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Gauging recovery of zooplankton from historical acid and metal contamination: the influence of temporal changes in restoration targets

Michelle E. Palmer[1*,‡], Wendel (Bill) Keller[2] and Norman D. Yan[1,3]

[1]*Department of Biology, York University, 4700 Keele Street, Toronto ON M3J 1P3, Canada;* [2]*Cooperative Freshwater Ecology Unit, Laurentian University, 935 Ramsey Lake Road, Sudbury ON P3E 2C6, Canada and* [3]*Dorset Environmental Science Centre, 1026 Bellwood Acres Road, Dorset ON P0A 1E0, Canada*

Summary

1. Clearly defined restoration targets are necessary to judge the effectiveness of management actions in restoring damaged ecosystems. However, the identification of appropriate targets is difficult in a rapidly changing world. Historical reference conditions commonly provide recovery targets, but they may not be appropriate if present-day environments have shifted in response to regional or global drivers. Such shifts may need to be incorporated into restoration targets to avoid erroneous conclusions about the recovery of ecosystems damaged by localized stressors. No previous study has examined whether the selection of historical vs. present-day reference conditions alters judgments of the recovery of historically damaged ecosystems.

2. We examined 35-year trends in the zooplankton communities of four lakes polluted by smelter emissions in Sudbury, Ontario, Canada. Recovery was assessed by comparing the Sudbury lakes to both historical (1983–1984) and present-day (2004–2006) conditions in a set of minimally impacted reference lakes in south-central Ontario.

3. Sudbury zooplankton communities improved substantially over time when compared with both the historical and present-day recovery targets. However, recovery occurred later, and improvements differed quantitatively when judged against the present-day vs. historical targets. These differences were attributable to regional shifts in zooplankton communities that happened after the historical sampling period but were reflected in the present-day data.

4. Species richness in two Sudbury lakes met recovery targets and communities in all four lakes became more similar to those in the reference lakes. However, the continued absence of many daphniids, cyclopoids and large calanoids indicated that the lakes had not fully recovered and further monitoring is needed.

5. *Synthesis and applications*. Our results show that the choice of reference condition can alter recovery assessments. This finding emphasizes the importance of establishing clearly defined restoration goals to ensure appropriate choice of reference conditions. Restoration is unlikely to be judged as successful if an historical reference point is used to guide management actions meant to restore an ecosystem to present-day regional conditions.

Key-words: acidification, adaptive management, biodiversity, multiple stressors, normal range of variability, reference condition approach, restoration ecology, shifting/sliding baselines, species richness, water quality

‡Present address: Environmental Monitoring and Reporting Branch, Ontario Ministry of the Environment, 125 Resources Road, Toronto ON M9P 3V6, Canada
*Correspondence author. E-mail: michelle.palmer@ontario.ca

Introduction

Ecological restoration, the practice of assisting the recovery of a damaged ecosystem (SER 2004), is a critical management option in an increasingly human-dominated landscape. To evaluate the success of a restoration project, recovery must be measured against an explicit restoration target that quantitatively defines the desired ecological endpoint such that practitioners can monitor the effectiveness of restoration activities (Hughes *et al.* 1990; Michener 1997). However, a primary dilemma for restoration scientists and practitioners is determining appropriate and realistic restoration goals amid a myriad of ecological, operational, financial and social constraints (Miller & Hobbs 2007; Thorpe & Stanley 2011; Wilson *et al.* 2011).

Restoration targets are predominantly set using a reference condition that typifies the state of the damaged ecosystem prior to, or in the absence of, significant anthropogenic disturbance (Reynoldson *et al.* 1997), a method that has had variable success (Leschen, Ford & Evans 2010; Toth 2010). While a return to the historical state is certainly an ideal restoration goal, it is often an unrealistic expectation (Hilderbrand, Watts & Randle 2005). Even when the perceived benefits of historical reconstruction supersede the prohibitive financial and social costs (e.g. Birch *et al.* 2010), the ecological impediments to restoring an ecosystem to its historical state are daunting (Cairns 2006; Pinnegar & Engelhard 2008). Cessation of the damaging activity does not guarantee success as changes in other, often unmonitored, natural and anthropogenic processes can alter the trajectory of the ecosystem away from the desired state (Campbell *et al.* 2009; Duarte *et al.* 2009). Global climatic change adds a further complication as climate-induced shifts in species distributions may render restoration targets based on historical climate conditions obsolete (Ravenscroft *et al.* 2010). This has raised concerns about the efficacy of historically based restoration targets and suggests present-day environmental conditions and confounding stressors should be considered when identifying restoration goals (Owen, Duncan & Pollard 2001; Nõges *et al.* 2007).

Despite these concerns, the consequences of using historical vs. present-day reference conditions to assess the recovery of a damaged ecosystem have not been tested. Shifting reference conditions, that is the shifting/sliding baseline syndrome (Pauly 1995), can have drastic ramifications for conservation planning, suggesting similar effects may be expected for recovery assessments. Huber, Greco & Thorne (2010) evaluated whether existing reserves met vegetation conservation objectives for the highly human-impacted Central Valley in California, United States, and found that a substantially greater area of land would need to be restored and conserved to meet conservation thresholds based on pre-industrial vs. present-day land cover data, with multibillion dollar ramifications. Similarly, Hermoso *et al.* (2011) found that the use of minimally disturbed vs. present-day scenarios of fish species distributions in an Iberian river basin led to very different recommendations for identifying priority conservation areas. Here, we investigate the impacts of using historical vs. present-day reference conditions to set recovery targets for zooplankton communities in lakes with severe and chronic industrial contamination.

Acid deposition is a primary threat to aquatic biological diversity (Sala *et al.* 2000). In Canada, the largest SO_2 emissions point source was the metal smelting operations near Sudbury, Ontario (Zeng & Hopke 1994). Mining of copper and nickel in Sudbury pre-dates the turn of the last century and early industrial practices led to 'world-class environmental devastation' including the acidification of over 7000 lakes (Gunn 1996). Most lakes within *c.* 70 km of the smelters were also contaminated by atmospheric deposition of heavy metals (Dillon *et al.* 1979). By 1920, lakes were dominated by acid- and metal-tolerant species (Dixit *et al.* 1995), and sensitive taxa were locally extirpated (Scheider, Adamski & Paylor 1975). More recently, the water quality and subsequently the biota (Keller *et al.* 2007) of Sudbury lakes have improved significantly following extensive land restoration efforts and a nearly 90% reduction in SO_2 and metal emissions since the 1960s (Lautenbach *et al.* 1995; Keller *et al.* 2007).

