Changes in the fish community of a limed lake near Sudbury, Ontario: effects of chemical neutralization or reduced atmospheric deposition of acids? Water Air Soil Pollut. 41: 113–136. doi:10.1007/978-94-009-2279-2_9.
- Gunn, J.M., Hamilton, J.G., Booth, G.M., Wren, C.D., Beggs, G.L., Rietveld, H.J., et al. 1990. Survival, growth, and reproduction of lake trout (Salvelinus namaycush) and yellow perch (Perca flavescens) after neutralization of an acidic lake near Sudbury, Ontario. Can. J. Fish. Aquat. Sci. 47: 446–453. doi:10.1139/f90-048.
- Gunn, J.M., Sein, R., Keller, B., and Beckett, P. 2001. Liming acid of and metal contaminated catchments for the improvement of drainage water quality. Water Air Soil Pollut. **130**: 1439–1444. doi:10.1023/A:1013908913162.
- Gunn, J.M., Szkokan-Emilson, E., and Kielstra, B.W. 2016. Catchment liming creates colonization opportunity for sensitive invertebrates in a smelter impacted landscape. J. Limnol. 75(s2): 50–58. doi:10.4081/jlimnol.2016.1201.
- Havas, M., Woodfine, D.G., Lutz, P., Yung, K., MacIsaac, H.J., and Hutchinson, T.C. 1995. Biological recovery of two previously acidified, metal-contaminated lakes near Sudbury, Ontario, Canada. Water Air Soil Pollut. 85: 791–796. doi:10.1007/BF00476926.
- 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., Keller, W., Paterson, M.J., Yan, N.D., Cannon, C.H., and Rusak, J.A. 2010. Communities contain closely related species during ecosystem disturbance. Ecol. Lett. 13: 162–174. doi:10.1111/j.1461-0248.2009.01411.x. PMID:20015255.
- Heneberry, J. 1997. Absence of large grazers: an obstacle to recovery in acid and metal damaged lakes. M.Sc. thesis, Laurentian University, Sudbury, Ontario, Canada, 108 p.
- 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. doi:10.4319/ lo.2000.45.8.1834.
- Holt, C., and Yan, N.D. 2003. Recovery of crustacean zooplankton communities from acidification in Killarney Park, Ontario, 1971–2000: pH 6 as a recovery goal. Ambio, 32: 203–207. doi:10.1579/0044-7447-32.3.203,. PMID:12839196.
- Hutchinson, T.C., and Havas, M. 1986. Recovery of previously acidified lakes near Coniston, Canada, following reductions in atmospheric sulphur and metal emissions. Water Air Soil Pollut. 28: 319–333.
- Jackson, M.B., Vandermeer, E.M., Lester, N., Booth, J.A., Molot, L., and Gray, I.M. 1990. Effects of neutralization and early reacidification on filamentous algae and macrophytes in Bowland Lake. Can. J. Fish. Aquat. Sci. 47: 432–439. doi:10.1139/f90-046.
- 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., and Smol, J.P. 2017. The ecological impacts of lakewater calcium decline on softwater boreal ecosystems. Environ. Rev. **25**: 245–253. doi:10. 1139/er-2016-0054.
- Jeziorski, A., Yan, N.D., Paterson, A.M., DeSellas, A.M., Turner, M.A., Jeffries, D.S., et al. 2008. The widespread threat of calcium decline in freshwaters. Science, 322: 374–1377. doi:10.1126 Science 1164949.
- Jeziorski, A., Keller, B., Paterson, A.M., Greenaway, C.N., and Smol, J.P. 2013. Aquatic ecosystem responses to rapid recovery from extreme acidification and metal contamination in lakes near Wawa, Ontario. Ecosystems, 16: 209– 223. doi:10.1007/s10021-012-9603-6.
- Jeziorski, A., Tanentzap, A.J., Yan, N.D., Paterson, A.M., Palmer, M.E., Korosi, J.B., et al. 2014. The jellification of north temperate lakes. Proc. Roy. Soc. B-Biol. Sci. **282**: 20142449. doi:10.1098/rspb.2014.2449.
- Kappes, H., and Haase, P. 2012. Slow, but steady: dispersal of freshwater molluscs. Aquat. Sci. 74: 1–14. doi:10.1007/s00027-011-0187-6.
- Keller, W. 1978. Limnological observations on the aurora trout lakes. Ontario Ministry of the Environment Rept., Sudbury, Ontario, 48 p.
- Keller, W. 1992. Introduction and overview to aquatic acidification studies in the Sudbury, Ontario, Canada area. Can. J. Fish. Aquat. Sci. 49(Suppl. 1): 3–7. doi:10. 1139/f92-294.
- Keller, W. 2007. Implications of climate warming for Boreal Shield lakes: a review and synthesis. Environ. Rev. 5: 99–112. doi:10.1139/A07-002.
