Assessing diatom shifts in embayments and lakes in and around Georgian Bay (Lake Huron) using paleolimnology

by

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Abstract

Freshwater ecosystems in Ontario are affected by a growing number of multiple stressors, with climate change often acting as a “threat multiplier”. Diatom-based paleolimnological approaches are used to provide the much needed long-term ecological information for embayments and lakes in and around Georgian Bay. In Chapter 2, the relative importance of nutrients and warming on the recent increase in sedimentary *Asterionella formosa* relative abundances in George Lake by comparing regional air temperature trends, 20 years of annually measured lake water nutrients (total nitrogen, total inorganic nitrogen, and total phosphorus), and long-term regional total inorganic nitrogen deposition data. Recent increases in *A. formosa* occur during the warmest period on record, even in the absence of nutrient enrichment. In Chapter 3, sedimentary diatom assemblages from two lakes in Killarney Provincial Park (north of Georgian Bay) are shown to clearly track the acidification of regional lakes around the turn of the 20th century in response to smelting activities in Sudbury, Ontario. Although the Killarney lakes showed signs of chemical recovery (increase in pH), the recent (post-1980s) diatom assemblages are not similar to either pre-acidification or acidification assemblages suggesting factors such as climate warming are partly driving recent diatom assemblage changes, rather than simply chemical recovery. In Chapter 4, diatom responses to shoreline development and climate warming in three embayments from southeastern Georgian Bay, two with shoreline development (impact) and one without (unimpacted). In the early 20th century, compositional changes in diatoms at the two impacted embayments are indicative of a modest increase in nutrient conditions. In the mid to late-20th and early 21st centuries, pronounced shifts towards higher abundances of lightly silicified pennate (*Asterionella formosa* and *Fragilaria crotonensis*) and/or small centric (*Cyclotella ocellata*, *C. comensis*, and *C. gordonensis*) planktonic diatoms at all three embayments were consistent with
a response to warming and associated changes in thermal and other physical properties. Collectively, my studies show that diatom assemblages are tracking long-term changes in limnological variables, but with the prevalence of multiple environmental stressors in a warming climate, diatom assemblages are on a new trajectory and therefore unlikely to return to pre-industrial scenarios.
Co-Authorship

Chapter 2 was co-authored by Kathleen M. Rühland, Andrew L. Labaj, Andrew M. Paterson, and John P. Smol, represents original work completed as part of this M.Sc. thesis. I completed the diatom and statistical analysis and was the primary author of the manuscript. Andrew L. Labaj obtained regional temperature records and lake water nutrient data and Andrew M. Paterson provided atmospheric deposition data. I drafted the manuscript and all co-authors assisted with the interpretation of results and edited the manuscript. This paper has been published separately in the Journal of Paleolimnology.


Chapter 3 was co-authored by Kathleen M. Rühland, and John P. Smol, represents original work completed as part of this M.Sc. thesis. I completed the diatom and statistical analysis and was the primary author of the manuscript. I drafted the manuscript and both co-authors assisted with the interpretation of results and edited the manuscript. This manuscript has been formatted for submission to Fundamental and Applied Limnology (formerly Archiv für Hydrobiologie).


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“It always seems impossible until it’s done”
- Nelson Mandela
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List of Abbreviations

ARA – Average Relative Abundance

$^{137}$Cs - Cesium-137

Chl-$a$ – Chlorophyll $a$

CRS – Constant Rate of Supply

CONISS – Constrained incremental sum of squares

DO – Dissolved Oxygen

$\text{H}_2\text{SO}_4$ – Sulfuric acid

$\text{HNO}_3$ – Nitric acid

LOESS – Locally weighted scatter-plot smoother

max. depth – Maximum depth

N – Nitrogen

P – Phosphorus

PCA – Principle Components Analysis

$^{210}\text{Pb}$ – Lead-210

$\text{SO}_2$ – Sulfur dioxide

TKN – Total Kjedahl Nitrogen

TIN – Total Inorganic Nitrogen

TN – Total Nitrogen

TP – Total Phosphorus

VRS – Visible Reflectance Spectroscopy
Chapter 1

General Introduction

1.1 Lakes as sentinels of environmental change

Human activities have always had impacts on aquatic ecosystems. However, the magnitude of anthropogenic effects has varied substantially over time. Since the industrial revolution, humans have become a major force affecting water quality with activities such as shoreline development, acidification, nutrient enrichment, contaminants and climate change. A growing number of studies have shown that lakes in Canada are subjected to multiple environmental stressors, resulting in novel ecological responses that are more complex than the response to any individual stressor (Rühland et al. 2010; Hawryshyn et al. 2012; Labaj et al. 2015). Multiple stressors can interact, synergistically or antagonistically impacting freshwater ecosystems resulting in “ecological surprises” (Christensen et al. 2006; Keller 2007; Ormerod et al. 2010). The situation is complicated further as climate warming can act as a “threat multiplier” (Smol 2010) on already-stressed aquatic ecosystems, exacerbating the effects of other stressors on ecosystem health. Hence, understanding and managing freshwater systems poses challenges for establishing attainable remediation targets, particularly in culturally and ecologically important international waterbodies such as the Laurentian Great Lakes and surrounding freshwater ecosystems. Additionally the lack or scarcity of long-term data, important for determining trajectories of ecosystem change and for establishing pre-impact conditions also pose challenges to determine realistic recovery goals. However, indirect proxy techniques, such as the paleolimnological approaches used in this thesis, can be used to reconstruct missing data sets.
1.2 Paleolimnology

