


Concurrent improvement and deterioration of epilimnetic water quality in an oligotrophic lake over 37 years

William D. Hintz ^{1,2*} Matthew S. Schuler,^{1,3} Jonathan J. Borrelli,¹ Lawrence W. Eichler,¹ Aaron B. Stoler,^{1,4} Vincent W. Moriarty,⁵ Laurie E. Ahrens,¹ Charles W. Boylen,¹ Sandra A. Nierzwicki-Bauer,¹ Rick A. Relyea¹

¹Darrin Fresh Water Institute, Department of Biological Sciences, Rensselaer Polytechnic Institute, Troy, New York

²Lake Erie Center, Department of Environmental Sciences, University of Toledo, Oregon, Ohio

³Department of Biology, Montclair State University, Montclair, New Jersey

⁴School of Natural Sciences and Mathematics, Stockton University, Galloway, New Jersey

⁵IBM Research, Yorktown Heights, New York

Abstract

Single-lake studies offer an opportunity for understanding, predicting, and mitigating local or regional threats to lake ecosystems. Our goal was to understand how concurrent environmental stressors such as climate change, eutrophication, and salinization affect long-term lake water quality. We report epilimnetic changes in 18 water-quality parameters collected at seven sites from 1980 to 2016 in Lake George, a large oligotrophic lake in the Adirondack Park, New York, USA. Improvements and deteriorations in water quality occurred over 37 years. We observed a 32% increase in chlorophyll *a* associated with an increase in orthophosphate, but not total phosphorus or a warming epilimnion (0.05°C/year). Salinization from road deicing salts contributed to the largest deterioration in water quality. However, chloride concentrations and the current rate of increase are low enough that few ecological impacts are likely to occur over the next few decades. Increasing calcium concentrations were not high enough to facilitate the persistence of invasive species in the lake such as zebra mussels (*Dreissena polymorpha*) but are sufficient for Asian clams (*Corbicula fluminea*) and the spiny water flea (*Bythotrephes longimanus*). Similar to other lakes, environmental legislation has supported recovery from acidification, indicated by reduced sulfate and nitrate, and increased alkalinity and pH. Declines in water quality were minor relative to other lakes, suggesting that decades of tourism and development occurred without major deterioration in water quality, but management efforts are needed to curb salinization in the Lake George watershed, particularly as it relates to sodium concentrations to prevent a loss of drinking water quality.

Multiple environmental stressors threaten the water quality of lake ecosystems and the services they provide (Carpenter et al. 1998; Strayer 2010; McCullough et al. 2019). Rising salinity from the use of road deicing salts, inputs from wastewater treatment facilities, and agricultural practices have increased the concentration of salts in many freshwater lakes (Dugan et al. 2017), threatening ecological community structure, water clarity, and drinkability (Hintz et al. 2017; Kelly et al. 2018). Climate change has altered lake hydrology, clarity, temperature, ice phenology, and water chemistry, disrupting ecosystem functions and reducing recreational opportunities (Adrian et al. 2009; Jeppesen et al. 2010). Despite the growing threat from multiple anthropogenic

stressors, proper management and legislative action has allowed the water quality of many lakes to recover. Notably, lakes in North America and Europe continue to recover from acidification (Stoddard et al. 1999). However, we have a limited understanding of how lake ecosystems respond to multiple concurrent environmental stressors over long periods of time. We need long-term studies that use multiple indicators of multiple stressors to demonstrate how lake water quality is responding to human-triggered environmental change.

Here, we use 18 water-quality indicator variables collected over 37 years from 1980 to 2016 to understand how multiple environmental stressors have changed the water quality of Lake George—a large oligotrophic lake in the Adirondack Park (New York; Fig. 1). Our goal was to identify contemporary threats to Lake George, an economically important ecosystem contributing to a regional \$2 billion USD tourist economy (Boylen et al. 2014). The lake is also a significant source of

*Correspondence: hintzwd@gmail.com

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

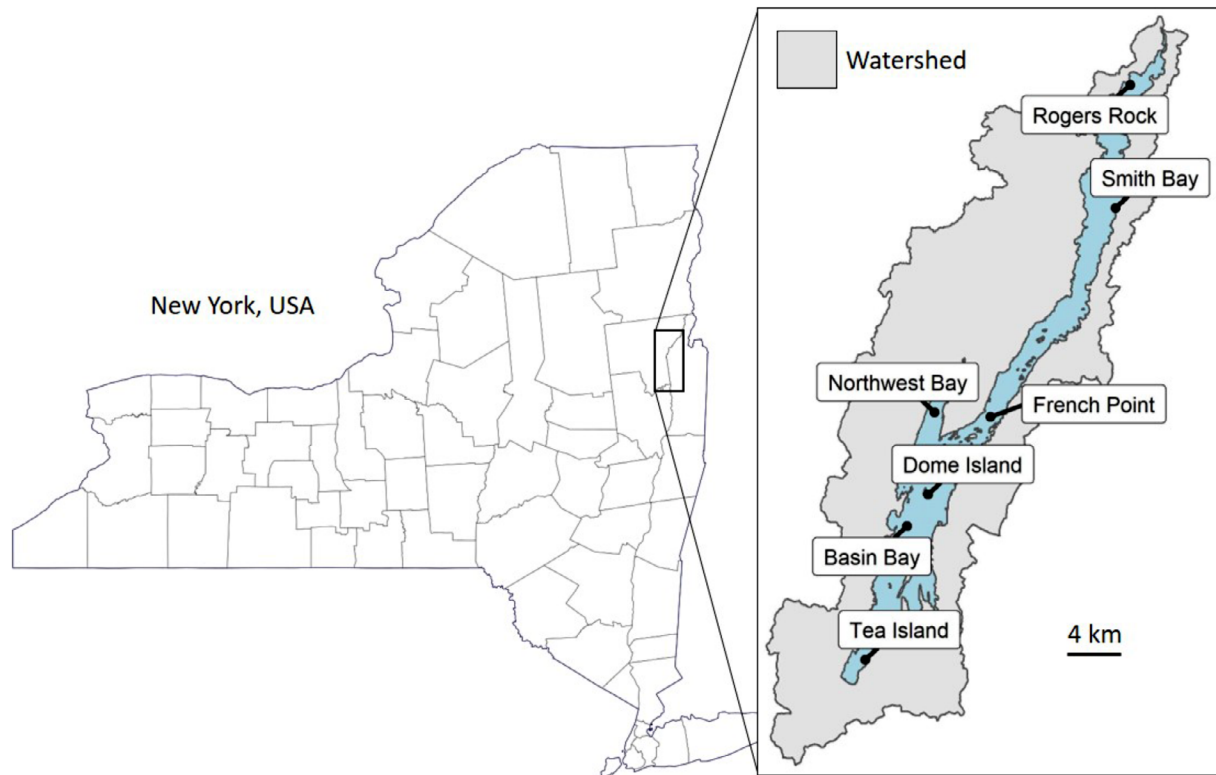


Fig. 1. Location of Lake George in the Adirondack Park of upstate New York, USA and the seven sites where 18 water quality variables collected during a 37-year offshore chemical monitoring program. [Color figure can be viewed at wileyonlinelibrary.com]

drinking water. Understanding the consequences of environmental stress and changes in the water quality of Lake George may also provide regional context for threats that other lakes face throughout the Adirondack Park and northeastern United States. Given a vibrant tourism industry and urban development primarily along the lake shoreline, we expected to observe increasing nutrient concentrations in Lake George. We predicted that increased nutrient concentrations would positively correlate with increased chlorophyll *a* concentrations and reduced water clarity. We also expected a warming epilimnion over

our 37-year study due to climate change (Swinton et al. 2015b). Additionally, we predicted that the use of road salts in the watershed (e.g., sodium chloride rock salt or brine) would be associated with increases in sodium, chloride, and water conductivity. Lastly, we wanted to understand the extent that Lake George has recovered from acidification, which has historically occurred throughout the region. We expected that reductions in sulfate and nitrate concentrations and increases in alkalinity and pH would indicate recovery from acidification.

Table 1. Methods used for the analysis of chemical analytes sampled from Lake George.