- Keller, W. 2009. Limnology in northeastern Ontario: from acidification to multiple stressors. Can. J. Fish. Aquat. Sci. 66: 1189–1198. doi:10.1139/F09-080.
- Keller, W., and Pitblado, J.R. 1984. Crustacean plankton in northeastern Ontario lakes subjected to acidic deposition. Water Air Soil Pollut. 23: 271–291. doi: 10.1007/BF00283204.
- 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., Gunn, J., and Conroy, N. 1980. Acidification impacts on lakes in the Sudbury, Ontario, Canada area. *In* Proc. Int. Conf. on the Ecological Impact of Acid Precipitation, Sandefjord, Norway. *Edited by* D. Drablos and A. Tollan. pp. 228–229.
- Keller, W., Pitblado, J.R., and Conroy, N.I. 1986. Water quality improvements in the Sudbury, Ontario, Canada area related to reduced smelter emissions. Water Air Soil Pollut. 31: 765–774. doi:10.1007/BF00284223.
- Keller, W., Yan, N.D., Holtze, K.E., and Pitblado, J.R. 1990a. Inferred effects of lake acidification on Daphnia galeata mendotae. Environ. Sci. Technol. 24: 1259–1261. doi:10.1021/es00078a015.
- Keller, W., Molot, L.A., Griffiths, R.W., and Yan, N.D. 1990b. Changes in the zoobenthos community of acidified Bowland Lake after whole-lake neutralization and lake trout (*Salvelinus namaycush*) reintroduction. Can. J. Fish. Aquat. Sci. 47: 440–445. doi:10.1139/f90-047.
- Keller, W., Dodge, D.P., and Booth, G.M. 1990c. 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., Pitblado, J.R., and Carbone, J. 1992a. Chemical responses of acidic lakes in the Sudbury, Ontario area to reduced smelter emissions, 1981 to 1989. Can. J. Fish. Aquat. Sci. 49(Suppl. 1): 25–32.
- Keller, W., Gunn, J.M., and Yan, N.D. 1992b. Evidence of biological recovery in acid-stressed lakes near Sudbury, Canada. Environ. Pollut. 78: 79–85. doi:10. 1016/0269-7491(92)90013-Z. PMID:15091931.
- Keller, W., Yan, N.D., Howell, T., Molot, L.A., and Taylor, W.D. 1992c. Changes in zooplankton during the experimental neutralization and early re-acidification of Bowland Lake near Sudbury, Ontario. Can. J. Fish. Aquat. Sci. 49(Suppl. 1): 52–62.
- Keller, W., Heneberry, J., and Gunn, J. 1999a. Effects of emission reductions from the Sudbury smelters on the recovery of acid and metal-damaged lakes. J. Aquat. Ecosys. Stress Recovery, 6: 189–198.
- Keller, W., Gunn, J., and Yan, N. 1999b. Acid rain: perspectives on lake recovery. J. Aquat. Ecosys. Stress Recovery, 6: 207–216. doi:10.1023/A:1009983318502.
- Keller, W., Heneberry, J., Clark, M., Malette, M., and Gunn, J.M. 1999c. Effects of emission reduction from the smelters in Sudbury on recovery of lakes within the metal deposition zone. *In* Proc. Mining and the Environment II, Sudbury, Ontario. *Edited by* D. Goldsack, N. Belzile, P. Yearwood, and G. Hall. pp. 483–492.
- Keller, W., Dillon, P.J., Heneberry, J., Malette, M., and Gunn, J. 2001a. Sulphate in Sudbury, Ontario, Canada, lakes: recent trends and status. Water Air Soil Pollut. 130: 793–798. doi:10.1023/A:1013858207380.
- Keller, W., Dixit, S.S., and Heneberry, J. 2001b. Calcium declines in northeastern Ontario lakes. Can. J. Fish. Aquat. Sci. 58: 2011–2020. doi:10.1139/f01-142.
- 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., Heneberry, J.H., and Dixit, S.S. 2003. Decreased acid deposition and the chemical recovery of Killarney, Ontario, lakes. Ambio, 32: 183–189. doi: 10.1579/0044-7447-32.3.183. PMID:12839193.
- Keller, W., Heneberry, J., Gunn, J., Snucins, E., Morgan, G., and Leduc, J. 2004. Recovery of acid and metal-damaged lakes near Sudbury Ontario: trends and status. Cooperative Freshwater Ecology Unit Tech. Rept. Laurentian University, Sudbury, Ontario. 53 p.
- Keller, W., Heneberry, J., and Leduc, J. 2005. Linkages between weather, dissolved organic carbon, and coldwater habitat in a Boreal Shield lake recovering from acidification. Can. J. Fish. Aquat. Sci. 62: 341–347 doi:10. 1139/f04-192.
