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

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Complete List of Authors:	Keller, Wendel (Bill); Laurentian University Heneberry, Jocelyne; Ontario Ministry of the Environment and Climate Change, Cooperative Freshwater Ecology Unit; Laurentian University Edwards, Brie A.; Ontario Ministry of the Environment and Climate Change, Cooperative Freshwater Ecology Unit; Laurentian University
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4 W. (Bill) Keller, Cooperative Freshwater Ecology Unit, Vale Living with Lakes Centre,
5 Laurentian University, Sudbury, Ontario, P3E 2C6, Canada

6 Jocelyne Heneberry, Ontario Ministry of the Environment Conservation and Parks, Cooperative
7 Freshwater Ecology Unit, Vale Living with Lakes Centre, Laurentian University, Sudbury,
8 Ontario, P3E 2C6, Canada

9 Brie A. Edwards, Ontario Ministry of the Environment Conservation and Parks, Cooperative
10 Freshwater Ecology Unit, Vale Living with Lakes Centre, Laurentian University, Sudbury,
11 Ontario, P3E 2C6, Canada

12
13 Correspondence:

14 W. (Bill) Keller, Cooperative Freshwater Ecology Unit, Vale Living with Lakes Centre,
15 Laurentian University, Sudbury, Ontario, P3E 2C6, Canada
16 Phone: 705 671 3858
17 Fax: 705 671 3857
18 Email: bkeller@laurentian.ca

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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 1970's have led to widespread chemical improvements in these lakes, and recovery has been observed for various aquatic biota. Studies of Sudbury area lakes are advancing our understanding of chemical and biological lake recovery; however, recovery is a complicated process and much remains to be learned. Biological recovery has often been slow to follow chemical recovery, and it has become apparent that the recovery of lakes from acidification is closely linked to interactions with other large-scale environmental stressors like climate change 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.

Keywords. Acidification, lakes, biota, recovery, Sudbury

Introduction

The mining and smelting of metals in the Sudbury, Ontario, Canada area began in the late 1800's (Winterhalder 1995a) and over time the Sudbury smelters became one of the world's largest sources of sulphur dioxide (SO₂) emissions, releasing ~ 2500 kilotonnes per year in the 1960's. 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 1960's (Gorham and Gordon 1960; OWRC 1970) and by the mid 1970's 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; Beamish et al. 1975; Conroy and Keller 1976; Conroy et al. 1976). By the mid 1970's, 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), programmes that expanded during the 1980's.

Based on large-scale chemistry surveys conducted in the 1980's it was estimated that over 7,000 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 lakewaters (Conroy et al. 1976, 1978) and sediments (Semkin and

66 Kramer 1976; Conroy et al. 1978) had accompanied acidification. As studies progressed, it
67 became apparent that widespread acidification damage had occurred to many biological
68 components of aquatic ecosystems including fish (Keller 1978; Matuszek et al. 1992), benthic
69 invertebrates (Conroy et al. 1976; Roff and Kwiatkowski 1977; Stephenson and Mackie 1986),
70 zooplankton (Spules 1975, 1977; Roff and Kwiatkowski 1977; Yan and Strus 1980; Keller and
71 Pitblado 1984; Yan and Geiling 1985; Yan et al. 1985; MacIsaac et al. 1987; Yan et al. 1988),
72 benthic filamentous algae (Keller et al. 1980; Vandermeulen et al. 1993) and phytoplankton
73 (Conroy et al. 1976; Kwiatkowski and Roff 1976; Yan and Stokes 1978; Yan 1979; Nicholls et
74 al. 1992). This biological damage, at various aquatic trophic levels, included the loss of acid-
75 sensitive species and reduced community richness. However, along with the documentation of
76 large-scale aquatic damage came the realization that lakes were already showing increases in pH
77 and reductions in Cu and Ni concentrations in the 1980's (Hutchinson and Havas 1986; Keller
78 and Pitblado 1986) in response to large reductions in SO₂ and metal emissions at the Sudbury
79 smelters in the early 1970's as well as declines in overall North American sulphur emissions.
80 The focus of aquatic studies in the Sudbury area began to change, from damage assessment to
81 investigating patterns of chemical and biological recovery. Additional emission reduction
82 programmes in the late 1970s and early 1990's, which, along with the earlier cuts, achieved >
83 90% reductions from previous peak levels of SO₂ (see for example Fig. 2 in Keller 2009) and
84 metal emissions, gave reason for guarded optimism for the future of northeastern Ontario lakes.
85 Expectations for ecosystem recovery were positive; however, the actual knowledge of chemical
86 and biological recovery processes was limited, and ongoing study was essential to track and
87 understand long-term recovery patterns. While much has been learned, many uncertainties
88 remain.

