Acidification in the Adirondacks: Defining the Biota in Trophic Levels of 30 Chemically Diverse Acid-Impacted Lakes

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The Adirondack Mountains in New York State have a varied surficial geology and chemically diverse surface waters that are among the most impacted by acid deposition in the U.S. No single Adirondack investigation has been comprehensive in defining the effects of acidification on species diversity, from bacteria through fish, essential for understanding the full impact of acidification on biota. Baseline midsummer chemistry and community composition are presented for a group of chemically diverse Adirondack lakes. Species richness of all trophic levels except bacteria is significantly correlated with lake acid−base chemistry. The loss of taxa observed per unit pH was similar: bacterial genera (2.50), bacterial classes (1.43), phytoplankton (3.97), rotifers (3.56), crustaceans (1.75), macrophytes (3.96), and fish (3.72). Specific pH criteria were applied to the communities to define and identify acid-tolerant (pH < 5.0), acid-resistant (pH 5.0−5.6), and acid-sensitive (pH > 5.6) species which could serve as indicators. Acid-tolerant and acid-sensitive categories are at end-points along the pH scale, significantly different at $P < 0.05$; the acid-resistant category is the range of pH between these end-points, where community changes continually occur as the ecosystem moves in one direction or another. The biota acid tolerance classification (batc) system described herein provides a clear distinction between the taxonomic groups identified in these subcategories and can be used to evaluate the impact of acid deposition on different trophic levels of biological communities.

Introduction

The Adirondack region of New York covers 2.6 million hectares and includes 2800+ lakes and 9400 km of streams (*1*). The region's susceptibility to acidification has been described on the basis of surface water alkalinity (*2*) and annual inputs of acid deposition (*3*). Adirondack surface geology is varied, resulting in chemically diverse lakes. A unique system for hydrologic classification has been used routinely (*4*).

The extent of regional acidification damage to water chemistry and biota first was documented through extensive field efforts including the 1984−1987 Adirondack Lakes Survey (ALS) and the 1984 Adirondack Biota Project (ABP), respectively. The ALS collected detailed chemistry and fisheries data from 1469 waters and determined that 54% above 600 m had a pH below 5.5; 25% of these waters were fishless (*5*). The ABP surveyed a subset of 50 ALS waters (*6*) and demonstrated that acidification decreases species diversity, richness, and biomass for phytoplankton (*7*), planktonic rotifers, (*8*) and crustacean zooplankton (*9*).

Although historical research demonstrated declines in species richness and diversity for plankton and fish, the acidity-trophic level relationships for bacteria and aquatic plants have not been quantified as an integrated set of acidification indicators. Previous Adirondack biotic studies usually comprised single annual sampling events or multiple sampling during the same year on widespread regional waters. These study designs potentially obscured relationships within and among biological communities as a result of annual differences in climate and regional variability. Earlier deficiencies were addressed in the present study by examining chemistry and biology over consecutive years in a group of waters within a small geographic subregion. The intent of this study was to assess the sensitivity of taxa among multiple trophic levels to acidification. It has provided a baseline upon which to evaluate future trends in Adirondack waters resulting from reduced emissions and deposition of acidic compounds in response to the 1990 Clean Air Act Amendments.

Methods

Study Sites. Thirty lakes (Figure S1 and Table S1, Supporting Information) were selected in the southwestern Adirondack Park from 52 sites monitored by the ALS since 1992 (*10*)

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because this region receives the highest deposition of atmospheric S from Midwest sources, lakes in this region are acid-sensitive, and restricting the geographic study area decreases the geologic, edaphic, and climatic variability that would complicate evaluation of differences among sites. Lake types were selected on the basis of a classification system (*4*) that considers depth of glacial till, hydrologic type, and concentration of dissolved organic carbon (DOC). The lakes are among a population of lakes that have acidified most between 1850 and 1990 (*11*).