- Keller, W., Heneberry, J., Leduc, J., Gunn, J., and Yan, N. 2006. Variations in epilimnion thickness in small Boreal Shield lakes: relationships with transparency, weather and acidification. Environ. Monit. Assess. 115: 419–431. doi:10.1007/s10661-006-7237-x. PMID:16614780.
- 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.
- Khan, F.R., Keller, W., Yan, N.D., Welsh, P.G., Wood, C.M., and McGeer, J.C. 2012. 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. PMID:22191513.
- Kielstra, B.W., Arnott, S.E., and Gunn, J.M. 2017. Subcatchment deltas and upland features influence multiscale aquatic ecosystem recovery in damaged landscapes. Ecol. Appl. 27: 2249–2261. doi:10.1002/eap.1609. PMID:28782919.
- Kwiatkowski, R.E., and Roff, J.C. 1976. Effects of acidity on the phytoplankton and primary productivity of selected northern Ontario lakes. Can. J. Bot. 54: 2546–2561. doi:10.1139/b76-274.
- Labaj, A.L., Kurek, J., Jeziorski, A., and Smol, J.P. 2015. Elevated metal concentra-

tions inhibit biological recovery of Cladocera in previously acidified boreal lakes. Freshwater Biol. **60**: 347–359. doi:10.1111/fwb.12496.

- Labaj, A.L., Korosi, J.B., Kurek, J., Jeziorski, A., Keller, W., and Smol, J.P. 2016. Response of *Bosmina* size structure to the acidification and recovery of lakes near Sudbury, Canada. J. Limnol. **75**(s2): 22–29. doi:10.4081/jlimnol.2016.1183.
- Lamothe, K.A., Jackson, D.A., and Somers, K.M. 2018. Long-term directional trajectories among lake crustacean zooplankton communities and water chemistry. Can. J. Fish. Aquat. Sci. doi.org/10.1139/cjfas-2017-0518.
- Larssen, T., Brereton, C., and Gunn, J.M. 2003. Dynamic modelling of recovery from acidification of lakes in Killarney Park, Ontario, Canada. Ambio, 32: 244–248. doi:10.1579/0044-7447-32.3.244. PMID:12839204.
- Lautenbach, W.E., Miller, J., Beckett, P.J., Negusanti, J.J., and Winterhalder, K. 1995. Municipal land restoration program: the regreening process. *In* Restoration and recovery of an industrial region. *Edited by* J.M. Gunn. Springer Verlag. pp. 109–122.
- 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.
- Luek, A., Morgan, G.E., Whissel, B., Gunn, J.M., and Ramcharan, C.W. 2010. Rapid and unexpected effects of piscivore introduction on trophic position and diet of perch (*Perca flavescens*) in lakes recovering from acidification and metal contamination. Freshwater Biol. 55(8): 1616–1627. doi:10. 1111/j.1365-2427.2009.02392.x.
- Luek, A., Morgan, G.E., Wissel, B., Gunn, J.M., and Ramcharan, C.W. 2013. Impaired littoral energy pathways cause a shift to pelagic resources by fish in recovering lake food webs. Ecol. Freshw. Fish, 22(3): 348–360. doi:10.1111/eff. 12030.
- Luek, A., Morgan, G.E., and Ramcharan, C.W. 2015. Biomass of benthic invertebrates unaffected by industrial damage to lakes despite effects on species composition. Hydrobiologia, 744: 101–114. doi:10.1007/s10750-014-2060-9.
- MacIsaac, H.J., Keller, W., Hutchinson, T.C., and Yan, N.D. 1986. Natural changes in the planktonic rotifera of a small acid lake near Sudbury, Ontario following water quality improvements. Water Air Soil Pollut. 31: 791–797. doi:10. 1007/BF00284225.
- MacIsaac, H.J., Hutchinson, T.C., and Keller, W. 1987. Analysis of planktonic rotifer assemblages from Sudbury, Ontario lakes of varying chemical composition. Can. J. Fish. Aquat. Sci. 44: 1692–1701. doi:10.1139/f87-208.
- MacPhee, S., Arnott, S., and Keller, W. 2011. Lake thermal structure influences macroinvertebrate predation on crustacean zooplankton. J. Plankton Res. 33: 1586–1595. doi:10.1093/plankt/fbr046.
- Manca, M.M., Bonacina, C., and Yan, N.D. 2016. What have we learned about ecological recovery from liming interventions of acid lakes in Canada and Italy? J. Limnol. 75(s2): 1–3. doi:10.4081/jlimnol.2016.1387.
- Matuszek, J.E., Wales, D.L., and Gunn, J.M. 1992. Estimated impacts of SO₂ emissions from Sudbury smelters on Ontario's sportfish populations. Can. J. Fish. Aquat. Sci. 49(Suppl. 1): 87–94.
