

## Drivers of water quality changes within the Laurentian Great Lakes region over the past 40 years

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### Abstract

Water quality of freshwater lakes within the Laurentian Great Lakes region is vulnerable to degradation owing to multiple environmental stressors including climate change, alterations in land use, and the introduction of invasive species. Our research questions were two-fold: (1) What are the temporal patterns and trends in water quality? (2) Are climate, invasive species and lake morphology associated with changes in water quality? Our study incorporated timeseries data for at least 20 years from 36 lakes in Ontario and Wisconsin sampled between 1976 and 2016. We evaluated patterns in water quality (total phosphorus [TP], total nitrogen, dissolved organic carbon [DOC], and chlorophyll *a* [Chl *a*]) using segmented regression analysis which identified significant breakpoints in Chl *a* and TP in the 1900s to mid-2000s after which Chl *a* and TP began to increase, whereas breakpoints in DOC exhibited increasing trends prior to the year 2000 with levels declining afterward. Next, we examined linear trends in water quality and climate (temperature and precipitation) using Sen slope analysis where, generally, over the past 40 years, lake TP and Chl *a* have significantly declined, whereas DOC has increased. Lastly, we conducted a redundancy analysis (RDA) to identify how climate, lake morphology, and the presence of invasive dreissenid mussels contributed to changes in water quality. The RDA revealed that precipitation, air temperature, and morphology explained 73.1% of the variation in water quality trends for the Great Lakes whereas precipitation, temperature, morphology, and occurrence of mussels explained 45.6% of the variation for smaller inland lakes.

Clean freshwater is an essential resource for human survival, ecosystem health, and sustainable economic development as it is used daily for drinking, fishing, irrigation, transport, and recreation. However, water quality is becoming increasingly degraded owing to anthropogenic stressors including climate change, urbanization, agriculture, and the introduction of invasive species (Michalak 2016). Lakes within the Laurentian Great Lakes region are already experiencing the combined effects of warming temperatures, changes in hydrology, inputs of excess nutrients, and non-native species invasions (Sterner et al. 2017). Consequences of multiple stressors on water quality include a higher risk of algal blooms, changes in water chemistry, and unprecedented disturbances to biodiversity in aquatic ecosystems (Jackson et al. 2016). Further, the structure and function of aquatic ecosystems may be altered as water quality could directly or indirectly influence a lake's response to environmental changes (Alberti 2005). For example, less favorable water quality conditions may result in

changes in life history traits in fish, such as smaller body sizes, that could ultimately affect the composition of fish assemblage and food web dynamics which may lead to negative impacts on not only fisheries but entire biological communities (Wrona et al. 2006). Lastly, climate change has been identified as one of the most influential stressors affecting water quality in North American lakes (Adrian et al. 2009; Michalak 2016). In particular, warming air temperatures have produced some of the most severe water quality impacts to date (O'Reilly et al. 2015; Michalak 2016; Woolway and Merchant 2019).

Increasing temperatures have been consistently found to promote the intensity, frequency, and duration of harmful algal blooms which may yield harmful toxins, release noxious taste and odor compounds, and ultimately disrupt overall lake production (Paerl et al. 2016). For example, in the Laurentian Great Lakes watershed, increasing air temperatures have led to shorter or no ice cover duration (Hewitt et al. 2018; Sharma et al. 2019), warmer water temperatures (O'Reilly et al. 2015), increased stratification (Stainsby et al. 2011), decreased dissolved oxygen concentrations (Nelligan et al. 2019; Yuan and Jones 2019), and favorable environments for toxic phytoplankton blooms (Rigosi et al. 2014; Ho et al. 2019). Climate

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change further affects water quality by altering regional hydrological patterns. Increased variability in precipitation influences the amount and frequency of nutrients being flushed into lakes from surrounding catchments. For example, Hudson et al. (2003) found that more rainfall delivers an excess amount of terrestrial-derived organic matter, specifically dissolved organic carbon (DOC), into lakes. This introduction of DOC, which is also referred to as brownification, may lead to adverse water quality conditions including color change, decreased light attenuation, and anoxia (Brothers et al. 2014). To better estimate future changes in water quality, there is a need to describe the historical relationship between water quality and climate across a gradient of lake types. In addition to changing climates, anthropogenic stressors such as land use changes (e.g., urbanization and agriculture) may increase nutrients into aquatic systems and lead to a degradation of water quality. Natural vegetation surrounding lakes all over North America have been replaced by constructed impervious surfaces, or areas equipped for irrigation and livestock (Ramankutty et al. 2018). Changes to these once natural landscapes results in lands that are treated with fertilizers and pesticides and produce more sewage and waste that can enter waterways (Paerl et al. 2016). Fortunately, over the past few decades, many initiatives have been implemented to reduce the amount of nutrients being discharged into lakes in the Laurentian Great Lakes watershed. For example, large decreases in total phosphorus (TP) and total nitrogen (TN) occurred in Lake Erie and Lake Ontario after the implementation of the 1972 US-Canada Water Quality Agreement (Dove and Chapra 2015). Further, North et al. (2013) showed that over time there have been declines in TP concentrations in Lake Simcoe as a result of better management practices. Yet, the new threat of climate change in addition to nutrient levels may be sufficient to tip the scales toward adverse water quality conditions and may promote harmful phytoplankton production (Paerl et al. 2016; Ho et al. 2019).

The introduction of invasive species into the Great Lakes basin has had a profound impact on lakes in the region (Karatayev et al. 2015). The establishment of non-native zebra (*Dreissena polymorpha*) and quagga (*Dreissena bugensis*) mussels within the Laurentian Great Lakes region has caused notable water quality and ecosystem modifications (Ricciardi and MacIsaac 2000; Karatayev et al. 2015). Zebra and quagga mussels can form thick colonies on aquatic plants and hard and soft surfaces which may interfere with water supplies for drinking, irrigation, and hydropower (Ricciardi and MacIsaac 2000). Waterbodies occupied by invasive dreissenid mussels have been associated with changes in nutrient cycling, increased water clarity (Lowe and Pillsbury 1995), and improved deep-water dissolved oxygen (Li et al. 2018). The filter feeding abilities of these invasive mussels have been shown to deplete chlorophyll, particulate nutrients, and food availability for other aquatic species (Stefanoff et al. 2018). Nutrient dynamics may also be altered which can promote harmful algal

blooms. For example, Vanderploeg et al. (2001) demonstrated that *Microcystis*, a species of toxic phytoplankton, was selectively rejected by zebra mussels. Simultaneously, the same mussels were reducing levels of competing algae, resulting in more available nutrients in the water column fostered by *Microcystis* forming noxious cyanobacterial blooms. The effects of dreissenid mussels in the Great Lakes have been extensively studied (Lowe and Pillsbury 1995; Ricciardi and MacIsaac 2000; Strayer et al. 2019), but their impacts on smaller inland lakes in relation to algae blooms and climate are less understood.

This study aimed to assess changes in water quality, defined here as chlorophyll *a* (Chl *a*), TP, TN, and DOC concentrations, for lakes in the Great Lakes basin, and to identify how climate change and other anthropogenic pressures may be driving those changes. To do this, we assessed water quality trends over the past 40 years in the Laurentian Great Lakes watershed and examined how they were related to a diverse set of physical, chemical, and biological variables (Table 1). By considering a suite of variables that may be influencing water quality, we specifically addressed the following questions: (1) What are the temporal patterns and trends in water quality? and (2) Are climate, lake morphology, and invasive dreissenid species associated with changes in water quality?