Paleolimnology is the science of reconstructing long-term environmental change using chemical, physical, and biological proxies preserved in lake sediments (Smol 2008). In the absence of direct long-term monitoring data, indirect approaches such as paleolimnology can be used to assess past environmental conditions. The long-term perspective on water quality changes provided by paleolimnological techniques can be used to make appropriate management decisions and set realistic restoration targets. Many different proxies can be used to assess water quality changes in paleolimnology. In this thesis, I will focus on sedimentary diatoms and spectrally-inferred sedimentary chlorophyll $a$ from dated sediment cores collected from lakes and embayments around Georgian Bay.

1.3 The Laurentian Great Lakes

The Laurentian Great Lakes are economically and ecologically important freshwater systems, as they provide drinking water and valuable ecosystem services to both Canada and the United States, and contain ~18% of the world’s surface fresh water (Assel et al. 2004). However, the water quality and quantity of the water within the Great Lakes has changed substantially over the past ~200 years in response to anthropogenic activities. The ecological concerns facing the Laurentian Great Lakes include, but are not limited to, algal blooms, introductions of non-native species, changes in water levels, and nutrient loadings, while recent warming has resulted in increases in summer water temperatures, early onset of thermal stratification, and decreases in the number of ice-covered days (Ricciardi 2006; Austin and Colman 2007; Jensen et al. 2007; International Upper Great Lakes Study 2009). These environmental changes can result in serious consequences for aquatic biota (Casselman 2002; Riley et al. 2008; Reavie and Barbiero 2013; Reavie et al. 2014), and understanding the impacts of simultaneous stressors in freshwater
ecosystems will prove important for the implementation of realistic restoration targets in the Laurentian Great Lakes in a warming world. Below I provide a brief introduction to my main study sites, all of which are situated in and near Georgian Bay (Lake Huron).

1.4 Georgian Bay

Georgian Bay, the largest bay of Lake Huron, is partially separated from the main lake basin by the presence of the Bruce Peninsula to the south and Manitoulin Island to the north (Fig. 1.1). Completely contained within the province of Ontario, Georgian Bay contributes substantially to the provincial economy by supporting seasonal recreational activities. The presence of provincial parks along the coast, as well as the development of cottages on the shores of smaller embayments and lakes around Georgian Bay, has made it an ideal location for year-round recreation and leisure. However, mining activities in the Sudbury area along with shoreline development in southeastern Georgian Bay have likely altered the water quality of the embayments and lakes in the region (e.g. Dixit et al. 1992a; Clark et al. 2015).

1.5 Multiple stressors affecting embayments and lakes in and around Georgian Bay

Sudbury, Ontario, located north of Georgian Bay, was a major center of metal smelting operations in Canada from the late-1800s (Watson and Richardson 1972) to the late-20th century. The smelting processes resulted in the release of large amounts of SO$_2$ and NO$_X$ compounds, which contributed to acid deposition and subsequent acidification of many poorly-buffered nearby lakes, as well as loss of vegetation in the Sudbury area (Gorham and Gordon 1960; Beamish 1976). Many lakes in Killarney Provincial Park, on the northern shores of Georgian Bay, were acidified in the 1920s as a result of acid deposition (Dixit et al. 1992). Although the implementation of SO$_2$ reduction programs in the 1970s and 1980s has led to the chemical recovery (specifically increase in pH) of many lakes to their pre-acidification levels, the biota
have not yet recovered to pre-acidification composition in the Sudbury area (Dixit et al. 2002; Labaj et al. 2015). In recent decades, climate warming has become an added stressor on the previously-acidified lakes, leading to changes in the thermal properties of many lakes in Sudbury (Keller 2007, 2009). The lack of complete biological recovery in Sudbury and Killarney Provincial Park lakes during the period of chemical recovery is not surprising, as regional climate warming is strongly influencing the aquatic biota (Labaj et al. 2015).

