Deciphering Climate-Driven Changes in Planktonic Diatom Communities in Lake Superior

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DECIPHERING CLIMATE-DRIVEN CHANGES IN PLANKTONIC DIATOM COMMUNITIES IN LAKE SUPERIOR

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A DISSERTATION
Submitted in Partial Fulfillment of the
Requirements for the Degree of
Doctor of Philosophy
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The University of Maine
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Climate change is affecting lake systems throughout the world, including Lake Superior, the world’s largest lake by surface area. Climate-driven physical changes in Lake Superior are well documented, but there is still substantial uncertainty of how recent biological changes are related to climate change. This research addresses these uncertainties using a variety of approaches to understand the effects of modern climate-driven changes on Lake Superior diatom communities. First, I developed models for environmental variables related to diatom abundance using 10 years of summer monitoring data. Second, I investigated changes in fossilized diatom relative abundances before, during, and after the Medieval Climate Anomaly (MCA, 950-1250 CE), a past period of warming with minimal anthropogenic impact. This is compared with sedimentary diatoms from the past two centuries. Third, I compared changes in fossilized diatom relative abundances before, during, and after the MCA with changes occurring throughout the same period in a smaller regional lake to investigate the relationship of lake size to diatom community resilience in Lake Superior.

Modern abundance patterns of *Cyclotella sensu lato* species, a dominant group of centric planktonic diatoms in Lake Superior, are complex, associated with multiple environmental variables, and suggest synergistic effects of nutrients and, in some instances, climate-driven physical change. Paleolimnological data from fossilized diatoms suggest that multiple variables including climate change,
as well as anthropogenic activities that alter nutrient cycling, are leading to novel shifts in modern diatom communities. Diatom shifts the past century have no analogue to past warming during the MCA, with no significant shifts in the diatom community occurring throughout the MCA. Diatom communities did shift during the MCA in a smaller, regional lake, suggesting the importance of lake size in mediating diatom community response to climate-driven change.

The more we understand the effects of climate change on lake ecosystems, the better we can protect and manage our drinking water and aquatic ecosystems. However, climate change is a complex, political, and polarizing topic; therefore, the American public has varying beliefs and values relating to climate change, making management of environmental issues relating to climate change especially difficult. Formal public education may be the best route to create an informed and engaged public. I investigated various aspects of climate change education in Maine middle and high schools via an online teacher survey. The survey assessed frequency and breadth of climate change topics in classes, teacher attitudes towards climate change and climate change education, knowledge level of various climate topics, and barriers to effective teaching.

Maine teachers address climate change across a wide variety of subjects, viewing climate change as a major concern and an interdisciplinary subject that should be taught more frequently and broadly. Teachers from multiple disciplines are interested in professional development around climate change education and identified barriers that could lessen effective teaching such as knowledge gaps, outside pressure, and fear of scaring students. Survey results informed suggestions to enhance climate education, such as targeted professional development, strengthening interdisciplinary links, and providing solutions and adaptation strategies.
DEDICATION

This research is dedicated to the strong women in my family. To my mother Helen Weekly, for endless support, love, and generosity whatever I do or wherever I go. I am more grateful to you than I could ever say and you inspire me more than you could even know. To my grandmother Fannie Cronin for unconditional love and support, and for sharing her passion for reading and quiet observation. To my grandmother Mary Rose Kireta for sharing her love of baking, her determination, and art of eye rolling. I could never ask for two more amazing and loving role models. To the incredible, brilliant, inspiring, and caring angel Sherry Miller, the best Nurse Practitioner the world will ever know. Foremost, this work is dedicated to Parker Jane. You inspired me to follow this dream. May you always follow yours.
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CHAPTER 1

INTRODUCTION

Climate change is affecting lake systems throughout the world, with surface water temperatures increasing since 1985 in many of the world’s largest lakes (Schneider and Hook 2010). The magnitude of these surface water temperature increases varies regionally, with the greatest recent rates of change occurring in mid to high latitudes in the northern hemisphere (Schenider and Hook 2010). Lake morphometry and average water temperature modify how increasing air temperatures affect the vertical thermal structure of lakes, with recent research suggesting greater changes in the thermal structure of deep lakes since 1970 (Kraemer et al. 2015). Collectively, these studies reveal that warming has altered water temperature and thermal structure in large lakes over recent decades.

Most of our understanding of biological response to climate change is based on research in substantially smaller systems, including temporal variation in diatom shifts related to anthropogenic warming (Smol et al. 2005; Rühland et al. 2015). Many climate parameters have been linked to diatom community changes in smaller systems, including: changes in seasonality (e.g., Bradbury et al. 1993; Wolin 1996), precipitation (Bradbury 1988), ice cover (e.g., Wolin 1996; Rühland et al. 2008), length of growing season (Smol et al. 2005), and thermal stability (e.g. Winder et al. 2009; Saros et al. 2012). Much less is known about biological responses to climate change in large lakes. The few studies that have been conducted in large lakes suggest links between climate and changes in pelagic communities. For instance, Lake Baikal is experiencing substantial changes in water temperature and ice cover, with expectations of major alterations in food webs and function with projected climate change (Moore et al. 2009). Diatom communities have abruptly shifted with climate in Lake Victoria (Stager et al. 1997), and have been related to long-term climatic fluctuations in Lake Malawi (Stone et al. 2011). The general paucity of data linking climate and biological response in large lakes limits our ability to clarify relationships in many of these lakes. For example, diatom ecological ranges in the Great Lakes system
can differ from those found in other systems, warranting cautions when applying ecological information from smaller systems without proper testing (Stoermer 1993). Although the relationship between recent algal shifts and climate change in the North American Great Lakes is still largely a puzzle, recent research has suggested links between diatoms and climate change in the Great Lakes (Reavie et al. 2014; Bramburger and Reavie 2016; Reavie et al. 2016).

The North American Great Lakes, hereafter referred to as the Great Lakes, contain 20% of the world’s available freshwater, and 90% of the available supply for the continental United States. The Great Lakes are a highly studied system, with a biannual monitoring program measuring chemical and biological parameters for the past three decades (GLNPO 2010), and well-documented changes in phytoplankton over the past two centuries using paleolimnology; however, the causes of these changes generally focused on cultural eutrophication (e.g. Stoermer et al. 1993; Schelske and Hodell 1995; Wolin et al. 1988). Lake Superior is the largest Great Lake and holds 10% of the world’s available freshwater. Lake Superior surface water temperatures are increasing at approximately twice the rate as air temperatures (Austin and Colman 2008), with a declining ice cover trend since the 1970s (Wang et al. 2012) and recent record low lake levels (Holden 2007). During this time, diatom community structure has changed (Reavie et al. 2014b; Chraïbi et al. 2014) and summer diatom abundance has decreased (Reavie et al. 2014a). The relationships among these recent physical and biological changes in Lake Superior are still poorly understood.

Diatoms are dominant members of Great Lakes phytoplankton and are likely key ecological indicators for understanding biological response to climate in this system. Diatoms are particularly well suited for investigating biological responses to physical and chemical changes as they respond rapidly to environmental change (Vinebrooke 1996) and leave fossil remains in lake sediments. The Environmental Protection Agency has been monitoring the Great Lakes for the past few decades (GLNPO 2010), with quality-controlled records of summer diatom communities and a suite of physicochemical parameters
since 2001. To date, no study has used these data for in-depth investigations of relationships with environmental drivers in Lake Superior for species found related to climate-driven changes in smaller systems.

However, the climate-driven changes in Lake Superior have occurred concurrently with other environmental changes, such as nutrient concentrations (Dove and Chapra 2015), making it difficult to isolate recent climate change effects on diatoms from other anthropogenic activities in the watershed that have also been altering Great Lakes’ water quality for more than a century. Investigating ecological change during past periods of increasing air temperatures can provide valuable perspectives on the contemporary effects of increasing air temperatures on Lake Superior diatom changes. The Medieval Climate Anomaly (MCA, 950-1250 CE) is a well-documented period of climate change in the Northern Hemisphere, with many areas experiencing temperature increases comparable to or greater than current warming (Mann et al. 2009). A large portion of the Great Lakes region is believed to have warmed during the MCA, with a temperature anomaly of ~0.4°C relative to a 1961-1990 reference period mean (Mann et al. 2009). Investigating diatom changes during the MCA allows for an investigation of diatom response to warming during a period with minimal anthropogenic impact. This could be compared to modern changes to tease apart the effects of climate from other anthropogenic impacts.

It is important to note that physical effects of climate-driven change can differ in large lakes from those found in small lakes. For example, increasing wind strength at a rate of 5% per decade over Lake Superior (Desai et al. 2009) differs from trends over many terrestrial areas of the United States, where surface wind speeds are decreasing (Pryor et al. 2009). Surface winds are a major driver of stratification in Lake Superior (Austin and Allen 2011), with increasing thermocline depths since 1995 (Reavie et al. 2016). This would differentially affect the average light available for epilimnetic diatom communities in the Great Lakes compared to smaller systems where increased stratification and
decreased mixing is expected with increasing temperatures (Winder et al. 2009). Additionally, thermocline depth in Lake Superior can vary due to near-inertial currents (Austin 2013). Increased variability of thermocline depth in large versus small lakes can lead to lessened responses of taxa in large lakes with climate-induced changes in epilimnion thickness (Boeff et al. 2016). It is possible that changes in thermocline depth and resulting light availability during the MCA is within the range of variability experienced before or after the MCA, thus not enough to elicit a measurable response in the diatom community.

Siskiwit Lake is on Isle Royale, an island in Lake Superior, and is an ideal location to study the effects of the same climate drivers on a smaller regional lake. The surface area, depth, and volume are much smaller for Siskiwit Lake than Lake Superior. Previous investigation has found diatom communities in Siskiwit Lake responsive to changes in climate since 1850, showing more than a 50% change in diatom assemblages since 1920 (Saros et a. 2012). A paleolimnological comparison of Lake Superior and Siskiwit Lake before, during and after the MCA will identify differences in diatom community response to past warming. Siskiwit Lake may be a more sensitive sentinel of regional climate change than Lake Superior.

My research addresses how climate-driven changes in Lake Superior affect planktonic diatom communities using three studies: 1. Investigating changes in contemporary abundances of *Cyclotella sensu lato* species in Lake Superior in relation to climate-driven change and other environmental variables; 2. Investigating changes in diatom assemblages before, during, and after the previous warming period of the Medieval Climate Anomaly, comparing changes to those in the sedimentary records since 1800; 3. Investigating changes in a smaller lake embedded in Lake Superior, Siskiwit Lake, to understand the effect of lake size on diatom community resilience to climate-driven changes.

As a trainee in the A2C2 IGERT program, the final research chapter of my dissertation evolved from my Collaborative Immersion Project, and focuses on the broader concept of how middle and high school teachers understand and teach climate change. That chapter is packaged as its own unit.
Chapters 2, 3, and 5 were written for publication in three different journals and will have various co-authors for each chapter. I have yet to target a journal for chapter 4. Chapter 2, “Contemporary abundance patterns of *Cyclotella sensu lato* taxa in Lake Superior: assessing responses to physical and chemical gradients and potential links to climate change,” will be submitted to the Journal of Plankton Research and include J.E. Saros as co-author. I designed this study with guidance from Jasmine Saros. Diatom and environmental data were collected and analyzed as part of the EPA’s Great Lakes National Program Office and were provided by Euan Reavie, who is the principal investigator for the phytoplankton monitoring program. I independently conducted all data analyses with guidance from Brian McGill and interpreted results with guidance from Jasmine Saros. Euan Reavie and Mark Edlund provided valuable taxonomic guidance and suggestions to a previous manuscript draft. Chapter 3, “Comparison of sedimentary diatom profiles during the Medieval Climate Anomaly and the 20th century in Lake Superior suggests recent changes are unique,” will be submitted to the Journal of Paleolimnology with J.E. Saros and V.L.S Chraibi as co-authors. I designed this study with guidance from Jasmine Saros. Core samples were obtained from Joe Werne and Molly O’Beirne, with $^{210}$Pb dating from data generated by Robert Hecky. I prepared the slides and counted the diatoms in the MCA core and performed all statistical analyses with guidance from Jasmine Saros. Data from the Post-1800 core were provided by Victoria Shaw Chraibi (originally published in Chraibi et al. 2014). Chapter 4, “Comparing Lake Superior and Siskiwit Lake sedimentary diatoms during the Medieval Climate Anomaly: Can a smaller regional lake be used as a sentinel of climate change?,” will include J.E. Saros and likely several others, such as M.B. Edlund, D. R. Engstrom, and K. E. Strock as co-authors. I designed this study with guidance from Jasmine Saros, using core material Mark Edlund and Daniel Engstrom had previously collected from Siskiwit Lake, with slides prepared previously by Kristin Strock. I enumerated the diatoms and analyzed the data with guidance from Jasmine Saros. Chapter 5, “Climate Science and Climate Change Education in Maine Middle and High Schools”, will be submitted to Maine Policy Review, with B. Grigholm, M.
Teisl, and M. Schauffler as authors. I co-designed the survey for this study with Bjorn Grigholm, with guidance from Molly Schauffler, Dan Capps, and Michelle Smith. I analyzed and interpreted data with guidance from Mario Teisl.

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CHAPTER 2

CONTEMPORARY ABUNDANCE PATTERNS OF CYCLOTELLA SENSU LATO TAXA IN LAKE SUPERIOR:
ASSESSING RESPONSES TO PHYSICAL AND CHEMICAL GRADIENTS AND POTENTIAL LINKS TO CLIMATE CHANGE

2.1 Abstract

Relative abundances of Cyclotella sensu lato diatom taxa have been shifting in freshwater lakes over the past 150 years. These shifts are often attributed to climate change, however specific drivers of changing abundances are currently unclear in Lake Superior, where abundances of several taxa have changed over the last century. We used multiple linear regression to identify relationships among environmental variables and cell densities of six species, four responsive to climate-driven change in smaller lakes and two with similar morphology: Discostella stelligera and the similar D. pseudostelligera, Lindavia comensis and the similar L. delicatula, Lindavia ocellata, and Lindavia bodanica. Nutrients, including nitrate, phosphorus, and silica, were important in explaining distributions of all taxa. Surface water temperature and light availability were tested variables associated with climate-driven physical change, using turbidity and thermocline depth as indicators of the light environment. We found that cell densities of two taxa were linked to physical variables associated with climate: Discostella pseudostelligera was associated with higher light availability and L. ocellata with lower water temperatures. Cyclotella sensu lato abundance patterns in Lake Superior are complex and associated with multiple environmental variables, suggesting synergistic effects of nutrients, and in some instances, climate-driven physical change, may alter relative abundances.

2.2 Introduction

Cyclotella sensu lato taxa are a group of planktonic centric diatoms that comprise three currently accepted modern genera: Cyclotella, Discostella, and Lindavia (Spaulding et al., 2010), with
Pantocosekiella recently proposed (Ács et al., 2016) to accommodate some members of the group. *Cyclotella sensu lato* taxa have shown marked shifts in abundance over the past 150 years in many lakes around the world (e.g. Hobbs et al., 2010; Rühland et al., 2015). Although some research suggests a general trend of increasing abundance of this group (Rühland et al., 2015), others have summarized increases or decreases in abundance as highly variable by species and location (Saros and Anderson, 2015). Changes in the relative abundances of *Cyclotella sensu lato* are often inferred as signals of warming-induced changes in the physical features of lakes, such as length of ice-free season (Rühland et al., 2008), or changes in water column stability (i.e., strength of stratification) or mixing depth (Winder et al., 2009; Saros et al., 2012). Previous research has revealed interspecific variation in the mixing depth optima of various *Cyclotella sensu lato* taxa in small lakes (Saros et al., 2012), largely owing to differences in requirements for photosynthetically active radiation (Saros et al., 2012, 2014; Malik and Saros, 2016), the availability of which is altered by changes in thermal structure. For example, warming temperatures may lead to earlier or stronger stratification, with a shallower epilimnion providing algal cells higher average light availability than a deeper epilimnion (Saros et al. 2016). Currently, many *Cyclotella sensu lato* taxa are widely accepted as indicators of climate-driven changes in smaller, oligotrophic to mesotrophic lakes in the Arctic (Smol et al., 2005; Malik and Saros, 2016) as well as alpine and boreal regions (Rühland et al., 2008; Winder et al., 2009; Saros et al., 2012). It should be noted that *Cyclotella sensu lato* relationships to thermal structure are also affected by nutrient availability (Kilham et al., 1996; Saros et al., 2014; Malik and Saros, 2016).
**Figure 2.1.** Light micrographs of *Cyclotella sensu lato* taxa in this study. (A) *Discostella stelligera*; (B) *Discostella pseudostelligera*; (C) *Lindavia comensis*; (D) *Lindavia delicatula*; (E) *Lindavia ocellata*; (F) *Lindavia bodanica*. Scale bars to left of each taxon indicate 10 µm. Images courtesy of Michael Agbeti from Lake Superior Great Lakes National Program Office samples (images C, D, F), Victoria Shaw Chraïbi from modern Lake Superior sediment (image A), Rex Lowe from Lowe, 2015a (image B), and Amy Kireta from Lake Superior sediment (E).

*Cyclotella sensu lato* taxa (Fig. 2.1) are an important component in modern diatom assemblages in Lake Superior, the world’s largest freshwater lake by surface area (Reavie et al., 2016). Relative abundances for this group have been changing in recent decades, with major shifts since ~1980 documented in multiple paleolimnological records (Chraïbi et al., 2014; Reavie et al., 2016). Specifically, *Discostella stelligera* (Cleve & Grunow) Houk & Klee and the morphologically similar *Discostella pseudostelligera* (Hustedt) Houk & Klee have fluctuated in recent decades across paleolimnological records with no clear increasing or decreasing trends (Reavie et al., 2016), however the timing of relative abundance changes differs spatially across the basin, supporting localized watershed effects (Chraïbi et al., 2014). *Lindavia comensis* (Grunow) T.Nakov et al. has generally been increasing since ~1970, although its relative abundance has been eclipsed by increases of the morphologically similar taxon *Lindavia delicatula* (Hustedt) T.Nakov et al., also reported as *L. comensis* “rough center with
process” (Chraïbi et al., 2014; Reavie et al., 2016) or *Cyclotella cf. delicatula* (Reavie and Kireta, 2015). *Lindavia ocellata* (Pantocsek) T.Nakov et al. has declined in the recent sediment record (Stoermer et al., 1985a; Chraïbi et al., 2014; Reavie et al., 2016). Relative abundances of *Lindavia bodanica* (Eulenstein ex Grunow) T.Nakov et al. increased in sedimentary profiles through the 1970s (Stoermer et al., 1985a) and have since been fluctuating (Chraïbi et al., 2014; Reavie et al., 2016).

There are several reasons why deciphering the ecology of *Cyclotella sensu lato* in Lake Superior will improve interpretations of the drivers of diatom community changes in this system. Taxa within *Cyclotella sensu lato* may have species-specific relationships to climate-driven physical changes in Lake Superior. Also, climate-driven changes have occurred concurrently with shifts in other environmental variables and the drivers of diatom community changes are currently unclear. Further, diatom autecology can vary among systems, with drivers in Lake Superior differing from those identified in other systems. Finally, large lake ecosystems such as Lake Superior often respond differently to climate forcing compared to smaller lakes, where most of the relationships between *Cyclotella sensu lato* and climate have been assessed. For example, while epilimnion thickness is controlled by transparency in smaller lakes, mechanical energy, like wind, is more important in larger lakes (>500 hectare) and can lead to greater interannual variability of epilimnion depths (Fee et al., 1996).

While climate change is a suspected driver of diatom community shifts, recent research in the Great Lakes has largely treated *Cyclotella sensu lato* as one group, therefore grouping autecology and finding unclear linkages between diatom community composition changes and water chemistry (Bramburger and Reavie, 2016; Reavie et al., 2016). Paleolimnological (e.g. Stoermer et al., 1985a; Chraïbi et al., 2014) and contemporary (e.g. Reavie et al. 2014b) studies suggest distinct environmental responses for individual *Cyclotella sensu lato* taxa in the Great Lakes, supporting the need to investigate relationships of discrete taxa with environmental drivers.
Although Lake Superior has undergone physical changes related to recent climate change (Austin and Colman, 2007; Desai et al., 2009), several other environmental variables have also changed recently (Reavie et al., 2016). Water chemistry and algal densities documented by the Environmental Protection Agency (EPA) (e.g. Reavie et al., 2014b) and Environment Canada (Dove and Chapra, 2015) suggest Lake Superior water quality has been changing over the past few decades. For example, spring total phosphorus (TP) has declined from 0.161 to 0.065 µM (reported as 5 to 2 µg L\(^{-1}\)) from 1970 to 2012, hypothesized to be related to changes in precipitation chemistry (Dove and Chapra, 2015).