## Methods

### Study area

Our study region includes lakes in Ontario and Wisconsin that are found within the Great Lakes basin or within neighboring watersheds. The Great Lakes basin is the largest freshwater system in the world, accounting for one-fifth of the freshwater surface on the planet (Van Der Leeden et al. 1990), and is home to millions of Canadian and U.S. residents who rely on the system for drinking water, recreation, industrial, and agricultural uses (Ducey et al. 2018). However, over the past few decades, lakes in this region have been experiencing increased anthropogenic pressures as the human population expanded from 46 to 52 million (Pendall et al. 2017). Land use around the small inland lakes in the Dorset, Turkey, Sudbury, and Experimental Lakes Area regions were limited to forestry and cottages, while lakes in the Wisconsin region experienced increases in urban development (Ducey et al. 2018). Lake Simcoe has experienced multiple pressures from increasing human activities over the past 200 years, including logging, damming, canal construction, agriculture, urban development, species invasion, and recently climate change (Hawryshyn et al. 2012). Further, Lakes Ontario, Erie, Huron, Superior, and Simcoe assimilate wastewater from numerous municipal water pollution control plants. Although our study includes only a small fraction of the tens of thousands of lakes in Ontario and Wisconsin, our study lakes represent a broad gradient of lake morphology and a range of

**Table 1.** Summary of key response variables to climate change for various physical, chemical, and biological parameters as well as any underlying mechanisms and climate drivers with explanations on external pressures and comments on our current understanding with advantages (A), and disadvantages (D).

| Lake properties     | Physical, chemical, and biological variables | Mechanisms  | Climate drivers                        | External pressures   | Comments   | References  |
|---------------------|--|---|--|--|--|---|
| Morphology          | Surface area                                 | Influenced by hydrology (drought and/or flood conditions), flow regulation (input/output and surface/ground waters) | PP, AT, EV                             | Surrounding catchment (land use change and development)  | Influences temperature effects, wind conditions and dilution capacity<br>A: Easily measured<br>D: Cannot draw many conclusion solely based on surface area             | Adrian et al. (2009), Moses et al. (2011),  |
|                     | Mean depth                                   | Dependent on water volume   | PP, EV                                 | Hydrological changes, wind mixing depending on depth   | A: Distribution, biomass and productivity of species<br>D: May affect turnover potential, depth may determine degree of deep-water mixing (possible anoxic conditions) | Newman and Reddy (1992), Li et al. (2018), Nöges (2009)   |
| Chemistry           | Phosphorus and nitrogen                      | Terrestrial runoff, anthropogenic inputs, internal reservoirs   | PP, AT, atmospheric deposition         | Current trophic status and nutrient availability, surrounding terrestrial catchment (farming, urbanization) and waste systems (sewage plants and treatments) yielding nutrients into lakes | A: Limiting nutrient for primary producers, regulates species composition and richness<br>D: Multiple stressors interacting, site-specific                             | Williamson et al. (2008), Dove and Chapra (2015), Baker et al. (2019)   |
|                     | DOC  | Relative contribution determined by allochthonous (from catchment) and autochthonous (within system) sources        | AT, PP, SR, CC, atmospheric deposition | Modified by acid deposition, ultraviolet radiation, fluxes of DOC from catchment (e.g., runoff), water residence time, trophic status  | A: Multiple effects on the physical, chemical, and biological lake processes<br>D: Highly determinant of transparency, dependent on local and system-specific factors  | Hudson et al. (2003), Hongve et al. (2004), Keller et al. (2008), Zhang et al. (2010), Williamson et al. (2015) |
| Community structure | Primary production                           | Ice-off/ice-on, stratification (intensity/duration),  | AT, PP, SR, CC                         | Characterized by interacting physical,   | A: Used as a measure of lake quality (e.g.,  | Vanderploeg et al. (2001), O'Reilly et al. (2015)   |

(Continues)

**Table 1.** Continued

| Lake properties | Physical, chemical, and biological variables | Mechanisms  | Climate drivers        | External pressures  | Comments   | References  |
|-----------------|--|---|------------------------|---|--|---|
|                 | Algal blooms                                 | nutrient loadings, trophic state, transparency<br>Period of stratification, nutrient loadings, trophic state, water residence time, lake mixing | AT, PP, SR, CC, WS     | chemical, and biological sources<br>Cultural eutrophication, climate change                       | Chl <i>a</i> concentrations)<br>D: Site-specific<br>A: Seasonal, easily detectable<br>D: Intensity and frequency highly dependent on when/where the sample was taken               | Paerl et al. (2016), Stefanoff et al. (2018)  |
|                 | Invasive species                             | Energy flow, nutrient dynamics, species assemblages, community structures   | AT                     | Anthropogenic change to environment, new networks of travel, transport and trades, climate change | A: Detect change over large special scale<br>D: Ability to predict outcomes of invasions are limited (generally negative)  | Lowe and Pillsbury (1995), Ackerman et al. (2001), Karatayev et al. (2015), Strayer et al. (2019) |
| Temperature     | Mean water temperature                       | Total lake heat budget  | AT, SR, PP, AV, CC     | Influenced by hydrology, ice phenology, morphology and transparency, climate change               | A: Easily and consistently measured, overall net temperatures of lake<br>D: Dependent on geomorphometric factors and mixing regimes, seasonal/interannual variability              | O'Reilly et al. (2015), Zhong et al. (2019)   |
|                 | Surface water temperature                    | Net heat energy input and losses across the air-water interface (latent and sensible heat fluxes)   | AT, WS, SR, PP, EV, CC | Nutrient loadings, turbidity, forest cover/state of riparian zone, transparency                   | A: Easily and consistently measured<br>D: Depends on seasonal variations (date of spring/fall overturn), lakes with different morphometric characteristics act in distinct manners | Sharma et al. (2008), O'Reilly et al. (2015)  |
|                 | Stratification                               | Seasonal turnover events, vertical distribution of heat   | AT, WS, PP             | Influenced by ice phenology, mixing regimes, warmer and longer summers                            | Dependent on thermal stability and influences community structures<br>A: Integrates climate changes of local region  | Stainsby et al. (2011), Richardson et al. (2017)  |

(Continues)

**Table 1.** Continued

| Lake properties | Physical, chemical, and biological variables | Mechanisms  | Climate drivers | External pressures  | Comments  | References   |
|-----------------|--|---|-----------------|---|---|--|
| Ice phenology   | Ice cover duration                           | Thawing in the spring and freezing in the fall, variations in ice structure, thickness, and decay | AT, SR, CC, PP  | Complex interplay of meteorological and limnological factors, influenced by latitude, interannual variability, climate change | D: Requires high-resolution spatial and temporal data<br>A: Sensitive indicator of climate (highly correlated to local weather)<br>D: Ambiguous definition of ice-on/ice-off, interannual variability | Moses et al. (2011), Adrian et al. (2009), Hewitt et al. (2018), Lopez et al. (2019) |

AT, air temperature; CC, cloud cover; EV, evaporation; P, precipitation; SR, solar radiation; WS, wind speed.

north temperate climates allowing the exploration of water quality patterns and drivers in diverse lake typologies.

### Data acquisition

#### Long-term temporal data

Long-term chemical and biological data were retrieved for a total of 45 sampling sites from a set of 36 lakes in Canada and the United States for periods  $\geq 20$  years between 1976 and 2016 (Table 2; Figs. S1, S2). Water quality variables included Chl *a* ( $\mu\text{g/L}$ ), TP ( $\mu\text{g/L}$ ), TN ( $\mu\text{g/L}$ ), and DOC (mg/L). Long-term data available for this region were amalgamated in this study resulting in an extensive dataset available for examining long-term changes. Data for each lake were consistently and continuously collected from year to year during the ice-free season (May–October), with all chemical and biological data consisting of surface water samples. Methods of data collection were consistent at each individual lake but may have differed among lakes depending upon the data source. We also acquired lake morphological characteristics, specifically surface area and mean depth, for each lake. Specific sampling details can be found in Center for Limnology 2012; desc.ca/; Hampton et al. 2017; iisd.org/ela/. We were not concerned about inconsistencies in sampling and analytical methods among lakes, as water quality trends were calculated for each lake individually. Data are available in a global chlorophyll and water quality database (Filazzola et al. 20207).

#### Historical meteorological data

Climate data were obtained from the Climate Research Unit (CRU) at the University of East Anglia (Harris et al. 2014). Monthly surface air temperature and precipitation means were downloaded from version 4.01 gridded timeseries dataset (covers the period 1901–2016) covering all land areas at a spatial resolution of  $0.5^\circ$ , where CRU data were specifically taken

for the latitude and longitude of each lake. Data were subsequently imported into *R* using the “ncdf4” package (<https://CRAN.R-project.org/package=ncdf4>; <http://www.R-project.org>). Using monthly climate means, we calculated seasonal means for each lake with seasons defined as winter (December–February), spring (March–May), summer (June–August), and fall (September–November).

### Data analysis

#### Temporal patterns in water quality

We quantified temporal patterns in each of the water quality timeseries by conducting linear, polynomial, and segmented regression models for each lake. Time was used as the predictor variable and Chl *a*, TP, DOC, and TN were response variables. Models with the lowest Akaike Information Criterion (AIC) were selected as the most parsimonious model. In cases where the segmented regression was the most parsimonious model, we subsequently calculated breakpoints in the long-term data. The segmented regression has been previously used in water quality studies to detect breakpoints, or abrupt shifts, in long-term datasets (Vanacker et al. 2015; Lopez et al. 2019). Segmented regression is based on the use of a continuous linear predictor represented by two or more straight lines (having different slopes) which are connected by a breakpoint (Vanacker et al. 2015). If significant, and represented as the best model fit, we reported the slope of the segmented lines before and after the year the data changed direction (breakpoint). We generated linear models using the function *lm*, polynomial models using the function *poly* (*x*, 2), and segmented regression models using the package “segmented,” function “segmented” (Muggeo 2008). All statistical tests were carried out in the statistical program *R* Version 3.4.4 (<http://www.R-project.org>).

