Compilation, Analysis, and Publication of Adirondack Effects Assessment Program (AEAP) Data and Associated Data Sets

Summary Report | Report Number 19-15 | March 2019

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Compilation, Analysis, and Publication of Adirondack Effects Assessment Program (AEAP) Data and Associated Data Sets

Summary Report

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NYSERDA Report 19-15 NYSERDA Contract 115876 March 2019

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Preferred Citation

New York State Energy and Research Development Authority (NYSERDA). 2019. "Compilation, Analysis, and Publication of Adirondack Effects Assessment Program (AEAP) Data and Associated Data Sets," NYSERDA Report Number 19-15. Prepared by Rensselaer Polytechnic Institute, Troy, NY. nyserda.ny.gov/publications

Abstract

Several research and monitoring programs have supported physical, chemical, and biological data collection efforts in New York State lakes for decades. Most of the data sets generated by these entities have been made publicly available in some form, but rarely together and often without accompanying sufficient descriptive information (metadata) to fully understand the long-term changes occurring in each waterbody. Compiling a long-term (~20 year) data set of 28 lakes in the Adirondack Park in New York, reveals substantial physical, chemical, and biological changes that have occurred in the Adirondack lakes. Increases in the concentration of dissolved organic matter (DOM) concentrations are occurring in many lakes—a process known as *browning*. Browning is occurring concomitant with other ecologically important water chemistry changes that may interact with or overwhelm any potential ecological response to browning itself. Changes in primary producers (i.e., phytoplankton) are occurring and are likely driven by water clarity losses associated with browning, independent of changes in nutrients. In contrast, concomitant declines in calcium (Ca) appear to play an important role in driving long-term changes in zooplankton communities. This indicates that long-term biological changes in lakes that are recovering from acidification in the Adirondack region of New York State depend on the trophic level of interest, thereby demonstrating that trophic responses are decoupling from one another. Concomitant chemical changes have important implications for understanding aquatic ecosystem responses to recovery from acid deposition, browning, and other environmental changes.

Keywords

Acid deposition, acid rain, climate change, recovery, browning, calcium, phytoplankton, zooplankton, lakes, long-term change

Acknowledgments

Funding for this project was provided by the New York State Energy Research and Development Authority (#115876) and National Science Foundation (EF-1638704).

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1 Project Focus

Physical, chemical, and biological data have been collected on a suite of New York State lakes in the Adirondack region for several decades. These include data collected by (1) the Adirondack Effects Assessment Program (AEAP), which has evaluated the biological communities, primarily phytoplankton and zooplankton, in 30 lakes over nearly two decades and (2) the Adirondack Lake Survey Corporation's (ALSC) sampling of 52 lakes, many of which are lakes that are sampled in the AEAP and over the same time period. In addition to these in situ lake data sets, long-term land use/land cover and gridded meteorological data are available for the entire region. However, while most of these data sets have been made publicly available in some form, they have never been compiled together, along with accompanying descriptive information (metadata) sufficient to fully understand long-term changes in physical, chemical, and biological characteristics of lakes. This project's goals include (1) compiling the data sets, (2) examining the data sets to understand the magnitude of physical, chemical, and biological changes that have occurred, and (3) identifying the most important changes that drive long-term trends in lake biology.

2 Context

Many lakes in the Adirondack region of New York State were severely impacted by past decades of acid deposition (Driscoll et al. 2016; Sullivan et al. 2018). Some lakes are recovering. For example, chemically, deposition has declined, resulting in rising pH levels in previously-impacted waterbodies (Sullivan et al. 2018). A range of other chemical changes are also occurring, such as declines in toxic forms of aluminum and an increase in dissolved organic carbon (DOC) concentrations in many lakes (Monteith et al. 2007). How these changes are affecting lake ecosystems, and food web components in particular, is largely unknown. Despite data on how lakes are recovering chemically from past acid deposition, little is known about how lakes have responded biologically. Given the importance of lake biology in regulating many services that surface water bodies provide to society (e.g., fisheries, drinking water quality, and algal blooms), it is imperative to understand the direction, magnitude, and drivers of biological changes occurring in lakes undergoing recovery from acid deposition. Research on the effects of recovery from acidification on phytoplankton and zooplankton are particularly lacking. Previous New York State Energy Research and Development Authority (NYSERDA)-supported data sets offer a tremendous opportunity to understand environmental changes occurring in New York State and in the Adirondacks in particular. In this project, long-term Adirondack lake data were cleaned (e.g., missing data were addressed, measurement units normalized, and a single data format was applied) and analyzed to identify long-term patterns and trends. The results of the research were submitted for publication in the peer-reviewed journal *Global Change Biology* (Leach et al. 2019).

3 Objectives

The main objectives of this project were the following:

1. **Clean and Compile AEAP and ALSC Data Sets.** Long-term Adirondack lakes data from the AEAP and ALSC data sets, associated metadata, land use/land cover, and meteorological data were cleaned. They were then compiled into a single well-described and formatted data set.
2. **Create and Submit a R Package of Lake Data and Metadata.** An R package containing the compiled Adirondack lake data and metadata was created and made publicly available. The package consisted of a set of reproducible R codes that included data processing tools (e.g., modeling, and time series techniques and analyses), documentation, and data. The R package was made publicly available on the Comprehensive R Archive Network (CRAN).
3. **Publish Compiled Data in Repository.** Using the compiled data resulting from the completion of Task 1, the compiled data set was published in *Nature Scientific Data* (Leach et al. 2018).
4. **Analyze Compiled Data for Trends in Zooplankton and Phytoplankton Response Metrics.** The compiled data set was analyzed to characterize trends through time in key zooplankton and phytoplankton response metrics, including phytoplankton biomass and chlorophyll a concentration, zooplankton biomass, and zooplankton community composition.
5. **Develop Manuscript.** Results from the analysis of the compiled data (Task 4) were communicated through tables and plots and summarized in a manuscript that was developed and published open-access in *Global Change Biology* (Leach et al. 2019).