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

93
94 **Sudbury lakes**

95 There is no “typical” Sudbury lake (Keller 1992). Lakes affected by the Sudbury smelter
96 emissions fall along a continuum, from very remote, dilute, oligotrophic systems in highly acid-
97 sensitive terrain distant from Sudbury, to urban lakes close to the smelters and subjected to urban
98 stressors such as nutrient and road salt inputs as well as atmospheric metal and acid deposition.
99 This diversity of Sudbury lakes greatly amplifies the broad, international value of the Sudbury
100 lake monitoring programmes. Relatively pristine lakes distant from the smelters are similar to the
101 dilute, acid-sensitive lakes that have typically been affected by long-range acid deposition in
102 other areas of North America and Europe (Garmo et al. 2014) offering valuable comparisons for
103 other regions. Because of these similarities Norwegian scientists visited some of these lakes in
104 the 1990’s to develop and test methods of assessing lake recovery, in anticipation of impending
105 benefits from European sulphur emission controls (Gunn and Sandoy 2003). The more urbanized
106 Sudbury lakes offer opportunities to better understand the aquatic effects of interacting multiple
107 stressors in heavily developed landscapes (Gunn and Keller 1995; Valois et al. 2011). The lakes
108 closest to the Subury smelters that were historically highly acidic and metal-contaminated offer
109 valuable comparisons to other lake regions directly affected by metal smelters in other areas of

Canada (Alpay 2006; Jeziorski et al. 2013) and 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 1980’s and 1990’s 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 1970’s (Lohi, Middle, Hannah) or the 1990’s (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, SO_4 , Ca and dissolved organic carbon (DOC) are presented in Tables A1 to A4 of the Appendix); 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; 1992a; 1999a, b; 2001a; Woodfine and Havas 1995). Changes included the expected declines in acidity and SO₄ concentrations (Figs. 2a, b). While 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. 2a).

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 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. 1990a; 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, 2a). 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 ~ 50 km southwest and ~ 110 km north of Sudbury, such as Nellie and Sunnywater lakes, respectively (Figs. 1, 2a). 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 SO_4 concentrations since 1981 (Fig. 2b). In the mid 1970's elevated lakewater SO_4 concentrations ($> 10 \text{ mg L}^{-1}$) were detectable to ~ 140 km from Sudbury (Conroy et al. 1978). Such elevated SO_4 concentrations now only occur in a few lakes very close ($< 10 \text{ km}$) to the Sudbury smelters (Fig. 3a), although concentrations over 5 mg L^{-1} extend to ~ 50 km, and lakewater SO_4 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. 2008a) that reflect regional background levels as affected by long range atmospheric transport (Fig. 3a).