Biological recovery of Sudbury's lakes has been routinely measured against a set of minimally impacted lakes that are within the same biogeographical region as Sudbury (Sprules 1977), but are beyond the influence of its smelters (Zeng & Hopke 1994). A regional reference condition approach was used because premining data are lacking and paleolimnological data are limited to species preserved in the sediments. Comparisons between Sudbury and these reference lakes have been very informative; however, continued use of the historical recovery target, which was based on data collected in the 1980s, has been questioned (Keller *et al.* 2002; Keller 2009). Changes in climate, acid deposition and lakeshore development have altered the thermal regime and water quality of the reference lakes over the last 25 years (Palmer *et al.* 2011; M.E. Palmer, N.D. Yan & K.M. Somers, unpublished data), and correlated shifts in their zooplankton communities have occurred (Yan *et al.* 2008). These regional stressors have caused similar physico-chemical changes in the Sudbury lakes (Keller 2009). To correctly assess recovery and avoid wrongly attributing differences between the reference and damaged lakes to acidification and metal contamination, restoration targets for Sudbury lakes may need to reflect present-day regional conditions.

This study provides the first comprehensive comparison of biological recovery using restoration targets developed from both historical and present-day reference conditions. We examined 35-year trends in the zooplankton communities of industrially polluted Sudbury lakes. Recovery was tested using historical (1983–1984) and present-day (2004–2006) restoration targets based on one set of minimally impacted, regional reference lakes. We found that damaged zooplankton communities have significantly improved over time and some community metrics have recovered in some lakes. Recovery occurred later, and improvements were reduced or enhanced when recovery was assessed using the present-day vs. historical reference condition. Our results prove that shifting baselines impact recovery assessment and underscore the importance of establishing clearly defined restoration goals to ensure appropriate choice of reference conditions.

Materials and methods

STUDY LAKES

Recovery was assessed for four lakes located within 13 km of Sudbury, Ontario (Fig. 1). Historically, the water quality of these lakes was severely degraded because of acid deposition and metal contamination (Fig. 2). As a result, fish were extirpated (Scheider, Adamski & Paylor 1975), phytoplankton biomass was dominated by acid-tolerant dinoflagellates (Yan 1979), and the depauperate zooplankton communities of the lakes were dominated by three acid and metal-tolerant species *Bosmina longirostris*, *Acanthocyclops vernalis* and *Chydorus sphaericus* (Yan & Strus 1979; for species naming authorities see ITIS 2012). To test whether habitat restoration would stimulate recovery, three of the lakes were subjected to intense restoration efforts. In the early- to mid-1970s, $CaCO_3$ and $Ca(OH)_2$ were added to Lohi, Hannah and Middle Lakes (Dillon *et al.* 1979). Small amounts of phosphoric acid were also added to Hannah and Middle Lakes in the mid-1970s (Yan *et al.* 1996), and their watersheds were treated with granular limestone and fertilizer in the early- to mid-1980s to support vegetation regrowth (Lautenbach *et al.* 1995). Following manipulations, pH increased to *c.* 6·5 in Middle, Hannah and Lohi Lakes (Fig. 2a). Lohi quickly reacidified, but pH rose above 6 by 1995. Clearwater Lake, which was used as a control to measure natural recovery, reached pH > 6 in 1999. Total copper and nickel contamination also decreased over time in the lakes (Fig. 2b,c). Metal contamination was greatest in Hannah and Middle Lakes, which were closest to the smelters. By 2007, copper concentrations in both lakes had decreased to 18 $\mu g\ L^{-1}$, while nickel concentrations had decreased to *c.* 100 $\mu g\ L^{-1}$. In Clearwater and Lohi Lakes, copper decreased from *c.* 90 to 9 $\mu g\ L^{-1}$, while nickel decreased from over 200 $\mu g\ L^{-1}$ to just over 50 $\mu g\ L^{-1}$. Zooplankton recovery was last assessed in Clearwater Lake in 2006 and in Hannah, Lohi and Middle Lakes in 2003 (Khan *et al.* 2012).

The 16 reference lakes (Fig. 1) were chosen from 47 candidates located *c.* 200 km from Sudbury in the Muskoka and Parry Sound Districts and Haliburton and Nipissing Counties of south-central Ontario. Principal components analyses on lake morphology and water quality parameters (Table 1) identified four atypical candidate lakes for removal. As our intent was to compare the Sudbury lakes to lakes representative of nonacidic, minimally impacted lakes, an additional 27 candidate lakes were removed as these lakes had pH < 6, a threshold separating acidic and nonacidic zooplankton communities (Holt, Yan & Somers 2003), or were invaded by the Eurasian cladoceran *Bythotrephes longimanus*, a predator that significantly alters zooplankton communities (Yan, Girard & Boudreau 2002) but had not yet spread to Sudbury's urban lakes. Copper and nickel concentrations in the reference lakes were below 2 $\mu g\ L^{-1}$.

DATA COLLECTION

The reference lakes were sampled monthly over the ice-free season (May–October) in 1983 (11 lakes) or 1984 (five lakes) and resampled in 2004 (nine lakes), 2005 (six lakes) or 2006 (one lake). Zooplankton were collected from the deepest point of the lakes using a conical 'DRC' plankton net with 76-μm mesh and a mouth diameter of 12·2 cm. The net was hauled vertically through the water column from 4 to 7 fixed depths, and haul contents were combined into a single monthly composite sample. Haul depths were chosen, so that the composite sample reflected the volumetric profile of the lake. Sample volumes were calculated correcting for the filtration efficiency of the hauls, measured using a current meter in the net mouth.