Analyte	Method
pH	Electrometric - Method 4500-H+ (American Public Health Association 1998)
Specific conductance	Wheatstone Bridge type meter - Method 120.1 (US EPA 1979)
Alkalinity	Titrimetric – pH 4.5 Method 310.1 (US EPA 1979)
Chloride, nitrate, and sulfate	Ion Chromatograph - Method 300 (US EPA 1979)
Chlorophyll <i>a</i>	Fluorometric - Method 10200 (American Public Health Association 1998)
Ammonia	Phenate Method -Method 4500-NH3 F. (American Public Health Association 1998)
Soluble silica	Molybdate Reactive -Method 4500-SiO2 E. (American Public Health Association 1998)
Total and total soluble phosphorus	Colorimetric—Persulfate Oxidation Method 365.2 (US EPA 1979)
Orthophosphate	Colorimetric—Method 365.2 (US EPA 1979)
Total nitrogen	Colorimetric—Persulfate Oxidation (Langner and Hendrix 1982)
Major cations and Metals (Ca, Na)	Atomic Absorption Spectroscopy – Flame Method 3111 (American Public Health Association 1998)

Table 2. Seven candidate linear mixed-effects models used to evaluate changes in water quality in Lake George, New York over 37 yr from 1980 to 2016. Models were evaluated against each other using Akaike's information criterion (AIC; Table S1).

Model	Structure in R	Fixed effect	Random effects
1	$Y \sim \text{Year} + (1 \text{Month}) + (1 \text{Site})$	Year	Month, site
2	$Y \sim \text{Year} + (1 \text{Month}/\text{Site})$	Year	Site nested within month
3	$Y \sim \text{Year} + (1 \text{Year}:\text{Month}) + (1 \text{Site})$	Year	Year \times month interaction, site
4	$Y \sim \text{Year} + (1 \text{Year}:\text{Month}) + (1 \text{Month}:\text{Site})$	Year	Year \times month interaction, site \times month interaction
5	$Y \sim \text{Year} + (1 \text{Year}:\text{SITE}) + (1 \text{Year}:\text{Month}) + (1 \text{SITE})$	Year	Year \times site interaction, year \times month interaction, site
6	$Y \sim \text{Year} + (1 + \text{Year} \text{SITE})$	Year	Slopes vary by year, intercepts vary by site
7	$Y \sim \text{Year} + (1 + \text{Year} \text{SITE}) + (1 \text{Month})$	Year	Slopes vary by year, intercepts vary by site, month

Methods

Study system

Lake George is a large, dimictic, oligotrophic lake with a volume of 2.1 km³ and a surface area of 11,400 ha. The catchment size is 606 km² with 210 km of shoreline and there is no agriculture within the catchment. The average depth of the lake is 18 m, with a maximum depth of 58 m. The hydraulic residence time is approximately 8 yr. While much of the watershed is a mix of temperate deciduous and coniferous forest types and undeveloped, nearly 1100 km of roads have been constructed within in the watershed and the shoreline is well-developed (Boylen et al. 2014).

Offshore chemical monitoring program

The offshore chemical monitoring program began in 1980 at six deep-water sites; a seventh site (Basin Bay) was added in 1995

(Fig. 1). We collected biweekly samples from April through November, with intermittent periods of monthly sampling. This allowed us to characterize abiotic and biotic variables from ice-off in the spring through fall turnover. At each site, we measured temperature (°C), conductivity ($\mu\text{S}/\text{cm}$), pH, and dissolved oxygen ($\text{mg O}_2/\text{L}$) using a calibrated hand-held YSI multiparameter sonde. Water clarity in the offshore chemical program was quantified using Secchi disk depth (m). We also collected hose-integrated (0–10 m), epilimnetic water samples from each site to measure chlorophyll *a*, total phosphorus, total soluble phosphorus, orthophosphate, nitrate, ammonium, total nitrogen, sulfate, sodium, chloride, calcium, soluble silica, and alkalinity (Table 1). While we started collecting most of these variables in 1980, we did not start measuring alkalinity until 1990 and total nitrogen until 1997. We used standard methods for preservation and holding times (Table 1).

Table 3. Eighteen long-term response variables measured during a 37-year study of water quality in Lake George (NY) from 1980 to 2016, except for total nitrogen collected from 1997 to 2016 and alkalinity collected from 1990 to 2016. Each variable includes the intercept, β_{Year} , and the confidence intervals from the linear mixed effects models.

Variable	Best fit model	Intercept	β_{Year}	\pm 95% CI
Chlorophyll <i>a</i> (ChlA, $\mu\text{g L}^{-1}$)	4	-21.272	0.0114	0.00437
Orthophosphate (OP, $\mu\text{g L}^{-1}$)	3	-26.995	0.0140	0.00487
Total soluble phosphorus (TFP, $\mu\text{g L}^{-1}$)	3	4.338	-0.0011	0.00474
Total phosphorus (TP, $\mu\text{g L}^{-1}$)	4	-7.382	0.0059	0.00676
Nitrate (NO_3 , $\mu\text{g L}^{-1}$)	4	0.381	-0.0002	0.00007
Ammonium (NH_4 , $\mu\text{g L}^{-1}$)	4	0.182	-0.0001	0.00005
Total nitrogen (TN, $\mu\text{g L}^{-1}$)	3	2.567	-0.0012	0.00041
Sulfate (SO_4 , mg L^{-1})	3	112.716	-0.0551	0.00228
Sodium (Na, mg L^{-1})	3	-368.926	0.1880	0.00749
Chloride (cl, mg L^{-1})	4	-652.288	0.3322	0.00947
Calcium (ca, mg L^{-1})	4	-69.017	0.0401	0.01319
Silica (Si, mg L^{-1})	4	-1.653	0.0013	0.00206
Temperature (T, °C)	4	-82.866	0.0486	0.01495
Secchi depth (Zsec, m)	3	13.261	-0.0022	0.01177
Alkalinity (ALK, $\mu\text{Equivalents L}^{-1}$)	3	-383.290	0.2058	0.01626
Conductivity (COND, $\mu\text{S cm}^{-1}$)	4	-2029.829	1.0713	0.05562
pH	3	-1.163	0.0044	0.00150
Dissolved oxygen (DO, $\text{mg O}_2 \text{L}^{-1}$)	4	13.113	-0.0014	0.00736

At the Darrin Fresh Water Institute (Bolton Landing, NY, USA), we used multiple quality control measures to evaluate the precision and accuracy of each analyte. To calibrate equipment and determine sample accuracy, we used known sample concentrations from the National Institute of Standards and Technology in the U.S. Department of Commerce. We used at least one known concentration for each ion and we maintained control charts for each analyte. We also monitored precision by reanalyzing 15% of all samples by retesting a single sample or analyzing a subsample. If quality control samples exceeded 10% of the expected value, we reanalyzed the sample. We followed these strict analytical protocols over the 37 years to ensure valid data comparisons.

As an extension of the offshore chemistry program, we collected subsurface photosynthetic active radiation (PAR) measurements for 22 yr (1995–2016) to quantify changes in water clarity and for comparison to collected Secchi depth measurements. We measured PAR with a Li-Cor Submarine Quantum sensor; surface radiation was measured simultaneously with a Li-Cor Deck Quantum sensor (LI-1400, Li-Cor, Lincoln, NB). We measured PAR at 2-meter depth increments from just below the lake surface to the depth where PAR intensity

reached 1% of surface light. From the PAR measurements, we calculated the light attenuation coefficient (K_d). We conducted profiles at eight sites on Lake George, four sites in the north basin and four sites in the south basin: Rogers Rock, French Point, Smith Bay, Sabbath Day Point (not included in the offshore chemistry program), Northwest Bay, Basin Bay, Dome Island, and Tea Island. We used profiles conducted at each site during the month of July from 1995 to 2016.