176

177 **Metals**

178 While lakewater metal (Cu, Ni) concentrations have also declined greatly in Sudbury area
179 lakes, residual metal contamination in water and sediments persists in the lakes closest to
180 Sudbury, and will likely continue for many years (Nriagu et al. 1998; Keller et al. 1999b). Some
181 of the lakes close to Sudbury are also affected by urban stresses such as road salting and nutrient
182 inputs from shoreline development (Gunn and Keller 1995; Pearson et al. 2002; Tropea et al.
183 2011), affecting metal toxicity and complicating patterns of recovery (Celis-Salgado et al. 2016).
184 In the 1970's metal (Ni, Cu) concentrations in lakewaters exceeding $30 \mu\text{g L}^{-1}$ for Ni and $25 \mu\text{g}$
185 L^{-1} for Cu were detected to ~ 40 and 80 km , respectively, from Sudbury (Conroy et al. 1976).
186 Currently (2015), elevated concentrations of these metals, exceeding Ontario Guidelines (MOEE
187 1994) for surface waters (Ni $25 \mu\text{g L}^{-1}$, Cu $5 \mu\text{g L}^{-1}$) are restricted to lakes within $\sim 20 \text{ km}$ of
188 Sudbury. However, slightly elevated Ni and Cu concentrations are still detectable in some lakes
189 up to $\sim 50 \text{ km}$ from Sudbury (Figs. 3b, 3c), a legacy of past widespread metal deposition on the
190 landscape.

191 In contrast to Cu and Ni, concentrations of total Al (Fig. 3d) do not show a relationship to
192 distance from the smelters, since acid-leaching of soils and increased lake acidity, not direct
193 atmospheric deposition, were the major factors causing elevated Al concentrations (Keller et al.
194 2003) in acidified lakes. While Al concentrations have greatly declined through time, they are
195 still (2015) highly correlated with pH ($r_s -0.78$, $p < 0.05$). The Extensive monitoring lakes with
196 the highest recent Al concentrations ($140 - 258 \mu\text{g L}^{-1}$) all still have $\text{pH} < 5.6$.

197

198 Calcium

199 Unexpectedly, large declines in Ca concentrations (Fig. 2c) were also observed in
200 Sudbury lakes as acidity decreased (Keller et al. 2001b) a pattern that was soon after documented
201 broadly in Precambrian Shield lakes across central and northern Ontario (Jeziorski et al. 2008;
202 Edwards et al. 2009). Ca concentrations in many formerly acidified lakes near Sudbury are now
203 much lower than diatom-inferred background conditions determined from paleolimnological
204 analyses of sediment cores (Keller et al. 2001b, 2003). Declines in lakewater Ca concentrations
205 averaging 55% (49 to 67%) have occurred in all Extensive monitoring lakes since annual
206 sampling commenced in 1981 (Fig. 2c). Declines in Ca (1981 vs 2015) were significantly
207 correlated ($r_s = 0.84$, $p < 0.05$) with declines in SO_4 . Considering charge balances ($\mu\text{eq L}^{-1}$) the
208 declines in Ca on average balance 46% of the declines in SO_4 (27 to 72% in individual lakes).
209 Almost all (40) of the 42 Sudbury area Extensive monitoring lakes considered here (Fig. 1) now
210 have $\text{Ca} < 2 \text{ mg L}^{-1}$ (Fig. 2c), and most (33) of these lakes now have Ca concentrations below 1.5
211 mg L^{-1} , an approximate threshold for damage to the most sensitive *Daphnia* species and chronic
212 stress in native crayfish in Precambrian Shield lakes (Ashforth and Yan 2008; Jeziorski et al.
213 2008; Cairns and Yan 2009; Edwards et al. 2015). However, the effect of Ca declines on aquatic
214 species is a complex issue, involving differing species sensitivities, lethal and sub-lethal
215 toxicity, and altered predatory interactions (Cairns and Yan 2009; Jeziorski et al. 2012; Riessen
216 et al. 2012; Azan and Arnott 2017; Jeziorski and Smol 2017). The only two Extensive
217 monitoring lakes with Ca still above 2 mg L^{-1} are urban lakes (Clearwater, Tilton; Fig. 1). Ca
218 concentrations in these lakes may have been affected by urban influences such as local watershed
219 development and dust control applications of CaCl_2 to gravel roads.

