IMPACTS OF CLIMATE CHANGE AND MULTIPLE STRESSORS ON WATER LEVELS AND PHYTOPLANKTON IN SMALL TEMPERATE LAKES WITHIN THE GREAT LAKES REGION OVER THREE DECADES

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ABSTRACT

Changes in climate influence water quantity and water quality through hydrological processes, thermal regimes, and ice phenology. This thesis investigates the impacts of climate change and additional anthropogenic stressors on water quantity and quality in two study areas with minimal anthropogenic disturbance within the Great Lakes region. Between 1984 and 2014, water levels dropped by an average of 50 cm in northern Wisconsin lakes. We found that 49% of the variation in water levels was attributed to decreased precipitation, and 30% was attributed to warmer air temperatures. Water levels are projected to rise by an average of 44 cm by the year 2070. In south-central Ontario, phytoplankton dominance shifted from diatoms to chrysophytes between 1984 and 2013. Changes in lake chemistry and lake morphometry explained 60% of the variation in phytoplankton biomass. Understanding how multiple interacting stressors affect lakes will help improve ecosystem management strategies.

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GENERAL INTRODUCTION

Global air temperatures are on average 0.87°C warmer than they were during the 1850-1900 pre-industrial period (IPCC, 2018). Similarly, temperatures have increased in the study regions of my thesis, namely Wisconsin and Ontario. For example, in northern Wisconsin, winter air temperature increased between 0.2-2°C and winter precipitation decreased by 10-20 mm between 1950 and 2006 (WICCI, 2011). Between 1984 and 2014, the regional climate in Wisconsin became warmer and drier, with a 0.21°C increase in air temperature and a 4.97 mm decrease in annual precipitation. Regionally, air temperature for the Ontario lakes increased by 0.83°C during the ice-free period, and autumn and winter became 1.2°C warmer. Precipitation and runoff decreased in eastern Canada between 1950 and 2012 (Hoegh-Guildberg et al., 2018). Winter precipitation in south-central Ontario increased by 23 mm during the study period. My thesis will investigate how the changes in climate have had an impact on lake ecosystems through water quantity and quality.

Climate warming carries risks of reduced water availability because of extreme drought and precipitation deficits (Hoegh-Guildberg et al., 2018). Warmer air temperatures lower water levels through enhanced evaporation rates. The drought of the 2000s particularly affecting Lake Superior was attributed to increased summer water temperatures and decreased ice cover, which led to increased evaporation (Assel et al., 2004; Assani et al., 2016). The same mechanism has doubled the evaporation rate measured in Lake Michigan-Huron since 1980 (Hanrahan et al., 2010). Climate conditions govern ice phenology, which affects the degree and duration of exposure of the lake to evaporative winter winds. Changes in precipitation timing and volume affect the degree of runoff entering the lake. Maintaining historical water levels is necessary for the provision of important ecosystem services, including lowered risk of flooding (Wantzen et al., 2008; Christensen and Christensen, 2003; IPCC, 2013), availability of drinking water and water for agriculture, and the continued use of waterways for recreation, fishing, and commercial shipping (Carpenter et al., 1992; Bronmark and Hansson, 2002).

Climate change poses an additional threat to water quality as climate variables govern lake physics, including thermal profile, hydrology, and ice phenology (Gerten and Adrian, 2002). Ice phenology affects the length of the growing season for phytoplankton, and changes in climate can impact water chemistry. Long term increases in air temperature may have contributed to increased NO_3 and NH_4 concentrations in the Ontario lakes, as nitrogen mineralization rates increase with warmer temperatures (Molot and Dillon, 1993). However, warmer air temperatures also encourage sulphur mineralization, affecting a lake's rate of recovery from acid rain (Williams, 1967; Strickland et al., 1984), and DOC production in the catchment (Palmer et al., 2014). Drought conditions can increase nutrient levels through reduced dilution, evaporative concentration, and diminished nutrient retention in soils (Gerson et al., 2016). A precipitation event following a drought transports sulphur and metals, re-acidifying lakes (Christophersen and Wright, 1981; Keller, 2007).

This thesis investigates the impacts of climate change and multiple stressors in two study areas with minimal anthropogenic impacts within the Great Lakes region. The first chapter aims to quantify the effects of climate change on water levels in seven lakes of northern Wisconsin. Our goals are to ascertain how water levels have changed in northern Wisconsin lakes between 1984 and 2014, to determine the main local and regional drivers of this change, and to forecast future levels under projected climate conditions for the next 30-50 years. The second chapter aims to identify local and regional drivers of phytoplankton biomass and variability in eight lakes in south-central Ontario between 1984 and 2013. Our goals are to establish how phytoplankton biomass has changed, to identify the local and regional drivers of community composition, and to determine the relative influence of lake morphometry, water chemistry, climate, and teleconnections indices on phytoplankton community and composition.

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CHAPTER 1: THE EFFECTS OF CLIMATE CHANGE ON WATER LEVEL FLUCTUATION IN NORTH TEMPERATE LAKES

Keywords: water level fluctuations, climate change, forecasting, local weather, large-scale climate drivers, time-series analysis

ABSTRACT

Fresh water is vital for human consumption, agriculture, recreation, fishing, and shipping. As climate changes, the quantity and quality of fresh water becomes vulnerable. Our study investigates how water levels have changed over the past 30 years in northern Wisconsin lakes, and the drivers of those changes. We also forecast water levels in 2050 and 2070 under scenarios of future climate change. During the study period (1984-2014), the regional climate became warmer and drier, with a 0.21°C increase in air temperature and a 4.97 mm decrease in annual precipitation. Concurrently, water levels dropped by an average of 0.02-1.12 m, with the greatest changes in autumn. Proportionally, approximately 50% of the variation in water level fluctuations was explained by decreased precipitation, and 30% of variation was explained by warming temperatures. From historical levels, water levels are projected to rise by an average of 0.72 m by the year 2050 and by 0.68 m by 2070, with regional climate projected to become warmer and wetter over the next century. These changes in water level could impact ecosystem services and lead to alterations in lake functioning, such as altered frequency of algal blooms, changes in water clarity, and shifts in the foraging and reproductive success of fish.

INTRODUCTION

Water levels in North America are changing. Long term water level fluctuations have been recorded since 1918 for Lake Superior, Michigan-Huron, St. Clair, and Erie. During the 1980s and late 1990s, water levels were above the long-term average. However, for the last 20 years, water levels have been continually declining and reached record lows in 2013 (White et al., 2008; Gronewald et al., 2016). The seasonal variation of water levels in the Great Lakes is between 0.2 m and 0.69 m (Lenters, 2001). Maintaining historical water levels is necessary for the provision of important ecosystem services, including lowered risk of flooding (Wantzen et al., 2008; Christensen and Christensen, 2003; IPCC, 2013), availability of drinking water and water for agriculture, and the continued use of waterways for recreation, fishing, and commercial shipping (Carpenter et al, 1992; Bronmark and Hansson, 2002).

Lake levels fluctuate seasonally and annually, and are influenced by local conditions and large-scale climate oscillations (Zohary and Ostrovsky, 2011). Air temperature, precipitation, cloud cover, and wind speed influence the water level in lakes through inputs and evaporation (Penman, 1948; Schindler, 2001; Adrian et al., 2009; Blanken et al., 2011). A 10-year study of Sparkling Lake, Wisconsin reported that variation in air temperature and humidity accounted for 46% of the variation in interannual evaporation rate and 54% of the variation in seasonal evaporation rate (Lenters et al., 2005). By the year 2055, winter temperatures in northern Wisconsin are projected to increase by 4.5°C and winter precipitation is projected to increase by 51 mm from current conditions (WICCI, 2011). Further, the degree of cloud cover influences water levels by affecting evaporation rates (Dai et al., 1999). There has also been a reduction in clouds, termed solar brightening, in areas where aerosol production has declined (Norris and

Wild, 2007; Haywood et al., 2011). It is in light of these projected changes that the importance of measuring and understanding changes in lakes is underscored.

While variation in water level over short time scales has been identified as being mainly dependent upon the precipitation from the previous year, interannual changes in level have been correlated with fluctuations in large-scale climate patterns reflecting oscillations in air pressure, sea surface temperature, or sunspot group number (Zohary and Ostrovsky, 2011; Clites et al., 2014). In North America, these include El Niño Southern Oscillation (ENSO), North Atlantic Oscillation (NAO), Atlantic Multidecadal Oscillation (AMO), Pacific North American Oscillation (PNA), Polar-Eurasian Oscillation (PE), Pacific Decadal Oscillation (PDO), Tropical/Northern Hemisphere Oscillation (TNH), Western Pacific Oscillation (WP), Quasi-Biennial Oscillation (QBO), and solar cycle (SS) (Polderman and Pryor, 2004; Ghanbari and Bravo, 2008; Sellinger et al., 2008). The dominant oscillations affecting the Great Lakes region are most influential on air temperature and precipitation volume during the cold season (Bonsal and Shabbar, 2010) and have been found to be correlated with dry or wet periods in the region (e.g. Ghanbari and Bravo, 2008; Rodionov and Assel, 2010).

Lakes integrate the impacts of changes of climate in their catchments (Magnuson et al., 1997; Jeppesen et al., 2009; Schindler, 2009). Because of this process, and their sensitivity to change, lakes have been proposed as indicators of climate change (Adrian et al., 2009; Schindler, 2009; Williamson et al., 2009). Many indicators of water quality, (such as chlorophyll *a*, dissolved organic compounds, and pH), are related to water quantity through concentration and loading (Håkanson et al., 2000; White et al., 2008; Hu et al., 2010), and lake water level has been suggested as a proxy for measuring climate change (Adrian et al., 2009). Water level could be an ideal indicator, as it is easy to measure and track, however quantitative relationships between water level and climate have not yet been well defined (Williamson et al., 2014; Adrian et al., 2009). Understanding the relationships between water levels and climate is essential for water management and regulation.

Research Objectives

The aim of this study is to quantify the effects of climate change on water levels in boreal freshwater lakes. We focus on seven lakes in northern Wisconsin with minimal point source anthropogenic impacts. We aim to answer two research questions: 1) How are water levels changing in northern Wisconsin lakes, and 2) What are the main local and regional drivers of this change? By investigating how lakes respond to climate change, we add to the knowledge base of how climate change may affect the north temperate landscape, and this may help improve our ability to mitigate negative responses on water levels.

METHODS

Data Acquisition

The study lakes are located in northern Wisconsin (Figure 1). Time series of recorded water levels for each lake were obtained from the North Temperate Lakes Long Term Ecological Research (NTL LTER) database. Water levels are monitored with a gauge at the shoreline approximately every second week and recorded in meters above sea level (North Temperate Lakes LTER). Regular monitoring of Big Muskellunge Lake (BM), Crystal Bog Lake (CB), and Crystal Lake (CR) began in 1981, and regular monitoring of Allequash Lake (AL), Sparkling Lake (SP), Trout Bog Lake (TB), and Trout Lake (TR) began in 1984. For consistency, our study period for these lakes is between 1984 and 2014. Biweekly lake level measurements were averaged into seasonal and annual means. Seasons were defined as spring (March, April, May), summer (June, July, August), and autumn (September, October, November). Two time series (CR Spring and TR Spring) were removed from analyses because of the large percentage of missing values (22 and 32% respectively). Three to 13% of water level data were missing from nine time series. These missing values were imputed with additive linear regression, bootstrapping, and predictive mean matching. This method was chosen because imputation by series mean or regression reduces variability in the data, reduces covariance and correlation estimates, and the regression method also overestimates model fit, whereas the predictive mean matching method avoids those distortions (Gelman and Hill, 2007). These analyses were performed in the R language environment using the aregImpute function in the Hmisc package (R Core Team, 2016).

Air temperature and precipitation data were obtained from the University of East Anglia Climate Research Unit (CRU). The data consists of gridded precipitation and air temperature time series variables from monthly observations at meteorological stations that were interpolated to the 0.5° scale (Harris et al., 2014). Monthly measurements of local temperature and precipitation were averaged into seasonal and annual means.

Large-scale climate drivers were obtained from the National Oceanic and Atmospheric Administration (NOAA) database (NOAA ESRL, 2016) and the Sunspot Index and Long-term Solar Observation database (SILSO, 2016). Indices were averaged into annual means, and are described in the Supplementary Material along with the mechanism of influence (Table S1).

A total of 126 climate projection scenarios were obtained for the years 2050 (an average of the years 2041-2060) and 2070 (an average of 2061-2080) from the most recent report of the Intergovernmental Panel on Climate Change (IPCC, 2013). Projections included 19 international General Circulation Models (GCMs) for monthly air temperature and precipitation. Each GCM consisted of two to four scenarios differing in greenhouse gas concentrations, air pollutant emissions, and land use, described as Representative Concentration Pathways (RCPs) (IPCC, 2013).

Data Analysis

How are water levels changing?

Sen’s slope analysis was used to identify long-term trends in historical water levels. Sen’s slope analysis was employed because it is a non-parametric estimator of the trend, i.e. it does not require any assumptions related to the distribution of the data, and the estimator allows for missing values in the data (Sen, 1968). These analyses were performed using the TheilSen function in the Openair package (R Core Team, 2016).

Autocorrelation function (ACF) and partial autocorrelation function (PACF) plots were examined to identify if there was temporal dependence in water levels at the annual and seasonal scales. If the autocorrelation at any particular time lag fell outside the 95% confidence interval, it was considered significant. When significant autocorrelations were identified, an autoregressive integrated moving average (ARIMA) model was developed to describe the degree to which water levels were correlated with those of previous years; the most parsimonious ARIMA model was chosen (Ives et al., 2010). These analyses were performed using the arima function in the tseries package (R Core Team, 2016).

What are the drivers of changing water levels?

Multiple linear regression (MLR) models and ARIMA models were developed for water levels at the annual and seasonal scale for each lake. The full model included local air temperature and precipitation at a seasonal scale, and climate indices at the annual scale. Multicollinearity was assessed between and within climate drivers. A forward selection procedure was performed with 9999 iterations and stopping criteria of $\alpha<0.05$ and $R^2>0.7$ to identify appropriate variables to be incorporated into lake models (Blanchet et al., 2008). Akaike Information Criterion (AIC) values were calculated for the MLR models, and were compared with the AIC values of the ARIMA models to determine which were better able to explain variation in water levels. We found that the MLR models had lower AIC values and were more parsimonious. These analyses were performed using the forward.sel function in the packfor package (R Core Team, 2016).

How will climate change influence water levels by 2050 and 2070?

We used MLR models with $R^2_{adj} > 0.7$ to forecast future water levels for 2050 and 2070 using future air temperature and precipitation values generated from the 19 general circulation models.

RESULTS

How are water levels changing?

At the annual scale between 1984 and 2014, water levels dropped in all seven lakes (Table 1), with an average decrease of 0.50 m, ranging from -0.23 m in Trout Bog ($p=0.03$) to -1.22 m in Big Muskellunge ($p<<0.001$). Within each lake, the greatest change at the seasonal scale was seen in autumn, on average decreasing 1.38 times more than the annual change (Table S2). Further, we found that annual water levels were autocorrelated with water levels in the previous year in six of the seven lakes in the study period (Table S3). Seasonally, water levels are dependent on levels of the previous year in 67.9% of the models. (Table S3).

What are the drivers of changing water levels?

An average of 61.4% of the variation in annual water levels was explained in our models, ranging from 22.4% in Trout Bog Lake to 81.9% in Big Muskellunge Lake (Table S4). 33.2% of this variation was attributed to the linear trend alone, and the remaining 66.8% of the variation explained was linked with weather, climate, and large-scale climate drivers.

Generally, declining water levels were associated with decreased regional precipitation. Proportionally, precipitation explained 48.9% of the variation in water levels. More specifically, precipitation explained an average of 65.5% of the variation in drainage lakes (Allequash and

Trout Lakes), and an average of 35.1% of the variation in seepage lakes (Big Muskellunge, Crystal, and Sparkling Lakes) (Table S4).

Warmer air temperatures were generally associated with lower water levels. Variation in air temperature explained an average of 29.6% of the variation in water levels. More specifically, air temperatures explained 45.5% of the variation in drainage lakes, and 24.2% in seepage lakes (Table S4).

Large-scale climate drivers proportionally explained 22.4% of the variation in lake levels in the models in which they were significant (Table S4). The most commonly significant driver was PDO, explaining 20.4% of the variation in the 12 models in which it was a significant driver. TNH Index was significant in four models and explained an average of 12.4% of variation. ENSO was a significant predictor in two models and explained 20.5% of the variation. WP, PE, and SS were significant in one model each and proportionally explained 62.6%, 19.9%, and 9.6% of the variation respectively (Table S4). Collectively, large-scale climate oscillations explained a greater proportion of variation in drainage lakes (28.6%) than seepage lakes (14.1%) (Table S4).

How will climate change influence water levels by 2050 and 2070?

Water levels are projected to decline by 0.68 m on average from 1984-2070 (Figure 2). There is no significant difference between the projected changes for the year 2050 and the year 2070. However, water levels are generally projected to rise under scenarios of climate change by an average of 0.4 m between current levels (1984-2014) and projected water levels in mid-to-late century (Figure S1).

DISCUSSION

Long term trends

Between 1984 and 2014, water levels dropped by an average of 50 cm in our study lakes. In northern Wisconsin, winter air temperature increased by 0.2-2.0°C and winter precipitation decreased by 10-20 mm between 1950 and 2006 (WICCI, 2011). The Great Lakes region has seen both wet and dry intervals in this period, with a period of high variability between 1973 and 2001 (Changnon, 2004). Net basin supplies were above average in the 1980s, which caused a uniformly wet period in the region (Assani et al, 2016). However, below average net basin supplies in the 1990s led to a drop in water levels and resulted in the consequent drought of the 2000s (Assani et al., 2016). The decrease we found in our study lakes is consistent with this overall decline of water levels in the region. A study conducted in 2008 found a drop of 0.1 m in 16 Ontario lakes between 1980 and 2003 (White et al, 2008). Between 1988 and 2001, water levels in Lakes Superior and Michigan-Huron also fell by 0.1 m (Lenters, 2001). Little Rock Lake, approximately 300 m from Sparkling Lake, experienced a loss of 1.1 m between 2001 and 2009 (Gaeta et al., 2013). Regional climate has been identified as a main driver of water level fluctuations in the Great Lakes basin, and recent fluctuations in Lakes Superior and Michigan-Huron have been attributed to changes in air temperature, ice cover, evaporation, and precipitation (Stow et al., 2008; Gronewald et al., 2016). Some of these factors were found to be important drivers in our study lakes.

Local drivers of changing water levels

Our water level models with considerations of weather, climate, and large-scale climate drivers explained an average of 61% of the variation in water levels. Approximately one third of this variation was explained by the linear trend of water levels, suggesting the long-term influence on lake water levels of climatic changes in the region. Lower water levels were correlated with lower rainfall and warming temperatures, with decreased precipitation accounting for 48.9% of the remaining variation in water levels, and 29.6% explained by warmer temperatures. Hanrahan and colleagues identified precipitation as the main driver of water levels in Lake Michigan-Huron (Hanrahan et al., 2010). Compared with southern Wisconsin, annual precipitation has been low since 1950, and declined by a further 5 mm during the study period (WICCI, 2011; Harris et al., 2014). Water levels increase with higher precipitation by increasing input through over-lake rainfall and runoff, and increased cloud cover, which, in addition to cooler air temperatures and less evaporation, resulted in the period of higher than average water levels in Lakes Superior and Michigan-Huron in the 1980s (Assel et al., 2004; Assani et al., 2016; Gronewald et al., 2016). Stow and colleagues identified that precipitation is the main driver of water levels in the Trout Lake watershed, whose positive correlation with levels of Lake Superior suggest regional climate to be a common driver (Stow et al., 2008).

Regional air temperature warmed by 0.21°C during the study period, and was correlated with a decline in the water levels of our study lakes. Air temperature decreases water levels by increasing water temperatures and evaporation rates. The drought of the 2000s particularly affecting Lake Superior was attributed to increased summer water temperatures and decreased ice cover, which led to increased evaporation (Assel et al., 2004; Assani et al., 2016). The same mechanism has doubled the evaporation rate measured in Lake Michigan-Huron since 1980 (Hanrahan et al., 2010). The extreme low levels in this region resulted in degraded water quality and decreased biodiversity due to the loss of wetlands, and in economic losses such as the scaling back of operations by water-dependent businesses like marinas (Chow-Fraser et al., 1998; Scott et al., 2005).

Large-scale climate drivers

We found that 22.4% of the variation in water levels was explained by large-scale climate drivers. Our models indicated that lower water levels were correlated with positive phases of AMO, PE, SS, TNH, and WP (Table S1). Assani and colleagues found that the positive phase of AMO was correlated with moderate drought in Lake Michigan-Huron, and Hanrahan and colleagues found average annual precipitation to be 18 cm less in positive phase years than negative phase years between 1916 and 1991 in Lake Michigan-Huron (Hanrahan et al., 2010; Assani et al., 2016).

Declining water levels were also correlated with negative phases of PDO and ENSO (Table S1). PDO was the most common index in our models, and was a significant predictor in 12 of the 24 cases. Mantua and colleagues identified that a positive phase of one standard deviation of winter temperatures was correlated with a 10 mm decrease of winter precipitation over the Great Lakes region (Mantua et al., 1997). The effects of El Niño are well-documented in the region. For example, the drought of the 2000s involved high intensity El Niño events, which resulted in a decrease in ice cover, an increase in temperature, and therefore increased evaporation in Lake Superior (Assel, 1998; Assel et al., 2000; 2004). The previous regional impacts are consistent with influence of the index on our study lakes, as declining water levels were correlated with the El Niño phase.

Landscape characteristics and water levels

We found a gradient of explained variation in water level models for seepage, drainage, and bog lakes. Weather, climate, and large-scale climate driver predictor variables explained the most variation in seepage lakes (Big Muskellunge with 82% variation explained, Crystal Lake with 77%, and Sparkling Lake with 76%), intermediate variation in drainage lakes (Allequash Lake with 33% and Trout Lake with 60%), and the two bog lakes differed the most in model success, with 79% of the variation explained in Crystal Bog and 22% of the variation in Trout Bog. We found that water levels in these lakes are primarily governed by precipitation and air temperature; therefore it follows that seepage lakes without surface connections would have a higher correlation with local climate. Earlier studies confirm that more highly connected lakes in this region are less coherent with changes in local climate, while lakes that were more isolated, or at higher altitudes, experienced water level fluctuations that were more dependent on changes in precipitation inputs (Kratz et al. 1997; Webster et al, 2000; Kratz et al., 2006; Ghanbari and Bravo, 2011).

Landscape position affects lake response within a flow system, and may also influence the degree of lake response to altered hydrological regimes (Riera et al, 2000; Kratz et al., 2006). Crystal Bog and Trout Bog Lakes are highest in the landscape and are also the smallest study lakes. Crystal, Big Muskellunge, Sparkling, and Allequash Lakes are progressively lower in position, with Trout Lake having the lowest position and correspondingly largest area. Kratz and colleagues hypothesized that lakes that are higher in the landscape have a restriction on water level due to the presence of a lower lake into which water may flow (1997). Surface water levels are also influenced by seasonal groundwater flow and geology around the lake (Anderson and Pint, 2002). The study region is composed of Precambrian bedrock, overlain by layers of glacial till and outwash approximately 50 m deep (Kenoyer and Anderson, 1989). Within 100 m of Crystal Lake, two silt layers of approximately 1 m thick are less permeable than the sandy glacial till in the area, which confine the flow of water (Kenoyer and Anderson, 1989; Kenoyer and Bowser, 1992). Ghanbari and Bravo studied how variation in precipitation in this area affects groundwater recharge, and found that it takes approximately 5 days for groundwater levels to respond to rainfall (2011). It is difficult to quantify the degree to which groundwater movement affects each lake, however the area between Crystal and Big Muskellunge Lakes, has been studied particularly closely. These two lakes are approximately 120 m apart, with most of the groundwater leaving Crystal Lake flowing into Big Muskellunge Lake, which is 1 m lower, except when a seasonal groundwater mound in response to snowmelt changes the direction of flow towards Crystal Lake (Kim et al., 1999). Overall, lakes in this region are closely connected through groundwater flow, and surface connectivity is poor, placing less emphasis on the importance of surface geology for water level fluctuations, and greater relevance on the influence of climatic change (Kenoyer and Anderson 1989; Kenoyer and Bowser, 1992).

Forecasted changes in water levels

Water levels in the majority of lakes are projected to rise over the next 30-50 years. In our study region, water levels are governed primarily by precipitation and air temperature, both of which are expected to increase in the next 30-50 years. For example, we forecasted autumn levels in

Big Muskellunge to be decreasing the most, as they experienced the greatest drop during the study period and are also projected to rebound the least over the next 30-50 years. Two anomalies in our lake projections are the annual levels of Crystal Lake and the fall levels of Sparkling Lake, which are both projected to decrease. Annual levels of Crystal Lake rise with greater spring and winter precipitation, a positive phase of the PDO, and a negative phase of the TNH, however, levels are expected to fall. This could be in response to the PDO remaining in a negative phase until 2025/35, and the associated decreased winter air temperature and precipitation, and decreased summer precipitation could result in a drop in level (Mantua et al., 1997; Changfang et al 2014; Assani et al., 2016).

Implications

Water levels in northern Wisconsin lakes declined over the past 30 years, and were found to be primarily driven by less precipitation and warmer air temperatures. These results were consistent with regional changes; Great Lakes water levels have been in general decline since the 1980s. Water level fluctuations carry ecosystem services via economic, social, and environmental impacts. For example, Schwartz and colleagues estimated that by 2050, due to projected decreases in water levels, the town of Goderich, Ontario on Lake Huron would be required to spend a minimum of $1.4 million to dredge their Inner Harbour, and between $200 000 and $600 000 to maintain access to harbour marinas (Schwartz et al., 2004). Further, the decline of Great Lakes water levels has facilitated the establishment of the invasive reed *Phragmites australis subsp. australis* (common reed), which opportunistically invades low-water coastal areas, and is posing an increasingly serious threat to biodiversity by outcompeting native species, trapping small animals in its dense growth, and reducing available habitat (Tulbure et al., 2007; Whyte et al., 2008; Tulbure and Johnston, 2010). A broader example of habitat loss are the several shallow (~1 m deep) study lakes and ponds on Ellesmere Island that were permanent features of the landscape, which dried out in the summer of 2006 in response to a changing climate (Smol and Douglas, 2007; Williamson et al., 2009b). Understanding how water levels are affected by climate change is essential to managers, as level fluctuations may have serious economic, social, and environmental impacts. Our study determined that water levels in northern Wisconsin are primarily governed by air temperature and precipitation, and are also influenced by large-scale climate drivers. By investigating how lakes respond to climate change, we add to the knowledge base of how climate change may affect the north temperate landscape, and this may help improve our ability to mitigate negative responses on freshwater availability.

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TABLES

Table 1: Average annual change in water level from 1984 to 2014 in each of the study lakes, expressed in meters.

Lake	Change (m)	95% CI		P
Allequash	-0.065	-0.245	0.040	0.19
Big Muskellunge	-1.088	-1.525	-0.539	<<0.001
Crystal Bog	-0.282	-0.375	-0.198	<<0.001
Crystal	-1.066	-1.522	-0.515	<<0.001
Sparkling	-0.741	-1.194	-0.208	0.01
Trout Bog	-0.155	-0.304	0.016	0.07
Trout	-0.099	-0.211	0.009	0.08

Table 2: Significant predictors of annual water level fluctuations in each study lake between 1984 and 2014. Seasonal values of local air temperature and precipitation, and annual values of climate drivers were included in the models. Adjusted R^2 and AIC values of models are provided.