Statistical analyses

We used linear mixed effects models with year as the fixed effect, to determine if any of the measured water-quality parameters in Lake George have changed over the 37-year study period. We fit the models in R version 3.6.1 (Team 2019) using lme4 (Bates et al. 2015). In the exploratory phase of our data analysis, some variables changed noticeably across sites and in different months (see Figs. S1-S18). For example, among sites temperature tended to be higher in June/July/August than in September or October. To account for these differences, we applied seven candidate model structures that allowed for different effects of the random variables of site and month on model intercepts (Table 2). For each variable,

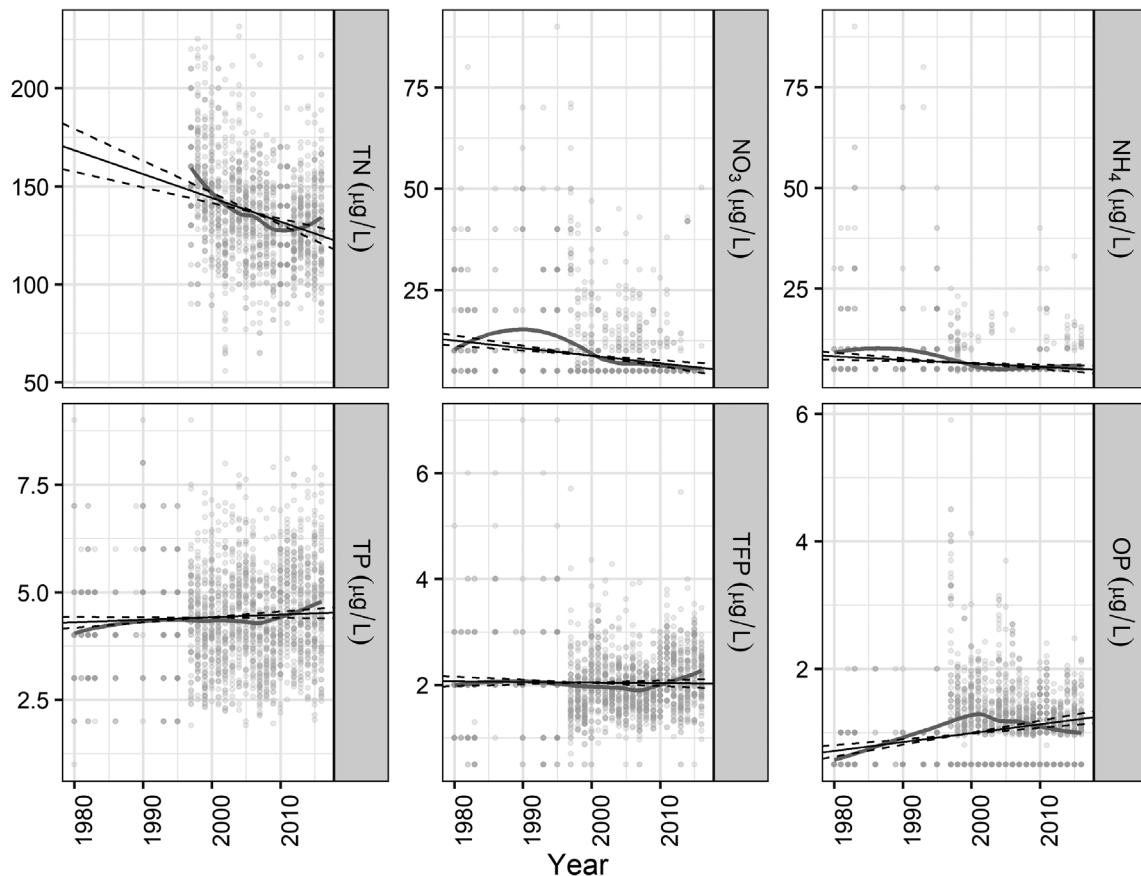


Fig. 2. Best fit linear mixed-effects models (solid black lines) and 95% confidence intervals (dashed black lines) for six nutrient response variables (total nitrogen, nitrate, ammonium, total phosphorus, total soluble phosphorus, and orthophosphate) collected at seven study sites during a 37-year study of Lake George (New York, USA). A loess curve (gray lines) illustrates nonlinearities in the data.

we chose the best model among the seven by selecting the one having the lowest Akaike Information Criterion (AIC) value. Using the best-fit model, we computed the 95% confidence intervals for the fixed effect of year. In our analyses, results from the alternative models did not contradict the best-fit model and model AIC values can be found in Table S1. The effect sizes (i.e., percent change) were calculated by using the model output by simply taking 2016 interpolated regression value divide by the interpolated regression value from 1980.

From the PAR surveys, we plotted light against depth and fit an exponential function to the curve for a given profile. The exponent from the negative exponential model fit to the profile data represents the rate of light decay at each site. To ensure high-quality profiles, we discarded any PAR surveys where the model R^2 for the exponential equation was less than 0.90. We analyzed trends in K_d with linear regression for each sampling site to determine whether K_d increased or decreased over the 22 yr that light profiles were collected.

Many of the environmental variables we measured can contribute to fluctuations in chlorophyll a . For example, temperature and nutrients can mutually influence chlorophyll a . As

such, we used partial correlation to identify potential mechanisms for changes in chlorophyll a during the 37-year study. Unlike the linear mixed-effects models, partial correlation did not account for variability among sites, or inter- or intra-annual variability, limiting our scope of inference. We used partial correlation to determine potential drivers of changes in Lake George chlorophyll a because the procedure accounts for the correlation or covariance among the environmental response variables (Crawley 2007). To complete the analysis, we had to remove X , Y pairs with missing data, which led to an $n = 1836$ rather than $n = 3034$. Our goal with the partial correlation analysis was to understand which variables were most strongly correlated with linear changes in chlorophyll a while holding the effects of the other variables constant. We added loess curves to accompany the linear mixed-effects model analysis to illustrate nonlinearities in the offshore chemistry program data.

To understand how water-quality parameters in Lake George changed relative to each other, we calculated the standardized effect size of each variable using z-scores. We then calculated 95% confidence intervals around the standardized effect size for the best model identified using AIC. By evaluating standardized

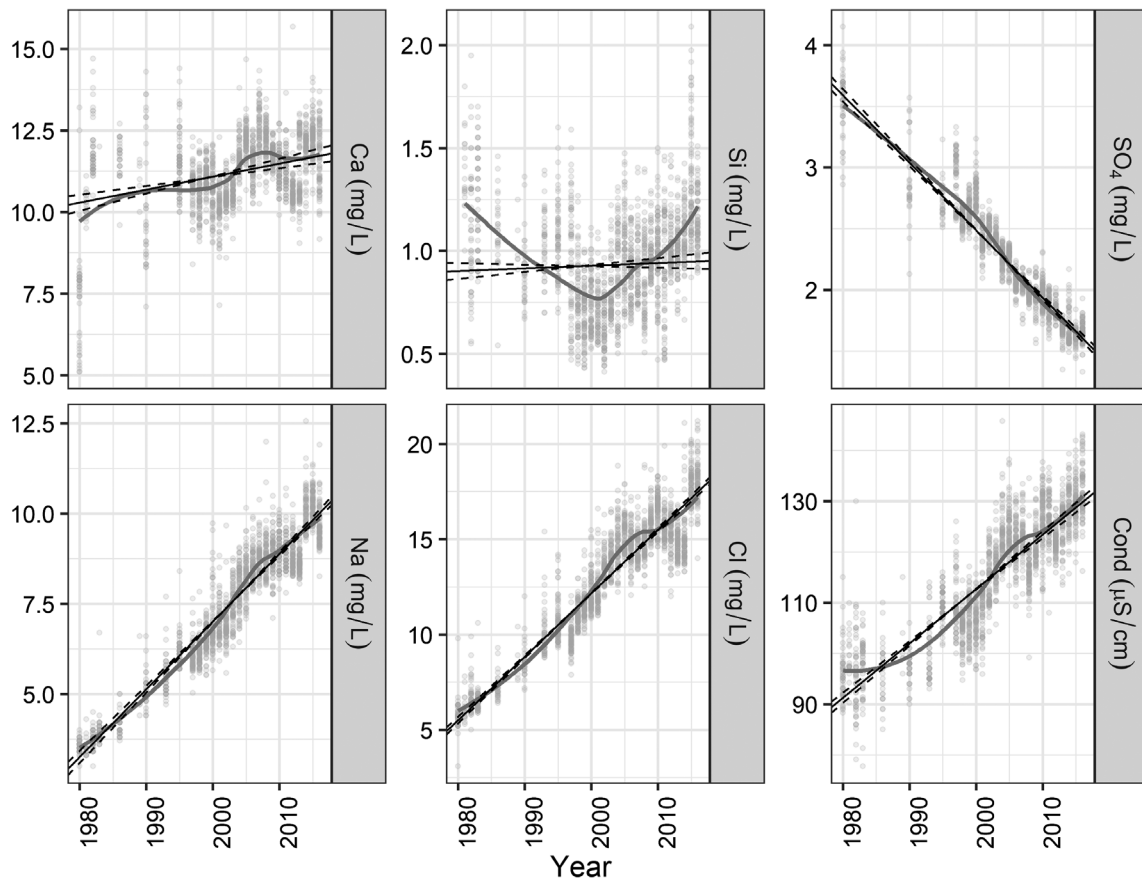


Fig. 3. Best fit linear mixed-effects models (solid black lines) and 95% confidence intervals (dashed black lines) for five ions (calcium, silica, sulfate, sodium, and chloride) and conductivity collected at seven study sites during a 37-year study of Lake George. We added a loess curve (gray lines) to illustrate nonlinearities in the data.

effect sizes, this increased our ability to identify the magnitude of positive and negative trends in the data and determine the magnitude of water quality changes occurring in Lake George since 1980.