Declining Ca concentrations are already having effects on lake zooplankton communities in Ontario (Jeziorski et al. 2014) inducing 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). While 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 ($\text{DOC} < 1.5 \text{ mg L}^{-1}$) 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 to 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 SO_4 ($r_s = -0.60$, $p < 0.05$) again suggesting that declines in sulphur deposition were a major factor affecting DOC increases. While generally, Ontario lakes are not at great risk of damage by UV-B irradiance (Molot et al. 2004) some very clear Sudbury area lakes may be exceptions. However, in 2015, only six of the 42 Extensive monitoring lakes had $\text{DOC} < 2 \text{ mg L}^{-1}$, a level below which UV attenuation is greatly reduced (Williamson et al. 1996).

In the relatively small ($< 500 \text{ ha}$) lakes that cover the northern Ontario landscape, lake clarity/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. 2015a) to aquatic organisms. Thus, it is likely that DOC increases are helping reduce metal

265 toxicity in Sudbury area lakes and that such benefits will increase as terrestrial systems recover
266 further, re-building organic soils and contributing increased organic matter inputs to lakes.

267

268 **Total phosphorus and nitrate**

269 All but six of the Extensive monitoring lakes did not show any evidence of temporal
270 changes in total phosphorus (TP) concentrations based on analyses of slopes over the 1981-2015
271 period. This conclusion is not surprising perhaps, since shoreline development is not heavy on
272 any of the Extensive lakes and most have none, although many lakes in south-central Ontario
273 have declined in TP even with increases in human activity (Eimers et al. 2009) from causes that
274 are not clear. More heavily urbanized lakes in Sudbury have shown evidence of cultural
275 eutrophication based on comparisons with background conditions estimated by hindcasts from
276 watershed TP models (Gunn and Keller 1995) and inferred from paleolimnological analyses of
277 diatoms in sediment cores (Tropea et al. 2011). Lake and watershed characteristics do not point
278 to any obvious explanation for the apparent decreases (Sans Chambre, Telfer) or increases (Bob,
279 Klock, Tillie, Crooked) in a few of the Extensive lakes. It is recognized, however, that the use of
280 single summer samples for TP analyses may limit the ability to detect trends since substantial
281 biological TP (and nitrogen) utilization may already have occurred at the time of sampling.
282 Future, more rigorous assessment of trends in nutrients, considering lakes with more frequently
283 collected, seasonal data, such as the Intensive lakes might be more revealing.

284 Atmospheric Deposition of N in the Sudbury area is primarily from long-range sources
285 since the Sudbury smelters have never been a large N source (Keller et al. 2003). While nitrate
286 (NO_3) 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. 2104). 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, 1992a, 1992b, 1993, 1995, 1996; Smol et al. 1998). While evidence of recovery was widely observed, changes were not always towards inferred background

308 conditions. In Sudbury area lakes with residual metal-contamination, communities of diatoms
309 have not begun to recover (Tropea et al. 2010). As well, even in lakes that were not heavily
310 metal contaminated, recovery trajectories do not necessarily track towards pre-industrial diatom
311 assemblages (Sivarajah et al. 2016, 2017) likely because of climate warming effects.

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

315

316 **Zooplankton**

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

328 Dispersal does not seem to greatly constrain recovery in lake-rich regions where there are
329 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). While most zooplankton species (both rotifers and crustaceans) seem to re-establish comparatively quickly (MacIsaac et al. 1986; Keller et al. 1992c; Havas et al. 1995; Keller et al. 2002), some species including hypolimnetic forms (*Daphnia longiremis*, *Cyclops scutifer*), and the so called “glacial opportunists” including *Senecella calanoides*, *Limnocalanus macrurus*, *Leptodiatomus sicilis* and *Diatomus 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) which 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. 2016b) as it has been for many decades (Yan et al. 1996b). 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 to lakewaters 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 non-mobile 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 (*Hyaella 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 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. 2010a, b; 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 1990's sediment concentrations of Ni and Cu still exceeded, often greatly, Ontario Sediment Quality Guidelines for the protection of aquatic life (75 and 110 $\mu\text{g g}^{-1}$ for Ni and Cu, respectively, MOEE 1993) out to ~ 50 km from Sudbury (Keller et al. 2004). While 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 $\mu\text{g g}^{-1}$ (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). Re-establishment 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; Gunn and Keller 1990; Gunn et al. 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).