Georgian Bay Littoral, encompassing the eastern and southeastern shores of Georgian Bay, contains the largest freshwater island archipelago in the Laurentian Great Lakes, for which it was designated a United Nations Educational, Scientific and Cultural Organization (UNESCO) Biosphere Reserve (UNESCO, 2010). The presence of islands and road-accessible embayments makes southeastern Georgian Bay an ideal location for permanent residences and seasonal recreational activities. However, recent limnological surveys from small embayments in southeastern Georgian Bay have recorded continuous low water levels, increases in macrophyte growth, declines in deep-water oxygen levels, higher nutrient levels relative to the open waters, and loss of cold-water fish habitat (Schiefer 2003; Schiefer et al. 2007; Chiandet and Sherman 2010). Nutrient enrichment resulting from human activities such as shoreline development has often been implicated as the cause for recent water quality changes and algal blooms in the embayments, although these changes have also occurred during a period of marked climate warming in the region. Recognizing the substantial changes in water quality of the embayments of southeastern Georgian Bay, in 2012 the Government of Canada provided an additional $29 million to the Lake Simcoe Clean-up Fund, in which southeastern Georgian Bay was included, to improve ecosystem function and services.
Other stressors, such as invasive species, contaminants, and cage aquaculture activities, have had negative impacts on the freshwater systems around Georgian Bay (e.g., Clerk et al. 2004). In addition to these local stressors, climate warming is acting as a regional stressor in Ontario and elsewhere.

In this thesis, a paleolimnological approach is used to assess long-term environmental change in the Georgian Bay area. Specifically, in Chapter 3 of this thesis, the effects of acidification and climate change on two lakes from Killarney Provincial Park are assessed. In Chapter 4, the combined effects of nutrient enrichment and climate warming on two embayments are compared to the effects of climate change alone on an unimpacted embayment from southeastern Georgian Bay.

1.6 Paleolimnological proxies

Diatoms (Bacillariophyta) are a diverse group of algae that are an integral part of most aquatic ecosystems because of their role as primary producers. Diatoms are excellent paleo-bio-indicators because they: 1) preserve well in most sediments, 2) are sensitive to limnological changes and rapidly respond to environmental change, 3) well represented by many species, and 4) are typically identifiable to the species level (Smol and Stoermer 2010). Diatoms have been used extensively for over a century in limnological and paleolimnological research to study environmental change in lotic and lentic systems, as assemblage composition typically responds sensitively to changes in nutrients and pH. For example, with paleolimnological approaches, diatoms have been used to effectively track eutrophication (Hall and Smol 2010) and acidification (Battarbee et al. 2010) over long time scales. Although diatoms do not necessarily respond directly to rising air temperatures, they do respond to changes in lake thermal properties induced by climate warming (Rühland et al. 2008, 2015). Diatoms have also been used to
analyze the impacts of anthropogenic effects such as hydrological changes (e.g., dam constructions; Rühland et al. 2010), cage aquaculture farming (Clerk et al. 2004), and shoreline development (Little et al. 2000). Diatoms have also been used to try to assess the effects of multiple stressors in lake ecosystems (Rühland et al. 2010; Hawryshyn et al. 2012).

Spectrally-inferred sedimentary chlorophyll \( a \) concentrations in lake sediments have been used to infer changes in whole ecosystem primary production, providing valuable information on shifts in lake trophic status (Das et al. 2005; Michelutti et al. 2005; Wolfe et al. 2006; Michelutti et al. 2010). Recently, increases in spectrally-inferred sedimentary chlorophyll \( a \) have been observed in many lakes, and often attributed to increased whole-lake primary production as a result of decreased ice cover and climate change (Michelutti et al. 2005; Labaj et al. 2015). Spectrally-inferred sedimentary chlorophyll \( a \) trends are frequently in agreement with the trends observed in diatom assemblages, providing a more comprehensive understanding of algal primary production in freshwater systems (Nelligan et al. accepted).

1.7 Thesis objectives and design

The overarching objective of this M.Sc. thesis is to assess the effects of acidification, nutrient enrichment, and climate warming on aquatic ecosystems in and around Georgian Bay using paleolimnology. This thesis consists of five chapters. Following this brief introductory chapter, three detailed data chapters are presented.Lastly, general conclusions (Chapter 5) briefly summarize the findings of this thesis and recommend opportunities for future developments.

In Chapter 2, the relative importance of nutrients and climate warming on the recent increase in the relative abundance of the diatom *Asterionella formosa* are explored. This study was inspired by recent paleolimnological studies that documented a marked increase in the
relative abundance of *A. formosa* across Boreal Shield lakes in Ontario, where warming-related changes to lake thermal properties have been described as a possible explanation for its increase in abundance (Rühland et al. 2010; Hyatt et al. 2011; Hadley et al. 2013; Barrow et al. 2014). However, studies from the mid-western United States suggest that increased nitrogen deposition is contributing to the recent success of *A. formosa* (Wolfe et al. 2003; Saros et al. 2005). Our study in Chapter 2 differs from previous research because annually measured lake water nitrogen data, direct measurements of regional inorganic nitrogen deposition, regional climate data, and high-resolution sedimentary *A. formosa* data are used to assess the relative importance of nitrogen and air temperature on the recent success of *A. formosa* in a Boreal Shield lake. An increase in the relative abundance of *A. formosa* is observed at George Lake, whilst measured lake water total nitrogen, total inorganic nitrogen, and regional total inorganic nitrogen deposition are declining. However, the marked increase in the relative abundance of *A. formosa* is occurring during the warmest period in the temperature record. Based on the evidence, the recent increase in *A. formosa* at George Lake and other lakes in Ontario is likely a response to regional warming rather than nitrogen deposition.