### Temporal trends in water quality

For each lake, we calculated a Sen slope (Sen 1968) to measure trends in TP, TN, DOC, Chl *a*, air temperature, and precipitation between 1976 and 2016. Sen slopes analysis is a nonparametric method that calculates the median of all pairwise slopes within a dataset to statistically test trends. Sen slopes are resistant to outliers and nonnormality and have been used in previous work to assess trends in water quality (O'Reilly et al. 2015; Rose et al. 2016; Strock et al. 2017). Sen slope values and their statistical significance were calculated in R using the package “openair” (Carslaw and Ropkins 2012; <http://www.R-project.org>). Missing data, owing to instances where some observational years were not sampled, made up < 5% of all data points. In these cases, missing data were imputed using a Multiple Imputation by Chained Equation approach using the “mice” package (Van Buuren and Groothuis-Oudshoorn 2011) to obtain a full dataset. The Sen slopes calculated for each lake over the selected timeframe were subsequently used as the response variables for investigating the associations between water quality and climate, lake morphology, and dreissenid species (dreissenid occurrence exclusively in small inland lakes). End sampling years ranged between 2011 and 2016 allowing us to compare timeseries data ending in the same decade.

Following our quantification of water quality trends by lake, we separated lakes into two groupings with “the Great Lakes” comprising Lake Ontario, Lake Huron, Lake Erie, and Lake Superior, and “inland lakes” comprising all remaining smaller inland lakes. This separation was implemented because large and small lakes behave quite differently owing to their difference in water volume (Moses et al. 2011). For example, Lake Ontario is the smallest of the Great Lakes, but was larger than all of the small inland lakes in our dataset combined, and therefore we expected it to exhibit different limnological responses (Beeton 1984). We compared the rate of change for the water quality of large vs. small lakes by assessing TP, TN, DOC, and Chl *a* Sen slope values for each grouping using the Mann–Whitney (MW) test. The nonparametric MW test is a common method to determine if there is a difference in medians between two groups when the data are not normally distributed (Ruxton 2006). A transparent workflow of all analyses in this study can be found online (<https://afilazzola.github.io/ChlorophyllTimeseries/>).

### Drivers of water quality trends

We investigated drivers of water quality trends in the Great Lakes and small inland lakes using a redundancy analysis (RDA) implemented in the *rda* function found in the “vegan” package for R (<https://CRAN.R-project.org/package=vegan>; <http://www.R-project.org>). RDA (package *vegan*, function *rda*) is a direct gradient ordination analysis which summarizes the linear relationship between a multivariate set of response variables to explanatory variables. We tested the significance of ordination axis using the broken stick model

(Peres-Neto et al. 2003; Legendre and Legendre 2012). We used an RDA rather than other ordination techniques, such as a Canonical Correspondence Analysis, because the response variables had a linear distribution that was identified from a detrended correspondence analysis with a gradient axis of less than 2 and an adjusted  $R^2$  could be calculated for each axis (Legendre and Legendre 2012). The Sen slopes for TP, TN, DOC, and Chl *a* calculated for each lake were used as the response variables. The data were standardized to provide a comparable unitless scale to compare lake morphology with water quality and climate variables. Explanatory variables for both RDAs included morphological characteristics (surface area, mean depth, and elevation) and climatic variables (winter, spring, summer, and fall temperature and precipitation), whereas dreissenid mussel invasion was only included for the small inland lakes RDA as all the Great Lakes are already invaded. Although the abundance and invasion history of dreissenids differs among the lakes, we have only included occurrence of dreissenid invasion as a predictor variable in the RDA. Prior to analyses, we assessed potential multicollinearity between seasonal climate and morphometric variables using a Spearman rank correlation matrix in R (package *corrplot*). Climate and morphometric variables that were highly correlated ( $r > 0.7$ ) were removed from the RDA.

## Results

### Temporal patterns in water quality

We calculated 60 significant segmented regression models identified for 25 lakes in the Laurentian Great Lakes region (Fig. 1; Table S2). Moreover, significant linear and polynomial models were developed for 11 and 8 lakes, respectively. Although Chl *a* has declined over the complete timeseries, we generally observed significant breakpoints in Chl *a* in the 1990s to the mid-2000s when Chl *a* began to increase for the Great Lakes and four inland lakes. For example, lakes in Muskoka, Ontario, and Wisconsin had significant breakpoints in Chl *a* between 1992 and 2006 after which Chl *a* concentrations began to increase. In contrast, four lakes exhibited decreasing trends after significant breakpoints between 1990 and 2008.

Similarly, TP concentrations in our study lakes have declined over the full timeseries, but segmented regressions revealed numerous significant breakpoints in TP in Ontario and Wisconsin in the 1990s to mid-2000s following which TP began to increase. For example, between 1990 and 2004 increases were observed after an abrupt shift in Lake Erie and Huron in addition to seven inland lakes. On the other hand, four lakes in northern Wisconsin began to experience negative TP concentrations after breakpoints in the late 2000s. Further for TN, both increasing and decreasing patterns were detected after significant breakpoints in the Laurentian Great Lakes region.

**Table 2.** Lake characteristics and data source of 36 lakes in the Laurentian Great Lakes watershed, with water chemistry and chlorophyll variables (with standard deviation in parentheses) being mean values for the study period.