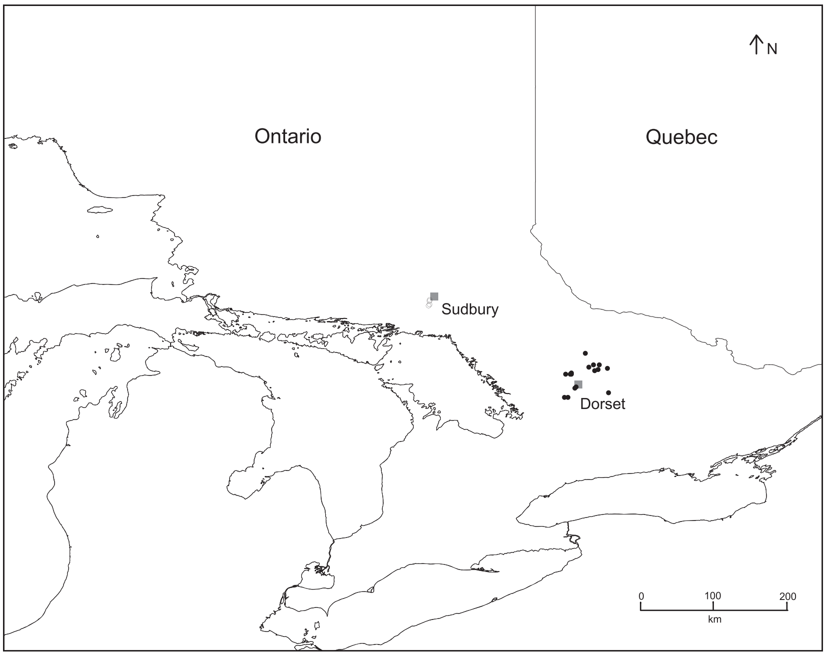

Fig. 1. Location of the study lakes in Ontario, Canada; the four Sudbury lakes are indicated by open circles and the 16 regional reference lakes are indicated by closed circles.

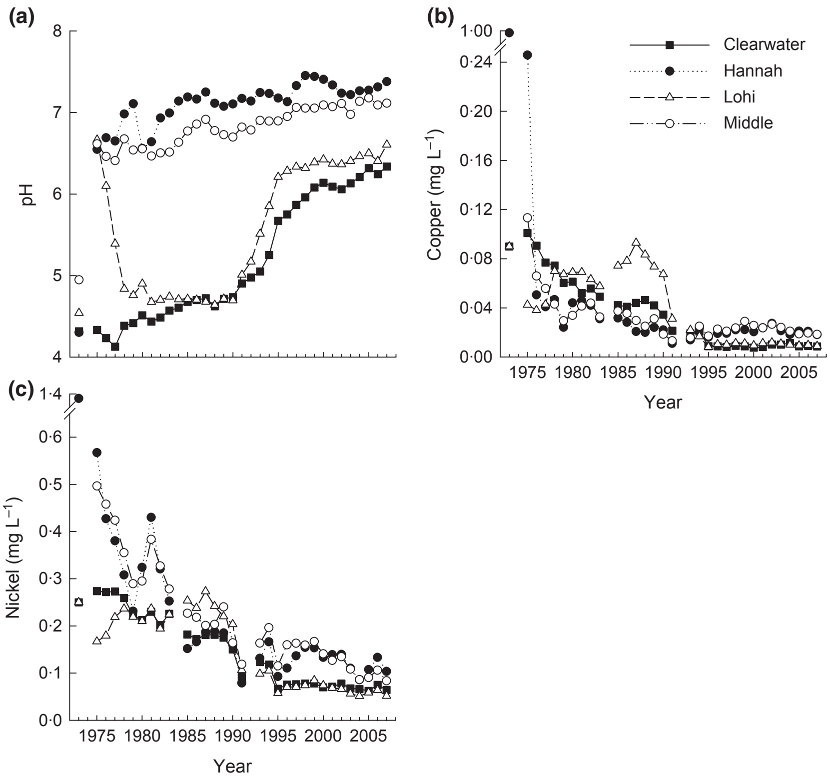

Fig. 2. Long-term trends in (a) pH, (b) copper and (c) nickel in the Sudbury lakes; reported values are ice-free season means.

Table 1. Summary of morphology and water quality parameters for the Sudbury lakes and 16 south-central Ontario regional reference lakes; present-day water quality values for the ice-free season are reported

	Sudbury lakes				Reference lakes		
	Clearwater	Hannah	Lohi	Middle	Median	Min.	Max.
Morphology							
Lake area (ha)	76·5	27·3	40·5	28·2	75·1	10·9	679·0
Max depth (m)	21·5	8·5	19·5	15·0	30·0	13·7	61·0
Shoreline (km)	5·0	2·7	4·5	3·2	5·8	1·5	29·3
Water quality*							
Calcium (mg L^{-1})	4·1	10·4	4·3	9·6	2·2	1·7	3·9
Chloride (mg L^{-1})	9·1	76·6	10·1	53·9	0·5	0·3	5·0
Chlorophyll a (μg L^{-1})	1·3	1·1	2·1	1·8	2·1	1·2	4·6
Dissolved organic carbon (mg L^{-1})	2·8	4·1	3·4	3·9	3·5	1·6	6·5
Iron (μg L^{-1})	33·5	76·2	66·7	70·8	61·2	25·9	307·4
pH	6·3	7·4	6·6	7·1	6·4	6·1	6·7
Sodium (mg L^{-1})	4·5	47·7	5·6	34·1	0·8	0·5	2·8
Sulphate (mg L^{-1})	9·9	17·7	9·5	18·3	5·3	4·5	6·3
Total nitrogen (μg L^{-1})	227·5	374·0	254·8	350·0	280·4	181·2	365·6
Total phosphorus (μg L^{-1})	4·2	8·5	6·1	7·1	6·0	3·4	8·3

*Water quality collection and analysis methods are reported in detail elsewhere (MOE 1983; Girard *et al.* 2007).

The Sudbury lakes were sampled during the ice-free season from 1973 to 2007, except 1980 when none of the lakes were sampled and 1990–1993 when Hannah and Middle Lakes were not sampled. Samples were collected weekly or fortnightly from 1973 to 1979 and monthly from 1981 to 2007. From 1973 to 1975, monthly samples represented a single vertical haul at the deepest point of the lakes using an unmetered Wisconsin net with 80-μm mesh and a mouth diameter of 11–29 cm. From 1976 to 1979, zooplankton were collected at 2- to 3-m vertical intervals at four pelagic stations per lake using a 30- to 34-L Schindler-Patalas Plexiglass trap with 30- to 80-μm mesh net and bucket. After 1980, samples were collected at the deepest point of the lakes using the DRC net hauled from four fixed depths based on lake bathymetry. Changes in sampling frequency and gear did not affect zooplankton community metrics (Yan & Strus 1979; Yan *et al.* 1996).

