Abstract

The lack of long-term data on the response of boreal lakes to climate change has been seen as an impediment to the assessment of the vulnerability and risks that northwest Ontario faces in light of future climate change. The overall objective of this thesis was to provide a centennial-to-multi-millennial perspective on the impacts of past climate change on boreal lakes in northwest Ontario. Second chapter has resulted in the development and application of a paleoecological model, based on the modern-day distributions of chironomid assemblages to lake depth, in a small boreal lake. Changes in the chironomid assemblages provided significant and strong support for the diatom-based inference techniques that estimated lower water levels, and consequently drought-like conditions, throughout northwest Ontario during the Medieval Climate Anomaly. Third chapter provides evidence that supports an early-to-mid-Holocene period of aridity, with reduced water levels across the boreal region in northwest Ontario. This conclusion was based on changes in diatom assemblages in well-dated sediment cores from three lakes spanning a distance of ~200 km across the boreal forest region. During the early-to-mid-Holocene, benthic diatom taxa predominate in all cores, suggesting lower lake levels by ~2-5 m, when compared to modern-day diatom assemblages from these lakes. Increases in planktonic diatom taxa to greater than 50% of the entire assemblage, occurs beginning ~4500 to 4000 cal yr BP, suggesting positive water balance over the last 4000 years in comparison to the mid-Holocene period. Fourth chapter provides evidence of enhanced primary production and higher abundances of cyanobacteria in three northwest Ontario lakes during the warmer early-to-mid-Holocene in northwest Ontario. This later study was based on changes in lake-water primary production from fossil pigments, spectrally-
inferred chlorophyll a, and diatom assemblages in well dated cores, taken from the main central basin of the three study lakes. The majority of indicators show a coherent pattern of enhanced primary production during the early-to-mid-Holocene period, with elevated concentrations of cyanobacterial pigments in two of the three lakes. If conditions become warmer and drier in the future in northwest Ontario, challenges associated to water quantity and quality should be expected.
Co-Authorship

This thesis is written in manuscript format outlined by School of Graduate Studies and Research. Each chapter is written in the form of specific journal to which paper was submitted or will be submit and contains its own literature cited in the specific format of journal style.

**Chapter 2** (Karmakar et al., 2014, *Quaternary Research*, 81: 251-259) was co-authored with Joshua Kurek, Heather Haig and my supervisor Brian F. Cumming. In this study I was responsible for the collection of all chironomid data, all statistical analyses, and figures. As primary author, I provided all major interpretations, synthesized information, and prepared the manuscript with input from all co-authors. Joshua Kurek was responsible for teaching my chironomid identification. Heather Haig was responsible for diatom study, interpretation and geochronology.

**Chapter 3** (Karmakar et al., *The Holocene*, in press) was co-authored with Kathleen R. Laird and my supervisor Brian F. Cumming. In this study I was responsible for the collection of all diatom data for Gall and Meekin Lake, statistical analyses, making figures and table. As primary author, I provided all major interpretations, synthesized information, and prepared the manuscript with input from all co-authors. Kathleen R. Laird was responsible for diatom counts, interpretation, and geochronology of the near-shore core of ELA Lake 239.

**Chapter 4** (Karmakar et al., in prep) will be co-authored with Peter Leavitt and my supervisor Brian F. Cumming. In this study I was responsible for the collection of all diatom data and fossil pigment for Gall and Meekin Lake, geochronology, all statistical analyses, and all figures. As primary author, I provided all major interpretations, synthesized information, and prepared the manuscript with input from all co-authors.
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of “skype” needs a special thanks that brought my family and dear ones closer during this
long journey and drive away my monotony and helplessness and recharged me with life
to move on…………….
# Table of Contents

Abstract ................................................................................................................................. ii
Co-Authorship ........................................................................................................................ iv
Acknowledgements .............................................................................................................. v
List of Supplemental Figures ............................................................................................ xii
List of Tables ........................................................................................................................ xiii
List of Abbreviations .......................................................................................................... xiv

Chapter 1 General Introduction ......................................................................................... 1
  1.1 Climate change ........................................................................................................... 2
  1.2 Paleoclimatology ....................................................................................................... 3
  1.3 Lakes and climate change .......................................................................................... 6
    1.3.1 Effects on phytoplankton ................................................................................... 8
  1.4 Paleolimnology and climate change .......................................................................... 10
    1.4.1 Diatoms as an indicator of lake-level fluctuation .............................................. 11
    1.4.2 Diatom as indicators of nutrients and lake trophic status ............................... 14
    1.4.3 Fossil pigments as an indicator of primary production .................................... 15
    1.4.4 Midge (Chironomid) and Chaoborus assemblages as biological proxy of lake-level and water quality .......................................................... 17
  1.5 Region-specific context of dissertation .................................................................. 19
  1.6 Broader significance of this thesis .......................................................................... 22
  1.7 Literature cited ......................................................................................................... 23

Chapter 2 Consensus among multiple trophic levels during high- and low-water stands over the last two millennia in a northwest Ontario lake ................................................................. 46
  2.1 Abstract .................................................................................................................... 47
  2.2 Introduction .............................................................................................................. 48
  2.3 Methods ................................................................................................................... 49
    2.3.1 Study site ......................................................................................................... 49
    2.3.2 Surface sample collection and midge processing ............................................ 51
    2.3.3 Assessment of changes in midges over the last 2000 years ............................ 52
    2.3.4 Numerical analyses of surface assemblages ................................................... 54
    2.3.5 Numerical analysis of downcore assemblages .............................................. 55
  2.4 Results ................................................................................................................... 56
    2.4.1 Midge assemblages from the modern surface sediments of Gall Lake .......... 56
Chapter 3 Diatom-based evidence of regional aridity during the mid-Holocene period in boreal lakes from northwest Ontario (Canada) ................................................................. 76
3.1 Abstract ............................................................................................................. 77
3.2 Introduction ..................................................................................................... 78
3.3 Study sites ....................................................................................................... 80
3.4 Methods .......................................................................................................... 82
  3.4.1 Field sampling and core location ................................................................. 82
  3.4.2 Geochronology ........................................................................................... 83
  3.4.3 Laboratory .................................................................................................. 86
  3.4.4 Numerical analysis ...................................................................................... 87
3.5 Results ............................................................................................................. 88
  3.5.1 Meekin Lake .............................................................................................. 89
  3.5.2 Gall Lake .................................................................................................... 92
  3.5.3 Regional patterns in diatom assemblages .................................................... 95
3.6 Discussion ....................................................................................................... 97
  3.6.1 Early to mid-Holocene changes in effective moisture ................................. 100
  3.6.2 Late Holocene changes in effective moisture .............................................. 103
  3.6.3 West to east gradient in effective moisture ................................................ 104
3.7 Conclusions .................................................................................................. 106
3.8 Acknowledgements ......................................................................................... 106
3.9 Literature cited .............................................................................................. 107

Chapter 4 Enhanced Primary Production in Headwater Boreal Lakes during the Early-to-mid-Holocene across Northwest Ontario ............................................................... 116
4.1 Abstract .......................................................................................................... 117
4.2 Introduction .................................................................................................... 118
4.3 Study sites ...................................................................................................... 120
4.4 Materials and Methods .................................................................................. 123
4.5 Results .................................................................................................................. 128
4.6 Literature cited ..................................................................................................... 149

Chapter 5 General discussion and future direction .................................................. 162
5.1 Literature cited ..................................................................................................... 169

Appendix A Pb\textsuperscript{210} and Cs\textsuperscript{137} profile for Meekin and Gall Lake ........................................ 173
Appendix B Analog analysis ....................................................................................... 175
Chapter 2

Figure 2-1. a) Map showing the location of the Winnipeg River Drainage Basin b) Bathymetry of Gall Lake with samples indicated. ........................................................................................................50
Figure 2-2. Diatom-inferred water depths from the Gall Lake near-shore core, five-hundred year periods that provide the framework for the present study .........................................................53
Figure 2-3. Distribution of the relative abundance of the dominant (>3%) chironomid taxa, the Chaoborus-to-chironomid index, and the PCA axis-1 scores .................................................................57
Figure 2-4. PCA biplot of chironomid assemblages........................................................................58
Figure 2-5. The relative abundance of the dominant chironomid taxa (>3%) in the 500-year time periods..........................................................................................................................60
Figure 2-6. Summary diagram showing relative abundances and concentrations of the three chironomid assemblage groups .....................................................................................61
Figure 2-7. a) Summary diagram between the relative abundance of profundal chironomid taxa, b) Comparison of summaries of changes in deviation from mean lake depth inferred for both the chironomid and diatom-based models .................................................................63

Chapter 3

Figure 3-1. A) Map showing the location of the three study lakes (Meekin, ELA Lake 239, and Gall Lake). B) Bathymetry map of Meekin Lake showing changes in lake depth and the coring location (black circle); C) Bathymetry of Gall Lake showing changes in lake depth and the coring location (black circle). ........................................................................................................81
Figure 3-2. A) Age-depth model for Meekin Lake and B) for Gall Lake, based on calibrated $^{14}$C dates (Table 1) ............................................................................................................................................85
Figure 3-3. The dominant (>5%) diatom taxa found in a near-shore (depth = 11.4 m) sediment core from Meekin Lake versus cumulative core depth. .................................................................90
Figure 3-4. The dominant (>5%) diatom taxa found in a near-shore (depth = 7.5m) sediment core from Gall Lake versus cumulative core depth. .................................................................93
Figure 3-5. Summary of the changes in diatom assemblages in sediment cores of the three lakes (Meekin, ELA Lake 239, and Gall Lake) west to east.................................................................96
Figure 3-6. Non-metric multidimensional scaling (nMDS) plot of diatom assemblages over the Holocene in: A) Meekin Lake; B) ELA Lake 239; C) Gall Lake. .................................................................99
Figure 4-1. Map showing the location of the three study lakes (Gall Lake, ELA Lake 239 and Meekin Lake) within the Winnipeg River Drainage Basin. .......................................................... 121

Figure 4-2. A) Age-depth model for the sediment cores from Gall Lake and B) for Meekin Lake, based on calibrated ¹⁴C dates (Table 1).................................................................................................................. 129

Figure 4-3. Concentration profile for selected fossil pigments in Gall Lake sediment core over time (cal yr BP).................................................................................................................. 131

Figure 4-4. Concentration profile for selected fossil pigments in ELA Lake 239 sediment core over time (cal yr BP).................................................................................................................. 133

Figure 4-5. Concentration profile for selected fossil pigments in the Meekin Lake sediment core over time (cal yr BP).................................................................................................................. 135

Figure 4-6. Summary of diatom-inferred total phosphorus (TP) values over the Holocene of Gall, ELA Lake 239 and Meekin Lake. Vertical box with zones and subzones represents dominant diatom assemblage (taxon >20%, see supplemental figures for detailed diatom stratigraphy) with major zones defined by constrained cluster analysis. ................................................................. 137
List of Supplemental Figures

Chapter 2
Supplemental figure 2-1. Relationship between observed depth and chironomid-inferred lake depth based on a transect of 31 surface-sediment samples from Gall Lake (Fig. 1B).......................... 75

Chapter 3
Supplemental figure 3-1. Concentrations of diatom taxa found in a near-shore (depth = 11.4 m) sediment core from Meekin Lake versus cumulative core depth................................................................. 114

Supplemental figure 3-2. Concentrations of diatom taxa found in a near-shore (depth = 7.5 m) sediment core from Gall Lake versus cumulative core depth................................................................. 115

Supplemental figure 3-3. Concentration of the dominant planktonic taxa Discostella stelligera versus calibrated age (yr BP)............................................................................................................... 115

Chapter 4
Supplemental figure 4-1. The dominant (>5%) diatom taxa found in Gall Lake sediment core (collected from center of the lake) versus cumulative core depth. .................................................. 158

Supplemental figure 4-2. Concentrations of diatom taxa found sediment core from Gall Lake versus cumulative core depth. 14C-estimated dates are indicated to the left. ........................................... 159

Supplemental figure 4-3. The dominant (>5%) diatom taxa found in sediment core (collected from center of the lake) from Meekin Lake versus cumulative core depth. ................................. 160

Supplemental figure 4-4. Concentrations of diatom taxa found in a sediment core collected from center of the lake from Meekin Lake versus cumulative core depth... ................................. 161
List of Tables

Chapter 3
Table 3.1. Summary of the $^{14}$C-dating results on pollen isolated from selected intervals from the nearshore sediment cores from Gall and Meekin lakes. ................................................................. 84

Chapter 4
Table 4.1. Summary of the $^{14}$C-dating results on pollen isolated from selected intervals from the deepwater sediment cores from Gall and Meekin lakes................................................................. 124
**List of Abbreviations**

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>$^{14}\text{C}$</td>
<td>Radioisotope of carbon (C)</td>
</tr>
<tr>
<td>$^{210}\text{Pb}$</td>
<td>Radioisotope of lead (Pb)</td>
</tr>
<tr>
<td>AMS</td>
<td>Accelerate Mass Spectrometry</td>
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<tr>
<td>ANOSIM</td>
<td>Analysis of similarity</td>
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<tr>
<td>B-P</td>
<td>Benthic- to-planktonic</td>
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<tr>
<td>CA</td>
<td>Correspondence Analysis</td>
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<tr>
<td>Cal yr BP</td>
<td>Calibrated years before present (BP)</td>
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<tr>
<td>CI-depth</td>
<td>Chironomid-inferred depth</td>
</tr>
<tr>
<td>Clam</td>
<td>Classical age depth model</td>
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<tr>
<td>CONISS</td>
<td>Constrained cluster analysis</td>
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<tr>
<td>C to D index</td>
<td>Chrysophyte scale-to-diatom index</td>
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<tr>
<td>DI-depth</td>
<td>Diatom-inferred depth</td>
</tr>
<tr>
<td>DI-TP</td>
<td>Diatom-inferred total phosphorus</td>
</tr>
<tr>
<td>DOC</td>
<td>Dissolved organic carbon</td>
</tr>
<tr>
<td>ELA</td>
<td>Experimental Lake Area</td>
</tr>
<tr>
<td>HPLC</td>
<td>High Performance Liquid Chromatography</td>
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<tr>
<td>KOH</td>
<td>Potassium hydroxide</td>
</tr>
<tr>
<td>IPCC</td>
<td>Intergovernmental Panel on Climate Change</td>
</tr>
<tr>
<td>LOI</td>
<td>Loss on ignition</td>
</tr>
<tr>
<td>MAT</td>
<td>Modern analog technique</td>
</tr>
<tr>
<td>MCA</td>
<td>Medieval Climate Anomaly</td>
</tr>
<tr>
<td>nMDS</td>
<td>non-metric multidimensional scaling</td>
</tr>
<tr>
<td>NW</td>
<td>Northwest</td>
</tr>
<tr>
<td>OM</td>
<td>Organic matter</td>
</tr>
<tr>
<td>PCA</td>
<td>Principal Component Analysis</td>
</tr>
<tr>
<td>PFE</td>
<td>Prairie-forest ecotone</td>
</tr>
<tr>
<td>RMSEP</td>
<td>Root mean square error prediction</td>
</tr>
<tr>
<td>TP</td>
<td>Total phosphorus</td>
</tr>
<tr>
<td>UV</td>
<td>Ultra violet</td>
</tr>
<tr>
<td>WA</td>
<td>Weighted average</td>
</tr>
<tr>
<td>WA_INV</td>
<td>Weighted average-inverse model</td>
</tr>
<tr>
<td>WRDB</td>
<td>Winnipeg River Drainage Basin</td>
</tr>
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Chapter 1

General Introduction

The focus of this dissertation is to use paleoecological approaches to better understand how lakes in the boreal region in northwest (NW) Ontario have changed over time in terms of water quantity and quality. More specifically, I employ techniques to understand changes in lake-level and water quality in NW Ontario, over the Holocene, to provide important possible analogs on how climate change may impact boreal lakes in the future. In this chapter, I introduce: climate change; paleoclimatology; briefly discuss the importance of the effects of climate on lakes; introduce the science of paleolimnology and finally provide a regional context for my study lakes.

My thesis research addresses three main research themes including: (1) a critical examination of the utility of chironomid-based indicators to infer lake-specific changes in water level over the past 2,000 years; (2) a regional examination of the changes in water balance of the boreal region of northwest Ontario over the Holocene; and (3) an investigation of the importance of enhanced lake-water production and cyanobacterial abundance during the early-to-mid Holocene time period that has been inferred to be warmer than present. Chapters 2 through 4 are written in manuscript format for scientific journals, which are then followed by a general discussion (Chapter 5). Chapter 2 investigates changes in chironomid assemblages within Gall Lake over past 2000 years and has been published in Quaternary Research (2014). Chapter 3 of my thesis investigates regional patterns of changes in diatom assemblages from near-shore cores and inferences of changes in lake-level over the past 10,000 years. This paper is accepted in the journal The Holocene. Chapter 4 investigates changes in lake-production over the past 10,000
years using fossil pigments, spectrally-inferred chlorophyll a, and changes in diatom assemblages from deep-water cores from Gall Lake, ELA Lake 239, and Meekin Lake.

1.1 Climate change
Climate change can be defined as “a change in the state of the climate that can be identified by changes in the mean and the variability for an extended period, typically decades or longer” (Intergovernmental Panel on Climate Change, IPCC, 2013). With the onset of the industrial revolution and burning of fossil fuels, the concentration of carbon dioxide (CO₂) and other greenhouse gases in the atmosphere has increased about 40%, and global mean surface temperature has increased 0.8 °C (1.4 °F) since 1900 (IPCC, 2013). The increases in greenhouse gases and their associated radiative forcing are consistent with the observed warming over the last century, and our understanding of how the climate system works. This led the IPCC (2013) to conclude that humans have clearly been the dominant cause of warming since the mid-20th century. The IPCC also concluded that human activities have contributed to global-scale changes in precipitation over land and the intensification of heavy rain fall events. Climate models predict a further increase between 0.3-4.8 °C by the end of the 21st century relative to the 1986-2005 time period (Collins et al., 2013), but with regional variation. Climate models also suggest that changes in precipitation will vary geographically. For example, high-latitude, equatorial and some sub-tropical regions may experience increases in precipitation whereas mid-latitude and some sub-tropical regions may exhibit decreases (Trenberth et al., 2007). Along with changing temperature, region-specific evaporation rates will increase resulting in changes in hydrological balance (Arnel, 1999). Changes in both temperature and precipitation could lead to changes in freshwater ecosystems, as well as water scarcity (IPCC, 2013). Climate change has also impacted
ecosystems, for example, a shift in the migratory pattern of some species, as well as shifts in the species abundances of many terrestrial, freshwater and marine species (IPCC, 2013).

Besides human-induced climate change, other drivers of climate include variations in solar activity, volcanic eruptions and changes in ocean circulation. For example, El Niño-southern oscillation (ENSO) is a major internal climate pattern that has affected the global environment (Royal Society and US National Academy of Science, 2014).

**1.2 Paleoclimatology**

To better understand anthropogenic climate change, it is important to understand long-term environmental changes over centuries to millennia. The climate over the Holocene in Europe has been divided very broadly into three main periods (Warner et al., 2008): the first phase coincide with the ‘Preboreal’ and ‘Boreal’ chronozones from ~11,600 to ~9000 yrs BP; the second phase coincides with the ‘Atlantic’ chronozone, which covers the period from ~9000 to 6000-5000 yrs BP, often called as ‘Hypsithermal’; and the third phase coincides with the ‘Subboreal’ and ‘Subatlantic’ chronozones from ~6000-5000 yrs BP to pre-industrial times, often referred to as ‘Neoglacial’ (Nesje and Dahl, 1993). The ‘Hypsithermal’ is especially relevant to recent warming as in the northern mid-to-high latitude regions experienced warmer conditions due to high summer insolation (Wanner et al., 2008). Evidence of abrupt climate change during the Holocene is known in paleoclimatic studies and has been related to changes in temperature and precipitation patterns (Alley and Agustsdottir, 2005). Several paleoclimatic studies have also provided evidence of large-scale ‘megadroughts’ in North America (Stine, 1994; Woodhouse and Overpeck, 1998; Cook et al., 2004, 2007; Stahle et al., 2011). Although the cause of past droughts is not clearly understood, they have been associated with changes in sea surface
temperature and are thought to be related to variation in oceanic circulation patterns on both the Pacific and Atlantic oceans (Feng et al., 2011).

There is a significant amount of evidence from the interior parts of North America (mainly mid-west) and the Pacific Northwest suggesting that the mid-Holocene was much drier and more arid in comparison to today (Wright et al., 1993; Williams et al., 2000; Thompson and Anderson, 2000), and that lake-levels were low across the North American Great Plains (Last, 1990; Fritz et al., 1991; Vance et al., 1993; Laird et al., 1996). Based on the numerous records, the mid-Holocene time period (mid-west North America) is characterized as warm and dries (Laird et al., 1996). Lake Winnipeg was a closed-basin lake from ~8.2-4.5 cal yrs BP, with the southern basin desiccated (today this basin has a maximum depth of ~11 m) and the parkland border much further to the east (Lewis et al., 2001). Lake Manitoba, which is the fourteenth largest lake in North America, located in the Canadian prairie, northwest of Winnipeg, was also impacted by the mid-Holocene climate. Pollen and mineralogy from lake sediment revealed that it was subject to fluctuating moisture conditions and warmer temperature during that time (~6000-5000 yr BP) (Teller and Last, 1982; Last and Teller, 2002). In the Canadian prairies, a diatom-based study from Oro Lake also suggested arid climatic conditions throughout the mid-Holocene time period (Laird et al., 2007). In two Minnesota lakes, estimated lake-level declines were between ~1-15 m (Cohen et al., 2006), and declines of up to ~10 m were estimated in some Rocky Mountains lakes (Shuman et al., 2009). A multiproxy study from Elk Lake, Minnesota, also provided evidence of the mid-Holocene drought (Dean, 1993; Wright et al., 2004). Several sites in Dakota indicated arid conditions in mid-Holocene period as well (Fritz et al., 1991; Juggins et al., 1994, Laird et al., 1996). For example, Devils Lake in North Dakota experienced a prolonged period of increasing salinity and a low-water stand during the ~8000-4000 yr BP
period (Fritz et al., 1991), Moon Lake in North Dakota also experienced very high salinity conditions during ~7000-5000 yr BP (Laird et al., 1996). Other proxies also indicate warmer and drier conditions during the early-to-mid-Holocene (Forman et al., 2001; Dean et al., 2002; Shuman et al., 2002; Miao et al., 2007), lower water levels and fluctuating condition also observed from Western Alberta from 8000 to 6000 cal yr BP (MacDonald, 1989). According to Kutzbach and Guetter (1986), recurrent widespread drought could be related to high summer insolation that resulted in higher temperature and increased precipitation and evaporation (Lewis et al., 2001). Similarly in northwest Ontario, modeling data showed that lake-level in Lake of the Woods fell below the outlets in Kenora during the mid-Holocene period (~7000-4000 yr BP).

In general, palaeoclimatic records from the Holocene suggest that prolonged droughts were a natural part of the climate system. Over the last several millennia, the Medieval Climate Anomaly (MCA, ~900-1400 AD) has been identified as a time of warm temperatures, with extreme drought-like conditions in many regions of the prairies and western North America (Bradley et al., 2003; Mann et al., 2009). In northwest Ontario, Laird et al. (2012) concluded that the MCA represented a relatively low-water stand in a network of six lakes from NW Ontario over the past 2000 years. However, the magnitude, spatial extent and cause of the MCA in North America are still a subject of active research and debate (Diaz et al., 2011).

Global warming will continue throughout the 21st century due to increases in human derived greenhouse gases (IPCC, 2013) and “therefore may be we are entering into a new era of megadroughts with potentially catastrophic consequences to water supply, agriculture, energy production and for maintaining aquatic environment” (Cook, 2012). The degree and magnitude of future megadroughts caused by human-induced global warming could be different than the past, as the predominant climate forcing is different. However, these records are still important
as they illustrate the sensitivity of the climate system. Past climate variability should be taken into account as we anticipate possible future scenarios on a warmer planet (Overpeck and Cole, 2006). Although the forcing mechanisms of the projected changes due to greenhouse gases are different than the enhanced insolation during the early-to-mid-Holocene, the response of lakes in the past can serve as an indication of the sensitivity of the lakes in this region, and provide a realistic scenario of potential outcome due to climate warming.