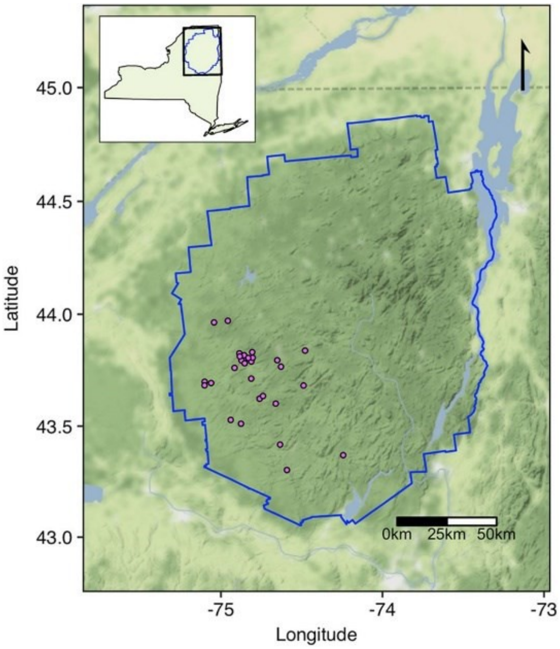
4 Study Area and Methods

4.1 Field Sites and Overview

The data compiled in this project were collected in 28 lakes located in the southwestern portion of the Adirondack Park in New York State (Figure 1). This area received high rates of atmospheric acid deposition (Jenkins et al. 2005). Due to the low-acid neutralizing capacity (ANC; Omernik and Powers 1983; Jenkins and Keal 2004), historically high-acidic deposition resulted in severe acidification of lakes in this region (Fakhraei et al. 2014; Driscoll et al. 1991). The study lakes are located in five of the six major sub-drainage basins in the Adirondack region and span a range of size, depth, watershed area, and hydrologic type (Table 1). The hydrologic classification scheme used was developed by Driscoll and Newton (1985) and is based on a combination of hydrology (drainage or mounded seepage lakes), underlying geology (thickness of glacial till or presence of calcite in the basin), and DOC concentration (high or low). When the three aspects of the classification scheme were combined, a characterization of the sensitivity to acidification of each lake was produced. Of the 28 lakes studied here, 20 are thin-till drainage lakes, the class considered the most sensitive to acidification. Of these 20 thin-till drainage lakes, two have historically high DOC concentrations (TDH), while the remaining 18 have historically low DOC concentrations (TDL).

Figure 1. Study Area

The 28 study lakes (purple points) are located in the southwestern and south-central Adirondack Park (outlined in blue). Inset shows park location within New York State.



There are six medium-till drainage lakes, two with historically high DOC concentrations (MDH) and four with historically low DOC concentrations (MDL). There is a single mounded seepage lake with historically low DOC (MSL) and one lake drains a watershed with deposits of carbonate (C), which eliminates sensitivity to acidification due to high ANC.

The lakes in this data set were included in two independent long-term monitoring programs that were established to assess the effects of acid deposition in Adirondack lakes; the Adirondack Effects Assessment Program Aquatic Biota Study (hereafter referred to as AEAP) and the Adirondack Long-Term Monitoring Program (ALTM). While both programs sampled more lakes than the 28 included in this data set, these 28 lakes represent the overlap between the two separate programs and thus provide a comprehensive view of the long-term physical, chemical, and biological characteristics of each lake. The data record starts in 1994 for all lakes and ends in 2006 for half of the lakes and in 2012 for the remaining half (Table 1). The physical, nutrient, and biological data presented here were collected and analyzed by the AEAP. Additional water chemistry data were collected and analyzed as part of the on-going ALTM program. Because these monitoring programs were independent there is overlap in the measured water chemistry analytes. For analytes that were measured by both programs, the most complete data record was used. Overlapping water chemistry measurements (i.e., those not selected for inclusion) can be found in the original data files (Data Citation 1: figshare https://doi.org/10.6084/m9.figshare.5686987.v2; 'data_inputs').

The in situ data represents a collation of AEAP and ALSC data, conducted in an overlapping set of lakes. As a result, not all parameters were collected at the same frequency or on the same day. Variables including mixed layer chlorophyll, phytoplankton and zooplankton biomass and taxonomy (enumerated to species), nutrients (total nitrogen and phosphorus), iron, and profiles of temperature and dissolved oxygen were collected two times per summer (typically in July and August) from 1994 to 2006 for half of the lakes and from 1994 to 2012 for the remaining half (Table 1).

Table 1. Summary of Lake Characteristics

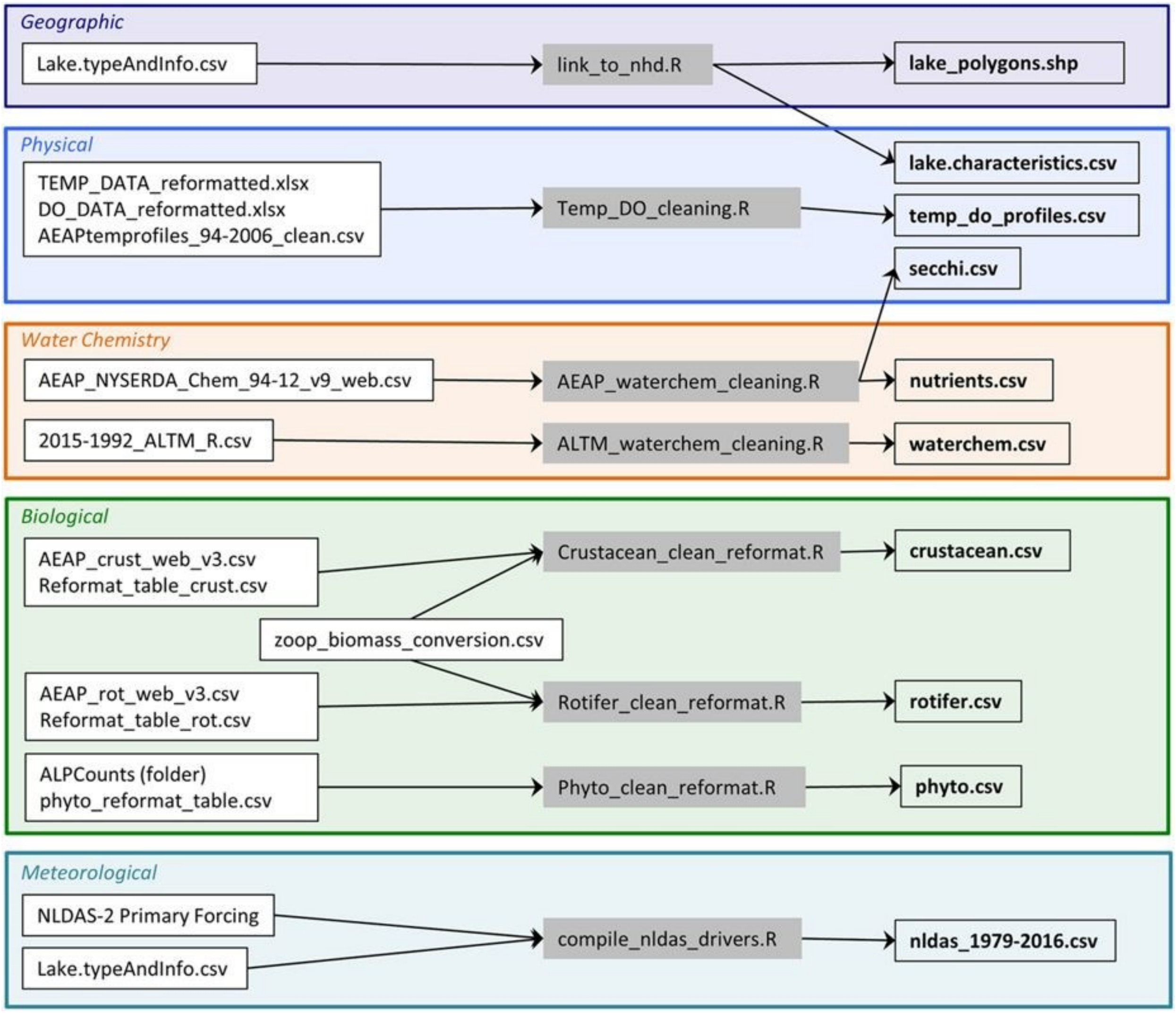
Geographic coordinates identify the lake, not necessarily the exact sampling location. End date refers to last year that all data types were available; all data start in 1994. Note that water chemistry extends to 2012 for all lakes. The asterisk (*) denotes water chemistry data typically collected by helicopter near the deep spot of the lake.

