

# Recovery of Crustacean Zooplankton Communities from Acidification in Killarney Park, Ontario, 1971–2000: pH 6 As a Recovery Goal

Despite reductions in atmospheric  $\text{SO}_4^{2-}$  deposition and resultant decreases in surface water acidity, widespread biological recovery from acidification has not yet been documented. Temporal trends in crustacean zooplankton species richness (number of species) and composition were examined between 1971–2000 in 46 Killarney Park lakes, Ontario, Canada, to assess the degree of biological recovery in lakes with significant water quality improvements, i.e. pH now  $> 6$ , compared to 2 other groups: *i*) lakes which never acidified; and *ii*) lakes which are still acidified (pH  $< 6$ ). Time trends in species richness could not be distinguished among the 3 groups of lakes, nor did changes in species richness indicate recovery. In contrast, the zooplankton community composition of lakes in which the pH increased to above 6, as measured by a multivariate index of species abundances, changed from a “damaged” state to one typical of neutral lakes. Some recovery in composition was also documented for the acidic lakes. While still acidic, the pH levels of these lakes have risen. The extent and pace of recovery in Killarney Provincial Park bodes well for the future of other acidified regions in North America and Europe.

## INTRODUCTION

Recent reductions in  $\text{SO}_2$  emissions in North America and Europe have led to widespread decreases in S deposition. In Canada, legislation was introduced in 1991 to reduce  $\text{SO}_2$  emissions by 40% of 1980 levels. These emission reductions, combined with those in the US (~40%), have led to strong downward trends in  $\text{SO}_4^{2-}$  deposition and in-lake concentrations (1). In some cases, increases in alkalinity and pH have resulted. For example, Keller and Pitblado (2) found an increase in pH among 209 acidic Sudbury area lakes between 1974–1976 and 1981–1983. However, exceptions to this trend do exist (1). Biological recovery can occur, but it has lagged behind improvements in water quality and has been less extensive (3).

A pH of 6 has been widely used in eastern Canada to discriminate between lakes damaged by acidification and those not damaged. This pH threshold has been identified in lab bioassays as well as field surveys, and from studies at the species level as well as the community level. For example, in a combined lab and field study, the  $\text{LC}_{50}$ 's of the zooplankton *Daphnia mendotae*, *D. retrocurva* and *Skistodiaptomus oregonensis* (pH 5.7–5.9) corresponded well with their declines in lakes of pH below 6 (4). The community structure of other taxonomic groups also changes as pH drops below 6.0 (5). For example, the species richness of fish, amphibians, zooplankton and benthic invertebrates decreases in lakes of pH  $< 6.0$  in eastern Canada (6).

There is some evidence that crustacean zooplankton communities can recover when lake pH levels rise to above 6.0. These examples are limited to: *i*) a few individual lakes (7); *ii*) experi-

mentally neutralized lakes (8–11); and *iii*) a few regional lake studies (3, 12). Studies of the first type include too few lakes to be considered definitive. The liming studies (type *ii*) may not be indicative of recovery in response to emission reductions given the rapidity of pH changes and increase in Ca content (10) that accompany liming. The regional studies, while promising, have not documented recovery to a state typical of circumneutral lakes. Hence, it is not certain if zooplankton communities of acidified lakes will recover once the pH rises to  $> 6.0$ .

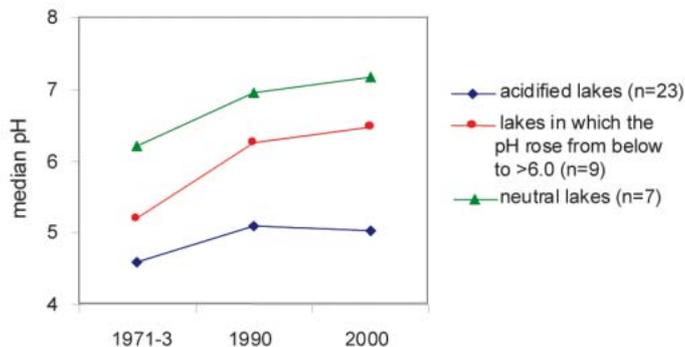
Detecting recovery is complicated (13, 14). While both classical ecosystem theory and international acid rain policies assume that recovery trajectories will reverse the monotonic trends of damage trajectories, the evidence suggests this simple reversal seldom occurs (9, 15). Instead, transient ecosystem dynamics, stochastic dispersal rates, and biological resistance result in unpredictable trajectories (5, 15, 16). For example, the recovery of zooplankton species composition did not mirror the damage pathway in one experimentally acidified lake in Wisconsin (15). The acid-sensitive species dominant prior to acidification, remained at low abundances after 5 years of water quality improvements, contrary to what was expected from the damage pathway.