Chapter 3 is an assessment of biological recovery of two acidified lakes in Killarney Provincial Park, Killarney (Ontario) using diatoms as paleolimnological bio-indicators. This study was inspired by previous work of Dixit et al. (1992) and Labaj et al. (2015). Dixit et al. (1992) retrieved sediment cores from Lumsden and George lakes (Killarney Provincial Park) in 1987 and assessed sedimentary diatom and chrysophyte assemblages. They concluded that these lakes were acidified and were showing signs of recovery in the most recent sediments based on the sedimentary diatom and chrysophyte assemblage shifts (Dixit et al. 1992). Twenty-five years later, Labaj et al. (2015) re-cored the same lakes and examined Cladocera assemblages and
spectrally-inferred sedimentary chlorophyll $a$. The increase in spectrally-inferred sedimentary chlorophyll $a$ in the most recent sediments across both lakes suggests that warming-related changes have resulted in an increase in primary production (Labaj et al. 2015), and is consistent with regional observations (Michelutti et al. 2010). My study specifically addresses whether diatoms from these lakes have completely returned to pre-acidification assemblages in response to chemical recovery (particularly pH) during a period of striking increases in regional temperatures. Diatom assemblages across both lakes responded to acidification, consistent with Dixit et al. (1992). However, the most recent diatom assemblages are substantially different from both pre-acidification and acidification assemblages, suggesting that factors other than chemical recovery are influencing the most recent diatom assemblages. We suggest that multiple stressors, particularly climate-related shifts to lake thermal properties, are playing an important role in influencing diatom assemblages. These previously-acidified lakes have crossed critical climate-related thresholds and are likely not going to return to pre-acidification assemblages.

In Chapter 4, the effects of shoreline development and climate warming on two embayments in eastern Georgian Bay are compared to the effects of climate warming alone on an embayment with almost no shoreline development. This work was motivated by recent observations of declining water levels during the 2000s, increases in macrophyte growth and cyanobacteria blooms, and declines in hypolimnetic oxygen and phosphorus release from the sediments in the embayments of Georgian Bay (Schiefer et al. 2006, 2007; Chiandet and Sheman 2010, 2014; Clark et al. 2015). In Chapter 4, diatom assemblages and spectrally-inferred sedimentary chlorophyll $a$ were analyzed in dated sediment cores from three large embayments of Georgian Bay. The availability of one embayment (Tadenac Bay) with no shoreline development provided an important opportunity to compare the effects of shoreline development
on two impacted embayments from Honey Harbour (North and South bays). Diatom assemblage changes in the late-1800s at the two impacted sites are indicative of slightly higher nutrient conditions, likely as a consequence of shoreline development such as permanent residences and recreational resorts. However, pronounced shifts towards more lightly silicified planktonic diatoms during the mid to late 20th century and early-21st century across all three embayments are consistent with similar observations from other southern Ontario lakes (Rühland et al. 2010; Hawryshyn et al. 2012). The synchronous diatom shift in the late-20th century is likely a response to changes in lake thermal properties, an effect of regional climate warming observed across lakes in Ontario.

Collectively, the data from this thesis show that embayments and lakes in and around Georgian Bay are responding to several stressors, with climate warming likely being a key variable over recent history. Furthermore, the algal assemblages of many freshwater systems have crossed critical climate-related thresholds and are likely not going to return to pre-disturbance conditions.

1.8 Acknowledgement

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1.9 References


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1.10 Figures

**Figure 1.1**: Map of Georgian Bay and major surrounding locations
Chapter 2

Why is the relative abundance of *Asterionella formosa* increasing in a Boreal Shield lake as nutrient levels decline?
2.1 Abstract

The freshwater diatom *Asterionella formosa* Hassall is a widely distributed species whose populations have been increasing in the recent sediments of numerous lakes worldwide. This taxon’s proliferation has commonly been associated with nutrient enrichment and, more recently, with 20th century increases in atmospheric nitrogen deposition. However, a growing number of studies have reported increases in *A. formosa* in the absence of increased nutrients and have thus raised questions about whether alternative causative factors (such as recent climate warming) may be important. Here we assess the relative importance of nutrients and climate warming on *A. formosa* by comparing regional air temperature trends and 20 years of annually measured (point measurements taken in June or July of each year) lake water nutrients (total inorganic nitrogen, total nitrogen and total phosphorus) with past changes in relative abundance of this taxon from a sediment core obtained from a soft-water, boreal shield lake (George Lake, Killarney, Ontario).