Lake	Coefficient	Predictors	Predictor P value	Model P value	Model R^2_{Adj}	R^2_{Adj} of H2O vs Year	Model R^2_{adj} when linear trend is taken into account	Total R^2_{Adj}	AIC
Allequash	-0.179	Intercept	0.02	0.02	0.15	0.21	0.12	0.33	-63.37
	-0.017	Temp Win	0.02						
Big Muskellunge	-1.333	Intercept	0	0	0.62	0.52	0.3	0.82	-9.79
	0.246	PDO	0						
	0.008	Pre spr	0						
	0.012	Pre win	0.01						
	0.083	Temp Fall	0.01						
Crystal Bog	-0.179	Intercept	0	0	0.4	0.65	0.14	0.79	-93.2
	0.003	Pre win	0.01						
	0.033	PDO	0						
	0.001	Pre spr	0.01						
Crystal	-0.933	Intercept	0	0	0.56	0.48	0.29	0.77	-3.82
	0.181	PDO	0						
	0.008	Pre spr	0						
	0.014	Pre win	0						
	-0.139	TNH	0.03						
Sparkling	-1.187	Intercept	0	0	0.65	0.32	0.45	0.76	-14.49
	-0.056	Temp spr	0.01						
	0.198	PDO	0						
	0.008	Pre spr	0						
	0.005	Pre sum	0						
	0.06	Temp fall	0.05						

Trout Bog	-0.202	Intercept	0.01	0.01	0.2	0.04	0.19	0.22	-44.85
	0.003	Pre spr	0.01						
Trout	-0.28	Intercept	0	0	0.55	0.1	0.49	0.6	-94.59
	0.002	Pre sum	0						
	0.037	ENSO	0.01						
	0.001	Pre spr	0.01						
	-0.109	AMO	0.03						

FIGURES

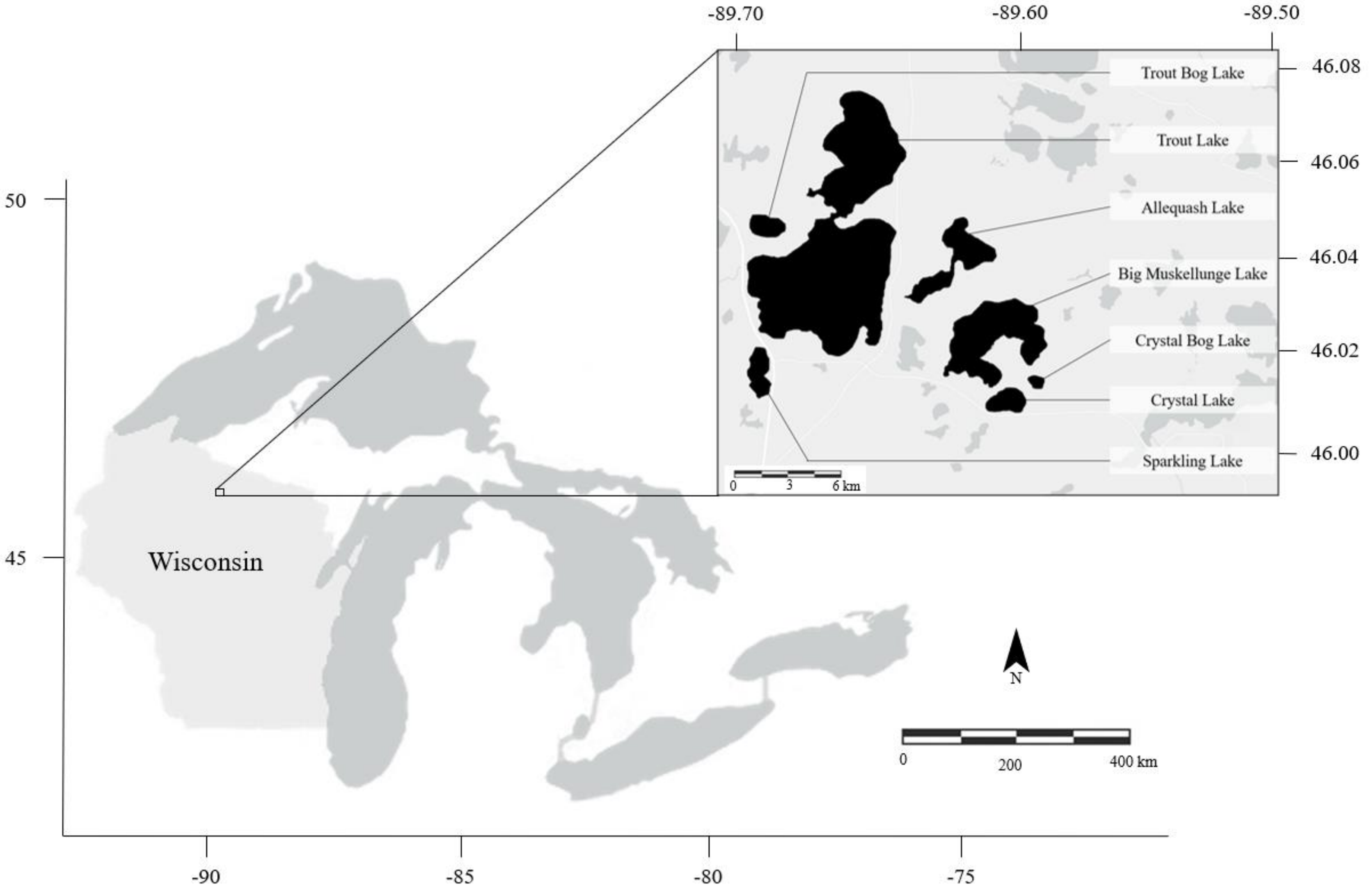

Figure 1: Map of the study region in northern Wisconsin, USA in relation to the Great Lakes region, with the locations of our seven study lakes (inset) in relation to each other.

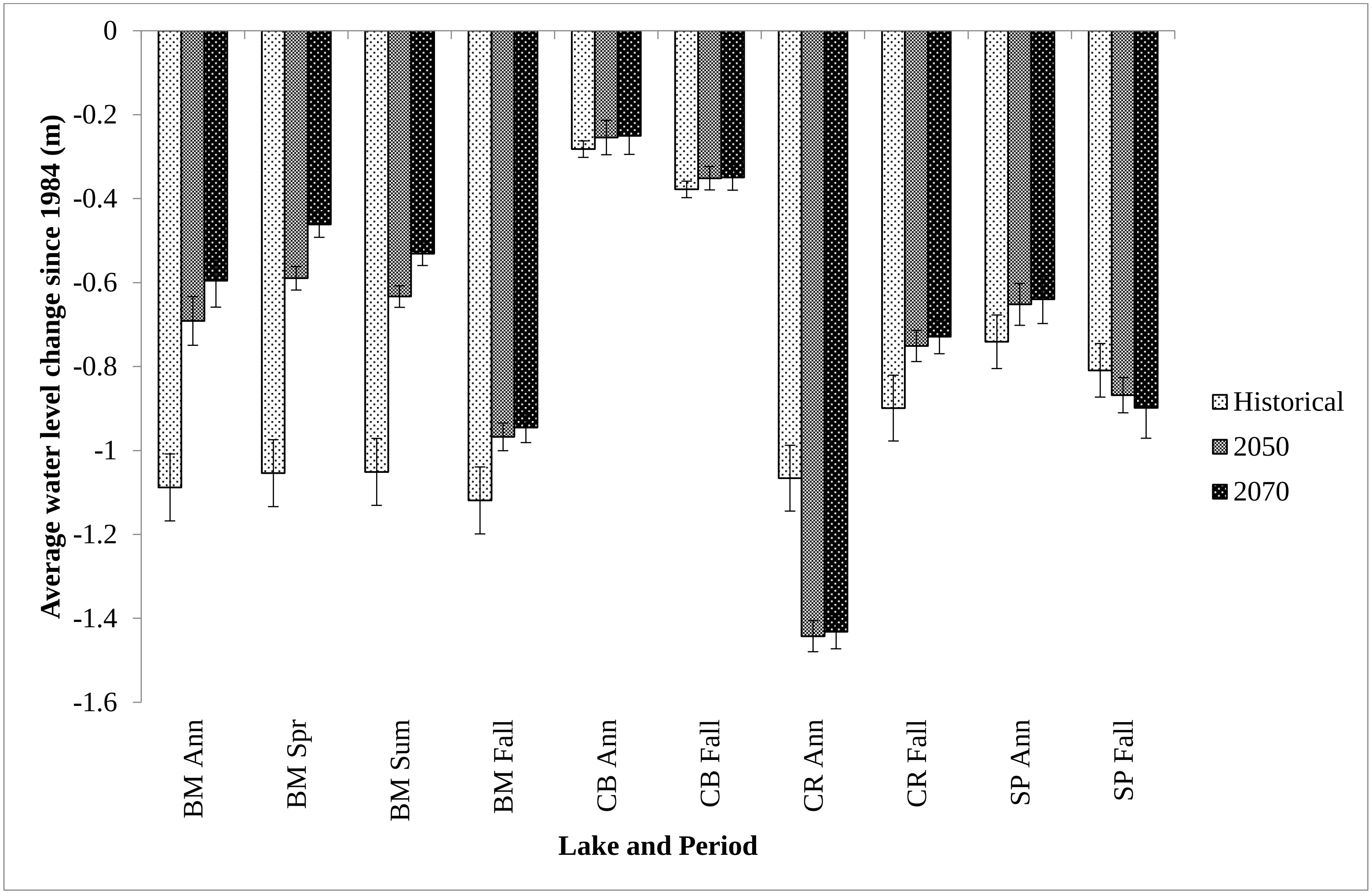

Figure 2: Average projected change in water levels since 1984 to the years 2050 (an average of the years 2041-2060) and 2070 (an average of 2061-2080), for four study lakes. Error bars represent the standard error of the values.

SUPPLEMENTARY MATERIAL

Table S1: Large-scale climate drivers and their influence on water level fluctuations in the study lakes between 1984 and 2014. Predicted effects (+/-) of a positive phase on water levels are shown outside parentheses, and observed effects (+/-) in bold parentheses.

Index	**Definition**	**Cycle length (yrs)**	**Effect in N. Wisconsin of positive phase**	**Phase in N. Wisconsin during study period**	**Predicted and (Modeled) Effect on water level of positive phase**	**Index Source**	**Information Source**
Atlantic Multidecadal Oscillation (AMO)	SST in N Atlantic	50-90	+ temp and - precip in summer	- (1995) +	- **(-)**	http://www.esrl.noaa.gov/psd/data/timeseries/AMO/	Mestas-Nunez and Enfield, 1999
North Atlantic Oscillation (NAO)	atmospheric pressure and winds in N Atlantic	no periodicity	+ temp and - precip in winter	+ (1985) - (1986) + (1988) - (1989) + (1993) - (1994) + (1996) - (1999) + (2001) - (2002) + (2003) - (2004) + (2005) - (2007) + (2008) - (2011) + (2012) - (2012) +	-	http://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/norm.nao.monthly.b5001.current.ascii.table	Barnston and Livezey, 1987
(El Niño Southern Oscillation (ENSO)	winds and SST in SE Pacific	2-7	- temp and + precip in winter	- (1986) + (1988) - (1990) + (1995) - (1997) + (1998) - (2002) + (2005) - (2006) + (2007) - (2009) + (2010) - (2012) + (2013) - (2014) +	+ **(+)**	http://www.esrl.noaa.gov/psd/enso/mei/table.html	Rasmusson and Carpenter, 1982
Pacific Decadal Oscillation (PDO)	SST in N Pacific	20-30	+ temp and - precip in winter	+ (2005) -	- **(+)**	http://www.esrl.noaa.gov/psd/data/correlation/pdo.data	Mantua et al., 1997

Polar-Eurasian Oscillation (PE)	strength and position of polar vortex	6-10	+ temp and - precip in winter	- (1990) + (1998) -	- **(-)**	ftp://ftp.cpc.ncep.noaa.gov/wd52dg/data/indices/poleur_index.tim	Rodionov and Assel, 2010
Quasi-Biennial Oscillation (QBO)	stratospheric circulation in tropics	2.35	- temp in winter	- (1985) + (1987) - (1988) + (1989) - (1990) + (1992) - (1993) + (1994) -(1995) + (1996) - (1997) + (1998) - (1999) + (2000) -(2002) + (2003) - (2004) + (2005) - (2006) + (2007) - (2008) + (2009) - (2011) + (2012) - (2013) +	**+**	http://www.geo.fu-berlin.de/en/met/ag/strat/produkte/qbo/index.html#access	Baldwin et al., 2001
Sunspot Index (SS)	total sunspot number	11	+ global temp	peaks in 1989, 2000, 2014	- **(-)**	http://www.sidc.be/silso/datafiles	Friis-Christensen and Lassen, 1991
Tropical/ Northern Hemisphere Oscillation (TNH)	shift in position of jet stream	interannual	- temp in winter	+ (1985) - (1988) + (1991) - (2002) + (2009) - (2011) +	- **(-)**	ftp://ftp.cpc.ncep.noaa.gov/wd52dg/data/indices/tnh_index.tim	Mo and Livezey, 1986; Barnston and Livezey, 1987; Barnston et al., 1991
Western Pacific Oscillation (WP)	strength and position of jet stream	no periodicity	+ temp and + precip in all seasons	- (1987) + (1988) - (1989) + (1990) - (1992) + (1994) + (1995) - (1998) + (2000) - (2001) + (2002) - (2004) + (2006) - (2009) + (2012) -	- **(-)**	ftp://ftp.cpc.ncep.noaa.gov/wd52dg/data/indices/wp_index.tim	Barnston and Livezey, 1987

Table S2: Average seasonal change in water level from 1984 to 2014 in each of the study lakes, expressed in meters. Significant results are shown in italics.

Lake	Time Period	Change (m)	95% CI		P
Allequash	**Spring**	0.019	-0.217	0.133	0.86
	Summer	0.003	-0.195	0.096	0.92
	Fall	*-0.254*	*-0.450*	*-0.056*	*0.01*
Big Muskellunge	**Spring**	*-1.054*	*-1.420*	*-0.508*	*0.002*
	Summer	*-1.051*	*-1.513*	*-0.512*	*<<0.001*
	Fall	*-1.119*	*-1.519*	*-0.611*	*<<0.001*
Crystal Bog	**Spring**	*-0.198*	*-0.298*	*-0.096*	*<<0.001*
	Summer	*-0.267*	*-0.360*	*-0.192*	*<<0.001*
	Fall	*-0.378*	*-0.496*	*-0.264*	*<<0.001*
Crystal	**Spring**	-	-	-	-
	Summer	*-0.806*	*-1.352*	*-0.304*	*0.01*
	Fall	*-0.899*	*-1.500*	*-0.412*	*0.01*
Sparkling	**Spring**	*-0.589*	*-1.060*	*-0.136*	*0.01*
	Summer	*-0.657*	*-1.032*	*-0.133*	*0.02*
	Fall	*-0.809*	*-1.156*	*-0.183*	*0.01*
Trout Bog	**Spring**	-0.065	-0.189	0.059	0.23
	Summer	-0.121	-0.282	0.043	0.13
	Fall	*-0.099*	*-0.453*	*0.025*	*0.03*
Trout	**Spring**	-	-	-	-
	Summer	-0.065	-0.161	0.031	0.27
	Fall	-0.081	-0.220	0.034	0.13

Table S3: ARIMA models for each study lake highlighting the coefficients of p,d, and q for each model, the intercept, and the Akaike Information Criterion used to select the best model. NS signifies non-significant results due to a lack of autocorrelation or missing values. NAs are written in the model column to signify missing data for that time period.

Lake	**Period**	**(p,d,q) model**	**Component**	**Coefficient**	**Intercept**	**AIC**
Allequash	**Ann**	(1,0,1)	AR	0.92	494.23	-59.76
			MA	-0.47		
	Spr	(0,0,0)	NS	NS	NS	NS
	Sum	(0,0,0)	NS	NS	NS	NS
	Fall	(1,0,2)	AR	0.95	494.31	-55.67
			MA 1	-0.91		
			MA 2	0.51		
Big Muskellunge	**Ann**	(0,0,0)	NS	NS	NS	NS
	Spr	(2,0,0)	AR 1	1.13	500.22	-4.66
			AR 2	-0.28		
			MA	0		
	Sum	(1,1,0)	AR	0.29	500.2	-10.49
			I	0		
			MA	0		
	Fall	(1,0,0)	AR	0.89	500.14	-3.46
			MA	0		
Crystal Bog	**Ann**	(1,0,0)	AR	0.83	501.31	-79.72
			MA	0		
	Spr	(1,0,1)	AR	0.91	501.35	-63.47
			MA	-0.53		
	Sum	(1,0,0)	AR	0.79	501.28	-73.88
			MA	0		
	Fall	(1,0,0)	AR	0.71	501.3	-48.89
			MA	0		
Crystal	**Ann**	(1,0,1)	AR	0.85	501.40	-13.35
			MA	0.42		
	Spr	NAs	NS	NS	NS	NS
	Sum	(1,0,0)	AR	0.8	501.38	7.07
			MA	0		
	Fall	(1,0,0)	AR	0.87	501.3068	-4.22
			MA	0		
Sparkling	**Ann**	(1,0,0)	AR	0.76	494.79	3.34

			MA	0		
	Spr	(0,0,1)	AR	0	494.8	12.47
			MA	0.81		
	Sum	(1,0,0)	AR	0.51	494.82	18.56
			MA	0		
	Fall	(1,0,0)	AR	0.74	494.74	4.32
			MA	0		
Trout Bog	**Ann**	(1,0,1)	AR	0.41	493.68	-51.16
			MA	0.4		
	Spr	(1,0,0)	AR	0.47	493.73	-41.15
			MA	0		
	Sum	(1,0,0)	AR	0.53	493.57	-43.27
			MA	0		
	Fall	(0,0,1)	AR	0	493.63	-40.03
			MA	0.83		
Trout	**Ann**	(1,0,0)	AR	0.45	491.83	-74.10
			MA	0		
	Spr	NAs	NS	NS	NS	NS
	Sum	(0,0,2)	AR	0	491.83	-70.73
			MA 1	0.07		
			MA 2	0.32		
	Fall	(1,0,0)	AR	0.37	491.8	-67.13
			MA	0		

Table S4: Significant predictors of seasonal water level fluctuations in each study lake between 1984 and 2014. Seasonal values of local air temperature and precipitation, and annual values of climate drivers were included in the models.

Lake	Period	Coefficient	Predictors	Predictor P value	Model P value	Model R^2_{Adj}	R^2_{Adj} of H2O vs Year	Model R^2_{adj} when linear trend is taken into account	Total R^2_{Adj}	AIC
Allequash	**Spr**	-0.226	Intercept	0.02	0.01	0.16	0.06	0.15	0.21	-51.42
		-0.021	Temp Win	0.01						
	Sum	-0.003	Intercept	0.83	0.04	0.11	0.07	0.1	0.17	-64.12
		-0.083	WP	0.04						
	Fall									
Big Muskellunge	**Spr**	-1.271	Intercept	0	0	0.58	0.53	0.28	0.8	-8.46
		0.24	PDO	0						
		0.009	Pre spr	0						
		0.125	Temp Fall	0						
	Sum	-1.392	Intercept	0	0	0.61	0.5	0.31	0.8	-7.31
		0.245	PDO	0						
		0.009	Pre spr	0						
		0.011	Pre win	0.01						
		0.089	Temp fall	0.01						
	Fall	-0.962	Intercept	0	0	0.61	0.53	0.29	0.82	-8.67
		0.183	PDO	0						
		0.015	Pre win	0						
		0.008	Pre spr	0						
		-0.134	TNH	0.02						
Crystal Bog	**Spr**	-0.13	Intercept	0	0	0.33	0.53	0.16	0.69	-86.79
		0.002	Pre spr	0						
		0.034	PDO	0.01						

	Sum									
	Fall	-0.344	Intercept	0	0	0.28	0.61	0.11	0.72	-68.29
		0.005	Pre ann	0						
Crystal	**Spr**									
	Sum	-0.044	Intercept	0.84	0	0.37	0.42	0.21	0.63	6.93
		-0.09	Temp spr	0						
		-0.224	TNH	0.01						
		0.006	Pre spr	0.03						
		0.017	Pre win	0						
		-0.012	Pre ann	0.03						
	Fall	-0.946	Intercept	0	0	0.59	0.47	0.31	0.78	-5.81
		0.176	PDO	0						
		0.016	Pre win	0						
		0.008	Pre spr	0						
		-0.158	TNH	0.01						
Sparkling	**Spr**	-0.517	Intercept	0	0	0.46	0.3	0.32	0.62	-2.15
		0.161	PDO	0						
		0.009	Pre spr	0						
		-0.002	SS	0.05						
	Sum	-0.278	Intercept	0.17	0	0.48	0.22	0.37	0.6	-0.94
		-0.061	Temp spr	0.02						
		0.007	Pre spr	0						
		0.135	PDO	0.01						
	Fall	-0.96	Intercept	0	0	0.65	0.31	0.45	0.76	-15.85
		0.024	Pre ann	0						
		0.155	PDO	0						
		-0.006	Pre fall	0						
		-0.047	Temp spr	0.02						

Trout Bog	**Spr**	0.433	Intercept	0.16	0	0.4	-0.02	0.41	0.39	-49.87
		0.004	Pre spr	0						
		-0.041	Temp sum	0.02						
	Sum	-0.231	Intercept	0	0	0.24	0	0.24	0.24	-43.65
		0.004	Pre spr	0						
	Fall	-0.552	Intercept	0	0	0.26	0.09	0.24	0.33	-36.15
		0.008	Pre ann	0						
Trout	**Spr**									
	Sum	-0.258	Intercept	0	0	0.32	0.02	0.31	0.33	-82.42
		0.002	Pre sum	0						
		0.002	Pre spr	0.01						
	Fall	-0.093	Intercept	0.1	0	0.59	0.08	0.54	0.62	-92.07
		0.002	Pre sum	0						
		0.061	ENSO	0						
		-0.035	Temp ann	0						
		-0.09	PE	0.01						

CHAPTER 2: PHYTOPLANKTON COMMUNITY RESPONSE TO MULTIPLE STRESSORS IN NORTH TEMPERATE LAKES OVER THE PAST THREE DECADES

Keywords: freshwater phytoplankton, climate change, abrupt shifts, teleconnections, multiple stressors, acid rain, lake brownification, algal blooms

ABSTRACT

There has been a significant increase in reports of algal blooms across Ontario since 1994. Multiple interacting stressors have impacted water quality during recent decades, including acid rain, calcium decline, brownification, and climate change. We analysed long-term records of phytoplankton biomass and lake chemistry from the Dorset Environmental Science Center, climate conditions, and teleconnections indices to identify the local and regional drivers of phytoplankton variability in eight study lakes in south-central Ontario between 1984 and 2013. Diatoms and chrysophytes were the most abundant groups, with a shift from diatom to chrysophyte dominance during the study period. Redundancy Analyses explained between 24% and 44% of the variation in phytoplankton biomass, with 60% of this variation explained by lake chemistry and morphometry. Climate warming and lake brownification have altered lake physics, extending the summer stratified period. This was detrimental for diatoms, which prefer colder temperatures and mixed hydrographic conditions, and favoured chrysophytes, a late summer opportunistic mixotroph that can thrive in stable conditions. Dinoflagellates, cyanobacteria, chlorophytes, and cryptophytes were not as abundant in our study lakes. Their relative abundances were driven by a combination of specific tolerances, competitive ability, and nutrient availability. Reduced Cation Exchange Capacity, local geology, and drought conditions have contributed to the slow recovery of our lakes to acid rain and affected the concentration and solubility of nutrients. Air temperatures are expected to become 0.2°C warmer per decade and precipitation to increase by 5-10% by the 2030-2052 period. By understanding how multiple stressors influence phytoplankton communities, we will be better able to anticipate harmful and nuisance blooms, improving water quality and public health.

INTRODUCTION

Harmful algal blooms (HABs) have been identified as potentially the greatest water quality threat to public health and aquatic ecosystems (Brooks et al., 2016). Across Ontario, between 1994 and 2009 there has been a significant increase in algal bloom reports, with a large proportion of these blooms containing cyanobacteria (Winter et al., 2011). Many bloom-forming phytoplankton, like chrysophytes and diatoms, are able to produce taste and odour compounds unpleasant to humans (e.g. Paterson et al., 2004; Cornwell et al., 2015), as well as more harmful toxic substances like the hepato- and neurotoxins produced by cyanobacteria, which include microcystins, nodularins, and anatoxin-a (O'Neil et al., 2012). Our study lakes are representative of lakes in south-central Ontario impacted by multiple environmental stressors (Palmer et al., 2011), without many of the confounding impacts of highly developed areas (e.g. Schindler, 1988; Yan et al., 2008). Multiple stressors, including climate change, acidification, and the introduction of invasive species, such as *Bythotrephes*, are important drivers of environmental change in this region (Yan and Pawson, 1997; Schindler, 1998; Watmough and Dillon, 2003; Paterson et al., 2004; Molot and Dillon, 2008; Yan et al., 2008; Keller et al., 2011; Jeziorski et al., 2014; Schindler et al., 2016). With increased stresses on freshwater systems, it is important to understand the corresponding changes to phytoplankton communities, in particular because of their influence on water quality, trophic web linkages, and the local economy. Our aim is to identify the main drivers of phytoplankton biomass in small lakes in south-central Ontario over the past 30 years.

Phytoplankton blooms are favoured by changes in climate (Paerl and Huisman, 2008; 2009). In the Great Lakes region, the frequency of heavy precipitation events and extreme high temperatures have increased over the past 50 years (Cruce and Yurkovich, 2011; Warren and Lemmen, 2014), and regional air temperatures increased by 0.25°C per decade between 1970 and 2000 (Kling et al., 2003; Hayhoe et al., 2010). Changes in temperature and nutrient availability influence the abundance and successional dynamics of algal species, as phytoplankton groups have different growth preferences (Nõges et al., 2003; Thackeray et al., 2008). For example, warmer air temperatures contribute to a decline in winter ice cover, resulting in earlier thermal stratification and a longer growing season (Magnuson et al., 2000; Hewitt et al., 2018). Increased precipitation can lead to increased runoff and an increase in dissolved organic carbon (DOC) concentrations within a lake (Schindler et al., 1990). Increases in water temperatures and DOC concentrations in response to warmer and wetter climates may influence spring phytoplankton communities, as light and temperature conditions change during stratification (Berger et al., 2014). A subsequent mismatch in the timing of phytoplankton and zooplankton peaks could lead to increased incidence of algal blooms from reduced grazing pressure (de Stasio et al., 1996). Phenological mismatches between phytoplankton and zooplankton are projected to be more pronounced in northern lakes under scenarios of climate change (de Stasio et al., 1996). Large-scale climate drivers, including the El Niño Southern Oscillation (ENSO) and North Atlantic Oscillation (NAO), also influence regional air temperatures and precipitation. ENSO was identified as the most likely synchronizing mechanism of changes in the thermal conditions and phytoplankton dynamics of freshwater lakes in North America (Gerten and Adrian, 2002). This finding is consistent with a study conducted by Palmer and colleagues, who identified ENSO and NAO as important drivers of climate, lake physics, and dissolved oxygen in south-central Ontario and Wisconsin (Palmer et al., 2014). They demonstrated coherent variation between climate, lake physics and dissolved oxygen. An increase in the frequency of extreme precipitation events led to increased epilimnetic nutrient loading during the stratified period, which in turn caused the epilimnion to become shallower (Palmer et al., 2014).

In addition, the lakes within our study region have also been impacted by several decades of metal smelting in Sudbury, Ontario. Smelting has resulted in sulphur deposition, calcium depletion, decreased phosphorus concentrations, and increased acidity of precipitation (Schindler, 1988). In the past two decades, there has been a general trend in acid rain recovery, although it is not uniform (Yan et al., 2008). When the pH is below 5, phytoplankton growth can be negatively affected. However, more acidic conditions may cause a dominance of acid-tolerant groups (Holopainen, 1992). Calcium depletion, a process associated with acid rain, can act as an environmental stressor in itself. Between 1985 and 2005, a 13% decline in calcium was reported in Canadian Shield lakes, which was linked with a decrease of between 60 and 67% of daphnia compared with pre-1850s values (Jeziorski et al., 2008). Calcium concentrations are low enough in some lakes to influence growth rates of invertebrates and zooplankton (Schindler, 2009). Factors influencing zooplankton populations have the potential to impact phytoplankton populations because of changes in grazing pressure (Wetzel, 2001). The depleted levels of calcium may have occurred with long-term acid deposition, but may also be the result of interactions between factors like climate change and clear cut logging (Schindler, 2009). The application of road salt in the watershed is an additional environmental stressor impacting our study lakes (Thunqvist, 2004; Watmough and Aherne, 2008; Dugan et al., 2017). An investigation of road salt application to central-Ontario lakes revealed that sodium concentrations increased between 250 and 350% in Dickie and Harp Lakes (Molot and Dillon, 2008).