| Lake  | Latitude, longitude<br>(decimal degrees) | Lake surface<br>area (ha) | Mean<br>depth (m) | Maximum<br>depth (m) | Elevation (m<br>above sea level) | TP*<br>( $\mu\text{g/L}$ ) | TN* ( $\mu\text{g/L}$ ) | DOC*<br>(mg/L) | Chl $\sigma^*$<br>( $\mu\text{g/L}$ ) | Sampling<br>year | Source<br>presence/<br>absence (P/A) |
|---|--|---------------------------|-------------------|----------------------|----------------------------------|----------------------------|-------------------------|----------------|---------------------------------------|------------------|--------------------------------------|
| Dorset, Ontario,<br>Canada                    |  |                           |                   |                      |                                  |                            |                         |                |                                       |                  |                                      |
| Blue Chalk                                    | 45.20, -78.94                            | 52.4                      | 8.5               | 23                   | 344                              | 6.1(0.6)                   | 204.1(18.9)             | 2(0.2)         | 1.8(0.4)                              | 1981–2013        | A                                    |
| Chub  | 45.30, -79.23                            | 34.4                      | 8.9               | 27                   | 344                              | 8.6(0.9)                   | 334.9(31.3)             | 5.4(0.8)       | 2.9(0.9)                              | 1984–2013        | A                                    |
| Crosson                                       | 45.08, -79.04                            | 56.7                      | 9.2               | 25                   | 332                              | 9.7(1.4)                   | 343(29.1)               | 4.6(0.5)       | 4(3.1)                                | 1981–2013        | A                                    |
| Dickie  | 45.15, -79.09                            | 93.6                      | 5                 | 12                   | 341                              | 9.7(1.4)                   | 343(29.1)               | 4.6(0.5)       | 4.3(2.0)                              | 1981–2013        | A                                    |
| Harp  | 45.38, -79.14                            | 71.4                      | 13.3              | 37.5                 | 327                              | 9.4(1.5)                   | 323.1(21.5)             | 5.4(0.7)       | 2.6(0.9)                              | 1981–2013        | A                                    |
| Honey   | 45.13, -79.10                            | 21.4                      | 3.3               | 5.8                  | 346                              | 6(0.7)                     | 261(23.3)               | 3.4(0.6)       | 2.2(0.6)                              | 1981–2013        | A                                    |
| Plastic                                       | 45.18, -78.82                            | 32.1                      | 7.9               | 16.3                 | 379                              | 4.9(1)                     | 197(27.5)               | 2.3(0.3)       | 2(0.6)                                | 1979–2013        | A                                    |
| Red Chalk East                                | 45.19, -78.94                            | 13                        | 5.7               | 34.3                 | 45.19                            | 6.6(0.8)                   | 305(22)                 | 3.2(0.4)       | 2.6(0.7)                              | 1984–2013        | A                                    |
| Red Chalk Main                                | 45.19, -78.95                            | 44.1                      | 16.7              | 38                   | 343                              | 4.7(0.4)                   | 273.1(18.2)             | 2.8(0.4)       | 2.1(0.7)                              | 1981–2013        | A                                    |
| Wisconsin, USA                                |  |                           |                   |                      |                                  |                            |                         |                |                                       |                  |                                      |
| Center for limnology<br>(NTL LTER)            |  |                           |                   |                      |                                  |                            |                         |                |                                       |                  |                                      |
| Allequash                                     | 46.04, -89.62                            | 1.6                       | 2.9               | 8                    | 500                              | 16.3(4.6)                  | 301(51.6)               | 4.2(0.3)       | 12.5(8.6)                             | 1986–2013        | A                                    |
| Big Muskellunge                               | 46.02, -89.61                            | 3.6                       | 7.5               | 21.3                 | 500                              | 9.7(4.8)                   | 345.2(56.4)             | 3.9(0.2)       | 3.8(1.3)                              | 1986–2013        | A                                    |
| Crystal                                       | 46.00, -89.61                            | 0.4                       | 10.4              | 20.4                 | 500                              | 7.6(2.6)                   | 181.8(28.7)             | 2(0.2)         | 3.5(1)                                | 1986–2013        | P                                    |
| Fish  | 43.29, -89.65                            | 0.8                       | 6.6               | NA                   | 18.9                             | 18(4.6)                    | 812.3<br>(154.2)        | 8(1.9)         | 6.9(3)                                | 1996–2013        | A                                    |
| Mendota                                       | 43.10, -89.41                            | 39.6                      | 12.8              | 25.3                 | 260                              | 47(19.1)                   | 996.1<br>(204.5)        | 5.9(1)         | 7.4(3)                                | 1995–2013        | P                                    |
| Monona  | 43.06, -89.36                            | 13.6                      | 8.2               | 22.5                 | 260                              | 45.6<br>(10.3)             | 880.6<br>(131.8)        | 6.1(0.8)       | 8.8(3.8)                              | 1995–2013        | P                                    |
| Wingra  | 43.05, -89.43                            | 1.4                       | 2.7               | 6.7                  | 260                              | 47.3<br>(20.1)             | 868(138.8)              | 6.4(1.5)       | 13.6(5.2)                             | 1996–2013        | A                                    |
| Sparkling                                     | 46.01, -89.7                             | 0.6                       | 10.9              | 20                   | 500                              | 7(2.3)                     | 229.6(39.7)             | 3.2(0.2)       | 3.8(1.3)                              | 1986–2013        | A                                    |
| Trout   | 46.03, -89.67                            | 15.7                      | 14.6              | 35.7                 | 500                              | 6.1(1.9)                   | 209.3(46.7)             | 3.1(0.2)       | 3.1(0.8)                              | 1986–2013        | A                                    |
| Simcoe, Ontario,<br>Canada                    |  |                           |                   |                      |                                  |                            |                         |                |                                       |                  |                                      |
| Center for<br>Environmental<br>Research       |  |                           |                   |                      |                                  |                            |                         |                |                                       |                  |                                      |
| Simcoe  | 44.44, -79.17                            | 722                       | 14.6              | 42                   | 219                              | 13.4(3.8)                  | 421(52.4)               | 4.1(0.3)       | 1.1(0.7)                              | 1982–2011        | P                                    |
| Turkey Lakes<br>Watershed,<br>Ontario, Canada |  |                           |                   |                      |                                  |                            |                         |                |                                       |                  |                                      |
| Environment and<br>Climate Change<br>Canada   |  |                           |                   |                      |                                  |                            |                         |                |                                       |                  |                                      |
| Batchawana<br>North                           | 47.07, -84.39                            | 5.9                       | 3.9               | 11.3                 | 370                              | 5.6(1.6)                   | 420(87.1)               | 4.1(0.4)       | NA                                    | 1982–2014        | A                                    |
| Batchawana<br>South                           | 47.06, -84.38                            | 5.8                       | 3.3               | 10.9                 | 370                              | 6.1(2)                     | 395.8(65.1)             | 4.8(0.5)       | NA                                    | 1982–2014        | A                                    |

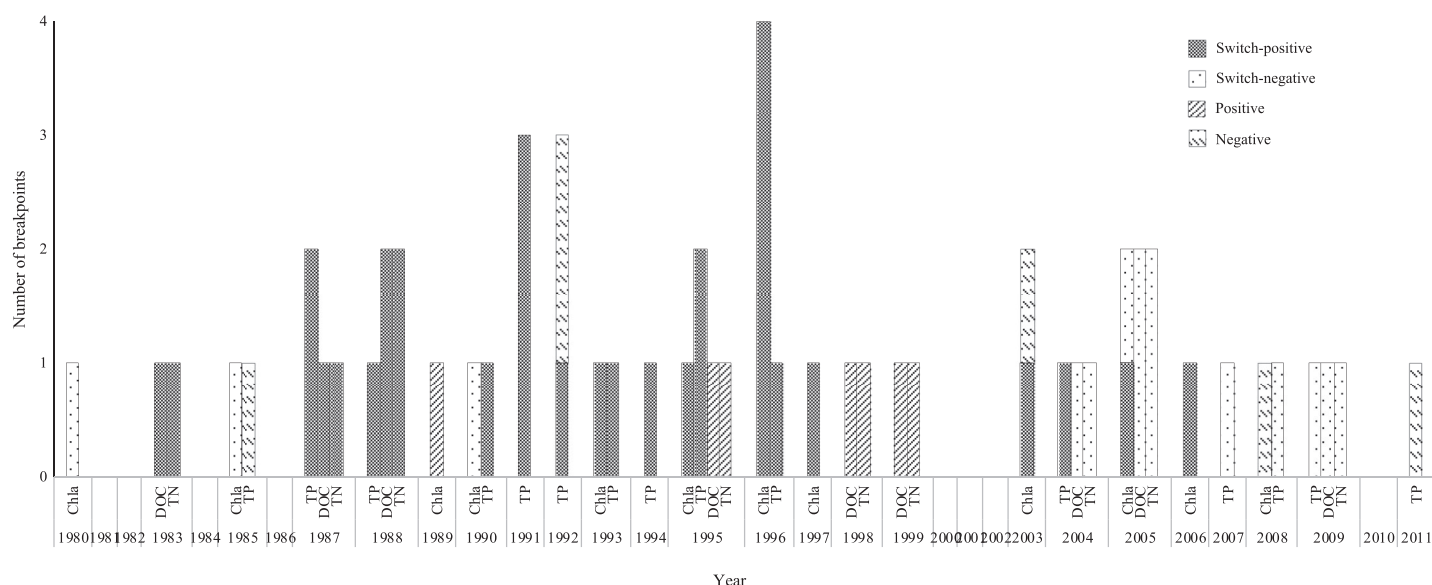
(Continues)