Meanwhile, concentrations of nitrate, the dominant form of nitrogen in Lake Superior, increased from \(~5\) to 25 µM in the past century (Sterner et al., 2007), and from \(<24\) to >27 µM (reported as \(<340\)-\(>380\) µg L\(^{-1}\)) from 1980-2010 (Dove and Chapra, 2015). Increases in nitrate in recent decades appear related to historical loadings and low availability of organic carbon, which is needed for denitrification to convert nitrate to unusable forms (Sterner et al, 2007; Sterner, 2011). Summer Secchi depths have significantly increased since the early 1970’s, correlated with decreases in surface chlorophyll concentrations (Dove and Chapra, 2015). Summer total algal abundances have fluctuated, ranging from 1,320 to 8,786 cells mL\(^{-1}\) and diatom abundance from 66 to 433 cells mL\(^{-1}\) between 2001-2010 (using data acquired from the U.S. EPA Great Lakes National Program Office, Great Lakes Biology Monitoring Program, Great Lakes Environmental Database). Reavie et al. (2016) tested correlations between *Cyclotella sensu lato* and environmental variables, but potential synergistic effects of these changing variables on species changes are yet to be investigated.

Potential differences in diatom resource physiology underscore the need to investigate linkages between *Cyclotella sensu lato* taxa and environmental drivers in Lake Superior. There are many examples of intraspecific variation in autecology, i.e. ecotype formation, with different resource requirements across freshwater regions for the same species (Guillard and Kilham, 1977; Lewis et al., 1997). For example, growth rates of *Cyclotella glomerata* H.Bachmann peak at low light (Kalff et al.,
1975) and high light (Carney et al., 1988) in different systems. Ecotype formation would lead to
mislabeled environmental drivers in a system as well as misguided paleolimnological inferences. While
the foundational research in diatom resource physiology was conducted in the Great Lakes (Kilham et
al., 1977; Tilman, 1977; Kilham, 1978; Tilman, 1981; Tilman et al., 1982), much of our understanding of
freshwater diatom ecology in the realm of climate-related parameters comes from smaller lakes
(Bradbury 1988), as well as large lakes in other regions, e.g., Yellowstone Lake (Kilham et al., 1996) and
Lake Tahoe (Winder et al., 2009). Stoermer (1993) cautioned against applying diatom environmental
preferences developed in other systems to the Great Lakes.

The unusually large size of Lake Superior results in different physical responses to climate
forcing than in smaller lakes, further supporting the need to specifically assess whether diatom
relationships to climate that were developed in other systems also apply here. Documented physical
responses to climate forcing in Lake Superior include surface water temperature increasing faster than
air temperature (Austin and Colman, 2007), increasing wind speeds over the lake (Desai et al., 2009),
and a significant increase in thermocline depth since 1995 (Reavie et al., 2016). Increasing regional wind
speeds contrast with trends of recent decreasing wind speeds over much of the contiguous United
States (Pryor et al., 2009). Although there has been a global trend towards deeper, steeper thermoclines
in lakes, deep lakes have experienced the largest changes in stratification (Kraemer et al., 2015). Lake
Superior has also shown different physical responses to climate forcing than other large lakes. For
example, wind and stratification patterns differ from Lake Ontario, a Great Lake with decreasing surface
winds and a shallower, more strongly stratified epilimnion (Huang et al., 2012). In addition, internal
seiches only develop to a significant extent in lakes with at least a 10 km fetch (Boyce, 1974). Thus, the
effects of thermal stratification on diatom taxa may be smoothed in large lakes due to the presence of
seiches (Boeff et al., 2016). Lake Superior experiences frequent seiches (Mortimer & Fee, 1976), creating
highly variable mixing depths, which would routinely expose phytoplankton to a variable light
environment. Further, near-inertial currents in Lake Superior are strongest during stratification and are also linked to changes in thermocline depth (Austin, 2013). Nevertheless, links between diatoms and climate-driven changes may also apply to Lake Superior. Although relationships with Cyclotella sensu lato are largely being developed in smaller systems (Smol et al., 2005; Saros et al., 2014), links between diatom community shifts and climate forcing have been found in other large lakes, such as Lake Baikal (Moore et al., 2009), Lake Tahoe (Winder et al., 2009), Lake Victoria (Stager et al., 1997), and Yellowstone Lake (Kilham et al., 1996).

We investigated which factors are related to Cyclotella sensu lato abundance in Lake Superior. We hypothesized similar relationships in Lake Superior between Cyclotella sensu lato taxa and climate-driven physical variables found in other studies, namely relationships related to light availability found by Saros et al. (2012) and Malik and Saros (2016): higher abundance of D. stelligera in higher light conditions; higher abundance of L. comensis in moderate light conditions; L. bodanica and L. ocellata with highest abundance at lower light conditions. Further, we tested two species that are morphologically similar to previously tested taxa, hypothesizing higher abundance of D. pseudostelligera in higher light conditions, as with D. stelligera, and higher abundance of L. delicatula in moderate light conditions, as with L. comensis. In this study, we used turbidity and thermocline depth as proxies for light availability. Specifically, we tested relationships between abundance of each taxon against the following physical and chemical variables: 1. Climate-driven physical parameters including: a. light availability: thermocline depth (thermocline) and turbidity, and b. surface water temperature (temperature); 2. Nutrients: total dissolved phosphorus (TDP), nitrates+nitrites (NOx), and silica; and 3. Specific conductance (conductivity).
2.3 Methods

2.3.1 Site Description

Lake Superior (47.7°N, 87.5°W) is the largest North American Great Lake, containing ~ 10% of the available fresh surface water in the world, more than all other Laurentian Great Lakes combined (Fig. 2.2). Bordering the United States and Canada, the surface area of Lake Superior is 82,100 km². It has an average depth of 147 m, with a maximum depth of 406 m.

![Map of Lake Superior indicating Great Lakes National Program Office sampling locations](image)

**Figure 2.2.** Map of Lake Superior indicating Great Lakes National Program Office sampling locations, with dashed box in insert showing location in North America, bordering the United States and Canada.

2.3.2 Dataset Description

The dataset was developed using data acquired from the U.S. EPA Great Lakes National Program Office, Great Lakes Biology Monitoring Program (GLNPO), Great Lakes Environmental Database which has been monitoring all five Laurentian Great Lakes for decades. Biannual phytoplankton and water chemistry sampling is conducted in spring and summer (typically April and August) at multiple standard stations for each lake aboard the ship R/V Lake Guardian, with a total of 19 biannual sampling locations for Lake
Superior (Fig. 2.2). We analyzed summer GLNPO monitoring data collected for Lake Superior from 2001 to 2011, which was the most complete dataset for our objective. Data used in this study are from summer sampling when the lake was under stratification and include three sites for each year from 2001-2005, and up to 19 sites for each year from 2007-2011, which were all the monitoring sites which had complete diatom and environmental data. Specific conductance data were not available for 2006 for sites with validated diatom data. Many physicochemical parameters were measured, including: surface temperature, thermocline, Secchi depth, total suspended solids, pH, NOx, total phosphorus, TDP, silica, dissolved organic carbon, turbidity, conductivity, chloride, diatom taxon abundances, chlorophyll, and total algal counts.

A standard operating procedure for phytoplankton collection and analysis was used (GLNPO, 2010). Briefly, whole water samples were collected from a rosette sampler on-board the R/V Lake Guardian. Phytoplankton samples were whole water composites, sampled at discrete depths within the epilimnion, integrating equal volumes from 1 m, 5 m, 10 m, and the lower epilimnion. If the epilimnion comprised less than the top 10 m, equal volumes of water were integrated from a maximum of four and a minimum of two sampling depths. Each sample was digested in nitric acid and subsequently in peroxide to isolate the diatom valves, which were then mounted on slides and counted using light microscopy standardized with high resolution (NA 1.4) oil immersion optics capable of 1000x magnification for detailed taxonomic identification to species-level or finer. Slides were enumerated by a single taxonomist and with quality control of data confirmed by a taxonomist at another lab.

2.3.3 Taxonomy

Taxa from two of the Cyclotella sensu lato genera were investigated in this study: Discostella Houk & Klee, and Lindavia (Schütt) De Toni & Forti (Fig. 2.1). The classification and nomenclature of this group have recently changed and no taxa in this study are currently included in the genus Cyclotella (Kützing).
We follow the classification scheme of Nakov et al. (2015) and have not adopted the recently proposed genus *Pantocosekiella* (Ács et al., 2016) for some of the taxa. Four taxa were identified for testing based on relationships reported with climate-driven physical change in previous studies (Saros et al., 2012; Malik and Saros, 2016): *D. stelligera*, *L. comensis*, *L. ocellata*, and *L. bodanica*. Two additional taxa were tested based on similar morphology to previously tested taxa: *D. pseudostelligera* and *L. delicatula*. For example, *D. pseudostelligera* has been previously combined with *Discostella stelligera* (Reavie et al., 2016), and *L. delicatula*, as *C. comensis* “rough center with process” or *L. cf. delicatula*, combined with *L. comensis* (Chraïbi et al., 2014; Reavie et al., 2016) in recent Great Lakes literature. There have been reports of similar environmental preferences of *L. delicatula* with *L. comensis* in Great Lakes-wide study (Reavie et al., 2016) and some overlapping autecology between *D. stelligera* and *D. pseudostelligera* in other systems (Lowe 2015 a,b).

2.3.4 Data Analysis

The following variables were selected to test relationships to taxon cell densities based on preliminary testing and environmental responses of diatoms in other studies (e.g. Saros et al., 2012; Malik and Saros, 2016; Reavie et al., 2016): TDP, NOx, thermocline depth, conductivity, silica, temperature, and turbidity. Most raw variables had a normal distribution (p=0.05), except for conductivity and turbidity which were each transformed by ¼ power to approximate normality. Correlations between water quality variables were tested using Pearson’s correlation. All variables were retained in the model-building process as correlations were below 0.5 and variance inflation factors of all constructed models were below 2, which is a conservative approach to avoiding collinearity in multiple linear regressions (Zuur et al., 2010).

Relationships among environmental variables and abundances of the four selected diatom species/complexes were determined using multiple linear regressions. Cell densities of each taxon were
transformed using $\frac{1}{4}$ power to approximate normality. The “best” subsets of variables for each species was determined using `regsubsets` in the `leaps` package in R (Lumley and Miller, 2009), comparing goodness of fit with model complexity. Various combinations of physicochemical variables were evaluated against diatom abundance to verify variable sub-selection. Mixed model approaches were tested using the `lme` package in R (Pinheiro et al., 2016) to account for site as a random variable, comparing Akaike Information Criteria (AIC) to determine model power (Johnson and Omland, 2004). Outlying samples were examined, and removal was tested against model output. Outlier samples were identified by examining plots of model residuals and leverage. Data were analyzed using R software (R Core Team, 2015).

2.4 Results

2.4.1 Environmental Variables

Environmental parameters of summer sampling varied across the dataset (Fig. 2.3). Conductivity ranged from 92-103 µS cm$^{-1}$ (average=99 µS cm$^{-1}$). Silica ranged from 30.3-40.9 µM (average=36.4 µM). Turbidity ranged from 0.09-0.6 NTU (average=0.27 NTU). Thermocline depth varied widely, ranging from 4-27 m (average=7 m), as did temperature, which varied from 10.1-20.3°C (average=14.4°C). NOx was consistently high across sampling events, ranging from 21.4-26.1 µM (average=23.6 µM). By contrast, TDP was universally low, ranging from 0.001-0.102 µM (average=0.05 µM). High nitrate and low TDP suggest a P-limited system across all sampling events; i.e., above a ratio of 3.4 DIN:TP (Bergström, 2010).
Figure 2.3. Data for environmental parameters plotted by year (n=103). The coefficient of variation (CV), the ratio of the standard deviation to the mean, is indicated for each parameter to indicate a standardized measure of dispersion, with larger values indicating greater dispersion. Note the inverted y-axis for thermocline depth.

2.4.2 Taxa

Cell densities used in model building ranged from <1-440 cells mL\(^{-1}\), with average total diatom abundance among species ranging from 0.7-53.7 cells mL\(^{-1}\), comprising ~1%-23.5% of average relative diatom abundances (Fig. 2.4, Table 2.1). Species with low occurrence or abundance include *D. stelligera,*
which was found at 17% of sites, and *L. comensis*, which was found at low average relative (1.8%) and absolute (<4 cells mL$^{-1}$) abundance, whereas taxa morphologically similar to the two, *D. pseudostelligera* (39.3 cells mL$^{-1}$) and *L. delicatula* (53.7 average cells mL$^{-1}$), occurred at much higher average densities (Table 2.1). Summer cell densities varied temporally and spatially, with peak abundances occurring in 2007 or 2008 for all species (Fig. 2.4). Cell densities of *L. bodanica* decreased in recent years; this was the only diatom with a qualitative temporal trend in this dataset (Fig. 2.4).

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Sites (n)</th>
<th>Sites (%)</th>
<th>Relative abundance</th>
<th>Density (cells mL$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>D. stelligera</em></td>
<td>17</td>
<td>17%</td>
<td>0.2-12%</td>
<td>0.1-62</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>1.0% (0.01)</td>
<td>0.7 (6)</td>
</tr>
<tr>
<td><em>D. pseudostelligera</em></td>
<td>103</td>
<td>100%</td>
<td>0.2-59%</td>
<td>0.2-150</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>19.8% (0.14)</td>
<td>39.3 (31)</td>
</tr>
<tr>
<td><em>L. comensis</em></td>
<td>100</td>
<td>97%</td>
<td>0.2-5%</td>
<td>0.1-22</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>1.8% (0.01)</td>
<td>3.8 (3)</td>
</tr>
<tr>
<td><em>L. delicatula</em></td>
<td>101</td>
<td>98%</td>
<td>0.2-85%</td>
<td>0.1-440</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>23.5% (0.2)</td>
<td>53.7 (70)</td>
</tr>
<tr>
<td><em>L. ocellata</em></td>
<td>102</td>
<td>99%</td>
<td>1.7-42%</td>
<td>1.4-240</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>20.4% (0.11)</td>
<td>42.6 (37)</td>
</tr>
<tr>
<td><em>L. bodanica</em></td>
<td>100</td>
<td>97%</td>
<td>0.2-44%</td>
<td>0.2-96</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>5.0% (0.07)</td>
<td>10.5 (16)</td>
</tr>
</tbody>
</table>

**Table 2.1.** Overview of *Cyclotella sensu lato* abundance in Lake Superior during summer sampling events (n=103) from 2001-2011 for species included in this study. Relative abundances are given as a percentage of the enumerated diatom communities.
2.4.3 Relationships with Environmental Variables

Multiple linear regression was used in model building as the AIC for the mixed model was higher than the original multiple linear regression model for each taxon, indicating site replication was not an important driver in species abundance changes. Approximately 6 outlying samples were identified for each multiple linear regression model based on model residuals and leverage. The adjusted $R^2$ improved slightly with removal of outlier samples for each model, although there was not strong evidence suggesting these samples were not representative of species relationships with environmental variables in Lake Superior. Ultimately, all samples were left in the final models as potential outliers fell in the 75% confidence intervals and their removal did not change the relationships with the environmental variables.

<table>
<thead>
<tr>
<th></th>
<th><em>D. pseudostelligera</em></th>
<th><em>L. comensis</em></th>
<th><em>L. delicatula</em></th>
<th><em>L. ocellata</em></th>
<th><em>L. bodanica</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>7.1</td>
<td>8.6*</td>
<td>27*</td>
<td>9.2*</td>
<td>7*</td>
</tr>
<tr>
<td>Conductivity$^{1/4}$</td>
<td>-0.02*</td>
<td>0.004*</td>
<td>0.002*</td>
<td>0.3*</td>
<td></td>
</tr>
<tr>
<td>NOx</td>
<td>-0.02*</td>
<td>-0.07*</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Silica</td>
<td>0.002*</td>
<td>0.14*</td>
<td>-0.07*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>TDP</td>
<td>0.14*</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Temperature</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Thermocline</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Turbidity$^{1/4}$</td>
<td>-2.3*</td>
<td>0.15</td>
<td>0.61</td>
<td>0.18</td>
<td>0.23</td>
</tr>
</tbody>
</table>

*Table 2.2.* Summary of multiple linear regression results for five *Cyclotella sensu lato* taxa. No relationships were found between *D. stelligera* and environmental variables. Regression coefficients are shown for each environmental variable explaining abundance changes for each taxon, with negative signs indicating negative relationships. Asterisks indicate significant relationships ($p<0.05$) and italics indicate borderline significance ($p<0.1$). Intercept is the variable for the multiple linear regression equation. Adjusted $R^2$ indicates the percent variation explained for each model.
Multiple linear regression models identified variables that were important to diatom abundances, explaining 12-61% of variation in diatom density, determined from adjusted $R^2$ values (Table 2.2). For each taxon, cell densities were related to various environmental parameters, ranging from 2-3 explanatory variables (Table 2.2). Environmental variables included in models had varying relationships with diatom taxa (Table 2.2; Fig. 2.5).

![Figure 2.4](image)

**Figure 2.4.** Cell densities (cells mL$^{-1}$) of key diatom taxa plotted by year (n=103 sampling events). The coefficient of variation (CV), the ratio of the standard deviation to the mean, is shown for each taxon to indicate a standardized measure of dispersion, with larger values indicating greater dispersion.

Higher *D. pseudostelligera* cell densities were related to lower turbidity and higher silica. Higher conductivity was related to higher abundance of the *D. pseudostelligera* at a borderline significant level ($P$-value=0.09) and was included because it increased explanatory power of the model and was considered important in contributing to species abundance patterns. Collectively, these three variables
explained 12% of the cell density variation of this taxon (adjusted $R^2=0.116$, P-value=0.002). Higher abundance of *L. comensis* was related to higher TDP and conductivity, explaining 15% of variation in cell densities (adjusted $R^2=0.149$, P-value=<0.001). Higher abundance of *L. delicatula* was related to higher conductivity and lower NOx and silica, explaining 61% of variation in cell densities (adjusted $R^2=0.613$, P-value=<0.001). Higher abundance of *L. ocellata* was related to lower temperature, and higher silica and conductivity, which explained 18% of variation in cell densities (adjusted $R^2=0.177$, P-value=<0.001).

Higher abundance of *L. bodanica* was related to higher TDP and NOx, with these two nutrients explaining 23% of variation in density (adjusted $R^2=0.225$, P-value=<0.001). No relationships could be determined for abundance of *D. stelligera*, with model testing identifying no significant variables and generating low explanatory power (adjusted $R^2< 0.03$).
Figure 2.5. Diatom abundance (cells mL$^{-0.25}$) in relation to environmental variables, with Pearson correlation coefficients ($r$) indicated on each plot. Only variables included in model building are depicted.
2.5 Discussion

In Lake Superior, two species had relationships with physical parameters related to climate, i.e. temperature, light, or thermocline depth: *D. pseudostelligera* and *L. ocellata* (Table 2.2). *Discostella pseudostelligera* had higher abundance with lower turbidity, which may be analogous to association with high light levels found in previous research in smaller lakes for *D. stelligera* (e.g. Saros et al., 2012; Malik and Saros, 2016), a relationship verified with a whole-lake mixing experiment (Saros et al. 2016). Higher *L. ocellata* abundance was related to lower surface temperatures and higher silica and conductivity, which partially coincides with experimental work by Malik and Saros (2016), who found interactive effects of temperature, nutrients, and light, although no relationships to light proxies were found in Lake Superior. Abundances of all five modeled species were related to changes in nutrients and were best explained by a combination of two or three environmental variables. We first review the environmental parameters in Lake Superior to provide context for these results.

2.5.1 Environmental Variables

An overview of nutrient conditions in Lake Superior is essential context before considering diatom responses. Lake Superior is considered ultraoligotrophic due to low primary production (Ostrom et al., 1998; Munawar et al., 2009). Dove and Chapra (2015) found that spring TP declined in Lake Superior from 1970 to 2010, suggesting gradual ultraoligotrophication of the lake over that period. In our study, TDP was always below 4 µM in the GLNPO dataset, hence small changes in the temporal and spatial variation of this limiting nutrient are expected to be ecologically important. NOx concentrations are relatively high, almost always greater than 22 µM. Sterner et al. (2007) and Sterner (2011) suggest the high and increasing concentrations of nitrate are related to reduced denitrification of high historic loadings due to limited organic carbon. Thus, Lake Superior has extreme and stoichiometrically unbalanced nutrient ratios for TN:TP and NO₃⁻:PO₄³⁻ (Sterner et al., 2007; Sterner, 2011). All measured...
NOx concentrations are more than ample for diatom growth and the ecological relevance of differing taxon distributions along this gradient of high N concentrations is unclear. There are two points, however, to consider: 1) we found no correlations between NOx and a suite of other measured environmental variables, suggesting that significant results of diatom abundances with NOx are at least not owing to co-variation with other measured variables; 2) models for taxa that included NOx also included other environmental parameters, possibly indicating synergistic effects between N and other variables. In terms of silica concentrations, they were always high and above 30 µM, and thus likely not limiting (Brzezinski, 1985).