Research Objectives

Previous work has investigated impacts on one phytoplankton group (e.g. diatoms in Enache et al., 2011 or Hadley et al., 2013), or has tracked recovery from one stressor (e.g. acid rain in Winter et al., 2008). Here, we update the single comprehensive look at the stressors structuring the phytoplankton community after a long-term effort of water quality improvement. In this study, we will answer three research questions: 1) How have phytoplankton biomass and variability in biomass changed over the past 30 years, 2) What are the local and regional drivers of phytoplankton community composition across all eight lakes in south-central Ontario, and 3) What is the relative influence of lake morphometry, water chemistry, climate, and large-scale climate drivers on phytoplankton community composition in eight study lakes in south-central Ontario? Our first objective is to identify patterns of changing variability between regions. Our second objective is to develop models describing responses in phytoplankton biomass with local and regional climate, and physical and chemical drivers. We hypothesize that both local (nutrients and weather) and regional (teleconnection indices) will influence phytoplankton biomass. Our third objective is to quantify the relative importance of each driving factor for phytoplankton biomass. We hypothesize that nutrient availability and air temperature will be the main driving factors of phytoplankton biomass.

METHODS

Data Acquisition

We obtained lake morphology, water chemistry, and phytoplankton biomass for eight lakes from the Ontario Ministry of the Environment and Climate Change Dorset Environmental Science Center (MOECC DESC). The study area is located within the Boreal Shield ecozone on the Precambrian Shield, and is comprised of exposed silicate bedrock, thin noncarbonate till, and thin acidic soil (Keller, 2007; Watmough and Aherne, 2008). The DESC has conducted a long-term monitoring program since the mid-1970s for Blue Chalk, Chub, Crosson, Dickie, Harp, Heney, Plastic, and Red Chalk lakes (Figure 1). Each lake is small (less than 1km^2), and all are dimictic except for Dickie which only mixes once per year (Paterson et al., 2008; Palmer et al., 2014). Red Chalk Lake has two basins which differ chemically, with approximately 10% of the east basin inflow coming from the main basin, which have been treated as separate lakes in our analyses, following Dillon et al (2003). We used a study period of 1984-2013 as the longest time period for which continuous data was available across all lakes.

Lake morphometry and long-term water quality data were obtained from each lake. Lake morphometry variables included lake surface area, maximum depth, and mean depth (Table A1). Water chemistry variables included ammonium, calcium, chloride, dissolved organic carbon, iron, total nitrogen, nitrate, total phosphorous, pH, silicate, sodium, and sulphate (Table A1). Water chemistry variables were measured biweekly throughout the study period, and recorded as whole-lake volume-weighted samples for analyses. Seasonal water chemistry means were calculated for the ice-free period (March to November), spring (March to May), summer (June to August), and fall (September to November). Further sampling details are described in Keller et al., 2008. Because phytoplankton biomass was expressed as an ice-free mean, only ice-free chemical variables were included as predictor variables in analyses.

Phytoplankton were collected using a PVC pump-and-hose system at depths within the euphotic zone (approximated as twice the secchi depth) at a deep station in each lake. Cell counts were converted to wet weight biomass and expressed as biovolume using geometric formulae for cell shapes. Sample concentrations were used to calculate lake-equivalent volumes, and samples were expressed as volume-weighted euphotic zone composites. Phytoplankton sampling periods ranged from weekly to biweekly (Dickie, Harp, and Plastic Lakes) or monthly (Blue Chalk, Chub, Crosson, and Red Chalk Lakes), and summarized as an ice-free mean (from March to November) (Paterson et al., 2008). Phytoplankton groups included diatoms, chlorophytes, chrysophytes, cryptophytes, cyanobacteria, dinoflagellates, and euglenoids, and were expressed as relative biomass (%) of the sample. Euglenoids did not exceed 2% relative biomass during the study period, and were excluded from analyses. Further details on sampling procedure may be found in Paterson et al., 2008.

Climate data (air temperature, precipitation, and cloud cover) were obtained from the University of East Anglia Climatic Research Unit (CRU) (Table A1). CRU data has a monthly temporal resolution and a 0.5°x0.5° spatial resolution (Harris et al., 2014), which corresponds to a grid of approximately 55.5 km. Teleconnection indices influencing the study region were obtained from the National Oceanic and Atmospheric Administration (NOAA) database, a summary of which can be found in Table A2 (Bonsal and Shabbar, 2010; NOAA ESRL, 2016).

Data Analysis

How has phytoplankton biomass changed over the past 30 years?

We assessed changes in phytoplankton abundance over time by imputing missing values to the phytoplankton time series, then plotting the absolute and relative biomass of each phytoplankton group in each lake during the study period. This was performed in the R language environment using the aregImpute function in the Hmisc package, and plotted using the ggplot2 package (Wickham, 2009; Harrell et al., 2015; R Core Team, 2018). We detected abrupt shifts in time series of log-transformed relative phytoplankton biomass and water chemistry variables using the MS Excel macro *Sequential Regime Shift Detector version 6.2* (SRSD) (Rodionov, 2004; 2006). Relative phytoplankton biomass was log-transformed using the decostand function in the vegan package (Oksanen et al., 2018). For the SRSD test, we set the significance level (α) to 0.05, the cut-off length (l) to 8, and Huber's weight parameter (h) to 6, following two studies of water chemistry and phytoplankton of Swedish lakes (Temnerud and Weyhenmeyer, 2008; Weyhenmeyer et al., 2013). When a cut-off length, (l, the minimum number of observations considered a stable regime) is chosen, the mean value and mean variance are calculated for the regime. Next, a range of difference is calculated using the regime mean, the critical value of the Student's t-test, the mean variance, and the regime length. Each following observation is sequentially tested to determine whether it falls outside this calculated range and is a statistically significant deviation from the current regime mean according to a t-test. If so, it is considered as the potential first year of a new regime, and if not, it is considered part of the current regime (Rodionov, 2004; 2006; Rodionov and Overland, 2005). Huber's weight parameter is a value by which outliers are multiplied so they are weighted by their inverse distance from the mean (Huber, 2005 cited in Temnerud and Weyhenmeyer, 2008). Autocorrelation of each variable was assessed using the Breusch-Godfrey test, which determines whether an observation is dependent upon that of the previous year AR1 (Breusch, 1978; Godfrey, 1978). This was performed in the R language environment using the bgtest function in the lmtest package (Zeileis and Hothorn, 2002; R Core Team, 2018). Results of the first SRSD were accepted if the variable was not autocorrelated. If a variable was found to be autocorrelated, a second SRSD test was performed using the same parameters as the first, but also prewhitening to filter out red noise (the first order autoregressive model AR1), and reducing the bias of the OLS estimator of the red noise coefficient rho using the Inverse Proportionality with 4 corrections (IP4) technique (Rodionov, 2006; 2015).

How has variability in phytoplankton biomass changed over the past 30 years?

We measured variability over time for each group in each lake by calculating rolling 3-, 5-, and 11-year windows of standard deviation of relative phytoplankton biomass, and plotting these over time to identify the variability within each group over the sampling period. It was decided that the 5-year window was most representative of variability. Rising standard deviation and other measures of variance have been shown to provide an indication of the potential occurrence of a regime shift (e.g. Carpenter et al., 2011). The calculations were performed with MS Excel, and results were plotted in the R language environment using the ggplot2 package (Wickham, 2009; R Core Team, 2018).

What is driving patterns of phytoplankton community composition across eight study lakes in south-central Ontario?

Redundancy Analyses (RDAs) (van den Wollenberg, 1977) were used to identify the environmental conditions that structure algal communities in the Dorset lakes. RDAs are an extension of multiple regression and allow a direct comparison between data matrices of interest, where the ordination of a table of response variables results in linear combinations of the variables in a table of predictor variables (Rao, 1964; Borcard et al., 2011). First, multiple regression of the response variables on the explanatory variables is carried out. Then, a principal component analysis (PCA) is performed on the matrix of fitted values to obtain eigenvalues and eigenvectors (Borcard et al., 2011). A PCA transforms the fitted values into linearly uncorrelated variables called principal components, which account for a descending amount of variance of the data (Hotelling, 1933; Jolliffe, 1990). Using the eigenvectors, site scores, species scores, and biplot scores are computed, which are the coordinates of the tips of the vectors representing, respectively, the study sites (points), the response variables (arrows), and the explanatory variables (arrows) (Borcard et al., 2011). The RDA with type II scaling is plotted so that the 3-dimensional diagram (correlation triplot) accounts for the greatest variance in the data and reveals similarities, dissimilarities and relationships between variables (ter Braak, 1994). The arrow length of environmental variables represents the relative effect size of the variable (Lepš and Šmilauer, 2003). The cosine of the angle between arrows represents the strength of linear correlation between them, and if the arrow directions coincide, the correlation is positive (Lepš and Šmilauer, 2003). An RDA was conducted at the regional level, including data from all lakes, as well as the individual lake level. Relative phytoplankton biomass was log-transformed, and a forward selection procedure was performed on a full model to identify significant predictor variables. A list of variables that were included in the full model used for forward selection can be seen in Table 1. This was done in the R language environment using the decostand function in the vegan package, and the forward.sel function in the packfor package (Dray et al., 2016; Oksanen et al., 2018; R Core Team, 2018). In addition, Moran Eigenvector Maps (MEMs) were calculated using the temporal component of the dataset (Legendre and Gauthier, 2014), and were included as predictor variables in our early analyses (Figure A1). MEMs represent temporal oscillations of varying scales during the study period, and were constructed to represent cyclical processes. However, when RDAs containing MEMs as predictors were compared with those without MEMs, we found that although the inclusion of MEMs raises the R^2_{adj} of the model, upon examination of the Variation Partitioning Analyses, the MEMs appear to be masking the relationships between phytoplankton variation and chemistry and were left out of the full model. The regional RDA including MEMs can be found in Figure A2. For each RDA, variables found to be multicollinear with other predictors were removed to arrive at the final model. This was done by calculating the Variance Inflation Factor (VIF) of each variable and removing the variable with the highest VIF statistic and least biological relevance until all remaining variables had a VIF below 10, following Borcard et al. (2011) and Hair et al. (2014), accompanied by a manual check that the remaining variables were uncorrelated. The VIF is a ratio describing the degree to which a variable is correlated with others in the dataset (Sokal and Rohlf, 2012). A higher VIF indicates redundancy, and that the variable may be preventing other better predictors from entering the model (Oksanen, 2012). These analyses were performed in the R language environment using the rda, vif.cca, and pcnm functions in the vegan package, and the cor.test function in the stats package (Oksanen et al., 2018; R Core Team, 2018). Variation Partitioning Analyses (VPAs) were conducted for each RDA to determine the proportion of variation explained by each category of predictors (Borcard et al., 1992). Our categories consisted of chemistry, climate, and teleconnections. We also included a morphometry category in the regional model. For the model including MEMs, they were grouped with teleconnections, as a maximum of four categories are allowed in VPAs. These analyses were performed in the R language environment using the varpart function in the vegan package, (Oksanen et al., 2018; R Core Team, 2018).

What are the drivers of phytoplankton groups in eight study lakes in south-central Ontario?

Locally weighted regression (loess) curves were applied to the untransformed time series of each phytoplankton group, climate variable, and chemistry variable to assess whether the change over time was linear or non-linear. A locally-weighted regression is useful for this function as it does not require a priori assumption of the data distribution (Cleveland and Devlin, 1988). A span width is specified, which defines the window of values to be considered “local” to the point being estimated. A low-degree polynomial (the default lambda is 2, quadratic) is fitted to the nearest specified span of points, and is weighted using a tri-cube function (Cleveland, 1979). The weight function gives greater weight to points nearer the x being fitted, and zero weight to points outside the range (Cleveland, 1979). Since the span width influences the bias and variance of the results, we applied a set of curves for each variable, setting the span width to be 0.10, 0.25, 0.50, 0.70, and 0.75 (between 10 and 75% of the data), to observe the range of resulting outputs. Relative phytoplankton biomass was log-transformed, and a forward selection procedure was applied to a full model of predictors. Using the significant variables, Multiple Linear Regression (MLR) models were developed for each phytoplankton group in each lake. MLRs simultaneously regress the response variable on several explanatory variables by minimizing the sum of squares between the observations and a line of best fit, with the goal of accounting for the variation in the response variable through a linear combination of the explanatory variables (Sokal and Rohlf, 2012). To model non-linear change over time, Generalized Additive Models (GAMs) were developed for each phytoplankton group in each lake, using both the restricted maximum likelihood (REML) and generalized cross validation (GCV) smoothing parameter estimation methods, the default thin plate regression splines, and specifying the Gaussian distribution family. GAMs describe a response variable through an additive combination of smooth functions of predictor variables (Lepš and Šmilauer, 2003). They are advantageous in non-linear modelling because no a priori assumption of distributions are required, the optimal smoothing parameter is automatically chosen to balance fit and smoothness, and they are a more flexible modelling approach as they use local rather than global values for fitting (Venables and Dichmont, 2004; Hastie and Tibshirani, 2006). However, none of these models were significant at the 0.05 alpha level, and are available in Table A3. These analyses were performed in the R language environment using the decostand function in the vegan package, the lm and loess functions in the stats package, and the gam function in the mgcv package, (Wood, 2017; Oksanen et al., 2018; R Core Team, 2018).

RESULTS

How has phytoplankton biomass changed over the past 30 years?

Diatoms and chrysophytes were the two dominant groups in our study lakes, each contributing up to 80% of the relative biomass during the study period (Figure 2). There was a shift from diatom to chrysophyte dominance over the course of the study period (Figure 2). Both dinoflagellates and cryptophytes had the greatest abundance during the first half of the study period, reaching 41% in 1990 in Heney Lake, and 38% in 1988 in Chub Lake respectively (Figure 2). Cyanobacteria peaked at 33% in Red Chalk Lake in 1985 and Chlorophytes peaked at 40% in Heney Lake in 1996, though both groups had relatively low biomass in our study lakes (Figure 2).

The breakpoint years of Diatoms and Chrysophytes were found to coincide in 1990, 1993, 1995, and 1999, with the mean relative biomass of each phytoplankton group shifting in opposite directions for each breakpoint (Table 1). Diatom and chrysophyte breakpoint years matched breakpoint years in dissolved organic carbon (DOC), ammonium (NH_4^+), and calcium. Diatoms abruptly shifted downwards and chrysophytes upwards coincidently with increases of DOC and NH_4^+, and a decrease of calcium. The abrupt decrease of chlorophytes in 2007 coincided with lower calcium and lower NH_4^+ (Table 1). Cryptophyte biomass abruptly decreased in 1990, 1992, and 2008, coinciding with higher DOC, lower iron, and higher sodium (Table 1). An abrupt increase of dinoflagellate biomass in 2006 coincided with an upward shift of DOC and downward shift of nitrate (NO_3^-) (Table 1). Cyanobacteria biomass had an abrupt increase in 2007, but this did not coincide with breakpoints in any of the water chemistry variables (Table 1).

How has variability in phytoplankton biomass changed over the past 30 years?

Most algal groups demonstrated a period of high variability during the late 1980s and early 1990s, followed by a gradual decrease and a second rise in the late 2000s (Figure 3). It is interesting to note that phytoplankton response to stressors of the system was not coherent by group nor by lake, as might be expected in lakes of such close proximity (Vogt et al., 2011). Diatoms and chrysophytes were the most variable groups, deviating on average by 8 and 13 standard deviations away from the long term mean, with different peak years for each lake, diatoms generally decreasing in variability with chrysophytes generally increasing, and both increasing during the last five years of the study period (Figure 3). Cyanobacteria, chlorophyte, and cryptophyte biomass had lower dispersion during the study period, generally peaking within the first ten years of the study period and remaining below 15 standard deviation points from the mean (Figure 3). Crosson Lake exhibited the most coherent pattern of phytoplankton variability, where diatom, dinoflagellate, and chrysophyte variability fluctuated similarly (Figure 3).

What is driving patterns of phytoplankton community composition across eight study lakes in south-central Ontario?

The regional RDA model explained 28% of the variation in the algal community biomass during the study period (Figure 4a, $R^2_{adj}= 0.244$, $N=270$, $P<0.05$). Diatoms were positively associated with deeper lakes that have higher calcium concentrations, lower ammonium concentrations, and higher pH, as well as less cloud cover and a negative phase of the Atlantic Multidecadal Oscillation (AMO) (Figure 4a). Conversely, chrysophytes were positively correlated with greater cloud cover, higher ammonium, and shallower more acidic lakes (Figure 4a). Dinoflagellates were associated with smaller lakes that have lower phosphorus and nitrate concentrations, as well as higher precipitation and a negative phase of the Pacific Decadal Oscillation (PDO) (Figure 4a). Cyanobacteria, chlorophytes, and cryptophytes seemed to be generalists within the region, which is evidenced by their closer proximity to the centroid (Figure 4a). The coloured points on the plot represent bins of 4 years of phytoplankton biomass. There is a temporal trend within the plot, suggesting that diatoms have decreased and chrysophytes have increased during the study period (Figure 4a). When we examined linear trends in our data, this finding was supported by a significant decrease in relative diatom biomass of 12.8% (representing a change of $47mm^3/m^3$), and a significant increase of 14.9% relative chrysophyte biomass during the study period (Table A4).

Drivers structuring phytoplankton biomass at the lake scale were similar to those of the regional RDA, with some notable exceptions. Contrary to the regional model, variables structuring diatom and chrysophyte biomass were not directly opposed for Crosson (Figure 7a, R^2_{adj}= 0.249, N=29, P<0.05), Harp (Figure 9a, R^2 adj= 0.327, N=29, P<0.05), Heney (Figure 10a, R^2_{adj}= 0.332, N=29, P<0.05), or Red Chalk Lake East (Figure 12a, R^2_{adj}= 0.323, N=29, P<0.05), in which chrysophytes were either generalists, or were positively correlated with sodium, DOC and higher pH. Blue Chalk (Figure 5a, R^2_{adj}= 0.382, N=29, P<0.05), Crosson, Harp, Plastic (Figure 11a, R^2_{adj}= 0.274, N=29, P<0.05), and Red Chalk East each shared common significant drivers for at least two phytoplankton groups as in the regional model. In lakes which either had one or no relationships in common with regional model, including both the worst (Dickie, Figure 8a, R^2_{adj}= 0.218, N=29, P<0.05) and best (Chub, Figure 6a, R^2_{adj}= 0.441, N=29, P<0.05) models, as well as Heney and Red Chalk Main (Figure 13a, R^2_{adj}= 0.237, N=29, P<0.05), silicate, nitrate, and DOC were important drivers. Phosphorus, DOC, and NO_3^- or NH_4^+ were important drivers in all lakes, and pH was important in four lakes. Local climate variables were significant drivers of five of the six phytoplankton groups in Red Chalk Main Lake, the deepest lake, and the only one for which climate was so important. The El Niño Southern Oscillation (ENSO) was the most frequently important teleconnection index, appearing in four lakes. Dickie (PDO and ENSO), Chub (Pacific/North American (PNA) and ENSO), Plastic (AMO and ENSO), and Harp (North Atlantic Oscillation (NAO) and AMO) Lakes each had two teleconnection indices as important for phytoplankton, while Blue Chalk (NAO), Heney (Quasi-Biennial Oscillation (QBO)), Red Chalk East (ENSO), and Red Chalk Main (NAO) Lakes each had one significant index (Figures 5 to 13).

In the regional VPA, primarily water chemistry variables structured algal community composition, contributing 33% to the total variation explained in the model (Figure 4b). The second most important group was morphology and chemistry, which explained 18% of the variation (Figure 4b). Within the region, significant chemistry variables included chloride (Cl^-), phosphorus, and sulphate (SO_4^{2-}), and morphological variables included maximum lake depth and surface area (Table 2). Teleconnections were the third greatest contributor to total variation explained, contributing 17% to the model (Figure 4b). The only teleconnection index significant at the regional scale was QBO (Table 2). Climate variables explained 11% of variation in the model (Figure 4b).

At the lake scale, the greatest proportion of variation was explained by water chemistry variables in all lakes, contributing between 32% (Red Chalk Lake Main basin) and 89% (Crosson Lake) to the models (Figures 5b to 13b). The most commonly significant chemistry variables included ammonium (NH_4^+) and nitrate (NO_3^-) (all lakes), DOC (six lakes), silicate (SiO_3^{2-}, four lakes), sulphate (SO_4^{2-}, three lakes), phosphorus (three lakes), pH (two lakes), and chloride (Cl^-, two lakes) (Table 2). Teleconnections contributed the second greatest proportion of variation explained in five lake models, ranging between 1.6% (Red Chalk East basin) and 27% (Heney Lake), and climate contributed the second greatest proportion in three lake models, ranging between 0% (Harp Lake) and 36% (Dickie Lake) (Figures 5b to 13b). Harp Lake was the only lake in which a shared term contributed a large proportion of variation to the model, where water chemistry together with teleconnections contributed 37% (Figure 9b). The most commonly significant teleconnection indices at the lake scale included ENSO (four lakes), AMO (three lakes), and PNA (two lakes), and climate variables included August water temperature (five lakes), cloud cover (four lakes), and air temperature (two lakes) (Table 2).

What are the drivers of phytoplankton groups in eight study lakes in south-central Ontario?

The loess curves revealed that all phytoplankton and water chemistry variables changed non-linearly over time. Regional MLR models of relative phytoplankton describe between 3 and 26% of the variation in biomass (Table 2). Maximum lake depth, cloud cover, precipitation, and three water chemistry variables were significant linear predictors of phytoplankton biomass in our study region. Diatom biomass was greater in deeper lakes with lower chloride concentrations (R^2_{adj}=0.26, P<<0.01, Table 2). Chrysophytes were more abundant and cryptophytes less abundant in shallower lakes with lower SO_4^{2-} concentrations and greater precipitation (R^2_{adj}=0.18, P<<0.01, Table 2). Chlorophyte biomass was greater with less cloud cover and greater phosphorus levels (R^2_{adj}=0.04, P=0.002, Table 2) and cyanobacteria biomass was greater with less cloud cover (R^2_{adj}=0.04, P=0.001, Table 2). There was significantly greater dinoflagellate biomass in lakes with smaller surface area and in a negative phase of the QBO (R^2_{adj}=0.13, P<<0.01, Table 2).

Lake level phytoplankton models explained between 10 and 60% of the variation in relative phytoplankton biomass (Table 2). The greatest congruency between the regional and lake models for variables structuring biomass was for diatom, chrysophyte, and dinoflagellate abundances. At the lake scale, Diatom biomass was significantly greater with higher concentrations of silicate, and lower concentrations of DOC, chloride, as well as when August water temperatures were cooler and during a positive phase of the NAO (R^2_{adj}=0.11-0.60, Table 2). Chrysophyte biomass was significantly greater with higher concentrations of nitrogen, chloride, and DOC, lower concentrations of silicate, and phosphorus, lower pH, and positive phases of the AMO and ENSO (R^2_{adj}=0.14-0.40, Table 2). Dinoflagellate biomass was significantly greater with high concentrations of DOC and chloride, low pH and nitrogen concentrations, and positive phases of the AMO and ENSO, and a negative phase of the PNA (R^2_{adj}=0.15-0.54, Table 2).

Cyanobacteria biomass was significantly greater with higher pH, higher concentrations of silicate and nitrate, low phosphorus concentrations, less cloud cover, and a positive phase of the PDO (R^2_{adj}=0.20-0.38, Table 2). Chlorophyte biomass was significantly greater with higher silicate concentrations and higher pH, lower nitrogen concentrations, less cloud cover, negative phases of the ENSO and PNA, and a positive phase of the PDO (R^2_{adj}=0.10-0.56, Table 2). Cryptophyte biomass was significantly greater with higher nitrate, phosphorus and sulphate concentrations, less cloud cover and precipitation, and a negative phase of the ENSO (R^2_{adj}=0.10-0.41, Table 2).

Water chemistry variables were important linear predictors of phytoplankton biomass, and most commonly included SO_4^{2-}, NO_3^-, pH, DOC, and SiO_3^{2-}. Climate variables and teleconnections were also important linear predictors, most commonly including cloud cover, August surface water temperature, ENSO, PDO, and AMO. None of the GAMs were significant and are included in Table A3.

DISCUSSION

Change in phytoplankton biomass and variability over time

Over time, the relative importance of diatoms in our study lakes diminished concurrently with the rise in importance of chrysophytes. Breakpoint years coincided for the majority of abrupt diatom and chrysophyte shifts. This suggests that these two most abundant groups are not only fluctuating in response to environmental changes but also relative to one another. Diatoms typically proliferate in the spring and autumn in oligotrophic temperate lakes, and chrysophytes tend to be most successful during periods of stratification (Reynolds, 1984; Sommer et al., 1986; Sandgren, 1988). This implies that either the duration of the stratification period lengthened, or that lake nutrient concentrations shifted over time to conditions favoured by chrysophytes. A lengthening stratification period could reflect earlier onset of stratification or a delay of autumn overturn, detrimental for diatoms by, respectively, accelerating sedimentation out of the epilimnion due to their reliance on mixed conditions (e.g. Lund, 1959; Lund et al., 1963; Reynolds, 1973; Reynolds and Wiseman, 1982), or reducing the window of overturn before winter, during which diatoms typically experience a second maximum (Sommer et al, 1986; Wetzel, 2001). Throughout the course of the ice free season, the uptake of nutrients by phytoplankton gradually depletes them from the epilimnion (Round, 1971; Morris, 1974; Reynolds, 1976; McCarthy, 1980), and subsequent sedimentation further sequesters nutrients in the hypolimnion (Reynolds, 1984). Thus, there is a general trend during the ice-free season from faster-growing r-selected species able to take advantage of the abundant nutrients towards slower-growing K-selected species that are more efficient in the utilization of lower nutrient concentrations (Banse, 1976; Kilham and Kilham, 1980; Sommer, 1981; Reynolds, 1984; Sommer et al., 1986; Sommer et al., 2012). The relative displacement of diatoms by chrysophytes could also reflect a shift in the proportion of nutrients over time towards conditions that are favoured by chrysophytes. Diatom and chrysophyte breakpoints coincide with abrupt shifts in ammonia (NH_4^+), dissolved organic carbon (DOC), and total phosphorus (TP). Diatom abundance reached a maximum and chrysophytes a minimum in Harp Lake, which had one of the highest mean TP concentrations in the study area. Greater TP levels favour the growth of faster growing smaller celled and unicellular species reflecting the relative efficiency of a larger surface area to volume ratio, and growth structure (Reynolds, 1984; Stockner, 1991). Both diatoms and chrysophytes have unicellular and colonial forms, and the colonial metalimnetic species would be favoured during stratification due to their access to nutrients (Sandgren, 1988). At this point we are unable to determine whether the shift of dominance from diatoms to chrysophytes reflects a shift from unicellular to colonial taxa. Chrysophytes increased during the study period, and were negatively correlated with TP. This is consistent with chrysophytes proliferating in low nutrient conditions (de M Huszar and Caraco, 1998), and supports their ability to dominate the later summer period of algal growth.

Dinoflagellates were the third most abundant group during the study period, and loosely mirrored the pattern of diatom abundance. They have a relatively slow generation time, are flagellated, and reach maximum population development during the warmest time of year (Padisak et al., 1998). Coupled with their K-selected growth strategy, dinoflagellates are also relatively large, and despite their ability for luxury P consumption (Heaney and Talling, 1980; Sommer, 1981), their lower SA/V ratio gives them a disadvantage in competition with smaller algae in early succession (Sandgren, 1988). However, dinoflagellates were not significantly correlated with TP in our lakes, similar to what de M Huszar and Caraco (1998) found in Wisconsin lakes.

Considering the similarity between dinoflagellate and chrysophyte growth strategies, we might expect similar temporal fluctuations in abundance. Dinoflagellate abundance may have been lower because of chrysophytes' competitive advantage in obtaining nutrition during an extended stratified season. Dinoflagellates abruptly increased with greater DOC and a reduction of nitrate (NO_3^-). Dinoflagellates have a low carbon uptake rate and low photosynthate production, which is more rapid at the beginning of the season (Sandgren, 1988) and declines as the season progresses and nutrients become scarcer. Dinoflagellates are also known to prefer hard water, which may be another factor preventing their reaching greater relative abundances in our lakes (Reynolds, 1984).