Measured lake water total phosphorus has always been very low and remains so to the present (<10 µg L⁻¹). Total inorganic nitrogen (TIN) and total nitrogen (TN) concentrations, however, show distinct declining trends (p < 0.05) at George Lake since the 1990s, when substantial increases in mean annual and mean winter air temperatures (p < 0.01) were also recorded. These declines in lake water nitrogen concentrations match declines in atmospherically deposited nitrogen in this region. Since the late-1980s and early-1990s, there has been a marked increase in the relative abundance of *A. formosa*, which had been virtually absent from the lake’s sediment record in earlier intervals. *A. formosa* trends closely track increasing regional air temperatures, but also clearly coincide with declines in lake water nutrients and decreases in regional nitrogen deposition (p < 0.01). These trends have also occurred in other lakes in the region. Our results show that increases in nitrogen deposition and/or nutrient enrichment are not pre-conditions for
increases in the relative abundance of *A. formosa*. Instead, warming-related changes including longer open water periods, changes in lake mixing regimes, and lake thermal properties might have contributed to the recent increase in the relative abundance of *A. formosa* in this lake and likely elsewhere.

### 2.2 Introduction

*Asterionella formosa* Hassall is an elongate, pennate diatom that forms star-shaped colonies by linking cells with mucilage pads at the foot-pole (Round et al. 1990). It has been reported in freshwater systems around the world (Tibby and Reid 2004; Dong et al. 2008; Hadley et al. 2013; Berthon et al. 2014; Hundey et al. 2014), and has often been considered to be indicative of moderate nutrient enrichment (Clerk et al. 2000; Reynolds et al. 2002; Bennion et al. 2011). Nonetheless, *A. formosa* has also been observed in notable abundance in nutrient-poor lakes (Rimet et al. 2009; Enache et al. 2011; Hadley et al. 2013), suggesting that *A. formosa* may have a relatively wide nutrient tolerance (Rimet et al. 2009).

Although *A. formosa* has been known to bloom during early-spring and late-fall, when lakes are well-mixed and nutrients are distributed throughout the water column (Maberly et al. 1994; Bertrand et al. 2003; Wang et al. 2012), peaks in this species have also been observed in the summer during thermally stratified periods (Solovieva et al. 2005; Becker et al. 2008; Rimet et al. 2009), and it may remain an important part of the phytoplankton community until fall overturn (Rimet et al. 2009). Importantly, the high surface area to volume ratio of *Asterionella* provides this taxon with one of the lowest sinking velocities of all freshwater diatoms (Round et al. 1990; Spaulding and Edlund 2009). The lower sinking velocities are further enhanced by the stellate structure of their colonial form (Jaworski et al. 1988; Round et al. 1990).
The relative abundance of *A. formosa* has been recently (~post 1980/1990) increasing or observed for the first time in paleolimnological studies across Ontario, Canada (Rühland et al. 2010, 2013; Hadley et al. 2013), as well as in many other regions globally (Solovieva et al. 2005; Stewart et al. 2008; Hobbs et al. 2010; Saros et al. 2011; Thies et al. 2012; Wang et al. 2012). In some previous paleolimnological studies from so-called “nitrogen hotspots”, such as the western Rocky Mountains of the United States, increases in *A. formosa* have been at least partly attributed to nutrient enrichment related to increased delivery of atmospheric nitrogen to these alpine lakes (Wolfe et al. 2003; Saros et al. 2005, 2011; Hundey et al. 2014; Sheibley et al. 2014). In regions where *A. formosa* has been increasing, but nutrient concentrations have not changed or have been declining, factors aside from phosphorus and nitrogen concentrations must be responsible for the diatom assemblage shifts (Rühland et al. 2010, 2015; Hyatt et al. 2011; Hadley et al. 2013). In these regions, changes in lake water thermal properties and mixing patterns induced by climate warming have recently been implicated as possible drivers of diatom assemblage shifts in these lakes (Rühland et al. 2010; Enache et al. 2011; Hyatt et al. 2011; Hadley et al. 2013).

In this study, we explicitly address the issue of whether nutrients or climate variables are the primary drivers of an increase in the relative abundance of *A. formosa* observed in Ontario Shield lakes. George Lake (Killarney, Ontario, Canada) provides us with an exceptional opportunity to directly examine possible triggers for the recent increase in this taxon that has been observed throughout Ontario. The rare existence of long-term data sets including 20 years of annually measured (point measurements taken in June or July) lake water nutrient concentrations from George Lake (total inorganic nitrogen (TIN), total nitrogen (TN), and total phosphorus (TP)), over three decades of regional TIN deposition data from three locations in our
study region of south-central Ontario, as well as 57 years of continuous regional air temperature data, allowed us a valuable opportunity to directly test whether increases in *A. formosa* relative abundances are associated with nitrogen concentrations and climate.