Lake	Lat.	Long.	Hydro. type	Max. depth (m)	Mean depth (m)	Lake volume (m^3 x 10^3)	Surface area (ha)	End date
Big Moose	43.81687	−74.856111	TDL	21.3	6.8	34882	512.5	2012
Brooktrout*	43.60097	−74.660624	TDL	23.2	8.4	2420	28.7	2012
Carry*	43.68204	−74.488558	MSL	4.6	2.2	62	2.8	2006
Cascade	43.7891	−74.812042	MDL	6.1	4.2	1719	40.4	2012
Constable	43.83101	−74.806420	TDL	4	2.1	435	20.6	2006
Dart	43.79376	−74.872572	TDL	17.7	7.3	3807	51.8	2012
G*	43.41714	−74.633945	TDL	9.8	4.5	1437	32.2	2012
Grass*	43.693	−75.060844	MDL	5.2	1.5	78	5.3	2006
Indian*	43.62286	−74.760748	TDL	10.7	3	981	33.2	2012
Jockeybush*	43.30278	−74.591444	TDL	11.3	4.5	786	17.3	2012
Limekiln	43.71301	−74.812459	TDL	21.9	6.1	11476	186.9	2012
Long	43.83789	−74.479025	TDH	4	2	33	1.7	2006
Loon Hollow*	43.9636	−75.042530	TDL	11.6	3.4	191	5.7	2006
Middle Branch*	43.69912	−75.100869	TDL	5.2	2.1	363	17	2006
Middle Settlement*	43.68281	−75.101427	TDL	11	3.4	545	15.8	2006
Moss	43.7814	−74.852986	MDL	15.2	5.7	2598	45.7	2012
North*	43.52775	−74.939567	TDL	17.7	5.7	10107	176.8	2012
Queer*	43.80596	−74.803521	TDL	21.3	10.9	5960	54.5	2006
Raquette	43.79492	−74.651303	MDH	3	1.6	24	1.5	2006
Rondaxe	43.76088	−74.915920	TDL	10.1	3	2733	90.5	2012
Sagamore	43.76605	−74.628371	MDH	22.9	10.5	7131	68	2012
South*	43.51096	−74.875888	TDL	18.3	8.3	16302	197.4	2012
Squash	43.82557	−74.886135	TDH	5.8	1.4	45	3.3	2006
Squaw*	43.63508	−74.739599	TDL	6.7	3.4	1249	36.4	2012
West	43.81189	−74.882960	TDL	5.2	1.5	152	10.4	2006
Willis	43.36963	−74.243171	MDL	2.7	1.6	229	14.6	2006
Willys*	43.97078	−74.957396	TDL	13.7	4.9	1188	24.3	2006
Windfall	43.80497	−74.830768	C	6.1	3.2	78	2.4	2006

4.2 Data Harmonization and Processing

The different data sources were harmonized using a combination of lake names and latitude/longitude records. Lake names were verified using the Geographical Names Information System database (https://nhd.usgs.gov/gnis.html) and latitude and longitude references. Further, to connect the data set with a physical water body, each site was linked with its corresponding polygon in the high-resolution U.S. Geological Survey's National Hydrography Dataset (NHD) and includes corresponding polygons and permanent identifiers for future use. Sampling date formats and lake names were also standardized so that data files can be easily linked by lake and sampling occasion in addition to permanent identifiers. See Figure 2 for a detailed workflow.

Figure 2. Workflow Diagram for Data Cleaning and Harmonization



All key harmonization and data conversion steps were done in the R scientific computing language, version 3.3.3 (R Development Core Team 2015). The data are available in two formats: as comma separated files (.csv) within the folder 'data' (https://doi.org/10.6084/m9.figshare.5686987.v2) and as an R Data Package wrapper, 'adklakedata' (https://doi.org/10.5281/zenodo.1181754), which automatically retrieves and makes the data files available in R.

There are several different categories of data in the data set: (1) geographic, (2) physical, (3) water chemistry, (4) biological, (5) meteorological, and (6) other (Table 2, Figure 2). Additionally, each .csv data file has an accompanying text file with the same name that contains a description of each column header, units of each variable, and other pertinent metadata. Data are split across files containing different types of data based on data structure, but all data files contain a column with the unique lake name and date on which the data were measured, which enables linking data files together for analysis. A list with a description of the files associated with the data set is provided in 'adklake_data_descriptions.txt' (https://doi.org/10.6084/m9.figshare.5686987.v2) and Table 3. This information is also available in the 'adklakedata' documentation available on CRAN (https://cran.r-project.org).

Table 2. Description of All Distributed Data Files

File Name	Metadata File Name	Description
Geographic		
lake_polygons.shp	lake_polygons.txt	Shape file containing the polygon of all 28 lakes from the National Hydrography Dataset (high-resolution).
Physical		
lake_characteristics.csv	lake_characteristics.txt	Geographical location and physical characteristics of all 28 lakes in the data set (include lake surface area, watershed area, hydrologic type, max and mean depth etc.) NHD identification numbers.
temp_do_profiles.csv	temp_do_profiles.txt	Water temperature and dissolved oxygen (profiles for each sampling event at 1 m depth intervals. The temperature data is resolved to 0.1 °C and the DO to 0.1 mg/L.
secchi.csv	secchi.txt	Secchi disk measurement for each sampling event, resolved to 0.1 m.
Water Chemistry		
waterchem.csv	waterchem.txt	Surface water chemistry parameters for each sampling event.
nutrients.csv	nutrients.txt	Nutrient and chlorophyll a concentration data for each sampling event.
Biological		
phyto.csv	phyto.txt	Cell counts and biovolumes for each sampling event. Typically identified to species.
rotifer.csv	rotifer.txt	Organisms L−1 for each sampling event. Typically identified to species.
crustacean.csv	crustacean.txt	Organisms L−1 for each sampling event. Typically identified to species but always to genus.
Meteorological		
nldas_1979-2016.csv	nldas_1979-2016.txt	Local meteorology for each lake subset from the North American Land Data Assimilation data set averaged to a daily interval.
Other		
adklake_data_descriptions.txt	---	List with descriptions of each file in the data set.
zoop_biomass_conversion.csv	zoop_biomass_conversion.txt	Formula and body size measurements used to convert organism count data to biomass. Includes references for formula, coefficients, and measurements.

The data were technically validated before publication to create a unified and compatible data structure across all data types. A series of manual quality assurance/quality control (QA/QC) steps were performed to verify that there were no data processing errors between the raw source files and final data tables. A random 1% of each data type was manually checked between the original and final data files. All physical data including temperature and dissolved oxygen profiles and Secchi disk depths were manually checked for out of range or unexpected values. Out of range values were corrected or removed where appropriate. The database and R code were revised as needed throughout these manual validation steps to correct mistakes.