Cyanobacteria reached a maximum of 33% of the phytoplankton biomass, the lowest maximum of our six groups. This is surprising because many of the factors we would expect to favour chrysophyte growth would also favour cyanobacteria, namely stable hydrographic conditions due to their ability to regulate buoyancy (Paerl, 1988), increased temperatures since their optimal growth temperatures are higher than those for other phytoplankton, between 25-40°C when others are around 23-25°C (Paerl and Huisman, 2008; 2009; Reynolds, 1984), and increased inputs of organic matter as cyanobacteria can excrete siderochrome which allow the chelation of trace metals and confer competitive advantage (Murphy et al., 1976; Simpson and Neilands, 1976). Perhaps the fact that our study lakes are P-limited oligotrophic systems (Paterson et al., 2009) limits the ability of cyanobacteria to succeed, since dominance is commonly found in eutrophic lakes (Sommer et al., 1986; Pearl, 1988; Reynolds, 1984). Cyanobacteria reached maximum total biomass in Harp Lake, which had one of the greatest mean concentrations of TP. Another important factor is that cyanobacteria generally prefer neutral to alkaline water (Shapiro, 1973; Padisak et al., 1998) and are replaced by chrysophytes and chlorophytes under acidic conditions (Shapiro, 1973). Our lakes have mean pH from 5.6 to 6.7 and increased by an average of 0.35 units during the study period. Cyanobacteria biomass was on average greater in the lakes with pH>6, the biologically relevant threshold between acidic and nonacidic lakes (Fogg et al., 1973; Neary et al., 1990; Doka et al., 1997).

Chlorophytes shared a break year with calcium and ammonium (NH_4^+). Chlorophytes did not dominate any lake community during the study period, which is typical for temperate lakes, except in nutrient extremes (Watson et al., 1997; Jeppesen et al., 2005). They reached a maximum in Heney Lake, which had the lowest mean NH_4^+ concentration. Chlorophytes are the most varied algal group, encompassing microalgal, flagellar, colonial, and filamentous forms, though it is likely that only the microalgal, nonmotile green algae, and desmids are in our study lakes, as the flagellar forms are characteristic of eutrophic water bodies (Happey-Wood, 1988). This diverse group has vernal, early-summer, mid-summer, and late-summer assemblages in temperate lakes (Happey-Wood, 1988), and the advantage shifting between assemblages as conditions changed may have been the reason for a lack of dramatic change in relative abundance during the study period.

Cryptophytes are a fast-growing group which develop in spring and early summer after the clear water phase (Sommer et al., 1986). Cryptophytes reached a maximum relative abundance in Chub Lake in 1988. Population peaks follow disturbances such as wind-driven mixing, and opportunistically increase in abundance when other phytoplankton groups are declining (Sandgren, 1988). Cryptophyte abundance decreased with greater DOC and sodium concentrations, and lower iron. DOC and sodium significantly increased between 1984 and 2003, but chrysophyte population abundances fluctuation seemed to reach approximately the same relative abundances from year to year without an obvious monotonic interannual trend. This could perhaps be reflecting annual dominance changes between the other groups. Much of the variation in fast growing opportunistic species is lost when we look at the entire season as an ice-free mean.

Drivers of community composition

Water chemistry

Limiting nutrients

Nutrient concentrations integrate the hydrological changes to a lake, such as precipitation, catchment runoff, and lake discharge (Fraterrigo and Downing, 2008; Cardille et al., 2009; Jeppesen et al., 2011). In our regional model, 33% of the variation in phytoplankton biomass was explained by water chemistry. Approximately 20 elements are required for the growth and healthy functioning of vegetative tissues (Campbell et al., 2008). Macronutrients that were significant drivers in our models included P, N, S, Ca, Na, Cl, and DOC. Micronutrients included Fe and Si. P, N, and Si, and are usually scarce enough in oligotrophic freshwaters to be considered limiting according to Liebig's Law of the Minimum (Pearsall, 1932; Odum, 1971). Our study lakes have minimal anthropogenic impact, with stable P loading (MWC, 2018) and are considered P-limited oligotrophic systems (Smith, 1982; Paterson et al., 2009).

Phosphorus is an essential macronutrient for all plants, and is a component of nucleic acids and ATP (Campbell et al., 2008). Regionally, phosphorus decreased by 0.87 μg/L during the study period, and was a significant driver of all six groups in lake level RDA models. Phosphorus is the major limiting nutrient in freshwater systems (Redfield, 1958; Schindler, 1977). In thermally stratifying oligotrophic lakes, phosphorus inputs influence the potential to switch between clear and turbid water regimes, which depends on the interaction between iron and oxygen in the hypolimnion (Caraco et al., 1991; Orihel et al., 2016). The form of phosphorus available to phytoplankton is orthophosphate (PO_4^{3-}) (Wetzel, 2001). At lower phosphorus inputs, phytoplankton production, sedimentation, and oxygen consumption are low, which allows iron in the oxidized state to bind to phosphorus, precipitating as insoluble ferric orthophosphate ($FePO_4$) and sequestering the nutrient in the sediments. When lake phosphorus inputs are higher, phytoplankton growth and subsequent decomposition are high, oxygen in the hypolimnion is depleted, and iron in the reduced state does not bind to phosphorus, which dissolves, recycling the nutrient (Folke et al., 2004). We measured phytoplankton variability over time because we thought it might reveal the likelihood of a regime shift in our lakes, which involves gradual changes in the environment leading to transitions among alternative stable states in food webs, driving abrupt reorganizations in the ecosystem (Scheffer et al., 1993; Carpenter and Brock, 2006; Ives and Carpenter, 2007; Carpenter et al., 2008). However, the mean total phosphorus concentration in our lakes ranged between 4.7 and 9.7 μg/L, classifying them as oligotrophic (CCME, 2004), and though relatively shallow, our lakes are deeper than the more susceptible “shallow lakes” in the literature of up to 4 m, and thus are unlikely to shift into a turbid eutrophic state (Janse et al., 2008; Koh et al., 2018). However, tracking variability was helpful in highlighting intervals of disturbance during our study period.

Locally, both NH_4^+ and NO_3^- were significant drivers of each phytoplankton group. Nitrogen is a component of chlorophyll, nucleic acids, and amino acids and thus is an essential macronutrient for protein synthesis and reproduction in phytoplankton (Campbell et al., 2008). When phosphorus concentrations are increased, nitrogen becomes the most limiting aquatic nutrient (Redfield, 1958; Wetzel, 2001). The volume of nitrogen inputs to a lake depends on the amount of regional anthropogenic nitrogen emissions (absorbed by precipitation), the productivity of the catchment in terms of leaf litter, and the proportion of wetlands in the catchment (Bergstrom et al., 2005; Dillon and Molot, 2005; Kortelainen et al., 2006). Nitrate (NO_3^-) is the common form of nitrogen entering freshwater lakes from the catchment through runoff and precipitation (Wetzel, 2001). Though nitrate is assimilated by phytoplankton, ammonium (NH_4^+) is the most energetically favourable substrate for cellular reactions as nitrate and nitrite (NO_2^-) must be reduced (Morris, 1974; Owens and Esaias, 1976; McCarthy, 1980). In our study lakes, total nitrogen ranged from 197 to 347 μg/L, and regionally, NH_4^+ increased by 17 μg/L in the first half of the study period, with no significant change during the second half. In the study region, anthropogenic nitrogen inputs from shoreline development are low (Molot and Dillon, 1993). Watmough and colleagues (2005) hypothesized that the increase could be related to climate-change driven mineralization and flushing of nitrogen into streams during warmer periods. Regionally, diatoms were more abundant in lakes with lower, and chrysophytes with higher NH_4^+ levels. Turnover rates for NH_4^+ are faster within the water column, and for NO_3^- are faster in lake sediments (Wetzel, 2001). Diatoms may have been more abundant with lower NH_4^+ levels because they rely on mixed conditions, which brings up NO_3^-. Greater chrysophyte abundances may have been associated with higher NH_4^+ levels because of their faster NH_4^+ assimilation rate. Dinoflagellates were the only group with lower abundance in greater nitrogen concentrations. This group's relatively large cell sizes allow it to outcompete the smaller celled algae when P and N are lowest.

Silicon is a common terrestrial element, being the principal component of more than 95% of rocks (Ingri, 1978). Our study area is on the Precambrian Shield in an area which has granitic bedrock, which is on average 73% silicon (Blatt and Tracey, 1997; Keller, 2007). Silicon is most commonly found and assimilated as silicon dioxide or silica (SiO_2) (Werner, 1977). Diatom abundance was greater in lakes with higher silica concentrations, but chrysophytes were correlated with lower silica concentrations. Silica is an essential element for diatoms and scaled chrysophytes, as it is used to form the frustules and scales. However, silica is not as readily recycled as nitrogen and phosphorus (Bailey-Watts, 1976; Lehman, 1980; Paasche, 1980), and typically depletes during the ice-free season, so levels might be lower during the stratified period during which chrysophytes proliferate. Lake pH affects the availability of silica, with lower concentrations found in more acidic lakes (Hutchinson, 1957; Willén, 1991). Silica is not only a component of the protective covering of a diatom, with about 90% of assimilated silica going towards the frustule (Paasche, 1980), but is also a component of the nucleus, nucleolus, chloroplast, golgi apparatus, vacuoles, ribosomes and mitochondria, and therefore halts the functioning of diatoms when unavailable (Sullivan and Volcani, 1981) as they are unable to store it (Willén, 1991).

Acid rain

Chrysophyte abundance was associated with a lower pH at the regional scale. However, chrysophytes increased regionally, and the mean pH increased during the study period. Chrysophytes prefer neutral to acidic waters (Sandgren, 1988). The greatest increases in pH were in Dickie, Harp, and Crosson lakes, but the relative abundance of chrysophytes did not significantly change in these lakes. Although our lakes are suitable for chrysophyte growth as they ranged in pH from 5.6 to 6.7, pH does not seem to be a driving factor for chrysophyte biomass. Relative diatom abundance was associated with a higher pH at the regional scale. Diatom abundance decreased while our lakes became less acidic during the study period. Diatoms prefer lakes within a pH range of about 4.5 to 7.5 (Birks et al., 1990; Dixit et al., 1992), but tolerance varies by taxon (Weckström et al., 1997; Cameron et al., 1999; Stoermer and Smol, 1999), and responses to changes in pH can be nonlinear (Birks et al., 1990). The pH became more alkaline in Chub, Crosson, Dickie, Harp, and Red Chalk Lakes, but of those lakes, diatoms saw significant (negative) change in only Harp and Red Chalk, suggesting that pH is not a direct driver of diatom abundance. At the local scale, cyanobacteria abundance was positively correlated with pH in Red Chalk Lake and negatively correlated with pH in Chub Lake. Red Chalk Lake was one of the most alkaline with a mean pH of 6.3, and Chub one of the most acidic with a mean pH of 5.7. This aligns with the finding that cyanobacteria prefer more alkaline lakes (Shapiro, 1973; Padisak et al., 1998). Relative cyanobacteria abundance increased in Harp and Heney Lakes, and pH increased in Harp but did not change in Heney. This would also suggest that lake pH was not a direct driver of cyanobacteria abundance. Cryptophytes were associated with more alkaline water in Plastic Lake. pH did not significantly change in this lake, but cryptophytes became relatively less abundant. This suggests that cryptophytes may be responding to variables associated with a changing pH, such as the rate of physiological/metabolic reactions, or availability of nutrients. Chlorophyte abundance was associated with greater alkalinity in Chub Lake. Chlorophytes are a very diverse group, and have a wide tolerance of pH (Sandgren, 1988). Though the lake became more alkaline, there was no significant change in chlorophyte abundance in this lake, suggesting that this RDA model may have been showing the clearer relationship between pH and cyanobacteria.

Lake acidification has been a concern in this region since the 1960s (Likens et al., 1996). Sulphur dioxide (SO_2), nitrogen oxides (NO_X), and other atmospheric pollutants from fossil fuel combustion bind with H^+ from water vapour to acidify precipitation. Acidification also occurs through dry deposition on catchment soils, which pulls H^+ from the soil solution. The most vulnerable lakes are low-order headwater lakes with unreactive geology, and base-poor soils (Quinlan et al., 2003), owing to their reduced buffering capacity. Our study lakes are headwater lakes with the exception of Red Chalk which is downstream of Blue Chalk Lake (Paterson et al., 2008), and the underlying bedrock is granitic (Keller, 2007), which is slow-weathering. The soils in our region are acidic podzols and brunisols typically less than 1 metre deep (Watmough and Aherne, 2008). At lower pH values, many of the negatively charged sites on soil surfaces are bound with acidic cations (strong, acid-forming) such as hydrogen (H^+), iron (Fe^{2+}), and aluminum (Al^{3+}), however runoff from acidic soils is unlikely to acidify freshwaters unless strong anions are present (such as sulphate and nitrate) (Reuss et al., 1987). Governmental action for emissions regulations resulted in a 50% reduction in sulphur deposition in 44 sampled lakes of the Muskoka-Haliburton region between 1981 and 2005 (Palmer et al., 2011), and emissions were successfully reduced to 50% those of 1980 in 1993 (Nixon and Curran, 1998; Stoddard et al., 1999; Keller et al., 2011). We found that sulphate concentration decreased in our lakes by 53%, from an average of 7.03 to 3.29 mg/L during the study period. However, lake recovery has been slow compared with what would be expected from the degree of emissions reductions. The pH of precipitation became less acidic by about 0.8 pH units since 1980 (Watmough et al., 2016), but the pH of our lakes only increased by 0.22 units since 1984. The pH in 33% of our lakes (four of eight compared with six at the beginning of the study period) increased from below to above 6, a biologically significant threshold separating acidic and nonacidic lakes (Holt et al., 2003). Chub, Crosson, Heney, and Plastic Lakes are still acidic.

Recovery from acidification has been slower partly due to soil cation exchange and the reduction of Cation Exchange Capacity (CEC). The CEC refers to the availability of negatively charged locations on the surfaces of soil particles and the ability of strong cations to replace weak cations bound at those locations. Base cations are the weakest acid cations in soils, and the main ones are calcium (Ca^{2+}), magnesium (Mg^{2+}), sodium (Na^{+}), and potassium (K^{+}) (Rayment and Higginson, 1992; Berthrong et al., 2009). Strong anions such as nitrate (NO_3^{-}), sulphate (SO_4^{2-}), and dihydrogen phosphate ($H_2PO_4^{-}$) transport cations from soils where they are leached into a lake (Campbell et al., 2008). Decreased deposition reduced direct acidification, but the loss of base cations throughout the course of previous emissions faster than the rate of natural replenishment depleted the reserve of cations in the soil (Reuss et al., 1987). This limited the improvement of acid neutralising capacity and pH recovery of lakes (Palmer et al., 2011).

Calcium depletion

Calcium enters lakes through the weathering of rocks, runoff, and atmospheric depositions (Watmough and Aherne, 2008). Our study lakes had a mean calcium concentration of between 1.6 and 2.6 mg/L, and are considered softwater lakes (OMOE, 1974; Health Canada, 2009). The lakes in our study region are within the Precambrian Shield, whose granitic bedrock and noncarbonate till have low calcium levels (on average 1.8% calcium oxide) and a very slow weathering rate (Shaw et al., 1967; Blatt and Tracy, 1997; Jeffries and Snyder, 1983; Urquizo et al., 2000; Keller, 2007). These lakes are particularly sensitive to acid rain because calcium carbonate is an important component in the carbon dioxide/ bicarbonate/ carbonate equilibrium (Butler, 1992). The absence of calcium hinders the ability of lake water to buffer pH fluctuations (Cole and Prairie, 2009). Acid rain intensified between 1960-1970 and leached the calcium from catchment soils to lakes faster than it could be replenished by natural inputs (Palmer et al., 2011; Jeziorski et al., 2014). Calcium leaching from catchment soils initially increased lake calcium concentrations, but as the stored calcium pool was depleted, lake calcium steadily declined (Likens et al., 1996; Stoddard et al., 1999; Keller et al., 2001). Tree removal, forest fire suppression, and a warming climate currently contribute to further reductions of calcium input to lakes and rivers in the region (Bayley et al., 1992, Schindler et al., 1996; France et al., 2000; Watmough and Aherne, 2008; Berthrong et al., 2009; Yao et al., 2009). In Plastic Lake, ice-free pH has remained relatively stable since the 1850s, from 5.7 around the time of settlement of the region, to about 5.8 in 2006, but calcium concentrations fell between 1980-2006 from 2.2 to 1.4 mg/L, and calcium declined in 36 Muskoka region lakes by a mean of 13% during that time (Jeziorski et al., 2008). The continued depletion of calcium has resulted in the decline of *Daphnia pulex,* a keystone herbivore, and the gradual increase of another large cladoceran with a tenth of the calcium requirement (Jeziorski et al., 2015), *Holopedium glacialis*, a process which has been termed lake jellification, due to the jelly-like polysaccharide coating of *Holopedium* (Jeziorski et al., 2015). *Daphnia* are stressed when calcium concentrations are under 2.5 mg/L, and die in lakes with less than 1.5 mg/L (Hessen et al., 2000; Ashforth and Yan, 2008; Jeziorski et al., 2008). Currently, six of our eight study lakes have calcium concentrations below 2.5 mg/L, and three are below 1.5 mg/L. A study of 36 Muskoka region lakes revealed that during the 1980s, there was one lake below the 1.5 mg/L threshold, compared with five lakes in 2006 (Jeziorski et al., 2008). Currently, 56% of 187 sampled lakes in Muskoka have calcium levels under 2.5 mg/L (MWC, 2018). By 2005, the relative abundance of Daphnia decreased in 60% of 770 lakes across Ontario (including 49 from our study region) with less than 1.5 mg/L of calcium, compared with pre-settlement abundances (Jeziorski et al., 2008). During the study period, calcium concentration declined by 21% in our lakes. In 31 south-central Ontario lakes between 1980-2005, Ca declined by a median 25% and *Holopedium* relative abundance increased by 3-37% in 17 of the 26 lakes uninvaded by *Bythotrephes* (Jeziorski et al., 2015). During the study period, calcium concentrations increased in Dickie and Harp Lakes, reflecting the addition of calcium chloride ($CaCl_2$) dust suppressant to the nearby roads (Yao et al., 2011). However it was not a significant driver of phytoplankton groups at the lake level. Calcium was positively associated with diatom abundance in Red Chalk Lake. Calcium decreased in this lake, but diatom biomass did not significantly change during the study period. So although calcium influences herbivore abundances, it is probably not directly affecting phytoplankton in our lakes.

Lake brownification

Lake transparency is a measure of the extent to which light penetrates the water column, or the amount of suspended particles, including phytoplankton, sediments, particulates from runoff, and organic matter in the water column. Dissolved Organic Carbon (DOC) is a main determinant of lake transparency and colour and therefore plays a large role in aspects of lake structure including epilimnion thickness (Cahill et al., 2005; Keller et al., 2006), and thermocline depth (Fee et al., 1996; Pérez-Fuentetaja et al., 1999). Coloured DOC best absorbs short wavelengths of light, ranging from blue to ultraviolet (Mostofa et al., 2013), which results in UV protection for phytoplankton and differential lake warming. The chromophores in dissolved organic matter (DOM) absorb solar radiation with a wavelength above 290 nm (Wetzel, 2001), and particularly attenuate UV-B (280-320 nm), UV-A (320-400 nm), and blue photosynthetically active radiation (400-495 nm) (Vincent and Roy, 1993; Kirk 1994a,b; Morris et al., 1995). This reduces negative impacts to phytoplankton due to UV exposure, which includes DNA damage, reduced capability of nutrient uptake, and depression of physiological processes (Vincent and Roy, 1993; Karentz et al., 1994; Moeller, 1994; Leu et al., 2007). In a study that modelled light attenuation in 65 glacial lakes across North America, when DOC levels are below 1-2 mg/L, the 1% attenuation depths are at their greatest, and are sensitive to small changes in DOC concentration (Williamson et al., 1996). The impacts on aquatic ecosystems may be nonlinear; recent studies have suggested that primary production becomes limited through light attenuation above a certain DOC concentration threshold, which ranges between 4.8 and 10 mg/L (Hanson et al., 2003; Seekell et al., 2015a,b; Solomon et al., 2015). Mean DOC concentration in our lakes ranged between 1.9 and 5.4 mg/L, and increased by 36% during the study period. The reduced light availability due to an increase in lake colour may result in a shift of lake productivity from phototrophic production towards light-independent heterotrophic production (Karlsson et al., 2009; Thrane et al., 2016). In addition to influencing the light environment in a lake (Fee et al., 1996; Thrane et al., 2014), DOC also affects lake physics (Keller et al., 2006; 2008). Coloured DOC absorbs solar radiation at the lake surface, warming the upper water layers at a much faster rate than lower layers, and thereby increasing the thermal density gradient and the amount of energy required for mixing (Snucins and Gunn, 2000). In 28% of 2,332 surveyed lakes representing 11,500 lakes across North America, the mean DOC concentration was 4.89 mg/L and the thermocline began within 1 m of the surface (Williamson et al., 1996). A shallow thermocline may result in the isolation of nonmotile phytoplankton in the epilimnion and their exposure to harmful UV radiation (Vincent and Roy, 1993; Milot-Roy and Vincent, 1994). In our study lakes, Palmer and colleagues (2014) found that increased DOC concentrations resulted in shallower thermoclines and greater thermal stability of the water column with delayed autumn mixing. Because of the impacts to thermal structure, humic lakes tend to have greater abundances of flagellate phytoplankton such as chrysophytes and cyanobacteria (Drakare et al., 2002; Willén, 2003) as well as phytoplankton adapted to low light conditions such as diatoms, cyanobacteria, chlorophytes, and cryptophytes (Richardson et al., 1983; Litchman, 2000; Jager et al., 2008; Winder et al., 2012; Maileht et al., 2013; Lenard and Ejankowski, 2017). We did not see an increasing trend in low-light adapted groups, which could be because DOC levels are not high enough in our study lakes to limit light. However, the increase of chrysophytes could have been due to the development of an extended stratification period and shallower thermocline during the study period. The increased carbon source could also have stimulated bacterial production (Ask et al., 2009) which provide an advantage for mixotrophic phytoplankton like chrysophytes (Urrutia-Cordero et al., 2017).

Over the long term, DOC concentrations and water colour have increased (brownification) across northern Europe and North America (Evans et al., 2005; Monteith et al., 2007; Palmer et al., 2011; Granéli, 2012; Hansson et al., 2013; Solomon et al., 2015), with hypothesized regional drivers in the literature including air temperature (Freeman et al., 2001; Evans et al., 2005; Larsen et al., 2011), precipitation (Hongve et al., 2004), atmospheric CO_2 concentration (Freeman et al., 2004), sulphur deposition (Monteith et al., 2007), and interactions between these drivers (Fenner et al., 2007; Clark et al., 2009; Clark et al., 2010). Lake pH and DOC concentrations have increased in our study lakes, suggesting that recovery from acid rain may be a contributing factor towards browning. Two recent studies have also found that the increase in DOC was correlated with changes in air temperature, precipitation, and sulphate deposition (Zhang et al., 2010; Palmer et al., 2014). The increase of summer and winter radiation and air temperature in the region accelerates the production of organic matter, its decomposition into DOC, and its release from soils (Freeman et al., 2001; Keller et al., 2008), and precipitation events transport DOC into lakes (Dillon and Molot, 1997; Correll et al., 2001; Keller et al., 2008).

Lake morphometry

Morphometry alone (comprising maximum lake depth and lake surface area) explained 8.7% of the total variation in the regional model, but morphometry and chemistry together contributed 18% to total variation explained. Lake morphometry is associated with water retention time and circulation dynamics. Water retention time is the ratio of lake volume to the flow in or out, which lengthens with increasing lake volume and depth (Quinn, 1992; Brooks et al., 2014).

Retention time impacts nutrient concentrations, with lakes of longer retention times retaining nutrients such as phosphorus (Brett and Benjamin, 2008; Kõiv et al., 2011), nitrogen (Kaste et al., 2003; Brooks et al., 2014) and base cations (Schindler et al., 1996) for longer, and reacting to droughts differently compared with lakes of faster retention times (Anderson et al., 2001; Pham et al., 2008; Romo et al., 2013). In larger lakes, wind is a major factor in determining mixing depth, with lakes of a longer fetch having more effective mixing (Hutchinson, 1957; Shuter et al., 1983; Patalas, 1984; Hanna, 1990). Wind-driven transport of surface heat to deeper layers determines the epilimnetic depth and the heat retention of the water column (Hutchinson, 1957; Wetzel, 2001). In smaller lakes (<10 km^2), wind-induced mixing is less important for regulating thermal structure than it is for circulation (Mazumder and Taylor, 1990). In the small (<5 km^2) Boreal Shield lakes, thermal structure is usually most influenced by lake transparency and not through variations in weather (Fee et al., 1996). Our study lakes are all less than 1 km^2, and all are dimictic except for Dickie Lake which is monomictic (Paterson et al., 2008; Palmer et al., 2014). In our regional model, diatom abundance was positively correlated with deeper lakes. Diatoms are found to have active chlorophyll even in deeper strata, and can grow at greater depths (Litchman, 2000; Jager et al., 2008; Maileht et al., 2013). Diatoms thrive in mixed environments. Because of their heavy frustules, they are reliant on water turbulence for maintenance in the epilimnion, and will aggregate in upwellings of Langmuir rotations (Reynolds, 1984). Chrysophyte abundance was positively correlated with shallower lakes. Chrysophytes can also thrive in mixed conditions, but can excel in stable and shallow epilimnia due to their ability for diel vertical movement (Sandgren, 1988). Dinoflagellate abundance was correlated with smaller lake area. Dinoflagellates are sensitive to abrupt changes in wind intensity, especially during the nocturnal period of reproduction (Pollingher, 1988). Abrupt wind changes might be proportionately more disruptive in smaller lakes (Mazumder and Taylor, 1990; Tanentzap, 2006).

Climate

Temperature

Climate variables including air temperature, precipitation, and cloud cover, explained 11% of the variation in our models. Regionally, air temperature became significantly warmer in each season. Temperature can directly control phytoplankton growth. During spring and autumn overturn when nutrient availability is high, phytoplankton production is controlled by water temperature, light availability, and the length of the ice-free period (Carlson, 1977; Fee et al., 1992; Shuter and Ing, 1997). When nutrient availability is lower, productivity varies with nutrient levels and is relatively less sensitive to changes in temperature (Shuter and Ing, 1997; Kling et al., 2003). Photosynthetic and metabolic rates are temperature dependent (Reynolds, 1984), so warmer temperatures may increase the growth rates of bacteria and phytoplankton (Goldman and Carpenter, 1974; Morris and Lewis, 1992; Fuh-Kwo and Ducklow, 1994). Regier and colleagues (1990) found that a 10°C increase in water temperature might quadruple primary production in the Great Lakes. Increasing temperatures are also expected to result in changes to community composition (Findlay et al., 2001; Strecker et al., 2004). The increase in growth rates may confer an advantage to phytoplankton with faster generation times, as well as those with smaller cell sizes (Rasconi et al., 2015). Species sizes overlap within the groups studied, so we are unable to make a more specific statement than that unicellular forms may be favoured over colonial or filamentous forms. As air temperatures become warmer, epilimnetic temperatures are expected to increase, but hypolimnetic temperatures may decrease in lakes with greater DOC concentrations (De Stasio et al., 1996; Snucins and Gunn, 2000; Keller et al., 2005). Between 1982 and 2005, 80% of the increase in autumn air temperature was transmitted to the epilimnia of our study lakes, and 50% to the metalimnia (Palmer et al., 2014). The increases were not reflected in the hypolimnetic temperatures, which are controlled by spring temperatures in dimictic lakes (Hondzo and Stefan, 1993), so phytoplankton that tend to live closer to the lake surface, and which prefer warmer temperatures might be favoured. Regionally, the trend of total phytoplankton biomass increased by approximately 19 mm^3/m^3 per year during the study period, so temperature may have directly influenced algal growth in our lakes. The increase may have been so slight (biomass ranged between approximately 3,000 and 39,000 mm^3/m^3) by being offset by decreased light availability for photosynthesis on cloudy days. Adams and colleagues (1993) found this mechanism in action in their Wisconsin study lakes. In our lakes, spring cloud cover significantly decreased but summer cloud cover significantly increased regionally. It is likely that the direct effects of temperature on phytoplankton abundance will have less of an impact than the effects of nutrient availability, and grazer abundance (McKee et al., 2002; Moss et al., 2003).

Climate variables may govern phytoplankton indirectly by affecting the physical aspects of lakes, including ice phenology, thermal profile, hydrology, and water chemistry (Gerten and Adrian, 2002; Adrian et al., 2009). Air temperature is closely linked with the thermal structure of North American lakes (Shuter et al., 1983). Lake heating is primarily radiative (Wetzel, 2001), and colder epilimnion temperatures were correlated with deeper mixing in a study of Ontario lakes (Keller, 2007), as mixing occurs more easily with a smaller temperature and density difference between layers. In a study of our lakes in 2014, Palmer and colleagues identified that between 1982 and 2005, lakes became warmer and more stable with greater warming of upper layers, and shallower mixing depths (2014). At the regional scale, September air temperature and DOC concentrations were the most important factors affecting mixing depth, whereas pH and DOC explained the most variability among lakes (Palmer et al., 2014). As discussed previously, DOC attenuates solar radiation and results in shallower more pronounced thermal gradients developing (Holloway, 1980; Fee et al., 1996; Pérez-Fuentetaja et al., 1999; Cahill et al., 2005). pH affects the photodegradation rate of DOC (Gennings et al., 2001). The warmer air temperatures, shallower mixing depths, and more stable thermal gradients likely resulted in delayed autumn overturn and ice-on (Palmer et al., 2014).