1.3 Lakes and climate change

Lakes are important sentinels of climate, but can respond to climate change in many different ways (Schindler, 2009; Williamson et al., 2009a, b). This thesis will focus on the climate sensitivity of temperate, lakes from the boreal region. Important drivers of climate change in boreal regions include increases in air temperatures, changes in seasonality, and variations in precipitation, resulting in direct and indirect effects on lakes. Modelling studies on northern-temperate Wisconsin lakes showed higher epilimnetic temperatures and longer ice-free periods under different global warming scenarios (e.g. 1×CO₂, 2×CO₂ de Stasio et al., 1996). During the 1970s and 1980s, the length of the ice-free season has increased in several sites in northern US and Canada (Comb, 1990; Schindler et al., 1990, 1996a; Hanson et al., 1992; Robertson et al., 1992; Anderson et al., 1996; McDonald et al., 1996). A 150-year analysis of ice-phenology from northern Hemisphere lakes and rivers indicated that ice-on has been delayed at a mean rate of 5.7 days/100 years, and ice-off has been occurring 6.3 days/100 years earlier (Magnuson et al., 2000a). Such changes can influence the onset of thermal stratification and the position of the thermocline (de Stasio et al., 1996). Longer thermal stratification could also affect the status of the oxidized microzone at the water-sediment interface, leading to internal loading of nutrients.
from the sediment (Wetzel, 2001). Changes in physico-chemistry of lakes due to climate change may also result in change in fish habitat and species composition (de Stasio et al., 1996). Also as a result of climate warming on the thermal regimes of lakes, temperate mid-latitude dimictic lakes may become monomictic, and northern latitude monomictic lakes may stratify during the summer months resulting in a dimictic regime (Schindler, 1997b).

Changes in the timing and magnitude of precipitation can also result in changes in temperate region lakes. For example, lower stream flow can decrease chemical exports from catchments (Dillon et al., 1994; Schindler et al., 1996a). During drought periods concentrations of many chemical variables could increase as a result of longer contact time with soils (Schindler et al., 1992; Hinton et al., 1997; Webster et al., 1996). Reduced stream flow as a result of decrease in precipitation and/or warmer temperatures can result in longer water retention times and higher concentrations of ions within lakes (Schindler, 1996a, b). For example, water renewal time increased about four-fold in Experimental Lake Area (ELA), northwest Ontario, Canada, lakes with relatively small climate change (Schindler et al., 1996a). A decline in precipitation has been shown to reduce runoff and there by decline dissolved organic carbon (DOC) in Canadian Shield lakes (Dillon et al., 1996, Schindler et al., 1996a, b). As a result of declines in DOC, water transparency and light penetration increased (especially UV penetration), and euphotic zone also increased (Schindler et al., 1990, 1992, 1996a, b) in ELA lakes. Alternatively, increases in precipitation with temperature changes may influence stream and subterranean flow, which will increase major ions, nutrients, and DOC in a lake (Adrian et al., 2009; Vincent, 2009; Zhang et al., 2010). Increased concentration of the coloured fraction of dissolved organic matter (CDOM) within a lake can have positive as well as negative effects on aquatic photosynthesis (Vincent et
al., 2007). For example, CDOM could help in absorbing photo-synthetically available radiation (PAR) and induce an increase in the rate of photosynthesis (Vincent et al., 2007).

1.3.1 Effects on phytoplankton
Phytoplankton is responsible for ~50% of the global net primary production, and they are an important source of energy to an aquatic ecosystem (Field et al., 1998). Algal communities are extremely sensitive to environmental changes (Reynolds, 1984) as alteration of the physical conditions within a lake will have strong effects on phytoplankton communities. Fluctuations in annual temperature, light availability, grazing pressure, and water column mixing are strongly related to phytoplankton dynamics (Sommer et al., 1986; Cloern, 1996; Winder and Sommer, 2012). The response of algae to climate warming can vary among different taxonomic groups. For example, one mesocosm experiment reported that cryptophytes and diatoms showed strongest response to warming (Winder et al., 2012). Changes in the thermal stratification patterns have effects on phytoplankton by the extending the growing season, or by changing vertical mixing (Schindler et al., 1996a; Rodriguez et al., 2001; Diehl et al., 2002; Smol et al., 2005). Water column mixing can influence nutrient availability and consequently phytoplankton production. Stronger stratification can suppress the upward flux of nutrients through vertical mixing resulting in nutrient-depleted surface waters (Livingstone, 2003; O’Reilly et al., 2003; Schmittner, 2005). Light and nutrients are two major factors which affect algal communities and biomass, both of which may be altered through climate change (Schindler et al., 1996a; Magnuson et al., 1997). Under reduced vertical mixing, cyanobacteria could thrive (Findlay et al., 2001). Also bloom-forming cyanobacteria have higher maximum growth rate compared to diatoms and green-algae at a temperature above 23 °C (Roberts and Zohary, 1987; Reynolds, 2006; Jöhnk et al., 2008). Temperature and related variables are recognized as important
predictors of cyanobacterial biomass across broad spatial and temporal gradients (Jöhnk et al., 2008; Kosten et al., 2012; Taranu et al., 2012).

Warming can also indirectly influence the phytoplankton spring bloom through its effect on ice-cover and patterns of lake mixing (Adrian et al., 1999; Winder and Schindler, 2004; Peeters et al., 2007). The mechanisms for determining the phytoplankton response to climate warming also differ strongly between shallow and deep lakes (Adrian et al., 1999; Peeters et al., 2007). In shallow temperate lakes, the spring phytoplankton bloom is mainly determined by increasing light availability (Sommer and Lengfellner, 2008), which is again co-related with solar radiation and the day length, which indirectly depends on lake specific features (for e.g. water transparency and depth). Conversely, in very deep lakes, phytoplankton starts growing with the depletion of strong mixing when phytoplankton is not transported out of the euphotic zone (Peeters et al., 2007).

Understanding the effects of temperature and nutrients on phytoplankton production can be complex, and models have been used to understand this complexity. For example, a phytoplankton community model study (Reynolds et al., 2001; Elliott et al., 2005) showed that the mean annual phytoplankton biomass increased with temperature and nutrient loading. Peak biomass was associated with increasing temperature for three spring-blooming species (Chlorella, Asterionella and Plagioselmis) (Elliott et al., 2006). Laboratory experiments also suggest that cyanobacteria can be more productive than Aulacoseira at warmer temperatures (Coles and Jones, 2000). Summer conditions favoured cyanobacterial blooms and Anabaena becomes the dominant algal taxon under higher temperature and nutrients (Elliott et al., 2006). Warmer climatic conditions may also favour development of cyanobacteria in lake ecosystems (Paerl and Huisman, 2008). Cyanobacteria can form significant blooms in many water bodies,
and are widely acknowledged as a threat to water quality in many regions of World (O’Neil et al., 2012), as many cyanobacteria can produce cyanotoxins (Carmichael et al., 1988). Cyanobacterial growth is favoured under warmer temperatures, due to their higher growth rates at higher temperatures relative to eukaryotic phytoplankton (Roberts and Zohary, 1987). Higher temperatures can also increase buoyancy capabilities of cyanobacteria and delay rate of sinking (Kromkamp et al., 1988; Reynolds, 2006; Carey et al., 2012), further favouring the abundance of cyanobacteria. Besides, temperature, high concentrations of nutrients are also recognised as important predictors of cyanobacterial blooms (Jöhnk et al., 2008; Kosten et al., 2012; Taranu et al., 2012), and temperature and nutrients together are the best predictors of cyanobacterial biomass (Beaulieu et al. 2013).

1.4 Paleolimnology and climate change
Paleolimnology is the science that uses various physical, chemical, and biological indicators contained within lake sediments to reconstruct the past environmental and ecological condition of a given lake (Smol, 2008). Lake sediment includes material from both within (autochthonous) and outside the lake basin (allochthonous), many of which can serve as important physical, chemical or biological indicators of past climate conditions (Cohen, 2003). The study of lake sediments can provide archives of Earth and ecosystem history which can be used to study a broad range of environmental and ecological questions. Importantly, some of these are related to climate change and effects on aquatic ecosystems at different spatial and temporal scales (Cohen, 2003).

Aquatic ecosystems are dynamic, and a change in one variable can cause a cascade on other variables (Stone and Fritz, 2004). According to Birks and Birks (2006) “Ecosystems can be
thought as an infinite network of integrations among biotic and abiotic components balanced between internal and external driving factors.” To better understand the dynamics of ecosystem paleolimnological techniques, which examine the physical and chemical characteristics in dated sediment cores, can be used to reconstruct past ecosystems and biotic response to past environmental change (Birks and Birks, 2006). To gain insight into environmental change, multiple proxies are desirable as each proxy will have different sensitivities as well as different strengths and weaknesses (NRC 2005; Smol, 2008). As such, I used a multiproxy approach in this dissertation. Detailed multi-proxy studies in paleolimnology and paleoecology are available, for example, Wright (1966), Birks and Birks (1980), Delcourt and Delcourt (1991), Cohen (2003), Lotter (2003), Pienitz et al., (2004), NRC (2005) and Smol (2008). Multiproxy studies address research question using multiple lines of evidence. Each proxy has its own environmental preferences, own spatial scale, and integration provides insights into different aspects of ecosystem and community dynamics (Birks and Birks, 2006). However, multiproxy studies are time consuming, labour intensive and challenging, and involve a large amount of data synthesis. None-the-less, well-designed multi-proxy studies can provide additional insights in understanding how lakes and the biological organisms respond to the external and internal forcings. My dissertation includes aquatic algae (diatoms, pigments) and invertebrates (chironomids, Chaoborus) assemblages from lake-sediment cores and addresses issues of climate-induces changes in water quantity and water quality in northwest Ontario.

1.4.1 Diatoms as an indicator of lake-level fluctuation

Diatoms are single-celled photosynthetic algae that have a taxonomically distinct cell wall that remains generally well preserved in lake sediments. The cell wall of diatom is known as a frustule and is made of two valves (Round et al., 1996). According to Cohen (2003), diatoms are
‘probably the single most valuable group of fossils for paleolimnological reconstruction’.

Diatoms are a highly diverse group as there are over 100,000 species and account for ~25% of global primary production (Round et al., 1996; Canter-Lund, 1995). High diversity and well-preserved morphologically-distinct valves, and species-specific responses to important environmental variables make them important paleolimnological proxies (Battarbee et al., 2001).

Climate warming could affect temperate lake systems in several ways including: changes in seasonality including the duration of the ice-free period, lake stratification, changes in thermal stratification, surface-water temperatures and water residence times (Schindler et al., 1996a; Benoy et al., 2007; Keller, 2007; Parker et al., 2009), which in turn could impacts on algal community. Diatoms have been shown to be a useful tool to determine lake-level change in lakes (Barker et al., 1994; Yang and Duthie, 1995; Brugam et al., 1998; Nguetsop et al., 2004; Punning and Puusepp, 2007). For example, in closed basin lakes, diatom species composition can change significantly over time in response to change in lake water level. Consequently, lakes located in semi-arid to arid regions diatom assemblage compositional changes in well dated core has been successfully used to reconstructing variation in salinity (Fritz et al., 2000; Laird et al., 2003) from different parts of North America. For example, a sediment core from Moon Lake, North Dakota (Laird et al., 1996) used diatoms to infer a period of low effective moisture (precipitation-evapotranspiration, P-ET) and high diatom-inferred salinity during mid-Holocene period (~7,300-4,700 cal yr BP).

Reconstruction of changes in lake water depth from drainage lakes is much more challenging. Due to the need for information from regions with drainage lakes a modified Digerfeldt method (Laird and Cumming, 2008, 2009; Laird et al., 2011, 2012) based on changes in diatoms that would be sensitive for reconstructing changes in lake-level fluctuation using
diatom assemblages from sediment cores from near-shore environments. This approach was firmly based on the modern-day relationship between diatom assemblages with water depth in individual lakes, which is known as the within lake calibration approach. The goal of this approach was to identify where present-day diatom assemblages started changing from benthic to planktonic, as this near-shore location would be a sensitive location for detecting any change in lake-level (see Laird et al., 2011 for details). The sediment cores used in Chapter 3 were located ~1.5 m deeper than the modern-day benthic-to-planktonic (B-P) diatom boundary identified in each lake (Laird et al., 2011; Kingsbury et al., 2012). The B-P diatom boundary is the water depth where there is a distinct change in the present-day diatom assemblage from primarily benthic diatoms to an assemblage dominated primarily by planktonic diatoms as water levels increase and is based on a within lake surface-sediment calibration across the depth gradient (Laird et al., 2011; Kingsbury et al., 2012). As lake-level declines, the B-P boundary will move towards the center of the lake and, conversely, will move back towards the lake shore with a rise in lake level (Laird et al., 2011). Retrieval of a core near this boundary provides a means of tracking this movement and provides an indication of changes in lake level. Near-shore cores have been shown to be much more sensitive in comparison to deep center cores to variations in lake level (Laird and Cumming, 2009; Haig et al., 2013; Ma et al., 2013).

Over the last 10,000 years, evidence for changes in hydrologic conditions in northwest Ontario is only available from one lake, Lake 239 (Laird and Cumming, 2008). Analyses of a near-shore core, taken at a depth of 13 m, indicated a change to a dominance of benthic diatom taxa, representative of modern diatom assemblages from depths of 4-6 m, in the mid Holocene (Laird and Cumming, 2008), suggesting that the lake-level was 7 to 9 meters lower than today at this time. This inference of lower water levels in the mid-Holocene period is consistent with
inferred warmer temperature of 1-2 degrees Celsius from pollen (Moos and Cumming, 2011), a
2-to-3 times increase in fire frequency (Moos and Cumming, 2012), and a change to a diatom
assemblage in a deep center core from this lake that was indicative of more nutrient-rich
conditions (Moos et al., 2009).

1.4.2 Diatom as indicators of nutrients and lake trophic status
Eutrophication can be defined as enrichment of an aquatic system with nutrients (Mason, 1991;
Wetzel, 2001). Both phosphorus (P) and nitrogen (N) are contributing factors for increasing
production within a lake system, when the demands for both nutrients are high. Oligotrophic
lakes can be dominated by desmids, diatoms and chrysophytes, but eutrophic lakes are generally
dominated by cyanobacteria (Cohen, 2003). Chrysophytes from an oligotrophic lake could take
advantage over other phytoplankton under low nutrient conditions; on the other hand in
eutrophic systems, they are outcompeted by other phytoplankton (Smol, 1995a; Van den Hoek et
al., 1995). According to Sommer (1990), there are species-specific optimal N: P ratios.
Phytoplankton species diversity, richness and evenness generally decline under nutrient
enriched-condition in lakes (Cottingham and Carpenter, 1998). Nutrient enrichment can result
from both human disturbance as well as natural variation.

    Enhanced primary production can occur due to climate warming, an increase in water-
renewal times (Adrian et al., 1995; Schindler, 2006). For example, in northwest Ontario, declines
in stream flow and lower lake-levels due to drought increased water residence times, and reduced
DOC. This resulted in enhanced water transparency and a larger euphotic zone, leading to
biological change (Schindler et al., 1996a; Findlay et al., 2001). In other regions, reduced
flushing rates and increased phosphorus (internal loading) from lake sediments due to summer
stratification were mentioned as possible drivers for enhanced production (Rippey et al., 1997).
Water residence time could also cause increase in phosphorus retention within a lake, which also causes nutrient enrichment (Rippey et al., 1997).

Diatoms from lake sediments are commonly used as indicator of lake eutrophication, and for tracking changes in trophic status over centuries. Diatom assemblages have been shown to be strongly related to lake water nutrients (e.g. Hall and Smol, 1992; Dixit and Smol, 1999). Several paleolimnological studies have used fossil diatom assemblages to track changes in the nutrient status of a lake over time scale ranging from decades to millennia (Fritz, 1989; Anderson, 1995a, b; Dong et al., 2008). Quantitative approaches such as diatom-inferred total phosphorus (DI-TP) models, have been used to quantitatively estimate changes in trophic status through analysis of diatom assemblages in well-dated sediment cores (Hall and Smol, 1992, 1999; Bennion et al., 1995; Lotter et al., 1998; Hall et al., 1999; Wessels et al., 1999; Garrison and Wakeman, 2000; Bradshaw and Anderson, 2001; Marchetto et al., 2003; Reavie et al., 2006; Smol, 2008). Several paleolimnological investigations have studied how lake production changed due to anthropogenic effect, human settlement, or changing land use (e.g. Fritz, 1989; Bradshaw et al., 2005; Ekdahl et al., 2007) or the effect of prehistoric Thule Inuit whalers in the High Arctic (Douglas et al., 2004). In summary, diatoms are one of the most widely used bioindicators to study changes in nutrient status of a lake from where little to no historical monitoring has been done.

1.4.3 Fossil pigments as an indicator of primary production

All algae and cyanobacteria contain chlorophyll $a$. Other chlorophylls and many of the carotenoids can be phyla specific. For example, diatoms contain the ubiquitous pigments chlorophyll $a$, $\beta$-carotene, chlorophyll $c1, c2, diatoxanthin$, and the accessory pigment, fucoxanthin. $\beta$-carotene is the principal carotene found in green plants and in the lake sediments.
Carotenoids, chlorophylls and their derivative products can persist within lake sediments for a long time, and are identifiable based on their pigments (Brown, 1969). Chlorophyll, and its derivatives, carotenoids from lake sediment have been used for over 70 years (Fox, 1944; Fox et al., 1944; Vallentyne, 1954, 1956; Leavitt, 1993; Leavitt and Hodgson, 2001). Fossil pigments are preserved well within sediments. For example, 56 000 years-old algal carotenoids have been recovered from marine sediments (Watts and Maxwell, 1977). Chlorophyll a is the most abundant pigment, and pheophytin a and pheophorbide a are derivatives that are commonly found in sediments (Daley et al., 1977; Leavitt and Hodgson, 2001). Degradative processes including herbivorous grazing, photo-oxidation, chemical or microbe-mediated oxidation can also play an important role in pigment preservation (Leavitt, 1993; Leavitt and Hodgson, 2001).

In early paleolimnological studies, fossil pigments were mainly used as a biochemical marker for the presence of phototrophic prokaryotes (Brown and Colman, 1963; Brown, 1968), or for the estimation of historic changes in lake production (Vallentyne, 1957; Fogg and Belcher, 1961; Belcher and Fogg, 1964). These pigments are now widely used in a number of ways including, indicators of algal and bacterial community composition (Zulling, 1981; Yacobi et al., 1990), changes in physical structure of lake (Hurley and Watras, 1991; Hodgson et al., 1998) and estimation of past ultraviolet (UV) radiation (Leavitt et al., 1997, 1999). Not surprisingly, fossil pigments are also used in a wide variety of studies that assess anthropogenic impacts on aquatic ecosystems, including eutrophication, acidification, fisheries management, land-use practices and climate change (Leavitt et al., 1994; Hall et al., 1999).

Carotenoid, such as myxoxanthophyll, canthaxanthin, and echinenone, have been attributed to changes in lake trophic status from oligotrophic to eutrophic conditions in a series of lakes from Minnesota (Santelman, 1981). Myxoxanthophyll and oscillaxanthin derived from
cyanobacteria were highly co-related with cultural eutrophication in a variety of lakes (Zullig, 1981, 1982; Griffiths et al., 1969; Gorham and Sanger, 1976; Guilizzoni et al., 1982, 1983). Presence of myxoxanthophyll and oscillaxanthin in Diss Mere (Norfolk, UK) were also related to eutrophication during 6000-5000 yrs BP (Fritz, 1989).

1.4.4 Midge (Chironomid) and Chaoborus assemblages as biological proxy of lake-level and water quality

Chironomids (Diptera, Chironomidae), are non-biting midges and have an aquatic larval stage. They are frequently used as an important biological proxy. Larvae grow and develop through four instars, and after each instar they shed their head capsules. Chironomids belong to the benthic fauna of most lakes, and some species prefer either near-shore or profundal environment. They also have different feeding habits including herbivores, detritivores, carnivores or filter feeders. Chironomids are good indicators of water quality, and they have been traditionally used in biomonitoring to assess the impact of nutrient enrichment (Seather, 1979; Wiederholm, 1983). Many environmental variables have been shown to be important for the development and distribution of midge larvae including: water temperature, macrophytes, substrate, food availability, and oxygen conditions (Walker and Mathewes, 1987, 1989; Walker et al., 1991; Warwick, 1989; Pinder, 1995; Broderson and Quinlan, 2006). Quantitative models have been developed to infer environmental variables from chironomids including summer temperature, deep-water oxygen, and lake trophic state (Walker, 1991, 1995; Lotter, 1998; Brook, 2001; Quinlan and Smol, 2002, 2010). Water depth has consistently been identified as an important variable related to the distribution of chironomid assemblages both within and between lakes (e.g. Walker et al., 1991, 2003; Olander et al., 1999; Porinchu and Cwynar, 2000; Quinlan and
Chironomid habitats range from the littoral, sublittoral to profundal zone. The littoral zone is characterized by greater habitat diversity due to littoral vegetation. A vertical up or downward shift in habitat will occur in this zone, whereas profundal and pelagic communities are not affected as directly by water depth and lake-level fluctuations (Hofmann, 1998).

The remains of *Chaoborus* are also important paleolimnological proxies. *Chaoborus*, commonly referred as phantom midges, are abundant in pelagic regions of freshwater lakes. Common *Chaoborus* taxa (Diptera: Chaoboridae) are *C. americanus*, *C. flavicans*, *C. punctipennis* and *C. trivittatus* (Uutala, 1990). *C. flavicans*, *C. punctipennis* and *C. trivittatus* commonly undergo diel vertical migration to minimize predation from fish (Franke, 1983, 1987; Voss and Mumm, 1999). Changes in *Chaoborus* assemblages can be tracked over time because the mandibles are well preserved in lake sediments. There are four developmental stages in the life cycle of *Chaoborus*, of which first- and second-instars can last up to a few weeks (Wood, 1956; Sweetman and Smol, 2006). Third- and forth-instar larvae consume a wide variety of prey including rotifers, copepods, daphnids and other smaller cladocerans. *Chaoborus* are better able to tolerate hypoxic conditions, in comparison to chironomids, due to the presence of a more impermeable exoskeleton (Munger et al., 1999), and their ability to migrate in the water column (except *C. americanus*). Chironomid and *Chaoborus* are good paleoecological indicators because: they have a strongly sclerotized head capsule that is resistant to degradation within the sediments (Walker, 2001); are abundant and identifiable to a meaningful taxonomic level (Brooks et al., 2007; Wiederholm, 1983); and are related to important limnological variables that can be quantified (Sheather, 1979; Pinder, 1995; Walker, 2001; Heiri and Lotter, 2003). Despite the difference in life history characteristics sometimes *Chaoborus* are counted are summed in
Chironomidae-based paleolimnological studies (e.g., Olander et al., 1997; Barley et al., 2006; Luoto, 2009). Several factors could relate to the distribution of Chaoborids, including climate-related factors (Lamontagne et al., 1994), oxygen levels (Quinlan and Smol, 2010), or lake morphometry (Luoto and Nevalainen, 2009). A study by Kurek et al., (2010) in northwest Ontario (146 Canadian Boreal Shield lakes) showed that water chemistry and lake morphometry are important environmental variables for the distribution of Chaoborus taxa. Relative abundance of C. flavicans generally increased in deeper lakes with high-pH, whereas C. trivittatus were strongly correlated with higher alkalinity, Na (sodium), and depth.

1.5 Region-specific context of dissertation

Northwest Ontario is a climatically sensitive region due to its geographic position at the confluence of three different air masses (the westerlies, Arctic air mass and the tropical airmass from the Gulf of Mexico). So understanding effects of past climate variability on boreal freshwater lakes from northwest Ontario is important in the context of future climate change as boreal forest region expected to be impacted by the anthropogenic climate change (Schindler and Lee, 2010). Over the past Holocene time period, areas adjacent to this region have experienced significant changes in ecosystem structure and function. Ten-thousand years ago, the Laurentide Ice sheet retreated northward of the Great Lakes Region and the boreal region shifted northward, and coniferous-deciduous forest extended from Minnesota to New Jersey (Delcourt and Delcourt, 1981). In the mid-latitude of the southeastern United States, the mesic deciduous forest also expanded likely due to the influence of the winter Pacific airmass and summer Maritime tropical airmass (Delcourt and Delcourt, 1981). During the mid-Holocene period, the mixed coniferous forest has expanded throughout the Great Lakes area and the prairie vegetation expanded eastward (Delcourt and Delcourt, 1981). Bryson (1966) concluded that droughts
occurred in the mid-continental region of North America during the Hypsithermal due to a strong zonal flow of the dry westerlies. From 7.5 to 4 Ka, Lake Winnipeg has experienced unexpectedly dry conditions, as indicated by the dessication of the southern basin. At this time the prairies expanded eastward into the boreal region (Baker et al., 1992). This change was attributed to the changes in the atmospheric circulation pattern where dry pacific airmass from the west blocked the moist tropical airmass from south (Baker et al., 1992).