Across the GLNPO data set, temporal trends and gradient lengths of chemical and physical parameters varied. Conductivity was the only variable with an apparent temporal trend, although variations of this scale (100 ± 4 µS cm\(^{-1}\)) were not expected to be ecologically relevant. Turbidity, used as a surrogate for light availability, was always below 1 NTU, likely not greatly limiting light across the range. Seiches and the Coriolis effect can influence thermocline depths in large lakes (Gorham and Boyce, 1989), and the large variations in thermocline depth (5 – 27 m) may also be related to Lake Superior’s near-inertial energy, which increases in strength with increased stratification and appears related to thermocline shifts of up to 10 m (Austin, 2013). The subset of Secchi data available for the current study revealed 93% of sampling events have thermocline depths shallower than the 1% PAR (GLNPO database), indicating more than adequate light availability in the epilimnion for this lake, which Sterner (2011) has referred to as having high water clarity. Nevertheless, light gradients can be important to individual taxa, as exemplified in studies of other oligotrophic lakes with similarly adequate light in the mixing depth (e.g. Saros et al., 2005; Saros et al., 2012).
2.5.2 Diatoms

Multiple environmental variables were important in explaining *Cyclotella sensu lato* abundances, highlighting the varied autecology of taxa in Lake Superior. These relationships expand on multiple drivers identified using correlations from data across the Great Lakes (Reavie et al., 2016), but narrowing the range to environmental gradients found in Lake Superior and investigating synergistic effects of variables. *Cyclotella sensu lato* taxa in Lake Superior have complex interactions with environmental variables, as has been found in other systems (summarized by Saros and Anderson, 2015). The varied interactions of *Cyclotella sensu lato* species with environmental variables are supported by asynchronous changes among taxa in the paleolimnological record (e.g. Stoermer et al., 1985 a,b; Chraïbi et al., 2014; Reavie et al., 2016). Relationships with environmental variables are detailed for each species below.

2.5.2.1 *Discostella stelligera*

No relationships were apparent between the abundance of this taxon and any environmental variable tested in this study. This lack of relationship may be due to low occurrence of *D. stelligera* in modern GLNPO summer samples (n=17, 4.4 average cells mL\(^{-1}\)).

Previous research has related *D. stelligera* to a variety of environmental variables. For example, Stoermer and Ladewski (1976) found a high temperature optimum for *D. stelligera* in Lake Michigan, another Great Lake, while Saros et al. (2012) found relationships with high light availability and shallower mixing depths in small alpine and boreal lakes. Further, in experiments with populations from arctic lakes, Malik and Saros (2016) found increased abundance with increased nutrients, light and temperature, but only when the algal community structure was diatom-dominated. In some lakes, *D. stelligera* flourishes when the epilimnion is shallower (Saros et al. 2016), whereas in others, blooms occur during spring (Boeff et al., 2016) or autumn turnover (Köster and Pienitz, 2006). These differences
have been attributed to interactive effects between light and nutrient limitation status on this species (Saros and Anderson, 2015; Malik and Saros 2016). A larger data set of *D. stelligera* distributions in Lake Superior may be necessary to decipher the ecology of this taxon in this lake.

### 2.5.2.2 Discostella pseudostelligera

Higher abundance of *D. pseudostelligera* with the lower end of the turbidity gradient supported our hypothesis of increasing cell densities with higher light levels. This is consistent with previous research identifying the importance of high light with sufficient nitrogen for *D. stelligera* (e.g. Saros et al., 2012; Malik and Saros, 2016), and, in this case, suggests a similar requirement of *D. pseudostelligera*.

Higher abundance of *D. pseudostelligera* with higher silica is consistent with research showing frustule silicification in this taxon is related to silica content in the water (Belcher et al., 1966). We did not find relationships between *D. pseudostelligera* and either phosphorus or temperature, contrasting correlations between greater abundance of a combined group of *D. stelligera* and *D. pseudostelligera* with lower phosphorus and higher temperature in a Great Lakes-wide study (Reavie et al., 2016). It is possible that relationships found in Reavie et al. (2016) could have been driven to a greater extent by *D. stelligera*, or the differences between our studies are due to different relationships of *D. pseudostelligera* with environmental parameters throughout the Great Lakes. As we could not determine relationships with environmental variables for *D. stelligera*, it remains unclear whether the two stelligeroid taxa have similar autecology in Lake Superior. However, *D. pseudostelligera* has been prominent in the sediment records over at least the past century (Chraïbi et al., 2014) whereas *D. stelligera* was much more prominent, with sparse occurrences of *D. pseudostelligera*, ~1000 years ago (Chapter 3), suggesting that these two taxa may differ in their relationships with environmental parameters in Lake Superior.
2.5.2.3 *Lindavia comensis*

The lack of relationship of *L. comensis* with either thermocline depth or turbidity did not support our hypothesis of greater cell densities under moderate to high light levels in Lake Superior. This contrasts the varying relationships to light reported for *L. comensis* in other systems. Specifically, *L. comensis* was related to moderate stratification depths with adequate nitrate availability, suggesting relationships with nutrients and intermediate light in experimental treatments in an alpine lake (Saros et al., 2012). By contrast, Reavie et al. (2016) found a positive correlation with *L. comensis* and thermocline depth in a study throughout the Great Lakes, suggesting an optimum at lower light availability. *Lindavia comensis* abundance was also not related to temperature in Lake Superior, thus providing no strong evidence that abundance is related to the climate-driven physical changes that we examined.

Higher abundance of *L. comensis* was related to higher ends of conductivity and TDP gradients. The positive relationship of *L. comensis* with phosphorus has been noted previously in the Great Lakes, with increasing abundances of Lake Superior populations with experimental phosphorus additions by Schelske et al. (1972). Nevertheless, in a recent study throughout the Great Lakes, where the phosphorus gradient is much longer (from 0.06 to >1.6 μM, reported as 2 to >50 μg L$^{-1}$), *L. comensis* was more abundant at the lower end of the phosphorus gradient (Reavie et al., 2016). Collectively, these studies indicate a positive effect of phosphorus for *L. comensis* in ultraoligotrophic Lake Superior, however, across the trophic states in the Great Lakes, *L. comensis* is found at low P conditions. The lack of relationship between *L. comensis* and nitrate contrasts relationships found in a moderate nitrate system (Saros et al., 2012), but is not surprising given the consistently high nitrate concentrations in Lake Superior. Another contrast is found by comparing sedimentary abundances in a nearby lake, where *L. comensis* increased with low biogenic silica concentrations and diatom-inferred high nitrate (Wolin and Stoermer, 2005). The present study found neither NOx nor silica important in describing abundance changes in Lake Superior.
*Lindavia comensis* can have high morphological variability, which in some cases, translates to autecological differences. For example, varying environmental preferences were identified among taxa morphologically similar to *L. comensis* in hardwater Swiss lakes by Hausmann and Lotter (2001), using six morphotypes to determine environmental relationships. Further work determining morphological variability of *L. comensis* in Lake Superior may also refine autecology of ecotypes of this taxon.

### 2.5.2.4 *Lindavia delicatula*

*Lindavia delicatula* abundance was not related to the proxy light measurements of turbidity or thermocline depth, thus our hypothesized relationship with moderate light was not supported. This contrasts relationships between *L. delicatula* (reported as *L. cf. delicatula*) and deepening thermocline, analogous to lower light, reported by Reavie et al. (2016) in a Great Lakes-wide study. Further, there was no evidence that changing abundance of *L. delicatula* was related to tested climate-driven physical changes in Lake Superior.

Higher abundance of *L. delicatula* was related to higher ends of the conductivity gradient. Additionally, differences in the consistently high nitrate and ample silica gradients were important to cell densities of *L. delicatula*, with higher abundances at lower ends of the gradients. Positive relationships to decreasing nitrate were also reported by Reavie et al. (2016). Differences in relationships with environmental variables compared to *L. comensis* support keeping the morphologically similar *L. delicatula* as a separate taxon. We did not find a relationship between *L. delicatula* and phosphorus, contrasting the relationship with lower phosphorus in a Great Lakes-wide study (Reavie et al., 2016), which had a much longer phosphorus gradient. As *L. delicatula* has yet to be widely reported (Burge and Edlund, 2015), there are no studies with which to compare our results more broadly beyond the Great Lakes.
2.5.2.5 *Lindavia ocellata*

Abundance of *L. ocellata* was not related to the proxy light measurements of turbidity and thermocline depth in Lake Superior, and thus do not support our hypothesis of higher cell densities with lower light. Previous studies have found relationships between *L. ocellata* and both high and low light availability. For example, Reavie et al. (2016) found correlations between *L. ocellata* and shallower thermocline, indicating a high light environment, in a study throughout the Great Lakes, while Malik and Saros (2016) found *L. ocellata* increased in experiments with low light, particularly when nutrients were added.

Higher abundance of *L. ocellata* in Lake Superior was related to lower surface water temperature, indicating an unexpected relationship to a climate-driven physical change. The relationship of *L. ocellata* with temperature was not found in a previous Great Lake study testing abundance and temperature in Lake Michigan (Stoermer and Ladewski, 1976), nor was any relationship with temperature determined in arctic lakes (Malik and Saros, 2016).

Abundance of *L. ocellata* increased with higher silica and conductivity, while no relationships with NOx or TDP were found. The lack of relationship with nitrogen and phosphorus in Lake Superior phytoplankton differs from the strong, independent effects of increased nitrogen and phosphorus on this taxon in experimental studies of oligotrophic lakes in the Arctic (Malik and Saros, 2016).

2.5.2.6 *Lindavia bodanica*

Abundance of *L. bodanica* was not related to thermocline or turbidity in Lake Superior, thus does not support our hypothesized relationship of greater cell densities with lower light. Cell abundance was not related to temperature, corresponding with no independent temperature effects found in other systems (Malik and Saros, 2016), but contrasting the high temperature optimum established by Stoermer and Ladewski (1976) for *L. bodanica* in Lake Michigan and relationships with warmer temperatures found in a number of boreal and tundra lakes (Pienitz, et. al, 1995).
Nutrient concentrations adequately described *L. bodanica* abundance in Lake Superior. The relationship found for higher abundances with higher phosphorus and lower nitrate was not noted in Reavie et al. (2016) for *L. bodanica* throughout the Great Lakes. The relationships found in Lake Superior are similar to those in Interlandi et al. (1999), who categorized *L. bodanica* as a relatively poor phosphorus but good nitrogen competitor in large lakes of Yellowstone National Park. They described *L. bodanica* as a low nitrogen specialist, with increased *L. bodanica* related to lower N:P ratios (Interlandi et al., 1999). This is further supported by sediment records indicating reduced abundances of *L. bodanica* with higher nitrogen loadings, again favoring a low N:P ratio (Kilham et al., 1996). No relationship was found between *L. bodanica* and silica, while previous research has reported both sedimentary increases (Bradbury, 1988) and decreases (Kilham et al., 1996) in *L. bodanica* abundance with a high Si:P ratio.

*Lindavia bodanica* had the strongest positive relationship with TDP among the tested taxa, with increased abundance related to increases in TDP along this notably low-concentration phosphorus gradient. In other lakes, *L. bodanica* is often found with mild to moderate phosphorus enrichment. For example, *L. bodanica* is more abundant in lakes in Yellowstone National Park at low N:P and low Si:P (Kilham et al., 1996). *Lindavia bodanica* is found in mesotrophic TP concentrations in multiple training sets (Camburn and Charles, 2000; Reavie et al., 1995; Ramstack et al., 2003), with optima between 0.3-0.4 µM (reported as 9-14 µgL⁻¹). However, in a Great Lakes wide study, Reavie et al. (2016) found no change in *L. bodanica* and no relationships between *L. bodanica* and environmental variables, consistent with Stoermer’s (1978) assessment that *L. bodanica* is a eurytopic diatom with a wide tolerance of nutrient concentrations across the Great Lakes. We place the findings of the current study in context of Lake Superior TDP concentrations that were always below 0.1 µM. This is so low in comparison to other nutrients that it is likely to be a major constraint limiting growth. The relationship between *L. bodanica*
and TDP underscores how small changes even at low phosphorus concentrations are important to the Lake Superior diatom community.

2.5.3 Summary of Cyclotella sensu lato Relationships with Environmental Variables

Complex, synergistic relationships with environmental variables affect cell densities of *Cyclotella sensu lato* species in Lake Superior. The relationships of the two taxa associated with climate-driven physical change are only significant in combination with other environmental variables. The relationship of *D. pseudostelligera* with higher light availability is only significant in combination with increasing silica, and potentially, increasing conductivity. Similarly, the relationship of *L. ocellata* with decreasing surface water temperature is only apparent in combination with increasing silica and conductivity. Furthermore, it should be noted that temperature is a difficult parameter to which to relate changes in diatom community structure. Anderson (2000) reviews evidence from multiple studies suggesting the importance of other factors related to temperature, such as thermal structure and mixing intensity, to diatom physiology. This is especially important to keep in mind when interpreting paleolimnological changes, as sedimentary records are incorporating changes in many variables, including watershed inputs and hydrodynamics over a variety of timescales (Anderson, 2000).

While the gradient is short, conductivity appears important to at least three taxa, with higher conductivity significantly related to higher abundances of *L. comensis, L. delicatula,* and *L. ocellata,* and contributing to explaining abundance changes of *D. pseudostelligera.* Higher silica was significantly related to higher cell densities of two taxa, *D. pseudostelligera* and *L. ocellata,* while lower silica significantly explained higher cell densities of *L. delicatula.* Lower NOx, in a consistently high gradient ranging from 21 to 26 µM, was significant for higher cell densities of two taxa, *L. delicatula* and *L. bodanica.* Similarly, higher concentrations of TDP, in a consistently low gradient ranging from 0.001-0.102 µM, were associated with greater cell densities of both *L. comensis* and *L. bodanica.* This suggests
important relationships between *Cyclotella sensu lato* taxa and the interactive effects of TDP, silica and NOx in this phosphorus-limited system.

Differences in *Cyclotella sensu lato* species autecology between this study and research in other regions suggest unique environmental optima for Lake Superior. Further, differences found between this study and research encompassing all the Great Lakes (Reavie et al., 2016) suggest the likelihood of unique drivers of *Cyclotella sensu lato* species within each Great Lake. Some of these differences may be explained by the smaller gradient of many environmental measures in Lake Superior compared to the Great Lakes and other regions, and the approach of the current study was to identify combinations of explanatory variables. Further, differences could also be due to the declining TP over recent decades and subsequent increasing stoichiometric imbalance (Sterner et al., 2007; Sterner, 2011; Dove and Chapra 2015). The nutrient conditions in Lake Superior may constrain responses to climate-driven physical changes. Specifically, low phosphorus concentrations limit diatom growth and reproduction, constraining response to changing temperature or thermal structure, in which case, we may expect weaker relationships with temperature shifts, thermocline depth, and turbidity. Malik et al. (2017) found that nutrient limitation status of different *Cyclotella sensu lato* taxa controlled growth responses to differing light intensities. In addition, difference in responses to climate-driven variables may also be related to lake size (Boeff et al., 2016). The temporal and spatial variations in thermocline depth in large lakes may explain the lessened response of taxa to thermocline shifts or turbidity (Boeff et al., 2016). Larger lakes experience greater internal energy than smaller lakes, which has the potential to alter the thermocline (Fee et al., 1996; Boyce, 1974). Diatoms experiencing periodic changes in thermocline depth due to seiches may be adapted to highly variable light availability. However, *L. ocellata* was related to stratification depth in a previous study of a large lake (Carney et al., 1988), although this relationship may vary with lake size. Specifically, the abundance of *L. ocellata* increased with intermediate stratification depths in the deep, oligotrophic Lake Tahoe (Carney et al., 1988) to
conditions more typical of deeper stratification in small lakes (Malik and Saros, 2016). It is unclear why relationships with light were not found for most tested Cyclotella sensu lato species in Lake Superior, although the relationships with other tested environmental variables suggest that light availability may have a more limited role in driving abundance shifts in Lake Superior than in other lakes.

2.5.4 Future work

Sampling at higher temporal and vertical spatial resolution as well as employing experimental approaches will clarify the importance of identified environmental variables for Cyclotella sensu lato species in Lake Superior. There is a need for continued species-level studies, particularly focusing on interactive effects of light and nutrients (Saros and Anderson, 2015) and specific testing within each Great Lake. Experimental approaches will help to determine mechanisms behind relationships with temperature, as well as further elucidate potential relationships with fluctuating thermoclines, stratification strength, and light availability. Finally, investigating changes in total phytoplankton composition will identify the role of community composition and interspecific competition in relationships with environmental parameters in Lake Superior, as phytoplankton composition appears to be an important factor in environmental responses in Arctic lakes (Malik and Saros, 2016).

2.6 Conclusions

Distributions of Cyclotella sensu lato in Lake Superior are related to multiple physical and chemical variables. Nutrients such as phosphorus, nitrate, and silica are important in explaining abundances of all tested species. Two taxa were related to climate-driven physical change: D. pseudostelligera, with increased abundance related to higher light, and L. ocellata, with increased abundance related to lower temperature, but only in combination with other variables. The limited relationships with climate-driven physical changes may be due to the increased importance of stoichiometric imbalance in the system.
(Sterner, 2011) and high variability of thermocline depths in large lakes (Austin, 2013; Fee et al, 1996) leading to greater variation in light availability than in smaller lakes (Boeff et al. 2016). Our findings suggest ecotype formation of *Cyclotella sensu lato* species in Lake Superior, underscoring Stoermer’s (1993) warning of applying environmental relationships developed for diatoms in other systems. Our results also suggest that multiple drivers are likely at work in eliciting recent diatom community changes in Lake Superior and must be considered when interpreting sedimentary records.
CHAPTER 3

COMPARISON OF SEDIMENTARY DIATOM PROFILES DURING THE MEDIEVAL CLIMATE ANOMALY AND THE 20TH CENTURY IN LAKE SUPERIOR SUGGESTS RECENT CHANGES ARE UNIQUE

3.1 Abstract

We examined the sedimentary diatom record from Lake Superior (Canada/USA) spanning the Medieval Climate Anomaly (MCA) to determine whether diatom assemblages changed during a previous warm, dry period. Changes in diatom species relative abundance were assessed in the core from ~500-1350 CE, with the MCA spanning from 950-1250 CE. From 500-1350 CE, sedimentary diatom assemblages were dominated by *Lindavia ocellata* and *Lindavia comensis*. No significant changes in the diatom community were found during the MCA. We contrast this with a significant change ~1940 in diatom assemblages preserved in another core from Lake Superior spanning ~1815-2010, and use recently established relationships between planktonic diatom taxa and multiple climate and lake physicochemical parameters from monitoring data. Results from the two cores suggest that multiple environmental drivers, including climate change as well as anthropogenic activities that alter nutrient cycling, are leading to novel shifts in modern diatom communities in Lake Superior. The lack of diatom assemblage change during the MCA further supports the unique environmental changes in Lake Superior during the past century due to anthropogenic impact.

3.2 Introduction

Lake Superior is the largest lake in North America and is often considered relatively pristine. Nevertheless, inferences from sedimentary diatom records suggest mild nutrient enrichment of the lake during the early 20th century, following local European settlement in the 19th century (Stoermer et al. 1985a, Chraïbi et al. 2014). With remediation efforts after enactment in 1972 of both the Clean Water
Act and the Great Lakes Water Agreement, diatom-inferred total phosphorus (TP) has declined in the lake (Chraïbi et al. 2014). In recent decades, research has also focused on the role of climate change on diatom community changes observed through routine biannual monitoring (Reavie et al. 2016; Bramburger et al. 2016; Chapter 1).