An alteration in ice phenology might change the timing, intensity, and composition of phytoplankton blooms (Gerten and Adrian, 2002). Between 1975 and 2004, the warming climate in the Great Lakes region has resulted in ice-off occurring 6.3 days earlier and ice-on occurring 9.9 days later (Jensen et al., 2007). Kling and colleagues hypothesized that a longer stratification period could shift the phytoplankton community towards blue-green algae, as they expected earlier ice-off and stratification (Kling et al., 2003), causing diatoms to decline. The timing of spring ice-off and mixing are dependent on winter and spring conditions (Hondzo and Stefan, 1993; Hewitt et al., 2018). In our study lakes, changes in air temperature and lake physics occurred in autumn, with the greatest increases in air temperature occurring after the early 1990s (Palmer et al., 2014). Based on models for Lake Mendota, Robertson and Ragotskie (1990) estimated that a 3 to 6°C increase in autumn air temperatures would delay overturn by 5 to 10 days. Because autumn overturn and ice-on were likely delayed in our study lakes, extending the growth period of late summer phytoplankton. During that time, phytoplankton that are better competitors for nutrients might be favoured, since they are depleted by the end of the growing season without further inputs from precipitation events. Diatoms proliferate in cooler temperatures. They dominate the ice-free period of Char and Meretta Lakes in Northern Canada (Kalff et al., 1975), and bloom in spring and autumn in temperate lakes. A delay in autumn overturn would shorten their growth period as they require mixed conditions to keep them in the epilimnion. Diatoms declined in the deepest lakes (Harp and Red Chalk Main). In Red Chalk, diatoms varied linearly with temperature, DOC, and ammonium (Table 2). Diatoms have decreased survival at lower depths and with decreased mixing, but are good competitors in environments with lower TP. Diatoms increased in Blue Chalk, Chub, and Dickie Lakes, which were among the lowest P concentrations.

Changes in temperature also indirectly affect phytoplankton through water chemistry. Warmer air temperatures have been shown to aid the recovery of acidified lakes by increasing base cation concentrations (Keller, 2007). Studies of alpine European lakes found that increasing air temperatures accelerated weathering rates, releasing base cations including calcium (Sommuraga-Wograth et al., 1997; Rogora et al., 2003). Since the underlying rock of our lakes is relatively low in calcium, they would receive minimal benefit from warming, perhaps affecting Harp Lake the most since its catchment contains proportionally more calcium (Dillon and LaZerte, 1992; Dillon et al., 1996). Sulphur in the soil is in organic forms of ester sulphates and carbon-bonded sulphates and in elemental form (insoluble), which must be mineralized for use by plants (Edwards, 1998). Ester sulphates (e.g. choline sulphate, phenolic sulphate) originate from microbial biomass (McLaren et al., 1985), and carbon-bonded sulphates (amino acids and sulpholipids) originate from decomposing vegetation (Tabatabai and Bremner, 1972; Neptune et al., 1975; Harwood and Nicholls, 1979). Atmospheric sulphur consists of inorganic SO_2 and H_2S which are oxidized into SO_4^{2-} (Bufalini, 1971; Kennedy, 1986). Oxidation rates increase with temperature, with the maximum rates occurring between 27 and 35°C (Tisdale and Nelson, 1975). Mineralization is carried out by soil microorganisms (bacteria, fungi, yeast), where organic sulphur is transformed to soluble inorganic forms (Brady, 1984). Inorganic sulphur in the soil solution is primarily in SO_4^{2-} form, and exists as mobile mineral sulphates by bonding with Ca^{2+}, Mg^{2+}, K^+, Na^+, NH_4^+, H^+, or Al^{3+} depending on the composition of the substrate (Hutchinson, 1979; Edwards, 1998). Mobilization is carried out by soil bacteria and microorganisms, where larger molecules of sulphur are reduced to smaller molecules, rendering them more mobile (Swank et al., 1985; Watwood et al., 1986). In cool wet conditions, immobilization and mineralization peak when conditions are optimal for microbial activity, in spring and autumn, and are lowest in winter (Swank et al., 1985; Strickland et al., 1987; Randlett et al., 1992). Mobilization is greater in warmer temperatures, with rates 5 times greater between 20 and 30°C than at 5°C (Strickland et al., 1984). Conditions favourable for sulphur mineralization are also favourable for nitrogen mineralization (Williams, 1967). Long term increases in air temperature may have contributed to increased NO_3^- and NH_4^+ concentrations, as anthropogenic nitrogen inputs are low in this region (Molot and Dillon, 1993). Ammonium bonds strongly with soil particles (Kaste and Dillon, 2003; Watmough and Dillon, 2003), and the mineralization and release of ammonium are greater during warm, dry periods (LaZerte and Scott, 1996; Qiu and McComb, 1996; Watmough et al., 2005). Palmer and colleagues (2011) suggested this process to explain the increasing ammonium levels during a period of constant deposition rates in our study region. The optimal temperature of the nitrification reaction is 26°C, nitrates are readily absorbed by plants, not requiring modification like ammonium

(Mengel and Kirkby, 1987). With warmer temperatures, more nitrogen would be available, encouraging algal growth. As air temperature increases, the production and release of DOC from soils also increases (Freeman et al., 2001; Keller et al., 2008), further enhancing the warming effect to lakes.

Precipitation

Though we saw a significant increase of snowfall over Red Chalk Lake, precipitation decreased in all other lakes, and annual precipitation decreased in the study region (Yao et al., 2009). Water flow has been further reduced in the Muskoka-Haliburton region owing to warmer air temperatures (e.g. Keller et al., 2008; Yao et al., 2009). Periods of reduced precipitation can decrease lake nutrient levels from less runoff, limiting algal production (Kling et al., 2003). Drought conditions can also increase nutrient levels through reduced dilution, evaporative concentration, and diminished nutrient retention in soils (Gerson et al., 2016). Droughts may result in increased DOC concentrations and associated changes in light climate and temperature profile (Yan et al., 1996) and lake re-acidification events (Bayley et al., 1992; Keller, 2007; Gerson et al., 2016). The DOC concentration in our study lakes between 1978 and 1998 was governed by winter precipitation and solar radiation (Hudson et al., 2003), with years of less UV radiation decreasing DOC degradation through photolysis (Molot and Dillon, 1997; Gennings et al., 2001), and years of less winter precipitation increasing lake DOC concentrations (Hudson et al., 2003). Regionally, chrysophytes and cryptophytes varied linearly with precipitation, sulphate, and lake depth (Table 2). Chrysophytes were more abundant in shallower lakes with more precipitation, including Chub and Dickie Lakes. Chrysophytes can thrive in mixed conditions due to their ability to vertically migrate (Sandgren, 1988). Their growth habit is characterised by rapid opportunistic growth followed by rapid decline (Sandgren, 1988). This was apparent in the large blooms in Crosson in 1990, 1996, and Red Chalk Main in 2002, which inflated the variability over time. Chrysophytes shared a breakpoint with DOC in 1990 in Crosson Lake, however none of the other variables had a high or low point in 1996 or 2002. These years did occur as the ENSO shifted from a negative to a positive phase, so perhaps chrysophytes bloomed in response to a nutrient pulse during the break of a drought, and these data were lost when averaged into an ice-free season value. Chrysophytes also prefer neutral to acidic pH (Sandgren, 1988). The rate of acidification recovery depends on the amount of stored sulphur (strongly tied with the amount of wetlands in the catchment), the occurrence of droughts, and the type and weathering rate of the catchment rocks (Dillon et al., 1996). Drought events may expose sulphur stored in previously submerged soil to oxygen and result in re-oxidation to SO_4^{2-} (Dillon et al., 1996; Keller, 2007), which is more soluble than the reduced compounds (Dillon et al., 2003). The warmer temperatures associated with droughts also encourage mineralisation, and the release of soluble SO_4^{2-} (Lofgren et al., 2001). Sulphur mineralization rates decline in conditions too wet for oxidation or too dry for microbial activity, with the highest rates occurring between 30 and 80% moisture (Williams, 1967; Watwood et al., 1988). A precipitation event following a drought mobilizes and transports sulphur and metals, increasing SO_4^{2-} in streams during larger runoff events, and acidifying lakes (Christophersen and Wright, 1981; Keller, 2007; Adkinson et al., 2008). Between 1980 and 1992, SO_4^{2-} exports peaked in streams during spring snowmelt but also in autumn after drought summers, but in years of average precipitation, SO_4^{2-} retention in catchments was directly correlated with the proportion of wetlands (Dillon et al., 1996). Wetlands have been identified as important sulphur storage sites (Dillon and LaZerte, 1992; Dillon et al., 1996; Dillon et al., 1997; Aherne et al., 2004).

Lakes with proportionally less wetland in their catchments will have lower storage capacity and more rapid recovery from sulphur deposition (Dillon et al., 1996). The catchment of Harp Lake has proportionally more glacial till, and has recovered the most, with SO_4^{2-} decreasing about 10% (Dillon and LaZerte, 1992; Dillon et al., 1996). Between 1980 and 1999, regional sulphur deposition had decreased by 35 to 40% compared with levels in the 1970s, resulting in lower SO_4^{2-} stream concentrations (Dillon et al., 1996; Watmough et al., 2005). However lake concentrations did not decline at the same rate, most likely because of summer droughts (Eimers and Dillon, 2002; Eimers et al., 2004), which dramatically increase sulphate release (Eimers and Dillon, 2002). Studies of Plastic Lake, which had the greatest SO_4^{2-} concentration in our study period, determined that SO_4^{2-} concentrations were driven by runoff chemistry, with the lowest concentration during snowmelt and the greatest in summer, as well as high SO_4^{2-} values of 10 to 25 times the long term average in streams draining in Dorset lakes in the autumn of years which had summer droughts (Dillon and LaZerte, 1992; Dillon et al., 1996).

Teleconnections

El Niño Southern Oscillation (ENSO)

Teleconnections, correlations between temporal fluctuations in meteorological parameters at separated geographical points (Wallace and Gutzler, 1981), explained 17% of the variation in our models. Radiative heating of the atmosphere generates the Polar, Ferrel, and Hadley circulation cells, which in conjunction with the Coriolis force, produce jet streams that affect global climate. The El Niño Southern Oscillation (ENSO) was the most important teleconnection index for our study lakes, being a significant predictor in all lake basin RDA models and in five lake MLR models. ENSO has a 2-7 year cycle and is one of the strongest drivers of interannual variability in the Canadian climate, aside from seasonal changes (Rasmusson and Carpenter, 1982; Gerten and Adrian, 2002; Shabbar, 2006). The SOI is defined as the difference in sea level pressure (around 1000 hPa) between Tahiti and Darwin (Diaz and Kiladis, 1992; Shabbar and Khandekar, 1996), where a negative SOI corresponds to warm water in the tropical Pacific and an El Niño phase. Radiative heating in the tropical Pacific Ocean alters currents in the troposphere (250-450 hPa, or 6-10km above sea level), which results in the formation of Rossby waves, transferring heat towards the poles, and affecting movement in the polar jet stream (250-350 hPa, or 7-12km above sea level) (Hoskin and Karoly, 1981; Rasmusson and Wallace, 1983). In Canada, the El Niño or La Niña circulation patterns emerge in autumn, are strongest in winter, and disappear by spring (Shabbar et al., 1997). During an El Niño winter, there is a stronger Aleutian low, and the polar jet stream shifts eastward, splits in the North Pacific, continuing eastward across Hudson Bay and across northern Florida (Shabbar et al., 1997). The region of southern Canada between these paths experiences warmer and drier weather compared with neutral years (Shabbar et al., 1997). Warmer temperatures begin in autumn over northwest Canada and stretch over most of southern Canada over the course of the winter (Shabbar and Khandekar, 1996), with Dorset experiencing on average 0.5-1°C warmer temperatures in an El Niño winter than a neutral winter (Shabbar and Khandekar, 1996; Shabbar, 2006). The southward diversion of the polar jet stream also alters tropospheric currents, decreasing the precipitation occurring from British Columbia to the Great Lakes region (Shabbar, 2006). Winter storms are also shifted further south (Smith and Ledridge, 1999), decreasing winter storm frequency in the Great Lakes region (Noel and Changnon, 1998; Angle et al., 1999). Dorset receives 0.3-0.4 mm/day less winter precipitation in an El Niño year (Shabbar, 2006). During a La Niña year, there is a weaker Aleutian low, the jet stream shifts westward, and crosses North America across the Great Lakes region, bringing moist air from the Pacific Ocean, and resulting in greater winter precipitation between British Columbia and the Great Lakes region (Shabbar et al., 1997). There is no significant temperature anomaly associated with the La Niña phase of ENSO in the Great Lakes region, though historically temperatures have been between 0 and 0.5°C cooler in Dorset (Shabbar and Khandekar, 1996). A study by Dillon and colleagues (1996) identified that drought years between 1970 and 1995 in Dorset catchments occurred following strong El Niño events. Drought events can lead to the re-oxidation and subsequent dissolution of sulphur stored in wetlands (Schindler et al., 1996), and Dillon and colleagues determined ENSO, NAO, and SO_4^{2-} deposition to be the best predictors of lake SO_4^{2-} concentrations (2003). Peaks in SO_4^{2-} concentrations occurred when streamflow was restored after the end of a drought (Dillon et al., 1996). The decomposition of DOC is more rapid with more acidic lake pH values (Gennings et al., 2001), so ENSO-related droughts contributing elevated SO_4^{2-} inputs may decrease lake DOC. Although a 2003 study did not find a link between ENSO and DOC lake concentration (Hudson et al., 2003), ENSO may indirectly affect DOC inputs through its influence on air temperature and precipitation magnitude and timing, as DOC increases during warmer years (Schindler, 1997; Curtis, 1998; Freeman et al., 2001) with drier winters and wetter summers (Urban et al., 1989; Easthouse et al., 1992; Hinton et al., 1997). Only a portion of variability in North American winter temperatures are explained by ENSO, as other teleconnections as well as regional phenomena are also important (Gerten and Adrian, 2002). During a warmer than average winter, the ice cover is likely to be less extensive. Assel (1998) found 15% less ice cover in four lakes in the Great Lakes region with a 1.2°C warmer than usual El Niño winters. Ice cover on the Great Lakes is typically decreased during the winters following El Niño events (Gerten and Adrian, 2002), and a study of 62 lakes and rivers across the Northern Hemisphere determined that freeze-up and break-up dates were related to the ENSO (Robertson et al., 2000) with earlier break-up in the Laurentian Shield region (Assel, 1998). Ice cover and timing of break-up affects the timing of the spring bloom, and influenced spring water column nutrient availability in a study of Lake Michigan (Behm, 1998). Nicholls (1998) also analysed a 19-year time series of Lake Huron phosphorous concentrations and found it to be negatively correlated with annual maximum ice cover in the Great Lakes, with greater than average phosphorous concentrations after the start of El Niño events and their associated winter air temperatures. They suggested that embayments receiving high P inputs (i.e. from Saginaw Bay) would in a neutral year have sediments settle until spring, and during an El Niño winter, the decreased ice cover allows wind energy to maintain nutrients in suspension, changing the trophic status (Nicholls, 1998). The ENSO also affects lake levels, with lower levels in an El Niño year and higher levels in a La Niña year (e.g. LaValle et al., 2000). Ecological responses to effects of ENSO are regional (Gerten and Adrian, 2002). Between 1976 and 2000, sulphate deposition declined by more than 50% in south central Ontario, but lake sulphate concentration only declined by approximately 25% (Dillon et al., 2003). When lake sulphate was modeled, Dillon and colleagues (2003) determined that the ENSO, NAO, and deposition were significant predictors, revealing that regional factors as well as local deposition control lake sulphate. These results are consistent with the research illustrating drought-related impacts on sulphur cycling. ENSO was an important predictor for each of our phytoplankton groups, and likely affected growth through its influence on drought frequency and magnitude, which in turn influence water chemistry.

Atlantic Multidecadal Oscillation (AMO)

The Atlantic Multidecadal Oscillation (AMO) was the second most important predictor in our models, and was significant in six RDA models and four MLR models. The AMO is a fluctuation in sea surface temperatures in the North Atlantic with a 65-80 year cycle (Enfield et al., 2001; Knight et al., 2005). The AMO drives summer precipitation in North America at decadal scales (Enfield et al., 2001; McCabe et al., 2004; Sutton and Hodson, 2005; 2007; Hu et al., 2011). The AMO switched from a cool to warm phase around 1995 (Enfield et al., 2001). During a warm phase, the North Atlantic subtropical high pressure system (NASH) weakens and shifts towards the north east, which diminishes its effect on North America, and allows warm continental air masses to develop, with a low pressure system (cyclonic flow) in the lower troposphere between British Columbia and the Great Lakes region and over Florida (Hu et al., 2011). These systems do not extend over the Great Lakes or southern Ontario, and Dorset receives reduced summer precipitation in a warm phase. In the cool phase, the NASH becomes stronger and shifts westward, affecting North American air circulation in the troposphere much more than in the warm phase, bringing maritime air in across the Great Lakes region, and forming of a high pressure system (anticyclonic flow) between British Columbia and the Great Lakes (Hu et al., 2011). A front develops in the upper troposphere between northward flowing maritime and southward flowing continental air, which crosses North America approximately over Lake Ontario. The instability that arises across this front precipitates storms in the Great Lakes region (Hu et al., 2011). Dorset receives greater summer precipitation in a cool phase. Mo et al. (2009) suggested that the greatest influence of AMO is to offset the effects of ENSO on drought, though their study concentrated on the southwest and great plains of the US. The AMO was important for four of our six phytoplankton groups. The AMO switched from a negative to a positive phase in 1995, after which the effects of ENSO would no longer have been mitigated and Dorset would have received a further reduction in summer precipitation.

North Atlantic Oscillation (NAO)

The NAO was important in five RDA models and one MLR model. The NAO is measured as the atmospheric pressure between Iceland and the Azores, and oscillates back and forth changing the wind speed and direction over the Atlantic Ocean approximately every 6-10 years (Hurrell et al., 2003). The NAO is a meridional shift in the polar jet stream, northward for a positive phase and southward in a negative phase (Riviere and Orlanski, 2007). In a positive phase, there is a low pressure system over Iceland at around 700 hPa (about 3km) and a high pressure system over the Atlantic near Portugal, which strengthens the polar vortex and jet stream, with the stronger zonal (latitudinal) flow closing off cold polar air from traveling south as well as bringing warm air from the Gulf of Mexico northward towards the Great Lakes region (Thompson and Wallace, 1998; Wang and Ikeda, 2000; Wang et al., 2005; Bai et al., 2015), resulting in warmer temperatures and decreased snowfall (Barnston and Livezey, 1987), and on average 47.6% less ice cover in the Great Lakes region (Bai et al., 2012). In a negative phase, there is a high pressure system over Iceland and a low pressure system over the midlatitude Atlantic, which weakens the polar vortex, encouraging the development of a ridge over western Canada and a trough over the Great Lakes in the polar jet stream, and this more meridional (longitudinal) flow leads to a colder than average winter in the Great Lakes region, with air temperatures 0.9 to 1.8°C colder (Klaassen, 2002), and 62.5% greater ice cover (Bai et al., 2012). The effects of the NAO are most evident throughout the winter, though they are present throughout the year, and were found to explain about one third of the variability in temperature in the northern hemisphere between

December and March (Gerten and Adrian, 2002). Bai et al. (2012) studied Great Lakes ice cover in winters from 1963 to 2010, and found that approximately half of the maximal ice cover winters occurred during negative NAO phases and half of the minimal ice cover winters occurred during El Niño events, implying that both phenomena are an important influence on ice condition (Bai et al., 2012). Klaassen (2002) found that since 1970, southern Ontario has received 10% less winter precipitation in negative NAO phase years, but that there was no significant link between NAO and drought years. However, Dillon and colleagues (2003) found that ENSO, NAO, and SO_4^{2-} deposition were important predictors for modeled lake sulphate concentrations in our study lakes between 1973 and 2000. The NAO was an important variable for diatoms, chrysophytes, and dinoflagellates in our models of Blue Chalk and Red Chalk Lakes. The NAO influences primary productivity through its effect on ice conditions (Gerten and Adrian, 2002). Straile and Adrian (2000) found that between 1979 and 1994, the NAO-related warming in Lake Muggelsee decreased ice cover and resulted in increased turbulence favouring a diatom bloom.

Conclusions and Implications

Phytoplankton biomass is driven by a combination of light availability, water chemistry, nutrient availability, lake thermal structure, and differences among groups including morphology, competitive ability, growth requirements, and specific tolerances to environmental conditions. Regionally, growth conditions are also influenced by local and large-scale climate patterns. Our RDA models explained 22 to 44% of the variation in phytoplankton biomass. Changes in lake chemistry and lake morphometry accounted for 60% of explained variation in our regional model.

Though emissions have declined following amendment of the US Clean Air Act in 1990, and the enactment of the Canada-US Air Quality Agreement in 1991 (EC, 2004) our lakes have yet to recover from acid rain deposition. Precipitation pH increased by 0.8 units since 1980 (Watmough et al, 2016) but our lakes only increased by 0.22 units since 1984. Chub, Crosson, Heney, and Plastic are still biologically acidic. Reduced Cation Exchange Capacity, local geology, and drought conditions contributed to the slow recovery, which has also affected DOC and calcium concentrations, and nutrient solubility. We did not see direct correlation between phytoplankton and pH, however it affects nutrient solubility and cycling. Recovery of soils from acidification increases DOC production by increasing the rate of biological activity (Andersson et al., 2000), DOC release from soils (Driscoll et al., 2007; Monteith et al., 2007; Zhang et al., 2010; Kerr and Eimers, 2012), and reduced solubility (Clark et al., 2010).

Our models have a large degree of unexplained variation. This variation may be explained by variables affecting phytoplankton growth and survival not included in our study, such as zooplankton grazing (Tirok and Gaedke, 2007), fungal and viral infections, parasitism (van Donk and Ringelberg, 1983) and fish predation (Jeppesen et al., 1997; Gliwicz, 2003; Jeppesen et al., 2004; Sørensen et al., 2011). Our models may have also been improved if we had not had limitations in the data, as we lacked more specific taxonomic information, and greater temporal resolution.

Global climate patterns influenced regional weather variables, which were modified by lake-specific characteristics (morphology, catchment composition, euphotic zone depth) affecting the production, recycling, input, and availability of nutrients in our study lakes throughout the study period. With multiple stressors acting on this region, water quality recovery does not imply biological recovery (Quinlan et al., 2008). DOC input can be managed through the management of forest fires and clearcutting, or removal of riparian vegetation (Meyer and Tate, 1983; Schindler et al., 1992; Delong and Brusven, 1994; Guyot and Wasson, 1994), and other land management decisions (Kritzberg, 2017). pH could be managed by applying lime to lakes, as they have done in Sweden (e.g. Bengtsson et al., 1980). Understanding how lakes will respond to climate change is important, as air temperatures in the Great Lakes region are expected to increase by 0.4 to 2.6°C and precipitation is to increase by the year 2065 (IPCC, 2013). These factors are expected to cause large scale changes to lake environments (Palmer et al., 2014). This study provides an idea of how phytoplankton will respond to these changing factors. By understanding how these stressors impact phytoplankton communities, we will be better able to anticipate harmful and nuisance blooms, improving water quality and public health.

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TABLES

Table 1: Detected breakpoint years and the direction of shift (increased or decreased mean after the break) in the time series of relative phytoplankton biomass and water chemistry variables in the eight Dorset study lakes between 1984 and 2013. The cut-off length l=8, Huber's weight parameter h=6, and significance level α=0.05. Bold numbers indicate a matching break date between phytoplankton and nutrients in a lake.

	Blue Chalk		Chub		Crosson		Dickie		Harp		Heney		Plastic		Red Chalk East		Red Chalk Main	
	Break	Dir.	Break	Dir.	Break	Dir.	Break	Dir.	Break	Dir.	Break	Dir.	Break	Dir.	Break	Dir.	Break	Dir.
Diatoms	1999	-			**1990**	-			**1993**	-							**1995**	-
					2009	+												
Chlorophytes	**2007**	-			1988	-					1996	+						
					2006	+					2002	-						
Chrysophytes	1999	+	1989	+	**1990**	+			**1993**	+					1990	+	**1995**	+
					2006	-												
Cryptophytes	**1992**	-			**1990**	-			1999	+	1990	-			1990	-		
									2008	-								
Cyanobacteria									2007	+								
Dinoflagellates	2004	+	2006	+			1997	-			1993	-	1994	-			2004	+
							2005	+			2006	+	**2006**	+				
Ca	1995	-			1995	-							1995	-	1995	-	**1995**	-
	2007	-			2007	-							2005	-	2009	-	2007	-
Cl			2008	-	2007	-	2006	+	2006	+	1999	+	2009	-	2008	-		
											2008	-						
DOC	2000	+	2003	+	**1990**	+					1998	+	**2006**	+	1999	+	2003	+
					2000	+												
Fe	**1992**	-	2007	+											2008	+	2009	+
	2003	+																
Na							2008	+	**2008**	+	1999	+			1995	-	1996	-

											2008	-					2003	+
NH4	1997	+	2009	-	1998	+	1993	+	**1993**	+	1991	+	1992	+			1998	+
	2007	-			**2009**	-	2004	-	2004	-	2007	-	2004	-			2007	-
NO3	2006	-	2002	-			1998	-	1998	-	2005	-	**2006**	-	2005	-	1998	-
pH			2001	+	1997	+	1995	+	1995	+								
							2009	+	2009	+								
TP	1998	+	1991	-	2001	-					2001	-	1992	-				
SiO3					2008	+							1998	-	2008	+	2009	+
SO4	2008	-											2008	-	1993	-		
															2008	-		
TN			2004	-					2009	-								

Table 2: Multiple linear regressions of log-transformed relative phytoplankton biomass (log(% of sample)) and absolute phytoplankton biomass (mm^3/m^3) at the regional and lake scales. Only significant results are reported.