Field and Laboratory Methods. Lakes were sampled three times yearly, from late June through early September, during midsummer thermal stratification and in the zone of maximum depth. Each sampling interval occurred during two consecutive weeks, one for remote lakes accessed by helicopter and the other for lakes accessed by vehicle. Water chemistry, phytoplankton, and zooplankton were sampled from 1994 to 1996. Bacterioplankton were collected during 2002; macrophyte and fish surveys were conducted between 1994 and 2006. Sampling protocols and laboratory methodologies are summarized in Table S2 (Supporting Information). Chemical analytical procedures followed standard EPA methods (Table S3, Supporting Information).

Bacterioplankton. Fifteen lakes were sampled in 2002 for rDNA gene sequence analyses (Table S2, Supporting Information). Samples (prefiltered [5 μm]) were filtered onto 0.22 μm mixed cellulose ester filters and stored at −80 °C. DNA extractions, PCR amplification of 16S rDNA genes, and cloning were carried out as described in Percent et al. (*12*). Ninety-six clones were chosen randomly for each sample and analyzed using Amplified Ribosomal DNA Restriction Analysis (ARDRA). Select clones representing different ARDRA patterns were analyzed by 16S rDNA sequencing in both directions using M13 primers. A total of 1923 clones were included in this analysis.

Phytoplankton. The analytical procedures for samples collected during 1994−1996 are described in Table S2 (Supporting Information). Samples were collected from the photic zone (surface to one percent light intensity) using an integrated hose technique. Taxa were identified to the lowest possible level and enumerated in randomly selected microscope fields. The 1994−1995 samples were analyzed in one lab, and the 1996 samples were analyzed in another. Samples were sent each year from both laboratories to the same outside consultant to provide quality assurance of taxonomic identifications. Differences in taxonomy were evaluated using multivariate ordinations of all sample data. Most taxa were recognizable between the two laboratories; however, some lumping of taxa was necessary.

Zooplankton. Replicate zooplankton samples were collected using a constant flow pump and the integrated hose technique (Table S2, Supporting Information). At least 100 L of water was pumped for each sample from most lakes, and a range of 150−200 L was collected in lakes having low zooplankton densities. Identifications were made for species whenever possible (Table S2, Supporting Information).

Macrophytes. Twenty-eight lakes were sampled for macrophyte community composition, distribution, and species dominance. Surveys occurred once in late July or August to ensure maximum standing crop using standard methodology (Table S2, Supporting Information). Communities were observed, and data (frequency and relative abundance) were recorded by SCUBA divers who followed line transects marked at 1 m intervals perpendicular from the shoreline to the extent of the littoral zone.

Fish. Fish sampling follows Daniels et al. (*13*) (Table S2, Supporting Information). Fish assemblages were sampled during the spring and fall. Our interest focused on species richness in each lake. In order to develop as complete a species list as possible for each lake, we used information from collections made during this study using trapnets, gill nets, and seines (*13*), snorkeling surveys, surveys conducted by other organizations (ALSC unpublished data), a comprehensive literature review, and information from museum collections. Although effort varied among lakes and lists developed in this way may have problems with accuracy (*14*), we believe that these lake-specific lists are accurate because fish, as a group, are relatively easy to recognize and identify and Adirondack lakes have been heavily sampled during the last several decades.

Results and Discussion

Chemical Characterization of Study Lakes. Lake characteristics and midsummer water chemistry are summarized in Table S1 (Supporting Information); basic chemical and productivity characteristics are summarized in Figure 1. Study lakes exhibited a broad pH range. Seven lakes had average midsummer pH from 4.5 to 5.0, nine between pH 5.1 and 5.5, four between pH 5.6 and 6.0, seven between pH 6.1 and 6.5, and three with pH above 6.5. Most lakes had summer acid neutralizing capacity (ANC) between about −50 and +50 μeq/L, which is the range within which biological effects would be expected. Midsummer sulfate (SO_4) and dissolved organic carbon (DOC) concentrations ranged from 70 to 107 μeq/L and 1.2 to 10.7 mg/L, respectively.