There are two methods for data access. One, the CSV files of all data can be downloaded directly from an online repository (https://doi.org/10.6084/m9.figshare.5686987.v2). This supports general use cases, as CSV is a common and widely supported data format. Two, an R package wrapper for the data set is available from CRAN (https://cran.r-project.org). This package, 'adklakedata', automates the downloading, local storage, and access of the data. Data are accessed using the 'adk_data' function which accepts a parameter for each data set (e.g.,'adk_data('tempdo')' for temperature and dissolved oxygen data). Visit https://cran.r-project.org/web/packages/adklakedata/adklakedata.pdf for more information on CRAN.

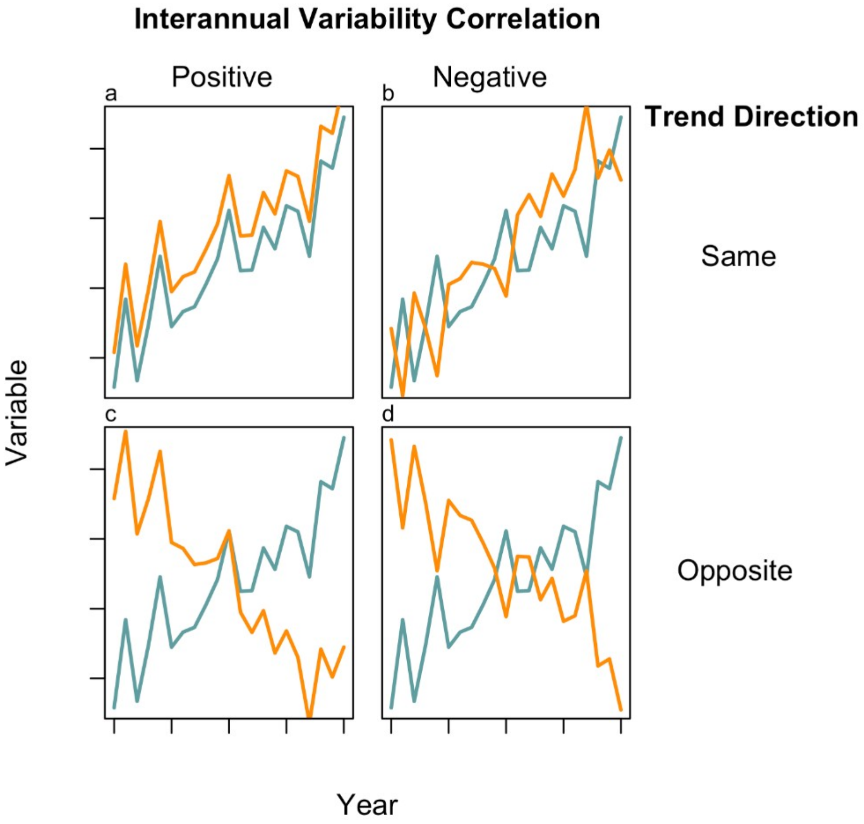
4.3 Trends

Overall trends through time were calculated for water chemistry parameters, three ecological responses, and climatic variables. To examine long-term changes in trophic structure, trends in community composition (proportion of total community biomass) for crustacean zooplankton and rotifer taxonomic groups were estimated. Trends were estimated using a Theil-Sen slope estimator (referred to here as the Sen's slope; Sen 1968), which is a nonparametric trend estimator technique robust to outliers and non-normality. The Sen's slope was calculated on annual average values across all sites (hereafter, lake population trends) and on the annual average values within a lake (hereafter, within lake trends). Because Sen's slope does not include statistical significance, trend significance was assessed with the nonparametric Mann-Kendall analysis.

It is difficult to infer process from time series data, particularly when multiple parameters are trending over the same time scale. Therefore, in addition to the long-term trends, correlations in the first derivatives of each time step in the series within each lake were also examined, which quantified correlations in the interannual variability (IAV) of any pairwise combinations of variables in the data set. This analysis is seasonally-robust because derivatives were calculated only from seasonally matched samples (i.e., first derivatives were only calculated for July to July or August to August samples across years). A Spearman rank correlation coefficient was used to quantify the magnitude and significance of these correlations. Strong positive or negative correlations in IAV can occur independent of the direction or magnitude of trends (Figure 3) and indicate that the yearly movements in the two variables are either mechanistically linked or responding to the same underlying driver.

Figure 3. Combinations of Trends and Correlation of Interannual Variability

Several, but not all, theoretical combinations of trends and correlation of interannual variability. Interannual variability and trend directions are independent of each other. Directional coherence between long-term trends are grouped by rows (a and b = same; c and d = opposite) and interannual variability correlations by columns (a and c = positive; b and d = negative). Correlations in interannual variability may also be high even if one, or both, of the variables are not trending over time.



A substantial challenge in long-term ecological data analyses is identifying causal drivers of change, particularly when many variables are trending at the same time. Comparisons of both the long-term trends and the correlations of interannual variability among variables provide one technique to better understand the temporal scales and assess mechanistic links. For example, mechanistically linked variables may exhibit both positive long-term trend correspondence and positive interannual variability correlation, such as bottom-up stimulation of primary production by DOC-associated nutrients resulting in positive correlations in both long-term and interannual variability between DOC, nutrients, and productivity. Conversely, correspondence in long-term trends with inverse interannual variability correlation suggests different mechanisms driving long-term change and interannual variability. Finally, variables may exhibit long-term trends without any interannual correlation, indicating that there may be some timescales at which the two variables operate independently. When coupled together, long-term trends and the significance and direction of correlations in IAV between variables can provide a better assessment of potential causality than either test could in isolation.

5 Project Findings

5.1 Long-Term Trends

Air temperature in the Adirondack region increased at a rate of 0.134 °C year^{-1} from 1994–2012 ($p = 0.044$; Figure 4a). Over this same period, lakes surface temperatures warmed (0.14 °C year^{-1}; $p = 0.016$) and thermoclines became shallower (-0.04 meters [m] year^{-1}, $p = 0.025$), but bottom water temperatures did not change ($p = 0.455$; Figure 4b). While there appeared to be cyclic changes in Palmer drought severity index (PDSI), there was no overarching trend ($p = 0.39$).