Boreal regions contain over 60% of the world’s fresh surface water, thousands of freshwater lakes and more than half of the carbon in forested regions (Schindler and Lee, 2010). This is a region with rolling topography with many lakes and hills of crystalline bedrock covered with shallow soils (McAndrews, 1982). My study lakes are located in the Winnipeg River Drainage Basin (WRDB), which is composed of two major watersheds; the English River Watershed and Lake of Woods or Rainy River Watershed. The WRDB has an area of 150,000 km², with the majority of this watershed in northwest Ontario (St. George, 2006). The WRDB is the source of drinking water for the city of Winnipeg as well as water for hydro-electric power generation. The eastern part of the WRDB is mainly composed of black spruce (Picea mariana), jack pine (Pinus banksiana), poplar (Populus spp.), along with white birch (Betula papyrifera), balsam fir (Abies balsamea), and larch (Larix spp.). The south and the west regions of my study area are mainly dominated by black ash (Fraxinus nigra), poplar, and white birch along with red maple (Acer rubrum) and balsam fir.

My research lakes are located within the forest along a west to east transect of ~100 to 250 km from the present-day forest-prairie boundary. All the study lakes are first-order lakes. Northwest Ontario is a humid-continental region, but droughts in this area can have important ecological and environmental repercussions. For example, a widespread drought affected most of
the WRDB in 2003/04, and was the main factor responsible for reduced energy production (St. George, 2006). This resulted in a net loss of over $400 million for Manitoba Hydro (Manitoba Hydro, 2004). Instrumental climate data for the last 100 years from northwest Ontario shows a significant warming trend of around 1-2 °C as well as an increase in precipitation (Laird et al., 2012). Increases in precipitation over the last 100 years were also recorded in the annual discharge of the Winnipeg River which increased ~60% over the 20th century (St. George, 2006). Within the trend of increasing precipitation, shorter-duration of decreases in precipitation have occurred at some of the northwest Ontario climate stations during the 1930s, 1950s and 1980s (please see, Fig. 2, Laird et al., 2012; Canadian Climate Data archive (http://ec.gc.ca/dccha-ahccd). Furthermore, without continued increases in precipitation to offset increases in evaporation due to warmer temperatures, water levels in this region could fall (Laird et al., 2012).

The 100-year perspective from the instrumental record from this region is insufficient to provide the full range of climate variability. For example, the main reference lake at the Experimental Lakes Area (ELA), Lake 239 (located ~50 km west of Kenora) showed major changes associated with a drought in the late 1980s (Schindler et al., 1996a). Among other changes, the drought drastically reduced runoff, resulting in a decrease in DOC, an increase in light penetration, and a deepening of the position of the thermocline (Schindler et al., 1997a). These modern observations help to inform interpretations from paleolimnological data. For example, a comparison of diatom assemblages from present-day and ~150 year-old sediments from almost 40 ELA ‘reference’ lakes, are consistent with recent warming, with increases in planktonic diatoms relative to pre-industrial assemblages, especially in the deep lakes (Enache et al., 2010). Similarly, in the nearby large and complex Lake of the Woods, recent changes in
diatom assemblages were related to records of climate warming and periods of extended ice-free conditions (Rühland et al., 2008).

To understand lake response under a warmer climate during the mid-Holocene time period, this thesis uses paleolimnological approaches. Based on climate-change predictions from general circulation models (GCMs), the boreal forest biome is expected to warm (Ruckstuhl et al., 2008). The border between Ontario and Manitoba is located near an ecotone between the Canadian prairies (west), and the forested boreal region (east). Such transitional boundaries are predicted to be highly sensitive to changing climate (Naiman and Decamps, 1990; Schindler et al., 1996a), and are a sensitive location for examining environmental change. Holocene shifts in the prairie-forest ecotone (PFE) have been extensively studied, beginning with the classic work of McAndrews (1966), and the more recent syntheses of many studies (Nelson and Hu, 2008; Williams et al., 2009). These recent syntheses support that the timing and rates of the PFE shifts were heterogeneous, with many records indicating an abrupt early-Holocene transition from forest to grassland, but a more gradual reforestation during the late Holocene (Umbanhowar et al., 2006). A west-to-east time-transgressive response to aridification was also documented with the early shift in the PFE (Williams et al., 2010). Williams et al. (2011) suggest this may be due to more arid sites being nearer to a threshold than less-arid sites.

1.6 Broader significance of this thesis

There is controversy whether mid-Holocene period is a good analog for understanding future climate change? This thesis will help determine the climate sensitivity of the boreal lakes of northwest Ontario during periods of time that were likely warmer and drier than present. With the unprecedented warm temperatures over the last several decades, industry and governments are struggling to understand the risks to water resources. This dissertation adds to the broader
literature of how multi-proxy approaches can be used to understand regional changes in water quantity and quality. Paleolimnological approaches and good study design can increase our understanding of past climate variability during times that were warmer than present. All three study lakes exhibited similar low-water stands during early-to-mid-Holocene period and higher water stands during last 4-5 thousands years suggesting a broad regional climate forcing. This thesis also supports the sensitivity of lakes to climate warming in northwest Ontario. Given the importance of the WRDB as a source of freshwater to both Ontario and Manitoba, results in this thesis will be of interest to policy makers, industry partners, and lake managers, and provide possible scenarios that could occur in the future.

1.7 Literature cited


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38


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Chapter 2

Consensus among multiple trophic levels during high- and low-water stands

over the last two millennia in a northwest Ontario lake
2.1 Abstract
We investigated the modern distribution of fossil midges within a dimictic lake and explored downcore patterns of inferred lake depths over the last 2000 years from previously published proxies. Modern midge distribution within Gall Lake showed a consistent and predictable pattern related to the lake-depth gradient with recognizable assemblages characteristic of shallow-water, mid-depth and profundal environments. Interpretations of downcore changes in midge assemblages, in conjunction with quantitative lake depth inferences across \textit{a priori} defined (based on diatom data) \textasciitilde 500-year wet and dry periods, demonstrated that both invertebrate and algal assemblages exhibited similar timing and nature of ecological responses. Midges were quantified by their relative abundance, concentrations and an index of \textit{Chaoborus} to chironomids, and all showed the greatest differences between the wet and dry periods. During the low lake-level period of the Medieval Climate Anomaly (MCA: AD 900 to 1400), profundal chironomids declined, shallow-water and mid-depth chironomids increased, chironomid-inferred lake level declined and the \textit{Chaoborus}-to-chironomid index decreased. The coherence between multiple trophic levels provides strong evidence of lower lake levels in Gall Lake during the MCA.
2.2 Introduction

To expand our knowledge of climate change in northwest Ontario over the past 2000 years, Laird et al. (2012) assessed the drought signal from near-shore sediment cores taken from a network of six small oligotrophic-to-slightly mesotrophic lakes. These lakes spanned a distance of ~250 km across the boreal forest region of the Winnipeg River Drainage Basin (WRDB). The cores were retrieved from a sensitive location in each lake, just deeper than the modern transition from planktonic diatoms to assemblages with increasing contributions from benthic taxa (Laird et al., 2011; Kingsbury et al., 2012). At this ecologically-relevant location, a small change in either light or lake depth can result in a shift in diatom assemblages, thereby providing the critical location for detecting drought through declines in water level and associated variables (details in Laird et al., 2011). This spatial network of sites provided clear evidence that a prolonged period of aridity occurred between AD 900-1400 (Medieval Climate Anomaly), and that conditions over the last 100 years were indicative of relatively high effective moisture (Laird et al., 2012), in agreement with regional hydrological monitoring (St. George, 2006; Parker et al., 2009).

The strength of quantitative (and by extension qualitative) reconstructions of lake level from biological proxies (such as diatoms) has been challenged (Juggins, 2013). The main criticism is based on the inability of modern calibration data sets to produce a consistent pattern of diatom optima to lake depth across regions. It was concluded that depth has limited or no direct effect on biota but acts as a surrogate variable for many underlying environmental factors. We agree that lake depth is a ‘composite’ and potentially complex environmental variable, but it is inextricably coupled to a range of biologically-important variables including temperature, substrate, wave action, light, food availability, and changing predator-prey interactions. Nonetheless, many studies show repeatable and well-defined relationships to water depth, for
diatom assemblages (Kingsbury et al., 2012), and chironomid assemblages (e.g., Kurek and Cwynar, 2009a; Engels and Cwynar, 2011; Luoto, 2012).

To further evaluate the sensitivity of biotic assemblages to historic lake-level shifts over the last 2000 years, we compared midge assemblages to independent inferences of changes in lake depth that were derived from diatom assemblages in Gall Lake (Laird et al., 2012; Haig et al., 2013). The strength of the relationship between midge assemblages and lake depth was assessed in Gall Lake across a depth gradient, thereby maximizing the possibility of detecting changes in midge assemblages with lake depth. Midge assemblages from three a priori chosen ~500-year periods of diatom-inferred water level (one low-water level and two high-water levels) were analyzed. Specifically, we predict that if midges are sensitive to changes in depth then midge assemblages during the arid period should be represented by more shallow-water taxa, and the abundance of Chaoborus, and deep-water chironomid taxa should decrease. Alternatively, if midges donot show a significant and consistent change, then either midges are not sensitive to subtle changes in lake depth, or the quantitative diatom inferences may not accurately represent lake-level changes in Gall Lake.

2.3 Methods

2.3.1 Study site

Gall Lake (50° 14” N, 91° 27” W) is located in northwest Ontario, Canada, within the eastern region of the English River Watershed (Fig. 2-1). The study site is ~20 km northwest of Sioux Lookout and is located within a forested region with minimal human disturbance (i.e. mainly forested, no cottages, and minimal human activity in the catchment). Average summer temperature in Sioux Lookout is 17.1 °C and average annual precipitation is ~820 mm
Figure 2-1. a) Map showing the location of the Winnipeg River Drainage Basin comprised of the English River Watershed and the Lake of the Woods/Rainy River Watershed (modified from Laird et al 2011). b) Bathymetry of Gall Lake with samples indicated. Contour lines represent depth intervals of 2 m. The black square represents the location of the piston core that was taken from a depth of ~7.5 m.
The catchment is characterised as boreal forest and is dominated by black spruce (*Picea mariana*), jack pine (*Pinus banksiana*), and poplar (*Populus* spp.), along with white birch (*Betula papyrifera*), balsam fir (*Abies balsamea*), and larch (*Larix laricina* spp.). Gall Lake is a small, headwater lake with a surface area of 19 ha and a maximum water depth of 18 m. The eastern basin has a gently sloping bottom from which surface-sediment samples were collected (Fig. 2-1b). Water chemistry indicates that Gall Lake (July, 2008, Kingsbury et al., 2012) has a low specific conductance (~25 µS/cm), low-to-moderate concentrations of total phosphorus (TP = 12.3 µg/L) and a relatively high concentration of dissolved organic carbon (DOC = 15.8 mg/L). During June 2010 and 2011, the metalimnion extended between 4 and 6 m at Gall Lake.

2.3.2 Surface sample collection and midge processing

To quantify the distribution of modern-day midge assemblages, subfossil remains were identified in surface-sediment samples (top 0-1 cm) taken from Gall Lake. Samples were collected along a transect at ~1m depth increments to the center of the lake (Fig. 2-1b) using a gravity corer (Glew, 1989). Samples from >15m depth were absent because sufficient sediment was no longer available. Standard procedures were followed to isolate midge remains from the surface sediments (Walker, 2001). Briefly, 15 g of wet sediment was deflocculated in 5% KOH for ~10 minutes at 200 °C, and then rinsed with running tap water through a 100-µm mesh sieve. Using a Bogorov counting tray and fine forceps, chironomid head capsules and *Chaoborus* mandibles were picked by hand under a dissection microscope at 20X magnification. Specimens were then placed onto cover slips and mounted on slides using Entellan®. Chironomid head capsules were identified using Wiederholm (1983) and the fossil key of Brooks et al. (2007). *Chaoborus* mandibles were identified using the fossil key of Uutala (1990). A minimum equivalent of 50
whole chironomid head capsules were counted per sample (Heiri and Lotter, 2001; Larocque, 2001; Quinlan and Smol, 2001).

2.3.3 Assessment of changes in midges over the last 2000 years

Three a priori 500-yr periods that represent primarily more mesic or arid conditions based on quantitative inferences from diatom assemblages (Fig. 2-2, Haig et al., 2013) were chosen for analysis of midges. These periods include two relatively mesic periods (from ~ AD 100 to 600, and from ~ AD 1400 to 1900; henceforth termed Wet 1 and Wet 2, respectively), and a period of aridity during the MCA (~ AD 900 to 1400; henceforth termed Dry 1). Diatom-inferred (DI) depths during the Wet 1 and Wet 2 generally ranged between 10 and 12 m, and during Dry 1 ranged between 8 and 10 m. Wet 1 is generally represented by an abundance of between ~65 and 85% planktonic diatom taxa. Wet 2 was more variable and represents an initial transition from arid conditions to a period of more mesic conditions, with planktonic diatom taxa representing ~60% of the relative abundance in the 1400s, to ~75 to 80% relative abundance between AD 1600 and 1900 (Haig et al., 2013). During the MCA (Dry 1) the percentage of planktonic diatoms was typically <70% (Laird et al., 2012; Haig et al., 2013). The subtle, but consistent changes among these periods, sets the stage for this study where we assess whether midge assemblages show a response consistent with the diatom inferences.

Chironomid head capsules and Chaoborus mandibles were analyzed in the top 50 cm of a near-shore piston core taken in 2010 from a water depth of ~7.5 m. We sectioned the core into ~0.25 cm intervals and samples were analyzed every other interval, resulting in bi-decadal temporal resolution during each of the 500-year periods. The chronology of the core is well established and based on both $^{210}\text{Pb}$ and AMS $^{14}\text{C}$ dates (Laird et al., 2012; Haig et al., 2013). Total $^{210}\text{Pb}$ was measured on a low-background gamma counter (Schelske et al., 1994) and
Figure 2-2. Diatom-inferred water depths from the Gall Lake near-shore core (Haig et al., 2013). Changes in the diatom assemblages and depth-based inferences were used to define three apriori five-hundred year periods that provide the framework for the present study (Wet 1, AD 100-600; Dry 1, AD 900-1400; and Wet 2, AD 1400-1900).
sediment age was determined using a constant rate of supply model (Binford, 1990). Four AMS $^{14}$C dates were determined for the deeper intervals based on AMS dates of pollen isolated from the sediments. Sediment age was based on the midpoint of the 2-sigma range with the highest relative area under the probability distribution using CALIB 6.01 (Reimer et al., 2009). Complete details of the age-depth model are in Haig et al. (2013).

2.3.4 Numerical analyses of surface assemblages

Chironomid counts were expressed as percent relative abundance of all identifiable chironomids. Chaoborus mandibles were expressed as an index of Chaoborus relative to chironomids $\frac{(# \text{ of Chaoborus mandibles/2})}{(# \text{ of Chaoborus mandibles/2} + (# \text{ of chironomid head capsules}))}$ (Quinlan and Smol 2010). This index is henceforth referred to as the Chaoborus-to-chironomid index. The dominant pattern of variation in the modern chironomid assemblages in Gall Lake was summarized by principal components analysis (PCA) using the computer program CANOCO v. 5 (ter Braak and Šmilauer, 2002), based on square-root transformed relative abundances. A depth-constrained cluster analysis was used to identify groups of similar chironomid assemblages in the modern surface sediments, determined using a squared-chord distance as a measure of dissimilarity (Grimm, 1987). Weighted-averaging (WA) was used to provide an estimate of the depth optimum for each chironomid taxon, with the weight being the relative abundance of a taxon at each depth. These weighted averages were then used to assign individual chironomid taxa to one of the three groups identified in the cluster analysis: a shallow-water, a mid-depth, and a profundal assemblage. WA regression and calibration with inverse deshrinking were used to develop and assess a predictive model for lake depth from chironomid assemblages. This model was developed using the program C2 1.6.5 (Juggins, 2003).
2.3.5 Numerical analysis of downcore assemblages

The same taxonomic references and counting strategies described above were used to analyse the midge assemblages in the sediment core over the last 2000 years. However, in the core, the midge assemblages were expressed in two ways: i) relative abundances (and/or indices) as described above and ii) as concentrations of chironomids and *Chaoborus* per gram dry weight of sediment. Individual chironomid taxa were also assigned to the groups defined above (shallow-water, mid-depth and profundal assemblages) to summarize the assemblage shifts. Correlations between the relative abundance data and the concentration data were run on the three groups to determine the degree of similarity between these metrics.

To assess if the chironomid assemblages were significantly different between the two 500-year mesic periods (Wet 1 and Wet 2) and the arid MCA (Dry 1), an Analysis of Similarity (ANOSIM) was performed using PRIMER 6.0 (Clarke, 1993). ANOSIM was run on relative abundance data after removing rare taxa (those taxa < 3% in at least one sample), and samples within the 500-year time periods were treated as replicates. ANOSIM is a non-parametric test which can differentiate between *a priori* defined groups. In the ANOSIM, a test-statistic (R) is generated based on rank similarities calculated within and between groups (Clarke, 1993). If R = 1 then all similarities within groups are greater than the similarities between groups. To identify which groups differed from each other, multiple pairwise ANOSIMs were run (i.e. Wet 1 versus Dry 1, Wet 1 versus Wet 2, and Dry 1 versus Wet 2). We hypothesized that, if the chironomid assemblages follow similar directional change as inferred from the diatoms, then Wet 1 and Wet 2 would be more similar, in comparison with either, Wet 1 and Dry 1, or Wet 2 and Dry 1. To aid in the comparison of changes in diatom and midge assemblages over the last 2000 years, a summary of the percent profundal chironomids and planktonic diatoms were compared, as were
diatom and chironomid inferences of lake depth. The chironomid-inferred depth reconstruction was assessed following procedures outlined by Telford and Birks (2011). If our reconstruction explains more variation than 95% of reconstructions (n=499) generated from models trained on random data, the reconstruction was considered statistically significant.

2.4 Results

2.4.1 Midge assemblages from the modern surface sediments of Gall Lake
Chironomid assemblages showed a distinct pattern of variation across the gradient of lake depth, and three depth-related zones were identified based on cluster analysis (Fig. 2-3). The profundal or deep-water assemblage was characterized by the highest abundances of *Chironomus anthracinus*-type and *Sergentia coracina*-type (10% and 50%, respectively). The mid-depth assemblage (Fig. 2-4) was characterized by a declining abundance of *S. coracina*-type and increased relative abundances of *Micropsectra contracta*-type, and *Micropsectra insignilobus*-type from ~10 to 6.25 m water depth. The shallow-water assemblage was generally characterized by higher abundances of taxa including: *Cladopelma*, *Microtendipes pedellus*-type, *Tanytarsus*, *Polypedilum*, *Tanytarsus mendax*-type, *Pagastiella*, *Tanytarsus chinyensis*-type, and *Zalutschia*. Several taxa were relatively ubiquitous across the depth gradient such as *Procladius*, *Psectrocladius sordidellus*-type, whereas *Psectrocladius* (*Monopsectrocladius*), *Heterotrisocladius marcidus*-type, and Tanytarsini (which likely include several taxa that are difficult to identify given the fragmentation of head capsules) showed relatively high abundances in the shallower to mid-depth region (Fig. 2-3). The three zones identified by the cluster analysis were also clearly supported by the first two PCA axes of the modern chironomid assemblages. The first axis differentiates the profundal taxa, *C. anthracinus* and *S. coracina*-types from the
Figure 2-3. Distribution of the relative abundance of the dominant (>3%) chironomid taxa, the *Chaoborus*-to-chironomid index, and the PCA axis-1 scores of the chironomid assemblages across a gradient of depth in Gall Lake. Chironomid taxa are arranged based on their weighted-average optima. Three zones were defined based on cluster analysis.
Figure 2-4. PCA biplot of chironomid assemblages. The first axis separates the profundal taxa (open triangles) *C. anthracinus* and *S. coracina*-types from the more diverse shallow-water (open rectangles) and mid-depth assemblages (open circles), which themselves are defined based on their depth optima.
more diverse shallow-water assemblage, whereas the mid-depth taxa are represented by negative loadings on the second axis, primarily from *M. contracta* and *M. insignilobus*-types. *Chaoborus* were represented by two taxa, *C. trivittatus* and *C. flavicans*-types. Similar to the transition in chironomid assemblages, the *Chaoborus*-to-chironomid index was much higher in the deeper waters and declined in an approximately linear fashion to 0 by ~3 m water depth (Fig. 2-3). A strong predictive model for lake depth was developed, based on the WA optimum of the 29 chironomid taxa present in the surface-sediment of Gall Lake (bootstrapped $r^2 = 0.80$; RMSEP = 1.95 m, $n = 31$, Supplemental 2-1).

### 2.4.2 Downcore midge and diatom assemblages

Generally, the abundances (Fig. 2-5) and concentrations (Fig. 2-6) of profundal taxa (e.g. *S. coracina*) are high during the wet periods and low during the dry period from 900 to 1400 AD. The dry period was also characterized by higher abundances of several mid-depth (e.g., *T. pallidicornis*-type, *P. nubeculosum*-type) and shallow-water taxa (e.g., *Polypedilum* and *Pagastiella*) (Fig. 2-5). There were two shallow-water taxa, *M. pedellus*-type and *Tanytarsus*, that were present in Wet 1, that were not present in Wet 2. The differentiation between 500-year periods was visually more apparent when the chironomid taxa were grouped into depth categories based on their abundance in the modern-day surface samples (Fig. 2-6). In Wet 1 and Wet 2, the relative abundance of profundal taxa ranged from ~20 to 50%, whereas in Dry 1, the abundance of profundal taxa was consistently < 20% (Fig. 2-6). Trends in the relative abundance data were similar to the patterns observed in the concentration data, which were significantly correlated for the profundal ($r = 0.85$, $n = 73$, $p < 0.05$), mid-depth ($r = 0.69$, $n = 73$, $p < 0.05$), and shallow-water ($r = 0.80$, $n = 73$, $p < 0.05$) groupings (Fig. 2-6). The *Chaoborus*-to-chironomid index was higher during the wet periods in comparison to Dry 1 (Fig. 2-6).
Figure 2-5. The relative abundance of the dominant chironomid taxa (>3%) in the 500-year time periods. Because of insufficient sediment availability ~ AD 600-900 was not included. The chironomid taxa are arranged according to their weighted-average optima and habitat categories.
Figure 2-6. Summary diagram showing relative abundances and concentrations of the three chironomid assemblage groups (shallow, mid-depth, and profundal), in the three *a priori* defined 500-year periods (Wet 1, Dry 1 and Wet 2). Chaoborus-to-chironomid index and the concentration of *Chaoborus* taxa are also shown.
During Dry 1, the *Chaoborus*-to-chironomid index reached the lowest sustained values of all three periods. The *Chaoborus*-to-chironomid index was significantly correlated to the concentration of *Chaoborus* (*r* = 0.93, *n* = 73, *p* < 0.05).

The ANOSIM results confirmed that the chironomid assemblages were significantly different between all three 500-year periods (Global *R* = 0.49, *p* < 0.001). However, the pairwise comparison between the Wet 1 and Dry 1 and Wet 2 and Dry 1 were higher (*R* = 0.71, 0.61, respectively, *p* < 0.001 for both) than between Wet 1 and Wet 2 (*R* = 0.31, *p* < 0.001). Chironomid taxa that exhibited the greatest mean differences between the wet and dry periods were profundal taxa such as *S. coracina*-type and *C. anthracinus*-type, and shallow-water taxa such as *Polypedilum* and *Pagastiella*, and mid-depth taxa such as *P. nubeculosum*-type and *T. pallidicornis*-type. Using untransformed relative abundance data, the chironomid-based reconstruction explained significantly (*p* = 0.03) more variation than 95% of reconstructions generated from models developed with random environmental data (Telford and Birks, 2011).

Comparison of the response of chironomid assemblages within the zones previously described by the diatom assemblages were similar and support a conclusion of overall lower water levels in Gall Lake during the MCA (Dry 1). Dry 1 is defined by a decline in planktonic diatom taxa from 70 to 80% consistently less than 70% between AD 900 and 1400 (Fig. 2-7A), and diatom-inferred decreases in lake level of just over 1 m (Fig. 2-7B).
Figure 2-7. a) Summary diagram between the relative abundance of profundal chironomid taxa in comparison to changes in the relative abundance of planktonic diatoms. b) Comparison of summaries of changes in deviation from mean lake depth inferred for both the chironomid- (CI-depth) and diatom (DI-depth)-based models over the last 2,000 years.
This trend during Dry 1 is mirrored in the chironomid assemblages with low abundances of profundal chironomids (Fig. 2-7A) and sustained lower chironomid-inferred water levels of ~1-2 m (Fig. 2-7). Similarly, during the two wet periods, the abundance of profundal taxa doubles, and inferred water levels are ~1-2 m higher than the average over the last 2000 years (Fig. 2-7).