Bacterioplankton. Fifteen lakes, including 14 epilimnetic and 7 hypolimnetic samples with pH ranging from 5.54 to 7.52, were sampled for bacterioplankton. 16S rDNA clones from these 21 independent libraries were examined and classified to class and, when possible, to genus, using the RDP Classifier (http://rdp.cme.msu.edu/classifier/classifier.jsp). Eighteen bacterial classes were observed, with 4−14 classes per lake (avg = 7.4 ± 2.3); and a loss of approximately 1.4 classes per unit decrease in pH (Figure 2). There were 6−29 genera per lake (avg = 16.1 ± 6.5), with a loss of 2.5 genera per unit decrease in pH. Representatives of the Actinobacteria and β-proteobacteria accounted for the majority of recovered clones. Sphingobacteria, α-proteobacteria, and the γ-proteobacteria classes also comprised significant components of the bacterial community. Richness generally increased with pH, but these relationships were not statistically significant (*12*).

Understanding how pH affects important bacterial groups may help identify bacterial indicators of acidification. In this study, the overall structure of bacterial communities was weakly correlated with pH. However, several specific groups such as α-proteobacteria were influenced by pH. These groups, including genera such as *Magnetospirillum*, unclassified *Rhodospirillales*, and unclassified *Alcaligenaceae*, may represent indicator organisms for acid impacted Adirondack lakes. Bacteria also may be influenced by alteration in primary producer communities and chemical effects on nutrient cycling that influence the availability of dissolved nutrients (*15*).

Phytoplankton. Over 220 phytoplankton taxa were observed, including 100 Chlorophyta, 60 Chrysophyta, 40 Cyanophyta and 5 Pyrrhophyta. Approximately one-half of the total taxa occurred in no more than one lake; 13 taxa occurred in 25 or more lakes, and three taxa were found in all 30 lakes (Table S4, Supporting Information).

The mean number of midsummer phytoplankton taxa decreased with pH (Figure 2), ranging from 21.3 taxa at pH > 6.3 to 7.4 taxa at pH < 5, reflecting a loss of approximately four taxa per unit decrease in pH. These results are consistent with surveys of 100 Adirondack lakes conducted in 1982 and 1984 (*7*). Findlay (*16*) and Graham et al. (*17*) found a strong positive correlation between measured lake water pH and the number of phytoplankton taxa in 22 lakes in Killarney Park (immediately downwind of Sudbury), Ontario and in the experimentally acidified (pH decreased from 6.7 to 4.5)