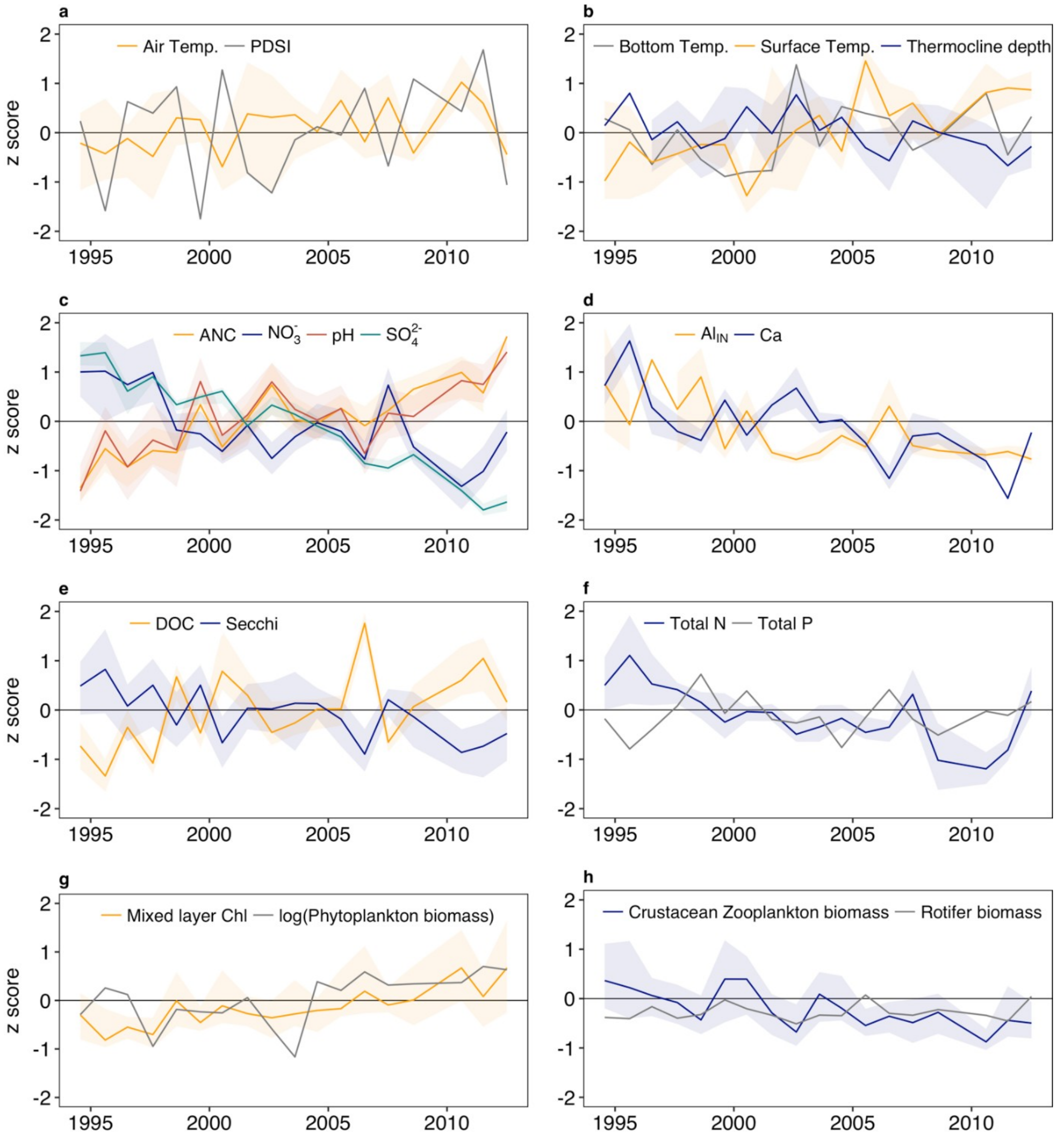
Lakes showed chemical recovery from acidification with positive trends in pH (0.019 pH units year^{-1}; $p = 0.002$) and ANC (0.966 microequivalents per liter per year [$\mu\text{eq L}^{-1}\ \text{year}^{-1}$]; $p < 0.0001$; Figure 4c), and negative trends in sulfate (SO_4^{2-}) (-0.109 milligrams per liter per year [$\text{mg L}^{-1}\ \text{year}^{-1}$]; $p < 0.0001$) and nitrate (NO_3^-) concentrations (-0.023 $\text{mg L}^{-1}\ \text{year}^{-1}$; $p = 0.005$; Figure 4c). Inorganic monomeric aluminum (Al_{in}) concentrations (-0.89 micrograms per liter per year [$\mu\text{g L}^{-1}\ \text{year}^{-1}$]; $p = 0.0135$; Figure 4d) and concentrations of base cations, including Ca (-0.014 $\text{mg L}^{-1}\ \text{year}^{-1}$; $p = 0.003$; Figure 4d), magnesium (Mg) (-0.003 $\text{mg L}^{-1}\ \text{year}^{-1}$; p value = 0. 0046) and potassium (K) (-0.0019 $\text{mg L}^{-1}\ \text{year}^{-1}$; $p = 0.0365$) also declined. Additionally, iron (Fe) increased across all lakes (0.005 $\text{mg L}^{-1}\ \text{year}^{-1}$; $p < 0.0001$). Across lakes, DOC concentrations increased (0.052 $\text{mg L}^{-1}\ \text{year}^{-1}$; $p = 0.023$; Figure 4e) and water clarity declined as indicated by increased water-color (0.655 platinum-cobalt [Pt-Co] units year^{-1}; $p = 0.002$) as well as shallower Secchi disk measurements through time (-0.046 m year^{-1}; $p = 0.0005$; Figure 4e).

Lake population trends showed that chlorophyll concentrations significantly increased (0.060 $\mu\text{g L}^{-1}\ \text{year}^{-1}$; $p = 0.0001$) and total phytoplankton biomass exhibited a near-significant positive trend (0.023 log mg wet weight per liter per year [$\text{WW L}^{-1}\ \text{year}^{-1}$]; $p = 0.076$; Figure 4g). This trend was not matched by trends in nutrients, with no significant trends in total phosphorus (TP) or total filterable phosphorus (TFP, which represents dissolved phosphorus [P]) across all lakes ($p = 0.8$ and $p = 0.14$, respectively; Figure 4f). Total nitrogen (TN) showed significant negative trends (-0.009 $\text{mg L}^{-1}\ \text{year}^{-1}$; $p = 0.0166$; Figure 4f) largely driven by declines in NO_3^-.

Zooplankton communities exhibited substantial changes through time. Lake populations trends of crustacean zooplankton biomass declined (-0.009 mg WW L^{-1} $year^{-1}$, p = 0.0096; Figure 4h) driven largely by declines in calanoid copepod biomass (-0.004 mg WW L^{-1} $year^{-1}$; p = 0.009), particularly *Leptodiaptomus minutus*, which comprised on average 48% of the crustacean zooplankton biomass in these lakes. Cyclopoid copepods and cladoceran grazers (Anomopoda and Ctenopoda) did not exhibit trends in biomass through time (p = 0.89, 0.96 and 0.98, respectively).

Figure 4. Time Series and Trends of Select Variables

Time series (and trends) of (a) air temperature (0.134 °C $year^{-1}$) and Palmer Drought Severity Index (PDSI; no significant trend), (b) surface (0.14 °C $year^{-1}$) and bottom water temperature (no significant trend) and thermocline depth (-0.04 m $year^{-1}$), (c) metrics of recovery from acidification including pH (0.019 pH units $year^{-1}$), ANC (acid neutralizing capacity; 0.965 µeq. L^{-1} $year^{-1}$), nitrate (NO^{3-}; -0.023 mg L^{-1} $year^{-1}$) and sulfate (SO_4^{2-}; -0.109 mg L^{-1} $year^{-1}$) concentrations, (d) inorganic monomeric aluminum (Al_{in}; -0.89 µg L^{-1} $year^{-1}$) and calcium (Ca; -0.014 mg L^{-1} $year^{-1}$) concentrations, (e) DOC (0.052 mg L^{-1} $year^{-1}$) concentration and Secchi disk depth (-0.046 m $year^{-1}$), (f) total nitrogen (TN; -0.009 mg L^{-1} $year^{-1}$), and total phosphorus (TP; no significant trend), (g) mixed layer chlorophyll concentration (0.06 µg L^{-1} $year^{-1}$) and log phytoplankton biomass (no significant trend), and (h) crustacean (-0.009 mg wet weight L^{-1} $year^{-1}$ and rotifer (no significant trend) biomass. Time series are shown here as a z score (standardized as (value – mean)/standard deviation)) for each variable. Lines represent lake population trends as median values for all lakes within a year and shaded areas show the 1st-3rd quartiles of each variable for that year. Lines shown in grey indicate non-significant trends, while all others represent significant trends ($p \leq 0.05$) based on a Mann-Kendall test statistic.