Lake	Response	log-transformed relative biomass				absolute biomass			
		Coefficient	Predictor	Model R^2_{adj}	Model P	Coefficient	Predictor	Model R^2_{adj}	Model P
Regional	Diatoms	6.65576	intercept	0.2556	2.20E-16	91.383	intercept	0.1025	1.98E-07
		0.80712	zmax			30.396	zmax		
		-0.26706	Cl			-15.203	NH4		
	Chlorophytes	10.27723	intercept	0.0369	0.002441	30.392	intercept	0.08021	5.24E-06
		-0.08847	Cloud			-7.613	zmax		
		0.14462	TP			3.602	NO3		
	Chrysophytes	3.083803	intercept	0.18	4.46E-12	-1456.1	intercept	0.04614	0.001383
		-0.27157	zmax			29.29	Cloud		
		-0.123115	SO4			54.81	NH4		
		0.016395	Precip			-49.45	zmax		
	Cryptophytes	7.007038	intercept	0.1051	3.92E-07	44.923	intercept	0.1042	4.51E-07
		0.27203	zmax			8.101	A0		
		0.188723	SO4			7.405	TP		
		-0.01904	Precip			5.473	PDO		
	Cyanobacteria	8.45023	intercept	0.04093	0.001395	19.47483	intercept	0.06263	0.0001525
		0.41238	zmax			-0.06487	SS		
		-0.02975	Cloud			3.09611	zmax		
						2.53676	TP		
	Dinoflagellates	-5.67718	intercept	0.1347	5.04E-09	37.417	intercept	0.1915	1.76E-13
		-0.64291	A0			-14.949	zmax		
		-0.02599	QBO			-12.468	NO3		
		0.16961	Cloud						
Blue Chalk	Diatoms	2.7977	intercept	0.31	0.002543				
		-0.349	DOC						

		0.8393	NAO						
	Chlorophytes	11.72616	intercept	0.56	0.0001067	28.519	intercept	0.2181	0.005411
		0.39744	SO4			-7.19	SiO3		
		0.38896	NH4						
		-0.13793	Cloud						
		-0.75705	PNA						
		-0.23534	TN						
	Chrysophytes	2.7296	intercept	0.2306	0.01108	223.68	intercept	0.1079	0.04271
		2.6017	AMO			-83.29	Ca		
		-0.3416	pH						
	Cryptophytes	2.847	intercept	0.1123	0.03944				
		0.2941	NO3						
	Cyanobacteria	11.7744	intercept	0.2295	0.01128	11.872	intercept	0.1581	0.01697
		-0.3847	SWT_8			4.667	ENSO		
		-0.3741	TP						
	Dinoflagellates	3.1951	intercept	0.2846	0.004147	29.34272	intercept	0.5728	3.36E-05
		6.9229	AMO			7.75694	DOC		
		-0.7245	pH			-0.21185	SS		
						8.12686	Na		
						7.86702	TP		
Chub	Diatoms	3.6496	intercept	0.1452	0.02157	93.95	intercept	0.3089	0.0008483
		-0.4809	TN			62.93	pH		
	Chlorophytes	4.3985	intercept	0.2828	0.004284	26.734	intercept	0.1224	0.03279
		-1.3504	ENSO			-9.018	ENSO		
		0.8095	PDO						
	Chrysophytes	3.219	intercept	0.2943	0.001156	314.75	intercept	0.1842	0.0104
		0.3712	NH4			-151.74	SiO3		
	Cryptophytes	2.64	intercept	0.1289	0.02911	68.244	intercept	0.1702	0.01353
		-1.8061	AMO			-21.185	SiO3		
	Cyanobacteria	4.6055	intercept	0.233	0.004045	11.8352	intercept	0.2535	0.007358

		1.0285	SiO3			-0.34313	QBO		
						-0.06329	SS		
						31.493	intercept	0.3401	0.001394
						-21.823	NO3		
						11.587	SiO3		
Crosson	Diatoms	4.8379	intercept	0.1512	0.01927				
		0.6795	SiO3						
	Chlorophytes	4.2011	intercept	0.2449	0.00319	44.242	intercept	0.7095	3.15E-07
		0.6487	SiO3			1.3855	Precip		
						-24.1999	NAO		
						-6.3575	SWT_8		
						-4.0624	Na		
	Chrysophytes	2.53916	intercept	0.3506	0.001122	3737.26	intercept	0.3319	0.001647
		-0.34437	NO3			-327.7	NO3		
		0.33861	ENSO			-317.81	Temp		
	Cryptophytes	13.41454	intercept	0.4101	0.0007557	36.876	intercept	0.1739	0.02889
		0.51912	SiO3			-9.163	ENSO		
		-0.54694	ENSO			6.345	TP		
		-0.17311	Cloud						
	Dinoflagellates	4.0347	intercept	0.1483	0.02033	-440.003	intercept	0.1401	0.02366
		0.8106	DOC			7.837	Cloud		
Dickie	Chrysophytes	7.39717	intercept	0.3991	0.0009529	3662.21	intercept	0.3468	0.001215
		-0.27552	SiO3			-141.17	SWT_8		
		-0.22342	SWT_8			-162.69	NO3		
		0.17955	Cl						
	Cryptophytes	3.8701	intercept	0.1204	0.034	-83.4227	intercept	0.2187	0.01363
		0.3745	SiO3			1.724	Precip		
						14.2142	Cl		
	Dinoflagellates	2.9416	intercept	0.3635	0.001952	27.564	intercept	0.3362	0.001509
		-0.7275	NH4			13.284	DOC		

		0.8414	DOC			-8.672	TN		
		0.8222	ENSO						
Harp	Diatoms	3.2021	intercept	0.5156	4.77E-06	144.6	intercept	0.5604	1.18E-06
		-0.6967	Na			-130.17	Na		
	Chlorophytes	17.8418	intercept	0.2578	0.006805				
		-0.2401	Cloud						
		0.31783	pH						
	Chrysophytes	3.0909	intercept	0.2739	0.00177	-1796.38	intercept	0.1579	0.01701
		0.4903	NH4			32.51	Cloud		
	Cryptophytes	2.3009	intercept	0.3086	0.0008524				
		2.1747	AMO						
	Cyanobacteria	23.585	intercept	0.2682	0.00563	38.0812	intercept	0.4036	0.0008671
		-0.8304	SWT_8			-14.4978	NH4		
		0.6659	pH			1.3246	QBO		
						-11.7063	NO3		
	Dinoflagellates	3.5513	intercept	0.3568	0.0009861				
		-0.7643	TN						
		0.549	Cl						
Heney	Diatoms	4.7328	intercept	0.1147	0.03776	3.5038	intercept	0.5388	8.40E-05
		-0.8052	NO3			-0.8232	NO3		
						-0.4299	TN		
						0.7672	ENSO		
						-1.2511	PNA		
	Chlorophytes	3.876	intercept	0.2771	0.004769	-729.152	intercept	0.3831	0.001321
		-0.5817	SO4			26.656	pH		
		-0.3562	ENSO			13.062	Cloud		
						21.203	TN		
	Chrysophytes	1.79631	intercept	0.1363	0.02538	335.48	intercept	0.3688	0.0007652
		0.13819	NO3			170.34	PDO		
						123.01	TN		

	Cryptophytes					27.667	intercept	0.1931	0.008769
						13.237	NH4		
	Cyanobacteria	4.2153	intercept	0.3808	0.000168	17.539	intercept	0.2504	0.007785
		-1.3497	SO4			-6.27	SO4		
						5.879	NH4		
	Dinoflagellates	3.5038	intercept	0.5388	8.40E-05	-668.933	intercept	0.2196	0.0134
		-0.8232	NO3			-28.379	NH4		
		-0.4299	TN			12.385	Cloud		
		0.7672	ENSO						
		-1.2511	PNA						
Plastic	Diatoms					28.113	intercept	0.1268	0.03024
						-12.175	SO4		
	Chlorophytes	-0.5033	intercept	0.1043	0.04563	-70.332	intercept	0.2283	0.01152
		0.4823	Temp			9.846	Temp		
						6.101	ENSO		
	Chrysophytes	2.15729	intercept	0.2	0.007682				
		-0.22264	TP						
	Cyanobacteria	6.0656	intercept	0.1962	0.00826	7.343	intercept	0.1132	0.03875
		0.8667	NO3			2.219	NH4		
	Dinoflagellates	4.9493	intercept	0.1574	0.01718	-576.796	intercept	0.3981	0.0004022
		0.7989	DOC			-37.799	NO3		
						10.756	Cloud		
Red Chalk East	Diatoms	1.94343	intercept	0.6001	1.52E-05	61.308	intercept	0.1595	0.01651
		-0.53359	DOC			-16.916	SiO3		
		0.46049	Temp						
		-0.17014	SWT_8						
		-0.2461	NH4						
	Chlorophytes	9.95307	intercept	0.1252	0.03111	27.155	intercept	0.1701	0.03076
		-0.12378	Cloud			-6.117	SiO3		
						5.376	NH4		

	Chrysophytes	3.74404	intercept	0.3635	0.0008554	304.74	intercept	0.2627	0.002226
		0.27453	DOC			97.58	DOC		
		-0.17751	Temp						
	Cryptophytes	8.49162	intercept	0.4043	0.0008547	35.362	intercept	0.5779	2.91E-05
		-0.04535	Precip			14.876	TP		
		0.4427	TP			-15.597	SiO3		
		-0.41035	SiO3			-22.785	NAO		
						12.311	ENSO		
	Cyanobacteria	26.0795	intercept	0.229	0.004373	235.8489	intercept	0.4645	0.0004922
		-0.3453	Cloud			-7.7939	SiO3		
						0.7333	QBO		
						7.5551	DOC		
						-3.602	Cloud		
Red Chalk Main	Chlorophytes					254.753	intercept	0.3805	0.001394
						-3.813	Cloud		
						-6.208	NO3		
						-5.606	Na		
	Chrysophytes	4.3303	intercept	0.3486	0.001169				
		-0.5596	Ca						
		0.3337	NH4						
	Cryptophytes	4.5373	intercept	0.1005	0.04885	36.458	intercept	0.2823	0.001488
		0.3562	SO4			-11.329	SiO3		
	Cyanobacteria	18.4959	intercept	0.3574	0.0009731				
		-0.6518	SWT_8						
		0.6732	PDO						
	Dinoflagellates	11.6143	intercept	0.4136	0.0002827	26.265	intercept	0.3832	0.0001585
		1.097	DOC			15.885	DOC		
		-0.3609	SWT_8						

FIGURES

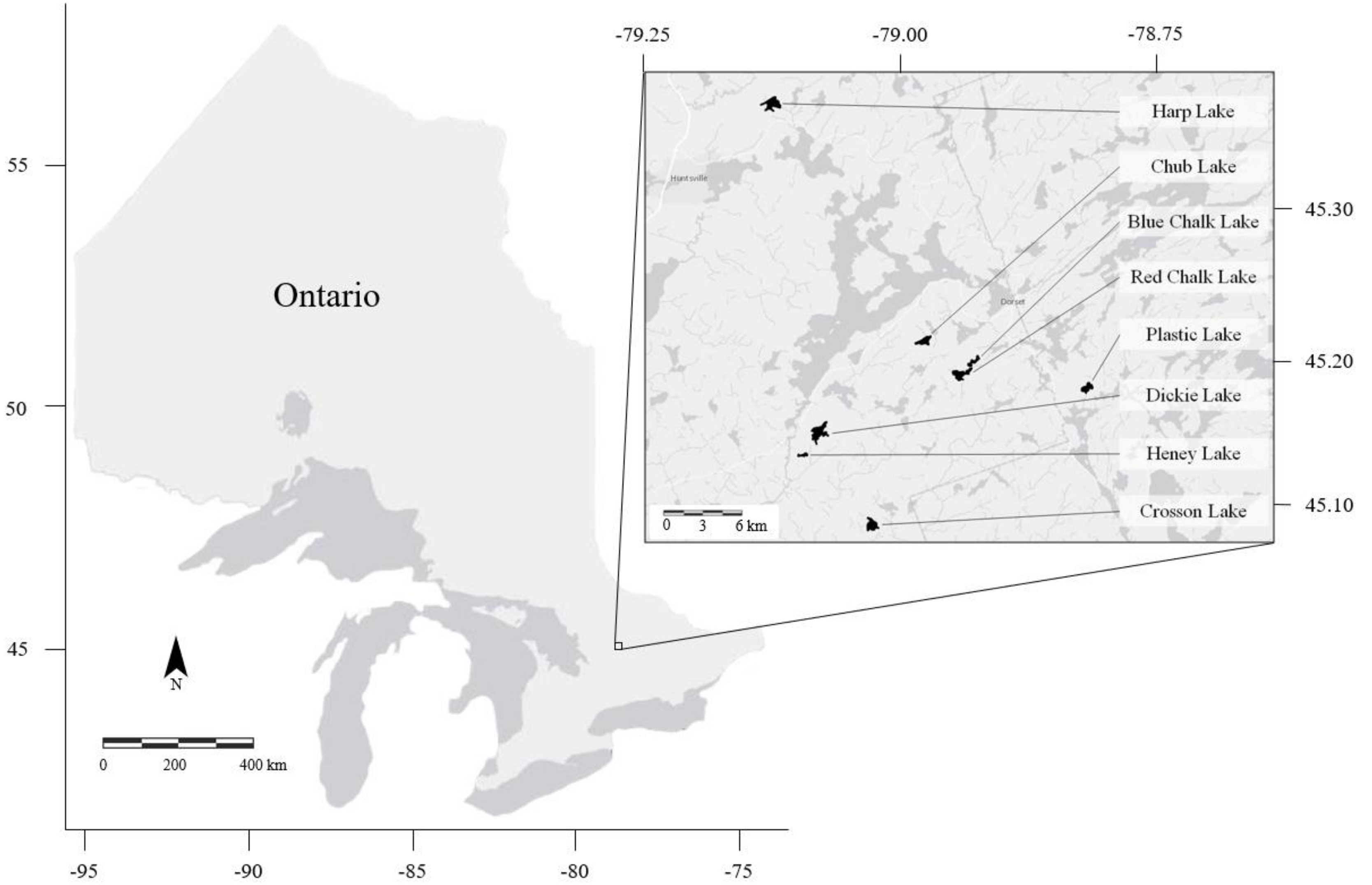

Figure 1: Map of the study region, with an inset of our eight study lakes in southern Ontario.

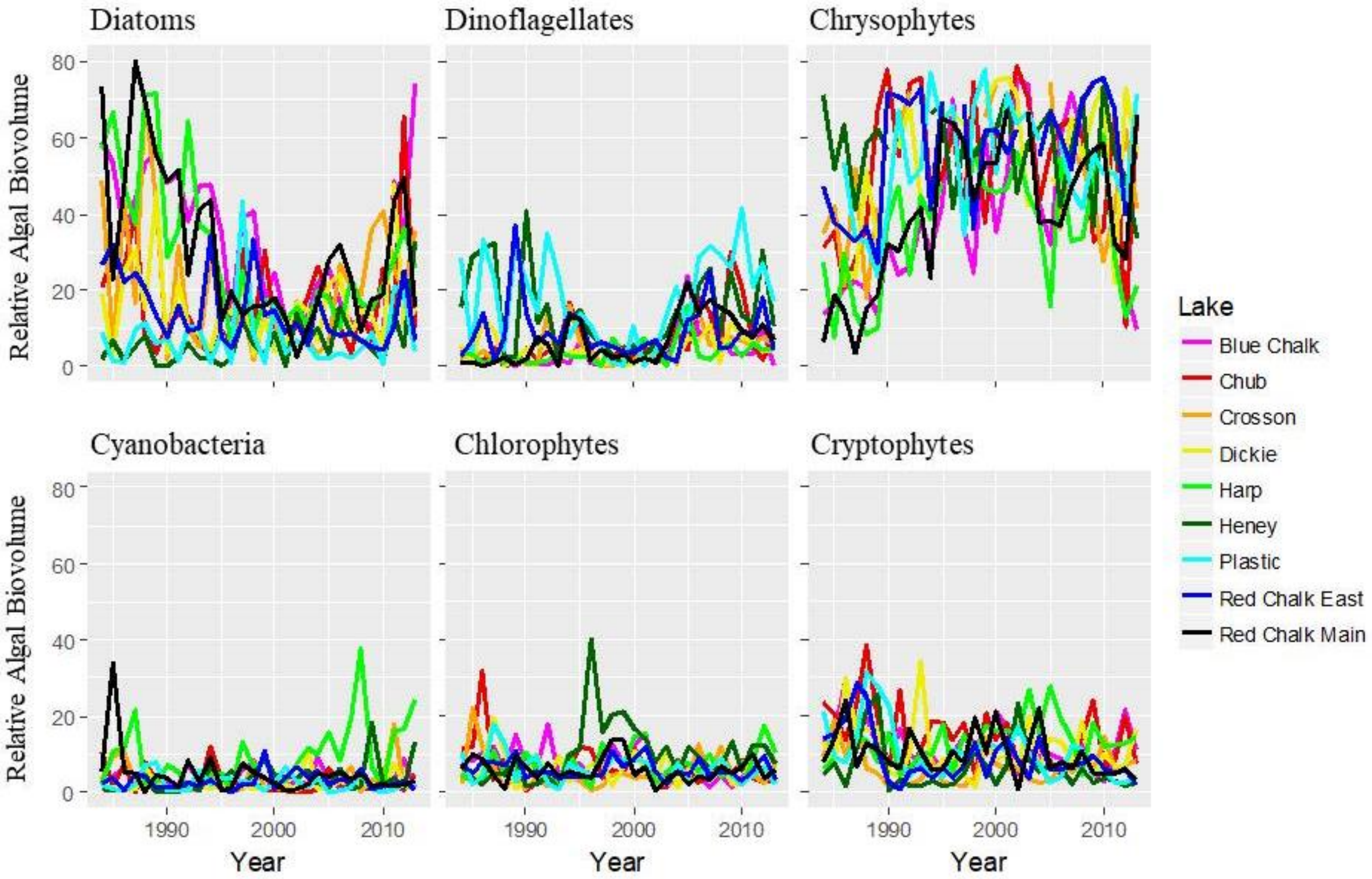

Figure 2: The relative biomass (%) of six algal taxa in each of the eight Dorset study lakes between 1984 and 2012.

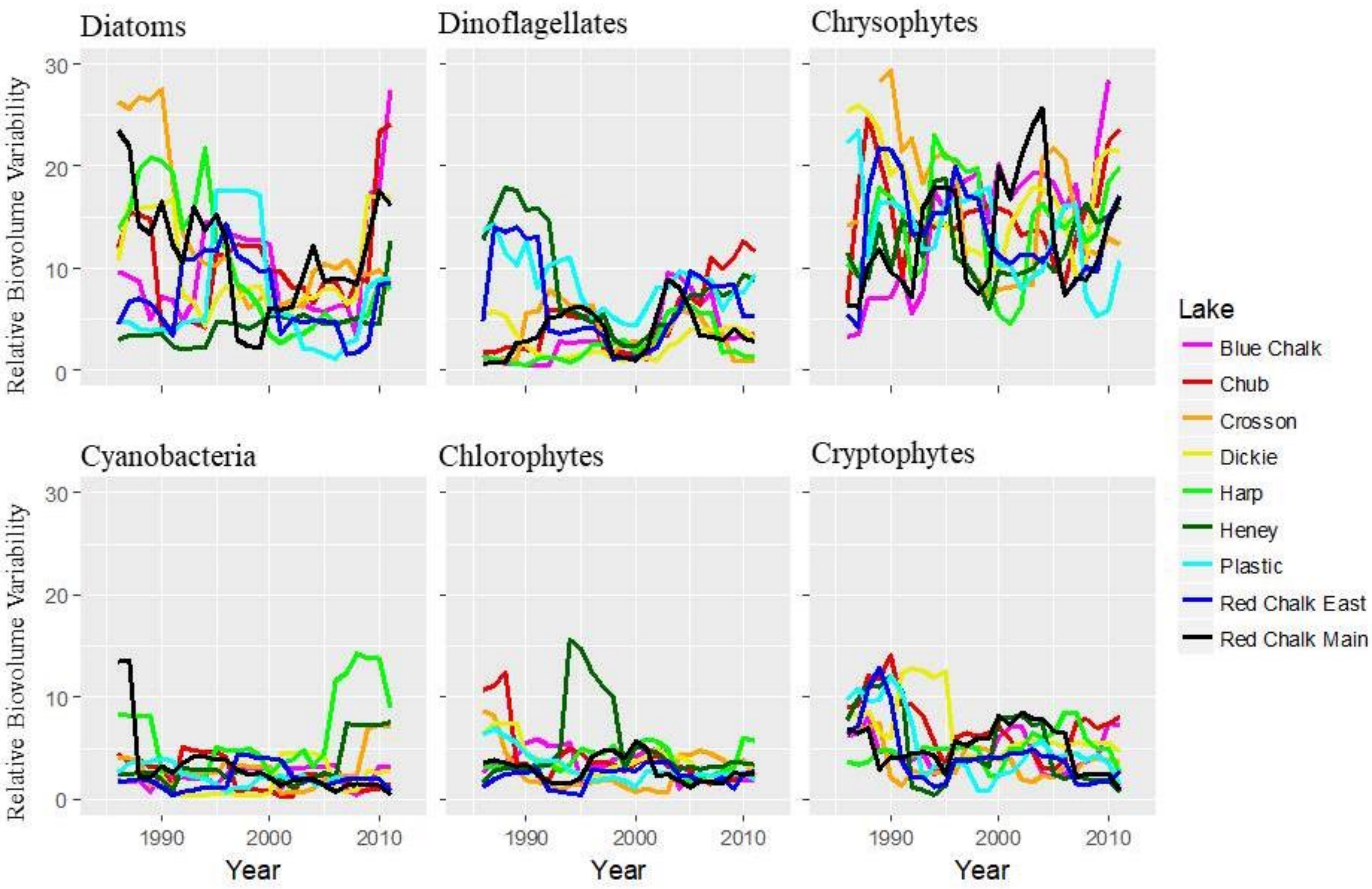

Figure 3: The variability of six algal taxa in each of the eight Dorset study lakes between 1984 and 2012. Variability was calculated as a 5-year moving window of standard deviation for each group

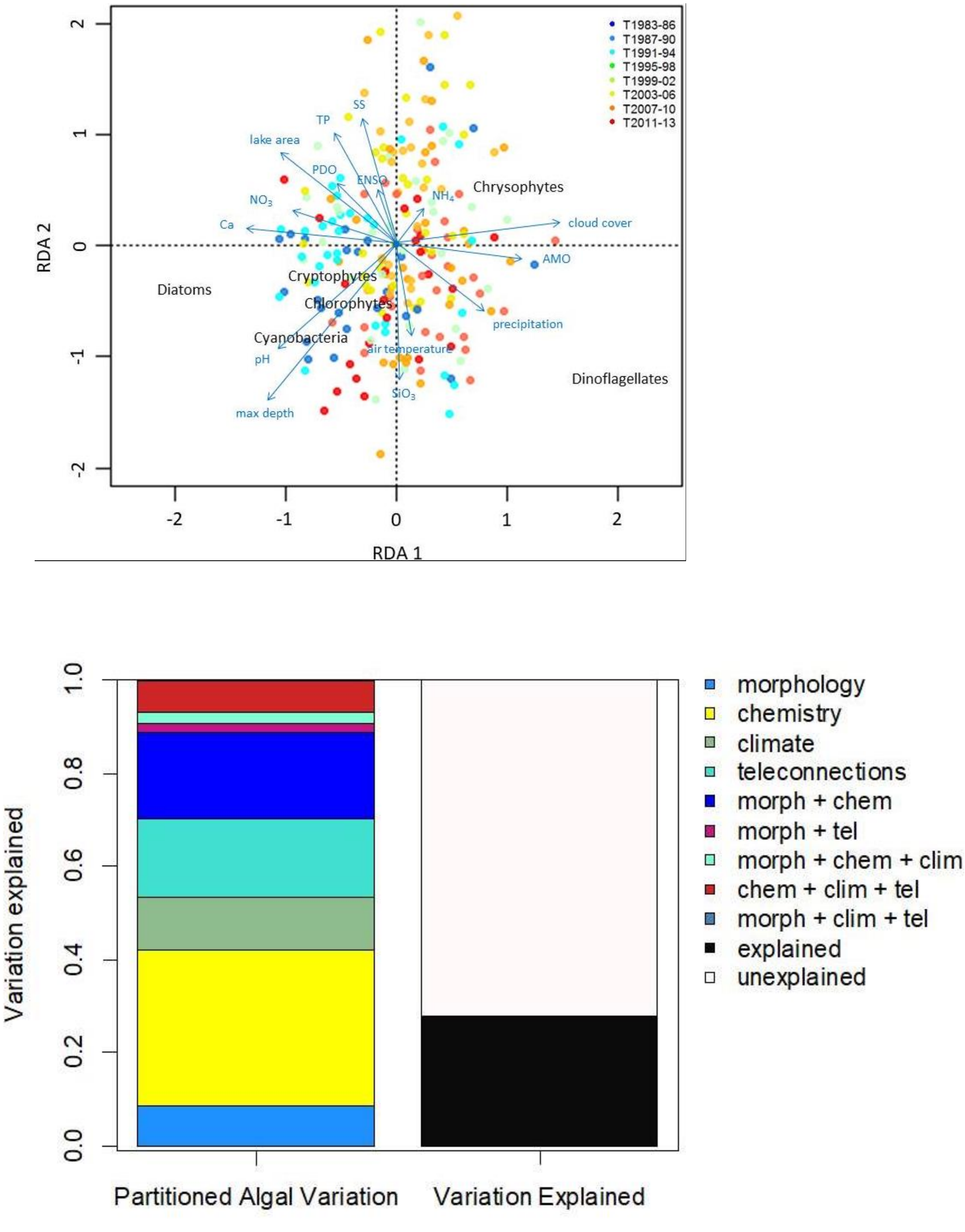

Figure 4: **(a)** Redundancy analysis plot including all study lakes, showing the response of six algal taxa to morphometric, chemical, and climatic variables, and **(b)** Variation partitioning analysis of the relative variation explained by each group of variables.

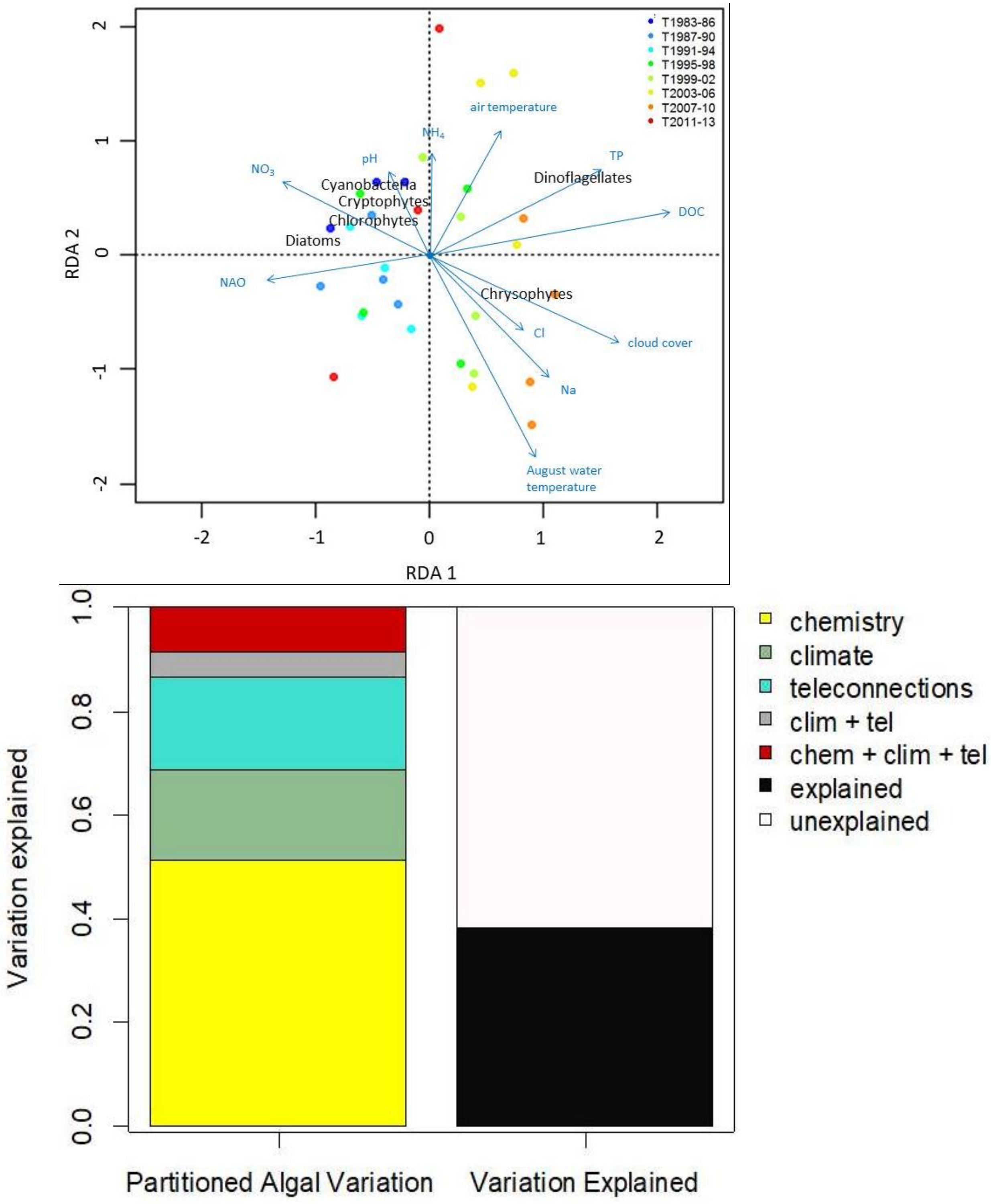

Figure 5: **(a)** Redundancy analysis plot showing the response of six algal taxa to chemical and climatic variables in Blue Chalk Lake, and **(b)** Variation partitioning analysis showing the relative variation explained by each group of variables.