In Lake Superior, changes in planktonic diatom assemblages in monitoring data spanning 2007-2011 (Reavie et al. 2016) and in sedimentary records since ~1970 (Chraïbi et al. 2014; Reavie et al. 2016) have been related to climate change. These inferences are based, in part, on the ecology of diatom taxa studied in smaller lake ecosystems. For example, changes in *Cyclotella sensu lato* taxa in Lake Superior are thought to be linked to climate-driven physical changes in the lake (Chraïbi et al. 2014, Reavie et al. 2014b). A group of planktonic centric diatoms that comprise three currently accepted modern genera, *Cyclotella*, *Discostella*, and *Lindavia* (Spaulding et al., 2010), *Cyclotella sensu lato* taxa have shifted in abundance over the past 150 years in many lakes around the world (e.g. Hobbs et al., 2010; Rühland et al., 2015). Increases in *Cyclotella sensu lato* taxa have been related to warming in other studies (Smol et al. 2005, Rühland et al. 2008), although more recent studies reveal mechanistic responses related to the effects of climate change vary among species within this group (Saros et al. 2012, Saros and Anderson 2015, Malik and Saros 2016). As examples, Winder et al. (2009) found smaller diatom taxa, including some *Cyclotella sensu lato* taxa, became more abundant with stronger stratification and decreased mixing intensity. Further investigation of individual *Cyclotella sensu lato* species has revealed varying relationships to light availability, which are further modified by interaction with other environmental variables. For example, cell densities of *Discostella stelligera* (Cleve and Grunow) Houk and Klee increase with light under P-limited conditions but show the opposite patterns with nitrogen and phosphorus co-limitation (Saros et al. 2012, Malik et al. 2017), and may also depend on diatom-domination of the lake algal community (Malik and Saros 2016). Cell densities of *Lindavia ocellata* (Pantocsek) T.Nakov et al. in experimental treatments are related to low light and nutrients (Malik and Saros 2016), while those of...
*Lindavia radiosa* (Grunow) De Toni & Forti increased with light regardless of nutrients (Saros et al. 2014). Reavie et al. (2016) attributed *Cyclotella sensu lato* increases throughout the Great Lakes to warming air and water temperatures, suggesting diatoms may be responding to changing thermocline depths, decreasing ice cover, and shifting water quality. However, the species within the *Cyclotella sensu lato* group that have been related to climate-driven changes in lake thermal structure in other systems (e.g. Winder et al. 2009, Saros et al. 2012) show variable responses in Lake Superior, making interpretations difficult.

Recent research has suggested that modern distributions of *Cyclotella sensu lato* taxa in Lake Superior are related to multiple, and possibly synergistic effects of, environmental variables, with limited effects of climate-driven physical variables (e.g., thermocline depth, light availability) on tested species (Chapter 2). The physical effects of climate forcing of Lake Superior are well documented and include surface water temperatures increasing faster than air temperatures (Austin and Colman 2007), wind speeds increasing over the lake (Desai et al. 2009), and thermocline deepening since 1995 (Reavie et al. 2016). However, other environmental changes have also occurred in Lake Superior over the past century, including changes in atmospheric chemistry and internal nutrient cycling processes which have led to decreasing phosphorus (Dove and Chapra 2015) and increasing nitrate (Sterner et al. 2007) in the water column. Given the changes in multiple lake parameters over the past century, determining the responses of diatom assemblages during a past warm period, prior to other strong anthropogenic effects, may help to decipher the effects of climate change on planktonic diatom taxa in this lake.

In some areas of the northern hemisphere, the Medieval Climate Anomaly (MCA) was a warmer, drier period spanning from 950-1250 CE (Mann et al. 2009). A global climate proxy network with regional weighting support a positive temperature anomaly of ~0.4°C in the upper Midwest relative to a 1961-1990 reference period mean (Mann et al. 2009). Other evidence supports that the MCA was marginally warmer than present and that the shift to warmer temperatures was abrupt, due to changes
in oceanic and atmospheric circulation in the North Atlantic basin occurring in centuries, decades, or less (deMenocal et al. 2000). Regionally, significant droughts occurred in the northern Great Plains during the MCA (Vance et al. 1992) and water table reconstructions of bogs in Minnesota and Michigan support temporal and spatial drought coherence (Booth et al. 2006).

We compared changes in the diatom community during the MCA (MCA Core) to those occurring over the last two centuries (Post-1800 Core) from two sediment cores recently collected in Lake Superior. The MCA Core was a deeper sedimentary core collected near the Keweenaw Peninsula (O’Beirne et al. 2017) and was used to examine diatom changes before, during, and after the MCA. The Post-1800 Core was collected near Isle Royale (Chraibi et al. 2014) and was used to examine more recent sedimentary diatom assemblages following European settlement. Coherent changes in recent centuries were found in sedimentary diatom profiles collected in different locations in Lake Superior (Chraibi et al. 2014), indicating the two coring locations used in this study should capture similar responses of planktonic diatom communities to climate-driven change. Our objective was to investigate potential changes in the diatom sedimentary record during the MCA, a previous warm period, to better understand how changes in the modern Lake Superior diatom community are related to climate change.

3.3 Materials and Methods

Lake Superior is located in central North America and is bordered by the United States and Canada, with an average depth 147 m, a maximum depth of 406 m, and surface area of 82,100 km². The two coring locations were near the central basin of the lake (Fig. 3.1).
Figure 3.1. Map of Lake Superior with dashed box in insert showing location in North America, bordering the United States and Canada. Coring locations are indicated for the MCA Core (star) and Post-1800 Core (circle).

3.3.1 MCA Core

To capture the period including the MCA, deeper sediments were obtained with a gravity core that was used as a trigger core to a Kullenberg piston corer aboard the Research Vessel (R/V) Blue Heron in 2009 (O’Beirne et al. 2013; O’Beirne et al. 2017). The MCA core was collected east of the Keweenaw Peninsula in the central southern portion of Lake Superior at 47°7′42″ N, 87°49′16″ W (O’Beirne et al. 2017). This area had one of the greatest sedimentation rates of recent cores collected across Lake Superior at 0.0252 g/cm²/yr (O’Beirne 2013). Subsamples were collected at 0.5-cm intervals by The University of Minnesota National Lacustrine Core Repository (LacCore) to provide fine temporal resolution.

An age model was created using ¹⁴C dates from the gravity core and ²¹⁰Pb dates from a multicore collected by the R/V Blue Heron at a nearby site at 47°7′4″ N, 87°49′12″ W in 2009, as the gravity core did not capture the sediment-water interface. O’Beirne (2013) developed an age/depth relationship to determine the starting interval for the gravity core using linear extrapolations from the
bottom of a corresponding multi-core, a method used to estimate dating in a previous study (O’Beirne et al. 2017). The current study differs from previous work by specifically targeting the gravity core and adding $^{14}$C dating, which has been historically difficult to accomplish using Lake Superior sediments. Radiocarbon dating was performed on pollen isolates extracted at the University of Maine using methods adapted from Vandergoes (2003) and Newnham et al. (2007). Livermore Lab analyzed accelerator mass spectrometry (AMS) radiocarbon dating (Stuiver and Polach 1977). Three AMS $^{14}$C dates extended the $^{210}$Pb age-depth Constant Rate of Supply model reported by O’Beirne et al. (2013; 2017). Age models and error estimates were generated with the R package (R Core Team 2015) with the contributed BChron package (Parnell 2016), using normal calibration for the $^{210}$Pb data and northern hemisphere terrestrial $^{14}$C calibration curve for the radiocarbon data, which determines the most likely age-depth estimates using Bayesian probability techniques. A total of 52 sediment intervals targeting the MCA and surrounding intervals were chosen for analysis.

Permanent microscope slides were made with Naphrax™, a mountant providing a high refractive index, and diatoms were examined under oil immersion at 1000X magnification (numerical aperture = 1.3) under light microscopy, counting 300 diatom valves per slide and converting raw counts to percent relative abundance. Species identifications were made with consultation of taxonomists working on water quality monitoring in Lake Superior as part of the Environmental Protection Agency’s Great Lakes National Program Office, which has biannually documented diatom communities in Lake Superior since 2001 (GLNPO, 2010). Taxonomic references included Krammer and Lange-Bertalot (1986-1991) as well as those specific to the Great Lakes (Reavie and Kireta 2015).
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<th>Group name</th>
<th>Included genera</th>
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<td>Stratigraphic plots</td>
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<td><strong>Achnanthes sensu lato</strong></td>
<td><em>Achnanthes</em> Bory, <em>Achnanthidium</em> Kützing, <em>Eucocconeis</em> Cleve ex Meister</td>
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<td><em>Aulacoseira</em> spp. (Ehrenberg) Thwaites</td>
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<td><strong>Cyclotella atomus</strong> Hustedt</td>
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<td><strong>Cyclotella atomus</strong> “fine form”</td>
<td>Adapted from <em>C. atomus</em> Hustedt by Reavie and Kireta (2016)</td>
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<td><em>Cyclostephanos</em> spp. (Cleve in Cleve &amp; Miller) Round in Theriot et al.</td>
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<td><em>’Cyclotella sensu lato</em> (Kützing) Brébisson</td>
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<td><strong>Discostella stelligera</strong> (Cleve &amp; Grunow) Houk and Klee</td>
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<td><strong>Fragilaria sensu lato</strong></td>
<td><em>Fragilaria</em> (O. Müller) Lyngbye, <em>Synedra</em> (Nitzsch), <em>Ulnaria</em> Nitzch</td>
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<td><em>Lindavia comensis</em> (Grunow) T.Nakov et al.</td>
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<tr>
<td><em>Lindavia comensis/ ocellata</em></td>
<td>Group containing species hard to distinguish between <em>L. comensis</em> and <em>L. ocellata</em></td>
</tr>
<tr>
<td><em>Lindavia ocellata</em> (Pantocsek) T.Nakov et al.</td>
<td></td>
</tr>
<tr>
<td><strong>Stephanodiscus conspicueporus</strong> Stoermer, Håkansson, &amp; Theriot</td>
<td></td>
</tr>
<tr>
<td><strong>Stephanodiscus</strong> spp. Ehrenberg</td>
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</tr>
<tr>
<td><strong>Tabellaria</strong> spp. Ehrenberg ex Kützing</td>
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</tr>
</tbody>
</table>

**Table 3.1.** Diatom taxa and combinations for the MCA Core.

*except for *C. atomus*, *C. atomus* “fine form”, *D. pseudostelligera*, *D. stelligera*, *D. stelligeroides*, *L. bodanica*, *L. comensis*, *L. ocellata*, and *L. michiganiana*

**except for *S. conspicueporus***
### Cluster Analysis

<table>
<thead>
<tr>
<th>Diatom Taxa</th>
<th>Authors and References</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Amphora spp.</strong> Ehrenberg ex Kützing</td>
<td></td>
</tr>
<tr>
<td><strong>Asterionella formosa</strong> Hassall</td>
<td></td>
</tr>
<tr>
<td><strong>Cocconeis spp.</strong> Ehrenberg</td>
<td></td>
</tr>
<tr>
<td><strong>Cymbella sensu lato</strong></td>
<td>Cymbella Agardh, Encyonema Kützing</td>
</tr>
<tr>
<td><strong>Discostella pseudostelligera</strong> (Hustedt) Houk &amp; Klee</td>
<td></td>
</tr>
<tr>
<td><strong>Eunotia/ Diatoma</strong></td>
<td>Eunotia Ehrenberg, Diatoma Bory de Saint-Vincent</td>
</tr>
<tr>
<td><strong>Lindavia bodanica</strong> (Eulenstein ex Grunow) T.Nakov et al.</td>
<td></td>
</tr>
<tr>
<td><strong>Lindavia michiganiana</strong> (Skvortzow) T.Nakov et al.</td>
<td></td>
</tr>
</tbody>
</table>
| **Navicula sensu lato**                                                   | Brachysira Kützing, Cavinula Mann and Stickly in Round, Crawf
| **Non.**                                                                 | Diatoms (Ehrenberg) Cleve, Eolimnia Lange-Bertalot & Schiller in Schiller &Lange-Bertalot 1997, FALLACIA (Kützing) Stickl
| **Non.**                                                                 |                                                                                       |
| **Nitschia spp.**                                                        | Denticula Kützing, Nitzschia Hassall, Simonsenia Lange-Bertalot, Tryblionella W. Smith |
| **Planothidium sensu lato**                                               | Planothidium Round and Bukhtiyarova, Psammothidium Bukhtiyarova & Round, Karayevia Round et Bukhtiyarova ex Round |
| **Urosolenia spp.** (Round & Crawford) emended Rott, Kling & McGregor    |                                                                                       |
| **Staurosira sensu lato**                                                 | Pseudostarosira Williams & Round, Punctastriata Williams & Round, Staurosira Ehrenberg, Staurosirella Williams & Round |
| **Surirella spp.** Turpin                                                 |                                                                                       |
| **Unknown centric**                                                      |                                                                                       |
| **Unknown pennate**                                                       |                                                                                       |

**Table 3.1 continued.** Diatom taxa and combinations for the MCA Core.  
Diatom taxa and combinations are listed in Table 3.1. Taxa were mostly combined into genus level groups that contained the associated species (e.g. *Aulacoseira* spp.) or broad taxonomic groups that contained multiple genera that have been erected from the base genus (e.g. *Fragilaria sensu lato* contained the genera *Synedra* and *Ulnaria*). Species that were abundant, and that had recently been tested for relationships with environmental drivers (Chapter 2), were not combined into groups, but were kept separate to investigate potential temporal changes of these taxa. Groups such as *Stephanodiscus* spp. and *Cyclotella sensu lato* indicate at least one taxon within these broader groupings was individually examined. *Cyclotella atomus* “fine form” was used following Chräibi et al. (2014) and Reavie et al. (2016) for a *Cyclotella* taxon described as *C. atomus* var. 1 in Great Lakes taxonomical reference (Reavie and Kireta 2015). This taxon appears morphologically similar to *Cyclotella atomus* Hustedt, was often less than 5 µm, and often had indistinct features. *Lindavia comensis/ocellata* was used for a group with similarities to both *Lindavia comensis* (Grunow) T.Nakov et al. and *L. ocellata* that could not be confidently distinguished to either taxon.

### 3.3.2 Post-1800 Core

A sediment core capturing the last two centuries was collected in 2010 from south of Isle Royale at 47°58’23”N, 88°27’58”W at a depth of 234 m with an Ocean Instruments model MC-400 multi-corer aboard the R/V Blue Heron (Chraïbi et al. 2014). Samples were extruded at 0.25-cm intervals. A $^{210}$Pb age-depth Constant Rate of Supply model was used to date the core (Chraïbi et al. 2014). A total of 21 sample intervals in 13 cm of sediment spanning 1815 – 2010 CE were used in this study. Samples generally integrated ~3-6 years.

Sedimentary diatoms were analyzed for a previous study (Chraïbi et al. 2014), using similar methods to the present study (e.g., light microscopy with oil immersion at 1000x magnification), with
400 diatom valves counted per sample and converted to relative abundance. Taxa were combined into
genus groups for the current study (Table 3.2), similar to combinations used in the MCA core.

<table>
<thead>
<tr>
<th>Group name</th>
<th>Included genera</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stratigraphic plots</td>
<td>Aulacoseira spp. (Ehrenberg) Thwaites</td>
</tr>
<tr>
<td>Cyclotella atomus Hustedt</td>
<td>Cyclotella atomus “fine form”</td>
</tr>
<tr>
<td>Discostella pseudostelligera (Hustedt) Houk &amp; Klee</td>
<td>Adapted from C. atomus Hustedt by Reavie and Kireta (2016)</td>
</tr>
<tr>
<td>Fragilaria sensu lato</td>
<td>Fragilaria (O. Müller) Lyngbye, Synedra (Nitzsch)</td>
</tr>
<tr>
<td>Lindavia comensis (Grunow) T.Nakov et al.</td>
<td>Ehrenberg, Ulnaria Nitzch</td>
</tr>
<tr>
<td>Lindavia delicatula Hustedt</td>
<td></td>
</tr>
<tr>
<td>Lindavia ocellata (Pantocsek) T.Nakov et al.</td>
<td></td>
</tr>
<tr>
<td>Urosolenia spp. (Round &amp; Crawford) emended Rott, Kling &amp; McGregor</td>
<td></td>
</tr>
<tr>
<td>Stephanodiscus conspicueporus Stoermer, Håkansson, &amp; Theriot</td>
<td></td>
</tr>
<tr>
<td>*Stephanodiscus spp. Ehrenberg</td>
<td></td>
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</tbody>
</table>

Table 3.2. Diatom taxa and combinations for the Post-1800 Core. Data modified from Chräibi et al. 2014

*except for S. conspicueporus
### Cluster Analysis

<table>
<thead>
<tr>
<th>Diatom Taxa</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Achnanthes sensu lato</strong></td>
</tr>
<tr>
<td>Amphora spp. Ehrenberg ex Kützing</td>
</tr>
<tr>
<td>Asterionella formosa Hassall</td>
</tr>
<tr>
<td>Cocconeis spp. Ehrenberg</td>
</tr>
<tr>
<td><strong>“Cyclotella sensu lato” (Kützing) Brébisson</strong></td>
</tr>
<tr>
<td>Cymbella spp. Agardh</td>
</tr>
<tr>
<td>Eunotia/ Diatoma</td>
</tr>
<tr>
<td>Lindavia bodanica (Eulenstein ex Grunow) T.Nakov et al.</td>
</tr>
<tr>
<td>Lindavia michiganiana (Skvortzow) T.Nakov et al.</td>
</tr>
<tr>
<td>Navicula sensu lato</td>
</tr>
<tr>
<td>Nitschia spp.</td>
</tr>
<tr>
<td>Planothidium sensu lato</td>
</tr>
<tr>
<td>Urosolenia spp. (Round &amp; Crawford) emended Rott, Kling &amp; McGregor</td>
</tr>
<tr>
<td>Surirella spp. Turpin</td>
</tr>
<tr>
<td>Tabellaria spp. Ehrenberg ex Kützing</td>
</tr>
<tr>
<td>Unknown centric</td>
</tr>
<tr>
<td>Unknown pennate</td>
</tr>
</tbody>
</table>

*Table 3.2 continued.* Diatom taxa and combinations for the Post-1800 Core. Data modified from Chräibi et al. 2014

*except for S. conspicueporus*


### 3.3.3 Statistical Analyses

Data were analyzed separately for each core using R core software (R Core Team 2015). Changes in the diatom community were analyzed using depth constrained chronological analysis. First, we determined
sample dissimilarity by creating a dissimilarity matrix by computing chord distances between samples in a core. In this case, we used the R base package (R Core Team 2015) to analyze dissimilarity using Hellinger distances, which is the distance determined using the Euclidean method with square root transformed relative abundance data. Next, hierarchical chronological clustering was determined using the rioja package (Juggins 2017). The chclust function implemented a constrained cluster analysis on the dissimilarity matrix using an agglomerative clustering technique, which joins groups from individual objects using local similarity over larger differences. In this case, we used a constrained Ward’s minimum variance method (Ward 1963) to determine subsequent groups of samples throughout the core, by minimizing the total within group sum of squares. A broken-stick analysis was used to determine significant zones of diatom reorganization from the hierarchical chronological clustering (Bennett 1996) using the vegan package (Oksanen et al. 2017) in R. The broken-stick analysis examines the zonation from the chronological clustering data, showing the reduction of sum of squares under a random distribution, identifying the number of zonation or clusters from the chronological clustering model better than the random model. Stratigraphic plots were made using the analogue package in R (Simpson and Oksanen 2016). Species were included in the stratigraphic plots if they occurred in at least 10 sample for the MCA Core and at least 5 sites for the Post-1800 Core and had a relative abundance of at least 5% in each core. Diatom community turnover was determined using detrended correspondence analysis (DCA) of square root relative abundance data using the vegan package (Oksanen et al. 2017) in R.

3.4 Results

3.4.1 MCA Core

The calibrated age-model indicated that the examined section of the core spanned ~500-1350 CE (Fig. 3.2), capturing about 450 years prior to the start of the MCA, the MCA period, and about 100 years post-
MCA. Each 0.5-cm sediment sample interval represented approximately a 7-year integrated sample. The 402 enumerated taxa were combined into 31 taxonomic groups (Table 3.2), with 14 final groups occurring in at least 10 samples with at least 5% relative abundance in one sample (Fig. 3.3).

