Rolf D. Vinebrooke, Mark D. Graham, David L. Findlay and Michael A. Turner

Resilience of Epilithic Algal Assemblages in Atmospherically and Experimentally Acidified Boreal Lakes

Algal assemblages can be highly responsive to environmental changes in recovering acidified lakes. We compared epilithic algal assemblages in boreal lakes during chemical recovery from atmospheric (Killarney Park, Ontario) and experimental (Lake 302S, Experimental Lakes Area, Ontario) acidification to assess the impact of spatial and temporal scale of severe acidification on taxonomic resilience (i.e. recovery rate). Resilience was measured as the distance traveled by lakes in ordination space during pH recovery based on canonical correspondence analysis. Resilience was relatively negligible in the Killarney lakes, suggesting that eight years of experimental acidification in Lake 302S had less impact on biological recovery than did decades of regional acidification. Increases in dissolved organic carbon, dissolved inorganic carbon, and calcium best explained temporal variance of epilithic species abundances in the recovering acidified lakes. In Lake 302S, contrasting trajectories of taxonomic resilience and resistance, i.e. displacement from reference conditions following a perturbation, indicated that ecological factors affecting epilithon differed at corresponding pH levels during recovery and acidification. Our findings reveal that modeling of ecosystem recovery from severe acidification must account for the spatial and temporal scale of the perturbation, and biological delay responses that result in differences between recovery and acidification trajectories.

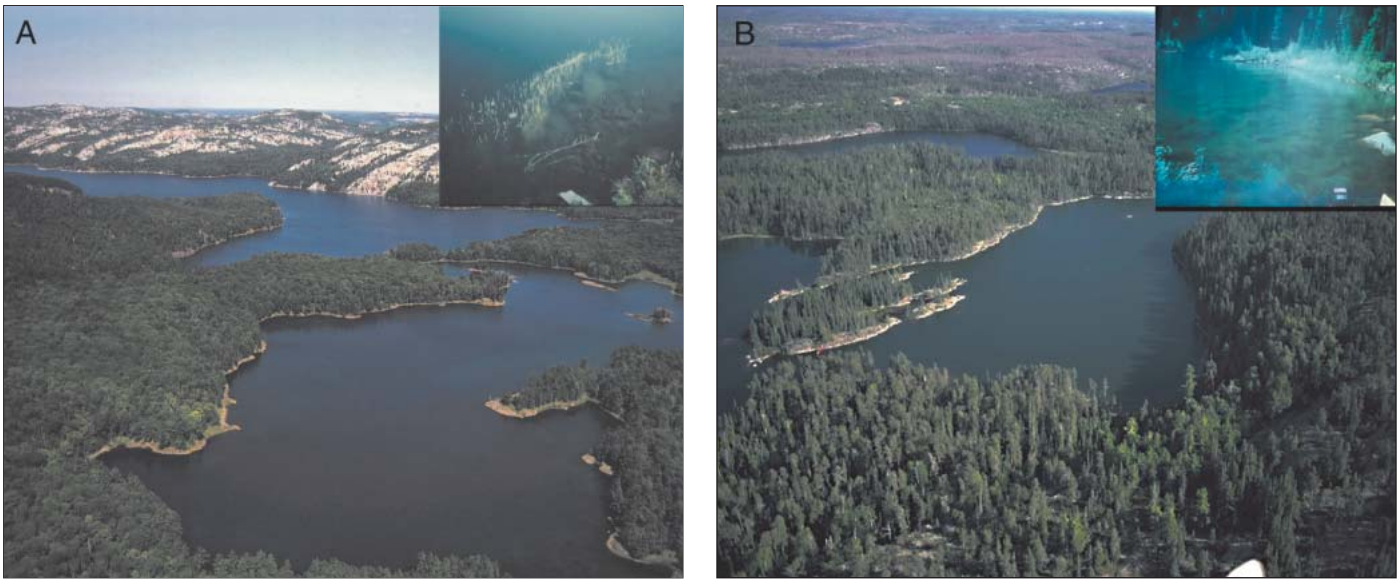
INTRODUCTION

The boreal biome contains the world's largest number of lakes that are sensitive to anthropogenic acidification. Thousands of poorly buffered Canadian boreal lakes (Fig. 1) were acidified during the 20th century by acid deposition generated from industrial activity (1). Since 1970, some boreal lakes have shown chemical and biological recovery because of reductions in acidic sulfur oxide emissions by Canadian industries (2–6). However, other lakes have shown limited recovery, while many continue to acidify (3). Therefore, evidence of resilience, i.e. recovery rate to anthropogenic acidification in boreal lake ecosystems is required to assess the need for further abatement of emissions of sulfur and nitrogen oxides.

Anthropogenic acidification of boreal lakes impacts several environmental variables (7). Increased acidity results in declines in dissolved organic carbon (DOC) and base cations (e.g. calcium), and elevated aluminum, concentrations in boreal lakes. As a consequence, biota experience increased exposure to DNA-damaging UV-B (280–320 nm wavelength) radiation and metal toxicity because DOC is the primary attenuator of ultraviolet (UV; 280–400 nm wavelength) radiation and organic chelator of metals in boreal lakes (8–11). Lake acidification also lowers the concentration of dissolved inorganic carbon (DIC), which limits rock-associated, i.e. epilithic, algae (12). Consequently, anthropogenic acidification impairs biodiversity and certain ecosystem processes in boreal lakes (7, 13).

Algal assemblages may closely track environmental changes in lakes owing to their wide dispersal potentials and relatively fast growth rates (14–16). In particular, taxonomic composition can be a more sensitive indicator than primary production because compensatory species dynamics make aggregate community functions more resistant against the impacts of acidification (14, 17). For example, taxonomic shifts in epilithon (15, 18, 19), phytoplankton (5, 19, 20), and diatom assemblages (21, 22) are more often detected than are changes in total algal biomass in recovering acidified lakes. Nevertheless, taxonomic resilience will depend on recruitment from local (within-lake) and regional

Figure 1. Atmospherically acidified Killarney lake at pH 5.0 (A, left panel) and experimentally acidified Lake 302S, Ontario, at pH 4.7 (B, right panel). Insets show characteristic proliferation of filamentous green algae in both acidified lakes. Photos: Killarney Lake, E. Snucins, Killarney algal inset, R. Vinebrooke; and Lake 302S, J. Shearer and algal inset, M. Turner.