Results

In our analysis of nutrients, we observed little change in total soluble phosphorus or total phosphorus concentrations over the 37 years (Table 3; Fig. 2). However, orthophosphate increased by $0.5 \mu\text{g L}^{-1}$, which represents a 70% (95% CI: 41–109%) increase over time. All measured nitrogenous analytes decreased during the period of study. Nitrate decreased by 54% ($6.7 \mu\text{g L}^{-1}$; 95% CI: 38–66%), ammonium decreased by 36% ($3.2 \mu\text{g L}^{-1}$; 95% CI: 19–53%), and total nitrogen (measured after 1997) decreased by 16% (0.0432 mg L^{-1} ; 95% CI: 11–20%).

Concentrations of the ions and polyatomic ions in Lake George changed from 1980 to 2016 (Table 3, Fig. 3). Sulfate decreased by 55% ($1.984 \text{ mg S L}^{-1}$; 95% CI: 53–57%). Among the different monatomic ions, sodium increased by 204% (6.76 mg L^{-1} ; 95% CI: 190–228%), chloride increased by 218%

(11.96 mg L^{-1} ; 95% CI: 204–230%), and calcium increased by 14% from (10.38 to 11.82 mg L^{-1} ; 95% CI: 9–19%). Soluble silica concentrations fluctuated throughout the study, but concentrations in 1980 were similar to those at the end of the study. Conductivity increased by 42% over the 37-year study (by $39 \mu\text{S cm}^{-1}$; 95% CI: 40–45%).

Accounting for the variability among sites and months, we found that epilimnetic temperature increased by 13% (1.8°C ; $0.05^\circ\text{C yr}^{-1}$; 95% CI: 9–18%) and alkalinity increased by 20% ($7.41 \mu\text{Equivalents L}^{-1}$; 95% CI: 18–22%; Fig. 4). We also observed a 2% increase in pH from 7.55 to 7.71. Epilimnetic dissolved oxygen fluctuated over the study period, but concentrations in 1980 were similar to those in 2016.

We assessed water transparency using Secchi depth measurements over all 37 yr and PAR surveys over the most recent 22 yr (Fig. 4). We found that Secchi depth did not change over time. Among the eight sights where we collected PAR light profiles, we found no change in K_d over time for seven of the sites (Figs. S19–S20; all $R^2 \leq 0.07$, $p \geq 0.227$) and an improvement in water clarity (i.e., a decrease in K_d) at the eighth site (Fig. S19; $R^2 = 0.18$, $p = 0.038$).

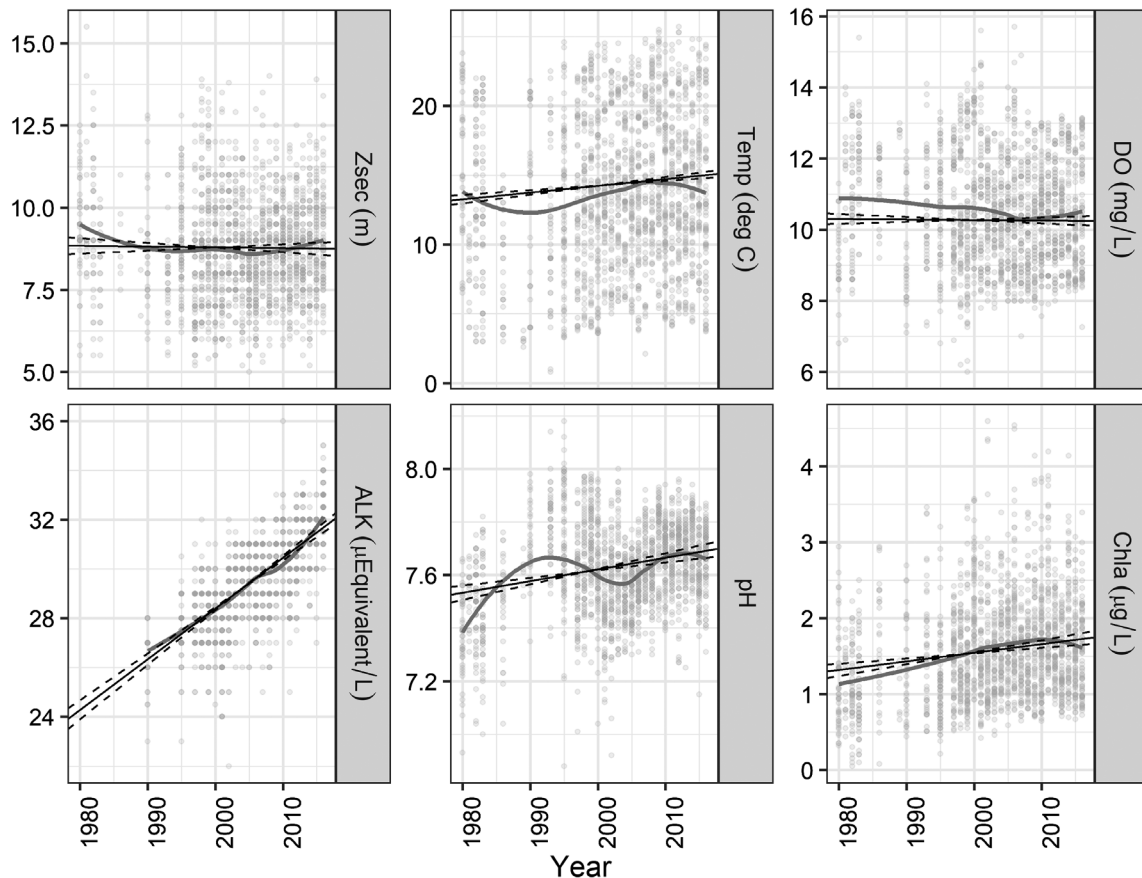


Fig. 4. Best fit linear mixed-effects models (solid black lines) and 95% confidence intervals (dashed black lines) for Secchi depth, temperature, dissolved oxygen, alkalinity, pH, and chlorophyll *a* collected at seven study sites during a 37-year study of Lake George (New York, USA). A loess curve shown in gray illustrates nonlinear patterns in the data.

Table 4. Pearson partial correlation coefficients and *p*-values between chlorophyll *a* and all other environmental variables to facilitate identifying what triggered a lake-wide 32% increase in chlorophyll *a* from 1980 to 2016 (*n* = 1836).

Variable	Partial correlation coefficient	<i>p</i> value
Total phosphorus	0.18	<0.001
Orthophosphate	0.12	<0.001
Sodium	0.12	<0.001
Chloride	0.12	<0.001
Secchi depth	-0.34	<0.001
Temperature	-0.23	<0.001
Alkalinity	-0.09	<0.001
Dissolved oxygen	-0.08	<0.001
Total soluble phosphorus	0.02	0.482
Nitrate	-0.02	0.450
Ammonium	0.01	0.758
Total nitrogen	0.04	0.116
Sulfate	0.02	0.411
Calcium	-0.03	0.207
Silica	-0.02	0.415
Conductivity	-0.01	0.605
pH	0.01	0.614

Across all study sites, average chlorophyll *a* increased by 32% (by 0.41 $\mu\text{g L}^{-1}$; 95% CI: 18–46%) from 1980 to 2016. We used partial correlation to determine which water-quality measurement accounted for the most variation in chlorophyll *a*. From this analysis, we determined that orthophosphate, total phosphorus, chloride, and sodium were positively associated with the change in chlorophyll *a*. In contrast, Secchi depth, alkalinity, temperature, and dissolved oxygen were negatively associated with chlorophyll *a* (Table 4).