2.5 Discussion

Based on the lack of reproducible depth optima in diatom assemblages in lake calibration datasets, Juggins (2013) concluded that composite variables such as lake depth need to be interpreted with great caution. Despite the recognized challenges with depth reconstructions (Kurek and Cwynar, 2009b; Velle et al., 2012), we contend that depth is an environmental variable that represents a biologically-important variable in both space and time. In this paper we examine changes in the present-day distribution of midges within a lake, and use this information to assess if diatom-based inferences of changes in lake depth are valid.

2.5.1 Modern-day distribution of midge assemblages

Gall Lake represents an excellent site from which to examine the distribution of midge assemblages across a gradient of lake depth. First, the morphometry of the lake, with a gently sloping eastern basin enabled assemblages to be sampled at a sub-meter resolution. This study with even sample distribution allowed a robust representation of depths, a factor not common in most datasets examining the relationship between midge assemblages and depth-associated gradients (Kurek and Cwynar, 2009a; Luoto, 2010, 2012; Cwynar et al., 2012). In addition to the simple lake morphometry, Gall Lake generally lacks macrophytes, except for a few emergent macrophytes at low densities, resulting in a less complicated near-shore environment. A drawback of the transect design is that the environmental variable (depth) and chironomid species assemblages would be strongly spatially autocorrelated. However, our goal was to
maximize the assemblage signal to depth. Quantitative and comparative assessments of spatial autocorrelation from within-lake chironomid distribution surveys showed little evidence that spatial autocorrelation is a significant concern (Velle et al., 2012; Engels and Cwynar, 2012; Luoto, 2012).

Three broad categories of chironomid assemblages were recognized across a depth gradient in Gall Lake and included: a shallow-water or littoral assemblage, a mid-depth assemblage, and a profundal assemblage. The profundal assemblage is relatively stable at water depths >10 m and is primarily composed of *S. coracina*-type and *C. anthracinus*-type. These two taxa reached peak abundances in the profundal zone and are generally absent at depth < 5 m. *S. coracina*-type, the most abundant deep-water taxon in Gall Lake, is a cold stenotherm (Brundin, 1956; Brodin, 1986) common to the profundal zone of deep lakes (Barley et al., 2006; Kurek et al., 2012). *S. coracina*-type was also identified as a deep-water taxon in two site-specific intra-lake data sets (Austrian Alps and Finland) and one regional multi-lake dataset (Luoto, 2012). In the Experimental Lakes Area of Ontario, Sergentia was abundant in lakes of at least ~8 m depth (Quinlan et al., 2012). *C. anthracinus*-type was present at a relative abundance of ~10% at depths >10 m in Gall Lake. According to Engels and Cwynar (2011), *C. anthracinus*-type is a deeper-water taxon. Other research has found *C. anthracinus*-type often abundant in the profundal region and has been described as an important indicator of low-to-moderate oxygen conditions (Brodin, 1986). The high *Chaoborus*-to-chironomid index at deeper locations in Gall Lake also supports this index as another proxy of lake depth. *Chaoborus*, both *C. flavicans* and *C. trivittatus*-types, were important in Gall Lake relative to chironomids at depths greater than 10 m, reaching abundances of 40% of the combined midge assemblages. This index declines gradually with depth from over 40% to essentially zero by a depth of ~3 m. However this index
is complicated by the fact that it relies on both a changing numerator (number of Chaoborus) and denominator (number of Chaoborus + number of chironomids), and can shift based on an increase or decrease in either chironomids or Chaoborus. The observation of higher index values at greater depths is not a surprise as Chaoborus, such as C. flavicans and C. trivittatus-types, often prefer deeper water and can tolerate moderate levels of predation from planktivorous fish (Kurek et al., 2010, 2011). However, this trend could also arise if chironomids were more abundant in near-shore areas and at lower abundances with increasing depth. Quinlan and Smol (2010) suggested that this index could be used as a proxy of anoxia. A high index value would arise if chironomids declined as a result of deteriorating oxygen conditions, as Chaoborus are tolerant of lower oxygen conditions (Quinlan and Smol, 2010), and have the ability to migrate to regions of higher oxygen, unlike profundal chironomids. Given the range of possible interpretations, changes in this index is problematic without additional long-term information on either the lake (e.g. water-quality, planktivorous fish populations), or other information from the core including the concentrations of both chironomids and Chaoborus.

We also identified a mid-depth chironomid assemblage, which can be viewed as a transition between habitats. Although the mid-depth zone is not as distinct as the other two zones in terms of assemblage composition, it can be defined by certain taxa and by the declines or increases of the dominant taxa of the adjacent zones and is clearly defined on axis 2 of the PCA ordination (Fig. 2-4). For example, members of the Tanytarsini group common to mid-depth include: M. contracta-type, M. insignilobus-type, and T. pallidicornis-type (Fig. 2-3).

The shallow-water chironomid assemblage in Gall Lake occurred at depths generally < 6 m and consisted of a diverse assemblage of many taxa at lower % abundance in comparison to the few, but more abundant chironomid taxa in the profundal zone. There is reasonable
agreement with shallow-water taxa observed in Gall Lake and other study lakes from north-temperate regions. *Tanytarsus, Microtendipes, Pagastiella, Cladopelma,* and *Zalutschia* are known to prefer the littoral zone (e.g. Sahmah, 1993; Walker and MacDonald, 1995; Kurek and Cwynar, 2009a). We also observed that *P. nubeculosum*-type is an indicative of the near-shore environment similar to Kurek and Cwynar (2009a), where they found *Polypedilum* at shallow depth.

While depth itself is not a direct, causal factor associated with the distribution of midges and diatoms, there are certainly a myriad of factors that co-vary in a consistent fashion over time. Juggin’s (2013) conclusion of a lack of consistency in diatom optima between datasets may partially rest in complexities associated with between-lake versus within-lake calibration datasets. Generally, the ‘noise’ associated with other environmental variables (i.e. nuisance or secondary gradients) in between-lake datasets is relatively large. This can obscure the relationship of biological assemblages to depth, but this does not imply that depth-specific habitat preference is ecologically unimportant. Given the robust changes in chironomid assemblages with depth, and the strong inferences models based on the optima of chironomid taxa, reconstruction of changes in lake depth and associated factors are certainly possible, and environmentally realistic. However, given the complexities of these reconstructions, multiple proxies should be examined to support inferences of changes in lake depth.

2.5.2 *Do midges support inferences of changes in lake level over the past 2000 years?*

Given the difficulties associated with the complexities of a composite variable such as lake depth, multiple lines of evidence should be used to assess environmental inferences associated with historic lake-level shifts. In present-day drainage lakes, Laird et al. (2011) summarize the evidence that supports core location as being critical for detecting changes in diatom
assemblages associated with a decline in lake depth. Core location is also critical for detecting a signal with midges and likely other common invertebrate indicators (e.g., Cladocera). Because chironomid assemblages at lake-water depths greater than ~8-10 m exhibit little change in overall assemblage structure (Fig. 2-3, Supplemental 2-1), and associated inferences of lake-depth plateau at depths greater than ~10 m, different coring locations within the lake will represent different sensitivities to detect shifts in lake level. For example, a core taken at a depth of ~8 m would likely be an ideal location to detect changes in lake level, whereas a core take from a deeper location would be less sensitive (i.e. further away from the depth at which assemblage changes related to depth are occurring; see Haig et al., 2013; Ma et al., 2013).

To assess the utility of midges as indicators of changes in lake depth over time, we examined midge assemblages in a core taken from a depth of 7.5 m in Gall Lake. Assessment of changes in midge assemblages was based on a number of metrics including: relative abundances and concentrations; a simplification of chironomid assemblages summarized as shallow, mid-depth and profundal categories; depth reconstructions based on overall chironomid assemblage composition; and changes in the Chaoborus-to-chironomid index, and the overall concentration of Chaoborus taxa. Consistent with the diatom based inferences, all of these metrics suggest an interpretation of a drop in water level during the MCA (Dry 1) relative to the 500-years periods preceding and following this period. A reconstruction of lake depth clearly indicates that lake level was ~1-2 m lower throughout the MCA, in comparison to the higher inferred lake levels during the Wet 1 and Wet 2 periods (Fig. 2-7). The consistency of inferences during these 500-year periods between diatom and chironomid proxies (Fig. 2-7) strongly suggests that Gall Lake experienced reduced water levels during the MCA, thereby adding additional support for a regional MCA signal (Laird et al., 2012).
2.6 Conclusion

Qualitative and quantitative reconstructions of lake depth can lead to environmentally-relevant and correct interpretations, as lake depth is an important, but indirect composite variable. Our findings suggest that knowledge about modern-day ecology and the distribution of midge assemblages are fundamental to understanding historic lake levels at Gall Lake. Additionally, midge-based inferences of lake levels provide additional evidence that the MCA in northwestern Ontario was arid. Multi-proxy paleolimnological studies based on: informed lake selection and coring location, limnological-based mechanisms, and spatially-extensive networks of lakes near ecotonal boundaries need to be developed to advance our understanding of climate change impacts on freshwaters. Such information enables water managers and policy makers to define realistic scenarios of hydrological changes that may occur in the near future.

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2.8 Literature cited


Walker, I.R., MacDonald, G.M. 1995. Distribution of Chironomidae (Insecta: Diptera) and other freshwater midges with respect to tree line, Northwest Territories, Canada. Arctic and Alpine Research 3, 258-263.
Supplemental Figure 2-1. Relationship between observed depth and chironomid-inferred lake depth based on a transect of 31 surface-sediment samples from Gall Lake (Fig. 1B). This model is based on a weighted-averaging regression and calibration model using non-transformed species abundances of 29 chironomid taxa.
Chapter 3

Diatom-based evidence of regional aridity during the mid-Holocene period in boreal lakes from northwest Ontario (Canada)
3.1 Abstract

Boreal regions and their freshwater ecosystems may be susceptible to future climate change under projected warmer conditions. Northwest Ontario is a boreal region adjacent to the climatically sensitive prairie-forest ecotone. Pollen records spanning the Holocene from near the Manitoba/Ontario border to lakes up to ~300-km east of the prairie-forest ecotone, indicate a warmer and possibly wetter mid-Holocene period across northwest Ontario from ~8000 to 4500 cal yr BP. To date only one Holocene-scale record of changes in effective moisture, as indicated through diatom-inferred changes in lake level (ELA Lake 239), is available from this region. Our study expands the regional context of Holocene climate change, with the analysis of diatom assemblages in sediment cores from two additional lakes, which span a distance of over 200-km across the present-day boreal forest, from 80-km west of ELA Lake 239 to ~150-km to the northeast. In cores from both lakes, benthic taxa predominate in the early-to-mid-Holocene period, with a low abundance of planktonic taxa, suggesting lower lake levels by ~2-5 m. Increases in the abundance of planktonic taxa to >50% occurred in both lakes beginning ~4500- to 4000 cal yr BP suggesting positive water balance over the last 4000 years in comparison to the mid-Holocene period. This new evidence supports a regional mid-Holocene period of aridity, with reduced water levels across the boreal region of northwest Ontario. If future climate change results in lower effective moisture, then conditions could become similar to the mid-Holocene period aridity, leading to real challenges for the management of water resources across the region.
3.2 Introduction

Boreal regions are globally significant biomes containing over 60% of the fresh surface water on the planet and more than half of the carbon stored in forested regions (Schindler and Lee, 2010). Boreal regions and their freshwater ecosystems may be extremely vulnerable to climate change, especially boreal regions situated adjacent to ecotonal regions (Frelich and Reich, 2010). One such region is northwest Ontario, a boreal region located adjacent to the semi-arid Canadian prairies to the west. Projections from General Circulation Models, using several emission scenarios, suggest that the temperatures in northwest Ontario will increase by a mean of ~2°C by 2020, and by > 3 °C by 2050 (Chiotti and Lavender, 2008). It is widely expected that warming will lead to the prairie biome shifting to the northeast, displacing the existing forest (Frelich and Reich, 2010). Warming will likely increase the occurrence and magnitude of fires, winds, insects and disease, which would further fragment the landscape and lead to a reduction in the extent of the boreal forest (Frelich and Reich, 2010).

Given the climatic sensitivity of ecotonal regions, it is important to understand how aquatic systems and water balance have changed over time in response to a changing climate. Fortunately, changes in climate over the Holocene period are relatively well known from studies of pollen from trees, shrubs and grasses preserved in lake sediments. In a synthesis of pollen data across the prairie-forest ecotone (PFE) in central Canada and the north-central USA, a rapid eastward expansion of prairie occurred between 10,000 and 8000 cal yr BP, with the prairie reaching its maximum extent by 6000 cal yr BP (Williams et al., 2009). Well-dated sediment cores that have been analysed for pollen are sparse in northwest Ontario. However, the few sites in this region indicate changes to a more open forest (parkland) during the early-to-mid-Holocene period (McAndrews, 1982; Björck, 1985; Lewis et al., 2001; Moos and Cumming,
Pollen-based inferences from the Experimental Lakes Area (ELA) Lake 239 in northwest Ontario, suggest conditions were wetter and approximately 1-2°C warmer than today during the mid-Holocene period (~8000 to 4500 cal yr BP). A synthesis of available pollen-based records from the North American Pollen Database, which span the Canadian prairie-boreal forest ecotone, indicate changes in vegetation at eight sites (Moos and Cumming, 2011). However, there were differences in the species changes dependent on lake location; the prairie lakes indicate changes in Poaceae and *Ambrosia* during the mid-Holocene period, whereas changes in Cupressaceae and *Ambrosia* are more apparent in the boreal region.

There is a scarcity of Holocene-scale records of hydrologic conditions from boreal regions, particularly in northwest Ontario (Laird and Cumming, 2008; Moos et al., 2009). This paucity of long-term hydrological changes largely reflects the difficulty in detecting changes in effective moisture from sedimentary evidence in drainage lakes, those with a surface outlet (Smol and Cumming, 2000). Currently, the only Holocene-scale record of effective moisture is from ELA Lake 239, a drainage lake within the Winnipeg River Drainage Basin (WRDB), a watershed that is ~150,000 km² in surface area. This record is based on a modified Digerfeldt approach, which is summarized in Laird et al. (2011). This approach identifies sensitive coring locations from near-shore regions with high rates of sediment accumulations to reconstruct changes in lake level from drainage lakes based on the diatom assemblages preserved in the lake sediments.

A primary focus of this study was to investigate the changes in sediment cores from two additional northwest Ontario lakes to assess whether the trends in water levels at ELA Lake 239 were representative of the region, with inferred low levels throughout the mid-Holocene period and a transition to higher water levels for the last ~4000 years. A secondary focus was to
determine whether there was a west-to-east gradient in the timing or magnitude of change as was seen in the northern U.S. prairies in the early to mid-Holocene period (Williams et al., 2010). The two study lakes, Meekin Lake and Gall Lake, were chosen from six previously studied unregulated low-order lakes in northwest Ontario that were investigated for changes in water level over the past ~2000 years (Laird et al., 2012). The rational for choosing these two lakes was that these two lakes maximized the west-to-east moisture gradient across the boreal region in northwest Ontario, with Meekin Lake closest to the modern-day prairie-boreal forest ecotone and Gall Lake ~200 km to the northeast situated in present-day boreal forest (Fig. 3-1A).

3.3 Study sites
Meekin Lake (N 49° 49', W 94° 46') is located in the western portion of the WRDB (in the Lake of the Woods/ Rainy River Watershed) just 22 km northwest of Kenora, and ~100 km away from the modern-day prairie-forest ecotone (PFE) boundary (Fig. 3-1A). The watershed is mostly forested with minimal anthropogenic activities in the catchment (Kingsbury et al., 2012). The predominant vegetation around Meekin Lake is balsam fir (Abies balsamea), poplar (Populus spp.), white birch (Betula papyrifera), with some red maple (Acer rubrum) and black ash (Fraxinus nigra). Meekin Lake is a relatively large (surface area = 78 ha, maximum depth = 13 m), first-order circumneutral lake (pH = 6.5) that is oligotrophic (total phosphorus (TP) = 9.7 µg/L) and moderately coloured (dissolved organic carbon (DOC) = 7.7 mg/L) (Kingsbury et al., 2012). Importantly, this lake had a gently sloping eastern basin (Fig. 3-1B), from which the near-shore core was taken from a depth chosen based on changes in modern diatom assemblages (Laird et al., 2011).

Gall Lake (N 50° 14', W 91° 27') is located within the eastern region of the WRDB (in the English River Watershed), approximately 20 km northwest of Sioux Lookout, and ~250 km
Figure 3-1. A) Map showing the location of the three study lakes (Meekin, ELA Lake 239, and Gall Lake) that are located within the Winnipeg River Drainage Basin. Black dash line is the modern-day prairie-forest boundary (from Weir, 1983). Meekin Lake is located in the Lake of the Woods/Rainy River Watershed, whereas Lake 239 and Gall Lake are located in the English River Watershed. B) Bathymetry map of Meekin Lake showing changes in lake depth (2 m contour intervals) and the coring location (black circle); C) Bathymetry of Gall Lake showing changes in lake depth (2 m contour intervals) and the coring location (black circle). Please see text for rationale of near-shore coring locations.
away from the PFE boundary (Fig. 3-1A). Similar to Meekin Lake, the watershed of Gall Lake is mostly forested with minimal anthropogenic activities in the catchment (Kingsbury et al., 2012). However, the vegetation is quite different being dominated by black spruce (*Picea mariana*), jack pine (*Pinus banksiana*), and poplar, with lesser amounts of white birch, balsam fir, and larch (*Larix* spp.). Gall Lake is also a first-order lake with a smaller surface area (19 ha), but with a greater maximum water depth (18 m) than Meekin Lake. Gall lake is slightly acidic (pH = 5.9), oligo-mesotrophic (TP = 12.3 µg/L), with a relatively high concentration of DOC (15.8 mg/L) (Kingsbury et al., 2012). Similar to Meekin Lake, Gall Lake has an eastern basin that is gently sloping (Fig. 3-1C), which allowed sufficient sediment accumulation and assessment of changes in the present-day distribution of diatom assemblages, enabled the identification of a sensitive coring location (Laird et al., 2011).

### 3.4 Methods

#### 3.4.1 Field sampling and core location

Prior to coring, high-resolution sub-bottom profiling was used to identify near-shore areas in each lake with high sediment deposition. Sub-bottom profiling was accomplished using a Knudsen 320M marine sounder with 200 kHz and 28 kHz transducers. A square-rod Livingstone piston corer (ID – 5.1cm), a corer designed to recover sediment in 1-m increments (Glew et al., 2001), was used to collect cores from each of the study lakes. The piston cores were wrapped in 1-m sections on site and subsequently sectioned into ~0.25-cm intervals in the lab.

Our modified Digerfeldt approach is outlined in detail in Laird et al. (2011), but is briefly described here. The sediment cores used in this study were located ~1.5 m deeper than the modern-day benthic-to-planktonic (B-P) diatom boundary (Laird et al., 2011; Kingsbury et al., 2012), as a means of determining a sensitive location to interpret lower lake levels in drainage
lakes, in comparison to deep center cores which have been shown to be much less sensitive to variations in lake level (Laird and Cumming, 2009; Haig et al., 2013; Ma et al., 2013). The B-P diatom boundary is the water depth where there is a distinct change in the present-day diatom assemblage from primarily benthic diatoms to an assemblage dominated primarily by planktonic diatoms as water levels increase and is based on a within lake surface-sediment calibration across the depth gradient (Laird et al., 2011; Kingsbury et al., 2012). As lake-level declines, the B-P boundary will move towards the center of the lake and move back towards the lake shore with a rise in lake level (Laird et al., 2011). Retrieval of a core near this boundary provides a means of tracking this movement and inferences of changes in lake level. The depth of the B-P diatom boundary in both of our study lakes were established by Kingsbury et al. (2012) and occurs at a depth of ~10 m in Meekin Lake, and a depth of ~6 m in Gall Lake, the difference thought to be related to the greater light transparency in Meekin Lake (Kingsbury et al., 2012). Consequently, the targeted depths for coring were set at 11.5 m for Meekin Lake, and a depth of 7.5 m for Gall Lake. We compare our results to the previously published Holocene sedimentary record from ELA Lake 239 (Laird and Cumming, 2008), in which the depth of the diatom B-P boundary was ~10-12 m and core retrieved at ~13 m.

3.4.2 Geochronology

The chronology for the sediment cores for Meekin and Gall Lakes were primarily based on accelerator mass spectrometry (AMS) estimates of age based on $^{14}$C dating (Fig. 3-2), as well as measurements of $^{210}$Pb activities on the uppermost samples from each lake. Briefly, 8 to 12 AMS $^{14}$C dates were obtained along the cumulative depth of the sediment cores from Meekin and Gall lakes (Table 3.1). The AMS $^{14}$C age estimates were based on the carbon from pollen isolated from lake sediments (Brown et al., 1989), which was subsequently measured at the Lawrence
Table 3.1. Summary of the $^{14}$C-dating results on pollen isolated from selected intervals from the sediment cores from Gall and Meekin lakes. All analyses were performed based on pollen isolated at the Limnological Research Center at the University of Minnesota, and dated at Lawrence Livermore National Laboratory.

<table>
<thead>
<tr>
<th>Lake name, core number and section</th>
<th>Sample depth (cm)</th>
<th>Cumulative depth (cm)</th>
<th>$^{14}$C Age (± 1 SD)</th>
<th>Calibrated $^{14}$C Age (± 2 sigma) calendar years BP (clam)</th>
<th>No. of CAMS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gall, C2S1</td>
<td>24-24.5</td>
<td>24-24.5</td>
<td>1125±53</td>
<td>958-1092</td>
<td>149853</td>
</tr>
<tr>
<td>Gall, C2S1</td>
<td>44-44.5</td>
<td>44-44.5</td>
<td>1760±35</td>
<td>1567-1740</td>
<td>149831</td>
</tr>
<tr>
<td>Gall, C2S1</td>
<td>63-63.5</td>
<td>63-63.5</td>
<td>2380±30</td>
<td>2342-2489</td>
<td>149832</td>
</tr>
<tr>
<td>Gall, C2S1</td>
<td>80-80.5</td>
<td>80-80.5</td>
<td>3110±30</td>
<td>3239-3385</td>
<td>149833</td>
</tr>
<tr>
<td>Gall, C2S2</td>
<td>27-27.5</td>
<td>110-110.5</td>
<td>4155±30</td>
<td>4582-4769</td>
<td>157795</td>
</tr>
<tr>
<td>Gall, C2S2</td>
<td>77-77.5</td>
<td>161-161.5</td>
<td>6005±35</td>
<td>6750-6767</td>
<td>157796</td>
</tr>
<tr>
<td>Gall, C2S3</td>
<td>21-21.5</td>
<td>196-196.5</td>
<td>7525±30</td>
<td>7968-8068</td>
<td>157797</td>
</tr>
<tr>
<td>Gall, C2S3</td>
<td>47-47.5</td>
<td>222-222.5</td>
<td>8045±40</td>
<td>8763-9030</td>
<td>157798</td>
</tr>
<tr>
<td>Meekin, C1S1</td>
<td>30.25-31</td>
<td>30.25-31</td>
<td>895±30</td>
<td>737-834</td>
<td>149837</td>
</tr>
<tr>
<td>Meekin, C1S1</td>
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<td>50-51</td>
<td>1605±30</td>
<td>1413-1552</td>
<td>147807</td>
</tr>
<tr>
<td>Meekin, C1S2</td>
<td>10.25-11</td>
<td>79.5</td>
<td>2020±30</td>
<td>1894-2051</td>
<td>149838</td>
</tr>
<tr>
<td>Meekin, C1S2</td>
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<td>2747-2808</td>
<td>147808</td>
</tr>
<tr>
<td>Meekin, C1S2</td>
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<td>149-149.5</td>
<td>3270±40</td>
<td>3437-3579</td>
<td>147809</td>
</tr>
<tr>
<td>Meekin, C1S2</td>
<td>85.25-85.5</td>
<td>154-154.5</td>
<td>3505±30</td>
<td>3696-3859</td>
<td>147835</td>
</tr>
<tr>
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<td>183.5-184</td>
<td>4110±30</td>
<td>4225-4709</td>
<td>157808</td>
</tr>
<tr>
<td>Meekin, C1S3</td>
<td>75-75.5</td>
<td>233-233.5</td>
<td>4995±30</td>
<td>5650-5758</td>
<td>157809</td>
</tr>
<tr>
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<td>5620±30</td>
<td>6313-6453</td>
<td>157810</td>
</tr>
<tr>
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<td>333-333.5</td>
<td>6640±30</td>
<td>7407-7575</td>
<td>157811</td>
</tr>
<tr>
<td>Meekin, C1S5</td>
<td>25-25.5</td>
<td>383-383.5</td>
<td>7885±30</td>
<td>8592-8777</td>
<td>157812</td>
</tr>
<tr>
<td>Meekin, C1S5</td>
<td>50-50.5</td>
<td>409-409.5</td>
<td>8280±35</td>
<td>9137-9405</td>
<td>157813</td>
</tr>
</tbody>
</table>
Figure 3-2. A) Age-depth model for Meekin Lake and B) for Gall Lake, based on calibrated $^{14}$C dates (Table 1), obtained by the clam software (Bläauw, 2010). Dates and errors are shown in blue. The grey area shows 95% confidence intervals based on 1000 iterations.
Liverpool National Laboratory. Radiocarbon dates were calibrated (using IntCal09, Reimer et al., 2009, under *clam* package) and age-depth models were created using ‘classical’ age-depth modelling (Blaauw, 2010). To determine the age at the top interval of the piston core, total $^{210}\text{Pb}$ was measured in the uppermost sediment in the first section of the piston cores from each lake. This activity was compared with a dated gravity core retrieved at the same depth as the piston core. The unsupported activity of $^{210}\text{Pb}$, along with percent organic matter and diatom assemblage data was used to determine the overlap between the gravity and piston cores in each lake (Laird et al., 2012).