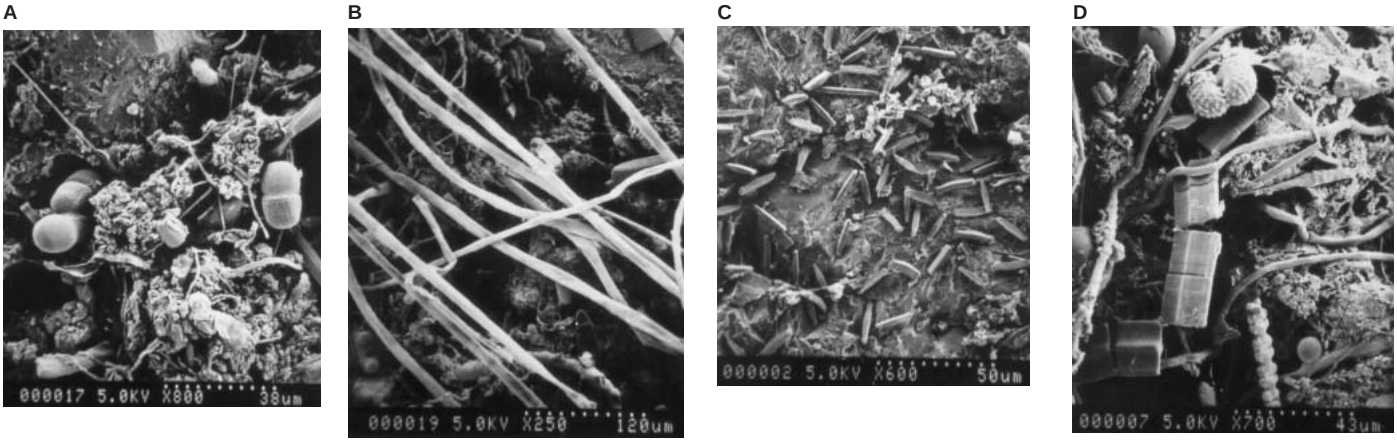


Figure 2. Scanning electron micrographs of epilithic algal assemblages in (A) highly acidified (pH < 5) clearwater lake; (B) highly acidified brownwater lake; (C) circumneutral clearwater lake, and (D) circumneutral brownwater lake. Photos: R. Vinebrooke.

(among-lakes) species pools, which can become impoverished in areas that have experienced decades of widespread atmospheric acidification (13, 18, 20).

Epilithic algal assemblages show distinct changes in taxonomic composition along gradients of lake acidity and DOC (15, 18), and during experimental lake acidification and recovery (12, 19). Filamentous green algae, saccoderm desmids, and certain diatom species replace cyanobacteria, placoderm desmids, and numerous other diatoms as species diversity declines with increasing lake acidity from pH 7 to 4 (Figs 1, 2). Epilithic desmids and filamentous green algae are also more abundant in brownwater (> 3 mg DOC L^{-1}) lakes than in clearwater lakes (Fig. 2). Abiotic factors are the key environmental determinants of epilithic algal abundance and taxonomic composition in boreal lakes during the early stages of recovery from severe acidification; however, grazing by macroinvertebrates and tadpoles becomes increasingly important above pH 6 (15, 18).

The primary objective of our study was to determine the influence of spatial and temporal scale of acidification on the resilience of epilithic assemblages during chemical recovery. We hypothesized that resilience would be more impaired by long-term, regional acidification (Killarney Park, Ontario) than by short-term, local acidification (Lake 302S, Experimental Lakes Area, Ontario). Resilience was measured as the distance traveled by lakes in ordination space during pH recovery towards reference lake conditions (pre-acidification Lake 302S). Our analyses also enabled us to assess the hypothesized potential of epilithic assemblages to function as indicators of recovery in acidified lakes (18).

MATERIALS AND METHODS

Study Lakes

Lake 302S is a small (10.9 ha surface area, 5.1 m average depth), dimictic headwater system located in the Experimental Lakes Area (49°40'N, 93°44'), which was established in 1968 for whole-ecosystem experiments and long-term ecological monitoring in northwestern Ontario (1). The catchment is unlogged boreal forest, consisting mainly of jack pine, red pine, and black spruce. The region experiences low rates of acid deposition (23). Lake 302S was monitored for 2 years before being gradually acidified over ten years (1982–1991) from pH 6.8 to 4.5 (24). The pH of Lake 302S was allowed to recover to target values (19) between 1991 and 2000 (Table 1; Fig. 3).

The 20 atmospherically acidified lakes that were surveyed are located in Killarney Provincial Park (46°3'N, 81°21'W), a 48 000-ha wilderness park situated 50 km southwest of Sudbury, Ontario. Lakes that were severely acidified by high sulfur deposition (> 20 kg SO_4 ha^{-1} yr^{-1}) over the past several decades are situated on the orthoquartzite ridges of the LaCloche Mountains (Fig. 1), whereas less-acidified lakes have sandstone, limestone, and wetlands in their catchments. Paleolimnological evidence suggested that acid deposition had shifted whole-lake algal community structure towards deepwater phytoflagellates and filamentous green phytobenthos in 4 Killarney lakes (Acid, Bell, George, O.S.A.) during the 20th century (25). All Killarney lakes are part of the Northern Lakes Recovery Study (NLRS), which is a Canadian-Norwegian investigation into the ecosystem recovery of lakes from anthropogenic acidification (26). Several of the lakes have shown pronounced pH recovery over the last decade (Fig. 3).

Sampling Protocols

In Lake 302S, water samples were collected monthly (May–October) from the upper water layer of uniform temperature, i.e. epilimnion, at the location overlying the deepest point in the lake. In each Killarney lake, surface water samples were collected during July from its outflow in 1992 (18) and at a mid-lake station from 1998–2000. Comparison of pH values for corresponding outflow and pelagic water samples showed that they were similar (± 0.1 pH units) for a subset of 6 Killarney lakes in 1992. Chemical analyses of water samples from Killarney lakes and Lake 302S were performed using standard procedures (27, 28).