The objective of this study was to determine if zooplankton communities of lakes in Killarney Provincial Park, Ontario, Canada, recovered to a state typical of neutral lakes, once the pH rose above 6. We posed 2 specific questions: *i*) did the temporal trajectories of the lakes in which the pH rose above 6 differ from 2 reference groups: those which never acidified (pH  $> 6$ ) and those which have remained acidic (pH  $< 6$ ); and *ii*) does this change in zooplankton communities represent recovery to a state typical of neutral lakes?

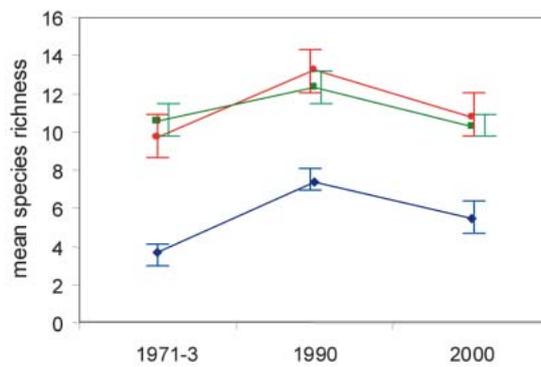
The lakes of Killarney Provincial Park, Ontario, Canada, were chosen to address these questions for two reasons: the availability of historical zooplankton data, and the recent improvements in water quality (2, 17). Many of the lakes were severely acidified by S emissions from long-range transport and nearby metal smelters throughout the 1900s; however, there have been remarkable improvements in water quality since local emissions were reduced in the 1970s and 1980s. Water quality improvements in these lakes are among the earliest—beginning in the early 1980s (2)—and most substantial examples documented (5). Acid-sensitive regions in Europe, such as in eastern Norway, have also experienced water quality improvements, but they are more recent and of less magnitude (18). Killarney Park lakes may therefore provide a preview of the benefits of reductions in S deposition in other acid-sensitive lakes.

## STUDY SITES

The 46 study lakes lie in and around Killarney Provincial Park, Ontario, Canada. The lakes vary widely in size (3–1088 ha, mean 137 ha) and maximum depth (2–61 m, mean 22 m). The current pH of the lakes also ranges widely (4.3–7.7), though a large portion are acidic (median pH 5.97). The lakes are mostly oligotrophic (mean TP  $12.3 \mu\text{g L}^{-1}$ ) and soft (mean Ca =  $96.2 \mu\text{eq L}^{-1}$ ), as is typical of Precambrian Shield lakes. Past



**Figure 1.** Changes in median pH from 1971–2000 for the 3 pre-selected lake groups based on water quality improvements. The groups were: the acidified lakes (pH always < 6), lakes in which the pH rose from < 6 to > 6, and the neutral lakes (pH always > 6).



**Figure 2.** Mean species richness (calculated from a single mid-lake site in midsummer) from 1971–1973, 1990, and 2000 of 3 lake groups based on water quality improvements. Error bars represent standard error.

zooplankton and water quality surveys were conducted roughly three decades and one decade ago (3, 19).

## DATA COLLECTION

Sprules (19) collected zooplankton and water quality samples from each lake between June and September, 1971–1973. Samples were taken at a single mid-lake station, except in multi-basin lakes where a sample was taken from each major basin. One vertical zooplankton haul was taken at each lake with a 25–30 cm diameter net of mesh size 75–110  $\mu\text{m}$ . Horizontal hauls were substituted in shallow lakes. The lakes were sampled again in 1990 by Locke et al. (3), at the same mid-lake sites. Three vertical zooplankton hauls were taken at each lake using a 25 cm diameter net of mesh size 76  $\mu\text{m}$ . We collected zooplankton and pH samples in July and August of 2000 from the same 46 lakes at the same mid-lake sites. Three vertical zooplankton hauls were taken at each site with a metered 12.5 cm diameter net of mesh size 80  $\mu\text{m}$ . The haul filtration efficiency averaged 77%. Samples were preserved in 70% ethanol.

The slight differences in sampling methodology over time do not influence our ability to detect community change. To determine the effect of net size on zooplankton community descriptions, 4 lakes were sampled with both a 30 cm diameter net of mesh size 80  $\mu\text{m}$  (single haul) and a 12.5 cm diameter net of mesh size 80  $\mu\text{m}$  (3 hauls). There were no significant differences in species richness or logged abundances of the 17 dominant species between the samples from the 2 nets, except for the abundances *Bosmina* (*Neobosmina*) *tubicen* and *Holopedium gibberum* ( $t = 5.01$ ,  $p < 0.01$  and  $t = 4.74$ ,  $p < 0.01$ , respectively). However, neither of these species is acid-sensitive. In addition, the variance in logged abundances of *Holopedium gibberum* between lakes, was significantly lower than for the other species ( $F = 12.03$ ,  $df = 63,7$ ,  $p < 0.005$ ), suggesting the variance associated with net size was not necessarily greater for this species.