Relative changes in water quality

Using standardized effect sizes (i.e., centered data), we compared the relative changes in each water quality variable. This allowed us to understand magnitude changes among the 18 water quality variables (Fig. 5). The largest decline observed was in the concentration of sulfate, which was two times greater than any other water quality variable. Following sulfate, the nitrogenous compounds exhibited the greatest concentration declines. An increase in alkalinity was the largest positive change over the study periods. Among the various ions, the rise of sodium and chloride exhibited the greatest relative increases, followed by a concomitant increase in conductivity.

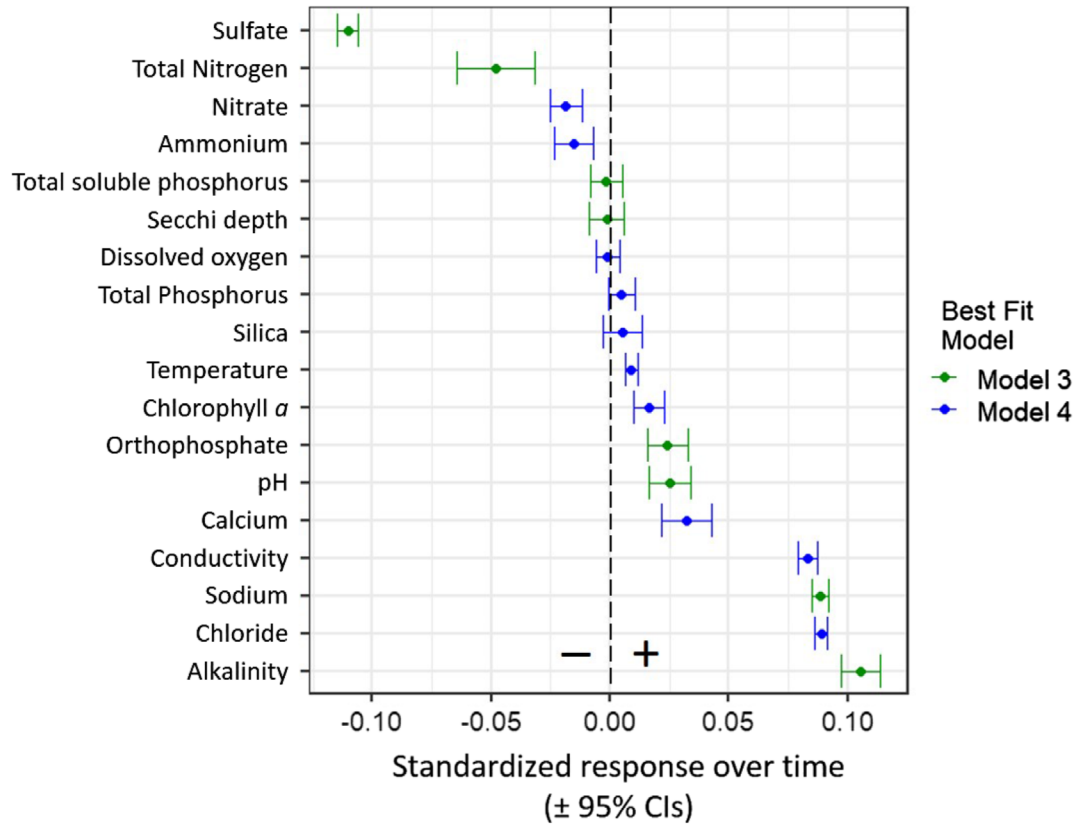


Fig. 5. Standardized effect size for the fixed effect of year (i.e., β) and 95% confidence intervals for the best-fit linear mixed effect model to determine which variables exhibited the greatest magnitude changes relative to one another in Lake George from 1980 to 2016. [Color figure can be viewed at wileyonlinelibrary.com]

Discussion

Water quality of lake ecosystems is influenced by multiple concurrent environmental stressors triggered by anthropogenic activities. Our goal was to identify how a large oligotrophic lake in the northeastern United States has responded to stressors such as climate change, acidification, and various regional pollutants over four decades. We show that some indicator variables suggest deterioration in the water quality in Lake George, others indicated improvement, and several exhibited stasis over 37 yr. Deterioration in water quality was associated with large percentage changes but relatively small absolute changes. However, these trends might signal areas of concern and a need for regulatory or management protections for Lake George and other lakes in the Adirondack region.

Epilimnetic warming of Lake George is consistent with surface water warming trends for lakes around world due to global climate change (Hondzo and Stefan 1993; George et al. 2007; Roesner et al. 2012; O'Reilly et al. 2015; Swinton et al. 2015b; Izmet'eva et al. 2016). In a study of 230 lakes distributed globally, O'Reilly et al. (2015) found that lake surface-water temperatures were increasing by $0.34^{\circ}\text{C decade}^{-1}$ (95% CI: $0.16\text{--}0.52^{\circ}\text{C}$). The epilimnetic temperature of Lake George has increase about $0.50^{\circ}\text{C decade}^{-1}$ (1.8°C over 37 yr; $0.05^{\circ}\text{C yr}^{-1}$), suggesting warming in Lake George might be higher than average but similar to other seasonally ice-covered lakes (O'Reilly et al. 2015). While currently unknown for our study system, the consequences of warming surface waters could trigger increases in algal blooms, methane emissions, and reductions in lake water levels and ecosystem stability (Smol et al. 2005; George et al. 2007; Brookes and Carey 2011; O'Reilly et al. 2015).

Another negative change in Lake George water quality was the increase in epilimnetic chlorophyll *a*. Although a 32% increase might seem substantial, the absolute increase was small; the chlorophyll *a* concentration increased from $1.30\ \mu\text{g L}^{-1}$ in 1980 to $1.71\ \mu\text{g L}^{-1}$ in 2016. The observed increase in Lake George chlorophyll *a* is similar to other large oligotrophic lakes around the globe (e.g., Lake Baikal; Hampton et al. 2008). A potential mechanism for increased chlorophyll *a* concentration in Lake George is the small increase in orthophosphate. Lake George is generally phosphorus limited. Increases in phosphorus are well known to trigger increases in chlorophyll *a* in phosphorus-limited lakes (Carpenter et al. 1996; Schindler et al. 2008). Interestingly, there was a correlation between total phosphorus and chlorophyll *a*, but total phosphorus did not increase over the 37-year study. At present, we cannot identify what triggered the increase in orthophosphate, but periods of nitrogen colimitation, changes in hypolimnetic salinity, oxygen dynamics, or shifts in anthropogenic nutrient sources should be explored.

Chlorophyll *a* is the best proxy of phytoplankton biomass (Huot et al. 2007), but the chlorophyll concentration of algae can change with environmental stimuli and gradients (e.g., Felip and Catalan 2000; Fennel and Boss 2003; Collins and Bell 2004).

More chlorophyll *a* per algal cell rather than higher algal biomass could have contributed to the 32% increase in epilimnetic chlorophyll *a* (e.g., Steele 1964). While we assume the increase in orthophosphate led to the increase in chlorophyll *a*, we cannot dismiss that temperature, changing ion concentrations, or ecological community structure might have independently or interactively increased the chlorophyll *a* concentration within algal cells. Further, like many lakes with a strong thermal stratification, Lake George maintains a deep chlorophyll maximum (DCM) for much of the year. The depth of the DCM varies over the course of a season and may appear as shallow as 5 m (Moriarty, unpublished vertical profiler data from Lake George). Although the depth of the DCM was not measured as part of our sampling program, it is possible upward migration of the DCM during the latter years could affect epilimnetic chlorophyll *a* (Leach et al. 2018).

Increasing concentrations of sodium and chloride were some of the most dramatic changes in Lake George over the 37 yr. Not surprisingly, there was a concomitant increase in conductivity. Because there are no natural processes that account for such dramatic increases in these ions, the source is anthropogenic and very likely due to the use of road deicing salts. While some Adirondack Park lakes show neutral or negative trends in chloride over several years (Dugan et al. 2017), our data suggest one of the larger lakes in the region has undergone significant road salt contamination, similar to many other lakes surrounded by urbanization in the region (Kelting et al. 2012).