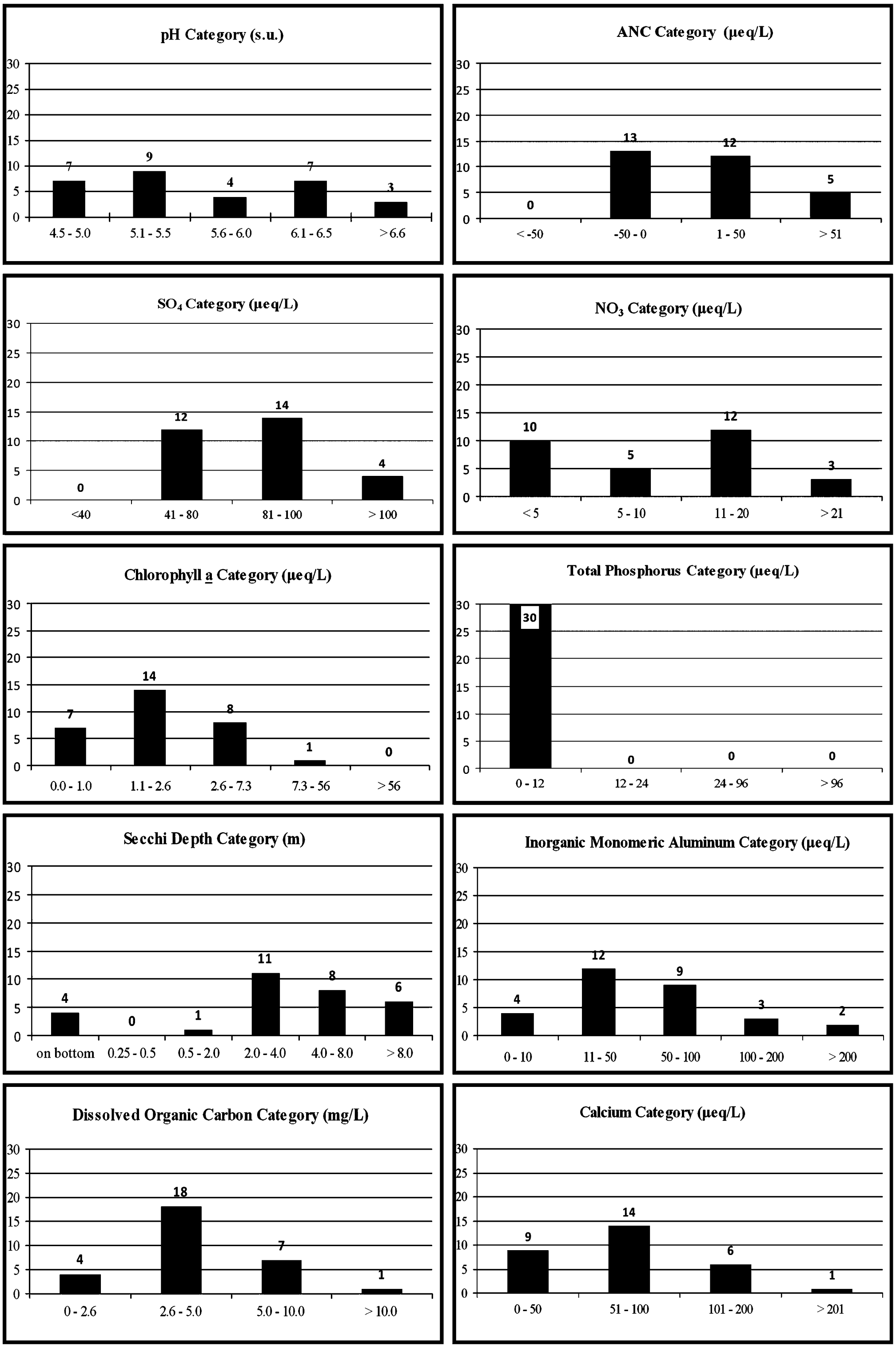

FIGURE 1. Physical, chemical, and biological attributes of 30 Adirondack study lakes. The *Y*-axis denotes the number of lakes in each category. The *X*-axis denotes major categories for the analyte under consideration. Lake placement in a category is based upon the average of midsummer values for each analyte collected during the period 1994–1996.

and recovered (pH increased to 6.0) Lake 302S in the Experimental Lakes Area in northwestern Ontario. Differences in numbers of taxa in pH ranges between our studies are primarily due to methodology. In particular, the number of taxa per category in the Lake 302S study is based on more samples. However, these differences do not affect the results of this study.

Taxa present in lakes having pH < 5.0 were considered acid-tolerant; those in lakes with pH 5.0–5.6 were considered acid-resistant, and taxa restricted to lakes above pH 5.6 were considered acid-sensitive. Of the 50 most commonly occurring phytoplankton taxa (i.e., those with biovolume or relative abundance >2% in 3 or more lakes), 35 taxa are acid-tolerant, 8 are acid-resistant, and 7 are acid-sensitive.

Zooplankton. *Rotifers.* Twenty-seven rotifer species were identified (Table S5, Supporting Information). Thirteen species were found in at least 50% of the study lakes. *Keratella taurocephela* was abundant or dominant in over two-thirds