To assess potential biases in pH associated with dissolved  $\text{CO}_2$ , pH was measured in the field, as well as in the lab after aeration. There was no significant difference in pH of aerated and non-aerated samples (paired  $t = 1.05$ ,  $p > 0.1$ ), as well as no bias to higher pH in aerated samples.

Water chemistry samples (alkalinity, Ca, Al, dissolved organic carbon (DOC), total phosphorus (TP), total nitrogen (TN), Cu

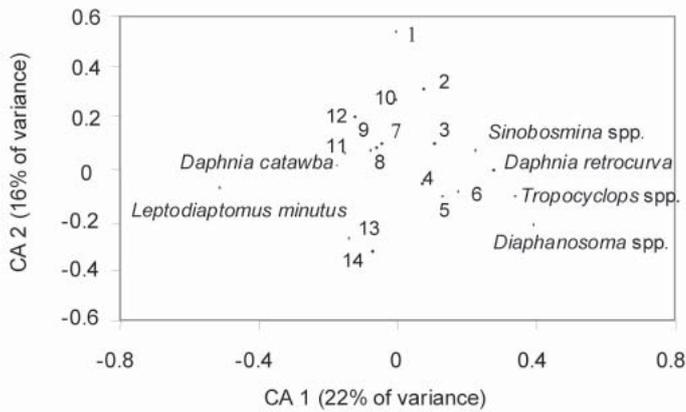
and Ni) were collected after fall turnover in November 2000, as a vertical composite of the top 5 m.

Crustacean zooplankton were identified and counted. The count protocol mirrored that of Locke et al. (3). Taxonomic discrepancies among studies (1971–1973, 1990 and 2000) necessitated pooling the counts of several species. *Diaphanosoma brachyurum* and *D. birgei* were pooled into *Diaphanosoma* spp. (20). *Tropocyclops prasinus mexicanus*, *T. prasinus prasinus* and *T. extensus* were pooled into *Tropocyclops* spp. (21). *Daphnia pulex* and *D. pulicarea* were pooled as well (22). The following species have recently been re-identified, necessitating the renaming in the 1971–1973 and 1990 records: *i) Daphnia galeata mendotae* has been re-identified as *Daphnia mendotae*; *ii) Bosmina longirostris* has been re-identified as *Sinobosmina* spp. (23). Immature cladocerans were included with adults. Immature copepods were excluded.

The 46 lakes were divided into 4 groups according to changes in pH from 1971 to 2000: *i)* lakes in which pH has risen from below to above 6.0 ( $n = 11$ ); *ii)* lakes which are still acidic (pH < 6.0) ( $n = 23$ ); *iii)* lakes which were never acidic (pH > 6.0) ( $n = 7$ ); and *iv)* lakes which have experienced stochastic changes around pH 6 ( $n = 5$ ) (Fig. 1). Only the first 3 groups were used in the analyses. The pH of 2 lakes rose to > 6.0 only in 2000. These 2 lakes were excluded on the assumption of insufficient time for zooplankton recovery (16).

## STATISTICAL ANALYSES

We used 2 zooplankton community metrics, species richness and correspondence analysis scores based on species abundances. Species richness was chosen because it has the most well documented and consistent relationship with pH (6, 24), despite the well-known dependence of species richness on sample size, sampling regime and calculation method (25–27). In this study, species richness was measured as the number of species in a count of 250 individuals sampled from vertical hauls at a single mid-lake station in each lake. Though this measure is not representative of the species richness of the entire lake, it does represent an index related to the numbers of species present and can be compared among lakes and years. A multivariate metric, correspondence analysis scores (CA) based on species abundances, was also used. Because it incorporates species abundances as



**Figure 3.** Species scores from correspondence analysis based on logged species abundances ( $\log(x+1) + 0.2$ ) from 39 lakes and 3 time periods: 1971–1973, 1990 and 2000. (1 = *Cyclops bicuspidatus thomasi*, 2 = *Daphnia mendotae*, 3 = *Skistodiaptomus oregonensis*, 4 = *Ceriodaphnia* spp., 5 = *Mesocyclops edax*, 6 = *Diaptomus reighardi*, 7 = *Epi-schura lacustris*, 8 = *Daphnia ambigua*, 9 = *Chydorus sphaericus*, 10 = *Daphnia longiremis*, 11 = *Polyphemus pedicululs*, 12 = *Eubosmina longispina*, 13 = *Holopedium gibberum*, 14 = *Neobosmina tubicen*).