- MOEE (Ministry of the Environment and Energy). 1993. Guidelines for the protection and management of aquatic sediment quality in Ontario. Ontario Ministry of the Environment and Energy Rept. Toronto, Ontario. 24 p.
- MOEE (Ministry of the Environment and Energy). 1994. Water management policies, guidelines, provincial water quality objectives. Ontario Ministry of the Environment and Energy Rept. Toronto, Ontario. 31 p. Moiseenko, T. 1994. Acidification and critical loads in surface waters: Kola,
- Moiseenko, T. 1994. Acidification and critical loads in surface waters: Kola, northern Russia. Ambio, 23: 418–424.
- Molot, L.A., Dillon, P.J., and Booth, G.M. 1990a. Whole-lake and nearshore water chemistry in Bowland Lake before and after treatment with CaCO₃. Can. J. Fish. Aquat. Sci. 47: 412–421. doi:10.1139/f90-044.
- Molot, L.A., Heintsch, L., and Nicholls, K.H. 1990b. Response of phytoplankton in acidic lakes in Ontario to whole-lake neutralization. Can. J. Fish. Aquat. Sci. 47: 422–431. doi:10.1139/f90-045.
- Molot, L.A., Keller, W., Leavitt, P.R., Robarts, R.D., Waiser, M.J., Arts, M.T., et al. 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., Høgåsen, T., et al. 2007. Dissolved organic carbon trends resulting from changes in atmospheric deposition chemistry. Nature, 450: 537–540. doi:10.1038/nature06316. PMID:18033294.
- Neary, B.P., Dillon, P.J., Munro, J.R., and Clark, B. 1990. The acidification of Ontario lakes: an assessment of their sensitivity with respect to biological damage. Ontario Ministry of the Environment, Dorset, Ontario, Tech. Rept. 170 p.
- Nicholls, K.H., Nakamoto, L., and Keller, W. 1992. The 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. Sci. Total Environ. 223: 99–117. doi:10.1016/S0048-9697(98)00284-8. PMID:9861730.
- 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.
- OWRC (Ontario Water Resources Commission). 1970. Preliminary report on the influence of industrial activity on the lakes in the Sudbury area, 1969–1970.

Ontario Water Resources Commision Report, Toronto, Ontario, 34 p. plus appendices.

- Pagnucco, K., Maynard, G.A., Fera, S.A., Yan, N.D., Nalepa, T.F., and Ricciardi, L.A. 2015. The future of species invasions in the Great Lakes-St. Lawrence River basin. J. Great Lakes Res. 41(Suppl. 1): 96–107.
- Palmer, M.E., and Yan, N.D. 2013. Decadal-scale regional changes in Canadian freshwater zooplankton: the likely consequence of complex interactions among multiple anthropogenic stressors. Freshwater Biol. 58(7): 1366–1378. doi:10.1111/fwb.12133.
- Palmer, M.E., Yan, N.D., Paterson, A.M., and Girard, R.E. 2011. Water quality changes in south-central Ontario lakes and the role of local factors in regulating lake response to regional stressors. Can. J. Fish. Aquat. Sci. 68: 1038– 1050. doi:10.1139/f2011-041.
- Palmer, M.E., Keller, W., and Yan, N.D. 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. doi:10.1111/1365-2664. 12007.
- Park, E.J., Jo, H.J., and Jung, J. 2009. Combined effects of pH, hardness and dissolved organic carbon on acute metal toxicity to *Daphnia magna*. Jour. Industr. Eng. Chem. 15: 82–85. doi:10.1016/j.jiec.2008.08.007.
- Paterson, A.M., Winter, J.G., Nicholls, K.H., Clark, B.J., Ramcharan, C.W., Yan, N.D., and Somers, K.M. 2008. Long-term changes in phytoplankton composition in seven Canadian Shield lakes in response to multiple anthropogenic stressors. Can. J. Fish. Aquat. Sci. 65(5): 846–861. doi:10.1139/f08-022.
- Pearson, D., Gunn, J.M., and Keller, W. 2002. The past, present, and future of Sudbury's lakes. *In Physical environment of the Sudbury region*. *Edited by* D.H. Rousell and K. Jansons. Geological Survey Special Volume. Sudbury, Ontario. pp. 195–215.
- Persaud, A.D., and Yan, N.D. 2003. UVR sensitivity of *Chaoborus* larvae. Ambio, **32**: 219–224. doi:10.1579/0044-7447-32.3.219. PMID:12839199.
- Pitblado, J.R., and Keller, W. 1984. Data report monitoring of northeastern Ontario lakes, 1981-1983. Ontario Ministry of the Environment and Energy Rept. Sudbury, Ontario. 9 p, plus appendices.