### 3.4.3 Laboratory

Diatom slides were prepared and enumerated at 4-cm intervals in the piston cores from both lakes. Briefly, a 50:50 molar mixture of concentrated sulfuric and nitric acid was added to approximately $~0.2-0.3$ g of wet sediment in a 20-ml glass vial, which was subsequently heated in a water bath at $~80$ °C for a period of 6-7 hours. After allowing the sample to settle for a period of 24 hours, the acid above the sample was removed by suction into a flask, and then rinsed with deionized water. This procedure was repeated, until the sample reached the same pH as the deionized water (around 8 rinses). The sample was then drawn down to a height of $~5$ ml at which time a known volume of microsphere solution (concentration – $2.0 \times 10^7$ spheres/ml) was added. A pipette was used to remove a small volume of the sample into a test tube, which was subsequently diluted with deionized water, before being pipetting onto a coverslip. In total, four successive dilutions from each slurry were made. The slurries on the coverslips were allowed to air dry ($~12$ hours) on a warming tray, at which point the coverslips were heated on a hotplate to remove any remaining moisture, before being permanently mounted onto glass microscope slides using Naphrax®.
Diatoms were enumerated using a Leica DMRB microscope with a 100x fluotar objective (NA = 1.3) and differential interference contrast optics at 1000x magnification. For each sample, a minimum of 400 diatom valves were counted along transects on the coverslip. Diatoms were identified down to the species level or lower using the following taxonomic references (e.g. Krammer and Lange-Bertalot, 1986, 1988, 1991a, b; Cumming et al., 1995; Lange-Bertalot and Melzeltin, 1996, and Camburn and Charles, 2000). Chrysophyte scales were also enumerated, but not identified to the species level. Estimates of the percent of organic matter in the sediments from both lakes were carried out every 4 cm in each of the cores following the methods outlined by Dean (1974). The chrysophyte scale-to-diatom index was calculated using the following formula: \[\text{number of scales/ (number of scales + number of diatom valves)} \times 100.\] Calculation of the concentration of diatoms is based on the addition of known concentration of microspheres and follows methods outlined in Battarbee and Kneen (1982).

3.4.4 Numerical analysis

To assess and summarize the changes in diatom assemblages over the Holocene, a number of techniques were used. First, both the relative abundance and concentration of individual diatom taxa were assessed. Secondly, to summarize the main diatom assemblages, taxa with a relative abundance >5% in at least two samples were plotted, and taxa with lower abundances were grouped into larger taxonomic categories (such as \textit{Achnanthes sensu lato}, \textit{Navicula sensu lato}, \textit{Fragilaria sensu lato}, etc.). Thirdly, a commonly used constrained clustering technique [CONISS, using a squared Euclidean distance as a measure of similarity] was undertaken with the aid of the computer program Tilia v. 2.02 (Grimm, 1987) to define the major periods of similar diatom assemblages. Fourth, the main trends in diatom assemblages were summarized and compared by two ordination techniques using square-root transformed species data:
Correspondence Analysis (CA) and non-metric multidimensional scaling (nMDS). Analyses were based on taxa ≥2% in one sample (including grouped categories). The computer program CANOCO v. 5 was used to calculate the CA and nMDS (ter Braak and Šmilauer P, 1998). This comparative approach between ordination methods provided an opportunity to assess the robustness of the two approaches. While nMDS has not been as commonly used to summarize paleolimnological data as principal component analysis (PCA) or CA (Legendre and Birks, 2012), nMDS has fewer assumptions on the structure of species data, on the interrelationship between the samples and can generally represent assemblage relationships in low-dimensional space (Clarke and Warwick, 2001). nMDS also provides the ability to choose the Bray-Curtis dissimilarity measure which is very suitable for data sets with lots of zero’s (Clarke and Warwick, 2001). Finally, a regional summary is provided by a comparison of the results from the two new study lakes (Meekin and Gall) with those from the previously published near-shore core from ELA Lake 239 (Moos et al., 2009) using graphics in Origin ver. 6.1 (Origin, 2000).

3.5 Results

Piston cores were obtained from a depth of 11.4 m in Meekin Lake in June 2009, and from a depth of 7.5 m in Gall Lake in June 2010. The cumulative length of the sediment cores were 440 and 230 cm for Meekin and Gall lakes, respectively, and in both cases, grey clays were present in the bottommost sections. The activities of $^{210}$Pb in the upper intervals of the piston cores from Meekin (0-0.5 cm interval) and Gall lakes (2.5-3 cm interval) corresponded to the years 1960 and 1975, respectively, based on the dated gravity cores from the same depth (Laird et al., 2012). A total of 12 and 8 pollen extracts were analyzed for $^{14}$C activity in the sediment cores from Meekin and Gall lakes respectively (Table 3.1, Fig. 3-2). Good correspondence between pollen-based radiocarbon dates to those derived from macrofossils from the same sediment levels of
lakes in northwest Ontario supports the utility of using pollen as the carbon source for $^{14}$C analysis (Laird & Cumming, 2008; Moos et al., 2009; Haig et al., 2013). Based on the clam age-depth models, the analysis of diatom assemblages at a 4-cm interval in the cores represents an approximate centennial-scale resolution for both lakes (~120-year resolution for Meekin Lake and 150-year resolution for Gall Lake).

### 3.5.1 Meekin Lake

A total of 190 diatom taxa were identified from the sediment core from Meekin Lake over the last ~9500 yrs. The zonation estimated by a constrained cluster analysis (Grimm, 1987) provides a framework to discuss the major changes in diatom assemblages that occurred over the Holocene (Fig. 3-3). Broadly, changes in the diatom assemblages showed differentiation into two main periods: an early to mid-Holocene (~9600 to 4800 cal yr BP) period that was dominated by benthic diatom taxa (Zone A); and a post-4800 cal yr BP period that was characterized by a dominance of a planktonic diatom assemblage (Zone B). Trends in these two periods are elaborated below.

**Zone A (~9500-4800 cal yr BP) Early to mid-Holocene period in Meekin Lake.** The earliest part of subzone A1 (~9600 to 8600 cal yr BP), was characterized by the lowest concentrations of organic matter (<20%), and low concentrations of diatoms (Supplemental 3-1), that were dominated by a diverse assemblage of benthic diatom taxa including: *Staurosirella pinnata* (Ehrenberg) Williams and Round, *Staurosira construens* (Ehrenberg) Williams and Round, *Navicula* sensu lato, *Cymbella* sensu lato, other benthic *Fragilaria* sensu lato and *Amphora* species (Fig. 3-3). The chrysophyte-to-diatom index was low and stable. The remainder of subzone A1 (~8600 to 6400 cal yr BP) was characterised by an almost doubling of organic
Figure 3-3. The dominant (>5%) diatom taxa found in a near-shore (depth = 11.4 m) sediment core from Meekin Lake versus cumulative core depth. $^{14}$C-estimated dates are indicated to the left. The diatom taxa are arranged by Correspondence Analysis (CA) axis-1 scores so that the changes in diatom assemblages across time are clearly shown. The chrysophyte scale-to-diatom index (C to D index), total diatom concentration and percent organic matter are also plotted. The zones and subzones are indicated, as defined by the constrained cluster analysis.
matter to ~40%, and increased abundances and doubling of the concentrations of a number of the benthic taxa, with the noted exception of *S. construens* which experienced declines in both relative abundance (Fig. 3-3) and concentration (Supplemental 3-1).

Subzone A2 (~6500 to 4800 cal yr BP) was characterized by declines in many of the benthic taxa, and increases in the relative abundances and concentrations of a number of planktonic taxa that achieved their highest relative abundances and concentrations, including *Tabellaria* spp., *Aulacoseira subarctica* (O’Muller) Haworth, and *Fragilaria tenera* (W. Smith) Lange-Bertalot. This zone was also characterized by the initial appearance of *Discostella stelligera* (Cleve and Grunrow) Houk and Klee and *Discostella pseudostelligera* Houk and Klee initially at low abundances which then increase to over 10% by ~4800 cal yr BP. Percent organic matter increased gradually over this period from ~40 to 50%, and the chrysophyte-to-diatom index remained low and variable throughout most of this subzone, decreasing to essentially zero by ~4800 cal yr BP.

*Zone B (~4800 to present cal yr BP) Mid-to-late Holocene in Meekin Lake.* The mid-to-late Holocene in Meekin Lake was characterised by large increases in the relative abundances and concentrations of *D. stelligera*, and *D. pseudostelligera* reaching combined relative abundances of ~40-75% (Fig. 3-3, Supplemental 3-1). The planktonic taxa, *T. flocculosa* strains 3p and 3 (*Tabellaria flocculosa* (Roth) Kutz strains (*sensu* Koppen), *A. subarctica* and *F. tenera* declined in both relative abundance and concentrations in Zone B, whereas the planktonic taxa *C. michiganiana* and other *Aulacoseira* (mainly *A. distans var humilis* Ehrenberg) increased. The relative abundance and concentrations of *S. pinnata* reached a record low at the beginning of this period, but then fluctuated between ~15 and 30% over the last ~4600 years.
3.5.2 Gall Lake

A total of 163 diatom taxa were identified from the sediment core from Gall Lake over the last ~9200 yrs. The zonation estimated by a constrained cluster analysis (Grimm, 1987) provides a framework to discuss the major changes in diatom assemblages that occurred over the Holocene (Fig. 3-4). Similar to the changes seen in the sediment core from Meekin Lake, changes in the diatom assemblages show differentiation into an early to mid-Holocene period (~9200 to 4000 cal yr BP), that was dominated by benthic diatom taxa (Zone A), and a post-4000 cal yr BP period that was characterized by a dominance of a planktonic diatom assemblage (Zone B). Trends in these two periods are elaborated on below.

Zone A (~9200 to 4000 cal yr BP) Early to mid-Holocene period in Gall Lake. The early to mid-Holocene period was composed of three distinct subzones (A1, A2, and A3; Fig. 3-4). Subzone A1 (~9200 to 8000 cal yr BP), was characterized by low concentrations of organic matter that increased from <5% to ~25% by ~7800 cal yr BP. From ~9200 to 8200 cal yr BP, low abundances and concentrations of planktonic taxa, including D. stelligera and Tabellaria, and some Aulacoseira taxa, co-existed with low concentrations of benthic taxa (S. construens, S. pinnata, Navicula sensu lato, Achnanthes sensu lato., and Cymbella sensu lato) followed by increases in the concentration and relative abundance of S. pinnata (Fig. 3-4, supplemental 3-2). The chrysophyte-to-diatom index was very low throughout Subzone A1.

Subzone A2 (~8000 to 5700 cal yr BP) was characterised by an initial increase in the organic matter to ~30% which then remained relatively constant. S. pinnata increased in relative abundance and concentration, as did many of the other benthic Fragilaria sensu lato (mainly Staurosirella leptostauron (Ehrenberg) Williams and Round (Fig. 3-4, Supplemental 3-2). Total
Figure 3-4. The dominant (>5%) diatom taxa found in a near-shore (depth = 7.5m) sediment core from Gall Lake versus cumulative core depth. $^{14}$C-estimated dates are indicated to the left. The diatom taxa are arranged by Correspondence Analysis (CA) axis-1 scores so that the changes in diatom assemblages across time are clearly shown. The chrysophyte scale-to-diatom index (C to D index), total diatom concentration and percent organic matter are also plotted. The zones and subzones are indicated, as defined by the constrained cluster analysis.
concentration of diatom valves increased throughout this zone, which was reflected primarily in increased concentrations of *S. pinnata*, other benthic *Fragilaria* sensu lato, *Achnanthes* sensu lato, and *Navicula* sensu lato (Supplemental 3-2). The chrysophyte-to-diatom index remained very low in this zone.

Subzone A3 (~5700 to 4000 cal yr BP) was characterized by declines in the previously common benthic taxa (*S. pinnata*, other benthic *Fragilaria* sensu lato, *Achnanthes* sensu lato, and *Navicula* sensu lato) that were replaced by other benthic taxa (e.g., *Achnanthidium minutissimum* (Kützing) Czarnecki, *Brachysira*, *Nitzschia*, *Cymbella* sensu lato), as well as some planktonic taxa, including *Cyclotella michiganiana* and small abundances of other planktonic taxa (e.g. *Aulacoseira tenella* (Nygaard) Simonsen, *D. stelligera*, and *Tabellaria*) (Fig. 3-4, Supplemental 3-2). Percent organic matter remained high, reaching a peak of just over 30%. Total concentration of all diatoms decreased, and the chrysophyte-to-diatom index remained very low.

**Zone B (~4000 to present cal yr BP)** Mid-to-late Holocene in Gall Lake. The mid-to-late Holocene in Gall Lake was characterised by large increases in the relative abundances and concentrations of planktonic taxa including *Asterionella formosa* (Hassall) Houk et Klee., *Aulacoseira distans* (Ehrenberg) Simonsen, *Aulacoseira tenella*, *D. stelligera*, *Cyclotella bodanica v. lemanica*, *Tabellaria* spp. (Fig. 3-4, Supplemental 3-2). Although the relative abundance of *C. michiganiana* remained constant, the concentration of this taxon declined somewhat from the previous zone (Fig. 3-4, Supplemental 3-2). Most of the benthic taxa that increased in Subzone A3 (e.g., *Achnanthidium minutissimum* *Brachysira*, *Nitzschia*, *Cymbella* sensu lato) remained relatively constant in both relative abundance and concentration in Zone B. Peak abundances of *D. stelligera*, the dominant planktonic taxon, were reached in the uppermost
three samples. Total concentration of all diatoms was lower throughout Zone B, and the chrysophyte-to-diatom index remained very low, but increased slightly until the last 1000 years, where this index greatly increased.

### 3.5.3 Regional patterns in diatom assemblages

Changes in the diatom assemblages in well-dated sediment cores over the Holocene along a west-to-east gradient across the boreal region (Meekin Lake, ELA Lake 239 and Gall Lake) were summarized by three metrics: changes in the main direction of variation in the diatom assemblages (CA axis-1 scores), changes in the percentage of planktonic diatoms; and changes in the dominant planktonic diatom in all three cores, *D. stelligera* (Fig. 3-5). Concentrations and % abundance of *D. stelligera* showed very similar patterns across all three lakes (Fig. 3-5 and Supplemental Fig. 3-3). The CA axis-1 scores captured 56.8% (Meekin Lake), 66.8% (ELA Lake 239) and 69% (Gall Lake) of the variance, and the patterns in all three metrics were similar. *Discostella stelligera* is the dominant planktonic taxon in all three lakes and the % abundance significantly correlated with the % abundance of planktonic taxa for all three lakes (Meekin, r = 0.9, n = 109, p = <0.05; Lake 239, r = 0.96, n = 72, p = <0.05; Gall, r = 0.88, n = 60, p = <0.05). In ELA Lake 239 and Gall Lake, the early-Holocene diatom assemblages initially contained planktonic taxa but at low concentration (Fig. 3-4, Moos et al., 2009) that quickly changed to dominance by benthic taxa by the mid-Holocene period. For the last ~4000 years, the diatom assemblages in all lakes reached high and relatively stable abundances of planktonic taxa, which were dominated by *D. stelligera*. Transition out of the dominance of the diatom assemblage by benthic taxa and the low lake levels of the mid Holocene began much earlier in Meekin Lake with increasing percentages of planktonic taxa starting ca. 6500 cal yr BP (Fig. 3-5). Whereas the
Figure 3-5. Summary of the changes in diatom assemblages in sediment cores of the three lakes (Meekin, ELA Lake 239, and Gall Lake) arranged in geographic position from west to east. Three metrics are shown to summarize the changes over the Holocene: A) Correspondence Analysis (CA) axis-1 scores, B) percent (%) planktonic taxa, C) percent abundance of the dominant planktonic taxon in all cores, *Discostella stelligera*.
initial increase in % planktonic taxa occurred later and with similar timing at ca. 5700 cal yr BP in ELA Lake 239 and Gall Lake (Fig. 3-5).

Changes in the diatom assemblages within three broad time periods were summarized by a nMDS plot (Fig. 3-6). The time periods used were: i) the period of deglaciation to ~8000 cal yr BP; ii) the mid-Holocene warm period (~ 8000 to 4000 cal yr BP), and iii) the neoglacial period (~4000 cal yr BP to present). In general, the three periods were distinct in their assemblages in each of the lakes as there is little overlap of the groups in ordination space (Fig. 3-6). The exception to this is the overlap between the early and mid-Holocene period in Meekin Lake and Lake 239, as our generalized time periods do not exactly correspond to the assemblage zones of the individual lakes (Figs. 3-3 and 3-4). In addition, in Lake 239 the initial assemblage after deglaciation had similar percentages to the early part of the late Holocene (albeit much lower concentrations, Fig. 3-5 and Supplemental Fig. 3-3) of some planktonic taxa (i.e. D. stelligera as a consequences these early-Holocene samples ordinate closer to the late Holocene assemblages. In Meekin and Gall lakes particularly, the mid-Holocene period is a period of gradual change of transition between the early and late Holocene assemblages, as represented by the broad placement of samples across nMDS axis space. Across all lakes, the late Holocene assemblages were very distinct from the other two periods and had the most similar composition within the period as represented by the tight cluster of samples (Fig. 3-6).

3.6 Discussion

The WRDB is an important source of water for ecosystems and human activities. Future climate projections for this region include temperature increases in excess of 2 °C over the next 20 years (Chiotti and Lavender, 2008). Instrumental records show that WRDB has experienced droughts during the 1930s, 1950s, and 1980s, but these droughts have been spatially asynchronous across
climate stations in northwest Ontario (Laird et al., 2012). However, periods of synchronous aridity have occurred across this region over the past 2000 years, as indicated by the regional drought during the Medieval Climate Anomaly (Laird et al., 2012). Given this climatic sensitivity over the last 2000 years, the goal of this study was to assess if synchronous changes in water balance have occurred over longer timeframes, especially in the mid-Holocene period, a time when temperatures have been inferred to be at least 1-2 °C warmer than present in the WRDB (Moos and Cumming, 2012). The impact of extreme aridity over the Holocene has been well studied on the northern prairies from loess records (Miao et al., 2005; Wolfe et al., 2006), pollen and other proxy records (Grimm et al., 2011) and from lake records (Laird et al., 2007), whereas changes in water balance over the Holocene in boreal regions is less studied. The recent synthesis of pollen records in the WRDB (Moos and Cumming, 2012) indicates a distinct change in the vegetation in the mid-Holocene period to a more open canopy forest with increased temperatures (particularly in the winter) and increased evapotranspiration (reduced effective moisture).

The impact of these inferred changes in effective moisture on lake ecosystems in the WRDB is poorly known. Influences of lake-level changes are mainly known from various proxies on one lake sediment record, ELA Lake 239, in northwest Ontario (Laird and Cumming, 2008; Moos et al., 2009; Moos and Cumming, 2011, 2012). The lack of studies to date on lake-level fluctuations in boreal regions is largely due to the problem of investigating hydrologic changes in drainage lakes (Smol and Cumming, 2000; Laird and Cumming, 2008). Our modified Digerfeldt approach for ELA Lake 239 (Laird and Cumming, 2008) was applied to the Holocene records from Meekin and Gall lakes to provide a more regional assessment of the changes in lake
Figure 3.6. Non-metric multidimensional scaling (nMDS) plot of diatom assemblages over the Holocene in: A) Meekin Lake; B) ELA Lake 239; C) Gall Lake. Three time periods are indicated i) deglaciation to ~8000 cal yr BP by solid square. ii) The mid-Holocene warm period (~8000 to 4000 cal yr BP) are shown by open diamond, and iii) the late Holocene (~4000 to present is shown by solid circle).
level in the WRDB. The estimated ages of sediments in the cores from Meekin and Gall lakes, based on AMS $^{14}$C-dating of pollen, provide strong evidence of continuous sedimentation and strong chronological control in the cores (Fig. 3-2). Consequently, changes in the diatom assemblages in Meekin and Gall lake cores, in conjunction with the previous record from Lake 239, enabled two important findings: i) the predominance of benthic diatom assemblages throughout the early-to-mid-Holocene period are consistent with prolonged declines in effective moisture inferred from pollen analysis in this region; and ii) the dominance of planktonic taxa over the last ~4000 years indicate that lake water levels have been much higher during this period which is consistent with cooler conditions inferred from the pollen inference in this region (Moos and Cumming, 2012).

3.6.1 Early to mid-Holocene changes in effective moisture

The dominance of benthic diatom assemblages from at least ~8000 to 5000 cal yr BP in all three lakes strongly suggests persistently low water levels across the region during the mid-Holocene warm period (Fig. 3-5), indicating that the pollen-inferred warmer temperatures and increased evapotranspiration resulted in a negative water balance in this region. The consistency between sites, which span a gradient of over 300 km through the present-day boreal forest, suggests the importance of extrinsic climate forcing (Williams et al., 2011).

The aridity of the mid-Holocene period (~8000-4000 cal yr ago) is well documented in the northern prairies of North America as well as regions to the west in the Rocky Mountains (Laird et al., 1996; Lewis et al., 2001; Shuman et al., 2009), with similar timing to those seen in our sites in northwest Ontario. The inferred declines in effective moisture had a large impact on lake levels within the region. Laird and Cumming (2008) suggest that ELA Lake 239 declined by at least 8 m during the mid-Holocene period. The consistently high % abundance and
concentrations of benthic taxa in Meekin and Gall lakes strongly suggests much lower water levels than present between ~8000 and 5000 years ago (Fig. 3-5), likely by as much as 2-3 m in Meekin Lake and 3-5 m in Gall Lake based on the modern distribution of *S. pinnata*, other benthic taxa and *D. stelligera* (Laird and Cumming, 2008; Laird et al., 2011; Kingsbury et al., 2012). The nMDS ordination also clearly showed that the diatom assemblages of the mid-Holocene period were unique in all three lakes in comparison to the early Holocene and late Holocene periods (Fig. 3-6).

The dominance of *Discostella* taxa today in both Meekin and Gall lakes and the presence of unique mid-depth assemblages (Kingsbury et al., 2012) preclude the usefulness of modern surface sample calibrations to provide adequate quantitative estimates of depth down core, due to the presence of several benthic taxa at higher abundances than those of the modern surface samples. For example, in Meekin Lake, the present-day abundance of *S. pinnata* reaches a maximum abundance of ~20% in the surface samples between a modern depth of 8 and 9 m (Laird et al., 2011). However, this taxon achieved a sustained and high relative abundance of greater than 40% in the early-to-mid-Holocene period. Similarly, the maximum abundance of *S. construens* is only ~5% in the surface samples, but the relative abundance in the core was consistently greater than ~20%. The same situation is present in Gall Lake in the early to mid-Holocene period, where the modern maximum of *S. pinnata* is ~30% occurring between 2-to-4 m depth (Laird et al., 2011), whereas in the core, abundances greater than 60% were common. This lack of adequate analogs is in part the result of models being based on % diatom taxa, a constrained metric in which if one taxon increases, others have to decrease. Other influences on analogs may be related to different physical and chemical conditions along the depth gradient today in comparison to the past. However, while specific benthic and planktonic taxa may differ
between the present and past, the B-P boundary appears to be a robust metric highly related to depth.