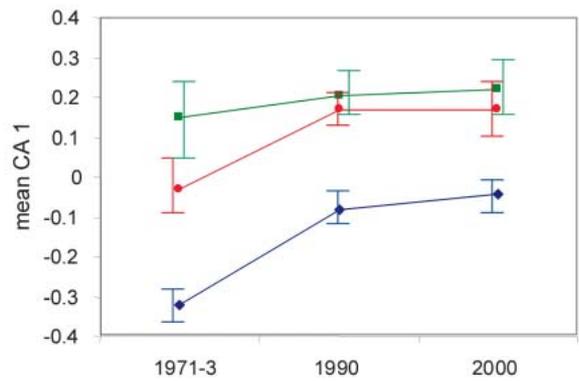
well as covariation patterns among species, it may provide a more sensitive indicator of recovery than richness. CA is not limited to linear species patterns and has the advantage of being robust to various data transformations compared to other common ordination methods (28). A small constant was added to each logged abundance ( $\log(x+1) + 0.2$ ) (29). It represented a minimum detection threshold and down-weighted species that were common in just a few lakes.

Using repeated measure ANOVA (30–32), trajectories of zooplankton community change of lakes in which the pH rose to  $> 6$  were compared to the 2 reference groups, those lakes which were not acidified (pH always  $> 6$ ) and those lakes which are still acidic (pH always  $< 6$ ). These 2 reference groups were termed the neutral and acidified lakes, respectively. Where significant differences in trajectories were detected, i.e. a significant treatment by time interaction term, the zooplankton communities of lakes that increased to pH  $> 6$  were compared to the neutral lakes (in both 1971–1973 and 2000) using t-tests. Recovery was documented by a nonsignificant test statistic for the year 2000 comparisons.

## RESULTS

Species richness varied from 1 to 17 (mean 7.7 species). Species richness was consistently lower in acidified lakes than in the other 2 groups of lakes (Fig. 2). The temporal trajectories did not significantly differ among the 3 lake groups, i.e. the treatment by time interaction term was not significant,  $F = 1.11$ ,  $df = 4,72$ ,  $p > 0.2$ . Instead, all 3 groups of lakes changed synchronously over time, i.e. the variance associated with years was significant,  $F = 20.25$ ,  $df = 2,32$ ,  $p < 0.001$ .

Species abundance data from all 3 time periods were merged in a correspondence analysis (Fig. 3). The first CA axis was most highly correlated with pH ( $r = 0.62$ ,  $p < 0.001$ ) compared to the other 3 axes ( $r = 0.30$ ,  $r = -0.15$  and  $r = -0.24$ ), and explained 22% of the total variance. Therefore, axis 1 was used as our recovery indicator. Differences in temporal trajectories of CA 1 were found among the 3 lake groups (treatment  $\times$  time  $F = 2.41$ ,  $df = 4,72$ ,  $p = 0.057$ , Fig. 4). However, in pair-wise comparisons, the trajectory of lakes in which the pH rose from below to  $> 6.0$  was not significantly different than that of the neutral lakes ( $F = 2.21$ ,  $df = 2,32$ ,  $p > 0.1$ ). This may have been an artifact of



- ◆ acidified lakes (n = 23)
- lakes in which the pH rose from  $< 6$  to  $> 6$  (n = 9)
- ▲ neutral lakes (n = 7)

**Figure 4.** Changes in mean CA axis 1 score based on logged species abundances in 3 lake groups of differing water quality improvements. Error bars represent standard error.

low power, as these 2 lake groups consisted of only 9 and 7 lakes each. To increase the power of the test in distinguishing between trajectories of lake groups, the number of time series points was reduced from 3 to 2 (1971–1973 and 2000) (33), as we were most interested in changes that occurred over the entire time period, from 1971 to 2000. In pair-wise comparisons of the reduced data set, the difference in trajectories of the lakes in which the pH rose to  $> 6.0$  and the neutral lakes approached significance ( $F = 3.42$ ,  $df = 1,16$ ,  $p = 0.086$ ). However, the trajectories of the lakes in which the pH rose to  $> 6.0$  were not different from the acidified lakes ( $F = 1.55$ ,  $df = 1,32$ ,  $p > 0.2$ ).