Figure 3.2. Age model for the MCA Core using $^{210}$Pb (14 dated positions shown near upper right) and $^{14}$C dating (3 dated positions shown near bottom left). The following samples were used for $^{14}$C dating:

- CAMS# = 171362, Sample ID = 3_30ME35LC, Fmodern = 0.8657 ± 0.0031, Conventional Radiocarbon Years = 1160 ± 30;
- CAMS# = 171363, Sample ID = 5_53.5ME58, Fmodern = 0.8217 ± 0.0033, Conventional Radiocarbon Years = 1575 ± 35;
- CAMS# = 171364, Sample ID = 8_87ME92LC, Fmodern = 0.7851 ± 0.0028, Conventional Radiocarbon Years = 1945 ± 30.
The diatom community was dominated by *L. ocellata* and *L. comensis*. Planktonic species dominated throughout the sediment core ranging from 80-93% relative abundance, with no apparent temporal changes in proportions of planktonic: benthic community ratios throughout the core (Chapter 4). Scores on the DCA axis 1 were variable but showed little temporal change, indicating little turnover over the time frame captured by this core (Fig. 3.3). Similarly, broken-stick analysis on the chronological hierarchical clustering indicated no significant changes over the diatom stratigraphic records over the time period of ~500-1350 CE. Non-significant, hierarchical breaks occurred at ~920 CE, with the next two hierarchical breaks occurring around 910 and 960 CE (Figure 3.4), which are not shown on the sediment profile (Figure 3.3). The fourth hierarchical break occurred at ~1305 CE. Although not significant according to the broken-stick analysis, the two broad breakpoints coincide roughly with the timing of the MCA, and the relative abundances of diatoms in assemblages in the three timeframes are described below.
Figure 3.3. Sedimentary diatom profile of the MCA Core. Taxa occurring in ≥10 samples with ≥5% relative abundance are sorted left to right by their weighted average optima of the y-axis variable, emphasizing species composition over time, with the biggest changes occurring in species to the left.

The column on the far right indicates community turnover using DCA axis 1 scores.

From ~500-900 CE, the diatom community was dominated by *L. ocellata* (average = 29%, range = 13-39%; Fig. 3.3). *Lindavia comensis* (average = 10%, ranging from 0-17%) and *C. atomus “fine form”* (average = 9%, range = 4-23%) were also abundant. *Stephanodiscus spp*, the group including all *Stephanodiscus* genera except *S. conspicueporus*, was also fairly abundant (average = 6%, range = 1-15%). Less common diatoms included *Achnanthes sensu lato* taxa (average = 5%), *S. conspicueporus*...
(average = 4%), *L. comensis/ocellata* (average = 4%), *D. stelligera* (average = 4%), and the group of
*Cyclotella sensu lato* taxa that included all species not analyzed individually (average = 4%).
Figure 3.4. Chronological hierarchical clustering of the MCA Core. The scale at the top indicates the distance measure between groups. Non-significant breaks are indicated by dashed lines, while the MCA period is approximated by the red box.
From 900-1300 CE, assemblages were again dominated by *L. ocellata*, with the average relative abundance 4% lower than in the previous section of the core, but a larger range of variation (average = 25%, range = 7-37%; Fig. 3.4). *Lindavia comensis* increased, with a 4% increase in average relative abundance (average = 13%, range = 4-31%), which may have been driven by high abundance in the sediment interval at 1215 CE. *Cyclotella atomus* “fine form” had a similar average abundance to the previous time period (average = 10%, range = 2-19%). Two groups each had a 2% increase in abundance: the *Cyclotella sensu lato* taxa (average = 6%, range = 1-11%) and *L. comensis/ocellata* (average = 6%, range = <1-13%). Less common diatoms also had similar abundance to the previous time period, such as *S. conspicueporus* (average = 5%) and *D. stelligera* (average = 4%).

From 1300-1350 CE, the biggest change was in *C. atomus*, with a 4% increased relative abundance compared to previous time periods (average = 5%, range = 0-14%). *Lindavia ocellata* was still dominant, but relative abundance further declined another 2% compared to the previous time period (average = 23%, range 11-31%; Fig. 3.4). The relative abundance of *C. atomus* “fine form” increased by 3% from the previous time period (average = 13%, range = 6-19%), while the relative abundance of *L. comensis* remained the same (average = 12%, range = 7-17%).
Figure 3.5. Sedimentary diatom profile of the Post-1800 Core. Taxa occurring in ≥5 samples with ≥5% relative abundance are sorted left to right by their weighted average optima of the y-axis variable, emphasizing species composition over time, with the biggest changes occurring in species to the left. The column on the far right indicates DCA axis 1 scores. The horizontal line indicates a significant breakpoint determined by broken-stick analysis from dissimilarity clusters from chronological hierarchical clustering.

3.4.2 Post-1800 Core

The diatom community over the last 200 years was dominated by *Discostella pseudostelligera* (Hustedt) Houk and Klee, *Lindavia delicatula* Hustedt, and *L. ocellata*. Planktonic species also dominated throughout this core, ranging from 82-91% relative abundance (Appendix A). The 90 enumerated taxa were combined into 26 taxonomic groups (Table 3.2), with 11 final groups occurring in at least 5 samples with at least 5% relative abundance in one sample (Fig. 3.5). There were no apparent temporal changes
in proportions of planktonic: benthic community ratios throughout the core (Chräibi et al. 2014).

Broken-stick analysis indicated a significant shift in diatom assemblages at ~1940 (Fig. 3.6); diatom community turnover was minimal until 1940 and then increased to the top of the core, as indicated by shifting DCA axis-1 scores (Fig. 3.5).

**Figure 3.6.** Post-1800 Core chronological hierarchical clustering. The scale at the top indicates the distance measure between groups. The significant break determined by broken-stick analysis is indicated by the horizontal line.
From 1815-1940, sedimentary diatom assemblages were dominated by *L. ocellata* (average = 18%, range = 13-27%; Fig. 3.6). Relative abundances of *D. pseudostelligera* (average = 15%, range = 9-19%) and *Aulacoseira* spp. (average = 15%, range 3-27%) were also high. Relative abundances of other taxa were lower, including *Stephanodiscus* spp. (average = 9%, range = 6-13%), *Fragilaria sensu lato* taxa (average = 8%, range = 6-11%) and *Urosolenia* spp. (average = 6%, range = 4-9%). Although *L. delicatula* had low relative abundance (average = 4%, range = 2-10%), it was present throughout the core.

From 1940-2010, *L. delicatula* was a dominant taxon, increasing 15% from the previous time period (average = 19%, range = 8-26%). *Discostella pseudostelligera* was similarly dominant, increasing 4% from the previous time period (average = 19%, range = 12-33%). Relative abundances of *L. ocellata* decreased 5% from the previous time period (average = 13%, range = 10-19%), while the relative abundance of *Fragilaria sensu lato* taxa increased 3% (average = 11%, range = 8-16%). *Aulacoseira* spp. decreased 10% from the previous time period (average = 5%, range 3-8%).

### 3.5 Discussion

There was very little change in the diatom community during the past warm, dry period of the MCA, based on small changes in the relative abundances of key taxa and the low species turnover. Although diatom assemblage changes surrounding the MCA are suggested by hierarchical clustering, they were not significant and were relatively small and variable throughout the core. Overall, we found little evidence of diatom shifts during the MCA. By contrast, diatom community structure shifted ~1940 in the Post-1800 Core, and community turnover continued to the top of the core (2010). These changes in diatom communities occurred during a period of multiple anthropogenic impacts (Stoermer 1985; Chraïbi et al. 2014) and climate change, with increasing air temperatures that have led to changes in surface water temperatures and lake stratification (Austin and Colman 2008).
It is possible that regional climate change during the MCA was not great enough to elicit pelagic changes in Lake Superior, however there is broad evidence of environmental change in the Great Lakes region during the MCA. Paleoclimate reconstructions from the Northern Great Plains of the US show the timing of this warm period in the central US coincides with the global MCA (950-1250 CE; Valero-Garcés et al. 1997). The MCA was characterized by periods of low effective moisture and low lake levels as indicated by records from other lakes in the area starting around 1000 CE (Last and Slezak 1986, 1988; Vance et al. 1992; Xia et al. 1997). Droughts in the western Great Lakes region largely overlapped with the MCA (1000-1300 CE), were associated with abrupt regional fire and vegetation changes (Booth and Jackson 2003), and likely affected a large mid-continent region (Booth et al. 2006). The effects of the MCA are also apparent in sedimentary diatom profiles of smaller regional lakes. In a lake isolated from Lake Michigan ~2250 years before present, Wolin (1996) found a distinct shift in diatom microfossils during the MCA. Given the extent of evidence for the warmer, drier conditions of the MCA in this region, we expected climate-related responses in the diatom community to occur during the MCA, with assemblages differing from the preceding interval. However, we found little evidence of diatom assemblage changes in Lake Superior over the 500-1350 CE period.

It is unclear why diatom assemblages in Lake Superior showed little response to climate change in the MCA, considering the multiple pathways by which climate has affected Lake Superior in the past century, including increased water temperatures, decreased ice cover, lengthened positively stratified season (Austin and Colman 2008) and increased wind speeds (Desai et al. 2009). It is possible that diatom communities were largely unaffected because the MCA lacked the other anthropogenic impacts occurring simultaneously with modern warming. It should be noted that the largest increases in open water surface temperature have occurred in the past three decades (Austin and Colman 2008), while the biggest changes in the diatom community post-1800 occurred ~1940. The lack of a significant change before, during, or after the MCA further suggests the changes in the paleolimnological record over the
past two centuries are related to a combination of environmental variables related to anthropogenic influences.

Some key differences were apparent in the diatom assemblages of the MCA versus Post-1800 cores. The biggest difference in diatom communities between the MCA and the past two centuries is the modern appearance of *L. delicatula* (average relative abundance of 4% up to ~1940 and 19% after), with increasing relative abundances in the past few decades, while we could not confidently confirm *L. delicatula* in any intervals from the MCA. Similarly, *D. pseudostelligera* was found throughout the past 200 years, retaining at least 10% abundance in recent decades, although it was rarely encountered in sediment deposited during the MCA (<1% abundance in 15% of samples). Conversely, while *D. stelligera* was never dominant in the MCA core, it was found in all MCA intervals, having a higher relative abundance (average = 3%) than in the past two centuries (average = 1%), and was absent in 25% of the sediment intervals deposited since 1940. Similarly, *L. comensis* was abundant during the MCA and decreased in the past two centuries, with a possible increase in recent decades. Only *L. ocellata* has retained high relative abundances through the numerous environmental changes occurring in Lake Superior over the past 1500 years.

The lack of diatom community reorganization during the MCA may also be due to weak relationships between diatom distributions and climate-related parameters in Lake Superior. A recent investigation using modern monitoring data suggested the importance of 6 environmental variables in explaining abundance changes for 6 planktonic diatom taxa, with 2-3 variables, which varied by species, best explaining abundance changes (Chapter 2). Changes in phosphorus, nitrate, silica, and conductivity had strong linkages to contemporary diatom distributions (Chapter 2). This suggests complex, synergistic effects of multiple variables to diatom community changes. Nutrient concentrations were related to changes in all tested species, while relationships to physical parameters associated with climate-driven forcing including turbidity, as a proxy for light availability, and temperature were weaker and found for 2
of the 6 tested taxa (Chapter 2). The study could not confirm relationships between any of the taxa and thermocline depth (Chapter 2). Additionally, the changes in the paleo record post-1800 have been related to multiple anthropogenic impacts including watershed development and inferred changes in nutrient concentrations (Stoermer 1985; Chraibi et al. 2014). Over the past-century, Lake Superior has had unprecedented and stoichiometrically unbalanced increases in nitrate (Sterner et al. 2007). Recent decades have been marked by decreased phosphorus concentrations (Dove and Chapra 2015), while the diatom record indicates response to enrichment with European settlement near the beginning of the 20th century (Stoermer 1985; Chraibi et al. 2014). The lack of change in the diatom community structure during the MCA suggests that changes in water chemistry were likely not as large as changes in the past century.

This research is a continuation of steps to understand the role of climate change in diatom shifts in Lake Superior (Reavie et al. 2016; Bramburger et al. 2016; Chapter 2). Continued analysis of the rich and growing monitoring data (GLNPO database), studies targeting seasonality of diatom blooms, further focus on sedimentary records capturing climatic events, and experimental methods are needed to understand complex drivers of Lake Superior diatom community changes. Further, paleolimnological investigations of diatom changes during the MCA in regional lakes may help illuminate reasons for the lack of community response in Lake Superior.

3.6 Conclusions

Diatom communities did not significantly change during the warm, dry conditions of the MCA. The most notable changes in the sedimentary diatom community occurred in the past century, in context of other anthropogenic impacts, including decreased phosphorus (Dove and Chapra 2015) and increased nitrate (Sterner et al. 2007). The lack of diatom community changes during the MCA and the increase post-1800 of taxa such as *D. pseudostelligera* and *L. delicatula* that are related to changes in nutrients and
conductivity, suggest that modern diatom communities in Lake Superior experience novel environmental conditions. This is further supported by the importance of multiple environmental variables in explaining abundance changes in modern monitoring data, with weaker and sometimes lacking relationships with physical parameters (Chapter 2). Changes of these environmental variables during the MCA do not appear large enough to have a notable effect on the diatom community. In contrast, the synergistic effects of multiple environmental variables are causing a novel shift in modern Lake Superior diatom communities, a shift that did not happen during a past period of warming.
4.1 Abstract

We examined the diatom profiles of a sediment core from Siskiwit Lake, a lake on an island in Lake Superior, to investigate regional response to climate-driven changes. The sedimentary record spanned a period before, during, and after the Medieval Climate Anomaly (MCA), a period of warming from ~950-1250 CE, to investigate diatom changes during a past warm, dry period with minimal human impact. This record was compared to a sedimentary record from Lake Superior covering the same time period. Diatom communities changed near the beginning of the MCA in the Siskiwit Lake core, but did not change in the Lake Superior core, indicating a community response to the effects of climate driven-change in Siskiwit Lake. However, *Discostella stelligera* did not have decreased abundance in Siskiwit Lake during the MCA, contrary to decreased abundance in modern samples that have been linked to a deepening epilimnion related to windier conditions during warming. Further, diatom-inferred mixing does not show significant changes throughout the MCA. Changes in the Siskiwit Lake diatom community near the beginning of the MCA include a marked decrease in benthic taxa relative abundance, suggesting decreased moisture balance led to decreased benthic habitat, which we propose was the dominant driver of diatom community changes. Our findings suggest the regional climate-driven changes during the MCA had a larger effect on Siskiwit Lake than on Lake Superior, highlighting the importance of lake size in mediating diatom community responses. Further, diatom community changes suggest different modern climate-driven changes, such as increased wind, in Siskiwit Lake compared to changes during the MCA.
**4.2 Introduction**

Climate change is occurring in the Great Lakes region, with water temperatures increasing faster than air temperatures in Lake Superior (Austin and Colman 2007). These changes are proposed to be affecting changes in the diatom communities, but the mechanisms are currently unclear (Reavie et al. 2014b, 2016). The relationship between climate change and the diatom community is complex, as changes in the planktonic summer diatoms are related to multiple environmental drivers, with limited response to climate-driven physical changes (Chapter 2). This, combined with evidence that changes in the paleolimnological record are related to multiple anthropogenic impacts (Chapter 3) leads to reinvestigation of a past period of warming with minimal anthropogenic influences.

The Medieval Climate Anomaly (MCA) was a warmer, drier period from 950-1250 CE, spanning many areas in the northern hemisphere (Mann et al. 2009). Mann et al. (2009) reported a positive temperature anomaly of ~0.4°C in the upper Midwest relative to a 1961-1990 reference period mean. There is evidence that the timing of MCA impacts in the Great Lakes region generally coincides with the global MCA, with paleolimnological records indicating the warm period in the central United States (Valero-Garcés et al. 1997). Impacts included droughts in the western Great Lakes region (1000-1300 CE) and associated abrupt regional fire and vegetation changes (Booth and Jackson 2003), likely affecting a large mid-continent region (Booth et al. 2006). Water table reconstructions of bogs in Minnesota and Michigan support temporal and spatial drought coherence (Booth et al. 2006).

Recent investigation on the Lake Superior paleolimnological record during the MCA adds to our understanding of the complex relationship between Lake Superior diatoms and climate change (Chapter 3). Relative abundances of Lake Superior diatom communities did not change during the previous warm, dry period of the MCA (Chapter 3); however, sedimentary diatom assemblages did change in the past 100 years (Stoermer et al. 1985a, Chraïbi et al. 2014). The lack of diatom change during the MCA compared to changes in the past century may be related to the combined influence of other factors.
anthropogenic impacts over the past century (Chapter 3). The lacking relationships of modern planktonic diatoms and paleolimnological changes during the MCA with climate-driven physical effects in Lake Superior may also be related to lake size. The role of lake size in differing diatom responses to modern climate-driven effects has been found in Maine Lakes (Boeff et al. 2016) and in other regional lakes near Lake Superior (Edlund et al. 2017). Climate-related changes in stratification, which is related to light availability for planktonic diatoms, are important to recent shifts in *Cyclotella sensu lato* taxa (Saros et al. 2012, Saros et al. 2014, summarized by Saros and Anderson 2015). The frequent seiches in Lake Superior (Mortimer and Fee 1976) create highly variable mixing depths, thus exposing phytoplankton to a variable light environment. In addition, near-inertial currents, internal currents with clockwise rotation in the open waters that can change vertical temperature profiles in Lake Superior, may cause large changes in the thermocline during stratification in Lake Superior (Austin 2013). Thus, the diatom community in Lake Superior may be more resilient to the physical effects of climate change.

One approach to understand Lake Superior’s potential resilience to past climate change is by studying changes in another regional lake experiencing the same climate forcing. Siskiwit Lake is embedded in Lake Superior, making it the largest lake, on the largest island (Isle Royale), in the largest lake in the world (Fig. 4.1). A boreal lake with surface area of 16.8 km$^2$, Siskiwit Lake contains several islands of it its own and is generally considered large in other contexts, although it is nearly 5,000 times smaller than Lake Superior (82,100 km$^2$). While Lake Superior has an average depth of 147 m (maximum depth = 406 m), Siskiwit Lake has a maximum depth of 45.1 m (Elias and VanderMeulen 2008). Siskiwit Lake tends to be an oligotrophic lake and the only lake on Isle Royale with mean total phosphorus and total nitrogen concentrations below EPA reference criteria, and a Secchi depth of at least 6 m (Damstra et al. 2014).
Diatom responses to climate change in Siskiwit Lake have been recently documented in samples over from the past two centuries (Saros et al. 2012). For example, decreases in *D. stelligera* and dominance of *L. bodanica*, which have different thermal mixing optima, indicate increased wind strength has led to deeper lake mixing depths in Siskiwit, starting around 1940 (Saros et al. 2012). Both centric diatoms, *D. stelligera* is associated with shallower stratification while *L. bodanica* is associated with deeper mixing (Saros et al. 2012).

Our objective was to test whether Siskiwit Lake, a smaller lake embedded in Lake Superior, is a more sensitive sentinel than Lake Superior to regional climate-driven changes during the MCA, a past warm, dry period with minimal human impact. We tested two responses of lake water quality: diatom community structure and total siliceous algal production. We expected diatom communities to experience different response magnitudes to climate-driven changes in these two systems. We hypothesized that sensitivity to climate change, as measured by overall diatom abundance and shifts in the community structure, would be greater in Siskiwit Lake, which, due to its smaller size, may not be
able to buffer climate effects as well as Lake Superior. Its smaller volume, area, and depth would be expected to make Siskiwit Lake more responsive to external climate forcing than Lake Superior. Thus, Siskiwit Lake would be less susceptible to average variation in thermal structure, with expected higher modifications to variations in light attenuation driven by warming, as well as changes in water chemistry and lake habitat that would be modified by a past warm, dry period. Thus, we would expect to see a more pronounced change in diatom communities in Siskiwit Lake near the start of the MCA due to increased thermocline depths and decreased light attenuation.

4.3 Methods

4.3.1 Siskiwit Lake Core (Siskiwit Core)

A 1.64 m core was collected from 31.8 m of water on August 9, 2011 at 47°59.65’N 88°48.3’W by pushing a 6.5 cm inner diameter polycarbonate tube outfitted with a piston in the sediments using a ridged drive-rod system (Fig. 4.2). This study extends a recent paleolimnological analysis by Saros et al. (2012). The core was subsampled at 0.5 cm intervals and a total of 35 non-contiguous samples covering the time period before, during, and after the MCA were targeted for diatom enumeration. A total of 300 diatom valves per slide were counted from permanent microscope slides made with Naphrax™, a mountant providing a high refractive index. Diatoms were examined under oil immersion at 1000X magnification (numerical aperture > 1.3) under light microscopy, with raw counts converted to percent abundance relative to total diatom counts. Taxonomy was generally by genus, while species were kept separate if they were found at high abundance or had recently been tested for relationships with environmental drivers (Chapter 2) to investigate potential specific changes (Table 4.1). Taxonomic references included those specific to the Great Lakes (Reavie and Kireta 2015) and those used by diatomists worldwide (Krammer and Lange-Bertalot 1986-1991).
Radiocarbon dating was performed on pollen isolates extracted at the University of Maine using adapted methods from Vandergoes (2003) and Newnham et al. (2007). Livermore Lab analyzed accelerator mass spectrometry (AMS) radiocarbon dating (Stuiver and Polach 1977). Four AMS $^{14}$C dates was used to extended the $^{210}$Pb age-depth Constant Rate of Supply model reported by Saros et al. (2012) from a nearby core at 48°00’02” N, 88°47’45” W, collected in 2010 from a 30 cm gravity core. Age models and error estimates were generated with the R statistical package (R Core Team 2015) using the BChron package (Parnell 2015), using normal calibration for the $^{210}$Pb data and northern hemisphere terrestrial $^{14}$C calibration curve for the radiocarbon data, which determines the most likely age-depth estimates using Bayesian probability techniques.
Diatom taxa and combinations are listed in Table 4.1, with taxa largely combined into genus groups containing all associated species (e.g. *Tabellaria* spp.) or broad taxonomic groups that contained multiple genera that have been erected from the base genus (e.g. *Cymbella sensu lato* with the genera *Cymbella* and *Encyonema*).