**Table 2.** Continued

| Lake   | Latitude, longitude<br>(decimal degrees) | Lake surface<br>area (ha) | Mean<br>depth (m) | Maximum<br>depth (m) | Elevation (m<br>above sea level) | TP*<br>( $\mu\text{g/L}$ ) | TN* ( $\mu\text{g/L}$ ) | DOC*<br>(mg/L) | Chl $\alpha^*$<br>( $\mu\text{g/L}$ ) | Sampling<br>year | Source/Dreissenids<br>presence/<br>absence (P/A)          |
|--|--|---------------------------|-------------------|----------------------|----------------------------------|----------------------------|-------------------------|----------------|---------------------------------------|------------------|---|
| Little Turkey                                  | 47.04, -84.41                            | 19.2                      | 6                 | 13                   | 370                              | 5.4(1.8)                   | 505.9<br>(119.8)        | 3.9(0.5)       | NA                                    | 1982–2014        | A   |
| Turkey   | 47.05, -84.42                            | 52                        | 12.2              | 37                   | 370                              | 5.4(2.7)                   | 430.1(76)               | 3.6(0.5)       | NA                                    | 1982–2014        | A   |
| Wishart  | 47.05, -84.4                             | 19.2                      | 2.2               | 4.5                  | 370                              | 8.9(15.9)                  | 429.7<br>(114.4)        | 4.5(0.5)       | NA                                    | 1982–2014        | A   |
| Sudbury, Ontario,<br>Canada                    |  |                           |                   |                      |                                  |                            |                         |                |                                       |                  | Ministry of<br>Environment,<br>Conservation and<br>Parks  |
| Aurora<br>Whitepine                            | 47.38, -83.63                            | 84.3                      | 7                 | 21.3                 | 422                              | 4(1.5)                     | 165.8(33)               | 3(0.6)         | 0.001(0)                              | 1990–2016        | A   |
| Clearwater                                     | 46.37, -81.05                            | 75.9                      | 8.4               | 21.5                 | 267                              | 5.1(7.8)                   | 218.7(48)               | 2.3(1)         | 0.002(0)                              | 1991–2016        | A   |
| Sans Chabre                                    | 46.72, -81.12                            | 14.5                      | 5.6               | 15                   | 385                              | 9.7(15.2)                  | 242.4(69.3)             | 2.7(0.5)       | 0.002(0)                              | 1988–2016        | A   |
| Laurentian Great<br>Lakes, Canada/<br>USA      |  |                           |                   |                      |                                  |                            |                         |                |                                       |                  | Center for<br>Environmental<br>Research                   |
| Erie   | 42.13, -83.11                            | 25,700                    | 19                | 64                   | 173                              | 24.7(11)                   | 539.7<br>(108.2)        | 2.1(0.2)       | 2.4(1.8)                              | 1977–2011        | P   |
| Huron  | 43.75, -81.73                            | 59,565                    | 59                | 229                  | 117                              | 11.2(8.3)                  | 529.5(96.7)             | 1.6(0.1)       | 1.2(0.9)                              | 1976–2011        | P   |
| Ontario  | 44.15, -77.39                            | 19,009                    | 86                | 244                  | 74                               | 13(6.6)                    | 484.2(68)               | 2.1(0.1)       | 1.3(0.8)                              | 1976–2011        | P   |
| Superior                                       | 48.48, -89.16                            | 82,097                    | 149               | 406                  | 180                              | 4.8(1.5)                   | 440.6(27.9)             | 1.7(0.1)       | 1.1(0.3)                              | 1980–2011        | P   |
| Experimental Lakes<br>Area, Ontario,<br>Canada |  |                           |                   |                      |                                  |                            |                         |                |                                       |                  | International Institute<br>for Sustainable<br>Development |
| 114  | 49.67, -93.76                            | 12.1                      | 1.7               | 5                    | 418                              | 14.2(3.6)                  | 655.3<br>(181.9)        | 8(1.2)         | 5.4(3)                                | 1978–2012        | A   |
| 224  | 49.69, -93.72                            | 25.9                      | 11.6              | 27.4                 | 409                              | 7.7(1.5)                   | 260.5(33.7)             | 3.1(0.4)       | NA                                    | 1982–2012        | A   |
| 373  | 49.74, -93.72                            | 27.3                      | 11                | 20.8                 | 424                              | 8.8(2.1)                   | 272.5(29.7)             | 4(0.2)         | NA                                    | 1983–2013        | A   |
| 442  | 49.78, -93.82                            | 16                        | 9                 | 17.8                 | 411                              | 14.7(3)                    | 469.4(67)               | 6.7(0.3)       | NA                                    | 1990–2012        | A   |
| 239  | 49.66, -93.72                            | 54.3                      | 10.5              | 30.4                 | 386                              | 7.3(1.8)                   | 316.2(34.6)             | 6.6(0.6)       | NA                                    | 1969–2012        | A   |

\*Ice-free means (for available data between 1976 and 2016).





**Fig 1.** The number and timing of abrupt shifts from 1980 to 2011 identified by segmented regression analysis in water quality. The change in pattern between the segmented lines before and after the breakpoint were described as negative (negative slope becoming more negative), switch-negative (positive slope becoming negative), positive (positive slope becoming more positive), and switch-positive (negative slope becoming positive).

**Table 3.** Summary of mean Sen slope values for chemical and biological variables by region (with sample size in parentheses). Lakes with < 20-year time series were not included in total mean values.

| Water quality variable                                 | Dorset       | ELA         | Great Lakes* | Lake Simcoe* | Sudbury                     | Turkey Lakes                | Wisconsin     |
|--|--------------|-------------|--------------|--------------|-----------------------------|-----------------------------|---------------|
| Mean TP ( $\mu\text{g L}^{-1}/\text{year}$ )           | -0.04(n = 9) | 0.03(n = 3) | -0.27(n = 6) | -0.1(n = 3)  | 0(n = 3)                    | -5.86 <sup>-5</sup> (n = 5) | -0.05(n = 5)  |
| Mean TN ( $\mu\text{g L}^{-1}/\text{year}$ )           | -0.28(n = 9) | 1.17(n = 3) | -0.25(n = 7) | 0.32(n = 3)  | 7.77 <sup>-4</sup> (n = 3)  | 7.48 <sup>-4</sup> (n = 5)  | -0.58(n = 5)  |
| Mean DOC (mg L <sup>-1</sup> /year)                    | 0.04(n = 9)  | 0.01(n = 3) | —            | 0.02(n = 3)  | 0.06(n = 3)                 | 7.91 <sup>-4</sup> (n = 5)  | -0.001(n = 5) |
| Mean Chl <i>a</i> ( $\mu\text{g L}^{-1}/\text{year}$ ) | -0.02(n = 9) | —           | -0.05(n = 6) | -0.04(n = 3) | -2.05 <sup>-5</sup> (n = 3) | —                           | -0.005(n = 5) |

Dark gray indicates increasing rate of change; light gray indicates decreasing rate of change; and — indicate no significant change or not enough data available.

\*Region where individual lakes had numerous sampling sites.

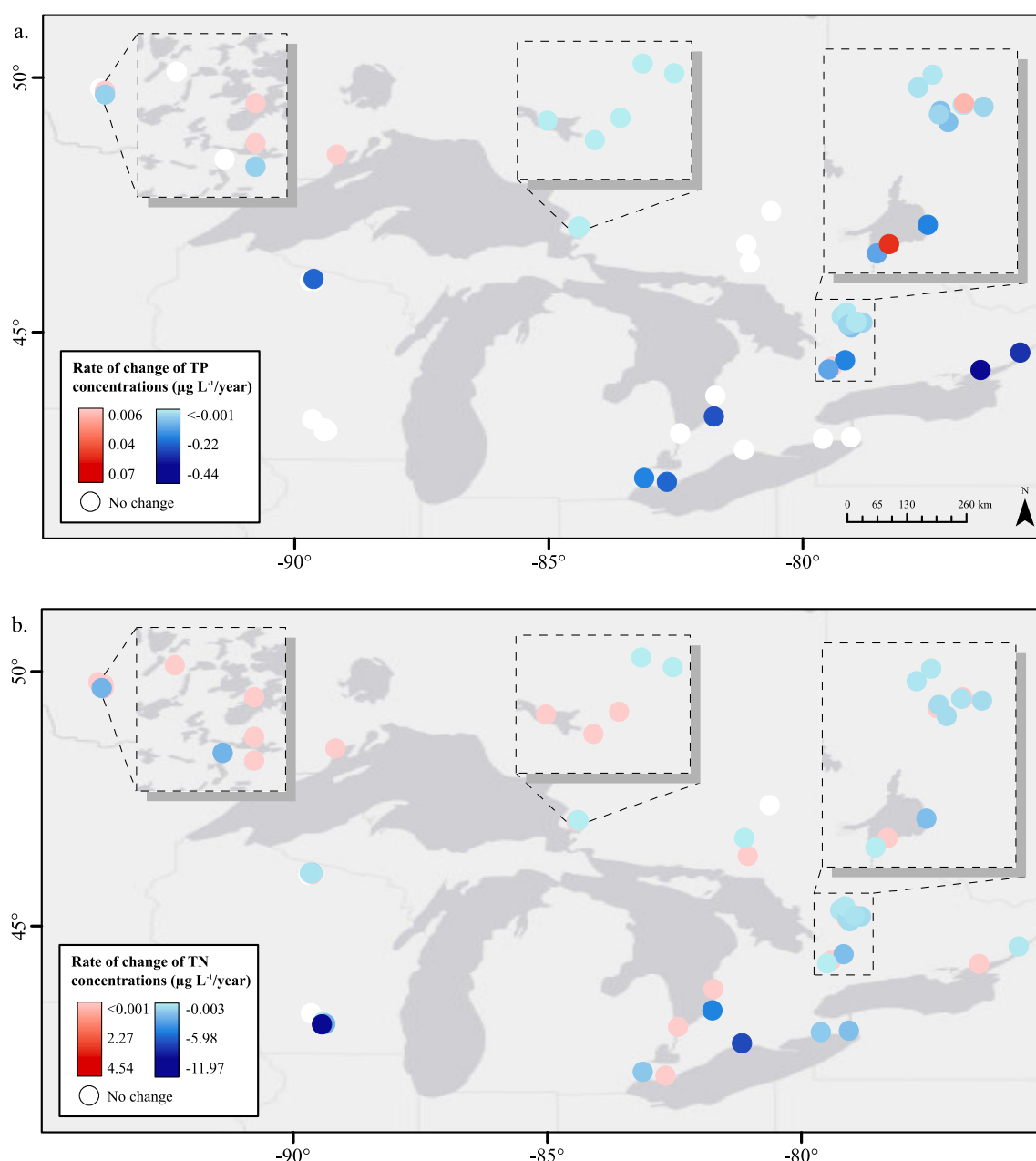
Generally, DOC has increased over time in our study lakes. Eleven lakes in Wisconsin, Dorset, Sudbury, ELA, and the Turkey Lakes Watershed all demonstrated significant breakpoints in DOC, such that after 1983–1999, DOC increased more rapidly. However, for northern lakes in Wisconsin and Heney Lake in Dorset, DOC began to decline after a significant breakpoint between 2004 and 2009. It is important to note that timeseries data for DOC for the Great Lakes did not meet the criteria for breakpoint analysis as we could only acquire data for 18 year periods.