In 1971–1973, CA 1 scores were higher for the neutral lakes than for the lakes in which the pH rose to  $> 6.0$  ( $t = -1.59$ ,  $df = 14$ ,  $p = 0.066$ ). By 2000, there was no significant difference in CA scores between these 2 groups ( $t = -0.46$ ,  $df = 14$ ,  $p > 0.2$ ). This result indicates that the zooplankton communities of lakes in which the pH rose to  $> 6$  changed from a “damaged” state to a state typical of neutral lakes.

The recovery of zooplankton species composition in lakes in which the pH rose to  $> 6.0$  was associated with changes in species abundances and not occurrences. *Daphnia retrocurva*, *Diaphanosoma* spp., *Sinobosmina* spp., and *Tropocyclops* spp. increased in abundance and *Leptodiaptomus minutus* and *Daphnia catawba* decreased (Fig. 5). *Daphnia mendotae* was the only taxon that recolonized and became dominant by 2000.

Even though the acidified lakes had a similar trajectory to that of the lakes which increased in pH to  $> 6.0$ , they did not recover to a state typical of neutral lakes. In addition, species richness remained low in these lakes and common dominant species of neutral lakes were absent.

## DISCUSSION

Zooplankton species composition did recover from a damaged to an undamaged state, in lakes which rose in pH to  $> 6.0$ . Some recovery was also found in the acidic lakes, though not to a state typical of neutral lakes.

This recovery is not an artifact of differences in morphometric and chemical conditions among lake groups. Lake size and maximum depth were not different among the 3 lake groups (ANOVA,  $F = 1.67$ ,  $df = 2,36$ ,  $p > 0.2$  and  $F = 0.41$ ,  $df = 2,36$ ,  $p > 0.5$ , respectively), suggesting that morphometry did not in-

fluence the observed recovery pattern. TP concentrations were not different among lake groups (ANOVA  $F = 0.28$ ,  $df = 2,36$ ,  $p > 0.5$ ), and therefore cannot explain observed patterns. Declining metal levels, e.g. Cu and Ni, have been associated with decreases in sulfur emissions, though are probably not influential in the current recovery process. Cu concentrations were below those of lakes unaffected by smelter emissions ( $2 \mu\text{g L}^{-1}$ ), (34) and Ni concentrations were below previously established thresholds of zooplankton species changes ( $40 \mu\text{g L}^{-1}$ ), (35). Declining Ca levels may be significant in recovery because Ca regulates toxic effects of acidity and metals, and daphnids in particular have a high Ca demand (36). However, Ca cannot explain the current recovery patterns because concentrations are generally above the lower threshold of Ca limitation (37, 38), but are too low to support hardwater species (39).

Biological conditions may, however, be able to explain some of the differences in recoveries among lake groups. Differences in predation regimes have been widely used to explain variability in zooplankton communities. Recovery may be limited by the re-establishment of biotic interactions typical of pre-disturbance ecosystems (16). Specifically, the recovery of zooplankton may be slowed or prevented by intense invertebrate predation pressure if fish do not recolonize recovering lakes (11, 40). In the present study, more than half of the acidic lakes were fishless in the mid-1990s (41). In contrast, the lakes in which the pH rose to  $> 6.0$ , and the neutral lakes, all contained fish with high frequencies of occurrences of both planktivores and piscivores. It is impossible to distinguish the effect of altered predation regime from low pH at this stage, since all lakes that lacked fish populations were also acidic. However, it is unlikely that fish and invertebrate predator populations recovered concurrently with *Daphnia* spp. due to the selective predation of fish and large invertebrates on large-bodied zooplankton such as *Daphnia*.

Recovery has occurred in the lakes which rose to  $\text{pH} > 6$  and, to an extent, in the acidic lakes, despite complexities commonly associated with recovery, such as changing environmental conditions, dispersal barriers and biological resistance (13, 16, 42). Recent unusual climatic events related to the Mt. Pinatubo eruption of 1991 and the El Niño events have increased variability in environmental conditions. For example, climate-driven water chemistry changes over the last 2 decades have resulted in re-acidification of some Ontario lakes (42–45), though these changes have not prevented recovery in Killarney lakes. Dispersal barriers have commonly been cited as an obstacle in recovery, particularly for hypolimnetic zooplankton such as *Mysis relicta*, and fish (16). Those species that are most readily available for dispersal may establish and become dominant instead of those typical of neutral lakes (16). In the current study, recovery represented changes in species abundances, not recolonization of new species. While dispersal barriers have not been important so far in the recovery process, they may become significant in future recovery of the acidic lakes. Finally, biotic re-