- Pollard, H.G., Colbourne, J., and Keller, W. 2003. Reconstruction of centuries old Daphnia communities in a lake recovering from acidification and metalcontamination. Ambio, **32**: 214–218. doi:10.1579/0044-7447(2003)032[0214: ROCDCI]2.0.CO;2.
- 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. pp. 51–65.
- Reasbeck, J.A. 1997. Changes in benthic macroinvertebrate community structure in acid and metal contaminated lakes following water quality improvements. M.Sc. thesis, Laurentian University, Sudbury, Ontario, Canada, 95 p.
- Riessen, H.P., Linley, R.D., Altshuler, I., Rabus, M., Söllradl, T., Clausen-Schaumann, H., et al. 2012. Changes in water chemistry can disable plankton prey defenses. Proc. Nat. Acad. Sci. **109**: 15377–15382. doi:10.1073/pnas.1209938109. PMID: 22949653.
- Roff, J.C., and Kwiatkowski, R.E. 1977. Zooplankton and zoobenthos communities of selected northern Ontario lakes of different acidities. Can. J. Zool. 55: 899–911. doi:10.1139/z77-118.
- Semkin, R.G., and Kramer, J.R. 1976. Sediment geochemistry of Sudbury-area lakes. Can. Mineral. 14: 73–90.
- Shurin, J.B., Winder, M., Adrian, R., Keller, W., Matthews, B., Paterson, A.M., et al. 2010. Environmental stability and lake zooplankton diversity – contrasting effects of chemical and thermal variability. Ecol. Lett. 13: 453–463. doi:10.1111/j. 1461-0248.2009.01438.x. PMID:20100243.
- Sivarajah, B., Rühland, K.M., Labaj, A.L., Paterson, A.M., and Smol, J.P. 2016. Why is the relative abundance of Asterionella formosa increasing in a Boreal Shield lake as nutrient levels decline? J. Paleolimnol. 55: 357–367. doi:10.1007/ s10933-016-9886-2.
- Sivarajah, B., Rühland, K.M., and Smol, J.P. 2017. Are diatoms recovering to pre-acidification assemblages in a warming world? Revisiting Killarney Provincial Park lakes (Ontario, Canada). Fund. Appl. Limnol. **190**: 13–28. doi:10. 1127/fal/2017/o981.
- Skeffington, R.A., and Brown, D.J.A. 1992. Timescales of recovery from acidification: implications of current knowledge for aquatic organisms. Environ. Pollut. 77: 227–234. doi:10.1016/0269-7491(92)90081-K. PMID:15091963.
- Smol, J.P., Cumming, B.F., Dixit, A.S., and Dixit, S.S. 1998. Tracking recovery patterns in acidified lakes: a paleolimnological perspective. Restor. Ecol. 6: 318–326. doi:10.1046/j.1526-100X.1998.06402.x.
- Snucins, E.J. 2003. Recolonization of acid-damaged lakes by the benthic invertebrates Stenacron interpunctatum, Stenonema femoratum, and Hyalella azteca. Ambio, 32: 225–229. doi:10.1579/0044-7447-32.3.225. PMID:12839200.
- Snucins, E.J., and Gunn, J.M. 2000. Interannual variation in the thermal structure of clear and colored lakes. Limnol. Oceanogr. 45: 1639–1646. doi:10.4319/ lo.2000.45.7.1639.
- Snucins, E.J., and Gunn, J.M. 2003. Use of rehabilitation experiments to understand the recovery dynamics of acid-stressed fish populations. Ambio, 32: 240–243. doi:10.1579/0044-7447-32.3.240. PMID:12839203.
- Snucins, E.J., Gunn, J.M., and Keller, W. 1995a. Restoration of the aurora trout to its acid-damaged native habitat. Conserv. Biol. 9: 1307–1311. doi:10.1046/j.1523-1739.1995.9051304.x-i1.

- Snucins. E.J., Gunn, J.M., and Keller, W. 1995b. Preservation of biodiversity: Aurora trout. In Restoration and recovery of an industrial region. Edited by J.M. Gunn. Springer Verlag. pp. 143-153.
- Sprules, W.G. 1975. Midsummer crustacean zooplankton communities in acidstressed lakes. J. Fish. Res. Board Can. 32: 389–395. doi:10.1139/f75-045.
- Sprules, W.G. 1977. Crustacean zooplankton communities as indicators of limnological conditions: an approach using principal component analysis. J. Fish. Res. Board Can. 34: 962–975. doi:10.1139/f77-149.
- Stephenson, M., and Mackie, G.L. 1986. Lake acidification as a limiting factor in the distribution of the freshwater amphipod *Hyalella azteca*. Can. J. Fish. Aquat. Sci. 43: 288–292. doi:10.1139/f86-037.