Monthly collections of epilithon from each lake were pooled to produce a single representative sample for each ice-free season, except for Lake 302S from 1996 to 1999 when samples were collected only in July and August. During the Killarney survey in 1992 and from 1998 to 2000, 5 rocks were retrieved monthly (June–October) from around the shoreline (~ 1-m depth) of each lake, and epilithon collected from a known area using a hard-bristle tootbrush (15, 18). In Lake 302S, at least 9 samples were collected on each occasion. Until 1995, triplicate collections of epilithon were taken approximately monthly from 3 different 1–2 m deep sites using a syringe equipped with a bristle brush (12, 29). Therefore, epilithon data for Lake 302S consisted of means over the ice-free season (May–September) from 1981 to 1995, and means based on mid-summer collections from 1981 to 2000.

Taxonomic enumerations of epilithic samples were performed using a modified Utermöhl technique (15, 18, 19). Each sample was enumerated by inspecting 100 random fields of view using an inverted light microscope (x125 – x1000 magnification) with phase contrast. Additional fields of views were enumerated if a minimum count of 100 viable cells of the most abundant taxon was not reached, which resulted in counts ranging between 300 and 1000 cells per enumeration. Chloroplast integrity was used as the criterion for cell viability. Estimates of taxon biovolumes were determined by converting cell counts using the appropri-

ate geometric formulae for each cell shape (30). Average cellular dimensions for each taxon were based on measurements of up to 30–50 cells in each sample.

Statistical Analyses

CCA was performed using CANOCO version 4.0 (31) to determine the environmental variables that best explained temporal shifts in epilithic assemblages during acidification and chemical recovery in Lake 302S and the Killarney lakes. CCA is a community-level, multivariate analysis that summarizes the maximum amount of variation in the taxonomic data set, and maximizes its correlation with linear combinations of measured environmental variables. Each linear combination of environmental variables is represented by a CCA axis and its eigenvalue (λ), which is a measure of the amount of explained species variance. The length and orientation of each environmental vector represents its magnitude and direction of maximum change in ordination space. The proximity and alignment of a species with a particular vector shows how closely the variation in its abundance is related to that environmental variable. Similarly, distances between site scores in ordination space reflect the degree of taxonomic dissimilarity of epilithic assemblages between different lakes, or across sampling years within a lake, e.g. Lake 302S.

Taxonomic and environmental data were screened prior to final CCA. Taxa that did not occur in at least 5 samples were defined as being rare, and removed from the species data prior to CCA to negate their potentially disproportional influence on the ordination. The Lake 302S-Killarney ordination was based on mean annual taxa abundances that were averaged over 5 sampling months from Killarney lakes (1992, 1998–2000) and Lake 302S (1981–1995), and standardized to the genus-level, to avoid confounding effects of differences in seasonality and taxonomic resolution between the two studies. Logarithmic transformation of mean annual biomass for each species was used to downweight the strong influence of highly abundant, large-celled taxa, e.g., filamentous green algae on CCA. Log-transformed environmental data were screened for insignificant and redundant variables to exclude superfluous variables that otherwise distort CCA ordination plots. The complete environmental data set consisted of pH, and dissolved fractions of aluminum, calcium, inorganic carbon, iron, magnesium, organic carbon, and total phosphorus. Hill's scaling was used to equalize taxon variances along all axes to generate site scores that were weighted averages of taxon scores (31). This scaling enabled us to focus on inter-sample distances because of our primary interest in relationships among sampling years in Lake 302S and lakes in the Killarney area. Statistical significance of each CCA was determined by Monte Carlo permutation testing of the eigenvalues.

Metrics used to quantify taxonomic resilience and resistance of epilithon were based on chi-squared distance (31) traveled by lake scores in ordination space towards or away from non-acidified, reference boreal lake conditions, respectively. Lake 302S prior to experimental acidification in 1982 served as a reference for nonacidified lake conditions. Resilience was quantified by dividing chi-squared distance traveled towards the CCA coordinates for nonacidified Lake 302S by the increase in pH between years in Lake 302S (1990–1999) and the Killarney lakes (1992–2000). Resistance of epilithon in Lake 302S was measured as departure of ordination scores during experimental acidification (1982–1990) from the score for Lake 302S in 1981 as a function of declines in pH.

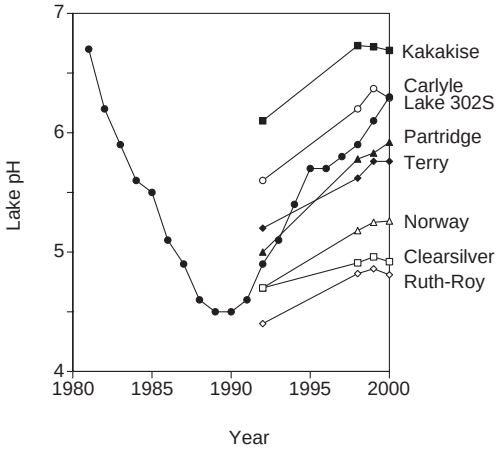


Figure 3. Temporal patterns of average annual ice-free epilimnetic pH values for Lake 302S (acidification experiment, 1982–1990; recovery, 1991–1999) and 7 Killarney lakes in which epilithon was first collected in 1992, and then resampled during 1998–2000.

RESULTS AND DISCUSSION

Lake 302S

CCA captured 29% of the total variance in the mid-summer (July –August) epilithic species data with its first 2 axes (Fig. 4). The 1st axis ($\lambda_1 = 0.46$) represented a significant ($p < 0.005$) temporal gradient of taxonomic responses by epilithic taxa to chemical changes during acidification between 1981 and 1990. Declines in epilimnetic pH ($r = 0.72$) and DIC ($r = 0.85$) best defined CCA axis 1, and accounted for 45% and 14% of the explained species variance, respectively. CCA axis 1 contrasted taxa that were common in Lake 302S prior to the experiment from originally rare taxa that increased in abundance during acidification. Specifically, filamentous cyanobacteria (*Anabaena*, (No. 1)) and diatoms (*Cyclotella* spp. (No. 45), *Gomphonema* spp. (No. 69), *Synedra* spp. (No. 91)) that were abundant before acidification were replaced by other diatoms (*Brachysira brebissonii* (No. 44), *Frustulia rhomboides* (No. 64), *Tabellaria quadriseptata* (No. 95)) during the decade-long acidification phase of the experiment (Fig. 4A).