Several variables within a lake vary with depth and influence the spatial distribution of diatom taxa, including substrate type, disturbance regime, temperature, nutrients and light availability (Laird et al., 2011 and citations within). Wave disturbance and light availability have been found to be two of the primary factors that characterize the vertical zonation of the diatom community across the depth gradient; whereas, the location of the B-P boundary is primarily influenced by changes in water depth and light availability (Laird et al., 2011). In the analysis of diatoms along three depth transects in Worth Lake, northwest Ontario, from different portions of the basin that had different wind orientations and wave disturbance, as well as varying complexity in bottom profiles and degree of slope, the estimated B-P boundaries were the same (Laird et al, 2010). Basin morphometry, and changes in water depth, can influence the sources of benthic and planktonic taxa to the sediments and their ratios, particularly in complex basins (Stone and Fritz, 2004). Here we chose lakes with relatively simple basin morphometry and cored in the part of the basin with a gentle slope to minimize these influences. Degree of light transparency can also change with changes in depth and turbulence; however, the analysis of invertebrate remains (which are not directly influenced by light) in Gall Lake show similar trends to the diatoms over the last two millennia, suggesting that changes in depth is one of the primary influences on both proxies (Karmakar et al., 2014).

The few other Holocene studies of lake level in adjacent regions to the WRDB suggest similar magnitude changes during the mid-Holocene period as estimated in our study lakes. In two Minnesota lakes, estimated lake-level declines were between ~1-15 m (Cohen et al., 2006), and declines of up to ~10 m were estimated in Rocky Mountains lakes (Shuman et al., 2009). In
the Canadian prairies, Lake Winnipeg was a closed-basin lake from ~4.5-8.2 cal yrs BP, with the southern basin desiccated (today this basin has a maximum depth of ~11 m) and the parkland border much further to the east (Lewis et al., 2001). The return to an open-lake system and rising lake levels in Lake Winnipeg is similar to the timing of increasing planktonic taxa in Meekin Lake, our site closest to the PFE.

3.6.2 Late Holocene changes in effective moisture
In all cores, planktonic taxa increase in abundance and remain abundant by at least 4000 years ago (Fig. 3-5). Modern-day diatom assemblages from all of our study lakes show a dominance of planktonic taxa in deep waters. In all lakes *D. stelligera* and *D. pseudostelligera* reach their modern-day maximum abundances of ~40-60% at depths greater than 10 to 12 m (Laird and Cumming, 2008; Kingsbury et al., 2012). In Meekin Lake, high abundances of *D. stelligera* and *D. pseudostelligera*, combined with abundances of many other planktonic taxa, suggest high and maintained water levels, of at least the depth of coring (11.5 m) over the past 4000-5000 years. Similarly, at Gall Lake and ELA Lake 239, many planktonic taxa were dominant post-4000 years ago (Fig. 3-5). In the Gall Lake Holocene record, *D. stelligera* exceeded abundances of ~35-40%, abundances observed at water depths > 8 m in the calibration set (Kingsbury et al., 2012), suggesting water levels have been at their highest at the coring site, over the past few hundred years and during other periods over the past 4000 years.

The sites in northwest Ontario suggest high lake levels were clearly established by ~4000 cal yr BP. This is similar to the broad-scale syntheses of lake-level conditions over the Holocene in North America to generally cooler, moister conditions which generally begin ~6000 -5000 cal yr BP, with ‘modern’ conditions in some lakes not established until ~3000-2000 cal yr. BP (Ritchie and Harrison, 1993; Thompson et al., 1993). More recent studies suggest a similar
timing to the onset of moisture conditions with the onset of higher lake levels generally by ~3000 cal yrs ago in the Great Lake region (Booth et al., 2002) and in the Rocky Mountains by ~3000-4000 cal yr BP (Shuman et al., 2009). However, changes in aridity have not been static over the past 4000 years. Higher resolution studies decadal-scale analyses from near-shore cores from Gall Lake indicate that a significant period of lower lake levels, much greater than any instrumental droughts, occurred during the MCA by both diatoms (Haig et al., 2013) and invertebrates (Karmakar et al., 2014). A synthesis across the WRDB also indicates a regional period of aridity during the MCA (Laird et al., 2012). Similarly, peatland records in the western Great Lakes region suggest several extreme drought events over the past 2000 years, including the MCA period (Booth et al., 2006). However, the low lake levels of the mid-Holocene period are clearly more extreme than during the last 2000 years.

3.6.3 West to east gradient in effective moisture
Holocene shifts in the prairie-forest ecotone (PFE) have been extensively studied beginning with the classic work of McAndrews (1966), and the more recent syntheses of many studies (Nelson and Hu, 2008; Williams et al., 2009). These recent syntheses support Umbanhowar et al. (2006) that the timing and rates of the PFE shifts were heterogeneous, with many records indicating an abrupt early-Holocene transition from forest to grassland, but a more gradual reforestation during the late Holocene. A west to east time-transgressive response to aridification was also documented with the early shift in the PFE (Williams et al., 2010). Williams et al. (2011) suggest this may be due to more arid sites being nearer to a threshold than less-arid sites. The length of our early-Holocene records varies, with only ELA Lake 239 recording the very early Holocene. Potentially the larger size and depth of Lake 239 enabled greater accumulation of sediments in the near-shore locations in the earliest history of the lake. The Lake 239 sedimentary record
clearly records an abrupt transition into the lower lake levels of the mid-Holocene period. This is only somewhat evident in the Gall Lake record, but timing of at least the lowest lake levels is much later. All three lakes do indicate a more gradual transition to the higher lake levels of the late Holocene.

Variability in the timing of low lake levels in the mid-Holocene period and transition to rising lake levels in the late Holocene varies within and between regions across much of North America (Thompson et al., 1993; Laird et al., 1996; Shuman et al., 2009). Our records also show variability in the timing of the transition to planktonic diatom taxa after the mid-Holocene low stands dominated by benthic taxa, with the earliest changes occurring in Meekin Lake ~1 millennia earlier than seen in ELA Lake 239 and Gall Lake (Fig. 3-5). Spatial and temporal variability in sediment records can be attributable to many factors, including spatial variability in climate and individual responsiveness of the lakes. Potentially the more western and closer location of Meekin Lake to the PFE explains the earlier onset of higher lake levels, whereas there may have been a lag in the response in the more northern site, as seen in Teed et al. (2009). However, the timing of the transition to higher lake levels is similar between Lake 239 and Gall Lake, thus physical characteristics of the lakes, and local geological and vegetational settings may have played more of a role in lake response than geographical position. The magnitude of change also does not have a clear west to east signal. We expected Meekin Lake to have the highest magnitude change and longest duration with its closer proximity to the modern PFE. However, the magnitude of change in % planktonic composition is similar across all lakes and the estimated decline in lake level is similar between Meekin and Gall lakes. There also was not a clear west to east signal of the low-lake levels of the MCA in either timing or magnitude of six study lakes in the WRDB (Laird et al., 2012). However, the overall similarity in the direction and
magnitude of response, and generally similar timing on both time scales (last ~2000 yrs and Holocene) suggests that a broad-scale forcing factor such as climate is likely a major driver of these changes (e.g. Williams et al., 2011).

3.7 Conclusions
Sediment cores collected adjacent to the B-P boundary appears to be a sensitive method to track changes in aridity from present-day drainage lakes. As such, this approach can provide a method to estimate changes in effective moisture in comparison to conditions today, in more humid regions from where such data have been difficult to acquire. Empirical evidence of the low-water levels during the mid-Holocene period across northwest Ontario during a time when climate was warmer by 1-2 °C warmer than today has important implications for mitigation and adaptation in this region. Increasing trends in precipitation over the last 100 years across northwest Ontario suggest that water scarcity may not be an issue in the near future (St. George, 2007). However, this study and other studies (Laird et al., 2012) suggests that northwest Ontario has experienced periods of synchronous aridity in the past and thus future warming could result in droughts across the region, similar to those of the past. What the future climate holds for regions of North America due to global warming is unclear, but a return to the aridity of the mid-Holocene period would bring significant ecological, environmental, and social challenges.

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Supplemental Figure 3-3-1. Concentrations of diatom taxa found in a near-shore (depth = 11.4 m) sediment core from Meekin Lake versus cumulative core depth. $^{14}$C-estimated dates are indicated to the left. The zones and subzones from Fig. 3 are shown to allow comparison across figures.
Supplemental Figure 3-3-2. Concentrations of diatom taxa found in a near-shore (depth = 7.5 m) sediment core from Gall Lake versus cumulative core depth. \(^{14}C\)-estimated dates are indicated to the left. The zones and subzones from Fig. 4 are shown to allow comparison across figures.

Supplemental Figure 3-3-3. Concentration of the dominant planktonic taxa *Discostella stelligera* versus calibrated age (yr BP) for the three study lakes arranged according to geographic position from west to east.
Chapter 4

Enhanced Primary Production in Headwater Boreal Lakes during the Early-to-mid-Holocene across Northwest Ontario
4.1 Abstract
Climate reconstructions based on pollen assemblages in northwest Ontario show that mean temperatures were 2-3 degrees above present-day conditions from ~8,500 to 4,500 years ago. Here we quantified changes in algal abundance and composition during the early-to-mid-Holocene period using pigments, spectrally-inferred chlorophyll $a$ and diatom assemblages in well-dated sediment cores from three lakes. All three indicators showed a coherent pattern of enhanced primary producers in two of the study lakes (Gall and ELA Lake 239), whereas only diatom assemblages suggested higher levels of nutrient in Meekin Lake. Overall, this study supports a regional pattern of enhanced primary producers during the early-to-mid-Holocene period, likely as a function of lower water levels and warmer temperatures. Elevated concentrations of cyanobacterial pigments also occurred in two of the three lakes during the warmer early-to-mid-Holocene, whereas pigments from purple sulfur bacteria provide evidence of enhanced deep-water anoxia at this time. These findings suggest that future climate warming could lead to regional eutrophication and expansion of potentially-toxic cyanobacterial populations.
4.2 Introduction

Increases in lake-water temperature as well as variations in precipitation and enhanced seasonality are expected to impact both abundance and composition of phytoplankton and phytobenthos. For example, temperatures have increased an average of 0.8°C (1.4°F) across northern hemisphere since 1900, and climate models predict an additional increase between 0.3-4.8 ºC by the end of 21st century relative to the 1986-2005 reference periods (Collins et al., 2013). Increase in regional air temperature is highly correlated with the surface water temperature of lakes, potentially leading to physical changes in lake including changes in mixing regimes and thermal stability (Adrian et al., 2009). Changes in physical characteristics may also have effects on nutrient, oxygen and biotic assemblages (Adrian et al., 2009). Further it is well known that climate influences the length of the ice-free periods (Schindler et al., 1996a; Rodriguez et al., 2001; Diehl et al., 2002; Smol et al., 2005) and many studies have demonstrated an increase ice-free conditions as air temperatures have increased (McKnight et al., 1996; Livingstone and Dokulil, 2001; Magnusson et al., 2000; Williams and Stefan, 2006). Climate warming can also increase water-residence times in lakes, through decreases in stream flow (Schindler et al., 1996a; Rippey et al., 1997). Declines in stream flow can result in lower lake-levels and longer residence times, but also a lower export of nutrients and dissolved organic carbon (DOC) from the catchment, with resultant increases in lake-water transparency, and changes in thermocline depth (Schindler et al., 1996a; Schindler et al., 1996b). Nutrient concentration can also be affected by the internal processes related to changes in the thermal structure and or primary production (Jeeppesen et al., 2005; Wilhelm and Adrian, 2008). All of these factors can influence the abundance and composition of primary producers, often in complex and unexpected ways (Findlay et al., 2001), and the response of lakes to climate change
can be vary between lakes with different characteristics (Adrian et al., 2006). Given this complexity, it is often hard to predict how primary producers in lakes will change under a warmer climate.

Warmer climatic conditions may also favour development of cyanobacteria in lake ecosystems (Paerl and Huisman, 2008). Cyanobacteria can form significant blooms in many water bodies, and are widely acknowledged as a threat to water quality in many regions of world (O’Neil et al., 2012), as many cyanobacteria can produce cyanotoxins (Carmichael et al., 1988). Cyanobacterial growth is favoured under warmer temperatures, due to their higher growth rates at higher temperatures relative to eukaryotic phytoplankton (Roberts and Zohary, 1987). Higher temperatures can also increase buoyancy capabilities of cyanobacteria and delay rate of sinking (Kromkamp et al., 1988; Reynolds, 2006; Carey et al., 2012), further favouring the abundance of cyanobacteria. Besides, temperature, high concentrations of nutrients are also recognised as important predictors of cyanobacterial blooms (Jöhnk et al., 2008; Kosten et al., 2012; Taranu et al., 2012), and temperature and nutrients together have been shown to be the best predictors of cyanobacterial biomass (Beaulieu et al. 2013).

An understanding of how past periods of warmer conditions have influenced primary producers in lakes will aid our understanding of this issue. Unfortunately, long-term records of changes in primary producers are rare, especially during periods of enhanced warmth. However, past period that were warmer than present do exist and the relationship between primary producers and warmth can be investigated using paleolimnological approaches. In particular, analysis of sedimentary pigments, inferences of chlorophyll $a$, and changes in diatom assemblages in well-dated sediment cores can provide robust records of historical changes in primary producers in response to climate (e.g. Hall et al., 1999; Garrison and Wakemane, 2000;
Reavie et al., 2006). To date, climate-related changes in lake trophic status during the warmer periods in the Holocene scale available from few lakes (e.g Fietz et al., 2007, Lake Baikal; Kirilova et al., 2009, central European Lake; Hickman and Schweger, 1990, Baptiste Lake, Alberta), with a particular absence of relatively small boreal lakes.

In this paper, we quantified historical changes in the abundance and composition to primary producers in three lakes from northwest Ontario to evaluate how early-to-mid-Holocene climate warming affected primary producers. Prior research from the Experimental Lake Area of northwest Ontario (NW), Canada revealed that during mid-Holocene time period, nutrient-rich planktonic diatom taxa were abundant and the concentration of biogenic silica was high, suggesting enhanced lake-water production at this time (Moos et al., 2009). At this time, the surrounding boreal region was characterized as parkland (McAndrews, 1982; Björck, 1985; Lewis et al., 2001; Moos and Cumming, 2011), with pollen-based inferences inferring that climate conditions were warmer than present by approximately 2-3°C, with enhanced precipitation and evaporation (Moos and Cumming, 2012). Lake-levels across this region were also low in comparison to the last 4-5 thousand years (Karmakar et al., 2014, in press). We take advantage of these well-known changes to address two questions: a) is enhanced primary production in lakes a common phenomenon in head-water lakes in NW Ontario during early-to-mid-Holocene period in comparison to the earlier and later in the Holocene; and b) did cyanobacterial communities become more abundant in the early-to-mid-Holocene?

4.3 Study sites

The Winnipeg River Drainage Basin (WRDB) is a large catchment (150,000 km²) located primarily in northwest Ontario, adjacent to the Canadian prairie region (Fig. 4-1). Instrumental records from the WRDB are limited, but show a warming trend of 1-2°C over the past century,
Figure 4-1. Map showing the location of the three study lakes (Gall Lake, ELA Lake 239 and Meekin Lake) within the Winnipeg River Drainage Basin. Lake 239 and Gall Lake are located in the English River Watershed, whereas Meekin Lake is located in the Lake of the Woods/Rainy River Watershed.
and spatially-asynchronous droughts on a sub-decadal scale (Laird et al., 2012). Three lakes were studied within the WRDB and sites were selected to span a spatial transect of over ~200 km (Fig. 4-1) across the boreal region. This region consists of rolling topography of hills and valleys located on crystalline bedrock with shallow soils (McAndrews, 1982). The easternmost site, Gall Lake is located in the English River Watershed (50° 14' N, 91° 27' W) whereas the westernmost site, Meekin Lake (49°49' N, 94°46' W) is located ~100 km from the modern-day prairie forest boundary. Finally, ELA Lake 239 (49°40′N, 93°44′W) was included in this study as it represents a more central location, and was the site of a previous investigation that motivated this study (Moos and Cumming, 2009).

Study lakes are all relatively small (19ha, Gall Lake; 78ha, Meekin Lake; and 56ha, ELA239) first-order lakes, with gentle sloping bathymetry in at least one basin. These lakes represent presently oligotrophic (Meekin and Lake 239) to slightly mesotrophic (Gall Lake) lakes (Kingsbury et al., 2012), with all sites containing few macrophytes. The vegetation near Gall Lake is dominated by black spruce (Picea mariana), jack pine (Pinus banksiana), and poplar (Populus spp.), along with white birch (Betula papyrifera), balsam fir (Abies balsamea), and larch (Larix spp.), whereas the vegetation near Meekin Lake, is consists of balsam fir, popular, white birch with some black ash (Fraxinus nigra) and red maple (Acer rubrum).

A previous paleolimnological study shows that lake level was low during the early-to-mid Holocene compared to the last 4 to 5 thousand years (Karmakar et al., 2014). Lower water levels in the early-to-mid-Holocene period is consistent with a pollen-inferred increase in temperature of 2-3 °C relative to present values (Moos and Cumming, 2011), a 2-to-3 times increase in fire frequency (Moos and Cumming, 2012), and a change to a diatom assemblage that is indicative of more productive conditions (Moos et al., 2009). A synthesis of available pollen-
based records from the North American Pollen Database, which span the Canadian prairie-boreal forest ecotone, indicate a clear identification of early-to-mid-Holocene warmth based on the changes in vegetation (Moos and Cumming, 2011). However, changes in pollen species were dependent on lake location, with the prairie lakes showing increases in Poaceae and *Ambrosia* during the early-to-mid Holocene, whereas changes in Cupressaceae and *Ambrosia* are more apparent in the boreal region.

### 4.4 Materials and Methods

In June 2011, a piston core was collected from the deepest region of the central basin in Gall and Meekin lakes with using a Livingstone square-rod piston corer, with an internal diameter of 5.1 cm (Glew et al., 2001). The total core lengths were ~5 and 9 m of sediment from Gall Lake and Meekin Lake, respectively. In the lab, each core was sectioned at 0.5-cm intervals into 10-oz Whirlpak® bags. A total of 10 (Gall Lake) and 13 samples (Meekin Lake) were sampled, and analysed along the length of both cores, for radiocarbon dates (Table. 4-1).

AMS $^{14}$C age estimates were based on analysis of carbon from pollen isolated at the Limnological Research Center at the University of Minnesota using the procedures of Brown et al. (1989), after which they were analyses for $^{14}$C activity at the Lawrence Liverpool National Laboratory. Radiocarbon dates were calibrated (using IntCal09, Reimer et al., 2009) and age-depth models were created using ‘classical’ age-depth modelling (*clam*; Blaauw, 2010). For deriving an age-depth model, *clam* calculates the weighted mean of all sampled calendar ages or the mid-point of the highest probability distribution, using an iterative algorithm, to calculate confidence 95% confidence intervals (Blaauw, 2010). To determine the age at the top interval of the piston core, total $^{210}$Pb was measured in the uppermost sediment in the first section of the
Table 1. Summary of the $^{14}$C-dating results on pollen isolated from selected intervals from the sediment cores from Gall and Meekin lakes. All analyses were performed based on pollen isolated at the Limnological Research Center at the University of Minnesota, and dated at Lawrence Livermore National Laboratory.

<table>
<thead>
<tr>
<th>Lake name</th>
<th>Sample depth (cm)</th>
<th>Cumulative depth (cm)</th>
<th>Material dated</th>
<th>$^{14}$C Age ($\pm$ 1 SD)</th>
<th>Calibrated $^{14}$C Age ($\pm 2$ sigma) calendar years BP (clam)</th>
<th>No. of CAMS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gall P1S1</td>
<td>30-30.5</td>
<td>30</td>
<td>Isolated pollen</td>
<td>445$\pm$30</td>
<td>466-533</td>
<td>157800</td>
</tr>
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<td>Gall P1S2</td>
<td>32.5-33</td>
<td>80</td>
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<td>1200$\pm$30</td>
<td>1056-1184</td>
<td>157801</td>
</tr>
<tr>
<td>Gall P1S2</td>
<td>82-82.5</td>
<td>130</td>
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<td>2035$\pm$30</td>
<td>1922-2064</td>
<td>157802</td>
</tr>
<tr>
<td>Gall P1S3</td>
<td>28-28.5</td>
<td>180</td>
<td>Isolated pollen</td>
<td>2695$\pm$30</td>
<td>2755-2849</td>
<td>157804</td>
</tr>
<tr>
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<td>3750$\pm$35</td>
<td>4062-4164</td>
<td>157803</td>
</tr>
<tr>
<td>Gall P1S4</td>
<td>27.5-28</td>
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<td>4785$\pm$30</td>
<td>5470-5561</td>
<td>157805</td>
</tr>
<tr>
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<td>157806</td>
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<td>157807</td>
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</tr>
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<td>7415$\pm$30</td>
<td>8181-8324</td>
<td>162179</td>
</tr>
<tr>
<td>Meekin P1S6</td>
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<td>Isolated pollen</td>
<td>8145$\pm$25</td>
<td>9008-9133</td>
<td>162180</td>
</tr>
<tr>
<td>Meekin P1S6</td>
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<td>Isolated pollen</td>
<td>8875$\pm$40</td>
<td>9886-10175</td>
<td>162181</td>
</tr>
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<td>Meekin P1S7</td>
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<td>616</td>
<td>Isolated pollen</td>
<td>10120$\pm$170</td>
<td>11242-12241</td>
<td>162182</td>
</tr>
<tr>
<td>Meekin P1S9</td>
<td>25-26</td>
<td>811</td>
<td>Isolated pollen</td>
<td>10945$\pm$40</td>
<td>12709-12912</td>
<td>162184</td>
</tr>
</tbody>
</table>
piston cores from each lake. This activity was compared with a dated gravity core retrieved at the same depth as the piston core.

**Estimates of primary producer abundance and composition**

Sedimentary pigment analysis was, undertaken following standard procedures Leavitt and Hodgson (2001). Briefly, pigments from a subsample of ~50 mg of freeze-dried sediment were extracted using a mixture of acetone, methanol, and water (80:15:5 by volume). Pigment extracts were then filtered through a 0.22-µm PTFE filter and after 24h were dried with inert N₂ gas. The dried pigment residues on the filters were then re-dissolved in a standard injection solution (combination of methanol, Sudan II tock solution and IPR stock solution) before introduction into an Agilent 1100 High Performance Liquid Chromatography (HPLC) system, equipped with a photo diode array detector. Pigments were differentiated on the basis of chromatographic position and light absorbance characteristics using detailed monographs and comparison with authentic standards (Leavitt and Hodgson, 2001).

Spectral analysis of chlorophyll a and associated degradation products in sediment samples was conducted following Michelutti et al (2010). Sediments were freeze dried and then sieved through a 125-µm mesh, and placed into glass vials. All reflectance spectra were obtained using a Model 6500 series Rapid Content Analyzer (FOSS NIRSystems Inc.). A ceramic reference paddle from the Rapid Content Analyzer was used as a reflectance reference, which was measured following every fifth sample. The sedimentary chlorophyll a concentration was inferred using an equation (chlorophyll a + derivatives = 0.0919 x peak area 650-700 nm + 0.0011) derived by Michelutti et al. (2010). This calibration was based on a total 35 sediment samples from five lakes that spanned a of broad range of trophic states (Das et al., 2005) and the mass ratios of lake sediment (Lake Louise sediment core at depth of 22.5cm) to algae (mixture of
cyanobacteria, pennate diatom and small chlorophytes from a tropical aquaria) at ratios of 250:1, 500:1 and 1000:1 (Wolf et al., 2006). The calibration was developed on the spectrophotometer described above.

Analysis of diatom assemblages was conducted using standard strewn mounts following the procedure of Wilson et al. (1996). Briefly, a sub-sample of ~0.2-0.3 g of wet sediment was digested in 20-ml glass vials using a 50:50 molar solution of concentrated sulfuric and nitric acids. Following the removal of the acid by aspiration, and daily rinses with distilled water every 24 hours until the sample was acid free. The diatom slurry was reduced to a volume of ~5 ml, to which a known aliquot of microsphere solution (8 ml of a 2.0 x 10^7 spheres/ml) was added to allow the calculation of diatom concentrations (Battarbee and Keen, 1982). Permanent slides were made by following the procedure of slide preparation procedure is outlined in Moos et al. (2005). For each diatom sample a minimum of 400 valves was enumerated using a Leica DMRB microscope with a 100x fluotar objective (NA = 1.3), and differential interference contrast optics at 1,000x magnification. For samples from the bottom section of the Meekin Lake sediment core (below cumulative depth of 608 cm), only ~ 200 valves were counted due to low diatom concentrations. Diatoms were identified down to the species level or lower using the standard taxonomic references (Krammer and Lange-Bertalot, 1986, 1988, 1991a, 1991b; Cumming et al., 1995; Lange-Bertalot and Melzeltin, 1996; and Camburn and Charles, 2000). Diatom data from ELA Lake 239 was available from a previous study (Moos and Cumming, 2009).