The composition of crustacean zooplankton became less dominated by calanoid copepods (-0.0097 proportion [prop.] mg WW L^{-1} $year^{-1}$, $p = 0.0016$) and the community composition shifted, with cladoceran grazers (Anomopoda) becoming proportionally more important over time (0.0022 prop. mg WW L^{-1} $year^{-1}$; $p = 0.019$). Though because cladoceran grazers did not exhibit trends in biomass through time, the observed increases in cladocerans as a proportion of the total crustacean zooplankton biomass within the community were driven by declines in calanoid copepod biomass not by an actual increase in cladocerans grazer biomass. Overall rotifer biomass did not show a significant trend ($p = 0.13$). Although the rotifer community became less dominated by Gastropus spp. (-0.004 prop. mg WW L^{-1} $year^{-1}$; $p < 0.0001$) and Keratella spp. (-0.004, p-value = 0.025), no individual rotifer group consistently increased to counter the declines in Gastropus and Keratella spp.

All long-term trends that were calculated are reported in Table 3.

Table 3. Overall Trends Reported for All Lakes in the Data Set

Subset of lakes includes 14 lakes with data record that spans from 1994–2012. Trends reported as ns are not significant (at $p \leq 0.05$). See Section 4.0 Study Area and Methods for detail on analysis technique. Note that there are no changes in the direction of significant trends between the full data set and the subset.

Variables	Overall Trend	Trend for Subset of Lakes
	(units $year^{-1}$)	**(units $year^{-1}$)**
Air temperature (°C)	0.134	0.162
Al_{in} (µg L^{-1})	-0.89	-0.92
ANC (µeq. L^{-1})	0.965	1.079
Bottom temperature (°C)	ns	ns
Ca (mg L^{-1})	-0.014	-0.014
Chlorophyll (µg L^{-1})	0.06	0.07
DOC (mg L^{-1})	0.052	0.052
Fe (mg L^{-1})	0.005	0.005
Phytoplankton biomass (log mg WW L^{-1})	0.023	0.0286
Mg (mg L^{-1})	-0.003	-0.003
Calanoid copepod biomass (mg WW L^{-1})	-0.004	-0.0057
NO_3^- (mg L^{-1})	-0.023	-0.034
PDSI (unitless)	ns	ns
pH (unitless)	0.019	0.023

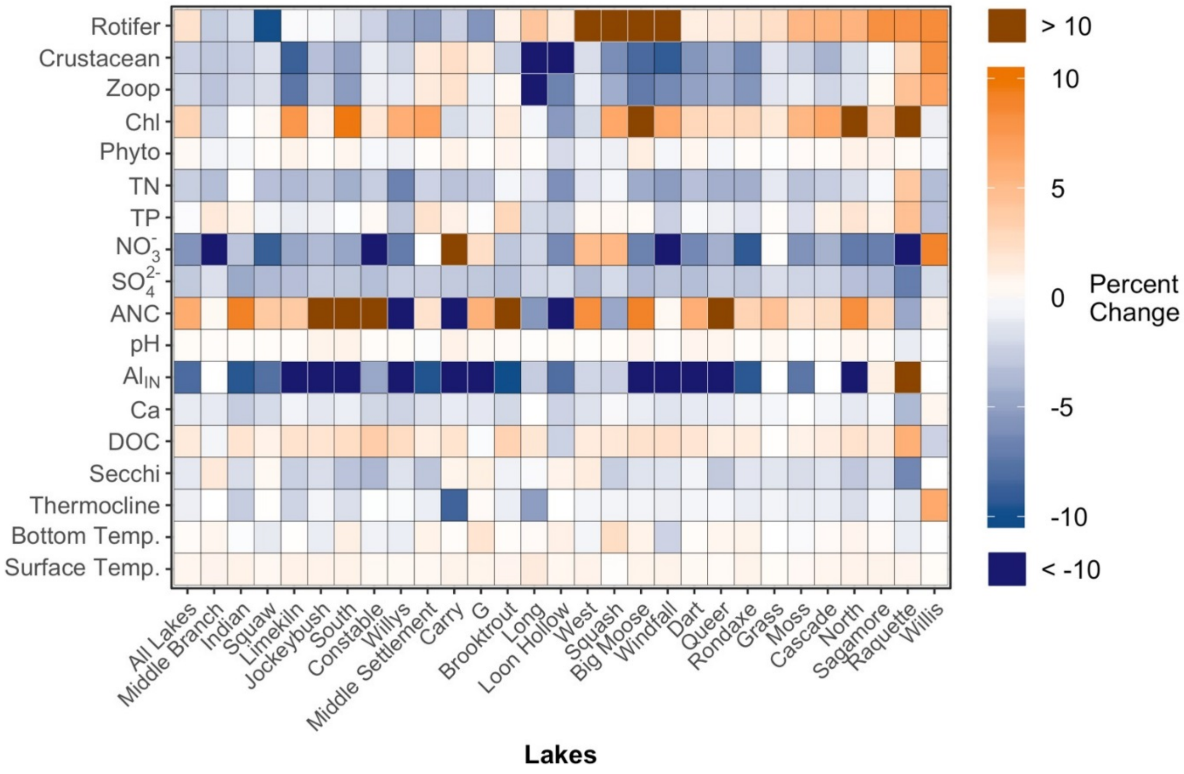
Table 3 continued

Variables	Overall Trend	Trend for Subset of Lakes
	(units year^{-1})	**(units year^{-1})**
Potassium (mg L^{-1})	-0.0019	-0.002
Proportion of biomass Anomopoda (prop. mg WW L^{-1})	0.0022	0.0033
Proportion of biomass Calanoid (prop. mg WW L^{-1})	-0.0097	-0.0117
Proportion of biomass Ctenopoda (prop. mg WW L^{-1})	ns	ns
Proportion of biomass Cyclopoid (prop. mg WW L^{-1})	0.004	0.006
Proportion of biomass Gastropus (prop. mg WW L^{-1})	-0.004	-0.004
Proportion of biomass Gymnomera (prop. mg WW L^{-1})	ns	ns
Proportion of biomass Keratella (prop. mg WW L^{-1})	-0.004	-0.004
	(units year^{-1})	**(units year^{-1})**
Proportion of biomass Polyarthra (prop. mg WW L^{-1})	ns	ns
Secchi disk depth (m)	-0.046	-0.054
SO42- (mg L^{-1})	-0.109	-0.12
Surface temperature (°C)	0.14	0.168
Total filterable phosphorus (µg L^{-1})	ns	ns
Thermocline depth (m)	-0.04	-0.047
Zooplankton: crustacean biomass (mg WW L^{-1})	-0.009	-0.0128
Zooplankton: rotifer biomass (mg WW L^{-1})	ns	ns
Zooplankton: total biomass (mg WW L^{-1})	-0.009	-0.012
Total Nitrogen (mg L^{-1})	-0.009	-0.011
Total Phosphorus (µg L^{-1})	ns	ns
Water color (Pt-Co units)	0.655	0.714

While there were many significant long-term lake population trends in physical, chemical, and biological characteristics, there was also substantial variability in both the magnitude and direction within lake trends for some characteristics among the population of lakes (Figure 5). For example, Al_{in}, TN, and SO_4^{2-} declined strongly across all lakes, though the concentrations varied; while ANC, TP, and the biological parameters showed higher variability in both the direction and magnitude within lake trends.