The 2nd CCA axis ($\lambda_2 = 0.26$) represented a temporal gradient of taxonomic responses by epilithon taxa to chemical recovery in Lake 302S between 1990 and 1999 (Fig. 4). CCA axis 2 was

Table 1. Limnological conditions of Lake 302S (1980–1999), Experimental Lakes Area, Ontario, and 20 survey lakes in Killarney Provincial Park, Ontario, sampled during July of 1992, and 1998–2000. Lake codes correspond to those that appear in the CCA plots.

Lake	Year	pH	Al ($\mu g\ L^{-1}$)	Ca ($mg\ L^{-1}$)	DIC ($mg\ L^{-1}$)	DOC ($mg\ L^{-1}$)
L302	1980–1981*	6.7	7	1.7	0.9	6.3
	1982–1990 **	5.2	38	2.4	0.4	4.0
	1991–1999 ***	5.5	43	2.1	0.4	3.6
Acid (A)	1998–2000	5.1	133	1.1	0.3	0.7
Bell (B)	1998–2000	6.3	38	1.9	4.2	5.4
Carlyle (CA)	1992	5.5	121	2.1	0.6	5.3
	1998–2000	6.3	26	6.3	0.3	3.3
Chain (CH)	1998–2000	4.8	197	1.3	0.3	4.5
Clearsilver (CS)	1992	4.7	309	1.8	0.1	1.4
	1998–2000	4.9	148	4.9	0.3	0.9
David (D)	1998–2000	5.1	67	1.2	0.3	1.3
George (G)	1998–2000	6.3	20	2.0	0.3	1.7
Helen (H)	1998–2000	7.0	16	2.5	1.0	3.3
Johnnie (J)	1998–2000	6.3	44	1.7	0.3	3.1
Kakakise (KA)	1992	6.1	74	2.1	0.6	2.7
	1998–2000	6.7	12	2.2	0.6	2.6
Killarney (KI)	1998–2000	5.1	136	1.5	0.3	0.3
Lumsden (L)	1998–2000	5.2	102	1.2	0.2	0.6
Nellie (NE)	1998–2000	4.6	458	1.4	0.2	0.3
Norway (NO)	1992	4.7	211	1.4	0.1	1.0
	1998–2000	5.2	113	1.5	0.3	0.8
O.S.A. (OSA)	1998–2000	4.9	139	1.9	0.3	0.3
Partridge (P)	1992	5.1	52	2.0	0.2	1.7
	1998–2000	5.8	37	2.0	0.5	1.7
Ruth-Roy (RR)	1992	4.4	311	0.8	0.1	0.8
	1998–2000	4.8	260	1.1	0.3	0.4
Teardrop (TD)	1998–2000	6.8	7	1.8	0.8	1.1
Terry (TE)	1992	5.2	201	1.4	0.3	6.5
	1998–2000	5.7	136	1.6	0.4	5.4
Tyson (TY)	1998–2000	6.2	32	1.8	0.3	4.2

* pre-acidification phase
** experimental acidification phase
*** pH recovery phase

positively correlated with increasing DOC ($r = 0.72$), which accounted for 41% of the total explained taxonomic variance. CCA axis 2 contrasted phytoflagellates (*Gymnodinium* (No. 98), *Cryptomonas* spp. (No. 120)) and cyanobacteria (*Pseudoanabaena* (No. 15)) from firmly attached filamentous green algae (*Bulbochaete* (No. 100), *Oedogonium* (No. 104)) that increased in abundance as Lake 302S recovered chemically between 1990–1999 (Fig. 4A). Interestingly, increased abundances of firmly attached epilithic taxa suggest that benthic herbivores had begun to recolonize Lake 302S as these algae can tolerate high grazing pressure (15, 32).

Ordination of sampling years showed that the taxonomic trajectories of epilithon during acidification and subsequent chemical recovery differed in Lake 302S (Fig. 4B). Although lake scores during acidification (1981–1990) tracked primarily along CCA axis 1, they later diverged during recovery (1991–1999) along CCA axis 2. In particular, differences between ordination scores for certain acidification and recovery years (e.g. 1983 *vs* 1997, 1987 *vs* 1992) indicated dissimilarity between epilithic assemblages despite corresponding epilimnetic pH values.

A possible explanation for differences between epilithic trajectories during acidification and recovery in Lake 302S involves biological delay responses by higher trophic levels. For example, extirpation and recolonization dynamics of certain benthic grazers differed in Lake 302S because species that were incapable of active aerial dispersal, e.g. amphipods, crayfish, tadpoles, remained absent or rare during chemical recovery (33). Therefore, benthic grazing probably differed at similar pH levels during acidification and chemical recovery in Lake 302S. Biological delay responses by epilithon that span years in Lake 302S could not be directly attributed to the algae because these relative fast-growing microorganisms have relative wide dispersal potentials and are more responsive to abiotic changes than are organisms at higher trophic levels (14, 16).