### 2.3 Site description

George Lake (46° 01.796' N, 81° 23.831' W), located in Killarney Provincial Park, Killarney (Ontario, Canada), is a deep (max depth = 39.7 m; Beamish et al. 1975), thermally stratified, ultra-oligotrophic (total phosphorus = 3.2 µg L\(^{-1}\)), circumneutral (pH = 6.3) lake (water chemistry data measured in August 2013; Alex Ross pers. comm. 2015). Due to its proximity to smelting operations taking place in Sudbury, and the poor buffering capacity provided by the underlying Precambrian Shield bedrock, George Lake began to acidify during the 1920s (Dixit et al. 1992). However, the implementation of SO\(_2\) reduction programs beginning in the 1970s has resulted in reduced regional acid deposition and an increase in pH back to pre-disturbance levels of many lakes in this region, including George Lake (Keller et al. 2003, 2006). George Lake is one of several lakes in Killarney Provincial Park that has been monitored for changes in various limnological characteristics (nutrients, metals, pH etc.) over the past three decades (since 1980) as part of the Sudbury Environmental Study Extensive Monitoring Programme (Keller et al. 2006), with annual lake water nutrient data (TIN, TN, TP) available since 1990. In addition to lake water chemistry, atmospheric deposition data (including TIN) have been collected at three meteorological stations at the Ontario Ministry of the Environment and Climate Change’s Dorset Environmental Science Centre (DESC) (approximately 200 km southeast of George Lake). These data have been collected since the mid-1970s as part of a long-term inland lake monitoring program (Yan et al. 2008a). This provides us with a unique opportunity to combine long-term, measured lake water nutrient concentration data (TIN, TN, TP), regional TIN depositional data,
and regional meteorological data, with sedimentary diatom data to assess the relative importance of nutrients and temperature on the increasing abundance of *A. formosa* at George Lake.

### 2.4 Methods

#### 2.4.1 Monitoring data

TIN, TN, and TP data were obtained from the Cooperative Freshwater Ecology Unit (Laurentian University, Sudbury, Ontario, 2012). The water chemistry analyses were conducted at either the Ontario Ministry of the Environment and Climate Change Laboratory in Toronto, Ontario (1990-1996, 1998-2001), or the Dorset Environmental Science Centre (1997, 2002-present). TIN ((NO$_2$ + NO$_3$) plus (NH$_3$ + NH$_4$)), TN (total Kjeldahl nitrogen (TKN) plus (NO$_2$ + NO$_3$)), and TP were point, surface water measurements taken in June or July of every year between 1990 and 2011. A detailed description of field methods and protocols regarding the water chemistry samples are presented in Keller et al. (2006). NH$_3$ + NH$_4$ data were not available for the year 2002, and were therefore not included in the figures and calculations.

Deposition data for selected solutes (including nutrients) are estimated from solute concentrations of bulk precipitation multiplied by precipitation volume. At each location, a bulk precipitation collector is located in an open area, with bulk precipitation sampled weekly for water chemistry, and daily precipitation data available from an adjacent weather station. Results herein are presented as total (annual) inorganic nitrogen deposition for each of three stations maintained by the Dorset Environmental Science Centre (Harp Lake: 45° 22.719’ N, 79° 08.102’ W; Plastic Lake: 45° 10.886’ N, 78° 49.245’ W; Dickie Lake: 45° 08.917’ N, 79° 05.410’ W).

A continuous air temperature record from Sudbury Airport climate station (46° 37.533’ N, 80° 47.867’ W; Climate Station ID: 6068150; World Meteorological Organization ID: 71730)
extends from 1956 to the present (Environment Canada Historical Climate Record: http://climate.weather.gc.ca/) and is the closest climate station to our study lake (80.5 km away). The mean annual and mean winter (December, January, February) temperatures between 1956 and 2012 were used to explore relationships with the relative abundances of *A. formosa*.

### 2.4.2 Field and Laboratory methods

A high-resolution sediment core was retrieved from the deepest part of George Lake in July 2012 using a Glew (1989) gravity corer. The sediment core was extruded on-site and sectioned at 0.25 cm intervals from 0 – 15 cm and at 0.5 cm intervals from 15 cm to the base of the core using a Glew (1988) extruder. All sediments were subsequently freeze dried prior to further analyses. 

$^{210}$Pb dates were estimated for the past ~150 years by measuring unsupported concentrations of $^{210}$Pb using gamma spectroscopy facilities available at the Paleoecological Environmental Assessment and Research Laboratory (PEARL), Queen’s University, Kingston, Ontario, Canada. The sediment core followed the characteristic $^{210}$Pb activities, and dates were estimated based on the constant rate of supply (CRS) model described by Appleby (2001). A second order polynomial function was used to extrapolate beyond background $^{210}$Pb activity. The $^{210}$Pb activity profile and $^{210}$Pb dates with associated errors are presented in the supplementary figure (Supplementary Fig. 2.1). Further details on radio-isotopic dating methods and results are found in Labaj et al. (2015).