Although increasing, present-day concentrations of sodium and chloride from road salts are unlikely to affect the biota of Lake George. Some of the most sensitive lake organisms can tolerate much higher salt concentrations before being impacted (Evans and Frick 2001; Elphick et al. 2011; Roe and Patterson 2014; Hintz et al. 2017; Hintz and Relyea 2017; Lind et al. 2018; Sinclair and Arnott 2018). For instance, low water hardness increases the toxicity of chloride from road salts triggering negative effects around $64\ \text{mg Cl}^{-1}\ \text{L}^{-1}$ for sensitive zooplankton species (Elphick et al. 2011). Current salt concentrations do not appear high enough to produce substantial negative effects on the abundance of large-bodied zooplankton (Hintz and Relyea 2017; Schuler et al. 2017; Searle et al. 2016; Sinclair and Arnott 2018; Stoler et al. 2017a,b), which might increase chlorophyll *a* concentration through a loss of grazing pressure (Hintz et al. 2017; Jones et al. 2017). Even though Lake George has low water hardness, it would take more than 135 yr to reach $64\ \text{mg Cl}^{-1}\ \text{L}^{-1}$ assuming trends follow those of the past 37 yr. Yet, it is unclear if shifts in species composition of phytoplankton has occurred, due to a change in species-specific concentration of chlorophyll *a*. Currently, species-level phytoplankton responses to road salt contamination remain to be explored (Hintz and Relyea 2019). Nevertheless, due to the unknown ecological impacts of road salts at low concentrations (Hintz and Relyea 2019), it would be wise to proactively curb road salt salinization in any lake ecosystem, including Lake George, which is on the lower end of road salt contamination among North American Lakes (Dugan et al. 2017).

Lake George is a drinking water supply for many in the region. A greater concern regarding road salt contamination in Lake George is the quality of drinking water. The concentration of sodium has gone from around 2–3 mg L⁻¹ to 10 mg L⁻¹ during our study period. The U.S. EPA and World Health Organization guidance level for sodium in drinking water is 20 mg L⁻¹ (USEPA 2003; World Health Organization 2003). Given the current rate of increase in Lake George, sodium concentrations would reach 20 mg L⁻¹ in 2068, less than 50 yr from present. Thus, efforts to curb salinization of Lake George through efficient and proactive deicing practices are necessary to prevent a loss of drinking water quality.

While our analyses confirm that increased orthophosphate is correlated with the increase in chlorophyll *a*, road salt contamination could potentially cause an increase in orthophosphate. Road salt can form a saline layer in the hypolimnion (Novotny and Stefan 2012), which can generate hypoxic or anoxic conditions near the benthos (Bridgeman et al. 2000; Ficker et al. 2018), triggering the release of phosphorus from lake sediments (Novotny and Stefan 2012; Wyman and Koretsky 2018; Hintz and Relyea 2019). However, if this were the case, we would likely have observed much higher epilimnetic chloride concentrations (>100 mg L⁻¹) because of mixing and turnover as reported in other lake systems (e.g., Wyman and Koretsky 2018). Nevertheless, we do not yet have data on hypolimnetic salt concentrations in Lake George to assess this hypothesis. Further study of salinized hypolimnetic habitats and the resulting ecological impacts is needed in salinized lakes in general.

Although the increase was small, a potential concern is whether the rising concentration of calcium in Lake George could contribute to the success and post-establishment impacts of calcium-limited invasive species. Currently, zebra mussels (*Dreissena polymorpha*) and spiny water fleas (*Bythotrephes longimanus*) are found in Lake George, but with limited, localized populations. Asian clams (*Corbicula fluminea*) are more widespread. The in-lake calcium concentration for zebra mussels is too low to exhibit a boon in population growth (Whittier et al. 1995). For instance, calcium concentrations <12 mg L⁻¹ are classified as “very low” risk of zebra mussel invasion while 12–20 mg L⁻¹ of calcium is classified as “low” risk and >20 mg L⁻¹ is considered “moderate to high” risk (Whittier et al. 2008). Over 37 yr, the average calcium concentration in Lake George increased from 10.4 mg L⁻¹ to 11.8 mg L⁻¹. At the current rate of increase, it would take over 200 yr to reach the moderate threshold of 20 mg L⁻¹ for zebra mussels. Thus, it does not appear the rising calcium concentrations will contribute to a sustained expansion by zebra mussels. Asian clams on the other hand exhibit adverse effects of low calcium concentration at approximately 6–10 mg L⁻¹ (Sousa et al. 2006; Sousa et al. 2008) and the spiny water flea does not appear to be calcium limited (Kim et al. 2012). While the Asian clam population in Lake George is relatively localized due to habitat availability and the spiny water flea is detected intermittently, current boat-inspection programs designed to inhibit the introduction of invasive species to Lake George are important as

calcium concentrations are high enough for the persistence of some but not all freshwater invaders.

Acidification from “acid rain” was a major environmental stressor for many North American and European lakes. The Acid Rain Program established by the United States Congress in 1990 under the Clean Air Act has curbed emissions that led to lake acidification. Emissions of sulfur dioxide were 40% lower in the early 2000s compared to emission in the 1980s and emissions of nitrogen oxides were 33% lower in the early 2000s than in the 1990s (National Science and Technology Council 2005). Although Lake George was never acidified to the point that triggered severe ecological effects such as a loss of fish populations (e.g., Beamish and Harvey 1972), likely due to calcium carbonate deposits in the watershed and on the lake bottom, the reduction in sulfate, nitrate, and increases in alkalinity and pH indicate recovery from acidification (Driscoll et al. 2003; Skjelkvale et al. 2005; Wright et al. 2005). Environmental regulations such as the Acid Rain Program under Clean Air Act in the United States and the Eastern Canada Acid Rain Program have clearly curbed acidification in Lake George similar to lakes throughout North America and Europe (Stoddard et al. 1999).

Water clarity can be a sentinel of biological or environmental change in lakes (e.g., Rose et al. 2017). Reductions in water clarity are often associated with increasing chlorophyll *a* concentrations (Tilzer 1988). While we found an increase in chlorophyll *a*, we did not find a reduction in water clarity in Lake George as measured by Secchi depth over 37 yr or by light attenuation surveys over 22 yr. No change in water clarity was indicated by Secchi depth or the light attenuation coefficient (K_d) except for one site, where water clarity slightly improved. Our findings are similar to reports from other oligotrophic lakes where small increases in chlorophyll *a* were reported, but water clarity did not decline (Hampton et al. 2008). The stasis in Lake George water clarity is encouraging, given the degree of shoreline development, introduction of invasive species, and epilimnetic warming due to climate change.

Conclusion

Deterioration in Lake George water quality was small compared to many lakes. The small increases in chlorophyll *a* and orthophosphate indicate that watershed-scale conservation efforts to protect the water quality of Lake George are robust, given the degree of development and tourism in the watershed. Yet, even small deteriorations in water quality might indicate larger threats on the horizon. For instance, while environmental policy has successfully reversed trends in acidification, the salinization of Lake George from the use of road deicing salts has increased substantially since 1980. We must consider lake morphology and spatial resolution regarding the salinization issue. Our study sites were offshore epilimnetic samples from deep-water sites, which do not reflect road salt concentrations in surrounding tributary streams, wetlands, ground waters, or the hypolimnetic zone (e.g., Swinton et al.

2015a). Importantly, studies examining the effects of road salts on freshwater lakes will need to consider peripheral habitats (i.e., tributaries, groundwaters, wetlands) and episodic effects, which will likely encounter much higher ion concentrations and are diluted by the time they reach pelagic study sites. Further, road salts can increase the concentrations of heavy metals and nutrients in lakes from peripheral habitats (Kaushal et al. 2018; Schuler and Relyea 2018). Thus, proactive policy and environmental management on the whole-catchment scale will be needed to protect our freshwater lakes from salinization (Schuler et al. 2019).

Our long-term study reveals concurrent improvements and deteriorations in the water quality, while many indicators exhibited 37 yr of stasis. Long-term measurement of multiple indicators of multiple stressors linked in space and time allows us to more fully understand changes in lake water quality than if we had only focused on a subset of variables over shorter time periods. This also allowed us to identify subtle changes in water quality that might not be apparent without similar spatial coverage and sampling intensity as applied here. Importantly, our approach can provide politicians, managers, and the public with a comprehensive picture of lake water quality to illustrate the effectiveness of management programs and policy.