Zooplankton were preserved in the field in 4–6% buffered sugar formalin. Crustacean zooplankton were subsequently identified and enumerated using ZEBRA, a semi-automated sample processing system (Girard *et al.* 2007). Adults and immature cladocerans were identified to species, while immature copepods were identified to suborder. For the reference lakes, a minimum of 250 individuals were identified and counted per sample. For the Sudbury lakes, all individuals within a sample were counted from 1973 to 1975, 350–400 individuals per sample were counted from 1976 to 1984, and a minimum of 250 individuals per sample were counted after 1984. The counting protocol ensured that unique counting categories (species or life stage) did not account for >20% of the total count. Abundances were calculated based on the fraction of the total sample volume processed. To accommodate nomenclature changes over time, *Alona*, *Bosmina*, *Ceriodaphnia*, *Diaphanosoma* and *Simocephalus* species were combined to genus; *Tropocyclops mexicanus* was combined with *Tropocyclops extensus*; *Daphnia catawba* and *Daphnia pulicaria* were combined with *Daphnia pulex*; and *Daphnia dentifera* and *Daphnia rosea* were combined with *Daphnia mendotae*. Owing to unequal detection effort over time, the macrozooplankton species *Leptodora kindtii* and *Polyphemus pediculus* were excluded.

RECOVERY TARGETS

Recovery was assessed using metrics shown to be sensitive indicators of recovery from acidification: crustacean species richness and multivariate ordination scores from correspondence analyses (CA) on cladoceran and copepod abundance matrixes (Yan *et al.* 1996, 2004; Keller *et al.* 2002; Frost *et al.* 2006). Richness was calculated as the number of species identified per month averaged over the ice-free season; monthly richness values for the Sudbury lakes prior to 1981 represented the average of weekly or fortnightly values. CA ordination scores, which incorporated both species relative abundances and interspecies covariation patterns, were calculated from ice-free mean abundances of common species (species present in $\geq 10\%$ of lakes or lake–year pairs). Abundances were $\log_{10}(x + 1) + 0{\cdot}2$ transformed to stabilize variances and further reduce the influence of rare species; immature copepods were excluded from analyses. Separate analyses for each Sudbury lake were executed in STATISTICA version 9 (StatSoft Inc., Tulsa, OK, USA). Lakes were considered recovered when their richness and ordination scores were within the typical range of variability of the reference lakes, that is within 2 standard deviations of the reference mean (Yan *et al.* 1996; Kilgour, Somers & Matthews 1998).

Results

SHIFTING REFERENCE CONDITION

Mean crustacean species richness in the reference lakes increased from 10·1 ± 1·3 species in 1983–1984 to 11·3 ± 1·3 species in 2004–2006 (paired *t*-test $t = 4$, $P = 0{\cdot}001$). This was due to a 0·7 ± 1·2 increase in cladoceran and a 0·5 ± 0·7 increase in copepod species richness (*P*-values <0·05). The species composition of the reference lakes also changed over time as indicated by an increase in lake scores along CA axis II (paired $t = 2{\cdot}1$, $P = 0{\cdot}056$; Fig. 3).

ASSESSMENT OF RECOVERY

As water quality improved, zooplankton communities changed in the Sudbury lakes. Over the study period, 24–32 zooplankton species were detected in the lakes. Ice-free mean crustacean richness increased from *c.* 2 to 4 species from 1973 to 1981 to 6·8 species in Clearwater and Lohi Lakes and *c.* 9·5 species in Hannah and Middle Lakes in 2007 (Fig. 4). Increases in richness were significant (Mann–Kendall trend tests *Z*-values >4·6, *P*-values <0·001) and were correlated with increases in pH and decreases in copper and nickel (Spearman rank order correlation coefficients = 0·60–0·92, *P*-values <0·001). In comparison with the historical richness target in the reference lakes (8–13 species), richness in Hannah and Middle Lakes had recovered by 2003 and 2004, respectively (Fig. 4a,b). Recovery in these lakes was delayed by 1–4 years when richness was compared with the present-day target of 9–14 species (Fig. 4c,d). Richness improved but did not recover in Clearwater and Lohi Lakes. When the median slope of the long-term trend (0·08 and 0·10 species year^{-1} for Clearwater and Lohi Lakes, respectively) was used to estimate the rate of recovery post-2007, richness in these lakes was projected to be within the historical recovery target by 2015–2017. In contrast, recovery was projected to occur 13 years later when the present-day richness target was employed. However, use of the long-term rate of recovery may be conservative if the trajectory of recovery since 2005 continues. Based on the recovery rate from 2005 to 2007 (0·50–0·60 species year^{-1}), richness in Clearwater and Lohi Lakes was projected to be within the historical recovery target by 2010–2011 and within the present-day recovery target by 2012–2013.

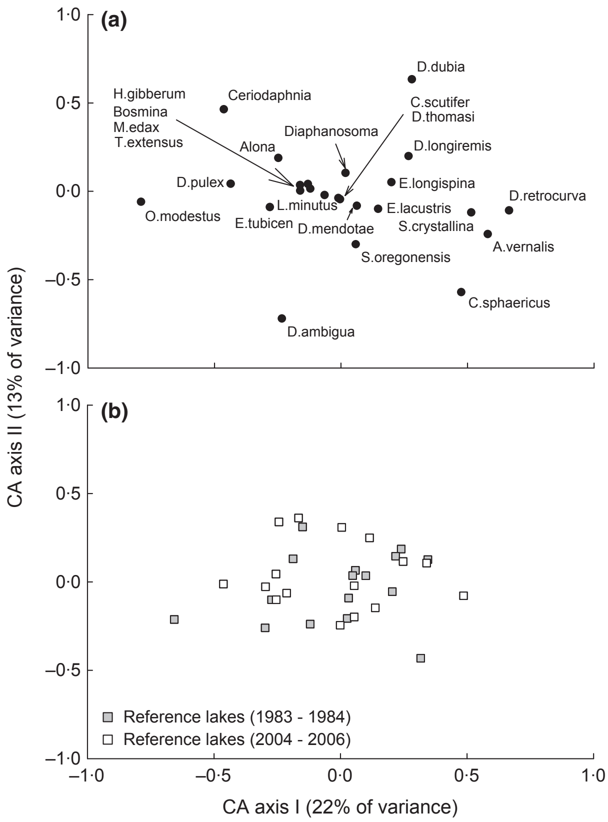

Fig. 3. Taxa (a) and lake (b) scores from a correspondence analysis of zooplankton community composition in the 16 south-central Ontario regional reference lakes using historical and present-day abundances of common taxa.