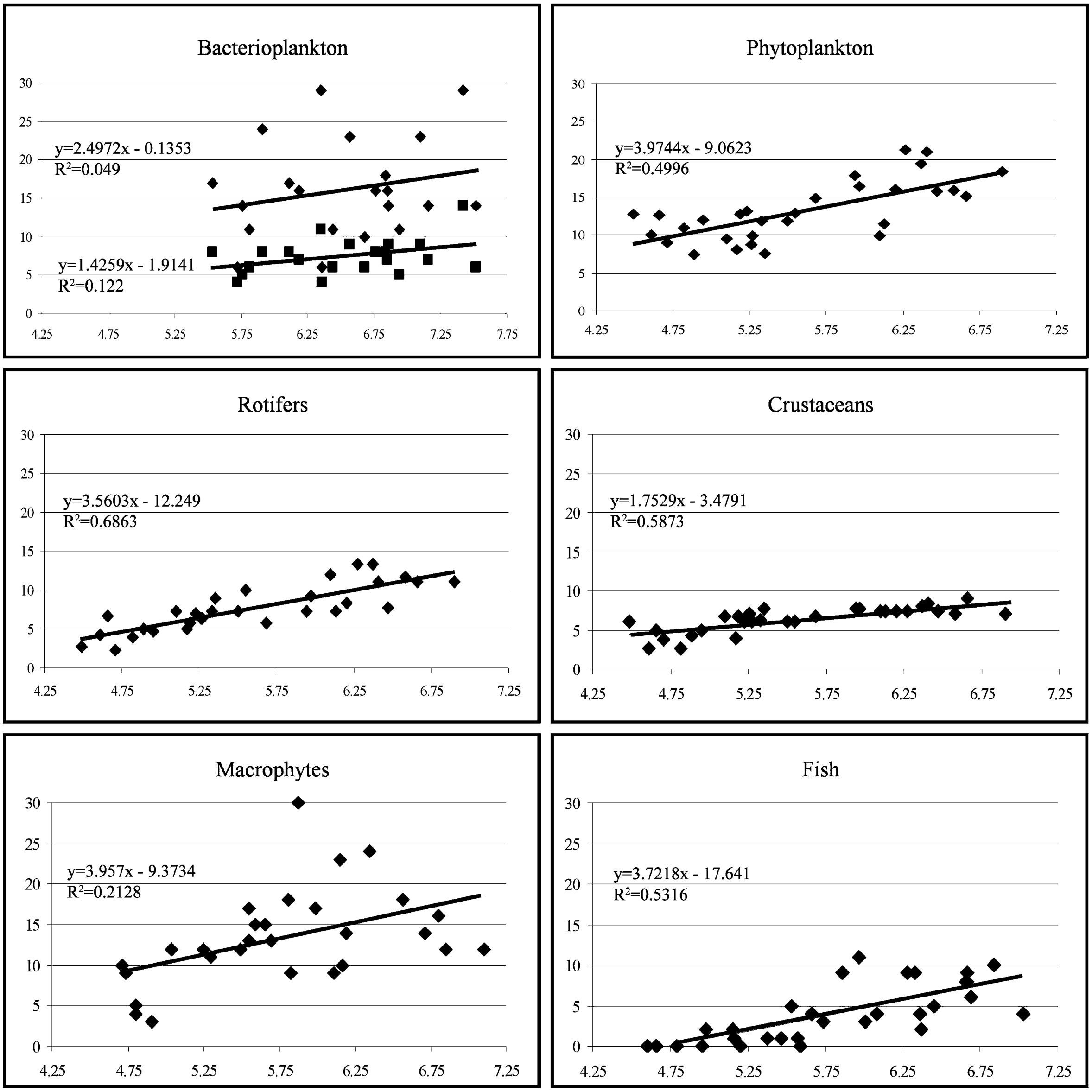

FIGURE 2. Species richness of biotic groups in Adirondack study lakes relative to midsummer epilimnetic pH in the sample years. The *Y*-axis denotes number of groups (bacteria), taxa (phytoplankton), or species (rotifers, crustaceans, macrophytes, fish). The *X*-axis denotes the pH range that occurred in the 30 study lakes. Note: In the bacterioplankton graph, two regressions were run on the basis of genera (diamonds) and classes (squares).

of the lakes. Seven species were dominant or abundant; 12 species were widespread in at least one lake, but 15 species had <5% of total density or were rare inclusions. Although there were higher densities in acidic lakes, there was no significant change in rotifer abundance with increasing pH across the full pH spectrum.