References

- Adrian, R., and others. 2009. Lakes as sentinels of climate change. *Limnol. Oceanogr.* **54**: 2283–2297. doi:10.4319/lo.2009.54.6_part_2.2283
- American Public Health Association. 1998. Standard methods for the examination of water and wastewater. Washington DC: American Public Health Association, American Water Works Association and Water Environmental Federation 20th Edition.
- Bates, D., M. Machler, B. M. Bolker, and S. C. Walker. 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**: 1–48. doi:10.18637/jss.v067.i01
- Beamish, R. J., and H. H. Harvey. 1972. Acidification of La Cloche mountain lakes, Ontario, and resulting fish mortalities. *J. Fish. Res. Can.* **29**: 1131–1143. doi:10.1139/f72-169
- Boylen, C., L. Eichler, M. Swinton, S. Nierzwicki-Bauer, I. Hannoun, and J. Short. 2014. The state of the lake: Thirty years of water quality monitoring on Lake George. Darrin Fresh Water Institute.
- Bridgeman, T. B., and others. 2000. A limnological survey of Third Sister Lake Michigan with historical comparisons. *J. Lake Reserv. Manag.* **16**: 253–267. doi:10.1080/07438140009354234
- Brookes, J. D., and C. C. Carey. 2011. Resilience to blooms. *Science* **334**: 46–47. doi:10.1126/science.1207349
- Carpenter, S. R., and others. 1996. Chlorophyll variability, nutrient input, and grazing: Evidence from whole-lake experiments. *Ecology* **77**: 725–735. doi:10.2307/2265497
- Carpenter, S. R., N. F. Caraco, D. L. Correll, R. W. Howarth, A. N. Sharpley, and V. H. Smith. 1998. Nonpoint pollution of surface waters with phosphorus and nitrogen. *Ecol. Appl.* **8**: 559–568. doi:10.2307/2641247
- Collins, S., and G. Bell. 2004. Phenotypic consequences of 1,000 generations of selection at elevated CO₂ in a green alga. *Nature* **431**: 566–569. doi:10.1038/nature02945
- Crawley, M. J. 2007. The R book. Chichester, UK: Wiley.
- Driscoll, C. T., K. M. Driscoll, K. M. Roy, and M. J. Mitchell. 2003. Chemical response of lakes in the Adirondack Region of New York to declines in acidic deposition. *Environ. Sci. & Tech.* **37**: 2036–2042. doi:10.1021/es020924h
- Dugan, H. A., and others. 2017. Salting our freshwater lakes. *P. Natl. Acad. Sci. USA* **114**: 4453–4458. doi:10.1073/pnas.1620211114
- Elphick, J. R. F., K. D. Bergh, and H. C. Bailey. 2011. Chronic toxicity of chloride to freshwater species effects of hardness and implications for water quality guidelines. *Environ. Toxicol. Chem.* **30**: 239–246. doi:10.1002/etc.365
- Evans, M., and C. Frick. 2001. The effects of road salts on aquatic ecosystems. Environment Canada - Water Science and Technology Directorate.
- Felip, M., and J. Catalan. 2000. The relationship between phytoplankton biovolume and chlorophyll in a deep oligotrophic lake: Decoupling in their spatial and temporal maxima. *J. Plankton Res.* **22**: 91–105. doi:10.1093/plankt/22.1.91
- Fennel, K., and E. Boss. 2003. Subsurface maxima of phytoplankton and chlorophyll: Steady-state solutions from a simple model. *Limnol. Oceanogr.* **48**: 1521–1534. doi:10.4319/lo.2003.48.4.1521
- Ficker, H., M. Luger, B. Pamminger-Lahnsteiner, D. Achleitner, A. Jagsch, and H. Gassner. 2018. Diluting a salty soup: Impact of long-lasting salt pollution on a deep Alpine lake (Traunsee, Austria) and the downside of recent recovery from salinization. *Aquat. Sci.* **81**: 7. doi:10.1007/s00027-018-0602-3
- George, G., M. Hurley, and D. Hewitt. 2007. The impact of climate change on the physical characteristics of the larger lakes in the English Lake District. *Freshw. Biol.* **52**: 1647–1666. doi:10.1111/j.1365-2427.2007.01773.x
- Hampton, S. E., L. R. Izmet'eva, M. V. Moore, S. L. Katz, B. Dennis, and E. A. Silow. 2008. Sixty years of environmental change in the world's largest freshwater lake – Lake Baikal, Siberia. *Glob. Change Biol.* **14**: 1947–1958. doi:10.1111/j.1365-2486.2008.01616.x
- Hintz, W. D., and others. 2017. Salinization triggers a trophic cascade in experimental freshwater communities with varying food-chain length. *Ecol. Appl.* **27**: 833–844. doi:10.1002/eap.1487
- Hintz, W. D., and R. A. Relyea. 2017. A salty landscape of fear: Responses of fish and zooplankton to freshwater salinization and predatory stress. *Oecologia* **185**: 147–156. doi:10.1007/s00442-017-3925-1
- Hintz, W. D., and R. A. Relyea. 2019. A review of the species, community, and ecosystem impacts of road salt salinization in fresh waters. *Freshw. Biol.* **64**: 1081–1097. doi:10.1111/fwb.13286

- Hondzo, M., and H. G. Stefan. 1993. Regional water temperature characteristics of lakes subjected to climate change. *Clim. Change* **24**: 187–211. doi:10.1007/bf01091829
- Huot, Y., M. Babin, F. Bruyant, C. Grob, M. S. Twardowski, and H. Claustre. 2007. Relationship between photosynthetic parameters and different proxies of phytoplankton biomass in the subtropical ocean. *Biogeosciences* **4**: 853–868. doi:10.5194/bg-4-853-2007
- Izmet'eva, L. R., and others. 2016. Lake-wide physical and biological trends associated with warming in Lake Baikal. *J. Great Lakes Res.* **42**: 6–17. doi:10.1016/j.jglr.2015.11.006
- Jeppesen, E., and others. 2010. Impacts of climate warming on lake fish community structure and potential effects on ecosystem function. *Hydrobiologia* **646**: 73–90. doi:10.1007/s10750-010-0171-5
- Jones, D. K., and others. 2017. Investigation of road salts and biotic stressors on freshwater wetland communities. *Environ. Pol.* **221**: 159–167. doi:10.1016/j.envpol.2016.11.060
- Kaushal, S. S., and others. 2018. Freshwater salinization syndrome on a continental scale. *P. Natl. Acad. Sci. U S A* **115**: E574–E583. doi:10.1073/pnas.1711234115
- Kelly, V. R., M. A. Cunningham, N. Curri, S. E. Findlay, and S. M. Carroll. 2018. The distribution of road salt in private drinking water wells in a Southeastern New York suburban township. *J. Environ. Qual.* **47**: 445–451. doi:10.2134/jeq2017.03.0124
- Kelting, D. L., C. L. Laxson, and E. C. Yerger. 2012. Regional analysis of the effect of paved roads on sodium and chloride in lakes. *Water Res.* **46**: 2749–2758. doi:10.1016/j.watres.2012.02.032
- Kim, N., B. Walseng, and N. D. Yan. 2012. Will environmental calcium declines hinder Bythotrephes establishment success in Canadian Shield lakes? *Can. J. Fish. Aquat. Sci.* **69**: 810–820. doi:10.1139/f2012-024
- Langner, C. L., and P. F. Hendrix. 1982. Evaluation of a persulfate digestion method for particulate nitrogen and phosphorus. *Water Res.* **16**: 1451–1454. doi:10.1016/0043-1354(82)90243-3
- Leach, T. H., and others. 2018. Patterns and drivers of deep chlorophyll maxima structure in 100 lakes: The relative importance of light and thermal stratification. *Limnol. Oceanogr.* **63**: 628–646. doi:10.1002/lno.10656
- Lind, L., and others. 2018. Salty fertile lakes: How salinization and eutrophication alter the structure of freshwater communities. *Ecosphere* **9**: e02383. doi:10.1002/ecs2.2383
- McCullough, I. M., K. S. Cheruvilil, S. M. Collins, and P. A. Soranno. 2019. Geographic patterns of the climate sensitivity of lakes. *Ecol. Appl.* **0**: e01836. doi:10.1002/eap.1836
- National Science Technology Council. 2005. National acid precipitation assessment program report to Congress: An integrated assessment. Washington, D.C.: National Science Technology Council.
- Novotny, E. V., and H. G. Stefan. 2012. Road salt impact on lake stratification and water quality. *J. Hydraul. Eng.* **138**: 1069–1080. doi:10.1061/(asce)hy.1943-7900.0000590
- O'Reilly, C. M., and others. 2015. Rapid and highly variable warming of lake surface waters around the globe. *Geophys. Res. Lett.* **42**: 10,773–10,781. doi:10.1002/2015gl066235
- Roe, H. M., and R. T. Patterson. 2014. Arcellacea (testate amoebae) as bio-indicators of road salt contamination in lakes. *Microbial Ecol.* **68**: 299–313. doi:10.1007/s00248-014-0408-3
- Roesner, R., D. C. Mueller-Navarra, and E. Zorita. 2012. Trend analysis of weekly temperatures and oxygen concentrations during summer stratification in Lake Plusssee: A long-term study. *Limnol. Oceanogr.* **57**: 1479–1491. doi:10.4319/lo.2012.57.5.1479
- Rose, K. C., S. R. Greb, M. Diebel, and M. G. Turner. 2017. Annual precipitation regulates spatial and temporal drivers of lake water clarity. *Ecol. Appl.* **27**: 632–643. doi:10.1002/eap.1471
- Schindler, D. W., and others. 2008. Eutrophication of lakes cannot be controlled by reducing nitrogen input: Results of a 37-year whole-ecosystem experiment. *P. Natl. Acad. Sci. U S A* **105**: 11254–11258. doi:10.1073/pnas.0805108105
- Schuler, M. S., and others. 2017. How common road salts and organic additives alter freshwater food webs: In search of safer alternatives. *J. Appl. Ecol.* **54**: 1353–1361. doi:10.1111/1365-2664.12877
- Schuler, M. S., and R. A. Relyea. 2018. A review of the combined threats of road salts and heavy metals to freshwater systems. *Bioscience* **68**: 327–335. doi:10.1093/biosci/biy018
- Schuler, M. S., M. Cañedo-Argüelles, W. D. Hintz, B. Dyack, S. Birk, and R. A. Relyea. 2019. Regulations are needed to protect freshwater ecosystems from salinization. *Philos. T. Roy. Soc. B.* **374**: 20180019. doi:10.1098/rstb.2018.0019
- Searle, C. L., C. L. Shaw, K. K. Hunsberger, M. Prado, and M. A. Duffy. 2016. Salinization decreases population densities of the freshwater crustacean, *Daphnia dentifera*. *Hydrobiologia* **770**: 165–172. doi:10.1007/s10750-015-2579-4
- Sinclair, J. S., and S. E. Arnott. 2018. Local context and connectivity determine the response of zooplankton communities to salt contamination. *Freshw. Bioll.* **63**: 1273–1286. doi:10.1111/fwb.13132
- Skjelkvale, B. L., and others. 2005. Regional scale evidence for improvements in surface water chemistry 1990–2001. *Environ. Pol.* **137**: 165–176. doi:10.1016/j.envpol.2004.12.023
- Smol, J. P., and others. 2005. Climate-driven regime shifts in the biological communities of arctic lakes. *P. Natl. Acad. Sci. U S A* **102**: 4397–4402. doi:10.1073/pnas.0500245102
- Sousa, R., C. Antunes, and L. Guilhermino. 2006. Factors influencing the occurrence and distribution of *Corbicula fluminea* (Müller, 1774) in the River Lima estuary. *Ann. Limnol. - Int. J. Lim.* **42**: 165–171. doi:10.1051/limn/2006017
- Sousa, R., C. Antunes, and L. Guilhermino. 2008. Ecology of the invasive Asian clam *Corbicula fluminea* (Müller, 1774) in aquatic ecosystems: An overview. *Ann. Limnol. Int. J. Lim.* **44**: 85–94. doi:10.1051/limn:2008017