Diatom slides were prepared using standard guidelines outlined by Battarbee et al. (2001). A minimum of 350 diatom valves were enumerated for each interval. The most common diatom taxa enumerated in the sediment core are stratigraphically presented as percent relative abundance data (Fig. 2.4). For clarity of display, we have grouped all *Eunotia* taxa as “*Eunotia sum*” in the figure. To enable a higher temporal resolution when comparing trends between *A.
*formosa* relative abundances and the instrumental records, *A. formosa* was enumerated for an additional seven intervals within the top 4 cm of the core (all intervals counted) and is presented separately in Fig. 2.5.

2.4.3 Data analysis

Trends in mean annual and mean winter air temperatures, regional TIN deposition data and lake water nutrient data were assessed using Mann-Kendall trend tests using the ‘Kendall’ package (McLeod 2011), developed for the R software environment (R Core Team 2014). Spearman Rank correlation coefficients were used to explore relationships between relative abundance of *A. formosa* and measured lake water total inorganic nitrogen (TIN) and the Sudbury air temperature data. To harmonize the temporal resolution of our paleolimnological proxy data and the annual-scale measured data (monitored TIN data from George Lake and mean annual and winter air temperature data from the Sudbury climate station), air temperature and nitrogen concentrations were averaged to represent the corresponding years represented by each sedimentary interval (*sensu* Sorvari et al. 2002). We focus particularly on TIN, as it has been suggested that TIN is a better measurement to explore nitrogen requirements of algae in lakes because TN contains a large organic fraction that is not readily bioavailable (Bergström 2010). Nonetheless, we also present total nitrogen, as well as lake water total phosphorus levels. Additionally, we calculated the TN/TP (Downing and McCauley 1992) and TIN/TP mass ratios (Bergström 2010).

2.5 Results

The measured lake water TIN and TN concentrations show significant declining trends (*p* < 0.05) at George Lake over the ~20 years (post-1990) of regular monitoring (Fig. 2.1). TIN was as high as ~154 µg L⁻¹ in the 1990s, whereas by 2010 it had declined to ~18 µg L⁻¹ (Fig. 2.1A). TN
also follows a general decreasing trend over the ~20 years of monitoring, with the exception of
the year 2002. Measured lake water TP has always been low and shows less variability than TIN
and TN, but nevertheless records a slight decrease over the ~20 year monitoring period. In 1995,
an uncharacteristically high TP reading (14 µg L⁻¹) was deemed to be an outlier (Keller et al.
2006) and not included in the analysis or figure. Mass ratios of TN/TP and TIN/TP at George
Lake have been relatively high (TN/TP - range: 31.3 – 140; mean: 71.4) (TIN/TP - range: 3.8 –
76; mean: 24.6). In addition to the declines in lake water nutrient concentrations at George Lake,
significant decreasing trends (p < 0.01) in regional total inorganic nitrogen deposition data from
all three meteorological stations were observed (Fig. 2.2).

Air temperature trends from the Sudbury Airport show significant increases (p < 0.01)
over the past 57 years (1956 – 2012) with mean annual and mean winter air temperatures having
increased by ~1.7 °C and ~2.5 °C, respectively (Figs. 2.3A,B). Particularly, notable increases in
mean annual air temperatures are observed post-1990s (Fig. 2.3A).

Discostella stelligera (Cleve and Grunow) Houk and Klee is the dominant diatom species
throughout the sediment core (Fig. 2.4). Tabellaria flocculosa Kützing str IIIp sensu Koppen has
also been present throughout the core and has been gradually increasing in relative abundance
since the 1900s. The first major shift in diatom assemblage occurs around the 1920s with a
notable decrease in the relative abundance of the circumnutral Cyclotella ocellata/tripartita
complex (C. ocellata Pantocsek; C. tripartita Håkansson) and a concomitant increase in the
relative abundance of acidobiontic Asterionella ralfsii W. Smith that were previously present in
trace abundances. The second notable shift in diatom assemblage composition occurs in the
1980s when Asterionella formosa and Psammothidium marginulatum (Grunow) Bukhtiyarova
and Round increase in relative abundances from previously trace abundances at the expense of *Achnanthidium minutissimum* (Kützing) Czarnecki and *A. ralfsii*.

*A. formosa* was present throughout the sediment core, albeit at trace abundances (mean relative abundance = 0.8%) before ~1980, after which it became a prominent part of the diatom assemblage (mean relative abundance = 6.8%) (Fig. 2.5). These increases occurred during the warmest decades on record, but also occurred during a period of notable nutrient decline (TN, TIN, and TP) (Figs. 2.2, 2.3, 2.6). The increase in the relative abundance of *A. formosa* is negatively correlated to TIN (Spearman Rank correlation: $R = -0.2571$, $N = 14$, $p = 0.37$). The increase in the relative abundance of *A. formosa* is positively correlated to mean annual air temperature (Spearman Rank correlation: $R = 0.3965$, $N = 19$, $p = 0.09$).