419 **Lake and watershed liming**

420 In contrast to other acid-affected areas of the world, particularly Scandinavia (Olem et al.
421 1991; Henrikson and Brodin 1995), large-scale lake liming programmes were not implemented
422 in Ontario because with an estimated 19,000 acidified lakes (Neary et al. 1990) liming as a lake
423 management strategy was not considered to be economically or logistically feasible. As well,
424 since liming is only a temporary interim step, not a solution, for the lake acidification problem,
425 the focus in Ontario was on achieving effective controls on acid-causing emissions (Keller
426 2009). A small number of whole-lake liming activities were, however, conducted in Ontario to
427 experimentally determine the responses of lake communities to reduced acidity (Dillon et al.
428 1979; Dodge et al. 1988; Keller et al. 1990c; Yan et al. 1995) or to assist with the restoration of a
429 unique strain of brook trout, the aurora trout, which had been eliminated from its natural lakes by
430 acidification (Snucins et al. 1995a, b).

431 In total, eight lakes were limed in Ontario, with seven in the Sudbury area. Lake liming
432 activities were successful in increasing lake pH (Dillon et al 1979; Molot et al. 1990a; Yan et al.
433 1995) and also substantially reduced lakewater metal concentrations in the highly metal-
434 contaminated lakes closest to Sudbury, although metal concentrations remained high (Dillon et
435 al. 1979). Positive responses to liming were observed in many groups of organisms, including
436 stocked lake trout (Gunn et al. 1990), phytoplankton (Molot et al. 1990b), littoral algae (Jackson
437 et al. 1990), zooplankton (Keller et al. 1992c), and benthic macroinvertebrates (Keller et al.
438 1990b; Carbone et al. 1998). However, in most of the limed lakes re-acidification occurred
439 relatively quickly, providing only limited opportunities to examine biological responses to
440 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 which 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 do 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 SO₂ fumigations from early metal smelting activities damaged vegetation in a large area surrounding Sudbury, leading to large-scale erosion (Winterhalder 1995a). Terrestrial damage left a large (17,000 ha) area barren of vegetation with severely eroded soils, within a 72,000 ha semi-barren area, around the Sudbury smelters (Winterhalder 1995a). However, with time, some natural re-vegetation has occurred (Winterhalder 1995b,c) with reduced smelter emissions (Potvin et al. 1995), and large-scale land restoration programmes including soil liming and tree planting have dramatically re-greened 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 re-forested areas is expected to have direct benefits to benthic invertebrates and ultimately to fish growth (Wesolek et al. 2010a; 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).

485 **Shifting reference conditions**

486 The fundamental nature of aquatic ecosystems in Ontario is changing in the face of
487 multiple anthropogenic stressors including climate warming, Ca decline, and invasive species.
488 Even in non-acidified Ontario lakes, chemistry and populations of zooplankton (Jeziorski et al.
489 2008; Yan et al. 2008; Palmer et al. 2011, 2013; Palmer and Yan 2013) and phytoplankton
490 (Paterson et al. 2008) have changed in recent decades. Variability in observed temporal changes
491 in lake plankton communities suggests that there can be strong heterogeneity in lake responses
492 within and across regions, due to influences such as climate change (Arnott et al. 2003b).
493 Paleolimnological studies suggest that cladoceran and diatom communities in some recovering
494 lakes are not moving back to their historical conditions, but rather they are moving to new
495 states, likely because of climate warming (Labaj et al. 2016; Sivaraja et al. 2016, 2017).