- Stockdale, A., Tipping, E., Lofts, S., Fott, J., Garmo, Ø.A., Hruska, J., et al. 2014. Metal and proton toxicity to lake zooplankton: a chemical speciation based modelling approach. Environ. Pollut. 186: 115–125. doi:10.1016/j.envpol.2013. 11.012. PMID:24370669.
- Strecker, A.L., and Arnott, S.E. 2005. Impact of *Bythotrephes* invasion on zooplankton communities in acid-damaged and recovered lakes on the Boreal Shield. Can. J. Fish. Aquat. Sci. 62: 2450–2462. doi:10.1139/f05-152.
- Strecker, A.L., Arnott, S.E., Yan, N.D., and Girard, R. 2006. Variation in the response of crustacean zooplankton species richness and composition to the invasive predator *Bythotrephes longimanus*. Can. J. Fish. Aquat. Sci. 63: 2126– 2136. doi:10.1139/f06-105.
- Szkokan-Emilson, E.J., Wesolek, B.E., Gunn, J.M., Sarrazin-Delay, C., Bedore, J., Chan, F., et al. 2010. Recovery of benthic invertebrate communities from acidification in Killarney Park lakes. Environ. Monit. Assess. 166: 293–302. doi:10.1007/s10661-009-1002-x. PMID:19479335.
- Szkokan-Emilson, E.J., Wesolek, B.E., and Gunn, J.M. 2011. Terrestrial organic matter as subsidies that aid in the recovery of macroinvertebrates in industrially damaged lakes. Ecol. Appl. 21: 2082–2093. doi:10.1890/10-1967.1. PMID: 21939045.
- Szkokan-Emilson, E.J., Kielstra, B.W., Watmough, S.A., and Gunn, J.M. 2013. Drought-induced release of metals from peatlands in watersheds recovering from historical metal and sulphur deposition. Biogeochemistry, 116: 131–145. doi:10.1007/s10533-013-9919-0.
- Szkokan-Emilson, E., Watmough, S.A., and Gunn, J.M. 2014. Wetlands as longterm sources of metals to receiving waters in mining-impacted landscapes. Environ. Pollut. **192C**: 91–103. doi:10.1016/j.envpol.2014.05.009.
- Szkokan-Emilson, E.J., Kielstra, B.W., Arnott, S.E., Watmough, S.A., Gunn, J.M., and Tanentzap, A.J. 2017. Dry conditions disrupt terrestrial-aquatic linkages in northern catchments. Global Change Biol. 23: 117–126. doi:10.1111/gcb. 13361.
- Tanentzap, A.J., Taylor, P.A., Yan, N.D., and Salmon, J.R. 2007. On Sudbury-area wind speeds: a tale of forest regeneration. J. Appl. Meteorol. Clim. 46: 1645– 1654. doi:10.1175/JAM2552.1.
- Tanentzap, A.J., Yan, N.D., Keller, B., Girard, R., Heneberry, J., Gunn, J.M., et al. 2008. Cooling lakes while the world warms: effects of forest regrowth and increased dissolved organic matter on the thermal regime of a temperate urban lake. Limnol. Oceanogr. 53: 404–410. doi:10.4319/lo.2008.53.1.0404.
- Tanentzap, A.J., Szkokan-Emilson, E.J., Kielstra, B.W., Arts, M.T., Yan, N.D., and Gunn, J.M. 2014. Forests fuel fish growth in freshwater deltas. Nat. Commun. 5: 4077. doi:10.1038/ncomms5077. PMID:24915965.
- Taylor, N.S., Kirwan, J.A., Yan, N.D., Viant, M.R., Gunn, J.M., and McGeer, J.C. 2016a. Metabolomics confirms that dissolved organic carbon mitigates copper toxicity. Environ. Toxicol. Chem. 35(3): 635–644. doi:10.1002/etc.3206. PMID:26274843.
- Taylor, N.S., Kirwan, J.A., Johnson, C., Yan, N.D., Viant, M.R., Gunn, J.M., et al. 2016b. Predicting chronic copper and nickel reproductive toxicity to Daphnia pulex-pulicaria from whole-animal metabolic profiles. Environ. Pollut. 212: 325–329. doi:10.1016/j.envpol.2016.01.074. PMID:26854702.
- Tropea, A.E., Paterson, A.M., Keller, W., and Smol, J.P. 2010. Sudbury sediments revisited: evaluating limnological recovery in a multiple-stressor environment. Water Air Soil Pollut. 210: 317–333. doi:10.1007/s11270-009-0255-x.
- Tropea, A.E., Paterson, A.M., Keller, W., and Smol, J.P. 2011. Diatoms as indicators of long-term nutrient enrichment in metal-contaminated lakes from Sudbury, Ontario. Lake Reserv. Manage. 27: 48–60. doi:10.1080/07438141.2011. 555935.