### 4.3.2 Lake Superior Core (Superior Core)

The Lake Superior Core was collected aboard the Research Vessel (R/V) *Blue Heron* in 2009, east of the Keweenaw Peninsula in central southern portion of Lake Superior at 47°7’42”N, 87°49’15.6”W. A gravity core was used as a trigger core to a Kullenberg piston corer; this site was targeted in a previous study (O’Beirne et al. 2017). Dating and diatom analysis on the gravity core was used in a previous study focused on changes in diatom communities in Lake Superior during the MCA (Chapter 3), with methods explained only briefly here. The University of Minnesota National Lacustrine Core Repository (LacCore) provided subsamples at 0.5 cm intervals. An age model was created using similar methods as described above for the Siskiwit core, with \(^{14}\text{C}\) dates from the gravity core and \(^{210}\text{Pb}\) dates from a multi-core capturing the sediment-water interface collected by the R/V Blue Heron at a nearby site at 47°7’4”N, 87°49’12”W in 2009. We used an age/depth model developed by O’Beirne et al. (2013) to determine the sedimentary intervals of the gravity core to be used for \(^{14}\text{C}\) dating (Chapter 3). A total of 52 non-contiguous sediment intervals targeting the MCA and surrounding intervals were chosen for analysis, with each 0.5 cm sediment sample interval represented approximately a 7-year integrated sample. Diatom samples were analyzed as described in Chapter 3. Of the 32 taxonomic groups 14 groups occurred in at least 10 samples with at least 5% relative abundance in one sample (Table 3.1) and were included in data analysis and graphical output.
4.3.3 Analyses

Diatom community data were analyzed, analyzing changes using depth constrained chronological analysis using R core software (R Core Team 2015). We first determined sample dissimilarity by creating a dissimilarity matrix, computing chord distances between samples in a core. In this case, we used the R base package (R Core Team 2015) to analyze dissimilarity using Hellinger distances, which is the distance determined using the Euclidean method with square root transformed relative abundance data. Next, hierarchical chronological clustering was determined using the rioja package (Juggins 2017). The chclus function implemented a constrained cluster analysis on the dissimilarity matrix using an agglomerative clustering technique, which joins groups from individual objects using local similarity over larger differences. In this case, we used a constrained Ward’s minimum variance method (Ward 1963) to determine subsequent groups of samples throughout the core by minimizing the total within-group sum of squares. A broken-stick analysis was used to determine significant zones of diatom reorganization from the hierarchical chronological clustering (Bennett 1996) using the rioja package (Juggins 2017) in R. The broken-stick analysis examines the zonation from the chronological clustering data, showing the reduction of sum of squares under a random distribution, identifying the number of zonation or clusters from the chronological clustering model better than the random model. Stratigraphic plots were made using the analogue package in R (Simpson and Oksanen 2016). Stratigraphic plots were made using the analogue package in R (Simpson and Oksanen 2016), plotting samples that were found in at least 5 samples with relative abundance of at least 5% in one of those samples. Species found in at least 5 samples with at least 5% abundance were chosen to represent non-rare diatom occurrence in the Siskiwit Lake core, which had a smaller number of samples (n=35) than Lake Superior (n=52), for which analyses included species found in at least 10 samples with at least 5% abundance. Detrended correspondence analysis (DCA) of square root relative abundance data was also used to determine diatom community turnover using the vegan package (Oksanen et al. 2017).
A mixing model was developed to infer changes in epilimnion depth for Siskiwit Lake using mixing optima developed by Saros et al. (2012), which applies the following mixing depth optima: *L. bodanica* = 14 m, *L. comensis* = 9 m, and *D. stelligera* = 4 m. Weighted averages were calculated for relative proportions of each of the three taxa from each sedimentary interval, providing estimated mixing depths throughout the sediment core.

Biogenic silica was analyzed by the Northern Arizona University Sedimentary Records of Environmental Change Lab using the wet chemistry method of Mortlock and Froelich (1989) and converted to biogenic silica flux based on the sediment accumulation rates extrapolated from $^{210}\text{Pb}$ analysis.
The calibrated age-model indicated that the Siskiwit Lake core covered a similar time interval to the previously dated Lake Superior core. The examined section of the core spanned ~470-1360 CE (Fig. 4.3), capturing about 500 years prior to the start of the MCA, the MCA period, and about 110 years post-MCA. Each 0.5 cm sediment interval represented ~20 - 22 years per sample. A total of 127 diatom taxa or taxonomic groupings were initially made for Siskiwit samples, later combined into 33 taxon or
broader groups based on similar species or (Table 4.1.). There were 14 taxa that were found in at least 5 samples with relative abundance of at least 5% abundance in one sample (Fig. 4.4). Broken-stick analysis on the chronological hierarchical clustering indicated a significant change in the diatom community with a hierarchical break at ~1070 CE (Fig. 4.5). Furthermore, a shift in diatom community turnover is also seen near this time in the DCA axis 1 scores (Fig. 4.5). Assemblages throughout Siskiwit Lake were dominated by *D. stelligera* (Fig. 4.4). Planktonic species ranged from 51-86%, with a notable decrease in benthic species at ~1070 (Fig. 4.6a).
Figure 4.4. Sedimentary diatom profile of the Siskiwit Lake core. Taxa occurring in ≥5 samples with ≥5% relative abundance are presented from left to right for taxa that changed the most through time, based on their weighted average optima of the y-axis variable, emphasizing species composition over time, with the biggest changes occurring in species to the left. The column on the far right indicates community turnover based on DCA axis 1 scores. The horizontal line indicates a significant breakpoint in dissimilarity clusters from chronological hierarchical clustering, while the MCA period is approximated by the red box.
Figure 4.5. Siskiwit Lake chronological hierarchical clustering. The scale at the top indicates the distance measure between groups. The horizontal line shows the significant break point from broken-stick analysis.
<table>
<thead>
<tr>
<th>Group name</th>
<th>Included genera</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stratigraphic plots</td>
<td></td>
</tr>
<tr>
<td><em>Achnanthidium</em> spp. Kützing</td>
<td></td>
</tr>
<tr>
<td><em>Achnanthidium minutissimum</em> (Kützing) Czarnecki</td>
<td></td>
</tr>
<tr>
<td><em>Aulacoseira</em> spp. (Ehrenberg) Thwaites</td>
<td></td>
</tr>
<tr>
<td><em>Lindavia michiganiana</em> (Skvortzow) T.Nakov et al.</td>
<td></td>
</tr>
<tr>
<td><em>Cymbella sensu lato</em></td>
<td><em>Cymbella Agardh, Enyonema Kützing</em></td>
</tr>
<tr>
<td><em>Discostella stelligera</em> (Cleve &amp; Grunow) Houk &amp; Klee</td>
<td></td>
</tr>
<tr>
<td><em>Lindavia bodanica</em> (Eulenstein ex Grunow) T.Nakov et al.</td>
<td></td>
</tr>
<tr>
<td><em>Lindavia bodanica/ radiosa/ planctonica</em></td>
<td>Group containing species hard to distinguish between <em>L. bodanica, L. radiosa</em> (Grunow) De Toni &amp; Forti, and <em>L. planctonica</em> Brunnthaler</td>
</tr>
<tr>
<td><em>Lindavia comensis</em> (Grunow) T.Nakov et al.</td>
<td></td>
</tr>
<tr>
<td><em>Lindavia ocellata</em> (Pantocsek) T.Nakov et al.</td>
<td></td>
</tr>
<tr>
<td><em>Pseudostaurosira</em> spp. Williams &amp; Round</td>
<td></td>
</tr>
<tr>
<td><em>Staurosira sensu lato</em></td>
<td>Group containing species in the genera <em>Staurosira</em> Ehrenberg and <em>Staurosirella</em> (Grunow in Van Heurck) Williams &amp; Round</td>
</tr>
<tr>
<td><em>Tabellaria</em> spp. Ehrenberg ex Kützing</td>
<td></td>
</tr>
</tbody>
</table>

**Table 4.1.** Diatom taxa and combinations for the Siskiwit Lake Core.

Cluster analysis

<table>
<thead>
<tr>
<th>Amaphora spp.</th>
<th>Amphora spp. Ehrenberg ex Kützing</th>
</tr>
</thead>
<tbody>
<tr>
<td>Asterionella formosa</td>
<td>Asterionella formosa Hassall</td>
</tr>
<tr>
<td>Cocconeis spp.</td>
<td>Cocconeis spp. Ehrenberg</td>
</tr>
<tr>
<td>Cyclotella meneghiniana</td>
<td>Cyclotella meneghiniana Kützing</td>
</tr>
<tr>
<td>Cyclotella atomus</td>
<td>Cyclotella atomus Hustedt</td>
</tr>
<tr>
<td>Lindavia comensis/ocellata</td>
<td>Group containing species hard to distinguish between L. comensis and L. ocellata</td>
</tr>
<tr>
<td>*Cyclotella sensu lato</td>
<td>*Cyclotella sensu lato</td>
</tr>
<tr>
<td>Eunotia spp.</td>
<td>Eunotia spp. Ehrenberg</td>
</tr>
<tr>
<td>Fragilaria sensu lato</td>
<td>Fragilaria sensu lato</td>
</tr>
<tr>
<td>Navicula/Achnanthes</td>
<td>Group containing specimens hard to distinguish between the genera Navicula Bory de Saint-Vincent and Achnanthes Bory</td>
</tr>
<tr>
<td>Nitzschia spp.</td>
<td>Nitzschia sensu lato</td>
</tr>
<tr>
<td>Urosolenia spp.</td>
<td>Urosolenia sensu lato (Round &amp; Crawford)</td>
</tr>
<tr>
<td>emended</td>
<td>emended Rott, Kling &amp; McGregor</td>
</tr>
<tr>
<td>Staurosira construens</td>
<td>Staurosira construens Ehrenberg</td>
</tr>
<tr>
<td>Staurosira cf. construens</td>
<td>Staurosira cf. construens</td>
</tr>
<tr>
<td>Stephanodiscus sensu lato</td>
<td>Stephanodiscus sensu lato Ehrenberg</td>
</tr>
<tr>
<td>Surirella sensu lato</td>
<td>Surirella sensu lato</td>
</tr>
<tr>
<td>Thalassiosira spp.</td>
<td>Cymatopleura W. Smith, Surirella spp. Turpin</td>
</tr>
<tr>
<td>Unknown centric</td>
<td>Unknown centric</td>
</tr>
<tr>
<td>Unknown pennate</td>
<td>Unknown pennate</td>
</tr>
</tbody>
</table>

**Table 4.1 continued.** Diatom taxa and combinations for the Siskiwit Lake Core.

*except for C. atomus, D. pseudostelligera, D. stelligera, L. bodanica, L. comensis, L. ocellata, and L. michiganiana

From ~470-1060 CE, the diatom community was dominated by D. stelligera (average = 30%, range = 18-44%; Fig. 4.5). Tabellaria spp. (average =10%, ranging from 4-15%), Achnanthidium sensu lato
(average = 9%, ranging from 6-15%), *Aulacoseira* spp. (average = 7%, range = 4-11%), and *Pseudostaurosira* spp. (average =7%, ranging from 2-13%) were also somewhat abundant. Less common diatoms included *Staurosira sensu lato* (average =5%), *L. michiganiana* (average = 5%) *Navicula* spp. (average = 4%), *L. ocellata* (average = 3%), *A. minutissimum* (average = 3%), and *L. bodanica* (average = 3%). Benthic assemblages were relatively high (average = 36%, ranging from 23-49%), although planktonic diatoms dominated (Fig. 4.6a).

From ~1080-1360, assemblages in Siskiwit Lake were again dominated by *D. stelligera*, with the average relative abundance 13% higher than in the previous section of the core (average = 43%, ranging from 30-61%). Relative abundances decreased 5% for *Achnanthidium sensu lato* (average = 4%, ranging from 1-6%), 4% for *Pseudostaurosira* spp. (average =3%, ranging from <1-6%), and 3% for *Tabellaria* spp. (average =7%, ranging from 3-7%). Relative abundance increased 4% for each *Aulacoseira* spp. (average = 7%, range = 4-11%) and *L. michiganiana* (average = 9%, ranging from 3-12%). Relative abundances were similar to the previous section of the core for *Navicula sensu lato* (average = 5%) and appeared to decrease 2% for *L. bodanica* (average = 1%). Although relative abundance of *L. comensis* was low (average = 1%, range = 0-6%), it was found consistently in intervals after 1250 CE, with only one occurrence in the previous section of the core, at 0.6% relative abundance at 770 CE. Relative abundance of benthic diatoms decreased 14% from the previous section of the core (average = 22%, ranging from 14-27%), with planktonic diatoms dominating (Fig. 4.6a).
Figure 4.6. Stratigraphic plots for percent relative abundance benthic diatoms for (a) Siskiwit Lake and (b) Lake Superior. The break at 1070 CE in Lake Siskiwit shows a significant change in the diatom assemblage from broken-stick analysis.

Lake Superior results are fully presented in Chapter 3. Briefly, planktonic species dominated throughout the sediment core ranging from 80-93% relative abundance, with no apparent change in proportions of planktonic:benthic community ratios throughout the core (Fig. 4.6b). DCA axis 1 scores were variable but showed little temporal change, indicating little turnover in Lake Superior (Fig. 4.7b). Similarly, broken-stick analysis on the chronological hierarchical clustering indicated no significant changes over the diatom stratigraphic records for Lake Superior (Chapter 3). The diatom community was dominated by *L. ocellata* (average = 26%, ranging from 7-39%) and *L. comensis* (average = 12%, ranging
from 0-31%). *Cylotella atomus* “fine form” (average = 10%, ranging from 2-22%), *Cyclotella sensu lato* taxa (average = 6%, ranging from 1-11%), *L. comensis/ocellata* (average = 5%, ranging from 0-13%), and *S. conspicueporus* (average = 5%, ranging from 1-10%) were also relatively abundant.
Figure 4.7. Sedimentary diatom profile of the Siskiwit Lake (a) and Lake Superior (b). Taxa occurring in ≥10 samples for Lake Superior and ≥5 samples for Siskiwit Lake with ≥5% relative abundance are ordered from left to right by taxa that changed the most through time, based on their weighted average optima of the y-axis variable, emphasizing species composition over time, with the biggest changes.
occurring in species to the left. The column on the far right indicates community turnover as DCA axis 1 scores. The horizontal line indicates a significant breakpoint from dissimilarity clusters from chronological hierarchical clustering. The MCA period is approximated by the red boxes.

The diatom inferred mixing depth model for Siskiwit Lake showed an average epilimnion thickness of 4.6 m (Fig. 4.8). The maximum mixing depth was 6.2 m (473 CE) and the minimum was 4.1 m (1084 CE). Changes in modeled stratification depth were not notable throughout the core.

![Figure 4.8. Modeled Siskiwit Lake mixing depth showing diatom-inferred changes in the mixing depth on the left, determined by the abundance weighted average optimal depth for three taxa, ordered from left to right by shallowest to deepest mixing depth optima. The MCA period is approximated by the red box.](image)
Biogenic silica in Siskiwit Lake averaged 0.7 mg/cm$^2$/yr (ranging from 0.5-1 mg/cm$^2$/yr; Fig. 4.9a) and averaged 1 mg/cm$^2$/yr in Lake Superior (ranging from 0.7-1.3 mg/cm$^2$/yr; Fig. 4.9b). There was no directional change in biogenic silica flux during the MCA (950-1250 CE) in either core.

Figure 4.9. Biogenic silica flux for Siskiwit Lake (a) and Lake Superior (b) before, during, and after the MCA, which is approximated by the red box.

4.5 Discussion and Conclusion

There was a significant change in the diatom assemblage in Siskiwit Lake approximately coinciding with the start of the MCA. Specifically, relative abundances of *D. stelligera* and *Aulacoseira* spp., and *L. michiganiana* increased. The increasing *D. stelligera* could signal shallowing of the epilimnion (Saros et al. 2012) while increased *Aulacoseira* spp. could signal increased turbulence (Bradbury et al. 1993) or a
deepening epilimnion (Reynolds et al. 2002). Examination of the mixing model suggests stratification depth was shallow throughout the MCA, as well as before and after. This leads us to speculate that changes in the diatom community around the MCA were not driven by changes in epilimnion depth. The change in proportion of planktonic to benthic taxa may better explain how the shift in the diatom community at ~1070 relates to climate-driven physical change in Siskiwit Lake. The significant breakpoint in diatom assemblages is related to a decline in relative abundance of periphyton, with an increased proportion of planktonic diatoms starting at the beginning and continuing through the MCA (Fig. 4.6a). We speculate that decreased precipitation throughout the region (Booth et al. 2006) could have led to decreased benthic habitats. Looking at the lake bathymetry, a decline in lake level could lead to a loss in benthic habitat from the shallower near-shore regions of the lake, as well as the shallower western basin (Fig. 4.2).

We can use modern climate-driven physical changes as proxies for lake-wide changes during a previous warming period. Modern changes in Lake Superior related to climate forcing include increasing wind speeds over the lake (Desai et al. 2009), increasing surface water temperature (Austin and Colman 2007), and significantly deepening thermocline depths (Reavie et al. 2016). However, our evidence does not suggest that the MCA was a windier period, contrary to conditions over Lake Superior related to modern warming. This is most apparent in the opposing trends in D. stelligera abundance in Siskiwit Lake during the two warming periods, with decreased abundance related to modern warming (Saros et al. 2012) and increased abundance during the MCA. The diatom-inferred stratification suggests that there does not appear to be the deepening stratification or decreased availability during the MCA, contrary to modern trends (Saros et al. 2012). Further, the relative abundances of planktonic taxa did not shift considerably during the MCA, suggesting minimal changes in planktonic habitat structure related to climate-driven warming. Although there are numerous studies documenting changes in lakes throughout central North America during the MCA (e.g. Last and Slezak 1986, Vance et al. 1992, Xia et
al. 1997), there is uncertainty about how much the air temperatures increased compared to changes in the last century (Mann et al. 2009).

Another climate-driven change that can affect diatom communities is decreased moisture balance, or the balance of water influx into or out of an area, leading to lake level changes and subsequently, changes to the proportion of pelagic to benthic habitat. Droughts in this region during the MCA have been noted in other studies (Vance et al. 1992; Booth and Jackson 2006) and have been linked to changes in diatom communities (Wolin 1996; Laird et al. 1998). The notable change in community structure with decreased percentage of benthic diatoms near the start of the MCA in Siskiwit Lake suggests that loss of benthic habitat due to lower water levels was the major driver of community shifts. Investigations into changing sedimentary planktonic and benthic abundances have been used in recent studies to infer water level changes (e.g., Moos et al. 2005, Heinsalu et al. 2008, Laird et al. 2011). Contrary to our findings, drier periods with lower water levels often lead to increased light availability to the lake sediment, increasing benthic habitats (Wolin and Stone 2010). For example, drought has been related to paleolimnological increases in benthic taxa in a smaller, shallower lake in Minnesota (Bradbury and Dieterich-Rurup 1993). Further, Wolin (1996) suggested lower lake levels during the MCA could have led to increased benthic forms in a regional lake with a maximum depth of less than 16 m. However, steep-sided lakes may be an exception to the expected benthic increases with lower lake levels (Wolin and Stone 2010). The importance of lake bathymetry to available benthic habitat was detailed by Stone and Fritz (2004). They found that Foy Lake in Montana had decreased periphyton around the MCA and attributed this decrease to a 6 m drop in water level related to drought (Stone and Fritz 2004). It is possible that the moisture balance was low enough to lose areas of benthic habitat in Siskiwit Lake. The changes we propose for lake level during the MCA would undoubtedly have had a larger impact in Siskiwit Lake than Lake Superior, where we would expect drought would lead to a proportionally smaller loss of benthic habitat in this large lake with small littoral zones.
However, drought may affect lakes in various ways. For example, drought could affect changes in nutrient input and internal nutrient cycling, affecting the resource availability for diatom species. The Great Lakes region is projected to have decreased average precipitation and lower inflows (Manguson et al. 1997), with expected decreases in total phosphorus loadings based on climate modeling (Robertson et al., 2016). However, predicting the effects of drought is difficult in Lake Superior. For example, little is known how nutrient fluxes in coastal wetlands contribute or modify nutrients in the lake, although Morrice et al. (2004) found a wide variation based on hydrology and seasonality, which would vary widely among Lake Superior wetlands (Trebitz et al. 2002). Further, changes in direct precipitation have increased importance in Lake Superior, which has a relatively small catchment area (127,700 km²) compared to its surface area (82,100 km²; Botts and Krushelnicki 1987). Precipitation is the primary source of lake phosphorus, with changes in recent precipitation hypothesized to be related to modern decreases (Dove and Chapra 2015). Future work is needed to determine whether the projected climate-driven changes would cause more diatom community response than occurred in Lake Superior during the MCA. We note that any modern changes would be occurring in a Lake that has substantially altered nutrient levels, such as high nitrate (Sterner et al. 2007) and that small changes in environmental parameters are related to changes in diatom abundance (Chapter 2).