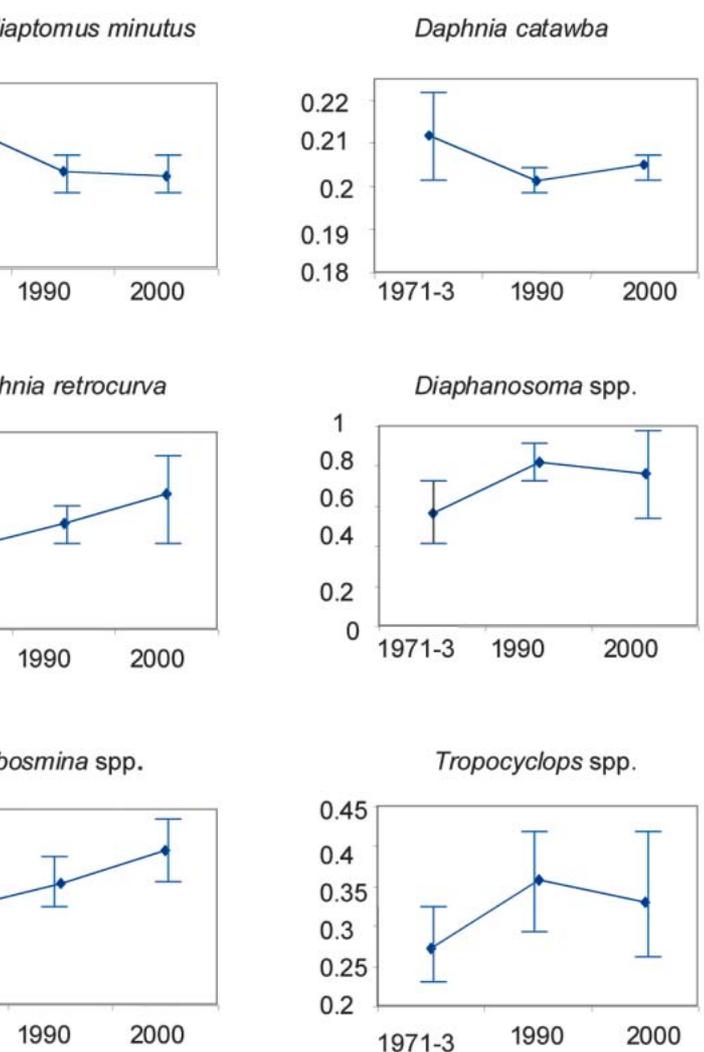


Figure 5. Changes in logged species abundances over time. Only those species with the greatest CA 1 weightings are shown. Error bars represent standard error.

sistance can prevent the re-establishment of community types typical of neutral lakes through intensive predation or competition in existing communities. Recovery pathways which do not mirror that of damage may result (13, 14). Though biotic resistance has not prevented recovery of lakes in which the pH rose to  $> 6$ , it may influence future recovery in acidic lakes. Despite these 3 common confounding influences, recovery has been documented in the majority of Killarney Park lakes.

One operational definition of recovery is a change in species composition to one typical of non-acidified lakes. This study documents such recovery for zooplankton communities as the pH rises from below to above  $\text{pH} 6.0$ . The recovery documented in this study adds to our evidence that recovery can occur to a state typical of non-acidified lakes given sufficient habitat quality improvements ( $\text{pH} > 6$ ). The recovery from acidification of many groups of aquatic biota continues, but the rates, patterns and extent in specific lakes may be complicated by environmental and biological factors, including changing abiotic conditions, dispersal barriers, and biotic resistance. Future monitoring will be required to track the extent and trajectories of recovery in Killarney Park. The degree of recovery documented herein bodes well for the future of other acid-sensitive regions in North America and Europe.