- Valois, A., Keller, W., and Ramcharan, C. 2010. Abiotic and biotic processes in recovering lakes: the relative roles of metal toxicity and fish predation as barriers to zooplankton re-establishment. Freshwater Biol. 55: 2585–2597. doi:10.1111/j.1365-2427.2010.02488.x.
- Valois, A., Keller, W., and Ramcharan, C.W. 2011. Recovery in a multiple stressor environment: using the reference condition approach to examine zooplankton community change along opposing gradients. J. Plankon Res. 33: 1417– 1429. doi:10.1093/plankt/fbr036.
- Van Zuiden, T.M., Chen, M.M., Stefanoff, S., Lopez, L., and Sharma, S. 2016. Projected impacts of climate change on three freshwater fishes and potential novel competitive interactions. Diversity Distrib. 22: 603–614. doi:10.1111/ddi. 12422.
- Vander Zanden, J., Wilson, K.A., Casselman, J.M., and Yan, N.D. 2004. Species introductions and their impacts in North American shield lakes. *In Boreal* Shield watersheds – lake trout ecosystems in a changing environment. *Editors* J.M. Gunn, R.J. Steedman, and R.A. Ryder. Boca Raton: CRC. pp. 239–263.
- Vandermeulen, H., Jackson, M.B., Rodrigues, A., and Keller, W. 1993. Filamen-

tous algal communities in Sudbury area lakes: effects of variable lake acidity. Crypto. Bot. **3**: 123–132.

- Vuorenmaa, J., Augustaitis, A., Beudert, B., Bochenek, W., Clarke, N., de Wit, H., et al. 2018. Long-term changes (1990-2015) in the atmospheric deposition and runoff water chemistry of sulphate, inorganic nitrogen and acidity for forested catchments in Europe in relation to changes in emissions and hydrometeorological conditions. Sci. Total Environ. 625: 1129–1145. doi:10.1016/j. scitotenv.2017.12.245. PMID:29996410.
- Watmough, S.A., and Aherne, J. 2008. Estimating calcium weathering rates and future lake calcium concentrations in the Muskoka-Haliburton region of Ontario. Can. J. Fish. Aquat. Sci. 65(5): 821–833. doi:10.1139/f07-196.
- Watson, G., Hunt, C., and Keller, W. 1999. Natural and enhanced aquatic ecosystem development at Inco's former Garson 10.2 open pit mine. *In* Proc. Mining and the Environment II, Sudbury, Ontario. *Edited by* D. Goldsack, N. Belzile, P. Yearwood, and G. Hall. pp. 419–428.
- Webster, N.I., Keller, W., and Ramcharan, C. 2013. Restoration of zooplankton communities in industrially damaged lakes: influences of residual metal contamination and the recovery of fish communities. Restor. Ecol. 21: 785– 792. doi:10.1111/rec.12013.
- Wesolek, B.E., Genrich, E.K., Gunn, J.M., and Somers, K.M. 2010. Use of littoral benthic invertebrates to assess factors affecting biological recovery of acidand metal-damaged lakes. J. N. Am. Benthol. Soc. 29(2): 572–585. doi:10.1899/ 09-123.1.
- White, C., Sayer, J.A., and Gadd, G.M. 1997. Microbial solubilization and immobilization of toxic metals: key biogeochemical processes for treatment of contamination. FEMS Microbial. Rev. 20: 503–516. doi:10.1111/j.1574-6976.1997. tb00333.x. PMID:9299717.
- Williamson, C.E., Stemberger, R.S., Morris, D.P., Frost, T.M., and Paulsen, S.G. 1996. Ultraviolet radiation in North American lakes: attenuation estimates from DOC measurements and implications for plankton communities. Limnol. Oceanogr. 41: 1024–1034. doi:10.4319/lo.1996.41.5.1024.
- Williamson, C.E, Overholt, E.P, Pilla, R.M., Leach, T.H., Brentrup, J.A., Knoll, L.B., et al. 2015. Ecological consequences of long-term browning in lakes. Nature Scientific Reports, 5: 18666. doi:10.1038/srep18666.
- 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.
- Winterhalder, K. 1995a. Early history of human activities in the Sudbury area and ecological damage to the landscape. *In Restoration and recovery of an* industrial region. *Edited by* J.M. Gunn. Springer Verlag. pp. 17–31.
- Winterhalder, K. 1995b. Natural recovery of vascular plant communities in the industrial barrens of the Sudbury area. *In* Restoration and recovery of an industrial region. *Edited by* J.M. Gunn. Springer Verlag. pp. 93–102.