### Temporal trends in water quality

In the Laurentian Great Lakes, TP, and Chl *a* concentrations decreased over time and DOC increased over time (Table 3; Fig. 2). Some of the strongest decreases in TP were observed in the Great Lakes, whereas the more northern inland lakes experienced a less intense decrease

in TP (Fig. 2a). The response of TN was mixed, with increases and decreases at various magnitudes (Fig. 2b). DOC showed an increasing trend throughout the landscape, however, there were no significant trends in DOC in the Great Lakes or lakes in the Turkey Lakes Watershed (Fig. 2c). Trends in Chl *a* decreased overall, except for some lakes in the Wisconsin region that increased (Fig. 2d). Over the entire Great Lakes, watershed temperature trends increased throughout all seasons. In most regions, winter precipitation trends increased and spring precipitation decreased. Climatic trends by region can be found in Table S1.

The rates of change in TP and Chl *a* were significantly different in the Great Lakes than in small inland lakes (MW test:  $p_{\text{TP}} = 0.01$ ,  $p_{\text{Chl } a} = 0.03$ ). TP and Chl *a* decreased at a faster rate in the Great Lakes ( $\bar{X}_{\text{TP}} = -0.25$ ,  $\bar{X}_{\text{Chl } a} = -0.2$ ) than in inland lakes ( $\bar{X}_{\text{TP}} = -0.05$ ,  $\bar{X}_{\text{Chl } a} = -0.02$ ).

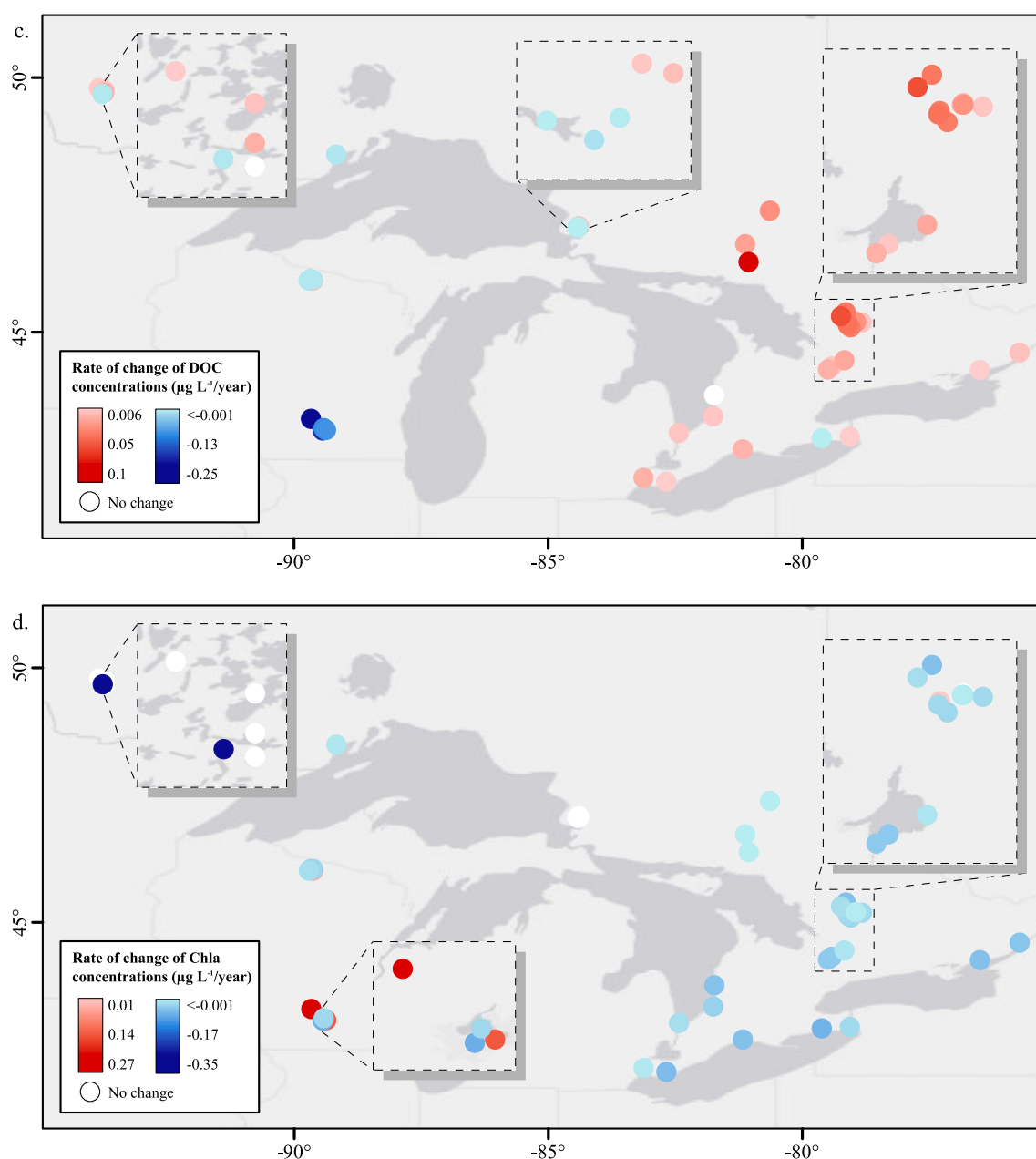


**Fig 2.** Lake specific trends in (a) TP, (b) TN, (c) DOC, and (d) Chl *a* concentrations during the study period (1976–2017) using Sen regression values. Positive temporal trends are depicted using shades of red and negative trends are depicted using shades of blue. A stronger shade in either trend direction denotes a faster trend regionally. White circles indicate no significant trends or no data available.

### Drivers of trends in water quality

The RDA explained 73.1% of the variation in changes in water quality over time for the Great Lakes (Fig. 3a). A broken-stick model revealed that the first RDA axis explained more variation than expected by chance alone; the first axis explained the most variation at 36.2%, and the second axis explained an additional 24%. Trends in TP were associated with RDA Axis 1, whereas Chl *a*, DOC, and TN were associated with RDA2 (Fig. 3a). In the Great Lakes, wetter springs were associated with

increases in Chl *a*, whereas higher DOC was correlated to warmer spring and winter temperature. The percentage of variation explained by the RDA for small inland lakes was 45.6% (Fig. 3b,c). The broken-stick model revealed that the first two RDA axes were significant; the first axis accounted for most of the variation (29%) and the second axis accounted for 11.7% of the variance. Trends in TP and DOC were associated with RDA1, whereas trends in TN and Chl *a* were associated with RDA2 (Fig. 3b). The presence of dreissenids combined with