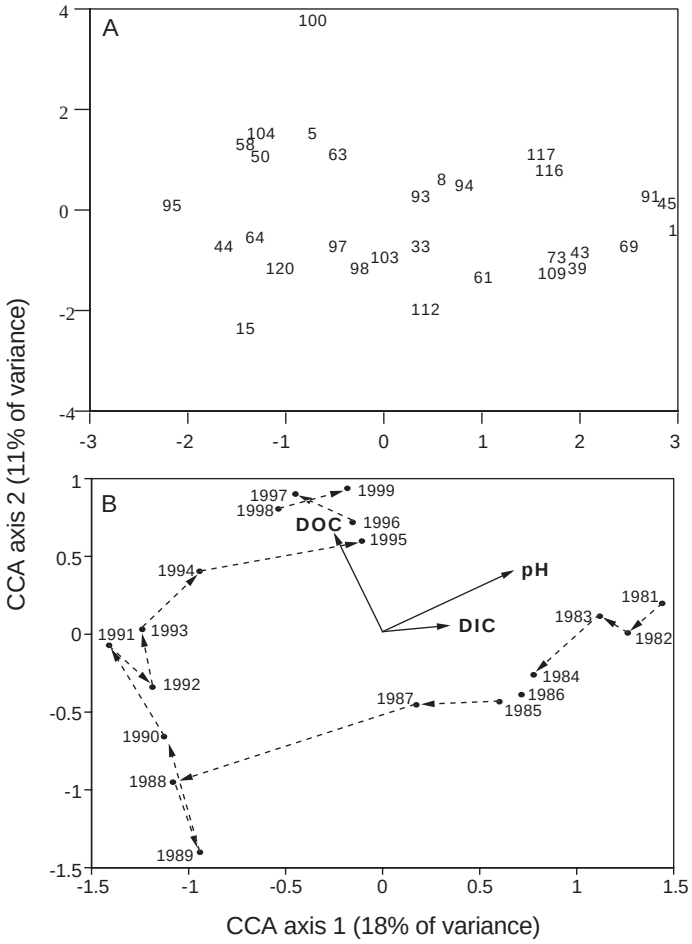


Figure 4. Association of (A) epilithic algal taxa; (B) sampling years (1981–1999), and water chemistry for experimentally acidified Lake 302S based on CCA using $\log_{10}$-transformed species biovolumes and water chemistry data averaged over July and August. Taxon numbers appear in Table 2.

Killarney Lakes

The first CCA axis explained 17% of the total variance in average annual (May–October) epilithic species abundances (Fig. 5). CCA axis 1 ($\lambda_1 = 0.21$) represented a significant ($F = 5.39$, $p < 0.005$) gradient that was best defined by DOC ($r = -0.74$), which accounted for 43% of the explained species variance. Dissolved Al was also strongly correlated ($r = 0.58$) with CCA axis 1, and accounted for 17% of the species variance explained by the CCA. Lake pH was also strongly associated ($r = 0.63$) with CCA axis 1, but it did not exert a significant influence independent of the covariable Al. The first axis separated species (*Homoeothrix juliana* (No. 7), *Tetmemorus laevis* (No. 35), *Zygogonium ericetorum* (No. 106)) that were abundant in highly acidified clearwater lakes (Clearsilver, Norway, Ruth-Roy) from several diatom species (*Gomphonema* spp. (No. 69), *Pinnularia* spp. (No. 84), *Stauroneis* spp. (No. 87)) that were more common in relatively circumneutral (Kakakise, Helen, Teardrop) and brownwater (Carlyle, Terry) lakes (Fig. 5).

The second CCA axis ($\lambda_2 = 0.11$) captured 9% of the total taxonomic variance, and represented a gradient of DIC ($r = 0.56$) and Ca ($r = 0.64$), which accounted for 16 and 24% of the explained variance (Fig. 5). The second axis primarily contrasted diatom species (*Achnanthes* spp. (No. 38), *Cymbella* spp. (No. 50)) in circumneutral lakes from desmids (*Euastrum* sp. (No. 28), *Cosmarium* spp. (No. 26)) and other diatoms (*Actinella punctuata* (No. 40), *Eunotia* spp. (No. 61)) that were disproportionately more abundant in dilute, brownwater lakes (Fig. 5).

Carlyle, Clearsilver, Kakakise, Partridge, and Terry were the only chemically recovering lakes (Fig. 3) that showed net movement in ordination space towards the upper left quadrant containing circumneutral lakes, such as Helen and Teardrop (Fig. 5B). In comparison, the magnitude or direction of trajectories of other acidified lakes (e.g. Norway, Ruth-Roy) varied greatly, and did not exceed those displayed by the circumneutral lakes. Therefore, our findings suggest that epilithic assemblages showed limited evidence of recovery from acidification despite substantial chemical improvements in many Killarney lakes between 1992 and 2000 (Table 1).

Comparison of Experimental and Atmospheric Acidification of Lakes

CCA axis 1 ($\lambda_1 = 0.18$) explained 20% of the total variance within the combined taxonomic data from Lake 302S and the Killarney lakes, and represented a significant ($p < 0.005$) environmental gradient most influenced by DOC ($r = 0.89$; Fig. 6). DOC accounted for 38% of the total explained taxonomic variance. Dissolved Ca ($r = 0.85$) was also correlated with CCA axis 1, accounting for 42% of the taxonomic variance. The first CCA axis contrasted species (*Cryptomonas* spp. (No. 120), *Gymnodinium* (No. 98), *Pseudoanabaena* (No. 15), *Tabellaria quadrisepta* (No. 95)) that were disproportionately more abundant in acidified Lake 302S versus several chlorophytes (*Actinotaenium cucurbita* (No. 22), *Cylindrocystis brebissonii* (No. 27), *Klebsormidium* (No. 101), *Microspora* (No. 102), *Penium cylindrus* (No. 31)) that were more common in the severely acidified, clearwater Killarney lakes (Acid, Clearsilver, Norway, OSA, Ruth-Roy; Fig 6A).

The second CCA axis ($\lambda_1 = 0.07$) explained 9% of the total species variance (Fig. 6), and was positively correlated with increasing DIC ($r = 0.53$). DIC accounted for 20% of the explained variance. CCA axis 2 separated desmids (*Arthodesmus* (No. 23), *Gonatozygon* (No. 29), *Netrium digitus* (No. 30)) and the green

alga *Coelastrum cambricum* (No. 110) that were common in the circumneutral Killarney lakes (Helen, Kakakise, Teardrop) from species (*Cryptomonas* spp. (No. 120), *Gymnodinium* (No. 98), *Pseudoanabaena* (No. 15), *Tabellaria quadrisepta* (No. 95)) that were more abundant in Lake 302S during the late stages of acidification, e.g. 1989–1993.