Figure 5. Percent Change in Each Variable Over Time for All Lakes and for Each Individual Lake

Significance of trends are not denoted. Rotifer and crustacean represent biomass of each group. All other abbreviations as follows: Al_{in} is inorganic monomeric aluminum, ANC = acid neutralizing capacity, Ca – calcium, Chl = chlorophyll concentration, DOC = dissolved organic carbon, NO_{3-} = nitrate, Phyto = phytoplankton biomass, TP = total phosphorus, TN = total nitrogen, Secchi, Thermocline = thermocline depth, and Zoop = zooplankton biomass.

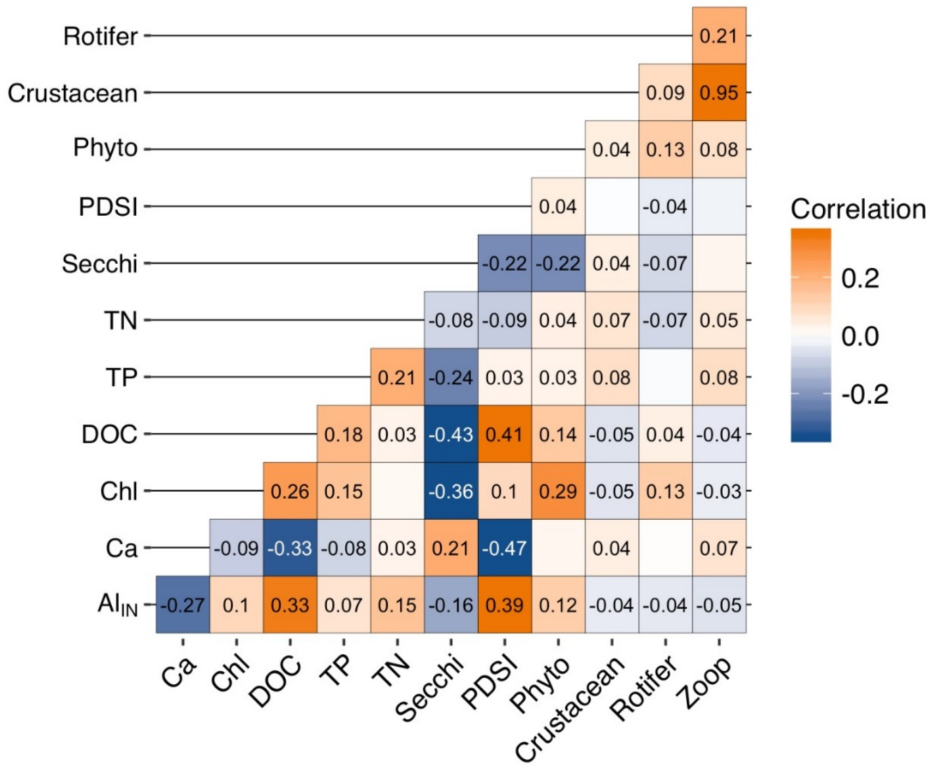


5.2 Correspondence Among Long-Term Trends and IAV

Within-lake correlations in IAV exhibited numerous significant correlations, indicating coherence in many chemical and biological variables (Figure 6). The top three IAV correlates with chlorophyll and phytoplankton biomass were Secchi depth (negative correlation), DOC, and TP (both positive; Spearman coefficient $\geq |0.15|$, $p \leq 0.05$; Figure 5). Long-term trends in chlorophyll and Secchi had opposite directions (chlorophyll increased while Secchi depth decreased), which corresponded with the negative IAV correlation between these two variables. Long-term trends in chlorophyll and DOC were in the same direction (both positive) and also corresponded with their positive IAV correlation. In contrast, chlorophyll and TP showed positive IAV but no correspondence in long-term trends (TP showed no trend over time).

Figure 6. Correlations of Interannual Variability Between Select Variables

Text in each square represents Spearman rank correlation coefficients and squares without values are non-significant correlations ($p > 0.01$). PDSI is Palmer Drought Severity Index, all other abbreviations as in Figure 4.



For zooplankton biomass, the top IAV correlates (ignoring rotifer and crustacean biomass) were phytoplankton biomass, TP, and Ca (all positive correlations; Spearman coefficient ≥ 0.07, $p \leq 0.05$; Figure 5) with DOC coming out as negatively correlated, but less correlated interannually (Spearman coefficient = -0.04, $p \leq 0.05$). Neither TP nor phytoplankton biomass had corresponding significant long-term trends to match the positive IAV correlation between zooplankton biomass and Ca, which showed long-term declines corresponding with the long-term zooplankton biomass declines. Breaking apart the zooplankton group, Ca was significantly, positively correlated with crustacean biomass but not significantly correlated with rotifer biomass ($p > 0.05$). $\mathrm{Al}_{\mathrm{in}}$ was negatively correlated with both crustacean zooplankton and rotifer biomass (coefficient = -0.04, $p \leq 0.05$).

Relationships between biomass of primary producers and consumers were also examined to understand potential trophic-mediated drivers of change. Chlorophyll and crustacean zooplankton biomass showed opposite long-term trends and a negative IAV (Spearman coefficient = -0.05, $p \leq 0.05$), while phytoplankton biomass showed positive IAV with crustacean zooplankton biomass (Spearman coefficient = 0.04, $p \leq 0.05$) yet no correspondence in long-term trends (phytoplankton biomass showed no long-term trend). Neither rotifer nor phytoplankton biomass showed long-term trends but showed positive IAV correlation (Spearman coefficient = 0.13, $p \leq 0.05$).

6 Implications

The results here indicate the recovery from acidification appears to be driving changes in lake biota, including both phytoplankton and zooplankton populations. While *browning* is frequently attributed as an important driver of ecological change, the results indicate that the direct chemical effects of recovery from acidification are overwhelming the consequences of browning for zooplankton. Long-term changes in the zooplankton community did not display previously predicted effects of browning despite the increase in primary producers potentially driven by browning. Thus, the long-term trajectories of these two trophic levels are uncoupled from one another. In turn, the results suggest that the ecological consequences of browning may be more dependent upon concomitant environmental changes than previously observed. This has broad implications for assessments of long-term ecological change associated with browning, given that recovery from acidification, which is driving long-term changes in the study lakes (Driscoll et al. 2016) is also considered a primary driver of increased DOC concentrations in many other regions (Monteith et al. 2007).