The proclivity of rotifer species to acidic conditions was assessed in terms of the lowest pH at which the species comprised at least 0.5% of the average total density in each lake. Rare species, not attaining 0.5%, were assessed at 0.1%. These levels provided benchmarks for excluding trace presences. Regardless, species absence generally was strongly related to pH. There were 16 rotifer species that could be considered acid-tolerant; nine could be considered acid resistant, and two could be considered acid-sensitive.

Crustaceans. Nineteen crustacean species were identified (Table S6, Supporting Information). Seven species occurred in more than 50% of the lakes. *Leptodiaptomus minutus* was abundant or dominant in over two-thirds of the lakes. Seven species were dominant or abundant; 11 species were widespread in at least one lake, but six species had <5% of total density or were rare inclusions. Siegfried et al. (*8*) also noted that zooplankton communities in low-pH lakes are dominated by a few taxa, including *Leptodiaptomus minutus*, *Mesocyclops edax*, and *Bosmina longirostris* (nomenclature changed to *Sinobosmina freyi*). No trend in overall crustacean abundance with decreasing pH was observed. Twelve crustacean species were considered acid-tolerant; two were considered acid-resistant, and five were considered acid-sensitive.

The relationship between zooplankton species richness and pH is complicated since it is affected by a variety of factors. Species richness is positively correlated with temperature to 15 °C (*18*) and with lake depth and watershed area (*19*) and negatively correlated with productivity (*20*) and elevation (*21*). Furthermore, zooplankton richness is greater in lakes with fish than in fishless lakes (unpublished data). Although many factors affect zooplankton richness, increasing lake acidity causes a decline. Figure 2 predicts loss rates of 3.56 rotifer species and 1.75 crustacean species per unit decrease in pH, explaining 69% and 59% of the variability in rotifer and crustacean richness, respectively. As acid-resistant and sensitive species decline, *Keratella* *taurocephala* typically becomes more abundant (*8*). Additionally, reduced exploitive competition with crustaceans may lead to high food resources and consequent high densities of *K. taurocephala* and other common rotifers (*22, 23*). This might account for the observed small increase in rotifer abundance with increasing pH seen in fishless lakes that had low overall crustacean densities. Many researchers also have reported a decrease in crustacean species richness with acidification (*24, 25*). Confer et al. (*24*) reported a loss rate of 2.4 crustacean species per unit decrease in pH in 10 Adirondack lakes, which is close to the 1.75 species reported here. The difference is probably due to lake selection choices and thought to be insignificant.

Macrophytes. Aquatic plant communities play a major role in structuring lake littoral zones, providing habitat for algae, zooplankton, other invertebrates, and fish (*26*). Within Adirondack waters, aquatic macrophyte species range from those that are highly resistant over a wide range of pH to species that are distinctly acid-sensitive or acid-tolerant (*27*).

A total of 763 specimens, including 52 species, were identified. Lakes had an average of 13.7 ($\pm$5.1) species. Drainage lakes had more species (14.4 $\pm$ 5.3) than seepage lakes (7.7 $\pm$ 8.7). Plants typically were distributed from the lakeshore (emergent species) to a maximum depth of 7 m. The bladderwort, *Utricularia purpurea*, was found as deep as 12 m (*28*).

Species were classified into three groups (Table S7, Supporting Information) based on pH of lowest occurrence: (1) acid-tolerant (22 species), (2) acid-resistant (13 species), and (3) acid-sensitive (17 species). Acid-tolerant species included *Potamogeton confervoides*, *Utricularia purpurea*, isoetids, and mosses. Acid-resistant species included *U. vulgaris* and *Vallisneria americana*. Certain species, such as *Eriocaulon aquaticum* and *Nuphar variegata*, thrive over a broad pH range, whereas, acid-sensitive charophytes and many *Potamogeton* species were not found below pH 5.6.

The number of plant species generally decreased with decreasing pH at a rate of four species per pH unit (Figure 2). A number of factors influence species richness: lake and littoral zone size, lake hydrologic type, habitat diversity, position in the landscape relative to other lakes, and water quality (*29*). Although seepage lakes exhibited a range of pH values, macrophyte species richness was uniformly low. Seepage lakes, with their lack of hydraulic connection to other lakes, have a substantially reduced probability of exchange of plant propagules. In drainage lakes, species richness increased with increasing pH.