Lake 302S separated from the Killarney lakes in ordination space as their epilithic assemblages became increasingly dissimilar during experimental acidification (Fig. 6). For instance, several tychoplanktonic species, such as *Pseudoanabaena* (No. 15), *Tabellaria quadrisepta* (No. 95), *Gymnodinium* spp. (No. 98), and *Cryptomonas* spp. (No. 120), became abundant in Lake 302S during acidification, but remained relatively rare in the highly acidified Killarney lakes. Comparison of separate CCAs for Lake 302S (Fig. 4) and the Killarney lakes (Fig. 5) suggested that a potential explanation for the taxonomic dissimilarity of their epilithon was that the species were affected by different environmental changes during atmospheric *versus* experimental acidification. Specifically, Al and Ca explained taxonomic differences among epilithon in the Killarney lakes, but not during acidification of Lake 302S. In Lake 302S, Al concentrations became elevated below pH 5, but remained well below the potentially phytotoxic levels recorded at similar pH values in the heavily acidified Killarney lakes (Table 1). Therefore, Killarney lakes and acidified Lake 302S differed both environmentally, and in terms of their epilithon, likely because the former experienced chronic whole-catchment acidification for several decades, whereas only the surface water of the latter was acidified for 8 years.

Taxonomic resilience of epilithon during pH recovery was relatively negligible in the Killarney lakes when compared to Lake 302S. For example, Carlyle Lake showed limited movement in ordination space when compared to the pronounced shift by Lake 302S (Fig. 6B). Furthermore, the slope of the linear relationship between chi-square distance traveled by Killarney lakes in ordination space and pH recovery was not significantly ($p > 0.05$) different from zero (Fig. 7), which showed that epilithic assemblages were not responsive to declining acidity between 1992 and 2000. In contrast, a positive relationship between chi-square distance and pH recovery showed that epilithic assemblages did respond to pH recovery in Lake 302S (Fig. 7). However, substantial unexplained variation in this relationship resulted from epilithic assemblages not consistently tracking pH recovery in Lake 302S. Therefore, epilithic algal recovery from experimental acidification of Lake 302S during the 1990s was dynamic, but also unpredictable at times in its direction. In fact, taxonomic trajectories during experimental acidification and recovery up to 1999 did not correspond (Fig. 4), suggesting that Lake 302S was recovering to a new alternate state.

Taxonomic responses by epilithon may have been more pronounced in Lake 302S because experimental acidification had not simulated the severity of environmental conditions in the heavily acidified Killarney lakes. For example, although DOC increased from 2 to 4 mg L^{-1} in Lake 302S during chemical re-

Figure 5. Association of (A) epilithic algal taxa; (B) lakes across sampling years (1992, 1998, 1999, 2000), and water chemistry for 20 atmospherically acidified lakes in Killarney Provincial Park, Canada based on CCA using log_{10}-transformed taxa biovolumes and water chemistry data averaged over June to October. Open symbols are used for the 7 chemically recovering lakes (see Fig. 3) that were sampled in 1992 and from 1998–2000. Solid symbols used for lakes that were only sampled from 1998 to 2000. Taxon numbers appear in Table 2, and Killarney lake codes are provided in Table 1.

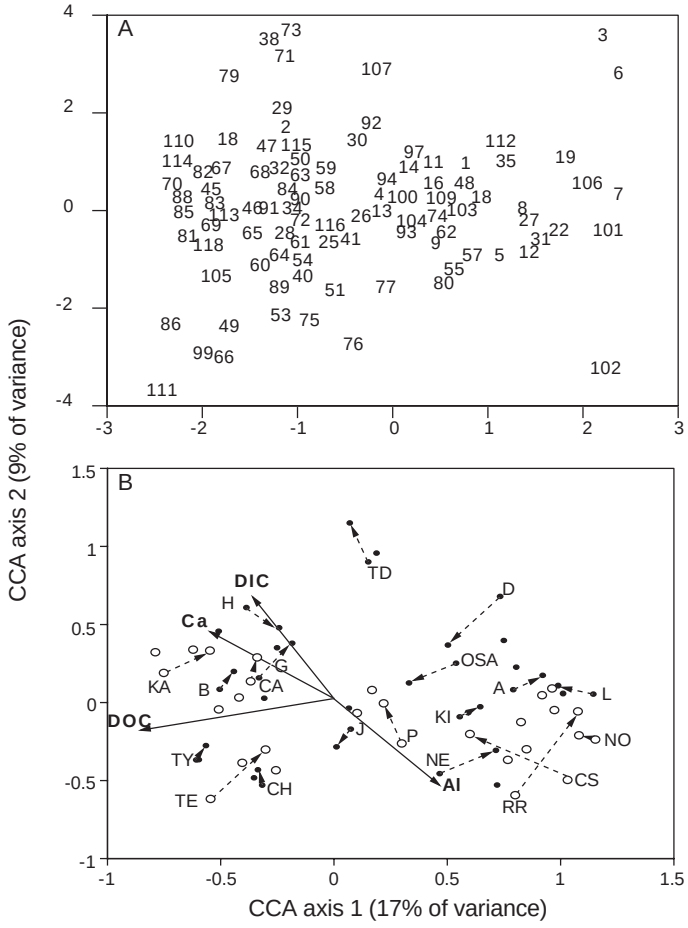
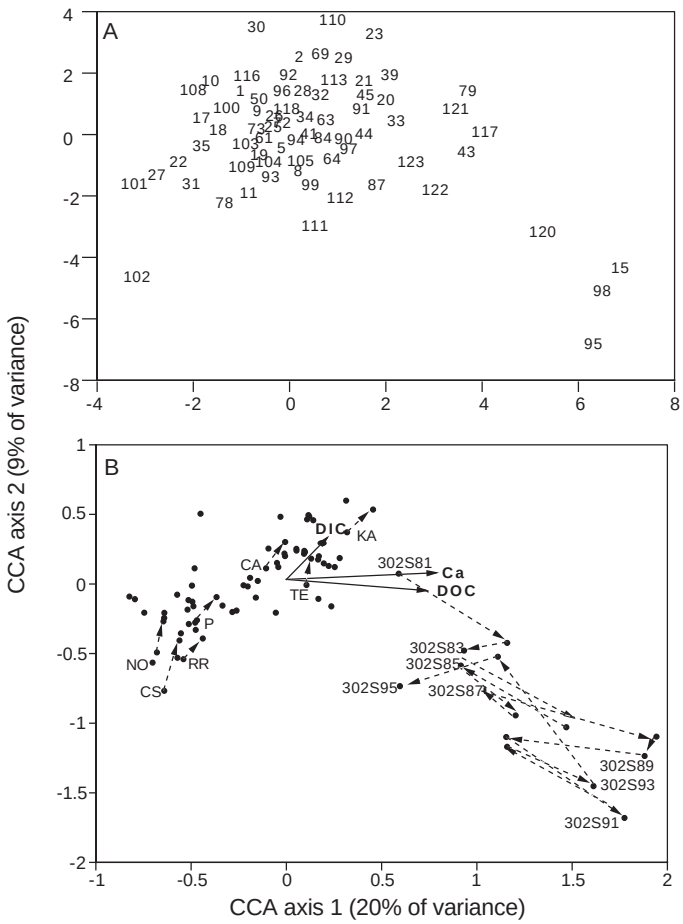