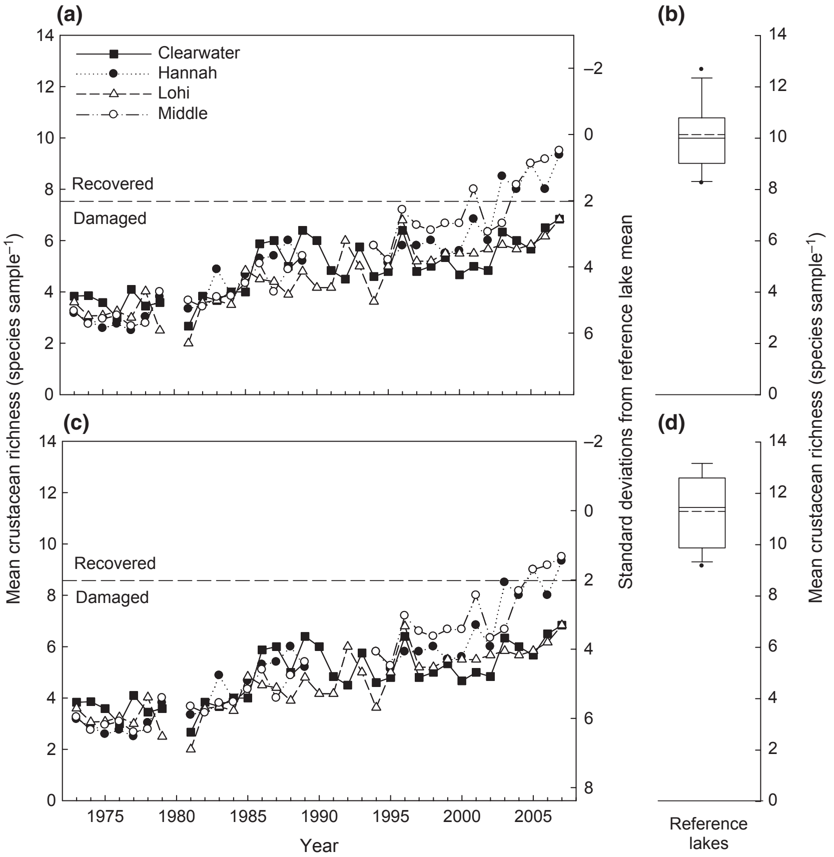

Fig. 4. Long-term trends in zooplankton richness in the Sudbury lakes compared with richness in the 16 south-central Ontario regional reference lakes: (a) damage and recovery in the Sudbury lakes compared with (b) historical richness in the regional reference lakes; (c) damage and recovery in the Sudbury lakes compared with (d) present-day richness in the regional reference lakes.

Correspondence analyses revealed a shift in the Sudbury zooplankton communities towards the reference lakes over time (Figs 5–8; see Appendix S1 and Fig. S1, Supporting information for species relative abundances over time). The first two CA axes explained 50–56% of the variance in the cladoceran communities of the study lakes and 64–72% of the variance in the copepod communities. Between the 1970s and mid-1990s, the cladoceran communities of the lakes were characterized by *C. sphaericus* and *Bosmina*, as well as *Simocephalus* in Clearwater, Hannah and Middle Lakes. By the late 1990s, *Ceriodaphnia* and *Diaphanosoma* were characteristic of all the Sudbury lakes, and *D. mendotae* was common in Hannah and Middle Lakes. However, the 2007 cladoceran communities of the Sudbury lakes were still distinguishable from the reference lakes, which were characterized by daphniids, *Eubosmina* spp., *Holopedium gibberum* and *Sida crystallina*. The cladocera of the Sudbury lakes did not recover over the study period. Shifts in the cladocera of the reference lakes (Fig. 3) and visual inspection of the CA 95% ellipses (Figs 5–8) indicate that the differences between the Sudbury and reference lakes were greater when using the present-day reference condition as compared with the historical target.

The copepod trajectories of the Sudbury lakes were characterized by the early disappearance of *A. vernalis* and the appearance of *Leptodiaptomus minutus*, *Orthocyclops modestus* and *T. extensus*. Despite this shift, the copepod communities of Clearwater, Hannah and Lohi Lakes did not recover over the study period when compared with copepod communities in the reference lakes, which were characterized by *Cyclops scutifer*, *Diacyclops thomasi*, *Epischura lacustris*, *Mesocyclops edax* and *Skistodiaptomus oregonensis*. The present-day copepod communities in the reference lakes were more similar to the Sudbury lakes than were the historical communities. Copepod community composition in Middle Lake was indistinguishable from both the historical and present-day copepod community reference conditions by 1994, indicating recovery.

Discussion

Reference ecosystems are 'moving targets' that can shift in response to large-scale regional drivers (Keller 2009). Our results demonstrate that these shifts alter the outcome of recovery assessments for ecosystems damaged by localized stressors. The limnology of our reference lakes changed between the early-1980s and mid-2000s (Palmer *et al.* 2011; M.E. Palmer, N.D. Yan & K.M. Somers, unpublished data). Surface waters warmed and thermal stability strengthened in response to increased air temperatures. Dissolved organic carbon and ammonia increased, probably due to climatic warming and increases in terrestrial export. Lake water acidity decreased as acid deposition declined, although improvements were tempered by decreased base cations because of long-term acidic leaching of lake watersheds. Chloride and sodium increased because of winter road salting. Metals,