Although invasive plant species were not found in these lakes, they do pose a threat to the region, and in some circumneutral Adirondack lakes, Eurasian watermilfoil (*Myriophyllum spicatum*) and curly leaf pondweed (*Potamogeton crispus*) have been found. Since no acidic lakes are known to contain invasive plants, it remains unclear as to whether acid pH reduces the probability of their becoming established.

Fish. Acidification has adverse impacts on fish populations. Fish presence/absence and species richness in Adirondack lakes are correlated with pH (*5*). However, species-specific habitat requirements and the widespread presence of non-native fish species complicate the analysis of fish presence/absence data from lakes of varying pH. Besides mineral acidity, fishless conditions can be caused by bog influence, limited access, poor spawning substrate, and winter-kill. Acidic deposition and mineral acidity are responsible for fishless conditions in an estimated 30% of Adirondack lakes categorized as fishless (*5*). Five study lakes were fishless, and four additional lakes have such small populations that they are considered functionally fishless. Six lakes were too large or inaccessible to trap, so richness results were obtained from previous surveys (ALSC unpublished data).

We observed a significant relationship between fish species richness and pH with a loss of 3.72 species per unit

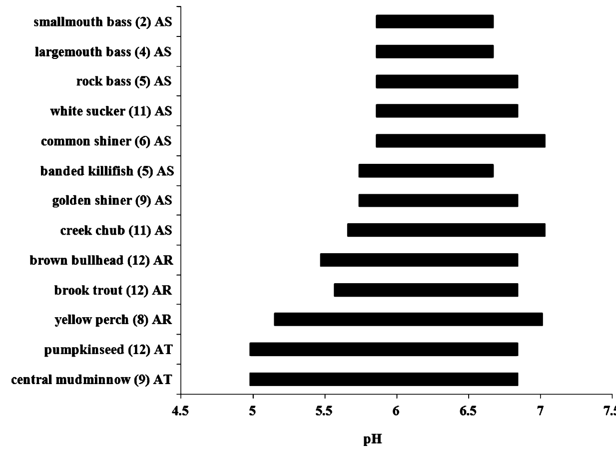

FIGURE 3. Fish species identified in the study lakes and their pH distribution. The number in parentheses is the total number of lakes in which the species occurred. The pH is the average pH for the year in which the sample was taken.

decrease in pH ($r^2 = 0.53$, $p < 0.05$; $n = 30$; Figure 2). Several of the larger lakes had greater richness, possibly due to increased habitat heterogeneity associated with increasing lake size (*30*). When lake area is taken into account [Richness $= 0.90(\text{pH}) + 0.30(\ln \text{lake area}) - 4.79$. $r = 0.88$], pH and lake area explain about 78% of the variance in species richness. Both β weights are significant and positive: β for pH $= 0.68$ and β for area $= 0.46$, so pH is the more important predictor of richness. Richness increases as both pH and area increase. The partial correlation for pH is relatively high, whereas the semipartial correlation is much lower, suggesting that pH explains a unique part of the variability in richness.

All fishless lakes had relatively low pH. In lakes with fish, individual species responded to pH in a variety of ways (Figure 3). Central mudminnow (*Umbra limi*), pumpkinseed (*Lepomis gibbosus*), and yellow perch (*Perca flavescens*) occurred in lakes across a wide pH range; other species were more restricted by pH. The lack of a strong relationship between fish distribution and pH, also noted by Driscoll et al. (*31*), suggests that fish may not respond to changes in pH as readily as other taxa until a threshold is reached (*5*). Most fish assemblages in these lakes are combinations of native and introduced fish (*32*). Some species can enter lakes intermittently; their presence in an assemblage may not be necessarily an indication that they are established and responding to long-term water chemistry.

A clear relationship between lake water chemistry and fish assemblages is not expected since physical lake characteristics are important in determining habitat suitability and non-native fish species have been introduced to many Adirondack lakes (*32, 33*). Such introductions have altered the native fish communities by eliminating forage species, thereby decreasing richness and diversity (*34*). Nevertheless, increased lake water acidity is associated with reduced species diversity, loss of sensitive species, and elimination of all fish from some lakes (*5*).