- Steele, J. H. 1964. A study of production in the Gulf of Mexico. *J. Mar. Res.* **22**: 211–222.
- Stoddard, J. L., and others 1999. Regional trends in aquatic recovery from acidification in North America and Europe. *Nature* **401**: 575–578. doi:[10.1038/44114](https://doi.org/10.1038/44114)
- Stoler, A. B., and others. 2017a. Leaf litter mediates the negative effect of road salt on forested wetland communities. *Freshw. Sci.* **36**: 415–426. doi:[10.1086/692139](https://doi.org/10.1086/692139)
- Stoler, A. B., and others. 2017b. Combined effects of road salt and an insecticide on wetland communities. *Environ. Toxicol. Chem.* **36**: 771–779. doi:[10.1002/etc.3639](https://doi.org/10.1002/etc.3639)
- Strayer, D. L. 2010. Alien species in fresh waters: Ecological effects, interactions with other stressors, and prospects for the future. *Freshw. Biol.* **55**: 152–174. doi:[10.1111/j.1365-2427.2009.02380.x](https://doi.org/10.1111/j.1365-2427.2009.02380.x)
- Swinton, M. W., L. W. Eichler, and C. W. Boylen. 2015a. Road salt application differentially threatens water resources in Lake George, New York. *Lake Reserv. Manage.* **31**: 20–30. doi:[10.1080/10402381.2014.983583](https://doi.org/10.1080/10402381.2014.983583)
- Swinton, M. W., L. W. Eichler, J. L. Farrell, and C. W. Boylen. 2015b. Evidence for water temperature increase in Lake George, NY: Impact on growing season duration and degree days. *Lake Reserv. Manage.* **31**: 241–253. doi:[10.1080/10402381.2015.1067660](https://doi.org/10.1080/10402381.2015.1067660)
- Team, R. C. 2019. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.
- Tilzer, M. M. 1988. Secchi disc - chlorophyll relationships in a lake with highly variable phytoplankton biomass. *Hydrobiologia* **162**: 163–171. doi:[10.1007/bf00014539](https://doi.org/10.1007/bf00014539)
- USEPA. 1979. Methods for chemical analysis of water and wastes. Cincinnati, OH: EPA-600/4-79-020. doi:[10.17226/1674](https://doi.org/10.17226/1674)
- USEPA. 2003. Drinking water advisory: Consumer acceptability advice and health effects analysis on sodium. Health and Ecological Criteria Division, Office of Water.
- Whittier, T. R., A. T. Herlihy, and S. M. Pierson. 1995. Regional susceptibility of Northeast lakes to zebra mussel invasion. *Fisheries* **20**: 20–27. doi:[10.1577/1548-8446\(1995\)020<0020:RSONLT>2.0.CO;2](https://doi.org/10.1577/1548-8446(1995)020<0020:RSONLT>2.0.CO;2)
- Whittier, T. R., P. L. Ringold, A. T. Herlihy, and S. M. Pierson. 2008. A calcium-based invasion risk assessment for zebra and quagga mussels (*Dreissena* spp). *Front. Ecol. Environ.* **6**: 180–184. doi:[10.1890/070073](https://doi.org/10.1890/070073)
- World Health Organization. 2003. Guidelines for drinking-water quality, 2nd ed. Health criteria and other supporting information. World Health Organization.
- Wright, R. F., and others. 2005. Recovery of acidified European surface waters. *Environ. Sci. Technol.* **39**: 64A–72A. doi:[10.1021/es0531778](https://doi.org/10.1021/es0531778)
- Wyman, D. A., and C. M. Koretsky. 2018. Effects of road salt deicers on an urban groundwater-fed kettle lake. *Appl. Geochem.* **89**: 265–272. doi:[10.1016/j.apgeochem.2017.12.023](https://doi.org/10.1016/j.apgeochem.2017.12.023)

Acknowledgments

We thank multiple funding sources that supported the offshore chemistry program including the FUND for Lake George, the Darrin Fresh Water Institute endowment fund, and in recent years the Jefferson Project at Lake George. During the 37-year effort to scientifically run the Lake George Chemistry Monitoring Program, over 75 individuals—field and laboratory staff, undergraduate and graduate interns, data managers and statisticians have been involved. We gratefully acknowledge their participation. Of note are those individuals who have provided specific expertise: Jeffrey Bartkowski, Tiffini Burlingame, Robert Bombard, Timothy Clear, Eric Howe, Dean Long, Bahram Momen, David Neils, Daniel Pope, Erik Posner, Shannon Shaver, and Reginald Soracco, Mark Swinton, and Jeremy Farrell. We thank Kevin Rose, Taylor Leach, Luke Winslow, Jeffrey Short, Jacek Maselko, and Richard Erickson for discussions during various phases of analysis and interpretation. We also would like to thank Benjamin Kraemer and anonymous reviewers who provide constructive comments that substantially improved our manuscript for publication.

Conflict of Interest

None declared.

Submitted 12 April 2019

Revised 30 July 2019

Accepted 27 September 2019

Associate editor: John Melack