Figure 6. Association of (A) epilithic algal taxa; (B) lakes across sampling years, and water chemistry for experimentally acidified Lake 302S and atmospherically acidified Killarney Lakes based on CCA using log_{10}-transformed taxa biovolumes and water chemistry data averaged over June to October for Killarney and May to September for Lake 302S. Taxon numbers appear in Table 2, and Killarney lake codes are provided in Table 1.



covery, lower levels of UV-attenuating DOC in the Killarney lakes did not change or declined between 1992 and 2000 (Table 1). Therefore, suppression of epilithon by DNA-damaging UV-B radiation (34, 35) could have been more severe in the Killarney lakes during chemical recovery. Higher Al:Ca ratios also suggested that epilithon experienced greater metal toxicity in the severely acidified Killarney lakes than in Lake 302S.

The relative weak response of epilithic assemblages to chemical recovery in the Killarney lakes may also reflect poor recruitment resulting from long-term acid deposition impoverishing local (7, 18) and regional (13) pools of algae and consumers. Decades of acidification of the Killarney lakes might have exhausted the supply of viable sedimentary resting stages, which are essential to community recovery following perturbation (36). In contrast, relatively high species turnover during recovery in Lake 302S could have resulted from emergence of viable resting stages that had to endure only 8 years of acidification. Interestingly, phytoplankton assemblages also showed higher relative taxonomic resilience in Lake 302S than in the Killarney lakes (5). Similarly, phytoplankton also required 2–7 years to taxonomically recover from a reacidification event in Swan Lake (4), which is located between the Killarney lakes and Sudbury. A possible explanation for the greater responsiveness of algal assemblages to chemical changes in Lake 302S is that it is located in a relative pristine region where species are readily available for colonization from numerous nearby lakes, e.g. Lake 302N, and wetlands.

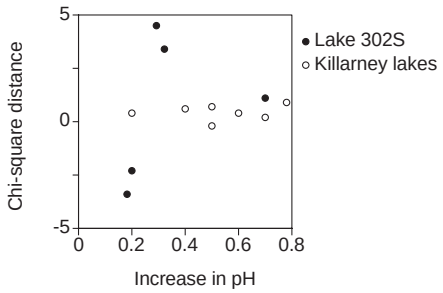


Figure 7. Net chi-square distance traveled by site scores in CCA ordination space towards coordinates for pre-acidification Lake 302S in 1981 (Fig. 6) as a function of pH recovery in Lake 302S (1990–1995) and 7 Killarney lakes (1992–2000). Lake 302S and the Killarney lakes are represented using solid and open symbols, respectively.

CCA consistently accounted for less than 30% of the total variance within the taxonomic data sets for epilithon from the Killarney lakes and Lake 302S, highlighting the importance of unmeasured environmental variables and habitat heterogeneity within the littoral zone. Variation in epilithic assemblages in these recovering acidified lakes might have been related to abiotic and biotic metrics that are difficult to quantify during synoptic surveys, such as acidification and nutrient pulses, length of ice-free growing season, solar irradiance and thermal regimes, and herbivory. In particular, unmeasured biotic factors, such as benthic grazing and competition, increasingly regulate epilithon during the advanced stages of chemical recovery, and therefore, may account for taxonomic variation within the less acidified (pH > 6) Killarney lakes (15, 18). In addition, unexplained variance in epilithic assemblages can be generated as a result of the pronounced heterogeneity of littoral habitats, which is difficult to quantify. Nonetheless, ordination of other surveyed aquatic communities also typically capture only 40% of the total species variance (5, 6).

CONCLUSIONS

Our findings agree with other reports of biological delay responses to chemical recovery in acidified lakes (2, 19, 37–40). Several possible explanations exist for epilithic delay responses to chemical recovery, which were pronounced more in the

Table 2. List of epilithic algal taxa used in canonical correspondence analyses. Taxon identification numbers correspond to those used in the CCA plots. Cyanobacteria (C), desmids (DE), diatoms (DI), filamentous green algae (FG), nonfilamentous green algae (G), dinoflagellates (DN), chrysophytes (CH), chryptophytes (CR), and euglenoids (E).