Climate change can lead to various physical and biological responses based on lake size. For example, physical response can differ by lake size. Increased air temperatures and lower dissolved organic carbon expected to lead to deepening epilimnia in small lakes, with no effect to epilimnia in large lakes (Fee et al. 1996). Stratification in larger lakes over 500 hectare, such as Lake Superior and Siskiwit Lake, is driven more by changes in wind (Fee et al. 1996). Large lakes tend to have a greater interannual variability of epilimnion depth, which could lead to greater variability in light availability (Fee et al. 1996). Greater variation in light availability could lessen the response of planktonic diatom communities to climate-driven changes in light availability. For example, Lake Superior experiences
frequent seiches (Mortimer and Fee 1976) and other types of motion only significant for lakes that have a fetch > 10 km (Boyce 1974), such as the Coriolis effect (Gorham and Boyce 1989), which could cause further variations in average light availability. As another example, Lake Superior’s near-inertial energy appears related to thermocline shifts up to 10 m (Austin 2013). Differences in diatom response to climate change has been proposed from changes in the sedimentary record of different sized lakes exposed to similar climate-forcing (Boeff et al. 2016, Edlund et al. 2017). However, lake size may influence the diatom community response to climate change in different directions. For example, Boeff et al. (2016) found that slow sedimentation and seiches may moderate stratification-driven diatom responses, while Edlund et al. (2017) found that shallower lakes generally had lower species turnover in the sedimentary record compared to deeper lakes. Lake Baikal, the world’s largest lake by volume, has had both strong physical and biological responses related to climate change (Moore et al. 2009). Changes in ice cover are related to shifts in the diatom community in Lake Baikal, as diatoms that bloom under the ice the form the largest peak algal bloom annually (Moore et al. 2009). The diatom community in Lake Superior does not appear to be intrinsically linked to changes affected by climate-driven forcing, in contrast to the strong linkages shown between physical changes and diatom changes in Lake Baikal.

In conclusion, the sedimentary diatom community changes in Siskiwit Lake during the MCA support a response to previous warming with minimal anthropogenic impact. In particular, drought appeared to be the major driver of changes in the diatom community, with decreased abundance of benthic diatoms suggesting a loss of benthic habitat. By contrast, diatom communities in Lake Superior revealed no significant change related to this warm, dry period. This suggests Lake Superior may be more resilient to past climate-driven forcing related to lower lake levels than the relatively smaller Siskiwit Lake, which may be a better sentinel of regional climate change. We note that although the functional and taxonomic diatom community showed change, siliceous algal productivity remained
constant, indicating that community-level changes provided a more sensitive response to climate-driven change. This study supports previous findings that diatom changes occurring in Lake Superior in the past century are related to multiple environmental variables, and that modern diatom changes may be outside of the range of diatom changes that have occurred within the past 1500 years (Chapter 3). This underscores the importance of understanding the mechanisms of modern diatom changes in Lake Superior and the differences in community response to climate change related to lake size.
CHAPTER 5

CLIMATE SCIENCE AND CLIMATE CHANGE EDUCATION IN MAINE MIDDLE AND HIGH SCHOOLS:

FINDINGS FROM A STATEWIDE TEACHER SURVEY

5.1 Abstract

This article shares findings from an online teacher survey of over 300 Maine middle and high school teachers. Results indicate that teachers in Maine are teaching about climate science and climate change across a variety of subjects and they view climate change as a major concern and an interdisciplinary subject that should be taught more frequently and broadly. We identify topics and strategies to further support climate education in Maine public schools.

5.2 Background

Climate change is one of the biggest global threats the world has ever faced. For example, climate change can impact water supplies (Vörösmarty et al. 2000), lead to increasing extreme weather events and cause structural and property damages (Mills 2005), decrease crop yields (Parry et al. 2004), and disconnect food webs and disrupt ecosystems (Magnuson et al. 1997). Further, the United States Department of Defense considers climate change a threat multiplier, with important implications for national security (Hagel, 2014). Climate science and the impacts of climate change are inherently complex and highlight the need for formal instruction through K-12 education. Marginalizing climate science in the classroom leaves the public susceptible to misperceptions and disinformation and ultimately vulnerable to the impacts of climate change and abrupt climate change. Unfortunately, climate change is an environmental, social and economic issue with political and polarizing opinions.
Presently, climate science is not being taught consistently, or sometimes even accurately, in the American school system (Wise, 2010). This partially explains the wide disconnect between climate scientists and the U.S. public. For example, despite 97% of active climate scientists agreeing that the planet is warming as a result of human greenhouse gas emission, only 42% of the U.S. population agrees (Pew Research, 2013). American teens and young adults have a poor understanding of basic climate-related topics, with less than 1/3 receiving passing grades on climate topics (Leiserowitz et al., 2011). Recently, Plutzer et al. (2016) reported the importance of teacher knowledge and values related to effective climate education. They found that confusion about climate science may lead to teachers covering unsupported claims about climate change in class.

In June 2017, the Maine-science listserv sent out information from the National Science Teachers Association (NSTA) regarding misleading climate propaganda sent to teachers nationwide from the Heartland Institute, a special interest group rejecting the scientific consensus on climate change (NSTA, 2017). The NSTA was founded in 1944, and is the largest organization in the world, with 55,000 members, committed to promoting excellence and innovation in science teaching and learning for all (NSTA, n.d). Describing this as an “unprecedented attack”, the NSTA offered support and resources, urging teachers to recycle the pseudo-teaching materials they received and to “just teach science in your classroom”, issuing three main points in response to the unsolicited propaganda (original emphasis maintained): “First, scientists don’t disagree about climate change or its causes. Second, labeling propaganda as science does not make it so. Third, science teachers are the critical bastion in the war against reason. And the special interests know it.”

A nationwide study identified problems in formal climate education by science teachers including 12% not emphasizing human causes, 30% stating global warming is likely due to natural causes, 31% sending confusing messages about scientific consensus about human causes (Plutzer et al.
Three suggested explanations can contribute to ineffective climate change education, including: outside pressure from parents, the community, or administration against teaching climate change; lack of knowledge of climate change evidence; and lack of awareness of extent of scientific agreement to human contributions of climate change (Plutzer et al. 2016). There is evidence that the atmosphere of climate education may be regional or improving, as Wise (2010) showed 15% of teachers felt outside pressure against teaching climate change in the state of Colorado, while a recent, nationwide study found 4% of teachers indicated that they felt outside pressure against teaching climate change (Plutzer et al. 2016). We wanted to investigate how climate change education was being taught in Maine schools as well as investigate differences between groups of teachers who did and did not teach classes related to science, technology, engineering, or mathematics. To understand the state of climate change in Maine public schools, we developed an online survey tool focused on all middle school and high school teachers throughout the state of Maine.

5.2.1 Study Goals

The main goal of this paper is to provide an overview of the current frequency and breadth of climate topics covered in Maine middle and high schools. We also attempt to capture attitudes Maine teachers have about climate change and climate change education as well barriers to effective teaching. We expected STEM teachers would present more climate change topics in their classes, be more knowledgeable about climate change topics, and indicate a greater preference for increased climate change education and professional development than non-STEM teachers. Using this information, we provide recommendations to further support and promote climate education.
5.3 Methods

The online survey was administered using Qualtrics software (Qualtrics, 2013) through the University of Maine system. Survey invites were sent out via email in spring 2014 and left for 3 weeks, with two weekly email reminders in between. Survey questions were expanded from questions used in Wise’s (2010) study of Colorado teachers. Details on original survey questions and response choices can be found in Appendix B. The survey tool included up to 41 questions addressing areas such as teaching content, barriers, attitudes, and demographics. Those teaching climate change were presented with the most questions. Participants were given the option to skip any questions they chose not to answer and were given the opportunity to enter for a chance for 1 of 5 $75 Amazon gift certificates. Participants were also given the opportunity to enter their contact information for notification of an upcoming curriculum-driven climate science workshop for teachers. Contact information for each of these was kept separate from survey data.

Attempted contacts were made via email for all Maine 6-12 grade teachers (n=2399) with contact information obtained from the Maine Department of Education website (Maine Department of Education, n.d.). The number of teachers who indicated that they taught some type of science course (n=962) was less than half of the total teachers we attempted to contact. The total response rate was 15% (n=369) of the contacted teachers.

To determine the differences between disciplines, teachers were divided into three groups: those that only teach STEM courses, which included biological, chemical, or physical sciences (n=231), those that only teach other subjects, termed non-STEM in this study (n=70), and those that teach both types of subjects (n=68), whose responses generally fell between the STEM and non-STEM groups and are not presented in this manuscript (Table 5.1). Data was queried using the R software package (R Core Team, 2015), with figures created using Microsoft Excel.
<table>
<thead>
<tr>
<th>GROUP</th>
<th>STEM (n= 231)</th>
<th>Non-STEM (n=70)</th>
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**Table 5.1.** Subjects taught by participants in the online survey (n=369). Italicized subjects indicate subjects self-identified by the participants by “fill in the blank”, while normal text indicates default survey options.

### 5.4 Results and Discussion

#### 5.4.1 Demographics

The demographics of respondents are grouped together to provide a broad picture of participants.

Teachers were mostly evenly dispersed between the age groups 35-44 (26%), 45-54 (25%), and 55-64 (28%), with younger teachers accounting 16% of respondents (n=329). There were nearly twice as many female respondents (66%) as male (34%, n=328). Most teachers had a Master’s (59%) or bachelor’s degree (34%). Political party and religious views spanned a broad spectrum, with the independent leaning democrats (Fig. 5.1) and Protestant (e.g. Baptist, Methodist) or Roman Catholic the most dominant self-identifications (Fig. 5.2). The teachers were evenly dispersed among grade levels (Fig. 5.3), and taught a wide variety of subjects, with a majority of identified subjects classified as STEM-related (Fig. 5.4).
Figure 5.1. Self-identified political views of teachers. Responses indicated for all teachers (n=324, STEM=204, non-STEM=61, both=59).

Figure 5.2. Self-identified religious views of teachers. Responses indicated for all teachers (n=324, STEM=203, non-STEM=61, both=60).
Figure 5.3. Grade levels taught by survey respondents. Responses indicated for all teachers (n=368, STEM=231, non-STEM=70, both=67).

Figure 5.4. Subjects taught by survey respondents. Responses indicated for all teachers (n=368, STEM=231, non-STEM=70, both=67).
5.4.2 Climate Change Topics in Classes

We asked the teachers a series of questions to assess how climate change is being taught in Maine middle and high schools. The majority of each STEM and non-STEM teachers indicated that they taught climate change occasionally across all their classes (Fig. 5.5). For those that taught climate change, they did so because they thought it was important (Fig. 5.6). The majority of STEM teachers indicated the Next Generation Science Standards (NGSS; Next Generation, n.d) were a reason they taught climate change, with less than half indicating that following curriculum standards was a reason. The state of Maine was a lead partner in developing the NGSS and although they are not yet officially adopted state standards many teachers chose to follow them. A minority of non-STEM teachers indicated curriculum standards were a reason they taught climate change, suggesting that the majority of non-STEM teachers are covering climate change topics that do not fall within their curriculum standards because they feel it is important.

![Figure 5.5](image.png)

**Figure 5.5.** Frequency climate change is taught across all classes. Responses grouped by STEM (n=229) and non-STEM (n=70).
Climate change was taught most frequently in environmental science and earth science classes, with the majority of teachers instructing about climate change at least a few times a year, with less than 6% indicating that they taught about climate change rarely or never (Fig. 5.7). Climate change was taught by at least 10% of teachers more than a few times a year across all subjects.

Climate change topics were categorized in 3 ways for analyses: a) topics related to 1. climate-related drivers or 2. components of the climate system; b) topics related to ecosystem effects of climate change; c) topics related to human effects or human impacts of climate change. Global warming was the climate-related driver topic covered by the majority of all teachers, while biogeochemistry was the climate-related component topic covered the least (Fig. 5.8a). Sea level rise and glacier melt were the climate-related environmental effect topics covered the most by STEM teachers, while animal/plant extinctions and storms/ hurricanes were the topics covered the most by non-STEM teachers (Fig. 5.8b). Human causes was the only climate topic categorized as “human-related” to be covered by the majority of each STEM and non-STEM teachers (Fig. 5.8c). Discussions on climate change impacts on society were more likely to be covered by non-STEM teachers, as were most other topics categorized as human-related. Heat waves were least likely to be talked about by non-STEM teachers and national security by STEM teachers. National security was a topic receiving minimal coverage by all teachers.
Figure 5.6. Reasons for teaching about climate change. Responses grouped by STEM (n=197) and non-STEM (n=42).

Admittedly, the categorization of topics is somewhat subjective between environmental and human effects (5.8b, c). For example, although sea level rise has human effects, we categorized it as an environmental effect. However, this coarse attempt to categorize topics is a first step to identify possible reasons varying climate change topics are being covered by different teachers.
**Figure 5.7.** Frequency climate change is taught in each class. Total responses (n) indicated in parentheses for each subject. Responses indicated for all respondents (n=364, STEM=226, non-STEM=70, those teaching both categories of classes = 68).
Figure 5.8. Climate-related topics covered or discussed in classes. Topics were related to the following:

a. drivers or components; b. ecosystem effects; c. human effects. Responses indicated for all respondents (n= 237) grouped by non-STEM (n=41), and STEM (n=196).

5.4.3 Teacher Attitudes toward Climate Change

Teachers were presented a series of statements addressing their attitudes toward various climate change topics and were assessed by their levels agreement with each statement. Both STEM and non-STEM teachers agreed with a series of statements related to the severity of climate change impacts,
with the majority of teachers in both groups agreeing with statements across all topics (Fig. 5.9).

Teachers had highest agreement that climate change is already a serious problem. Teachers also identified human impacts as the biggest drivers of recent climate change and the relationship between climate change and recent extreme weather events. The two topics related to rapid and abrupt climate change were where agreements between STEM and non-STEM teachers most differed, with STEM teachers were more likely to agree with statements related to abrupt climate change and tipping points.

![Bar Chart: Agreement with Climate Statements]

**Figure 5.9.** Agreement with the following climate statements. Results are shown for teachers who indicated that they agree with the climate statements. Other choices were not sure or disagree. Responses indicated for and STEM (n=207) and non-STEM (n=62) teachers.
We combined STEM and non-STEM teachers into a single group to examine which societal issues Maine teachers were most concerned about. Teachers indicated that climate change was a major concern, second only to quality of the environment (Fig. 5.10). Over 90% of teachers are at least moderately concerned about climate change, with nearly 60% very concerned about it. The majority of Maine teachers are also very concerned about poverty and energy prices. Teachers were least concerned about topics such as the size and power of the federal government and illegal immigration.

These results

STEM and non-STEM teachers had similar attitudes about climate change education, with nearly all teachers agreeing that students should learn about climate change in school (Fig. 5.11). Over 90% of each group believed that students should learn potential climate change solutions, with slightly more non-STEM teachers in agreement. The biggest topics of disagreement between groups were: 1. personal contributions to climate change, for which 10% more STEM teachers agreed with, and 2. whether some areas of the world would benefit from climate changes, for which 17% more STEM teachers agreed (Fig. 5.11).
Figure 5.10. Level of concern for each of the following societal issues. Responses indicated for all teachers (n=325) who taught STEM courses (n=206), non-STEM courses (n=60), and those who taught courses in both STEM and non-STEM categories. (n=59).
Figure 5.11. Agreement with the following attitude statements about climate change. Results are shown for teachers who indicated that they agree with the climate statements. Other choices were not sure or disagree. Responses indicated for STEM (n=207) and non-STEM (n=62) teachers.

Teachers indicated that climate change is an interdisciplinary topic, choosing among a broad range of topics they thought important for students to learn in public school. The majority of teachers in both groups indicated that all of the proposed climate topics were important for students to learn (Fig. 5.12a, b, c). Nearly all teachers indicated that greenhouse effect, global warming, impact on society, human causes and human health were important for students to learn. There were larger discrepancies between teacher groups for specialized topics such as biogeochemistry, which involves biological
chemical processes that govern the composition of environment. Meanwhile, topics that may be more familiar to most teachers, such as related to biodiversity, the variety and variability of species, and ecosystems, had high agreement between groups. We also note some inconsistencies for what teachers believe should be taught and what is being taught. For example, the majority of teachers think that national security should be taught (Fig. 5.12), yet few teachers cover this topic (Fig. 5.8). The majority of teachers in each group indicated climate change should be taught in 7 of the 15 offered subjects (Fig. 5.13). However, there were some differences in which subjects had higher agreement for STEM or non-STEM teachers. For example, STEM teachers were in higher agreement for teaching climate change in chemistry, biology, and physics, while non-STEM teachers had higher agreement for other sciences, geography, and social studies.
Figure 5.12. Climate system topics that are important for high school students to learn. These are the combined responses of “Very important” and “Somewhat important”. Climate components were related to the following: a. drivers or content; b. ecosystem effects; c. human effects. Responses indicated for all teachers (n=334) who taught STEM subjects (n=208), non-STEM subjects (n=67), and those who taught courses in both STEM and non-STEM categories (n=59).
Figure 5.13. Subjects in which Maine students should learn about climate change. Responses indicated for STEM (n=210) and non-STEM (n=67).

5.4.4 Barriers

A series of questions addressed barriers to effective climate education. Time was the biggest barrier for teachers of both groups (Fig. 5.14). All barriers were greater for non-STEM teachers, including resources, familiarity with topic, and curriculum standards. The majority of STEM teachers identified resources as a
barrier, while nearly half of STEM teachers identified topic familiarity as a barrier, making it a major barrier for effective climate education for both STEM and non-STEM teachers. A significant minority of both groups (from nearly 1/4 - 1/3 of teachers) indicated fear of scaring students or outside pressure as barriers. Personal choice was a barrier to nearly half of non-STEM teachers, and nearly 20% of STEM teachers. This question had the option for an open-ended response for the “other” category, with a total of 19 teachers writing detailed responses. Based on preliminary analysis, the largest group of these answers appear related to curriculum fit (37%). However, there were a few polarized responses such as: “I’m not sure that in this area there’s consensus on whether or not any recent changes in the climate are not anything more than a cyclical event” -STEM teacher; “I’m a very liberal minded person teaching in a very conservative minded community. Climate change is very important to me personally, but to teach it…would directly contradict what is taught in many of our students’ homes” -STEM teacher; “Bias...as reflected here”-teacher who teaches both STEM and non-STEM subjects (results not presented for this group). Although the largest source of outside pressure came from parents, only a small minority of teachers indicated that pressure against teaching climate change was a barrier for them (Fig. 5.15). Similarly, a minority of teachers indicated they felt pressure to teach climate change coming mainly from other teachers, while pressure from students appeared to be both for and against teaching climate change.
To dive deeper into student pressure, we examine another question that asked “Do your students express opinions about learning about climate change in school?” followed by an open-ended response detailing those opinions. The majority of teachers indicated that their students do express opinions on learning about climate change (STEM teachers = 65%; non-STEM teachers = 76%). Detailed responses on these opinions were provided by 124 teachers. Preliminary analysis suggests that nearly half of these responses indicate students were concerned or engaged with climate change, and nearly 1/3 of respondents indicated their students expressed varying opinions. Smaller minorities of students express disbelief of climate change, similar to beliefs shared by their parents or other teachers.
Figure 5.15. Outside pressure related to teaching climate change. Responses indicated for all teachers (n=339), who taught STEM courses (n=210), non-STEM courses (n=67), and those who taught courses in both STEM and non-STEM categories (n=62).