## References and Notes

- Stoddard, J.L., Jeffries, D.S., Lukewille, A., Clair, T.A., Dillon, P.J., Driscoll, C.T., Forsius, M., Johannessen, M., Kahl, J.S., Kellogg, J.H., Kemp, A., Mannio, J., Monteith, D., Murdoch, P.S., Patrick, S., Rebsdorf, A., Skjelkvåle, B.L., Stainton, M.P., Traaen, T., van Dam, H., Webster, K.E., Wieting, J. and Wilander, A. 1999. Regional trends in aquatic recovery from acidification in North America and Europe 1980–1995. *Nature* 401, 575–578.
- Keller, W. and Pitblado, J.R. 1986. Water quality changes in Sudbury area lakes: a comparison of synoptic surveys in 1974–1976 and 1981–1983. *Water Air Soil Pollut.* 29, 285–296.
- 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.
- Havens, K.E., Yan, N.D. and Keller, W. 1993. Lake acidification: effects on crustacean zooplankton populations. *Env. Sci. Tech.* 27, 1621–1624.
- Schindler, D.W., Frost, T.M., Mills, D.H., Chang, P.S.S., Davies, I.J., Findlay, L., Malley, D.F., Shearer, J.A., Turner, M.A., Garrison, P.G., Watras, D.J., Webster, K., Gunn, J.M., Brezonik, P.L. and Swenson, W.A. 1991. Comparisons between experimentally- and atmospherically-acidified lakes during stress and recovery. *Proc. R. Soc. Edinb. Sect. B Biol. Sci.* 97, 193–227.
- Doka, S.E., Mallory, M.L., McNicol, D.K. and Minns, C.K. 1997. Species richness and species occurrence of five taxonomic groups in relation to pH and other lake characteristics in southeastern Canada. 2179. *Fish. Oceans, Environ. Can.*, Burlington, Ontario.
- 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.
- Hörnström, E., Ekström, C., Froberg, E. and Ek, J. 1993. Plankton and chemical-physical development in six Swedish west coast lakes under acidic and limed conditions. *Can. J. Fish. Aquat. Sci.* 50, 688–702.
- Appelberg, M., Lingdell, P.E. and Andren, C. 1995. Integrated studies of the effects of liming acidified waters (Iselaw-Programme). *Water Air Soil Pollut.* 85, 883–888.
- Yan, N.D., Keller, W., Somers, D.M., Pawson, T.W. and Girard, R.E. 1996. Recovery of crustacean zooplankton communities from acid and metal contamination: comparing manipulated and reference lakes. *Can. J. Fish. Aquat. Sci.* 53, 1301–1327.
- Stenson, J.A.E. and Svensson, J.E. 1995. Changes of planktivore fauna and development of zooplankton after liming of the acidified lake Gårdsjön. *Water Air Soil Pollut.* 85, 979–984.
- Skjelkvåle, B.L., Anderson, T., Halvorsen, G.A., Raddum, G.G., Heegaard, E., Stoddard, J. and Wright, R. 2000. The 12-year report: Acidification of surface water in Europe and North America; Trends, biological recovery and heavy metals. *O-86001. Norwegian Institute for Water Research*, Oslo, Norway, 115 pp.
- Keller, W., Gunn, J.M. and Yan, N.D. 1999. Acid rain- perspectives on lake recovery. *J. Aquat. Ecosyst. Stress Recov.* 6, 207–216.
- O'Neill, R. 1999. Recovery in complex ecosystems. *J. Aquat. Ecosyst. Stress Recov.* 6, 181–187.
- Frost, T.M., Montz, P.K. and Kratz, T.K. 1998. Zooplankton community responses during recovery from acidification in Little Rock Lake, Wisconsin. *Restor. Ecol.* 6, 336–342.
- 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.
- Keller, W., Heneberry, J.H. and Gunn, J.M. 1999. Effects of emission reductions from the Sudbury smelters on the recovery of acid- and metal-damaged lakes. *J. Aquat. Ecosyst. Stress Recov.* 6, 189–198.
- Skjelkvåle, B.L., Wright, R.F. and Henriksen, A. 1998. Norwegian lakes show widespread recovery from acidification; results from national surveys of lakewater chemistry 1986–1997. *Hydrol. Earth Syst. Sci.* 2, 555–562.
- Sprules, W.G. 1975. Midsummer crustacean zooplankton communities in acid-stressed lakes. *J. Fish. Res. Bd Can.* 32, 389–395.
- Korínek, V. 1981. *Diaphanosoma birgei* n.sp. (Crustacea, Cladocera). A new species from America and its widely distributed subspecies *Diaphanosoma birgei* spp. *lacustris* n.ssp. *Can. J. Zool.* 59, 1115–1121.
- Dussart, B.H. and Fernando, C.H. 1990. A review of the taxonomy of five Ontario genera of freshwater cyclopoid Copepoda (Crustacea). *Can. J. Zool.* 68, 2594–2604.
- Dodson, S.I. 1981. Morphological variation of *Daphnia pulex* Leydig (Crustacea: Cladocera) and related species in North America. *Hydrobiol.* 83, 101–114.
- DeMelo, R. and Hebert, P.D.N. 1994. A taxonomic reevaluation of North American Bosminidae. *Can. J. Fish. Aquat. Sci.* 72, 1808–1825.
- Sprules, W.G. 1975. Factors affecting the structure of limnetic crustacean zooplankton communities in central Ontario lakes. *Verh. int. Ver. Limnol.* 19, 635–643.