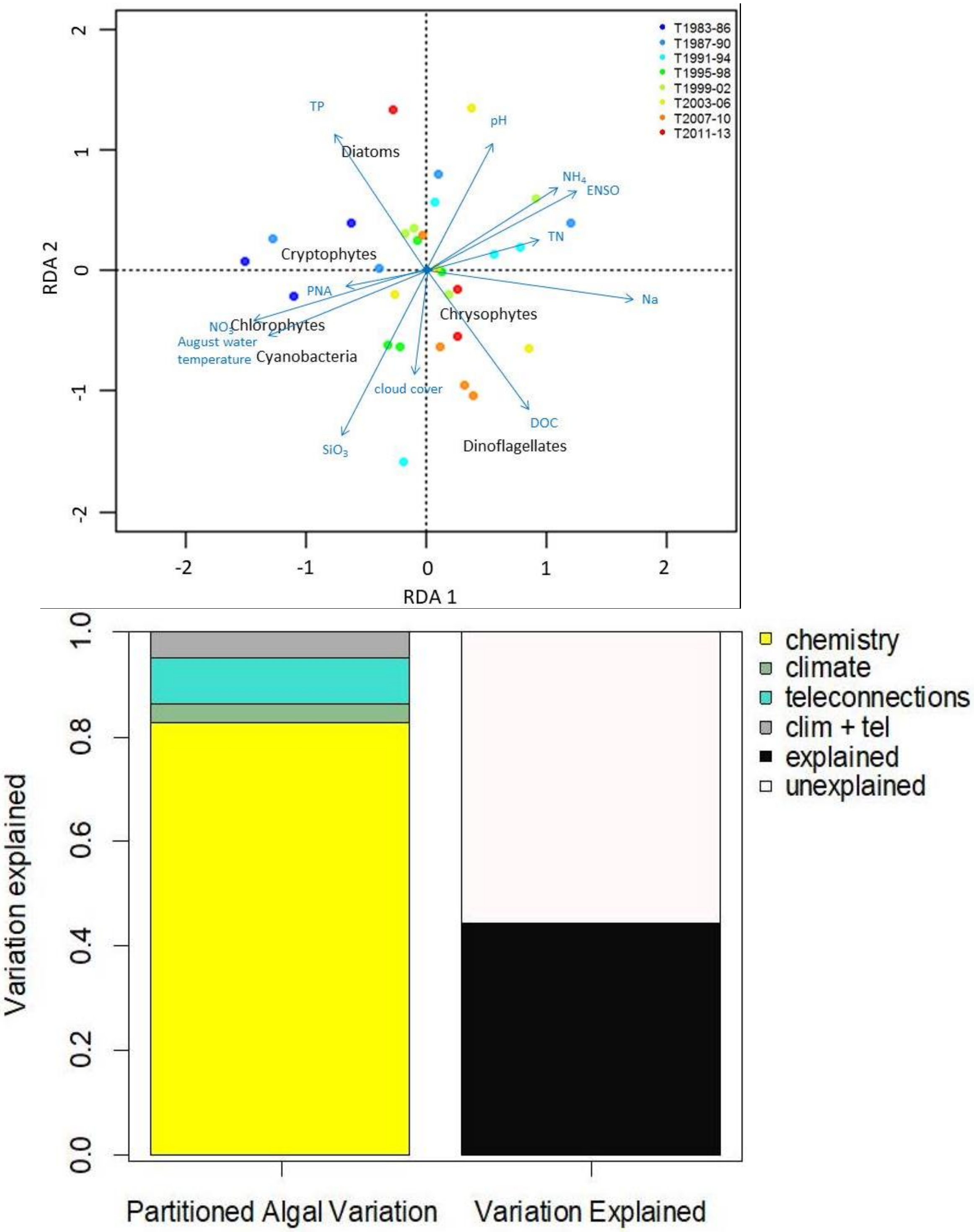

Figure 6: **(a)** Redundancy analysis plot showing the response of six algal taxa to chemical and climatic variables in Chub Lake, and **(b)** Variation partitioning analysis showing the relative variation explained by each group of variables.

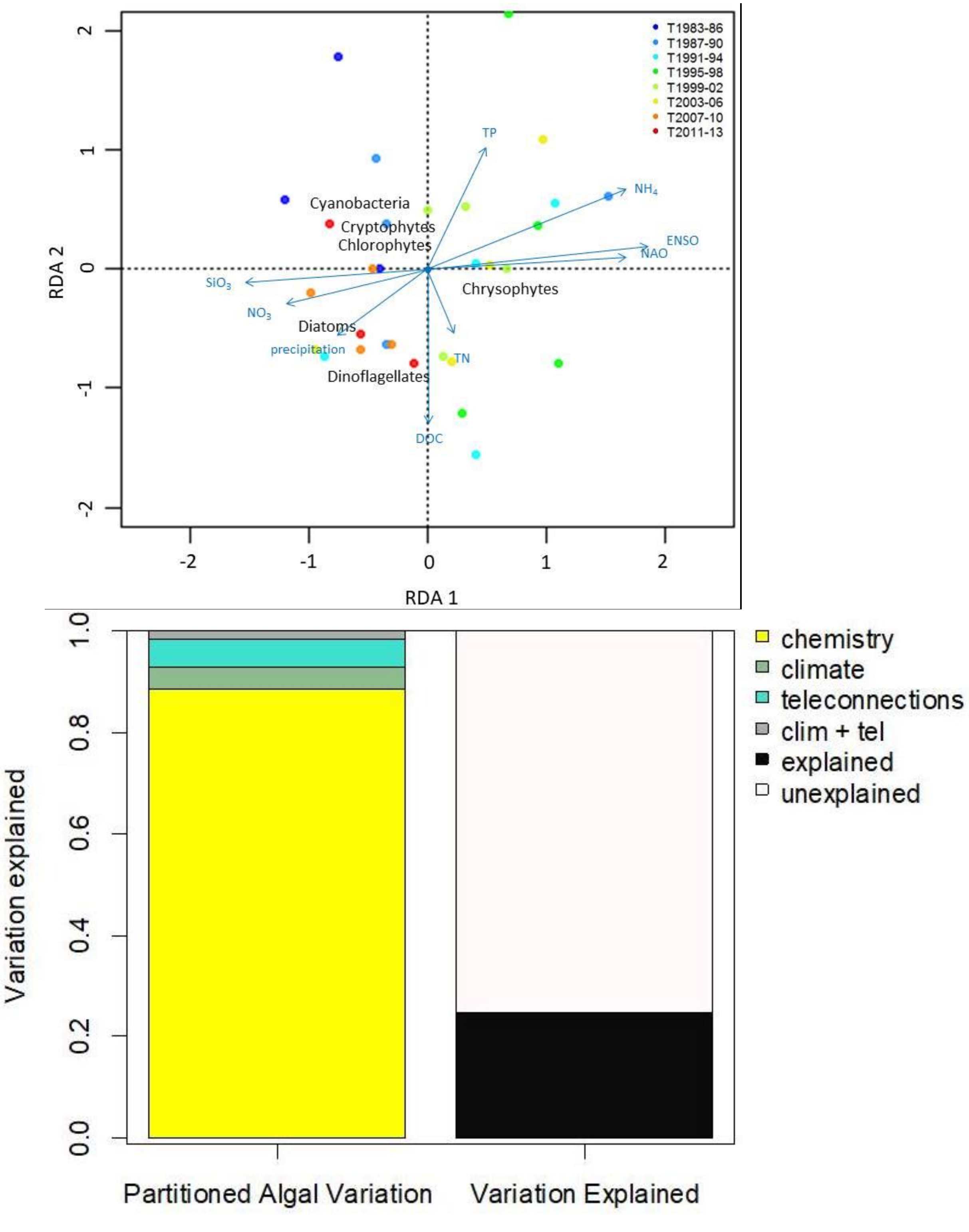

Figure 7: **(a)** Redundancy analysis plot showing the response of six algal taxa to chemical and climatic variables in Crosson Lake, and **(b)** Variation partitioning analysis showing the relative variation explained by each group of variables.

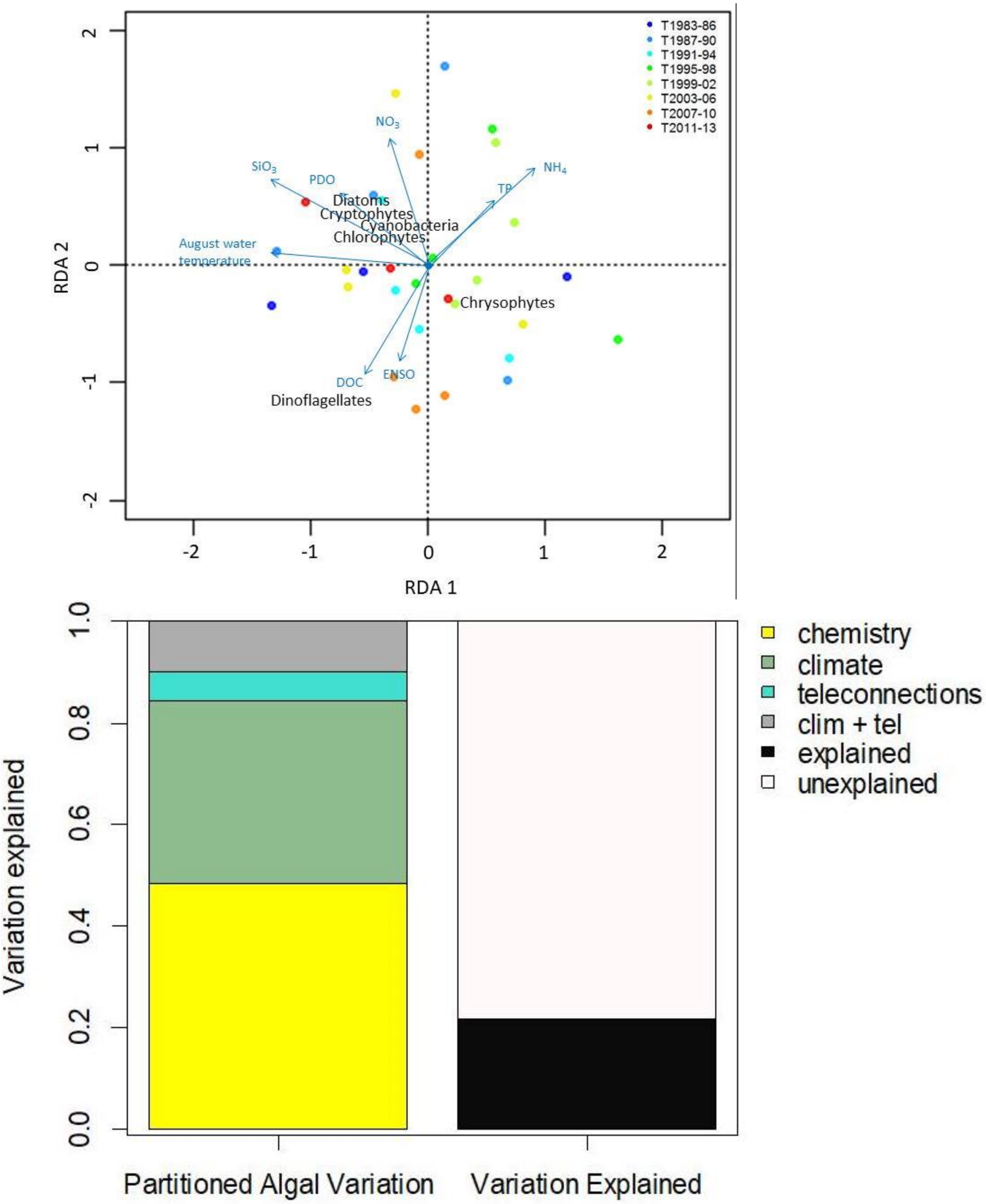

Figure 8: **(a)** Redundancy analysis plot showing the response of six algal taxa to chemical and climatic variables in Dickie Lake, and **(b)** Variation partitioning analysis showing the relative variation explained by each group of variables.

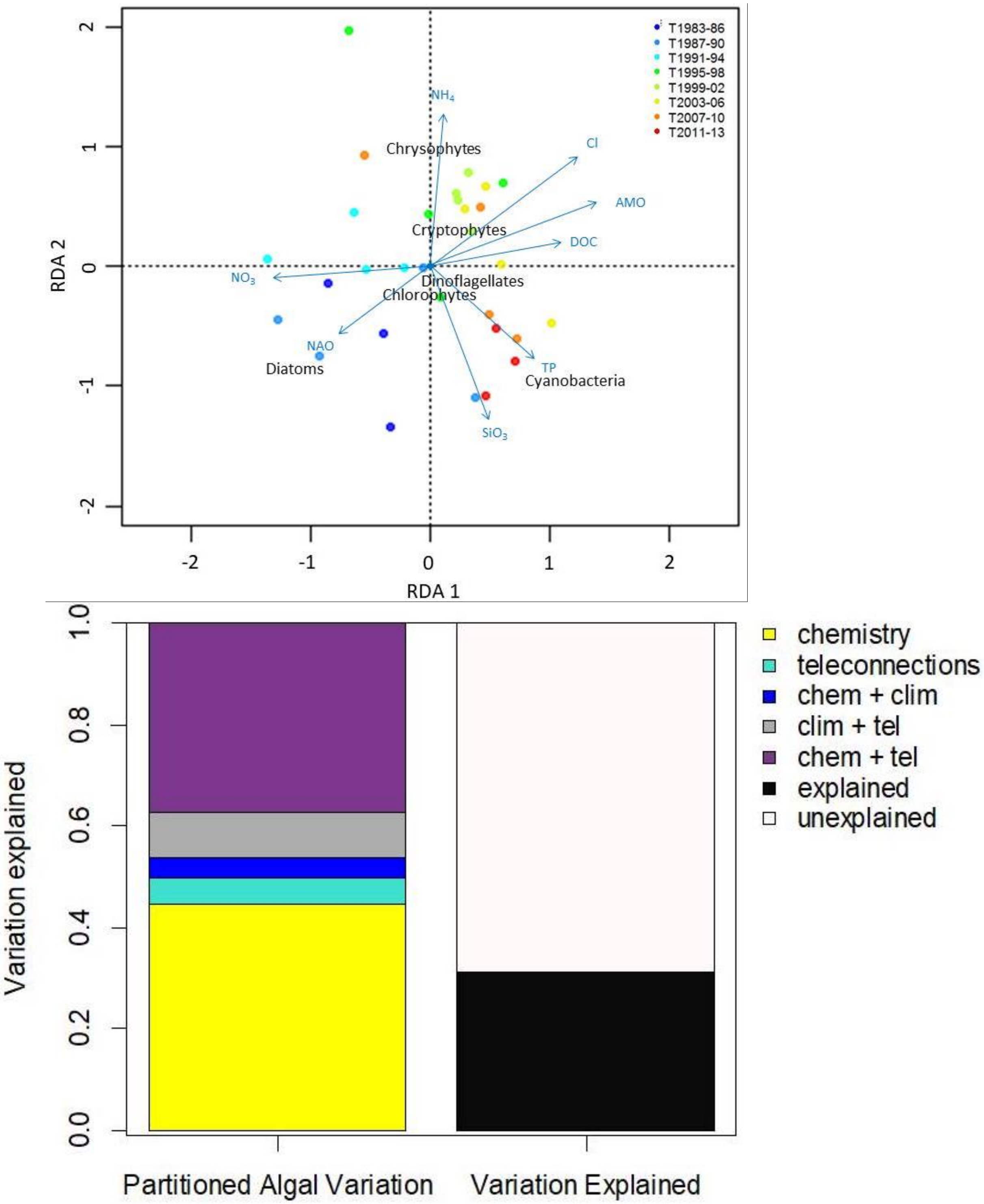

Figure 9: **(a)** Redundancy analysis plot showing the response of six algal taxa to chemical and climatic variables in Harp Lake, and **(b)** Variation partitioning analysis showing the relative variation explained by each group of variables.

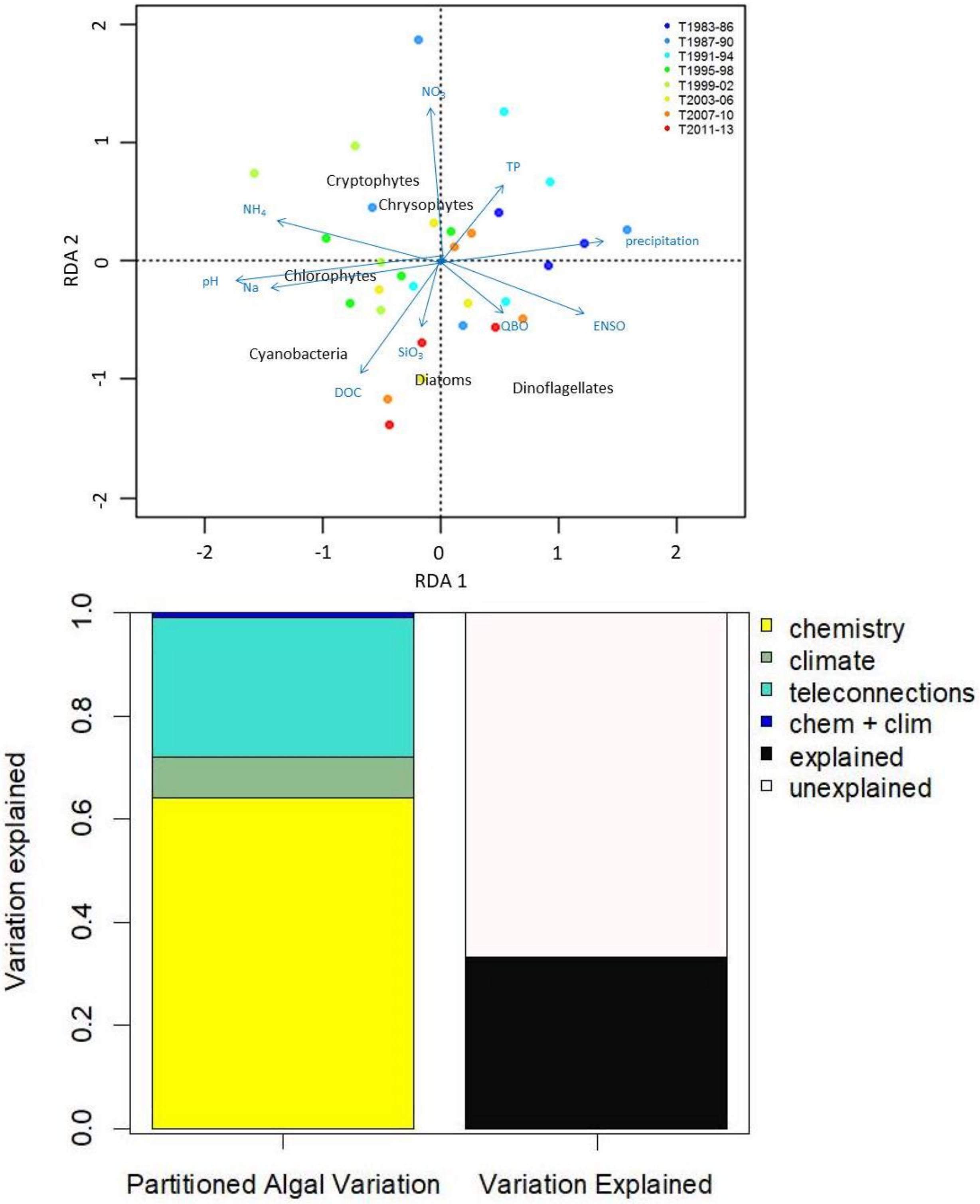

Figure 10: **(a)** Redundancy analysis plot showing the response of six algal taxa to chemical and climatic variables in Heney Lake, and **(b)** Variation partitioning analysis showing the relative variation explained by each group of variables.

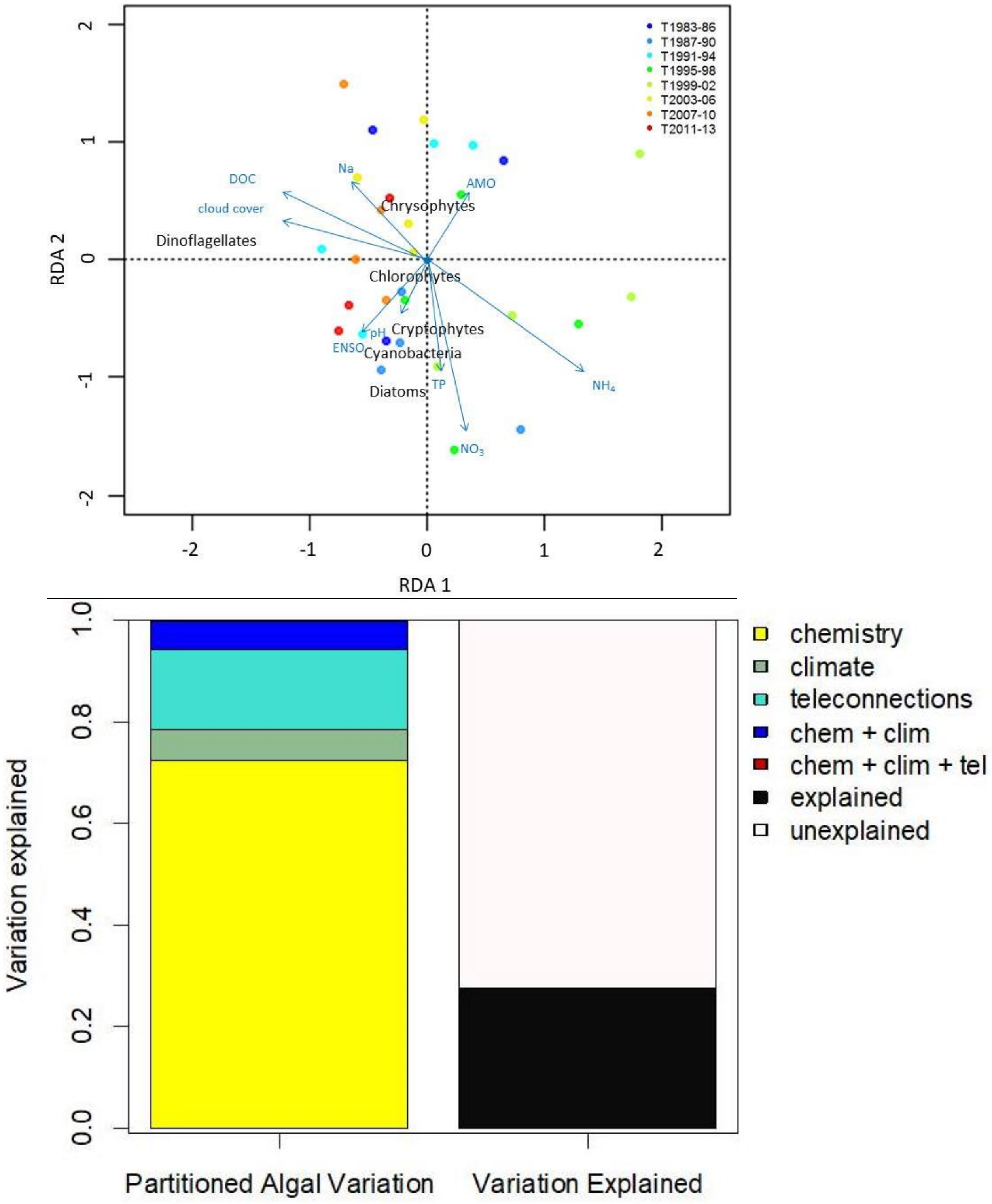

Figure 11: **(a)** Redundancy analysis plot showing the response of six algal taxa to chemical and climatic variables in Plastic Lake, and **(b)** Variation partitioning analysis showing the relative variation explained by each group of variables.

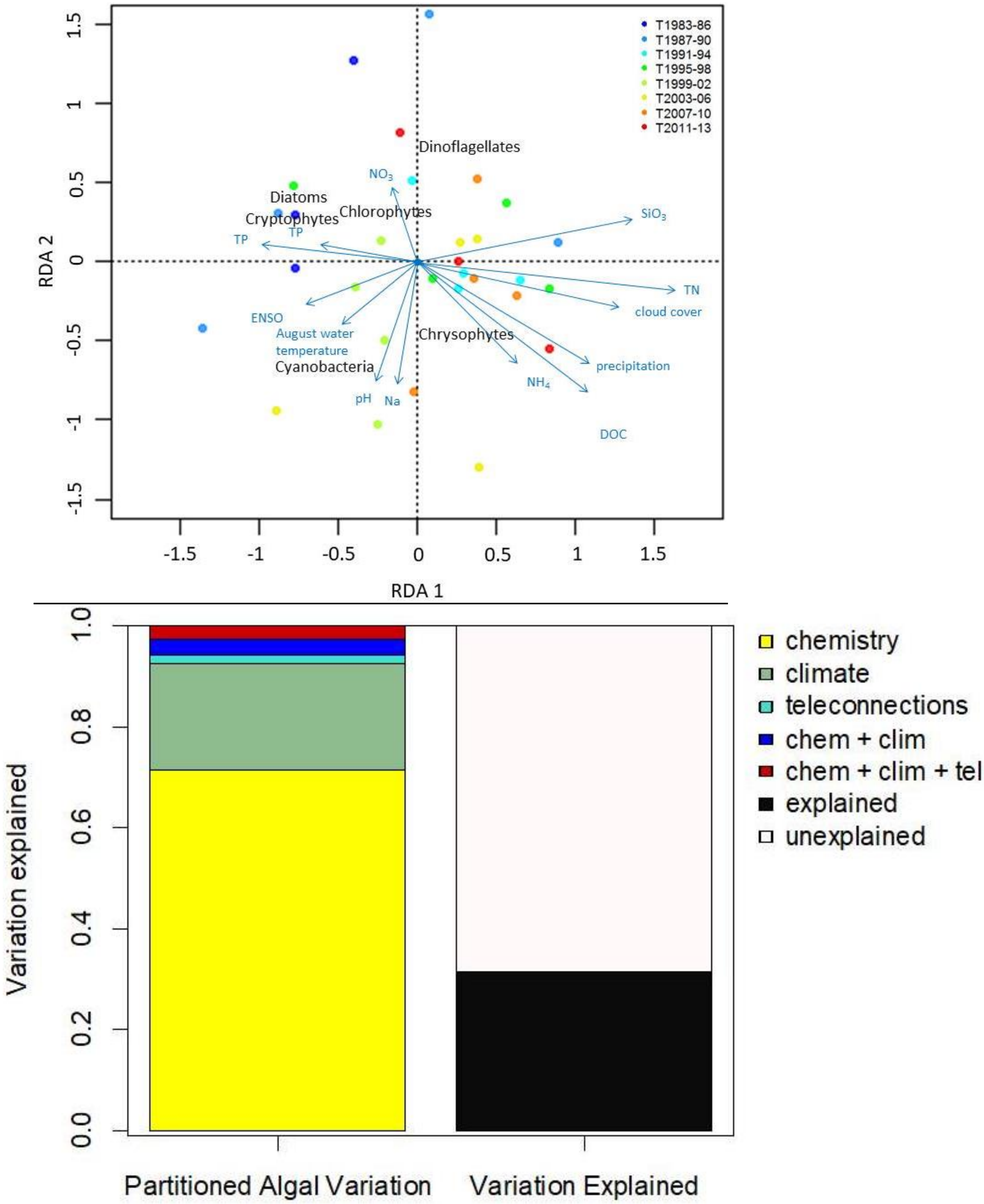

Figure 12: **(a)** Redundancy analysis plot showing the response of six algal taxa to chemical and climatic variables in Red Chalk Lake East, and **(b)** Variation partitioning analysis showing the relative variation explained by each group of variables.