It has previously been argued that DOM may be an important source of limiting nutrients (Kissman et al. 2013; Solomon et al. 2015), although the nutrient content of DOM has rarely been quantified (Daggett et al. 2015; Kissman et al. 2013; Vähätalo et al. 2003). In the study lakes, there were no significant increases in total or filterable P. Indeed, lakes with positive chlorophyll (11 of 28 lakes) or phytoplankton biomass trends (5 of 28 lakes) all showed either stable or declining TP trends through time (Table 3). Given the lack of trends in P despite increasing DOM, the results imply there was no fertilization effect from increasing DOM because the DOM is either a poor source of P, or other concomitant factors are suppressing P increases.

Despite the lack of correlation in long-term P and DOC trends in the data set, among-lake average DOC and P concentrations were positively correlated ($R^2 = 0.39$, $p < 0.001$). This suggests that the processes that drive P and DOC spatial correlation are different from the processes driving long-term change in DOC and P. Such a disconnect could come from complex, non-linear soil pH or Al-P or Fe-P adsorption processes (Huser et al. 2018). Due to this mismatch between spatial and temporal DOC-P relationships, space-for-time substitution may yield biased predictions of biogeochemical and ecological change and be inappropriate to understand long-term changes in lakes associated with browning.

Chlorophyll increases, while likely driven by browning, were not due to a fertilization effect from increasing DOC. Rather, browning-driven decreases in light levels and thermocline shoaling may have driven observed increases in chlorophyll. Under lower light conditions compensatory increases in chlorophyll can occur as phytoplankton produce more chlorophyll per unit biomass, which may have contributed increases in chlorophyll independent of increases in phytoplankton biomass as high DOM and associated low-light levels are known to limit primary production (Karlsson et al. 2009). The mixed layer sampling regime used here would have missed chlorophyll below the thermocline, particularly when the thermocline and the euphotic zone are well separated. As an alternative explanation for the increases in chlorophyll, it is possible that the loss of important zooplankton grazer released phytoplankton from top-down control thereby contributing to increasing chlorophyll trends. Consistent with this, long-term trends in chlorophyll and crustacean biomass were in opposite directions (Figures 4g and 4h) and the IAV was negatively correlated (Figure 6). However, crustacean biomass was positively correlated on an interannual basis with phytoplankton biomass, suggesting bottom-up, rather than top-down trophic interactions.

The long-term decline in crustacean zooplankton biomass was most likely driven by declining Ca concentrations. The study lakes had long-term, significant declines in Ca concentration that corresponded with declines in crustacean biomass (Figure 6). Additionally, the interannual variability between these Ca and crustacean biomass was positively correlated (Figure 6), indicating that in years when Ca concentrations were high that crustacean biomass was also high. Declines in surface water Ca concentrations is driven by soil base cation depletion (Driscoll et al. 2001) and has been widely observed in aquatic systems recovering from acidification (Stoddard et al. 1999; Keller et al. 2001; Skjelkvåle et al. 2005; Hessen et al. 2017). Crustacean zooplankton require Ca to build and harden their exoskeletons (Stevenson 1985) and dissolved ionic Ca in their environment, rather than food, is their main source (Cowgill 1976). Crustacean zooplankton, particularly Daphnia, show reduced reproduction and population growth rates at Ca concentrations < 1.5 mg L^{-1} (Ashforth and Yan 2008; Arnott et al. 2017; Azan & Arnott 2017). Additionally, a recent series of mesocosm studies showed that calcium levels < 1.0 mg L^{-1} reduce the population growth rates of several important freshwater copepod species, including L. minutus, which dominated the crustacean zooplankton biomass in the study lakes (Arnott et al. 2017).

Seven lakes crossed the 1.0 mg L^{-1} threshold, while an additional 10 lakes crossed the 1.5 gm L^{-1} threshold by the end of the study period (either 2006 or 2012). Three lakes started below 1.0 mg L^{-1} in 1994 but continued to decline, and all lakes showed calcium concentrations < 3.5 mg L^{-1} by the end of the study period. In addition to the observations, previous studies in other regions have linked shifts in crustacean zooplankton community composition (Tessier and Horwitz 1990) and long-term declines in Daphnia with declining calcium (Jeziorski et al. 2008).

One unexplored factor that may contribute to long-term declines in crustacean zooplankton is the recovery of fish populations in previously acidified lakes. Soil acidification mobilized Al_{in} resulting in high concentrations of Al_{in} in Adirondack lakes and streams which can be toxic to many fish species at concentrations > 55 μg L^{-1} (Driscoll et al., 2001; Baldigo et al., 2007). Approximately 40% of study lakes in the first two years of the data set showed Al_{in} concentrations above this threshold, but most declined substantially though time (Figure 4d). Recovering fish populations could have increased top-down predation pressure, thereby causing the observed decline in zooplankton biomass. However, the data and past published research suggest that this is unlikely. Interannual variability in Al_{in} and zooplankton biomass were not positively correlated, as would be expected from a top-down aluminum-mediated increase in fish predation. Additionally, while there has been documented recovery of fish populations in some lakes (Josephson et al. 2014; Sutherland et al. 2015) there is high cross-lake variability in recovering fish populations, with many Adirondack lakes showing little evidence of fish recovery (Baldigo et al. 2016). While comprehensive time series data are not available to understand if fisheries have recovered in the study lakes, a recent study based on fisheries surveys that included 24 of the 28 study lakes (excluding Big Moose, Cascade, G, and South) indicate highly variable recovery, with only four lakes that showed increased total fish biomass > 10% and most with no or negative change in fish biomass between approximately 1985 and 2010. Slow and highly variable recovery of fish populations suggest that changes in fish populations were unlikely a primary factor driving the consistent declines in crustacean zooplankton across lakes.

7 Conclusions

Recovery from acidification is producing large changes in many physical, chemical, and biological lake characteristics in lakes of the Adirondack region in New York State (Table 3). While increases in dissolved organic matter, termed *browning,* have been attributed as a primary driver of many of these changes, the results indicate that other concomitant water chemistry changes may be just as important as driving some types of long-term change as browning. The degree to which the results are generalizable to regions where browning is occurring independent of recovery from acidification is unknown and highlights the need for integrative long-term studies that address multiple components of environmental change that often occur simultaneously. However, given that recovery from acidification is considered a primary driver of browning (Monteith et al. 2007), the results are likely generalizable to many other lakes in New York State as well as many other regions.

The drivers of changes in both phytoplankton and zooplankton communities reveal long-term trends that are decoupled from one another but consistent with the effects of recovery from acidification and in some instances, independent of browning. The chlorophyll increases in Adirondack lakes were likely driven by changing optical conditions associated with browning but not a fertilization effect. The most likely drivers of zooplankton declines were dominated by variables that change concomitant with increases in DOM, primarily Ca limitation on crustacean zooplankton, not necessarily the direct or trophic-mediated effects of changing DOM. Lastly, the response of fish population to acidification recovery has a well-documented link with Al_{in} toxicity, though recovery has been slower than expected. With different ultimate drivers of browning yielding potentially different concomitant chemistry changes, long-term ecological changes associated with browning may ultimately depend on the overarching driver causing browning and the interactions of multiple concomitant physical and chemical changes. The results suggest that managing for the effects of recovery from acidification and browning in particular is complex in both space and time and requires understanding of trophic level-specific effects.

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