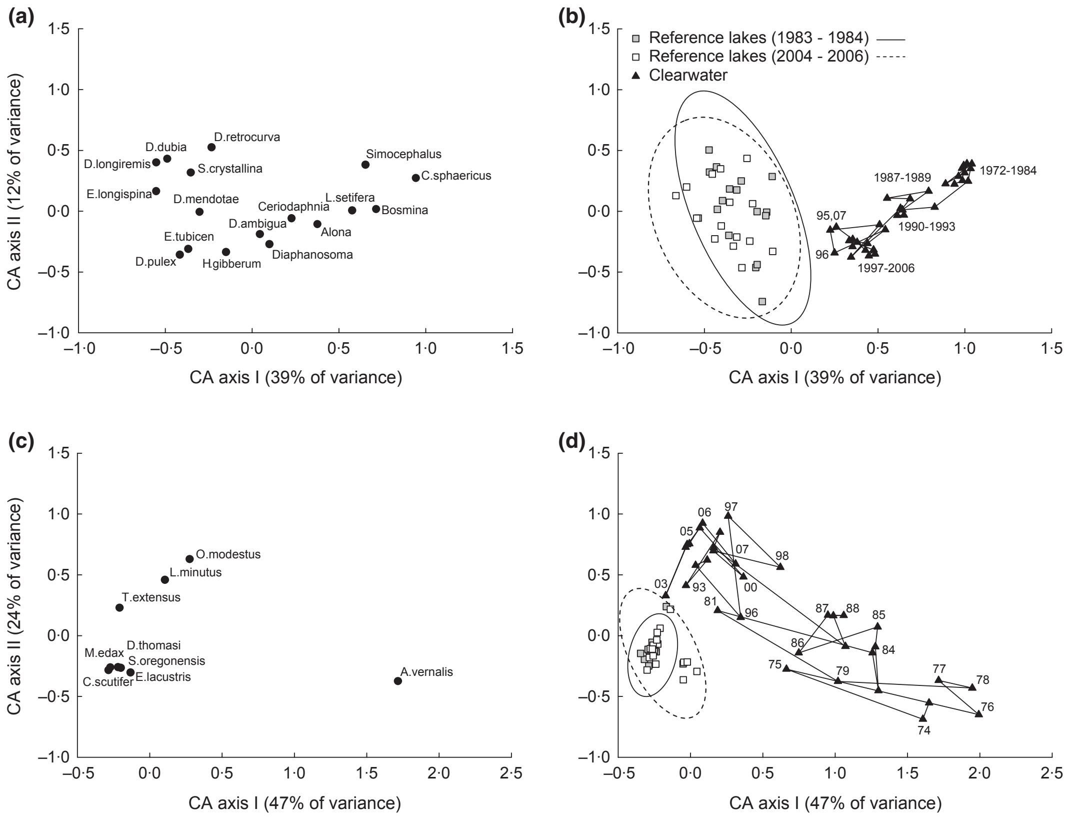

Fig. 5. Correspondence analyses (CA) of cladoceran and copepod communities in Clearwater Lake and the 16 south-central Ontario regional reference lakes based on the abundances of common taxa: (a) cladoceran taxa scores, (b) lake scores for cladoceran CA, (c) copepod taxa scores, (d) lake scores for copepod CA.

phosphorus and chlorophyll also changed, probably responding to interactions of acid deposition and climate change. Concurrent with these physico-chemical changes, zooplankton communities changed and crustacean species richness increased. Regional stressors driving changes in the reference lakes are similarly impacting the Sudbury lakes (Keller 2009). Therefore, Sudbury zooplankton communities probably reflect local and regional pressures, and recovery targets must be set using present-day reference conditions that incorporate these regional shifts if the goal is to restore lakes to a state typical of lakes in the region that have not been impacted by severe and chronic acidification and metal contamination.

Despite the many physico-chemical changes that occurred in the reference lakes between sampling periods, the lakes are still minimally impacted in comparison with most lakes in regions with extensive human development. This is reflected in the small temporal shift in zooplankton communities relative to the large variability among reference lakes. However, these small temporal shifts still altered recovery assessments. Hence, the choice of reference condition will be even more important in regions subjected to greater natural and anthropogenic pressures. When the damaged Sudbury lakes were compared with the present-day targets, recovery was predicted to occur 1–13 years later and community compositions at the end of the study period were more similar to reference lake copepod communities but less similar to cladoceran communities. Even these fairly small differences between recovery assessments could have significant financial and operational consequences as restoration projects and associated recovery monitoring often require extensive resources (Wilson *et al.* 2011).

As expected (Snucins *et al.* 2001; Persson 2008), Sudbury zooplankton communities improved substantially over the 35-year study period as water quality improved. By the mid-2000s, mean species richness in two of the four Sudbury lakes was within the range of richness observed in the south-central Ontario reference lakes. Ours is the first report of recovery of zooplankton species richness in Hannah and Middle Lakes. Biological recovery in these lakes occurred over 30 years after lake neutralization. Despite substantial improvements, full recovery did not occur in Clearwater and Lohi Lakes, which had lake water pH > 6 since the mid-1990s. Previous studies have suggested that a decade is adequate for zooplankton recovery from acidification (Keller & Yan 1998; Frost *et al.* 2006). The prolonged damage reported here may be attributable to the severity and extended duration of stress as the lakes were contaminated over 60 years ago (Yan *et al.* 2004). Although only the Middle Lake copepod community recovered, community changes in all the lakes were promising. Many taxa typically present in the reference lakes

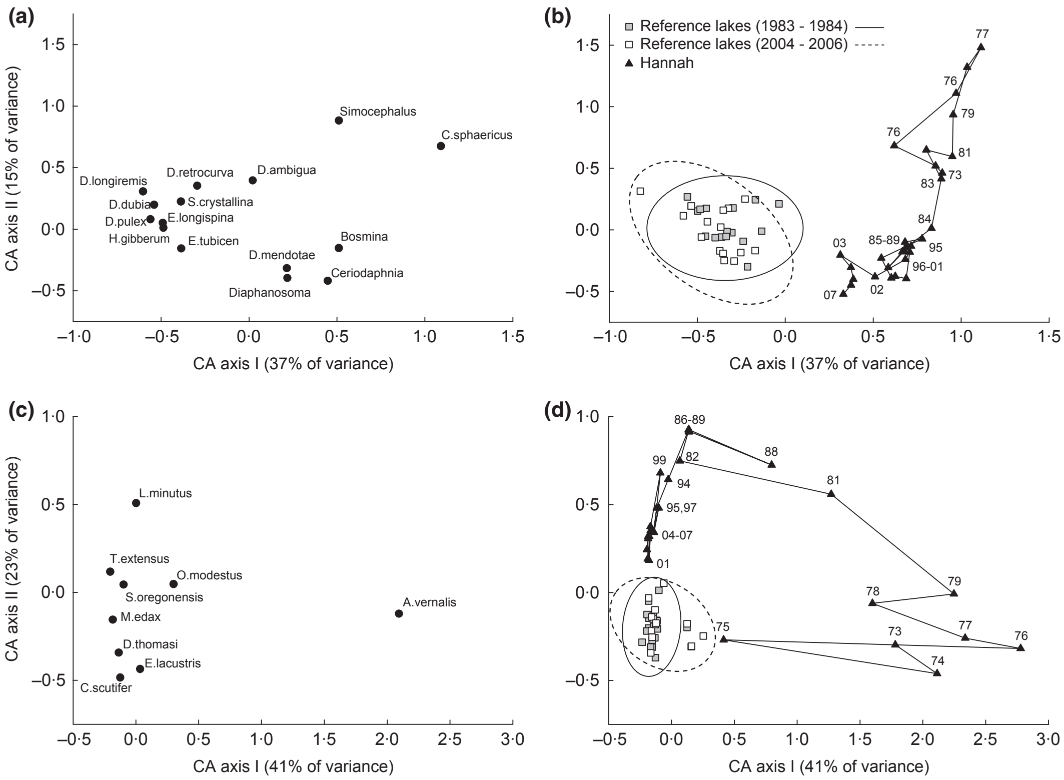

Fig. 6. Correspondence analyses (CA) of cladoceran and copepod communities in Hannah Lake and the 16 south-central Ontario regional reference lakes based on the abundances of common taxa: (a) cladoceran taxa scores, (b) lake scores for cladoceran CA, (c) copepod taxa scores, (d) lake scores for copepod CA.