496 Exotic invasive species are not yet widely distributed in inland lakes in Ontario; however,
497 when present the exotic invader *Bythotrephes* has had dramatic effects on resident zooplankton
498 populations (Boudreau and Yan 2003; Yan et al. 2008). Future expansions of this invader, likely
499 with severe consequences for resident zooplankton, including reduced species richness and
500 altered community structure (Strecker and Arnott 2005; Strecker et al. 2006), appear to be
501 inevitable (Pagnucco et al. 2015). Range expansion of native species as well as exotic species
502 can have dramatic effects on aquatic ecosystems. The northward expansion of bass (*M.*
503 *dolomieu*, *Micropterus salmoides*, *Ambloplites rupestris*) with a warming climate has the
504 potential to significantly alter food webs in northern Ontario lakes, through heavy predation by
505 bass on littoral food resources (Vander Zanden et al. 2004; Alofs and Jackson 2015). Recovering
506 lakes without established fish communities and lacking top predators may be particularly at risk
507 of invasion (Alofs and Jackson 2014). Climate change is also predicted to threaten the re-

508 establishment and persistence of many native cool- and cold-water fish species, further
509 increasing the invasibility of northern lakes (Edwards et al. 2016; Van Zuiden et al. 2016).

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

518

519 **Summary**

520 Once viewed as an international icon of environmental devastation, the Sudbury area now
521 provides one of the best examples in the world of successful environmental restoration and
522 recovery. Sudbury area studies have given a powerful demonstration of the environmental
523 benefits of air pollution controls. Long-term monitoring of lakes in the region has shown
524 remarkable chemical improvements after very large reductions of sulphur and metal emissions
525 from area smelters and reduced acid deposition from long-range sources. Because of the large,
526 relatively early regional sulphur emission reductions, lakes in the Sudbury area allowed
527 documentation of the lake recovery process before the implementation of substantial emission
528 controls in other areas. This evidence of aquatic ecosystem recovery was crucial in establishing
529 the necessity of sulphur emission controls during the international debates about the effects of

530 acid deposition and the need for action. Results from Sudbury area lakes have also led to the
531 development of a number of conceptual models of chemical and biological recovery processes
532 (Keller and Yan 1998; Yan et al. 2003; Keller et al. 2007) that continue to guide international
533 lake recovery studies. While the major contribution of Sudbury lake studies has been to
534 acidification research, these long-term data series, especially for zooplankton, have also had
535 substantial additional value for limnology in general. For example, Sudbury lake monitoring data
536 have helped advance the understanding of broad ecological issues related to relationships of
537 aquatic community change with environmental change (Helmus et al. 2010; Shurin et al. 2010;
538 Lamothe et al. 2018), and have allowed real-world validation of metal toxicity models for
539 aquatic invertebrates (Khan et al. 2012; Stockdale et al. 2014; Balistrieri et al. 2015).

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

550

551 **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 lake monitoring 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 datasets 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 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 need 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 lake monitoring 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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1190 **Appendix**

1191 Appendix Figs. A1 to A4 are provided on the following pages.

Draft

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Figure captions

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.

Fig. 2. Linear mixed-effect model slopes describing the observed temporal trends over the period 1981-2015 for pH (a), SO_4 (b), Ca (c) and DOC (d) for 42 Extensive monitoring lakes shown in Fig 1. Slopes are presented in rank order and display the 95% confidence interval for each lake. Lake specific slope was calculated as the conditional mean random effect slope, and standard error for each lake was calculated as the standard error of the conditional mean of each random effect slope. The 95% CI was then calculated as the mean slope ± 1.96 times its standard error. Slopes were deemed significant if their 95% CI did not overlap zero. CI's for SO_4 are too narrow to show at this scale. All lakes had increases in pH and decreases in SO_4 and Ca over this period. All but five lakes had increases in DOC.

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 SO₄ concentrations in eight Dorset, Ontario lakes in July 2015 is also shown in panel a (horizontal dashed lines).

Fig. A1. Time series for pH for 42 Extensive monitoring lakes sampled once annually in the summer epilimnion, 1981-2015.

Fig. A2. Time series for SO₄ for 42 Extensive monitoring lakes sampled once annually in the summer epilimnion, 1981-2015.

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.

Keller et al. Fig. 1.

Lake specific slope and 95% Conf. Int.

Keller et al. Fig. 2.

Keller et al. Fig. 3

Table 1. List of abbreviations for the Extensive monitoring lakes shown in Fig. 2 and the Appendix.

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