Teachers were presented with the following when asked about best teaching practices related to the conflicting viewpoints: “Scientists are in 97% agreement that climate warming is influenced by humans. Yet surveys indicate that Americans are still skeptical that changes are caused by humans.” Most STEM and non-STEM teachers identified the following as the best teaching practice: that all claims should be discussed, with scientific evidence emphasized (Fig. 5.16). Yet, nearly 1/3 of non-STEM teachers thought that all conflicting viewpoints should be presented for the student to decide, nearly 3 times the proportion of STEM teacher responses. A small proportion of each group, again led by non-STEM teachers, believed that discussion be exclusively focused on the scientific consensus. Finally, a small proportion of mostly non-STEM teachers indicated that teachers should not teach that humans can alter climate change.
Some barriers to teaching climate change include those related to any subject, such as time, resources, and curriculum standards. Others are specific to polarizing topics such as evolution, and include barriers such as presenting unbiased scientific evidence and outside pressures (Griffith and Brem, 2005; Wise, 2010). Maine teachers appear to face similar outside pressure against teaching climate change as the 4.4% found by science teachers across the U.S (Plutzer et al., 2016). However, as the current study focused on all teachers, we believe the barriers against teaching climate change, especially from parents, may be heightened for Maine teachers. Further, other studies have shown that the serious nature of climate change may frighten some students (Liverman et al., 2010), a concern shared by Maine teachers. The barriers identified in this study can have a large impact on teaching effectiveness and may even be more common than indicated. For example, a number of teachers...
indicated parent and community beliefs relate to student beliefs, with a majority of students expressing opinions on climate change. Although opinions may not have been categorized as pressure against teaching, these beliefs and opinions likely have an impact on effective teaching.

5.4.5 Knowledge and Misperceptions

Unfamiliarity with climate topics and misperceptions can also be barriers to effective climate education. We asked a series of questions addressing common misperceptions and teacher knowledge by asking respondents to self-identify comfort levels, pooled as “very” and “somewhat comfortable” for a variety of climate-related topics. A majority of teachers agreed with the common misperception that the ozone layer was related to recent global temperature increases, with 74% of non-STEM teachers and 53% of STEM teachers in agreement (Fig. 5.17). Nearly 1/4 of STEM teachers believed the misperception that human carbon dioxide emissions were a tiny fraction of the total, with slightly less non-STEM teachers agreeing. Most teachers indicated they were comfortable with their knowledge about the greenhouse effect and global warming (Fig. 5.18). The majority of STEM teachers were at least somewhat comfortable with all topics related to climate drivers or ecosystem effects except for biogeochemistry (Fig. 5.18a, b). STEM teachers also indicated higher knowledge of human-related topics such as human causes and human health, while non-STEM teachers had higher knowledge of impact on society and national security (Fig. 5.18c). National security was among the topics for which teachers in each group felt least knowledgeable. A minority of non-STEM teachers felt comfortable with the more science-based topics of climate change such as atmospheric chemistry and Earth’s radiative balance. The only topics a majority of STEM teachers indicated they felt very comfortable with were the greenhouse effect and biodiversity. However, there were no suggested topics a majority of non-STEM teachers indicated they felt very comfortable with (results not shown).
Figure 5.17. Agreement with the following climate misconceptions. Responses indicated for STEM (n=207) and non-STEM (n=62) teachers.
Figure 5.18. Comfortable with knowledge of different climate topics. Topics were related to the following: a. drivers or content; b. ecosystem effects; c. human effects. Responses were pooled for “very” and “somewhat comfortable” for each group. Responses indicated STEM (n=186) and non-STEM (n=41) teachers.

Survey results indicate Maine teachers had above average knowledge on several climate-related topics. For example, almost all Maine teachers agree that the planet is warming due to human causes, much higher than the 42% of the U.S. populations, which includes 27% of Americans that do not
recognize the Earth is warming (Pew Research, 2013). However, there only two topics STEM teachers felt they were very comfortable teaching, and several topics that non-STEM teachers were not even somewhat comfortable with, including the Earth’s radiative balance and biogeochemistry. Although these topics are certainly beyond what is covered in most subjects, a general understanding of how these components relate to climate change, especially in terms of misperceptions and faulty arguments against climate change and human-related drivers, may be helpful for teachers across disciplines.

Our results also show that Maine teachers share some widespread misperceptions. For example, the majority of Maine teachers share the misperception of the proposed relationship between the ozone layer and global temperature rises. Wise (2010) revealed that a majority of science teachers in Colorado provided formal instruction related to “the hole in the ozone contributing to global warming”. Although we did not test formal instruction, a slight majority of STEM teachers and nearly 3/4 of non-STEM teachers agreed with this fallacy. Further, we consider some misperceptions shared by even a small minority of teachers to be alarming and have potentially large implications. For example, nearly 1/5 of STEM teachers and 1/4 of non-STEM teachers mistakenly believe that most scientists disagree about the causes of recent climate change. Although not directly tested, Maine teachers may be above the national average, where more than half of science teachers are unaware of the high percentage of scientific agreement of human impacts being a main cause of climate change (Plutzer et al., 2016). However, this misunderstanding by even a minority of teachers is particularly disturbing if teachers are misrepresenting the scientific consensus to students. Further, misperceptions that climate change will not happen for hundreds of years or that increasing carbon dioxide has little effect on the climate may instill severe misunderstandings of climate change to a great number of students, leading to inaction and maladaptation. Fortunately, a high percentage of both STEM and non-STEM teachers indicated that they were interested in professional development on topics of climate change (Fig. 5.19). However, results suggest that survey respondents may be unrepresentatively concerned about climate change and
knowledgeable about climate topics and the role of human impacts. We find the incidence of misperceptions especially alarming as we suspect the larger teaching community may have less concern and climate knowledge and likely have a higher incidence of misperceptions.

![Percentage of teachers interested in professional development on climate change. Responses indicated for all teachers (n= 329). Who taught STEM (n=205) and non-STEM (n=64).](image)

**Figure 5.19.** Percentage of teachers interested in professional development on climate change. Responses indicated for all teachers (n= 329). Who taught STEM (n=205) and non-STEM (n=64).

5.5. Conclusions and Recommendations

In conclusion, Maine teachers view climate change as a major concern that is already being addressed across multiple disciplines in schools. However, teachers feel like a broad scope of topics are important for students to learn across a wide range of subjects, with more frequency and breadth than is currently being covered. Maine teachers seem to have a clearer understanding about climate topics and the scientific consensus of human causes of global warming than the rest of the country (compared to results from Plutzer et al. 2016). However, this study identifies the gaps in climate change content in classes and teacher misperceptions. The urgency and impacts of climate change require that teachers have a thorough understanding of climate change drivers and implications to share with their students, the future decision-makers who will need to address these challenges. Teachers want to learn more about climate change and ensure related topics are covered broadly over multiple disciplines. We
highlight recommendations to support effective and comprehensive coverage of climate change education in Maine schools.

Professional development directed at three main areas would target some of the barriers to effective teaching found by this study. First, misperceptions should be met with supporting scientific evidence to clarify confusion. Second, workshops or teaching materials should target topics for which teachers identified being less comfortable in their knowledge levels. Third, topics that teachers identified as important for students to learn about but are not currently covered to a great extent should be prioritized. As an example, national security is an area where there is a mismatch between attitudes and practice that may be related to knowledge or comfort level with this topic.

Although increased professional development may be a solid strategic starting point to help support climate change education, study results emphasize the interdisciplinary nature of climate education, which will be a difficult challenge to meet. Results suggest that the interdisciplinary nature of climate change is also a major reason for the disconnect between topics teachers believe important for students to learn and what is being taught. For example, the human-related topics were identified by many teachers as among the most important for students to learn about; however, these are among the least likely topics currently covered in classes by either STEM and non-STEM teachers. Providing linkages between what is covered in various subjects can help ensure more comprehensive coverage. The importance of interdisciplinary linkages for STEM education is already known. For example, Keller (2012) details how STEM education should be interdisciplinary and meaningful for students. Climate change may be the ideal topic to link multiple disciplines, due to the interdisciplinary nature of climate drivers and impacts, as well as the significant local and global effects of current and future climate change. Further, climate change education fits very well with several of the “deeper learning” skills such as adaptability, complex communication, and systems thinking referred to by Keller (2012). However, the
interdisciplinary nature of climate change goes beyond STEM education. As challenging as understanding interdisciplinary linkages can be, we underscore how comprehensive climate change education will likely only occur across STEM and non-STEM subjects.

Finally, linking teachers with solutions and adaptation strategies about climate change can help alleviate some of the fear students may feel when presented with this complicated problem. Some teachers have indicated that their student feel hopeless or wonder what they can do when discussing climate change. Teachers can be connected to a number of resources that offer adaptive and mediating actions. Discussion could also focus on local effects and adaptation strategies to empower students and help develop preparedness.
CHAPTER 6
CONCLUSIONS

This research took multiple approaches to understand how planktonic diatoms in Lake Superior are related to climate-driven physical changes in the lake. By investigating changes in contemporary abundances of *Cyclotella sensu lato* species in Lake Superior in relation to climate-driven change and other environmental variables, I found that relationships between planktonic diatoms and environmental variables in Lake Superior are complex and synergistic. Although changes in some taxa may be related to climate-driven physical changes, these relationships are weaker than relationships with other variables such as changing nutrient concentrations. By investigating changes in diatom assemblages before, during, and after the previous warming period of the Medieval Climate Anomaly (MCA), the importance of multiple modern stressors was supported by the lack of diatom change in the paleolimnological record. These findings also supported that environmental changes over the past century are leading to novel shifts in modern diatom communities, with no analogue to changes during a past warm, dry period with minimal anthropogenic impact. By investigating paleolimnological changes in Siskiwit Lake during the MCA, I found changes in the diatom community related to decreased benthic diatoms, suggesting drought led to decreased water levels in Siskiwit Lake. This suggests the importance of lake size in mediating diatom community response to climate-driven change, while suggesting that the climate-driven changes in the region differed than those occurring with contemporary warming.

In chapter 2, I found distributions of *Cyclotella sensu lato*, a dominant group of planktonic diatoms in Lake Superior, are related to multiple physical and chemical variables. Nutrients were important in explaining abundances of all tested species, particularly phosphorus, nitrate, and silica. Relationships with climate-driven physical change were found for two taxa: *D. pseudostelligera*, with increased abundance related to higher light, and *L. ocellata*, with increased abundance related to lower temperature, but only in combination with other variables. No relationships were found with tested
species and thermocline depth in Lake Superior. The limited relationships with climate-driven physical changes may be due to the increased importance of stoichiometric imbalance in the system (Sterner, 2011) and high variability of thermocline depths in large lakes (Austin, 2013; Fee et al, 1996) leading to greater variation in light availability than in smaller lakes (Boeff et al. 2016). The relationships with environmental variables suggest ecotype formation of *Cyclotella sensu lato* species in Lake Superior, underscoring Stoermer’s (1993) warning of applying environmental relationships developed for diatoms in other systems.

In Chapter 3, I found that diatom communities did not significantly change due to the warm, dry conditions of the MCA. This is compared to the sedimentary record post-1800, where the most notable changes in the sedimentary diatom community occurred in the past century, simultaneously with other anthropogenic impacts, including decreased phosphorus (Dove and Chapra 2015) and increased nitrate (Sterner et al. 2007). Diatom communities may have been largely unaffected during the MCA due to a lack of other anthropogenic impacts that are occurring concurrently with contemporary warming. Post-1800 increases in taxa such as *D. pseudostelligera* and *L. delicatula* that are related to changes in nutrients and conductivity in modern monitoring samples suggest that modern diatom communities in Lake Superior experience novel environmental conditions. The changes in environmental variables during the MCA do not appear large enough to have a notable effect on the diatom community, suggesting the synergistic effects of multiple variables are related to novel modern shifts.

In chapter 4, I found that sedimentary diatom community changes in Siskiwit Lake during the MCA support a response to previous warming with minimal anthropogenic impact, particularly lower lake levels due to drought. A lack of change in planktonic diatom species related to different light regimes suggests that community changes were not related to changes in thermal structure. Further, a diatom inferred mixing model did not show significant changes in epilimnion depth before or after the MCA. However, notable and sustained decreases in periphyton abundance coincided roughly with the
start of the MCA. This is contrasted with the lack of diatom community change in Lake Superior during the MCA where lake level decreases would likely not have the magnitude of benthic habitat change as in Siskiwit Lake.

The multiple approaches in chapters 2, 3, and 4, build upon our understanding of the effects of climate-driven changes on Lake Superior planktonic diatom communities. Results from chapters 2 and 3 suggest the importance of multiple anthropogenic impacts driving modern diatom changes, using evidence from both modern monitoring data and the paleolimnological records. Chapter 4 provides insight into potential climatic changes throughout the Lake Superior region during the MCA. Inferences from the Siskiwit Lake record in chapter 4 suggest that the climate-driven physical effects during the MCA were potentially different than those today. For instance, warming temperatures during the MCA may not have been as dramatic as contemporary warming in the region. The primary driver of diatom change in Siskiwit Lake during the MCA appears to be drought. The lack of change in planktonic diatom species indicates relatively stable epilimnion depths during the MCA, suggesting a less windy period than with modern warming. This lack in thermal structure change may be another reason for the lack of diatom community structure change in Lake Superior during the MCA.

As we better understand the effects of climate change on environmental quality, we need to place this understanding in context of the complex, political, and polarizing role of climate change for society. Better understanding does not inherently lead to better management, and it is important to ensure alignment of scientific findings with society’s understanding and desire to act. Thus, chapter 5 attempted to better understand formal climate change education in Maine public middle and high schools and identify recommendations for more effective teaching.

Maine teachers view climate change as a major concern and a topic that should be addressed in multiple disciplines in schools. Although already teaching various climate-related topics across multiple subjects, teachers indicated a desire for an increased variety of interdisciplinary topics to be taught
across multiple subjects. Professional development addressing misperceptions, knowledge gaps, and topics that teachers identified as high priorities for students to learn, would help create a more climate-literate public. Strengthening interdisciplinary links to ensure a comprehensive climate-change related curriculum across STEM and non-STEM subjects is also necessary to fill several topic gaps. Finally, providing students with positive solutions and adaptation strategies can help meet the challenges of climate change.


Juggins, S. (2017) rioja: Analysis of Quaternary Science Data, R package version (0.9-15). ([http://cran.r-project.org/package=rioja](http://cran.r-project.org/package=rioja)).


APPENDIX A: Percent relative abundance benthic diatoms and planktonic diatoms for the Post-1800 Core

Figure A. Stratigraphic plot showing the percent relative abundance benthic diatoms and planktonic diatoms for the Post-1800 Core
# APPENDIX B: Teacher Survey Questions and Answer Choices

Table A. Original question format as presented in the survey with answer choices.

<table>
<thead>
<tr>
<th>Question</th>
<th>Answer choices</th>
</tr>
</thead>
<tbody>
<tr>
<td>Q2. Generally speaking, do you consider yourself to be a(n): (PLEASE CHECK ONE BOX)</td>
<td>Strong democrat; Not so strong democrat; Independent leaning democrat; Independent; Independent leaning republican; Not so strong republican; Strong republican; Other; Refused</td>
</tr>
<tr>
<td>Q2. Is your religious background...? (PLEASE CHECK ONE BOX)</td>
<td>Protestant (e.g. Baptist, Methodist); Roman Catholic; Jewish; Other Christian; Other non-Christian/-unspecified; Agnostic/ Atheist; None; Other</td>
</tr>
<tr>
<td>Q3. What grade(s) do you teach? (PLEASE CHECK ALL THAT APPLY)</td>
<td>Grade 6; Grade 7; Grade 8; Grade 9; Grade 10; Grade 11; Grade 12</td>
</tr>
<tr>
<td>Q4. What subject(s) do you teach? (PLEASE CHECK ALL THAT APPLY)</td>
<td>Biology; Earth Science; Physics; Chemistry; Social Studies; History; Geography; Science (other); English/Lit; Art; Health; Environmental Science; Math; General Science; Economics; Other</td>
</tr>
<tr>
<td>Q5. Why do you teach about climate? (PLEASE CHECK ALL THAT APPLY)</td>
<td>Other Standards; Curriculum Standards; Part of NGSS Standards; I feel it is Important</td>
</tr>
<tr>
<td>Q6. How much do you teach about or discuss climate change in any of your classes? (PLEASE CHECK ONE BOX)</td>
<td>Not at all; Occasionally; Frequently</td>
</tr>
<tr>
<td>Q7. How frequently do you teach or discuss climate change in each of / your classes? (PLEASE CHECK ONE BOX IN EACH ROW)</td>
<td>Never; Rarely; A few; times/year; 5-9 times/yr; Several times/month; Several times/week</td>
</tr>
<tr>
<td>Q8. Which of the following topics related to climate do you teach or discuss in your class(es)? (PLEASE CHECK ALL THAT APPLY)</td>
<td>Heat waves; Drought; Storms/hurricanes; Floods; Vector-borne disease; Wildfires; Coral bleaching; Ocean acidification; Glacier melt; Sea ice melt; Human migration; Water scarcity; Food scarcity; Sea level rise; Air quality; Human conflict; Animal/plant extinctions; Earth's radiative balance; Greenhouse effect; Human causes; Global warming; Human health; Biodiversity/ecosystems; Atmospheric chemistry; Historical climate; National security; Biogeochemistry; Abrupt climate change; Impact on society; Carbon dioxide</td>
</tr>
</tbody>
</table>
Q9. Please indicate your level of agreement with the following: (PLEASE / CHECK ONE BOX IN EACH ROW) | Strongly agree; Somewhat agree; Not sure; Somewhat disagree; Strongly disagree
---|---
Q10. Please identify your level of concern with the following (PLEASE / CHECK ONE BOX IN EACH ROW) | Very concerned; Moderately concerned; A little concerned; Not at all concerned
Q11. Please indicate your level of agreement with the following: (PLEASE / CHECK ONE BOX IN EACH ROW) | Agree; Not sure; Disagree
Q12. How important do you think it is for high school students to learn the following climate system component topics? (PLEASE CHECK ONE BOX IN EACH ROW) | Very important; Somewhat important; Less important; Not important; I don’t know
Q13. In which school subject(s) should Maine students learn about climate change? (PLEASE CHECK ALL THAT APPLY) | Biology; Earth Science; Physics; Chemistry; Social Studies; History; Geography; Science (other); English/Lit; Art; Health; Environmental Science; Math; General Science; Economics; Other
Q14. What barriers to teaching climate change do you perceive? (PLEASE CHECK ONE BOX IN EACH ROW) | Major barrier; Minor barrier; Not a barrier
Q15. Have any of the following pressured you about teaching climate change? (PLEASE CHECK ONE BOX IN EACH ROW) | Pressure to teach climate change; No pressure; Pressure against teaching climate change
Q16. Scientists are in 97% agreement that climate warming is influenced by humans. Yet surveys indicate that Americans are still skeptical that changes are caused by humans. What do you think are best teaching practices to respond to potential conflicting classroom viewpoints about climate (check one box) | Teachers should not teach that humans can affect climate change; Discussion should only be about the scientific consensus; Other practices; Teachers should acknowledge and/or allow arguments brought forth by climate change skeptics; All sides should be presented to let the students decide; All claims should be discussed, with an emphasis on evaluating the scientific evidence
Q17. Please indicate your level of agreement with the following: (PLEASE / CHECK ONE BOX IN EACH ROW) | Agree; Not sure; Disagree
Q18. Rate your comfort level with your knowledge of the different climate topics: (PLEASE CHECK ONE BOX IN EACH ROW) | Very comfortable; Somewhat comfortable; Neutral; Somewhat uncomfortable; Very uncomfortable
Q19. Are you interested in professional development on climate change? (PLEASE CHECK ONE BOX) | Yes; No
BIOGRAPHY OF THE AUTHOR

Amy Kireta was born in Steubenville, Ohio on February 6, 1975. She was raised in Toronto, Ohio and graduated from Toronto High School in 1993. She attended the University of Akron and graduated in 1996 with a Bachelor’s degree in Psychology. She returned to biological sciences to pursue a Master’s degree in Aquatic Ecology, studying the effects of invasive dreissenid mussels and round goby on algal communities, graduating from Bowling Green State University in 2001. From there, she moved to northern Minnesota to work on environmental variables driving diatom changes in the Great Lakes and large U.S. rivers with the University of Minnesota Duluth’s Natural Resource Research Institute, at the Ely Field Station, starting under the direction of the late, great Dr. John Kingston. After receiving her degree, Amy will be returning to Minnesota to work as the Outreach Specialist for the Swenson College of Science and Engineering at the University of Minnesota Duluth, bringing her passion to support STEM education and her desire to share excitement for science. Amy is a candidate for the Doctor of Philosophy degree in Ecology and Environmental Science from the University of Maine in May 2018.