established persistent populations in the Sudbury lakes, including the acid- and metal-tolerant *Bosmina*, *Diaphanosoma*, *L. minutus* and *T. extensus* (Holt, Yan & Somers 2003; Yan *et al.* 2004). Acid- and metal-sensitive taxa, including *D. mendotae*, *Eubosmina tubicen*, *E. lacustris*, *H. gibberum*, *C. scutifer* and *S. oregonensis* (Yan & Strus 1979; Keller & Yan 1991, 1998; Holt, Yan & Somers 2003), also persisted in some of the lakes. However, the continued scarcity of most daphniids, *E. longispina*, cyclopoids and large calanoids suggested continued stress, a condition also typical of other nonacidic Sudbury area lakes with high metal concentrations (Valois, Keller & Ramcharan 2011).

Others have discussed the barriers to recovery in these lakes in detail (Yan *et al.* 1996, 2004; Keller *et al.* 2002). Here, we provide a brief overview. These barriers fall into two groups, those that affect recolonization and those that affect habitat quality (Keller & Yan 1998). Most taxa are not expected to be limited by colonization as natural dispersal vectors exist and nearby uncontaminated lakes, although reduced in number because of widespread acidification, have been shown to act as colonist sources (Pollard, Colbourne & Keller 2003). Lake sediments also provide an abundant source of cladoceran and calanoid resting eggs that can remain viable for decades (Hairston 1996). However, the number of colonists from egg banks can be reduced by decreasing egg viability with age and severity of pollution, emergence under water quality conditions that do not support survival and sediment deposition, which can bury eggs thus blocking cues that induce hatching (Gray & Arnott 2009). Unlike parthenogenetic cladocerans, sexually reproducing copepods must also find a mate, but the colonist numbers may be too low to breach Allee effect thresholds (Gray & Arnott 2011). Hypolimnetic taxa may be particularly restricted by colonization. The hypolimnetic species *Daphnia longiremis*, *E. longispina* and *C. scutifer* were present in 75–100% of the reference lakes but were rarely, if ever, detected in the Sudbury lakes. Prior to water quality improvements, water transparency in the Sudbury lakes was unusually high and seasonal warming of deep waters inhibited summer stratification (Yan *et al.* 2004). However, the availability of cool, deepwater habitat quickly increased following reductions in acidity and water clarity in the three deeper Sudbury lakes. The continued absence of hypolimnetic taxa despite the resurrection of suitable habitat has been attributed to low dispersal ability of deepwater species (Keller & Yan 1998; Keller *et al.* 2002). Although colonization barriers exist, most taxa common in the reference lakes were detected at least once in the Sudbury lakes, suggesting colonist mortality because of inhospitable habitat quality rather than lack of colonists has largely limited recovery.

Habitat factors hypothesized to affect recovery of Sudbury zooplankton include food availability, predators, continued metal contamination and urban stressors.

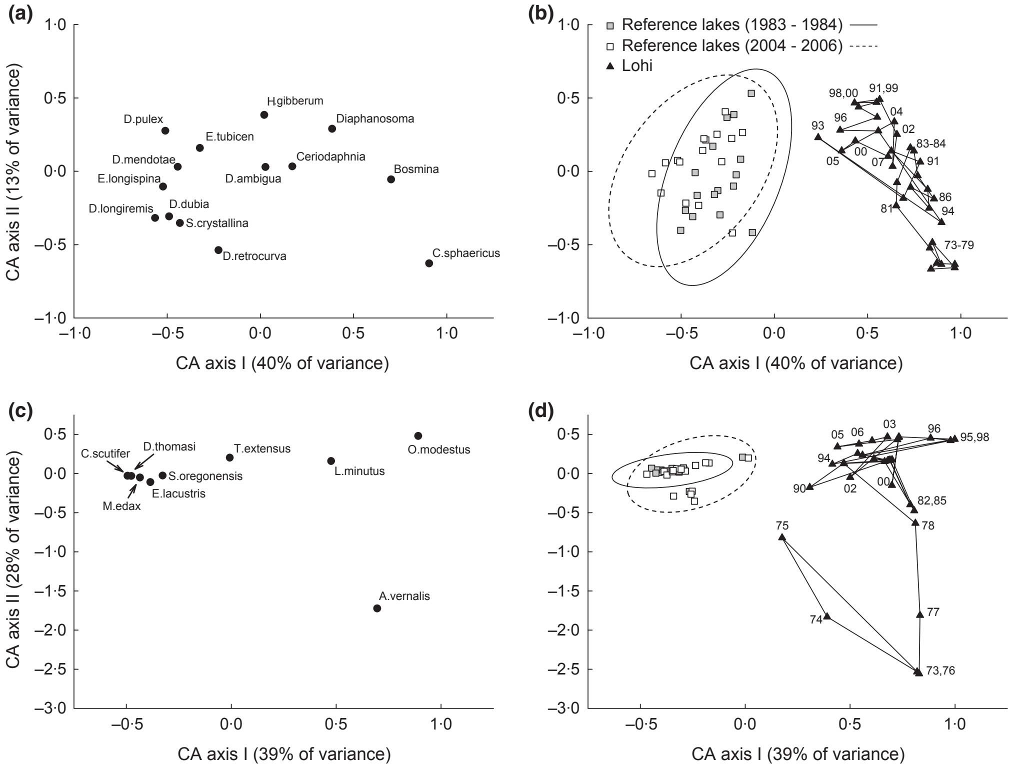

Fig. 7. Correspondence analyses (CA) of cladoceran and copepod communities in Lohi Lake and the 16 south-central Ontario regional reference lakes based on the abundances of common taxa: (a) cladoceran taxa scores, (b) lake scores for cladoceran CA, (c) copepod taxa scores, (d) lake scores for copepod CA.