- Winterhalder, K. 1995c. Dynamics of plant communities and soils in revegetated ecosystems: a Sudbury case study. *In* Restoration and recovery of an industrial region. *Edited by* J.M. Gunn. Springer Verlag. pp. 173–182.
 Winterhalder, K. 1996. Environmental degradation and rehabilitation of the
- Winterhalder, K. 1996. Environmental degradation and rehabilitation of the landscape around Sudbury, a major mining and smelting area. Environ. Rev. 4: 185–224. doi:10.1139/a96-011.
- Woodfine, D.G., and Havas, M. 1995. Pathways of chemical recovery in acidified, metal-contaminated lakes near Sudbury, Ontario, Canada. Water Air Soil Pollut. 85: 797–803. doi:10.1007/BF00476927.
- Yan, N.D. 1979. Phytoplankton community of an acidified, heavy metal-

contaminated lake near Sudbury, Ontario: 1973–1977. Water Air Soil Pollut. 11: 43–55. doi:10.1007/BF00163517.

- Yan, N.D., and Geiling, W. 1985. Elevated planktonic rotifer biomass in acidified metal-contaminated lakes near Sudbury, Ontario. Hydrobiologia, 120: 199– 205. doi:10.1007/BF00045163.
- Yan, N.D., and Stokes, P. 1978. Phytoplankton of an acidic lake, and its responses to experimental alterations of pH. Environ. Conserv. 5: 93–100. doi:10.1017/ S0376892900005531.
- Yan, N.D., and Strus, R. 1980. Crustacean zooplankton communities of acidic, metal-contaminated lakes near Sudbury, Ontario. Can. J. Fish. Aquat. Sci. 37: 2282–2293. doi:10.1139/f80-275.
- Yan, N.D., Keller, W., Pitblado, J.R., and Mackie, G.L. 1988. Daphnia-Holopedium relationships in Canadian Shield lakes ranging in acidity. Verh. Internat. Verein. Limnol. 23: 252–257.
- 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. PMID:27755679.
- Yan, N.D., Keller, W., and Gunn, J.M. 1995. Liming of Sudbury lakes: lessons for recovery of aquatic biota from acidification. *In* Restoration and recovery of an industrial region. *Edited by* J.M. Gunn. Springer Verlag. pp. 195–204.
 Yan, N.D., Keller, W., Scully, N.M., Lean, D.R.S., and Dillon, P.J. 1996a. Increased
- Yan, N.D., Keller, W., Scully, N.M., Lean, D.R.S., and Dillon, P.J. 1996a. Increased UV-B penetration in a lake owing to drought-induced acidification. Nature, 381: 141–143. doi:10.1038/381141a0.
- Yan, N.D., Welsh, P.G., Lin, H., Taylor, D.J., and Filion, J.-M. 1996b. Demographic and genetic evidence of the long-term recovery of Daphnia galeata mendotae (Crustacea; Daphnidae) in Sudbury lakes following additions of base: the role of metal toxicity. Can. J. Fish. Aquat. Sci. 53: 1328–1344. doi:10.1139/f96-066.
- Yan, N.D., Keller, W., Somers, K.M., Pawson, T.W., and Girard, R.E. 1996c. 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/f96-065.
- Yan, N.D., Leung, B., Keller, W., Arnott, S.E., Gunn, J.M., and Raddum, G.R. 2003. Developing conceptual ecological frameworks for the recovery of aquatic biota from acidification. Ambio, **32**: 165–169. doi:10.1579/0044-7447-32.3.165. PMID:12839190.
- Yan, N.D., Girard, R., Heneberry, J.H., 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., Paterson, A.M., Somers, K.M., and Scheider, W.A. 2008a. An introduction to the Dorset special issue: transforming understanding of factors that regulate aquatic ecosystems on the southern Canadian Shield. Can. J. Fish. Aquat. Sci. 65: 781–785. doi:10.1139/f08-077.
- Yan, N.D., Somers, K.M., Girard, R.E., Paterson, A.M., Keller, W., Ramcharan, C.W., et al. 2008b. Long-term trends in zooplankton of Dorset, Ontario, lakes: the probable interactive effects of changes in pH, TP, DOC and predators. Can. J. Fish. Aquat. Sci. 65: 862–877. doi:10.1139/f07-197.
- Yan, N.D., Bailey, J., McGeer, J., Manca, M., Keller, W., Celis-Salgado, M., et al. 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. doi:10.4081/jlimnol.2016.1226.

Appendix

Appendix Figs. A1 to A4 are provided on the following pages.







Fig. A3. Time series for Ca for 42 Extensive monitoring lakes sampled once annually in the summer epilimnion, 1981–2015.

Fig. A4. Time series for dissolved organic carbon (DOC) for 42 Extensive monitoring lakes sampled once annually in the summer epilimnion, 1981–2015.