**Numerical analysis**

Fossil pigment and spectrally-inferred chlorophyll a data were graphed using the computer program Tilia v.2.0.2 (Grimm, 2004). Diatom species with greater than 5% abundance in at least one sample were also graphed using Tilia. The correlation between HPLC measured
chlorophyll \(a\) and NIRS chlorophyll \(a\) (Chlorophyll \(a\) concentration was converted mg/ g OM for comparison) was based on interpolated data, as the same intervals were not measured for all samples. For all cores, we used cluster analysis to identify depth-constrained zones to aid in descriptions of broad-scale trends in the sedimentary sequences over time. For diatoms, both percent relative abundance and concentration data were calculated at a resolution of 8-cm intervals for Gall Lake, and 16-cm intervals for Meekin Lake. The chrysophyte scale to diatom index (C to D index) was calculated using the formula: \((\text{scales/diatoms} + \text{scales}) \times 100\). Diatom-inferred values for TP were developed based on a 268 calibration set of freshwater lakes from British Columbia, from which surface samples and measured water chemistry were available. The range of TP of the British Columbia model was 5–322 μg/l. Log TP was reconstructed with a simple weighted average model with inverse deshrinking (bootstrapped \(r^2 = 0.51,\) RMSEP = 0.34, Moos et al., 2009) using the computer program C2 (Juggins, 2003). To determine the suitability of using the modern dataset from British Columbia at reconstructing TP from lakes from northwest Ontario, we assessed the similarity between the diatom assemblages in the cores from Gall and Meekin lakes, in comparison to the modern-day diatom assemblages. This was accomplished using the modern analog techniques (MAT) in C2 (Juggins, 2003), and was based on the best match between calibration dataset samples and fossil samples using Bray-Curtis similarity coefficient as distance matrix (species relative abundance data were square-root transformed). The core samples were deemed suitable if they were within the distribution of the 90% highest similarity coefficients calculated between matches of each calibration sample with the next closest sample in the modern dataset. Poor or no analogs were determined if the similarity between the fossil (core) and modern samples was in the lowest 10\(^{th}\) percentile of the
similarity coefficients between best modern to modern comparison in the calibration dataset (Appendix B).

4.5 Results

The cumulative length of the sediment cores from Gall and Meekin lakes are 450 and 870 cm, respectively. In both cases, grey clays were present in the bottommost sections of the cores. The activities of $^{210}$Pb in the upper intervals of the piston cores from Meekin (3-4 cm interval; $^{210}$Pb activity= 1833.97 Bq/kg; $^{137}$Cs activity= 396.41 Bq/kg) and Gall lakes (2.5-3 cm interval; $^{210}$Pb activity= 1381 Bq/kg; $^{137}$Cs activity= 256.09 Bq/kg) correspond to the activities in $^{210}$Pb-dated gravity cores taken from similar locations that were dated to the years 1995 for Meekin lake, and 1977 for Gall Lake (Karmakar and Cumming, Appendix A). In both lakes, the calibrated ages show a consistent change, almost linear change, to older samples with increasing cumulative depth in the cores. The age-depth models constructed using classical age-depth modeling (Blaauw, 2010) show a strong age-depth relationship, with errors typically < 100 years, but with higher uncertainty prior to 9,000 cal yr BP in Gall Lake, and 9,500 cal yr BP in Meekin Lake. Based on the sedimentation rates from the age-depth models, the analysis of fossil pigment, spectrally-inferred chlorophyll $a$, and diatom assemblages at 8-cm intervals (in Gall Lake) represents an integrated sample of ~23 years sampled at an approximate temporal resolution of every 190 year over the Holocene. Similarly, for the sediment core from Meekin Lake, the analysis of three proxies at a 16-cm interval in the core represents an integrated sample of ~16 years sampled at an approximate 250-years temporal resolution. For the sediment core from Lake 239, the fossil pigment and spectrally-inferred chlorophyll $a$ analyses at a 16-cm intervals represents an integrated sample of ~45 years at an approximate resolution of every 150 years (Moos et al., 2009).
Figure 4-2. A) Age-depth model for the sediment cores from Gall Lake and B) for Meekin Lake, based on calibrated $^{14}$C dates (Table 1), obtained by the classical age-depth model under “clam” package in R software (Blaauw, 2010). Cumulative depth vs calendar years BP dates and errors are shown in blue. The grey area shows 95% confidence intervals of the inferred dates based on 1000 iterations.
Fossil Pigments and Spectrally-inferred chlorophyll a

Cluster analysis on the concentrations of fossil pigments in Gall Lake sediments (Fig. 4-3) identified four main zones during the Holocene: i) an early Holocene period, *circa* 11,200 to 9,200 cal yr BP (Zone A1, Fig. 4-3); ii) an early-to-mid-Holocene period, *circa* 9,200 to 7,400 cal yr BP (Zone A2); iii) a mid-Holocene period, *circa* 7,400-4,300 cal yr BP (Zone B1); and iv) a late-Holocene period from *circa* 4,300 cal yr BP to present (Zone B2). In early Holocene, the organic content of the sediment was low <10% with corresponding low concentrations of pigments and spectrally-inferred chlorophyll a. Pigment concentrations of chlorophyll, β-carotene, spectrally-inferred chlorophyll a, achieved their highest concentrations during the early-to-mid-Holocene time period, and remain high until approximately 4,200 cal yrs BP. The ratio of chlorophyll a: pheophytin a, an indicator of good preservation, remains high until *circa* 4,200, where it drops and remains relatively constant for the remainder of the Holocene.

Myxoxanthophyll, canthaxanthin, and echinenone initially increase in the early Holocene and continue to at similar or higher levels (echinenone) throughout the in the early-to-mid-Holocene when organic matter increases to almost 40%. The pigment okenone, unique to purple sulfur bacteria, becomes dominant in the early-to-mid-Holocene, where after it declines to below detection limits by 6,800 cal yr BP. In the mid-Holocene period, myxoxanthophyll declines below detection, while canthaxanthin and echinenone persist, but at slightly lower concentrations than the previous zone. In the late Holocene, concentrations of echinenone drop.
Figure 4-3. Concentration profile for selected fossil pigments (pigments which shows significant changes over Holocene and related to primary production and blue-green algal assemblage) in Gall Lake sediment core over time (cal yr BP). Pigments includes: chlorophyll a (Plantae, algae), chlorophyll b (Plantae, Chlorophyta, Euglenophyta), β-carotene (all plants), diatoxanthin (Bacillariophyceae, Dinophyta, Chrysophyta), myxoxanthophyll (colonial cyanobacteria), canthaxanthin (colonial cyanobacteria), echinenone (all cyanobacteria), okenone (purple sulphur bacteria), Chlorophyll a to Pheophytin A (an index of preservation), and organic matter (%) are also shown. The sub-zones (A1, A2, B1, B2) are shown as defined by the constrained cluster analysis.
to levels similar to those in the early Holocene. The HPLC measured chlorophyll $a$ and spectrally-inferred chlorophyll $a$ are significantly correlated ($r = 0.54$, $n = 55$, $p = <0.0001$).

In the sediment core from Lake 239, three major time periods based on changes in the concentrations of fossil pigments (Fig. 4-4) were identified: i) an early-Holocene period, *circa* 10,000 to 8,500 cal yr BP (Zone A, Fig. 4-4); ii) an early-to-mid-Holocene period, *circa* 8,500 to 4,000 cal yr BP (Zone B1); and iii) a late-Holocene period, *circa* 4,000 to present (Zone B2). During early Holocene the concentrations of all pigments are low (Fig. 4-4). During the early-to-mid-Holocene, the concentration of chlorophyll $a$ and $\beta$-carotene increase, as does diatoxanthin and myxoxanthophyll. Similarly, the spectrally-inferred chlorophyll $a$ was highest from *circa* 8,500-4,000 cal yr BP (Fig. 4-4), as was the ratio between chl $a$ and pheophytin a. Organic matter increased from approximately 5% to around 20% by the end of the mid Holocene, where it remained relatively constant for the remainder of the Holocene. During the late Holocene, myxoxanthophyll decreases sharply at 4,000 yrs. BP, but canthaxanthin remains high. The HPLC measured chlorophyll $a$ and spectrally-inferred chlorophyll $a$ are significantly correlated ($r = 0.5$, $n = 48$, $p = <0.0002$).
Figure 4-4. Concentration profile for selected fossil pigments (pigments which shows significant changes over Holocene and related to primary production and blue-green algal assemblage) in ELA Lake 239 sediment core over time (cal yr BP). Pigments includes: chlorophyll a (Plantae, algae), β-carotene (all plants), diatoxanthin (Bacillariophyceae, Dinophyta, Chrysophyta), myxoxanthophyll (colonial cyanobacteria), canthaxanthin (colonial cyanobacteria), echinenone (all cyanobacteria), Chlorophyll a to Pheophytin A, and organic matter (%) are also shown. The sub-zones (A, B1, B2) are shown as defined by the constrained cluster analysis.
In the sediment core from Meekin Lake, three major time periods based on changes in the pigment concentrations were identified (Fig. 4-5): i) a late glacial-to-early-Holocene period, *circa* 13,600 to 10,400 cal yr BP (Zone A1, Fig. 4-5); ii) an early-to-mid-Holocene period, *circa* 10,400 to 5,000 cal yr BP (Zone B1); and iii) a late Holocene period, *circa* 5,000 cal yr BP to present (Zone B2). During early Holocene, pigment concentrations were low. At this time organic matter was also low, but the chlorophyll *a* to pheophytin *a* ratio was high. During early-to-mid-Holocene, pigments including myxoxanthophyll, echinenone, canthaxanthin, chlorophyll *a* and β-carotene all increase, as does the percent organic matter from 10 to 30%. Interestingly, myxoxanthophyll increases only in the early Holocene, and only for a period of two-thousand years. During late Holocene, the concentration of both chlorophyll *a* and β-carotene continue to increase, achieving levels higher than the mid-Holocene. Carotenoids such as canthaxanthin, also increase to higher levels than seen in the mid-Holocene. The spectrally-inferred chlorophyll *a* increased quickly during the early-to-mid-Holocene followed by relative stability over the last 5,000 years (Fig. 4-5). A similar pattern is seen in the percent organic matter. The two measures of chlorophyll *a* are significantly correlated (*r* = 0.85, *n* = 52, *p* = <0.0001).
Figure 4-5. Concentration profile for selected fossil pigments (pigments which shows significant changes over Holocene and related to primary production and blue-green algal assemblage) in the Meekin Lake sediment core over time (cal yr BP). Pigments includes: chlorophyll $a$ (Plantae, algae), $\beta$-carotene (all plants), diatoxanthin (Bacillariophyceae, Dinophyta, Chrysophyta), myxoxanthophyll (colonial cyanobacteria), canthaxanthin (colonial cyanobacteria), echinenone (all cyanobacteria), Chlorophyll $a$ to Pheophytin A, and organic matter (%) are also shown. The sub-zones (A, B1, B2) are shown as defined by the constrained cluster analysis.
Diatom composition and inferred total phosphorus concentration

All three lakes underwent large changes in diatom species composition. The general trends in diatom-inferred total phosphorus (DI-TP), and the changes in the dominant diatom taxa, are summarized for all lakes (Fig. 4-6). The detailed diatom assemblages in the cores from Gall and Meekin lakes, for both percent abundance and concentrations are shown in supplemental figures 1 to 4. The high degree of similarity between the relative abundance data and the concentration data in both Gall (cf. Supplemental Figs. 4-1 and 4-2), and Meekin Lake (cf. Supplemental Figs. 4-3 and 4-4), suggests that similar interpretation would result if made on interpretations of relative abundance, concentration or accumulation data (i.e. sedimentation rates are approximately linear, cf. Fig. 4-2). The detailed diatom assemblages from the core from Lake 239 can be found in Moos and Cumming (2009). Briefly, *Aulacoseira subarctica* and *Fragilaria crotonensis* were two dominant nutrient-rich diatom taxa within Lake 239 during ~9000 to ~4500 cal yr BP which also contributed to the higher diatom-inferred TP.

The center cores from Gall Lake and Lake 239, span only the last 10,000 years, whereas the core from Meekin Lake extends to circa 12,500 cal yr BP (Fig. 4-6). High concentrations of DI-TP occur prior to 2,000, 3,000 and 4,000 cal yr BP for the sediment cores from Gall Lake, Lake 239 and Meekin Lake, respectively. However, the highest inferred DI-TP values occurs prior to 6,000 (Gall Lake), 7,000 (Lake 239) and 9,000 (Meekin Lake) cal yr BP years for the sediment cores from these same three lakes. In all three sites, a transitional zone between the most productive periods to a late-Holocene period dominated by *D. stelligera*, also appears time transgressive, occurring later in the east, than in the west (Zone B1 in Gall, Zone B in Lake 239 and Zone B1 in Meekin Lake; Fig. 4-6).
Figure 4-6. Summary of diatom-inferred total phosphorus (TP) values over the Holocene of Gall, ELA Lake 239 and Meekin Lake, arranged in geographic position from east to west. Vertical box with zones and subzones represents dominant diatom assemblage (taxon >20%, see supplemental figures for detailed diatom stratigraphies) with major zones defined by constrained cluster analysis. Diatom taxon names are abbreviated (Ach = Achnanthes sensu lato, Ast for = Asterionella formosa, Aul ten = Aulacoseira tenella, Aul sub = Aulacoseira subarctica, Aul isl = Aulacoseira islandica, Cyc mic = Cyclotella michiganiana, Cyc oce = Cyclotella ocelata, Fra cro = Fragilaria crotonenesis, Dis ste = Discostella stelligera, Sta pin = Staurosirella pinnata, Ste med = Stephanodiscus medius)
A similar time transgressive pattern is seen in the scaled chrysophyte to diatom index (C to D index), with the first large increase in this ratio occurring at circa 5,000 yr. BP in the Gall Lake core (Supplemental Fig. 4-1), c. 8,600 yr. BP in Lake 239 (Moos and Cumming, 2009), and circa 9,000 in Meekin Lake. A similar time-transgressive pattern is also present in the ratio of chlorophyll a to pheophytin a, with higher ratios between circa 9,000 and 4,000 cal yr BP in Gall Lake, 8,500 and 4,200 cal yr BP in Lake 239, and 13,000 and 7,000 cal yr BP in Meekin Lake. Specific changes in the relative abundances and concentrations of dominant diatom taxa in Gall and Meekin Lakes are outlined below.

Depth-constrained cluster analysis identified four major time periods during the Holocene based on changes in the diatom assemblages. For the sediment core from Gall Lake this resulted in four time periods (Supplemental Fig. 4-1): i) an early-Holocene period, circa 10,000 to 8,000 cal yr BP (Zone A1, Supplemental Fig. 4-1); ii) early-to-mid-Holocene period, circa 8,000 to 5,500 cal yr BP (Zone A2); iii) the mid-to-late-Holocene period, circa 5,500 to 2,000 cal yr BP (Zone B1); and iv) a late Holocene period, circa 2,000 to present (Zone B2). Both percent relative abundance (Supplemental Fig. 4-1) and concentration (Supplemental Fig. 4-2) data were similar in terms of overall changes in diatom taxa. The early Holocene was dominated mainly by benthic diatom taxa such as *Achnanthes sensu lato* (40%), *Navicula senso lato* (20%), *Staurosirella pinnata* (30%) (Ehrenberg) Williams and Round, and *Amphora* taxa. During the mid-Holocene time period, *Cyclotella michiganiana* Skv. is more abundant, and *S. pinnata*, *Staurosira contruens* (Ehrenberg) Williams and Round are dominant. The mid-to-late-Holocene period was mainly dominated by *Asterionella formosa* (Hassall) Houk et Klee, *Aulacoseira tenella* (Nygaard) Simonsen, *C. michiganiana*, *Cyclotella bodanica* v. *lemanica* (O. Müll. Ex Schrot) H. Bachmann, *Tabellaria flocculosa* str 3P, *T. flocculosa* str 3 (*Tabellaria flocculosa* (Roth) Kutz
strains (*sensu* Koppen), *Fragilaria tenera* (W. Smith) Lange-Bertalot. *S. pinnata* declines by 5,000 years ago. The C to D index increased at around *circa* 6,500 cal yrs BP, reaching stable but variable levels by *circa* 5,000 cal yrs. BP (Supplemental Fig. 4-1). During late-Holocene, *circa* 2,000 yrs BP to present, the planktonic diatom taxon *Discostella stelligera* (Cleve and Grunrow) Houk and Klee, became consistently more dominant, and less variable, and *A. distans* increased.

Four major zones were also defined in the core from Meekin Lake based on large changes in the diatom assemblages including: i) an early-Holocene period, *circa* 13,800 to 11,200 cal yr BP (Zone A1); ii) an early-to-mid-Holocene period, *circa* 11,200 to 8,000 cal yr BP (Zone A2, Supplemental Fig. 4-3); iii) a mid-Holocene period, *circa* 8,000 to 5,000 (Zone B1); and iv) a late Holocene period, *circa* 5,000 to present (Zone B2). Both relative percent data (supplemental Fig. 4-3) and concentration data (supplemental Fig. 4-4) showed similar trends in changes in the dominant taxa throughout the sediment record. During early-Holocene period, Meekin Lake was dominated by *Stephanodiscus medius* Håkasson, *Aulacoseira islandica* (O. Müller) Simonsen. The early-to-mid-Holocene period was dominated by *S. pinnata* (15-40%) and *A. subarctica* (15-35%) (O’Muller) Haworth, as taxa including *S. medius* and *A. islandica* declined (Supplemental Figs. 4-3 and 4-4). During the mid-Holocene period *A. subarctica* (35-50%) dominated the assemblage, but declines in relative abundance and concentration, whereas other diatom taxa such as *Aulacoseira ambigua*, *Cyclotella michiganiana*, *Fragilaria crotonensis* Kitton, *Stephanodiscus minutulus* increased. *Aulacoseira ambigua* (Grun.) O. Müller, *D. stelligera* (20-35%), *F. crotonensis* Kitton, *F. tenera*, *S. pinnata*, *Tabellaria* were present. In the late Holocene, *D. stelligera* and *Discostella pseudostelligera* Houk and Klee, increase to become the dominant taxa, and other planktonic taxa (*Cyclotella* and *Tabellaria*) remained subdominant. The C to D index within this lake was low in comparison to other two study lakes, although past
~4,000 years this index was high compare to early-and mid-Holocene periods. Most dominant diatom taxa in the calibration set are well represented in the down core samples and the analogs for Meekin Lake were stronger in comparison to the analogs for Gall Lake. For Gall Lake, diatom taxa such as Aulacoseira tenella, Fragilaria brevistriata, Amphora inariensis, Brachyseira neoexilis, Navicula explanata, Achnanthes subatomoides and Navicula pupula were more than 30% in fossil samples but were not present in the modern calibration set. For Meekin Lake, Aulacoseira islandica, Achnanthes clevei, A. delicatula, Amphora inariensis were only present in fossil samples, resulting in poor analogs in the early Holocene.

Discussion

Deep-water sediment cores across an east-to-west transect were used to quantify historical changes in abundance and composition of primary producers in northwest Ontario. Analysis provided clear evidence for higher primary producer abundance during the warmer early-to-mid-Holocene period as well as enhanced populations of cyanobacteria. In general pigments-and diatom-based analysis provided similar historical patterns of change in primary producers, although Meekin Lake did not show a consistent pattern of lake-production across all proxies. The interpretation of multiproxy data can be difficult, when different proxies give conflicting results. Taken as a whole, these finding suggest that future climate warming may expand cyanobacterial populations, as well as overall lake production.

Enhanced primary production in lakes during the warmer early-to-mid-Holocene

This study provides clear evidence of enhance primary production in lakes during the early-to-mid-Holocene, a time period that is estimated to have been 2-3°C warmer than today. The evidence of enhanced primary production is based on the combined evidence of high concentrations of sedimentary pigments and spectrally-inferred values of chlorophyll a in the
sediment cores from Gall Lake and Lake 239, and evidence for higher nutrient levels in all three study lakes, based on diatom species assemblages and diatom-based inferences of TP. Low effective moisture prevailed during the mid-Holocene time period in all of three study lakes in comparison to the late Holocene period (Karmakar et al., 2014). During this time, there was significant change in terrestrial vegetation to a more open boreal forest (Moos and Cumming, 2011). In both Gall Lake and Lake 239, elevated concentrations of chlorophyll $a$ and $\beta$-carotene suggested higher primary production in the early-to-mid-Holocene, occurring between 9,000 and 4,000 years ago in Gall Lake (Fig. 4-3), and between 8,200 and 4,000 years ago in Lake 239 (Fig. 4-4). However, in Gall Lake, there was also an indication of different limnological conditions between 9,000 and 7,000 years ago, as indicated by the consistent present of deep-blooming purple sulfur bacteria, an obligate anaerobe, suggesting either permanent stratification and anoxia, or seasonal anoxia in this lake. Water temperature as well as stratification is related to the change limnological condition within a lake thus shifts in relative phytoplankton species composition, algal blooms, and species interactions (Huisman et al., 2004; Adrian et al., 2006, Winder and Hunter, 2008). The ratios between chlorophyll $a$ to pheophytin a, an indicator of good pigment preservation, is either a result of either enhanced primary production and/or preservation (Leavitt, 1988). A high ratio of chlorophyll $a$ to pheophytin a is also present in Meekin Lake from the early Holocene until 7,500 years ago, much earlier than in the cores from Gall Lake and Lake 239. However, the core from Meekin Lake suggests that primary production over the past 5,000 years in Meekin Lake was higher than in the early-to-mid-Holocene, a trend opposite that observed in the other sites. The diatom assemblage data broadly support the inferences recorded in the pigments, with the exception of the trends in the pigments in Meekin Lake. That is, diatom assemblages during the early-to-mid-Holocene suggest that productive
conditions occurred at this time in all lakes (Fig. 4-6). The highest diatom-inferred total phosphorus inference occur before 8,000 years in Meekin Lake, by 7,000 years in Lake 239, and by 6,000 years in Gall Lake, a timing that suggests a west-to-east time-transgressive trend. Similarly, the transition to the dominance of the oligotrophic diatom *D. stelligera* occurs by 5,000 year ago in Meekin Lake, 2,000 years ago in Lake 239, and 1,000 years ago in Gall Lake. This is very similar to the shift in the prairie-forest ecotone from west to east time-trasngressive response to aridification, where more arid sites being nearer to the less arid site (Williams et al., 2010, Williams et al., 2011).

The time transgressive pattern is also supported by the earlier timing of lake-level rise inferred by the nearshore core in Meekin Lake (Karmakar et al., 2014), the lake that is closest (~100 km) to the modern-day prairie-forest boundary (Fig. 4-1). There are broad-scale pattern of higher primary production during early-to-mid-Holocene period inferred from fossil pigment, diatom assemblage and spectrally-inferred chlorophyll *a*, changes across the region are either time transgressive, with earlier changes in the west, or due to lake-specific differences. This enhanced lake production could be defined by the phenomenological concept of abrupt change (when one or more variable in a system rapidly jump to one state to another) (Williams et al., 2011). Given the strong chronology of the age-depth models, it would seem unlikely that the observed temporal lags between lakes are due to imprecise dating. It is possible that climate condition varied across our west-to-east transect of sites, with an earlier warming in the west and a delayed response in the east. Inferences of changes in climate conditions during the mid-Holocene period has been undertaken across the prairie-forest boundary in northwest Ontario based changes in pollen assemblages (Moos and Cumming, 2011). The cores from the prairie lakes showed an increase in herbaceous pollen during early-to-mid-Holocene whereas the eastern
lakes, currently located in the boreal region, showed changes from Cupressaceae and *Pinus* (Moos and Cumming, 2011), and larger inferred temperature changes in the cores from the prairie sites. Perhaps, the western part of the WRDB experienced an earlier warming with enhance moisture that influenced the western most Meekin Lake, and not the sites further to the east. Future research on these cores should provide answers to this question.