No.	Taxon	Algal group
1	*Anabaena* spp.	C
2	*Aphanocapsa* spp.	C
3	*Calothrix fusca*	C
4	*Chroococcus pallidus*	C
5	*Chroococcus* spp.	C
6	*Hapalosiphon* spp.	C
7	*Homoeothrix juliana*	C
8	*Lyngbya* spp.	C
9	*Merismopedia glauca*	C
10	*Merismopedia tenussima*	C
11	*Merismopedia* spp.	C
12	*Oscillatoria ornata*	C
13	*Oscillatoria* spp.	C
14	*Oscillatoria tenue*	C
15	*Pseudoanabaena* sp.	C
16	*Phormidium tenue*	C
17	*Filamentous cyanobacteria*	C
18	*Rhaboderma lineare*	C
19	*Dinobryon* spp.	CH
20	*Chrysochromulina laurentiana*	CH
21	*Kephyrion* sp.	CH
22	*Actinotaenium cucurbita*	DE
23	*Arthodesmus* spp.	DE
24	*Arthodesmus extensus*	DE
25	*Closterium* spp.	DE
26	*Cosmarium* spp.	DE
27	*Cylindrocystis brebissonii*	DE
28	*Euastrum* spp.	DE
29	*Gonatozygon* spp.	DE
30	*Netrium digitus*	DE
31	*Penium cylindrus*	DE
32	*Pleurotaenium* spp.	DE
33	*Spondylosium planum*	DE
34	*Staurastrum* spp.	DE
35	*Tetmemorus laevis*	DE
36	*Tetmemorus* spp.	DE
37	*Xanthidium* sp.	DE
38	*Achnanthes* spp.	DI
39	*Achnanthes minutissima*	DI
40	*Actinella punctata*	DI
41	*Anomoeoneis serians*	DI
42	*Anomoeoneis vitrea*	DI
43	*Aulacoseira* spp.	DI
44	*Brachysira brebissonii*	DI
45	*Cyclotella* spp.	DI
46	*Cymbella amphicephala*	DI
47	*Cymbella lunata*	DI
48	*Cymbella microcephala*	DI
49	*Cymbella minuta*	DI
50	*Cymbella* spp.	DI
51	*Eunotia arcus*	DI
52	*Eunotia bactriana*	DI
53	*Eunotia bidentula*	DI
54	*Eunotia bilunaris*	DI
55	*Eunotia exigua*	DI
56	*Eunotia flexulosa*	DI
57	*Eunotia incisa*	DI
58	*Eunotia pectinalis*	DI
59	*Eunotia pectinalis var. minor*	DI
60	*Eunotia serra*	DI
61	*Eunotia* spp.	DI
62	*Fragilaria acidobiontica*	DI
63	*Fragilaria* spp.	DI
64	*Frustulia rhomboides*	DI
65	*Frustulia rhomboides var. crassinerva*	DI
66	*Frustulia rhomboides var. saxonica*	DI
67	*Gomphonema acuminatum*	DI
68	*Gomphonema gracile*	DI
69	*Gomphonema* spp.	DI
70	*Gomphonema truncatum*	DI
71	*Gyrosigma* sp.	DI
72	*Melosira* spp.	DI
73	*Navicula* spp.	DI
74	*Navicula subtilissima*	DI
75	*Neidium affine*	DI
76	*Neidium iridis*	DI
77	*Neidium iridis var. amphigomphus*	DI
78	*Neidium* spp.	DI
79	*Nitzschia* spp.	DI
80	*Pinnularia abaujensis*	DI
81	*Pinnularia biceps*	DI
82	*Pinnularia major*	DI
83	*Pinnularia microstauron*	DI
84	*Pinnularia* spp.	DI
85	*Pinnularia streptoraphe*	DI
86	*Stauroneis anceps*	DI
87	*Stauroneis* spp.	DI
88	*Stenopterobia intermedia*	DI
89	*Stenopterobia* spp.	DI
90	*Surirella* spp.	DI
91	*Synedra* spp.	DI
92	*Tabellaria binalis*	DI
93	*Tabellaria fenestrata*	DI
94	*Tabellaria flocculosa*	DI
95	*Tabellaria quadrisepta*	DI
96	*Pennate diatoms*	DI
97	*Peridinium* sp.	DN
98	*Gymnodinium* sp.	DN
99	*Binuclearia tatrana*	FG
100	*Bulbochaete* spp.	FG
101	*Klebsormidium subtillisimma*	FG
102	*Microspora* spp.	FG
103	*Mougeotia* spp.	FG
104	*Oedogonium* spp.	FG
105	*Spirogyra* spp.	FG
106	*Zygogonium ericetorum*	FG
107	*Zygogonium tunetanum*	FG
108	*Zygogonium* spp.	FG
109	*Chlamydomonas* spp.	G
110	*Coelastrum cambricum*	G
111	*Crucigenia* sp.	G
112	*Oocystis* spp.	G
113	*Pediastrum* spp.	G
114	*Pediastrum tetras*	G
115	*Scenedesmus quadricauda*	G
116	*Scenedesmus* spp.	G
117	*Sphaerocystis schroeteri*	G
118	*Tetraedron* sp.	G
119	*Small greens*	G
120	*Cryptomonas* spp.	CR
121	*Rhodomonas minuta*	CR
122	*Trachelomonas hispida*	E
123	*Trachelomonas volvocina*	E

Killarney lakes than in Lake 302S. Firstly, long-term regional acidification and biological impoverishment of Killarney lakes may have delayed arrival by extirpated algae, or grazers that increasingly regulate epilithon during chemical recovery (15, 32). In contrast, the ubiquity of microbes and benthic grazers in relatively pristine areas, e.g. ELA, suggests that epilithic delay responses in Lake 302S were less hampered by poor species dispersal (7, 16). Secondly, we hypothesize that the persistence of acid-tolerant species can result in competitive exclusion of other species, thereby further delaying biological responses to chemical improvements (37). For example, acid-tolerant filamentous green algae suppress other epilithic species if acid-sensitive grazers, such as tadpoles, do not become re-established during chemical recovery (15, 32). Conversely, epilithic species may be unable to colonize recovering acidified lakes despite favorable abiotic conditions because of suppression by acid-tolerant grazers. For instance, high abundances of omnivorous minnows may suppress epilithic algae without affecting the filamentous green algae until the arrival of piscivorous fish in recovering acidified lakes (33). In addition, long-term regional acidification of the Killarney lakes may have generated more extreme abiotic conditions than did the localized experimental acidification of Lake 302S, which could further delay biological responses to chemical recovery. Finally, epilithic assemblages may not return to their original composition in recovering acidified boreal lakes because other global stressors, e.g. climate change, stratospheric ozone depletion and increased UV-B irradiance, may have altered these ecosystems during the intervening period (1, 41).

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