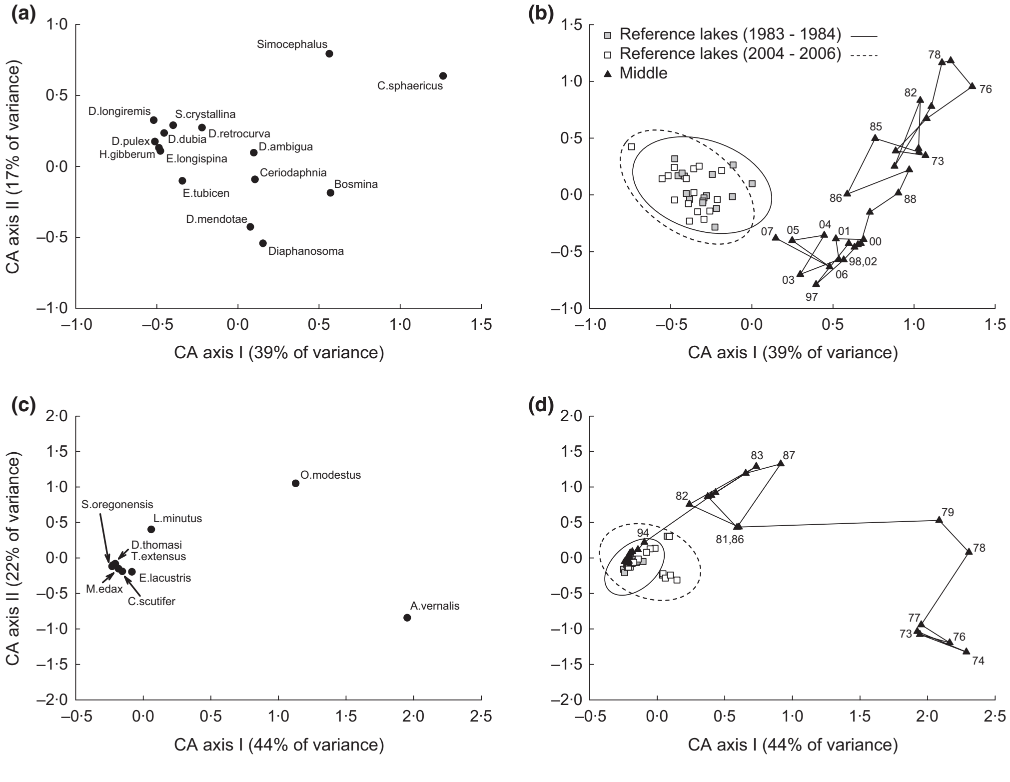

Fig. 8. Correspondence analyses (CA) of cladoceran and copepod communities in Middle Lake and the 16 south-central Ontario regional reference lakes based on the abundances of common taxa: (a) cladoceran taxa scores, (b) lake scores for cladoceran CA, (c) copepod taxa scores, (d) lake scores for copepod CA.

Although phytoplankton communities in the Sudbury lakes were degraded by acidification (Yan 1979), food was unlikely to be a limiting resource for herbivorous zooplankton in recent years because chlorophyll concentrations and phytoplankton communities resembled those in the reference lakes (Yan & Dillon 1984; Winter *et al.* 2008). Predators seem more likely to have had an impact, as piscivores are commonly lacking and small, planktivorous Yellow Perch *Perca flavescens* have become very abundant in Sudbury lakes, perhaps contributing to poor daphniid recovery (Yan *et al.* 2004; Valois, Keller & Ramcharan 2010). Zooplankton recovery was also likely to be limited by continued metal contamination. Elevated metals can depress the reproduction and survival of many zooplankton species (Koivisto, Ketola & Walls 1992), and present-day metal concentrations in the Sudbury lakes exceeded the Ontario Provincial Water Quality Objective of 5 $\mu g\ L^{-1}$ for copper and 25 $\mu g\ L^{-1}$ for nickel (MOEE 1994). In a survey of 46 Sudbury area lakes, Valois, Keller & Ramcharan (2011) found that low relative abundances of daphniids, cyclopoids and large calanoids were related to high metal concentrations. In our lakes, zooplankton recovery was greatest in Middle and Hannah Lakes, which had relatively high metal concentrations compared with Clearwater and Lohi Lakes. However, Hannah and Middle Lakes also had higher pH, cation and dissolved organic carbon levels, which almost certainly reduced metal bioavailability and metal toxicity (Khan *et al.* 2012). Declining calcium could also hinder zooplankton recovery, but calcium levels were consistently greater than the minimum concentration required by *Daphnia*, which have high calcium requirements relative to other zooplankton (Jeziorski & Yan 2006; Ashforth & Yan 2008). Finally, recovery of some taxa, including *H. gibberum*, may be impeded by urban stressors such as nutrient inputs, run-off from winter road salting and shoreline development (Valois, Keller & Ramcharan 2011).

CONCLUSIONS AND IMPLICATIONS

In this study, we showed that recovery assessments for damaged lake communities differed when historical vs. present-day reference conditions were used to set recovery targets. Our intent was not to disqualify the use of historical reference conditions, but to provide evidence of the impact choice of restoration targets can have. Managers and practitioners need to clearly define the goals of individual restoration projects to ensure appropriate targets are used to assess restoration success or failure. The likelihood of restoring an ecosystem to a previous condition, as well as the realities of time and money, must be considered when setting restoration targets (Hannah, Midgley & Millar 2002; Toledo, Agudelo & Bentley 2011). Historical targets, based on data from the impacted ecosystem or reference ecosystems, are appropriate if the goal is to restore an ecosystem to the historical state and can be useful when present-day data are unavailable, particularly for minimally impacted regions. In contrast, present-day targets can be advantageous as they integrate the influence of confounding stressors and provide an assessment of how the damaging agent of concern impacts ecosystems under current environmental conditions (White & Walker 1997). Use of inappropriate or out-dated restoration targets could cause inaccurate restoration assessments and lead to overengineered projects (Owen, Duncan & Pollard 2001; Palmer 2009). To avoid these pitfalls, an adaptive approach where restoration targets are re-evaluated periodically may be the best solution (Owen, Duncan & Pollard 2001; Nõges *et al.* 2007).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Annual changes in the relative abundances of common zooplankton taxa in the Sudbury lakes.

Appendix S1. Description of annual changes in the relative abundances of common zooplankton taxa in the Sudbury lakes.