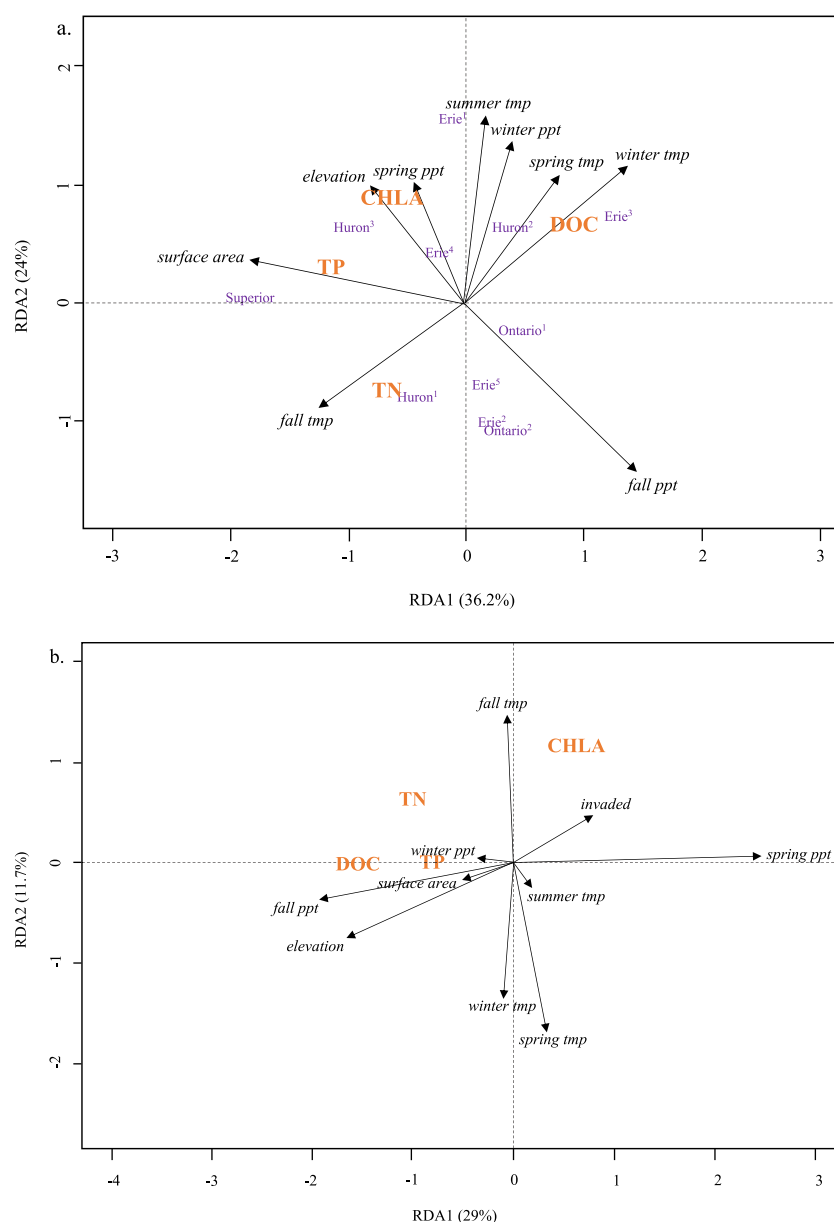
**Fig 2** (Continued)

cooler winter and spring temperatures was associated with increasing Chl *a* in inland lakes. Lower altitude inland lakes receiving less fall precipitation were associated with decreases in DOC and TP. TN was not influenced by climate, lake morphology, or dreissenid invasion in either the Great Lakes or small inland lakes in this study region.

## Discussion

Our study provided an overview of the temporal trends, patterns, and drivers of water quality for north temperate lakes

within the Laurentian Great Lakes region. In this study, we examined 20 to 40-year time series from 36 North American study lakes with a broad range of morphometric characteristics to document how multiple environmental stressors have affected water quality. We found that water quality has changed over time, with increasing DOC levels in most lakes. TP and Chl *a* were mostly decreasing in the Great Lakes region, although Chl *a* has been increasing more recently. Climate, temperature and precipitation, and lake morphology were all found to be important drivers for DOC and Chl *a* concentrations in the Laurentian Great Lakes watershed. Our results show that there have been



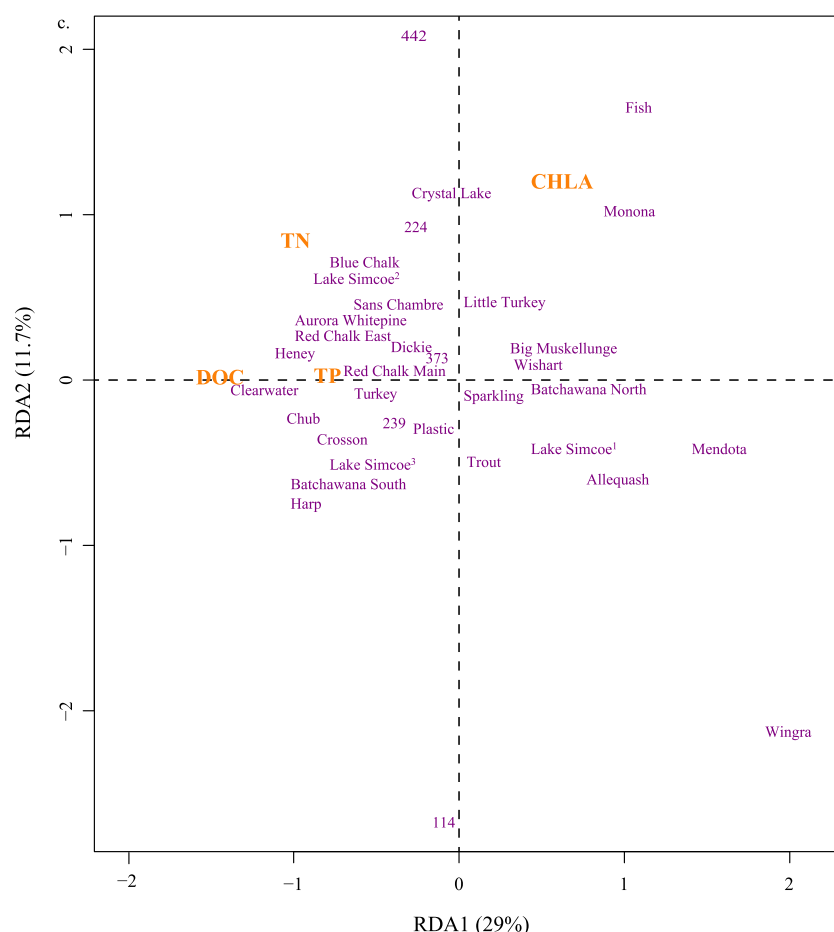
**Fig 3.** Redundancy analysis (RDA) of trends in lake water quality over time for (a) the Great Lakes and (b) inland lakes. Only the first two RDA axes are shown which explain 80.1% of the variation for the Great Lakes and 55.4% of the variation for small inland lakes. Climate variables are italicized and represented by arrows, water quality data are colored in orange, and lake name is colored in purple. (c) Magnified portion of the RDA of inland lakes only depicting ordination of lakes (purple) and water quality data (orange). Superscripts (1–5) denote different sampling locations within the same lake. ppt, precipitation; tmp, temperature.

significant changes in water quality over time which can potentially influence key limnological processes and ecosystem services.

### Temporal trends and patterns in water quality over the past 40 years

Although TP concentrations were generally declining linearly over the complete time series, clear breakpoints in the 1990s and 2000s suggested that TP had once again started

increasing in the Great Lakes. Numerous sampling locations within the Great Lakes could have experienced increases in TP for several reasons, including the decline in dreissenid densities (Kovalenko et al. 2018), increased air temperatures (O'Reilly et al. 2015; Zhong et al. 2019), and increased urban land cover (Croft-White et al. 2017). Similar to breakpoints in the Great Lakes, some northern inland lakes were also experiencing increased TP concentrations following an abrupt shift; however, stressors affecting local catchments and



**Fig 3** (Continued)

meteorology are more likely to be the source of change (Quinlan et al. 2008). When analyzing linear Sen regressions, we observed significant declines in TP concentrations for 20 of our study lakes over time. TP decreased in Lakes Erie, Huron, and Ontario at a significantly faster rate than in small inland lakes coinciding with multiple initiatives that targeted the reduction of TP entering the Great Lakes over the past four decades, including the 1972 Great Lakes Water Quality Agreement (De Pinto et al. 1986; Baker et al. 2019). Many smaller lakes, regardless of human activity (e.g., Dickie and Harp Lakes having high cottage densities while Plastic Lake has none) or undisturbed forested watersheds (e.g., the Turkey Lakes), also experienced decreasing trends in TP. Eimers et al. (2009) found that lower TP concentrations in streams during the spring resulted in decreased TP exports to lakes found in the Dorset region suggesting that changes in TP exports may be governed by terrestrial processes releasing P prior to and during snowmelt (Palmer et al. 2011). Consequently, the causes and consequences of long-term TP change in this region are uncertain and should remain the focus of future research.