- Arnott, S.A., Magnuson, J.J. and Yan, N.D. 1998. Crustacean zooplankton species richness: single- and multiple-year estimates. *Can. J. Fish. Aquat. Sci.* 55, 1573–1582.
- Fisher, R.A., Corbet, A.S. and Williams, C.B. 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. *J. Anim. Ecol.* 12, 42–58.
- Magnuson, J.J., Benson, B.J. and McLain, A.S. 1994. Insights on species richness and turnover from long-term ecological research: fishes in north temperate lakes. *Amer. Zool.* 34, 437–451.
- Jackson, D. 1993. Multivariate analysis of benthic invertebrate communities: the implication of choosing particular data standardizations, measures of association, and ordination methods. *Hydrobiol.* 268, 9–26.
- Rusak, J.A., Yan, N.D., Somers, K.M., McQueen, D.J. and Ramcharan, C.W. 2001. Differences in the variability of crustacean zooplankton communities between manipulated and reference lakes. *Arch. Hydrobiol.* 56, 171–186.
- Chapman, M.G. 1999. Improving sampling designs for measuring restoration in aquatic habitats. *J. Aquat. Ecosyst. Stress Recov.* 6, 235–251.
- Green, R.H. 1993. Application of repeated measures designs in environmental impact and monitoring studies. *Austral. J. Ecol.* 18, 81–98.
- Paine, M.D. 1996. Repeated measures design: Letter to the Editor. *Environ. Tox. Chem.* 15, 1439–1441.
- Legendre, P. and Legendre, L. 1998. *Numerical Ecology*. Elsevier, New York, 853 pp.
- Yan, N.D. and Miller, G.E. 1984. Effects of deposition of acids and metals on chemistry and biology of lakes near Sudbury, Ontario. In: *Environmental Impacts of Smelters*. Nriagu, J. (ed.). John Wiley and Sons Inc., pp. 243–282.
- Munzinger, A. 1990. Effects of nickel on *Daphnia magna* during chronic exposure and alterations in the toxicity to generations pre-exposed to nickel. *Water Res.* 24, 845–852.
- Keller, W., Dixit, S.S. and Heneberry, J. 2001. Calcium declines in northeastern Ontario lakes. *Can. J. Fish. Aquat. Sci.* 58, 2011–2020.
- Alstad, N.E.W., Skardal, L. and Hessen, D.O. 1999. The effect of calcium concentration on the calcification of *Daphnia magna*. *Limnol. Oceanogr.* 44, 2011–2017.
- Fryer, G. 1980. Acidity and species diversity in freshwater crustacean fauna. *Freshwater Biol.* 10, 41–45.
- Tessier, A.J. and Horowitz, R.J. 1990. Influence of water chemistry on size structure of zooplankton assemblages. *Can. J. Fish. Aquat. Sci.* 47, 1967–1943.
- Nyberg, P. 1984. Impact of *Chaoborus* predation on planktonic crustacean communities in some acidified and limed forest lakes in Sweden. *Inst. Freshwater Res. Drottningholm Rep.* 61, 154–166.
- Snucins, E. and Gunn, J.M. 1998. *Chemical and Biological Status of Killarney Park Lakes (1995–1997)*. Ontario Ministry of Natural Resources, Sudbury, 132 pp.
- Yan, N.D., Keller, W., Scully, N.M., Lean, D.R.S. and Dillon, P.J. 1996. Increased UV-B penetration in a lake owing to drought-induced acidification. *Nature* 381, 141–143.
- Arnott, S.F., Yan, N.D., Keller, W. and Nicholls, K. 2001. The influence of drought-induced acidification on the recovery of plankton in Swan Lake, Ontario, Canada. *Ecol. Appl.* 11, 747–763.
- Devito, K.J., Hill, A.R. and Dillon, P.J. 1999. Episodic sulphate export from wetlands in acidified headwater catchments: prediction at the landscape scale. *Biogeochemistry* 44, 187–203.
- Gunn, J.M., Snucins, E., Yan, N.D. and Arts, M.T. 2001. Use of water clarity to monitor the effects of climate change and other stressors on oligotrophic lakes. *Environ. Monit. Assess.* 67, 69–88.
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**Catherine Holt is currently a graduate student at the School of Resource and Environmental Management, Simon Fraser University in Vancouver, Canada. While performing this research she was at York University in Toronto, Canada. Her current interests are forecasting recruitment of Pacific salmon in changing environmental and ecological conditions.**

**E-mail: cholt@sfu.ca**

**Norman D. Yan is an associate professor in the Department of Biology at York University in Toronto, and works in partnership with the Dorset Environmental Science Centre of the Ontario Ministry of the Environment. His main research interests are the effects of multiple environmental stressors, including acids, metals, a changing climate and nonindigenous species, on the plankton of Canadian Shield lakes.**

**E-mail: nyan@yorku.ca.**

**Their address: Department of Biology, York University, 4700 Keele St., Toronto, Ontario, M3J 1P3, Canada.**