Many introduced fish are predatory species that have a negative impact on native fishes, particularly small, column-dwelling forms (*34*). Thus, the introduction of non-native piscivorous fish increases fish species richness but ultimately can be responsible for decreasing it. Similarly, the range of pH inhabited by individual species may be confounded by the presence of exotic species. Minnows absent from low-pH lakes may have been extirpated by introduced predators rather than sensitivity to low pH. Caution should be used when assessing relationships between fish and pH, particularly when the assemblage contains exotic species (*32, 34*).

TABLE 1. Mean Number of Species (Standard Error) That Occurred within Each Biota Acid Tolerance Category (batc) for Different Levels of Biota Investigated in the 30 Study Lakes[a]

trophic level	acid-tolerant, pH < 5.0	acid-resistant, pH 5.0−5.6	acid-sensitive, pH > 5.6
phytoplankton	17.0(1.79)a	15.8(1.50) a	24.5(1.31)b
rotifers	4.2(0.75)a	7.1(0.63) b	9.9(0.55) c
crustaceans	4.2(0.34)a	6.2(0.29) b	7.5(0.25) c
macrophytes	6.4(2.06)a	13.3(1.88) b	15.8(1.09)b
fish	0.4(1.87)a	2.9(1.59)ab	6.4(0.99)b

[a] The data for phytoplankton, rotifers, and crustaceans were three midsummer collections each year during 1994, 1995, and 1996; macrophyte and fish data were collected between 1994 and 2006. Different roman letters (a,b,c) indicate significant mean differences ($P < 0.05$) across rows based on the Tukey multiple mean comparison test performed after a significant ANOVA F test using the MIXED Procedure of the SAS System.

Biota Acid Tolerance Classification (batc) System. The effect of acidification on trophic levels from bacteria to fish was assessed in a group of chemically diverse lakes in the southwestern Adirondacks. Although the bacterioplankton failed to exhibit a direct richness response to pH, the α-proteobacteria warrants additional investigation to identify potential indicator organisms and their relationship to primary producers occurring in the same ecosystem. Tables S4−S7 (Supporting Information) identify the major phytoplankton, rotifer, crustacean, and macrophyte species likely to occur in Adirondack waters that range from chronically acidified to unimpacted by acidification. Figure 3 provides similar information for fish. These results suggest an order to the progressive decline of species as lakes acidify. The relative abundances indicate the likelihood of encountering a particular species from the above groups within collections from Adirondack lakes. The significant response between pH and species richness observed in this study provides the basis for a biota acid tolerance classification (batc) system across the pH gradient of the study lakes (Table 1). Acid-tolerant (pH < 5.0), acid-resistant (pH 5.0−5.6), and acid-sensitive (pH > 5.6) species were identified within each trophic level and serve as important indicators for future efforts to evaluate the response of impacted aquatic ecosystems to changing levels of acid deposition and interactions among multiple stressors (*35−37*). Within each trophic level, the acid-tolerant and acid-sensitive categories were significantly different at $P < 0.05$, providing a clear distinction between the taxonomic groups identified in these subcategories. Within the rotifers and crustacean zooplankton, statistical testing provided a further distinction among the three subcategories along the pH gradient. The primary requirement for data interpretation along this chemical and biological gradient is regular long-term monitoring within a consistent group of waters, thereby removing any climatic and geographic variability that can otherwise confuse results collected during a brief time period over a broad geographical area (*38*). This classification system is versatile and will have considerable value in assessing ecosystem recovery if and when regional lakes respond to reduced acid deposition.

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Supporting Information Available

Map of study lake locations (Figure S1). Summary data on the water chemistry and characteristics of the study lakes (Table S1). Summary data for water chemistry measurements, field and laboratory methods, and biotic taxonomy used in this study (Tables S2 and S3). Summary of data on phytoplankton, rotifer, crustacean, and aquatic plant species (Tables S4−S7). This material is available free of charge via the Internet at http://pubs.acs.org.

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