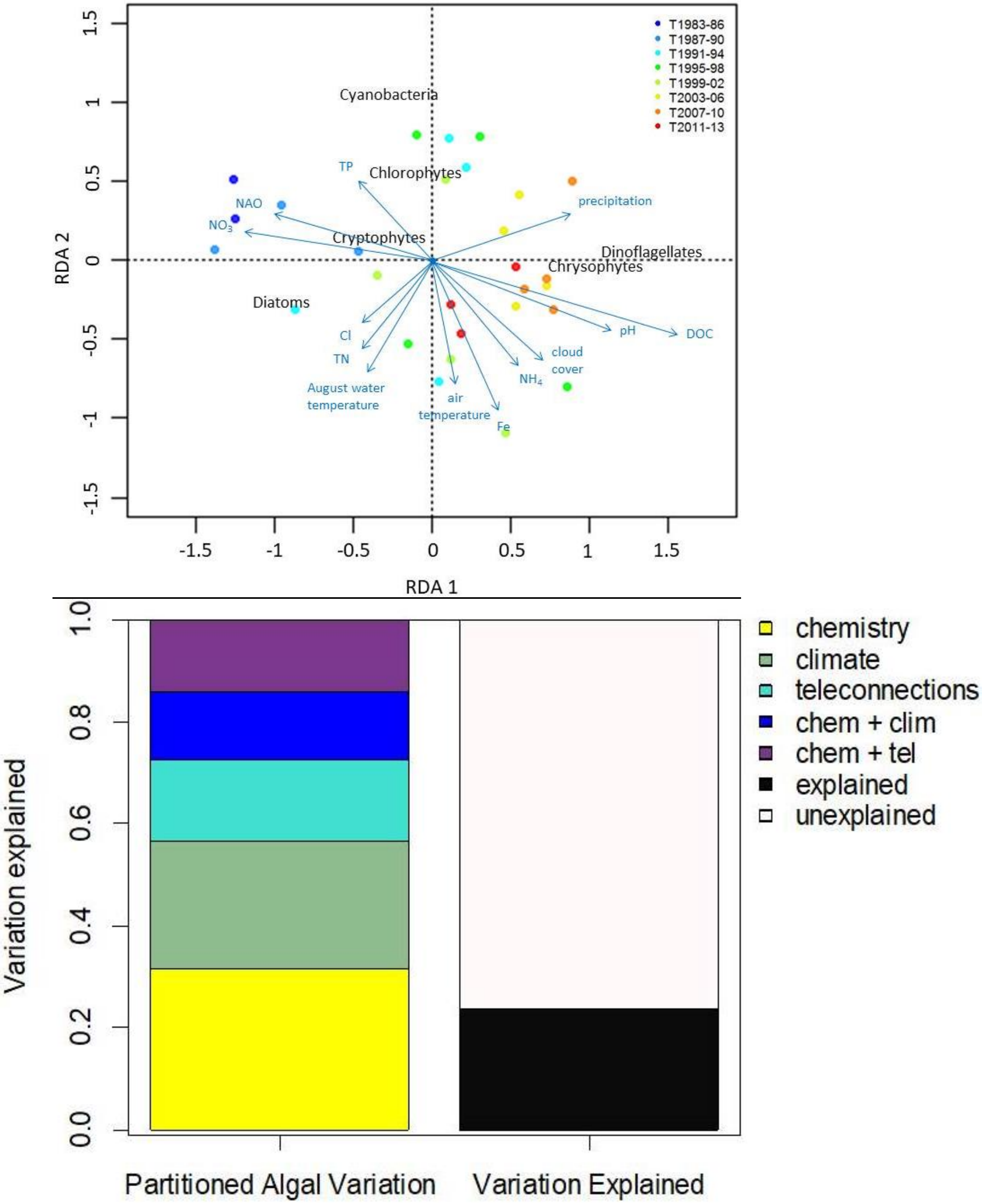

Figure 13: **(a)** Redundancy analysis plot showing the response of six algal taxa to chemical and climatic variables in Red Chalk Lake Main, and **(b)** Variation partitioning analysis showing the relative variation explained by each group of variables

SUPPLEMENTARY MATERIAL

Table A1: Dataset compiled to answer our research questions, including sources from which it was obtained, and the frequency of the observations.

Variable Type	Variable Category	Variable	Frequency of Observations	Data Source
Predictor	Morphometric	Lake Surface Area (ha)	-	DESC Database
		Mean Lake Depth (m)	-	DESC Database
		Maximum Lake Depth (m)	-	DESC Database
	Climatic	Historical Air Temperature (°C)	Monthly	CRU Database
		Historical Precipitation (mm)	Monthly	CRU Database
		Historical Cloud Cover (% of month)	Monthly	CRU Database
		Historical Water Temperature in August (°C)	Annually	DESC Database
		Climate Driver Indices	Monthly	NOAA, NCAR, and SILSO Databases
	Chemical	pH	Seasonal	DESC Database
		Dissolved Organic Compounds, DOC (mg/L)	Seasonal	DESC Database
		Total Nitrogen, TN (µg/L)	Seasonal	DESC Database
		Total Phosphorus, TP (µg/L)	Seasonal	DESC Database
		Silicate, SiO_3 (mg/L)	Seasonal	DESC Database
		Calcium, Ca (mg/L)	Seasonal	DESC Database
		Chloride, Cl (mg/L)	Seasonal	DESC Database
		Iron, Fe (µg/L)	Seasonal	DESC Database
		Sodium, Na (mg/L)	Seasonal	DESC Database
		Ammonium/Ammonia, NH_4 (µg/L)	Seasonal	DESC Database
		Nitrate/Nitrite, NO_3 (µg/L)	Seasonal	DESC Database
		Sulphate, SO_4 (mg/L)	Seasonal	DESC Database
Response	Biological	Relative Phytoplankton Biomass (%)	Ice-free (Mar-Nov) mean	DESC Database

Table A2: Reported influence of relevant teleconnection indices in the study region.

Index	Definition	Cycle Length (yrs)	Effect in Dorset of positive phase	Phases in Dorset during study period	Index Source	Information Source
Atlantic Multidecadal Oscillation (AMO)	SST in North Atlantic	50-90	+temp and -precip in summer	- (1995) +	http://www.esrl.noaa.gov/psd/data/timeseries/AMO/	Mestas-Nunez and Enfield, 1999
El Nino Southern Oscillation (ENSO)	winds and SST in South East Pacific	2-7	-temp and +precip in winter	- (1986) + (1988) - (1990) + (1995) - (1997) + (1998) - (2002) + (2005) - (2006) + (2007) - (2009) + (2010) - (2012) + (2013) - (2014) +	http://www.esrl.noaa.gov/psd/enso/mei/table.html	Rasmusson and Carpenter, 1982
North Atlantic Oscillation (NAO)	atmospheric pressure and winds in North Atlantic	no periodicity	+temp and -precip in winter	+ (1985) - (1986) + (1988) - (1989) + (1993) - (1994) + (1996) - (1999) + (2001) - (2002) + (2003) - (2004) + (2005) - (2007) + (2008) - (2011) + (2012) - (2012) +	http://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/norm.nao.monthly.b5001.current.ascii.table	Barnston and Livezey, 1987
Pacific Decadal Oscillation (PDO)	SST in North Pacific	20-30	+temp and -precip in winter	+ (2005) -	http://www.esrl.noaa.gov/psd/data/correlation/pdo.data	Mantua et al., 1997
Pacific / North American (PNA)	atmospheric pressure between Hawaii and central Canada	Dec-Apr, + phase associated with El Nino phase of ENSO	-temp in winter, -precip year round	+ (1988) - (1991) + (1994) - (1994) + (1996) - (1997) + (2002) - (2003) + (2008) - (2009) + (2014) - (2014) +	http://www.cpc.ncep.noaa.gov/data/teledoc/pna.shtml, https://www.ncdc.noaa.gov/teleconnections/pna/	Barnston and Livezey, 1987
Quasi-Biennial Oscillation (QBO)	stratospheric circulation in tropics	2.35	(positive=westerly phase) -temp in winter	- (1985) + (1987) - (1988) + (1989) - (1990) + (1992) - (1993) + (1994) -(1995) + (1996) - (1997) + (1998) - (1999) + (2000) -(2002) + (2003) - (2004) + (2005) - (2006) + (2007) - (2008) + (2009) - (2011) + (2012) - (2013) +	http://www.geo.fu-berlin.de/en/met/ag/strat/produkte/qbo/index.html#access	Baldwin et al., 2001
Sunspot Index (SS)	total sunspot number	11	+global temp	peaks in 1989, 2000, 2014	http://www.sidc.be/silso/datafiles	Friis-Christensen and Lassen, 1991

Table A3: Generalized Additive Models of log-transformed relative phytoplankton biomass (log(% of sample)) using both restricted maximum likelihood (REML) and generalized cross validation (GCV) smoothing parameter estimation methods, and thin plate regression splines.

Lake	Response	Predictor	REML method						GCV method					
			k'	edf	k-index	p-value	Model df	Model AIC	k'	edf	k-index	p-value	Model df	Model AIC
Blue Chalk	Diatoms	intercept					6.487	73.126					11.547	65.442
		DOC	9	2.78	1.01	0.45			9	4.19	1.33	0.93		
		NAO	9	1	0.85	0.15			9	5.35	0.97	0.38		
	Chrysophytes	intercept					8.030	68.258					7.235	65.665
		AMO	9	1.61	1.37	0.97			9	1.64	1.36	0.96		
		pH	9	3.26	0.82	0.15			9	3.59	0.84	0.18		
	Cryptophytes	intercept					4.488	69.648					4.134	68.668
		NO3	9	2.02	1.21	0.82			9	2.13	1.22	0.84		
	Cyanobacteria	intercept					4.710	84.739					7.953	82.458
		SWT_8	9	1	1.33	0.94			9	1	1.35	0.95		
		TP	9	1.41	0.93	0.29			9	4.95	1.12	0.67		
	Dinoflagellates	intercept					4.000	122.538					10.397	117.506
		AMO	9	1	0.83	0.12			9	3.54	0.89	0.2		
		pH	9	1	1.06	0.56			9	4.86	1.07	0.57		
Chub	Diatoms	intercept					3.000	92.793					3.000	92.793
		TN	9	1	1.1	0.66			9	1	1.1	0.65		
	Chlorophytes	intercept					4.000	93.078					4.000	93.077
		ENSO	9	1	1.21	0.81			9	1	1.21	0.8		
		PDO	9	1	1.31	0.92			9	1	1.31	0.95		
	Chrysophytes	intercept					3.000	53.462					3.000	53.462
		NH4	9	1	1.38	0.97			9	1	1.38	0.96		
	Cryptophytes	intercept					4.728	71.556					3.973	70.424
		AMO	9	2.19	1.1	0.67			9	1.97	1.08	0.55		

	Cyanobacteria	intercept					3.000	123.279					3.000	123.278
		SiO3	9	1	1.17	0.77			9	1	1.17	0.73		
Crosson	Diatoms	intercept					9.629	91.806					9.141	89.703
		SiO3	9	6.79	1.23	0.87			9	7.14	1.28	0.9		
	Chlorophytes	intercept					3.000	93.850					3.000	93.850
		SiO3	9	1	1.49	0.99			9	1	1.49	1		
	Chrysophytes	intercept					7.852	41.198					7.060	39.387
		NO3	9	3.97	0.96	0.32			9	4.06	0.97	0.38		
		ENSO	9	1	1.28	0.93			9	1	1.27	0.9		
	Cryptophytes	intercept					5.000	78.310					9.384	77.415
		SiO3	9	1	1.38	0.96			9	1	1.4	1		
		ENSO	9	1	1.11	0.66			9	3.32	1.14	0.69		
		Cloud	9	1	1.11	0.62			9	3.06	1.36	0.96		
	Dinoflagellates	intercept					3.000	123.475					3.000	123.475
		DOC	9	1	1.02	0.49			9	1	1.02	0.43		
Dickie	Chrysophytes	intercept					5.901	40.154					5.450	39.425
		SiO3	9	1	1.12	0.7			9	1	1.12	0.68		
		SWT_8	9	1.53	1.14	0.66			9	1.45	1.13	0.68		
		Cl	9	1	0.85	0.15			9	1	0.86	0.14		
	Cryptophytes	intercept					5.370	81.555					5.554	79.451
		SiO3	9	2.7	1.38	0.95			9	3.55	1.48	1		
	Dinoflagellates	intercept					10.166	94.717					12.467	86.711
		NH4	9	1	0.97	0.35			9	4.1	1.11	0.65		
		DOC	9	4.68	1.48	0.99			9	5.37	1.48	1		
		ENSO	9	1.28	1.43	0.99			9	1	1.34	0.94		
Harp	Diatoms	intercept					3.000	64.547					3.000	64.546
		Na	9	1	0.85	0.17			9	1	0.85	0.12		
	Chlorophytes	intercept					4.777	78.804					8.885	76.192
		Cloud	9	1.45	1.13	0.69			9	3.52	1.23	0.84		
		pH	9	1	0.94	0.31			9	3.36	0.97	0.4		

	Chrysophytes	intercept					3.000	72.928					3.000	72.928
		NH4	9	1	1.24	0.83			9	1	1.24	0.87		
	Cryptophytes	intercept					3.368	56.485					7.752	51.398
		AMO	9	1.2	1	0.46			9	5.75	1.43	0.98		
	Cyanobacteria	intercept					4.491	110.665					4.241	110.228
		SWT_8	9	1	0.98	0.38			9	1	0.98	0.36		
		pH	9	1.27	1.26	0.89			9	1.24	1.26	0.89		
	Dinoflagellates	intercept					5.612	97.195					4.914	96.151
		TN	9	2.1	1.22	0.83			9	1.91	1.22	0.84		
		Cl	9	1	1.17	0.8			9	1	1.17	0.82		
Heney	Diatoms	intercept					3.000	130.304					3.000	130.303
		NO3	9	1	1.13	0.7			9	1	1.13	0.74		
	Chlorophytes	intercept					6.981	85.793					6.390	84.093
		SO4	9	3.19	1.32	0.91			9	3.39	1.33	0.93		
		ENSO	9	1	1.38	0.98			9	1	1.38	0.98		
	Chrysophytes	intercept					3.879	19.975					3.472	19.292
		NO3	9	1.54	1.37	0.98			9	1.47	1.37	0.96		
	Cyanobacteria	intercept					3.559	120.351					3.294	119.863
		SO4	9	1.31	1.45	0.99			9	1.29	1.45	0.99		
Plastic	Chlorophytes	intercept					3.021	88.134					3.009	88.114
		Temp	9	1.01	1.21	0.79			9	1.01	1.21	0.88		
	Chrysophytes	intercept					4.329	36.421					3.704	35.443
		TP	9	1.84	1.21	0.8			9	1.7	1.2	0.82		
	Cyanobacteria	intercept					3.000	118.817					3.000	118.817
		NO3	9	1	1.28	0.94			9	1	1.28	0.94		
	Dinoflagellates	intercept					4.131	120.809					3.644	119.987
		DOC	9	1.72	1.13	0.76			9	1.64	1.12	0.68		
Red Chalk East	Chlorophytes	intercept					3.000	54.976					3.000	54.976
		Cloud	9	1	1.12	0..61			9	1	1.12	0.64		
	Chrysophytes	intercept					4.811	29.811					4.544	29.116

		DOC	9	1.47	0.98	0.42			9	1.54	0.98	0.4		
		Temp	9	1	1.26	0.86			9	1	1.26	0.92		
	Cryptophytes	intercept					7.204	78.589					6.800	77.177
		Precip	9	1	1.35	0.95			9	1	1.33	0.96		
		TP	9	2.58	1.25	0.88			9	2.8	1.27	0.93		
		SiO3	9	1	0.92	0.28			9	1	0.92	0.28		
	Cyanobacteria	intercept					6.209	93.483					5.357	91.823
		Cloud	9	3.38	0.23	0.88			9	3.36	1.23	0.85		
Red Chalk Main	Chrysophytes	intercept					8.053	69.986					6.199	67.522
		Ca	9	2.51	0.91	0.26			9	2.15	0.9	0.21		
		NH4	9	2.37	1.26	0.88			9	2.04	1.23	0.89		
	Cryptophytes	intercept					3.000	84.800					3.000	84.800
		SO4	9	1	1.38	0.97			9	1	1.38	0.99		
	Cyanobacteria	intercept					6.802	97.128					6.111	95.767
		SWT_8	9	3.12	1.37	0.96			9	3.11	1.37	0.97		
		PDO	9	1	0.96	0.32			9	1	0.96	0.28		
	Dinoflagellates	intercept					4.509	109.551					3.000	123.307
		DOC	9	2.01	1.18	0.76			9	1.87	1.18	0.83		
		SWT_8	9	1	1.03	0.052			9	1	1.04	0.46		

Table A4: Linear regressions of both relative and absolute phytoplankton groups over time.

		Relative				Absolute			
Lake	Phytoplankton Group	Trend	R^2_{adj}	P	Δ during study period (% total biomass)	Trend	R^2_{adj}	P	Δ during study period (mm^3/m^3)
Regional	Diatoms	-0.442	0.046	0.000236	-12.806	-1.618	0.015	0.02459	-46.913
	Chrysophytes	0.513	0.043	0.000348	14.868				
	Cryptophytes	-0.201	0.059	3.16E-05	-5.820				
	Dinoflagellates	0.152	0.020	0.01061	4.409	0.964	0.033	0.001523	27.959
BC	Diatoms	-0.984	0.196	0.008309	-28.545				
	Chlorophytes	-0.219	0.198	0.007932	-6.356				
	Chrysophytes	1.238	0.211	0.006169	35.888	11.13	0.163	0.01547	322.77
	Cryptophytes	-0.251	0.107	0.04335	-7.285				
	Dinoflagellates	0.241	0.154	0.01821	6.978	1.166	0.210	0.006398	33.805
CH	Cryptophytes	-0.389	0.156	0.01763	-11.275				
	Dinoflagellates	0.344	0.164	0.01527	9.976	1.722	0.155	0.01766	49.947
DI	Dinoflagellates					1.132	0.136	0.0254	32.840
HR	Diatoms	-1.411	0.391	0.00013	-40.925	-13.344	0.450	3.01E-05	-386.976
	Cryptophytes	0.258	0.125	0.03134	7.468				
	Cyanobacteria	0.409	0.155	0.01789	11.849				
	Dinoflagellates	0.144	0.136	0.02559	4.169				
HE	Diatoms	0.357	0.198	0.00806	10.350	1.751	0.180	0.01117	50.791
	Cyanobacteria	0.189	0.138	0.02473	5.477	0.807	0.140	0.02356	23.403
PL	Cryptophytes	-0.445	0.263	0.002199	-12.908				
RE	Diatoms	-0.491	0.207	0.006708	-14.224				
	Chrysophytes	0.884	0.193	0.008769	25.648	7.466	0.100	0.04961	216.514
	Cryptophytes	-0.350	0.189	0.009565	-10.136				
RM	Diatoms	-1.284	0.272	0.00185	-37.222	-5.861	0.127	0.03016	-169.969
	Chrysophytes	1.374	0.300	0.001024	39.837				
	Dinoflagellates	0.424	0.345	0.000383	12.284	1.748	0.358	0.000288	50.701

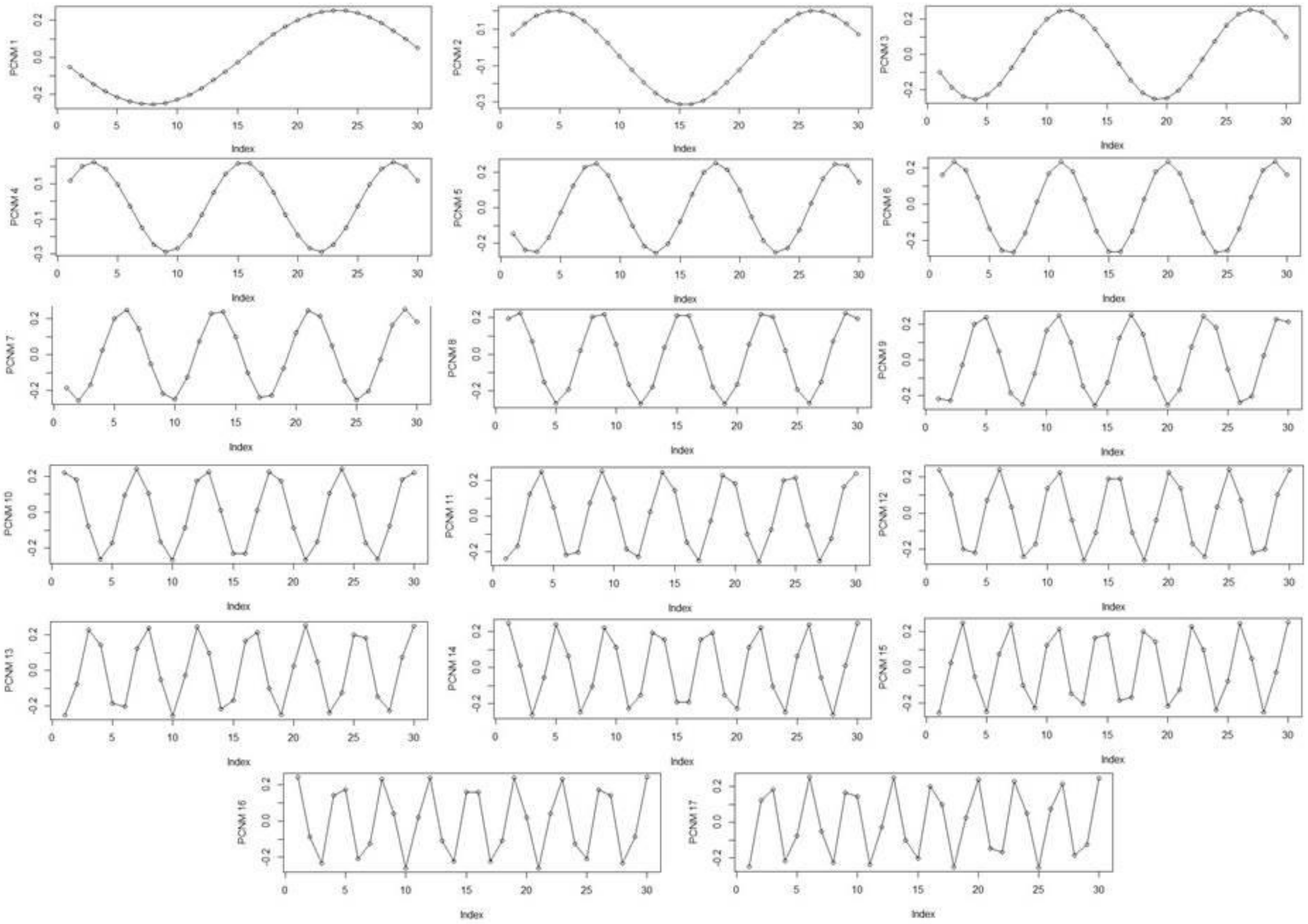

Figure A1: Moran Eigenvector Map periods constructed to represent cyclical processes in the study region between 1984 and 2013.

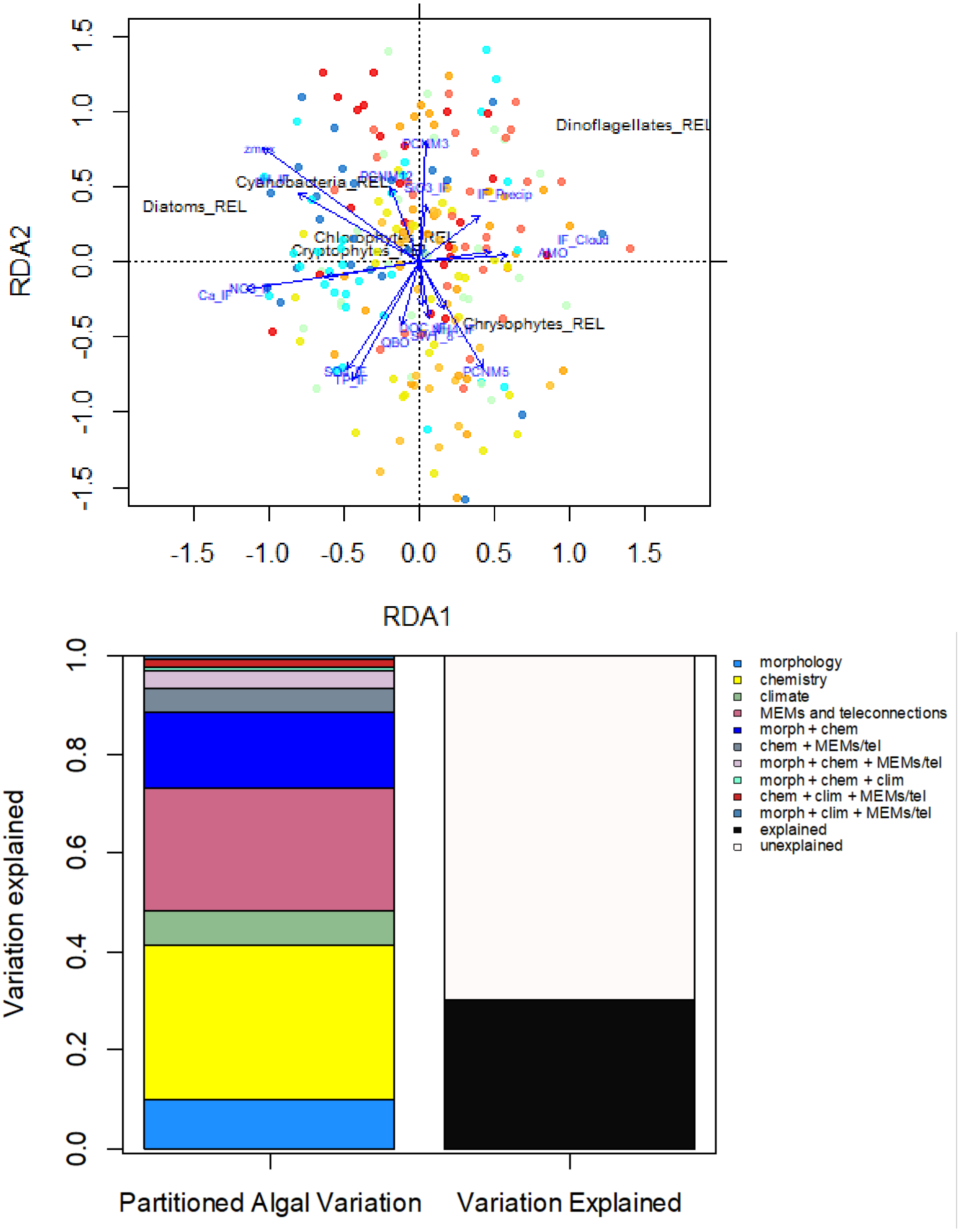

Figure A2: **(a)** Redundancy analysis plot including all study lakes, showing the response of six algal taxa to morphometric, chemical, and climatic variables, and MEMs, and **(b)** Variation partitioning analysis of the relative variation explained by each group of variables.

GENERAL CONCLUSION

In this thesis, we investigated the impacts of climate change on water quantity and water quality. We studied two relatively undisturbed regions using long-term ecological data. We found that water levels have declined and water quality has become further degraded over the past 30 years in response to multiple environmental stressors.

Between 1984 and 2014, water levels dropped by an average of 50 cm in our Wisconsin lakes, ranging from 23 to 122 cm, with the greatest changes in autumn. Our models explained between 22% and 82% of the variation in water levels. Precipitation explained 49% of the variation in level fluctuations, and 30% was explained by air temperatures. With regional climate projected to become warmer and wetter over the next century, water levels are projected to rise by an average of 36 cm by the year 2050 and by 44 cm by 2070. These changes in water level could lead to alterations in water chemistry, the health and size of wetlands, the frequency of algal blooms, and provision of ecosystem services.

In our Ontario lakes, diatoms and chrysophytes were the most abundant groups, with a shift from diatom to chrysophyte dominance between 1984 and 2013. Redundancy Analyses explained between 24% and 44% of the variation in phytoplankton biomass, with 60% of this attributed to changes in lake chemistry and lake morphometry. Changes in the phytoplankton community were driven by a combination of nutrient availability, competitive ability, and specific tolerances. Warmer air temperatures, periods of reduced precipitation, reduced Cation Exchange Capacity, and local geology have contributed to the slow recovery of our lakes to acid rain and affected the concentration and solubility of nutrients. In addition, lake brownification and climate warming have altered lake physics, extending the summer stratified period.

Global air temperatures are projected to increase by 0.2°C per decade and are likely to be 1.5°C warmer than pre-industrial temperatures by the 2030-2052 period (IPCC, 2018). The Great Lakes region is among the locations that will experience the greatest warming extremes (Hoegh-Guildberg et al., 2018). Although the region is expected to become drier due to a strong regional link between temperature and soil moisture, mean precipitation is expected to increase by 5 to 10%, and the Great Lakes region is at risk for more heavy precipitation events (Vogel et al., 2017; Hoegh-Guildberg et al., 2018). Adaptation options that reduce the risks from climate warming include ecosystem-based adaptation, biodiversity management, and sustainable water management (IPCC, 2018). In our study lakes, this might mean mechanical mixing to counteract the effects of enhanced stratification, sustainable groundwater management (water withdrawal for consumption and irrigation) to manage water levels as well as the severity of drought impacts, and managing forest fires to control DOC inputs to lakes. Management options for mitigating negative impacts of ecosystem changes might include liming lakes to accelerate recovery from acidification, removing vegetation and managing clearcutting to control DOC in the catchment, and the addition of calcium to promote daphnia population growth. By investigating how lakes respond to climate change, we may be better able to anticipate climate-related impacts. Water levels fluctuations may have serious economic, social, and environmental impacts. A better understanding of how multiple interacting stressors affect biological communities like phytoplankton will enable improved ecosystem management strategies, improving water quality and public health.

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