Nutrient loading and climate change both affect chlorophyll production in lakes (Richardson et al. 2018; Shuvo, O'Reilly et al., in review). Significant segmented regressions in Chl *a* identified breakpoints in the 1990s to the mid-2000s after which Chl *a* began to increase. Recent increases in Chl *a* may be a result of this region being a warming “hotspot” (O'Reilly et al. 2015) as well as a decadal regime shift from a cold to a warm state in 1997/1998 (due to a shift in the Pacific Decadal Oscillation toward its negative phase) (Van Cleave et al. 2014; Zhong et al. 2016). When examining Sen slopes over time, we observed decreases in Chl *a* at 30 study sites across the entire study region, which may be explained by improved waste water treatment and aquatic mitigation measures that have contributed to lower TP loadings in the region (Dove and Chapra 2015). However, chlorophyll levels can be spatially and temporally heterogeneous. For example, despite the decreasing linear trends in Chl *a* in Lake Huron over the study period, there have been several reports of toxic phytoplankton blooms in select locations, resulting in temporary high concentrations of Chl *a* in some locations (Vanderploeg et al. 2001).

In the Laurentian Great Lakes region, changing climate and hydrologic conditions have been suggested as drivers explaining extensive increases in DOC and brownification of lakes (Williamson et al. 2015). After performing segmented regression analysis, we found that seven lakes, in ELA, Dorset, Sudbury, and Turkey Lakes region, experienced even faster positive trends in DOC following a significant breakpoint in the data before the year 2000. Further, we found that 17 of our study lakes showed significant increasing linear trends in DOC, which was also consistent with previous findings reporting increasing DOC in lakes in the regions of Sudbury, Dorset, ELA, and in numerous lakes throughout Quebec (Keller et al. 2008; Zhang et al. 2010; Couture et al. 2012). Keller et al. (2008) demonstrated that higher temperatures may increase DOC export from catchments substantially given that the supply of DOC in lakes generally reflects temperature related processes of organic matter production and decomposition. In combination with warming temperatures, trends in DOC may depend on hydrological conditions. For example, Hongve et al. (2004) found that altered hydrological pathways, during periods of increased or intensive rainfalls, may increase DOC concentrations by flushing accumulated DOC from organic-rich matter from the upper soil. Further, changes in DOC may also be linked to a complex combination of regional variables such as longer ice-free periods, a reduction in solar radiation, or decreasing trends in precipitation sulfate concentrations (Zhang et al. 2010; Couture et al. 2012; Marcarelli et al. 2019).

We observed a considerable amount of temporal variation in TN trends and patterns over the study period. Both increasing and decreasing trends and numerous breakpoints in TN may have corresponded to changes in surrounding terrestrial catchments. For example, trends in non-point sources of nitrogen, specifically agricultural fertilizer use (Williamson et al. 2008), and point sources from human waste water treatments (Williamson et al. 2008) would affect TN in surface waters. TN levels in smaller, less disturbed lakes are influenced by the extent of surrounding wetlands (Gren 1995).

## Drivers of water quality trends

### *Impact of lake morphology on water quality trends*

Lake morphology, specifically surface area and mean depth, can alter the primary mechanisms by which climate and other stressors affect water quality, and must be taken into consideration when making broad statements about a lake's ability to integrate its surrounding environment (Adrian et al. 2009). Generally, lakes with smaller surface areas may experience increased temperatures, longer ice-free periods, and richer algal biomass (Moses et al. 2011). Lake depth has been shown to play an integral role in transparency and Chl *a* concentration as deeper lakes have a higher dilution potential making it possible for these lakes to be clearer with lower nutrient and Chl *a* levels (Nöges 2009). Shallow lakes can mix more easily during wind events, allowing more sediment

resuspension, which have been shown to act as a source of nutrients for phytoplankton growth (Nöges 2009).

### *Great Lakes water quality*

We found that increased DOC concentrations were positively associated with warming seasonal temperatures in the Great Lakes, similar to earlier studies which demonstrated that warmer geographic regions in the Northern hemisphere were more likely to experience accelerated changes in DOC (Weyhenmeyer and Karlsson 2009). In our study, winter temperature emerged as a significant driver governing DOC concentrations in large lakes as documented previously (Karlsson et al. 2008).

Our results showed a significant decline in TP in Lake Erie, Huron, and Ontario which parallels previous patterns in the Great Lakes (Dove and Chapra 2015). Initial declines in TP levels in the Great Lakes were brought about due to mandated changes in discharges, sewage treatments improvements, and phosphate reductions in detergents (Dove and Chapra 2015). Subsequent declines were hypothesized to have originated from the dreissenids filtering lake water after colonization (Ackerman et al. 2001). For example, similar to our findings, Dove and Chapra (2015) found declines in TP in Lake Erie and Ontario over a 42-year period to be 8 and 11  $\mu\text{g/L}$ , respectively.

### *Small inland lake water quality*

We observed that fall precipitation was strongly and positively associated with long-term trends in DOC in small inland lakes which also influenced TP and TN (Fig. 3b). An increase in precipitation is anticipated to increase export of terrestrial DOC into an aquatic system, as DOC mass export and runoff are tightly coupled (Dillon and Molot 2005). However, as shown in inland lakes in the Great Lakes region, increased spring precipitation did not correspond to an increase in lake DOC (Fig. 3b). In early spring, when soils and peat are still frozen, heavy precipitation may fail to export DOC locked in frozen soil and wetland and in fact may dilute lake DOC to some extent (Hudson et al. 2003; Heinz and Zak 2018). Not all of the small lakes in our dataset followed the broad patterns we found for Chl *a*. Interestingly, our analysis showed that Chl *a* increases were common in the most southern and dreissenid invaded lakes in Wisconsin. It has been established that dreissenids are effective ecosystem engineers, and have altered the cycling of nutrients in the near-shore zone creating a new littoral material processing function termed "the nearshore shunt" (Lowe and Pillsbury 1995; Stefanoff et al. 2018). Moreover, Chl *a* concentrations in southern Wisconsin may have simply been an outcome of landscape interactions. Regions such as Madison, WI, are highly developed and increased TP level may have led to more Chl *a* in Wisconsin lakes, despite there being an overall decreasing trend.

The small lakes in southern Wisconsin (Mendota, Monona, Wingra, and Fish Lake) exhibited increased variability in water



quality variables, specifically Chl *a*, compared to all other small lakes in the Great Lakes region. On a spatial basis, this might partly be explained by catchment areas being more heavily populated in southern geographic regions (when compared to the five northern Wisconsin lakes). However, since specific weather conditions vary widely between regions, the southern Wisconsin lakes may act as sentinels for future responses of degraded water quality and increased Chl *a* as these lakes tend to experience warmer and wetter climates relative to our other study sites.

### Implications and future directions of changing water quality

As shown in our study and many others, freshwater resources are experiencing significant changes with extensive implications for human and ecosystem health (Michalak 2016). Therefore, maintaining proper water quality has emerged as a key environmental issue (Michalak 2016). We observed significant changes in water quality expressed as TP, TN, DOC, and Chl *a* in nearly all lakes in our study region. We found that climate and the invasion of dreissenids were significant drivers of water quality in the Laurentian Great Lakes watershed and that lake morphology (surface area and mean depth) mediated lake responses to the drivers. Our water quality analysis revealed that there have been improvements in water quality in some lakes with declines in TP and subsequently Chl *a* concentrations, owing to better water management strategies over the past 40 years (De Pinto et al. 1986). However, we still do not know how climate and other anthropogenic factors will affect water quality in the future.

Temporal trends and patterns in water quality in lakes are influenced by many interacting factors including lake morphology, community structure, nutrient loadings, and environmental conditions (Table 1). Likewise, lakes are spatially heterogeneous, and large lakes in particular, can possess broad gradients in water quality. Continuously monitored water quality data including accurate long-term spatial records providing numerous sampling points per lake over a long time series, were unavailable for these small inland lakes, although we did acquire data for multiple sites (including nearshore and offshore) of the larger lakes to obtain a snapshot of how water quality may be changing over time. We acknowledge the unavoidable limitations of excluding spatial heterogeneity in our dataset, but future studies incorporating the combination of high temporal resolution data as well as numerous sampling points within a lake would further increase our understanding of spatial and temporal dynamics in water quality.

Maintaining water quality conditions provides extensive ecosystem services with vast socio-economic implications. Freshwater lakes in the Great Lakes region provide clean drinking water to millions of people in Canada and the United States and support multi-billion-dollar industries including fisheries, recreation, transportation, and tourism (Krantzberg and De Boer 2008). For example, water quality changes are

predicted to impact commercial and sport fishing by creating a new set of environmental challenges for non-generalist species, and by shifting the ranges of highly valued cold water fishes, such as lake trout, northward (Sharma et al. 2007; Van Zuiden et al. 2016). While there have been some successes over the past 40 years in understanding and mitigating the effects of numerous stressors on freshwater lake ecosystems, further research, monitoring, and restoration efforts are greatly needed in order to safeguard our vital freshwater resources for future generations.

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## Conflict of Interest

None declared.

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