The overall trend of increasing primary production could be related to several mechanisms, many of which would co-vary. Increased regional air temperature may result in enhanced thermal stratification, which again could affect the physical properties, nutrient availability or resource availability within lake and subsequently changes in primary producers. Not only the water temperature but also negative effective moisture condition or low water-stand condition during early-to-mid-Holocene time period had an effect on lake-water production, changing community structure mediated by water temperature, stratification, water transparency (reduced DOC) and hence change in trophic status.

**Cyanobacteria during the warmer early-to-mid-Holocene**

In all three lakes, cyanobacterial pigments are present throughout the Holocene period, but were much more pronounced during early-to-mid-Holocene time period (e.g. Gall Lake and Lake 239, Fig. 4-3 and 4-4). Among the three study lakes, Gall Lake (~9,000-4,000 cal yr BP) and Lake 239 (~8,500-4,000 cal yr BP) showed similar pattern of increasing cyanobacterial pigment concentration during early-to-mid-Holocene. Elevated abundance of cyanobacterial population again supports that water temperature was higher during that time and hence bloom-forming cyanobacteria took the advantage over other phytoplankton. This is not surprising, because warm and stable waters favors cyanobacteria (Jöhnk, 2008), and increases in cyanobacteria at higher temperatures has been reported in lakes of very different mixing regimes.
(Jöhnk, et al., 2008). High temperature can also influence buoyancy and delay sinking (Kromkamp et al., 1988; Reynolds, 2006; Carey et al., 2012). In the United States, models based on modern surveys show that nitrogen, phosphorus and water temperature are the best predictors of cyanobacteria biomass (Beaulieu et al., 2013).

In the Gall Lake core, the abundance of cyanobacteria is high in the early-to-mid-Holocene in comparison to the late Holocene. This pattern is consistent with the enhanced primary production at this time. The pigment, myxoxanthophyll, which represents colonial cyanobacteria algal groups, was present in the early Holocene within Gall Lake and then disappeared between 7,500-5,000 cal yr BP, when okenone, a pigment from purple-sulfur bacteria, increased. Presence of sulfur bacteria could be related to seasonal bottom-water anoxia. High-latitude lakes sediment contains well preserved bacterial communities due to low light penetration, low temperature and bottom-water anoxia (Hodgson et al., 2004). Similarly, in Lake 239, myxoxanthophyll was present throughout the mid-Holocene (~8,000-4,000 cal yr BP) within Lake 239 but disappeared after ~4000 cal yr BP. Myxoxanthophyll was also present in the Meekin Lake sediment core, but only during the very early Holocene (~10,500-8,000 cal yr BP). In studies of lake eutrophication, increases in myxoxanthophyll and/or oscillaxanthin in sediments have been interpreted as a signal of increased production (e.g. Griffiths and Edmondson, 1969; Gorham and Sanger, 1975; Grffiths, 1978; Zullig, 1981, 1982; Guilizzoni et al., 1982, 1983; Swain, 1985). However evidence of eutrophication from changes in climate are relatively rare (e.g. Fritz et al., 1989).

Complexity and interpretation of proxy data

In most cases, the inferences of enhance primary production during the warmer early-to-mid-Holocene period agreed. However, in Meekin Lake, both chlorophyll a and β-carotene
suggested that production was higher in the late Holocene period, resulting in a paradox with the diatom assemblage data that suggested higher production in the early-to-mid-Holocene. Pigment accumulations in lake sediments are often correlated with primary production, often as a result of increased production. However the concentrations of pigments found in lake sediments are the result of the difference between production and degradation (Leavitt, 1988), with less degradation associated with rapid burial, and/or enhanced preservation under anoxic conditions (Fritz, 1989). Rapid burial following depth could also be related to lower lake levels, but lower lake levels could result in enhanced photodegradation, if sufficient light penetrates to the lake bottom. The dominant diatom in Meekin Lake in the early-to-mid-Holocene is *A. subarctica*, reaching a relative abundance close to 60 percent. Subdominant planktonic taxa include *S. minutulus*, *F. crotenensis*, and *A. ambigua*. All of these taxa have high optima to lakewater total phosphorus (Wilson et al., 1996; Ginn et al., 2007), and therefore the total phosphorus inference could be high at this time. *Aulacoseira subarctica* an important spring and/or hypolimnetic bloomer (Interlandi et al., 1999), a diatom that is a highly silicified often benefiting from turbulent conditions (Gibson et al. 2003). Similarly, *A. ambigua* has been interpreted as an indicator of more turbulent conditions, requiring moderate to high light levels and high Si levels (Bradbury and Dietrich-Rurup, 1993). A possible explanation for the paradox between the diatoms and the pigments are perhaps low lake levels during the mid-Holocene, combined with warm waters and turbulent conditions, resulting in unfavourable preservation of pigments, whereas the deep more stratified waters in the late Holocene were more conducive to pigment preservation. Each proxy has its own bias, and no proxy is perfect. Interpretations from different proxies should provide insights into how complex ecosystem work (Birks and Birks, 2006). The present paradox between the pigments and the diatoms in Meekin Lake is complex, but likely
related to the specific dynamics of Meekin Lake, a relatively shallow system, with a large fetch (Kingsbury et al., 2012), in comparison to the other study lakes.

Relevance of findings to regional climate change in NW Ontario

Warm temperatures over the last several decades in northwest Ontario (Laird et al., 2012), combined with future projections for a further increase of over 2°C over the next 20 years (Chiotti and Lavender, 2008), have scientists, governments and industry struggling to understand the risk of climate warming on water resources. Using the longer temporal perspective, provided by fossil pigment and diatom analysis in well-dated sediment cores, we find that the observed changes in lakes during the past 40 years are small, in comparison to changes observed during the Holocene. Understanding how warmer periods in the past have impacted lakes, and how these changes compare to monitoring and instrumental record can help define risks and assess vulnerabilities. At present, governmental organizations consider the central region of Ontario to be at minimal risk from climate change on water quantity, and 20-50 years away from any negative impacts water quality (Chiotti and Lavender, 2008). However, these assessments are based on limited data and are over very large regions.

If the past can provide insights into the future, it can be argued the response of lakes to warming scenarios in the past can, at least, provide possible scenarios to which society should expect in the future. Limnological measurements at the Experimental Lakes Areas (ELA) in northwest Ontario have provided valuable insights into the response of boreal lakes to a warming climate. These include many observations of changes associated with climate warming over the past 40 years. These have included physical, chemical and biological changes in lakes, streams and terrestrial catchments during droughts (Schindler et al. 1980, 1990, 1992, 1996a, b, Bayley et al. 1992a, b), as well as changes in stream flow, lake level, water retention times, change in
dissolved organic carbon (DOC), water transparency, and thermal structure of the lake (Schindler et al. 1990, 1992, 1996 a, b). Change in phytoplankton biomass during drought periods was initially counter intuitive as production increased when nutrients decreased, as climate-induced physical and chemical changes created new phytoplankton niches (Findlay et al., 2001). Warmer condition exacerbate symptom of eutrophication with increased cyanobacterial blooms caused by longer periods of stratification (Schindler, 2001).

When a longer temporal perspective is taken, the observed changes in lakes over the last 40 years that were recorded at ELA, many be considered small, in comparison to changes over the instrumental periods. Instrumental records show that WRDB has experienced droughts during the 1930s, 1950s, and 1980s, but these droughts have been spatially asynchronous across climate stations in northwest Ontario (Laird et al., 2012). Similarly, when changes to lakes over the last 2,000 years are much greater than those seen over the instrumental record. Periods of synchronous aridity have occurred across this region over the past 2,000 years, as recorded in a network of six lakes (Laird et al., 2012), thereby providing challenges to companies such as Manitoba Hydro that depend on the WRDB for hydropower generation. The regional-scale period of aridity in northwest Ontario occurred between 900 to 1400 CE, a time period commonly referred to as the Medieval Climate Anomaly (Laird et al., 2012), suggests that the boreal region in northwest Ontario, is indeed sensitive to regional-scale changes in moisture balance. Finally, changes over the Holocene dwarf the relatively constant conditions seen over the last 2,000 years, thereby supporting the assertion that the longer temporal perspective, the more complete the picture of lake response to climate.

The estimated aridity of the mid-Holocene is of a similar magnitude to the projected changes over the next 20 years, and is dwarfed by projected changes by 2050 (Chiotti and
Lavender, 2007). Consequently, it can be argued that the changes in water quantity and quality that occurred when the climate was warmer and more arid than present in the early-to-mid-Holocene, may have relevance as potential climate scenarios that we may face in the future. At worst, information on warmer periods in the past can provide empirical data suggests that this region is climate sensitivity. Lower lake levels inferred from near-shore sediment cores, collected from the sensitive planktonic-benthic transition ecotone of diatoms in these lakes (Laird et al., 2011), suggests that net effective moisture was much lower than today during the early-to-mid Holocene across northwest Ontario (Karmakar et al., 2014). The predominance of benthic diatoms at coring locations that currently would support a planktonic assemblage, in combination with the inferred arid conditions from pollen assemblages, led Karmakar et al. (2014) to suggest that water levels were at least 2-5 m lower than today, and that positive water balance is only a more recent phenomenon that occurred over the last 4000 years. It is clear from this study, that boreal lakes can experience significant changes in lake primary producers and deterioration of water quality. More productive lakes, with increased abundance of cyanobacteria, could become a more common phenomenon in the future under a warmer climate.

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4.6 Literature cited


Supplemental figure 4-1. The dominant (>5%) diatom taxa found in Gall Lake sediment core (collected from center of the lake) versus cumulative core depth. $^{14}$C-estimated dates are indicated to the left. The diatom taxa are arranged by Correspondence Analysis (CA) axis-1 scores so that the changes in diatom assemblages over time are clearly shown. The chrysophyte scale to diatom index (C to D index) is shown. The zones and subzones are indicated, as defined by a constrained cluster analysis on the diatom relative abundance data.
Supplemental figure 4-2. Concentrations of diatom taxa found sediment core from Gall Lake versus cumulative core depth. $^{14}$C-estimated dates are indicated to the left. The zones and subzones are indicated as defined by a constrained cluster analysis on the diatom concentration data.
Supplemental figure 4-3. The dominant (>5%) diatom taxa found in sediment core (collected from center of the lake) from Meekin Lake versus cumulative core depth. $^{14}$C-estimated dates are indicated to the left. The diatom taxa are arranged by Correspondence Analysis (CA) axis-I scores so that the changes in diatom assemblages over time are clearly shown. The chrysophyte scale to diatom index (C to D index) is shown. The zones and subzones are indicated, as defined by a constrained cluster analysis on the relative abundance data.
Supplemental figure 4-4. Concentrations of diatom taxa found in a sediment core collected from center of the lake from Meekin Lake versus cumulative core depth. $^{14}$C-estimated dates are indicated to the left. The zones and subzones are indicated as defined by a constrained cluster analysis on the diatom concentration data.
Chapter 5

General discussion and future direction

Regional studies of past climate change and effects on lakes is important to increase our understanding of natural climate variability, and the impacts climate has had on aquatic ecosystems, as well assessing the vulnerabilities and risks to aquatic resources in a region. According to the recent IPCC report (2013), effects of climate related change will vary regionally. Our Earth had experienced anomalous climate condition during early-to-middle Holocene with much wetter conditions in Africa and parts of Asia, and drier and arid condition in central North America (Waner et al., 2008). Region specific studies are the only way to better understand the sensitivity of climate effects on different ecoregions. My dissertation uses paleolimnological approaches to provide information to increase our understanding of how freshwater boreal lakes, from northwest Ontario, have responded to climate change, over a variety of time scales. This information will be useful in addressing the dearth of long-term data on the impacts of climate change on boreal lakes. Paleolimnological studies are one means to provide information on the sensitivity of freshwater ecosystem to past changes in climate (e.g., Battarbee et al., 2004; Pienitz et al., 2004; Smol, 2008). The study location of northwest Ontario was chosen because it represents a climate-sensitive region, since this region is located only 100-km from the present-day prairie-forest boundary. It is widely expected that the prairie biome will shift and displace the existing forest, and that warming will interact with other important drivers of change such as fires, winds, insects and disease to remove forests from the landscape (Frelitch and Reich, 2010). However, transitions from one ecosystem to another can lead to surprises that are sometimes counter-intuitive (Shuman et al., 2009).
Over the last several decades temperature in northwest Ontario have increased (Laird et al., 2012). Additionally future projections suggest increase over 2°C over the next 20 years (Chiotti and Lavender, 2008). This has left many individuals as well as governments and industry struggling to understand the risk of climate warming on water resources. Limnological measurements at the ELA in northwest Ontario have provided valuable insights into the response of boreal lakes to a warming climate. These have included physical, chemical and biological changes in lakes, streams and terrestrial catchments during droughts (Schindler et al. 1980, 1990, 1992, 1996a, b, Bayley et al. 1992a, b), as well as changes in stream flow, lake level, water retention times, change in dissolved organic carbon (DOC), water transparency, and thermal structure of the lake (Schindler et al. 1990, 1992, 1996 a, b). However, precipitation increased in northwest Ontario over the last century as indicated by changes in streamflow (St. George, 2007), potentially suggesting that precipitation may offset overall changes in water supply due to increased temperature. To better understanding how warmer periods in the past have impacted lakes, and how these changes compare to monitoring and instrumental record can help define risks and assess vulnerabilities. At present, governmental organizations consider the central region of Ontario to be at minimal risk from climate change on water quantity, and 20-50 years away from any negative impacts water quality (Chiotti and Lavender, 2008). When a longer temporal perspective is taken, the observed changes in lakes over the last 40 years that were recorded at ELA, many be considered small, in comparison to changes over the instrumental periods. Instrumental records show that WRDB has experienced droughts during the 1930s, 1950s, and 1980s, but these droughts have been spatially asynchronous across climate stations in northwest Ontario (Laird et al., 2012). The estimated aridity of the mid-Holocene is of a similar magnitude to the projected changes over the next 20 years, and is dwarfed by projected changes
by 2050 (Chiotti and Lavender, 2008). Consequently, it can be argued that the changes in water quantity and quality that occurred when the climate was warmer and more arid than present in the mid-Holocene, may have relevance as potential climate scenarios that we may face in the future.

My thesis has been innovative in that I have developed new approaches to study and assess previously inferred changes in lake level over the last several millennia (Chapter 2), where we tested our hypothesis with two different biological proxies of different trophic status (primary producer and invertebrates). This study led to a better understanding of how modern chironomid assemblages change in lakes according to the complex gradient of lake depth, and has provided evidence that support the previous diatom-based inferences of lower water levels during the Medieval Climate Anomaly (MCA) (Laird et al., 2012; Haig et al., 2013). My research also assessed if previously known changes in lake-level that were assessed from a single lake in northwest Ontario, could be considered a regional representative (Chapter 3). By assessing changes in diatom assemblages over the Holocene from sediment cores from two additional lakes that were separated by hundreds of kilometers, a regional view of changes in effective moisture was developed (Chapter 3). Finally, my dissertation provides evidence that changes in water quality also occurred during the warmer early-to-mid-Holocene in northwest Ontario. A multiproxy approach was used to study changes in lake-water primary production using fossil pigments, spectrally-inferred chlorophyll a, and diatom assemblages in well dated cores, taken from the main central basin of three lakes. Not only was primary production elevated during the early-to-mid-Holocene, but cyanobacteria were generally more abundant in majority of the cores studied. This dissertation has built on previous studies and approaches studying the importance of past climate on terrestrial and aquatic environments in northwest Ontario. This dissertation
shows the benefit of studying a climatically-sensitive region, and the value of using both near-shore and deep-water cores to address issues of changes on lake level and water quality. By design, this thesis attempts to track changes in water level by studying cores taken from sensitive near-shore locations (Chapters 2 and 3), as well as evaluating changes in overall lake-water quality, which are better assessed using cores taken from the deep center basin of each lake (Chapter 4). In its entirety, this dissertation, attempts to shows the utility and strength of using multiproxy and multiple-core approach to provide regional inferences on the sensitivity of boreal lakes to climate and other environmental change.

The research in Chapter 2, builds on previous research undertaken in northwest Ontario. In Chapter 2, the validity of the diatom-based inferences of changes in lake-level over the last two thousand years is assessed (Laird et al., 2012; Haig et al., 2013; Ma et al., 2013) by developing and applying an independent approach for Gall Lake. In this chapter, a within-lake assessment of the distribution of chironomid assemblages in Gall Lake, was used to assess the validity of previous lake levels that were inferred based on changes in diatom assemblages. From the modern-day within-lake calibration set, chironomid assemblages showed changes associated with lake-water depth. Lake depth was viewed as a composite environmental variable, associated with many different environmental variables, including habitat, temperature, oxygen and food availability. Many chironomid taxa were clearly associated with shallower habitat, and two taxa, C. anthracinus and S. coracina, were more abundant in the deeper profundal zone. The knowledge of the present-day distributions of chironomids with lake depth in Gall Lake, were then applied to a near-shore sediment core, taken from a depth of 7.5 m. A hypothesis testing framework, using the inferences of centennial-scale low- and high-water level changes inferred from diatom assemblages (Haig et al., 2013), was used to assess the response of the chironomid
assemblages. Three \textit{a priori} defined time periods that spanned approximately equal 500-year periods (two wet periods, one before, and one after the MCA; and one dry period, during MCA) were chosen. Midge assemblages were quantified using both relative abundance and concentration metrics. Species compositions from different time periods were statistically assessed using a multivariate Analysis of Similarities. Statistically significant differences were found in the species composition between wet and dry periods, with profundal taxa declining, as expected, during the low-water stand of the MCA. This study provided further evidence that supported the diatom-based inference of low water-levels during the MCA (Laird et al., 2012; Haig et al., 2013). The hypothesis testing framework used in this chapter has been advocated for use in paleolimnology, however it is not frequently used (Birks, 1996, 1998).

Chapter 3 was inspired by previous research on Lake 239 from the Experimental Lakes Area (ELA). This included the 40-plus years of chemical and biological monitoring data from this lake, where climate-driven limnological changes were documented (e.g. Schindler et al., 1996a; Parker et al., 2009), as well as a number of paleolimnological investigations have been carried out on this lake to provide a longer-term perspective of climate-driven change on this lake (Moos et al., 2005; Laird and Cumming, 2008, 2009; Moos et al., 2009; Moos and Cumming, 2011, 2012). Pollen records spanning the Holocene from near the Manitoba/Ontario border to lakes up to ~300-km east of the prairie-forest ecotone, indicate a warmer and possibly wetter mid-Holocene period across northwest Ontario from ~8000 to 4500 cal yr BP. However, prior to this thesis, only one Holocene-scale record of changes in effective moisture, as indicated through diatom-inferred changes of lake level in Lake 239, was available from this region. Our study expands the regional context of Holocene climate change, with the analysis of diatom assemblages in sediment cores from two additional lakes, which span a distance of over 200-km
across the present-day boreal forest, and 80-km west of ELA Lake 239 to ~150-km to the northeast. In cores from both lakes, benthic taxa predominate in the early-to-mid-Holocene period, with a low abundance of planktonic taxa, suggesting lower lake levels by ~2-5 m, when compared to modern-day diatom assemblages from these lakes (Kingsbury et al., 2012).

Increases in the abundance of planktonic taxa to greater than 50% of the assemblages occurred in both lakes beginning ~4500-4000 cal yr BP, suggesting positive water balance over the last 4000 years in comparison to the mid-Holocene period. This new evidence supports a regional early-to-mid-Holocene period of aridity with reduced water levels across the boreal region; this finding is consistent with changes in vegetation inferred from pollen assemblages during this time period (Moos and Cumming, 2011). If climate change results in lower effective moisture in the future, then conditions could become similar to the mid-Holocene period aridity, leading to challenges for aquatic organisms, as well as the management of water resources across northwest Ontario.

In many regions around the world, a significant increase in cyanobacterial blooms has been reported over the past few decades (O’Neil et al. 2012), and both nutrients and climate have been used as causal explanation of such changes. The idea of enhanced primary production in northwest Ontario due to changes in water levels and warmer conditions was first raised by Moos et al., (2009). In a study based on both near-shore and deep-water cores, Moos et al., (2009) showed that from 8,500 to ~4,500 cal yr BP, when water levels were lower in the near-shore cores, there was a dominance of high-nutrient diatom taxa and higher concentration of biogenic silica in the deep-water core from ELA Lake 239, a core that was taken from a depth of ~28 m. Based on this finding, in conjunction with the findings of regionally-low water levels across northwest Ontario (Chapter 3) and warmer temperatures (Moos and Cumming, 2011) at
this time, we hypothesized that primary production in lakes would increase, as might undesirable blue-green cyanobacterial bloom. For testing this hypothesis, fossil pigments, spectrally-inferred chlorophyll a and diatom assemblages were analyzed in deep-water cores from all three lakes (Gall Lake, Lake 239 and Meekin Lake). These lakes, as mentioned earlier, span a ~200-km gradient across the boreal forest region of northwest Ontario. Overall Chapter 4 supports a regional early-to-mid-Holocene period of enhanced lake production. All three indicators show a coherent pattern of enhanced production in two of the study lakes (Gall and ELA Lake 239), whereas in Meekin Lake a more nutrient-rich early to mid-Holocene was evident only from the diatom assemblage. Enhanced lake-water production was also associated with elevated concentrations of cyanobacterial pigment in two of the three lakes (Gall Lake and Lake 239), and the occurrence of purple sulfur bacteria in one lake (Gall Lake). This study suggests that if a shift in climate in northwest Ontario becomes warmer and drier in the future, then challenges for water managers will not only be restricted to decreased water quantity, but also to water quality since overall production and increases in cyanobacteria could also occur, as they have in the past.

This study has shown that first-order boreal lakes are indeed sensitive to both changes in climate over the Holocene, as well as the last 2,000 years. However it has also raised questions associated with a time-transgressive pattern across this region (Chapter 4). At this point, this pattern is speculative given that only cores from three sites have been analyses. Additional sites from both western and eastern locations across northwest Ontario would be necessary to validate this finding, as would analysis of pollen assemblages from Meekin and Gall lakes (Danesh, unpublished data). Analysis of other biological proxies (e.g., Cladocera, protozoan, soft algae) would certainly add to our understanding of environmental changes in this region. For example, scaled chrysophytes, a well-known paleolimnological proxy, were highly abundant in Gall lake.
over the last 5000 years, and would be useful to compare to recent changes that have occurred at the Experimental Lakes Area over the last 200 years (Flear, 2012), let alone, over the Holocene.

In this study, a within-lake calibration set was used to interpret changes in chironomid assemblages in the Gall Lake sediment core (Chapter 2). More information could be gleaned on the important controlling factors of chironomid assemblages in a between-lake calibration set (e.g., Quinlan et al., 2012) for the greater region, especially if the calibration lakes spanned from the prairies, across the forest-prairie boundary and well into the boreal forest. Finally, many new techniques are now available, for example, X-ray fluorescence (XRF) scanning techniques which are rapid and non-destructive and give high resolution geochemical data of the sediment core (ITRAX). These approaches could further enrich the interpretations that are being based on biological proxy data in northwest Ontario.

5.1 Literature cited


Bayley, SE., Schindler, DW., Beaty, KG., Parker, BR., Stainton, MP., 1992b. Effects of multiple fires on nutrient yields from streams draining boreal forest and fen watersheds: nitrogen and phosphorus. Canadian Journal of Fisheries and Aquatic Sciences, 49: 584–596.


Appendix A

**Pb $^{210}$ and Cs$^{137}$ profile for Meekin and Gall Lake**

The activities of $^{210}$Pb in the upper intervals of the piston cores from i) Meekin (3-4 cm interval; $^{210}$Pb activity= 1833.97 Bq/kg ; $^{137}$Cs activity= 396.41 Bq/kg ) and Gall lakes (2.5-3 cm interval; $^{210}$Pb activity= 1381 Bq/kg; $^{137}$Cs activity= 256.09 Bq/kg) correspond to the activities in $^{210}$Pb-dated gravity cores taken from similar locations years ~1995 for Meekin lake, and ~1977 for Gall Lake

i) **Meekin Lake**

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Appendix B

Analog analysis

Measures of similarities between the diatom assemblages in the cores of i) Gall Lake, and ii) Meekin Lake and the modern calibration dataset of diatom assemblages in the 268 freshwater lakes from British Columbia. Similarities between modern and fossil assemblages are best on the best match (highest Bray-Curtis Similarity between the core and modern samples. All similarity coefficients are calculated using a Bray-Curtis similarity coefficient following a square-root transformation of the relative abundances of diatom taxa. The 50\textsuperscript{th} and 90\textsuperscript{th} percentiles of the distribution of the Bray-Curtis lowest similarity coefficients are shown between the best-match between each modern sample with any other modern sample in the modern calibration dataset of 268 lakes. Similarity coefficients less than 0.44 are considered poorer analogs.