### 2.6 Discussion

#### 2.6.1 Increases in *A. formosa* despite nitrogen decline

Observed increases in the relative abundance of *A. formosa* over recent decades in George Lake, despite notable decreases in measured lake water TIN, TN, and TP, are consistent with the reported expansion of this taxon in many lakes in Ontario. Importantly, declining nitrogen in George Lake is reflective of a wider-scale regional trend across south-central Ontario, where atmospheric bulk deposition of N (specifically NO$_3^-$ – an important component of TIN and TN) has been decreasing (Kothawala et al. 2011; Fig. 2.2). Although atmospheric nitrogen deposition has increased at a global scale, certain regions are known to have had declining deposition patterns (Vet et al. 2014). For example, the well-documented declines in eastern North America (including south-central Ontario) are often attributed to the implementation of regulations to reduce emissions from coal plants and mining activities in the eastern United States and Canada (Vet et al. 2014). The marginal decline in TP concentrations at George Lake over two decades is
also consistent with regional trends observed in other Ontario lakes where TP concentrations have been declining over approximately the past three decades (Dillon and Molot 2005; Keller et al. 2006; Yan et al. 2008b; Palmer et al. 2011). The high TN/TP and TIN/TP mass ratios also suggest that this lake has been primarily phosphorus (P) limited over the past 20 years.

Although *A. formosa* has been observed to increase in lakes during periods of nutrient enrichment (Clerk et al. 2000; Little et al. 2000) including high altitude, oligotrophic, nitrogen-limited lakes where nitrogen deposition is considerable (Saros et al. 2005; Hundey et al. 2014), the evidence provided by a growing number of studies suggests that the recent and geographically widespread increase in the relative abundance of *A. formosa* (as well as other pennate planktonic diatoms such as *Fragilaria tenera* (W. Smith) Lange-Bertalot and *Tabellaria flocculosa* str. IIIp) can also occur in the absence of nutrient enrichment (Solovieva et al. 2005; Stewart et al. 2008; Thies et al. 2012; Wang et al. 2012; Hadley et al. 2013; Michelutti et al. 2015a, b; Rühland et al. 2015). For example, Hadley et al. (2013) surveyed a suite of lakes from our study region in south-central Ontario and observed a significant regional increase in the relative abundance of *A. formosa* from surface sediment samples collected in 2007/08 compared to those collected from 1992. Importantly, they did not observe any directional relationship between nutrients (TN and TIN) and the relative abundance of *A. formosa* over these time periods, as increases in the relative abundance of *A. formosa* occurred even with no increase in total inorganic nitrogen concentration. Instead, limnological factors linked to climate warming (changes in thermal stratification and mixing regimes, longer ice-free periods) were implicated as the likely causative factors.

Based on the data presented from George Lake, as well as similar profiles from southern Ontario where nutrients have been either decreasing or not changing (Rühland et al. 2010; Hyatt
et al. 2011; Hadley et al. 2013; Barrow et al. 2014), we conclude that an increase in N is not a pre-condition for the increase in the relative abundance of *A. formosa*, particularly in oligotrophic, P-limited systems that typify the southern Canadian Shield. This suggests that alternative factors, such as regional warming, may explain the recent increases in the relative abundance of *A. formosa* in shield lakes from Ontario and likely elsewhere.

### 2.6.2 Asterionella formosa: a sentinel of warming in Ontario?

The rise in *A. formosa* from the mid-1980s to the present occurs during the warmest period in the Sudbury meteorological record (Fig. 2.6). Marked increases in regional air temperatures, with concomitant increases in epilimnetic temperatures of many temperate lakes in Ontario (Keller 2007), have also resulted in longer ice-free periods (Futter 2003), earlier onset and later breakdown of thermal stratification (Cahill et al. 2005; Stainsby et al. 2011), and increased thermal stability (Hadley et al. 2014) and all of the associated lake water property changes. Longer ice-free periods and changes to vertical mixing and thermal stratification patterns have led to the alteration and reorganization of diatom assemblages in Northern (Rühland et al. 2008, 2010, 2015; Hawryshyn et al. 2012; Winder and Sommer 2012) and Southern (Michelutti et al. 2015 a, b) Hemisphere lakes where small planktonic cyclotelloid taxa and planktonic pennate taxa such as *A. formosa* and *F. tenera* are favoured.

The advancement of spring diatom blooms in recent decades has been widely reported from many lakes (Maberly et al. 1994; Straile 2002; Winder and Schindler 2004; Winder and Sommer 2012), and has often been linked to climate-related changes in physical processes such as thermal stratification (Winder and Schindler 2004) and the timing of ice break up (Weyhenmeyer et al. 1999; Adrian et al. 2006). However, in addition to climate, other potential drivers changing diatom bloom dynamics have been proposed, and these changes may
sometimes be species-specific (Thackeray et al. 2008). For example, an earlier onset of thermal stratification in nutrient-enriched Lake Windermere (UK) appeared to drive the advancement of the spring peak in *Cyclotella* taxa whereas the advancement of the spring peak in *Asterionella formosa* appeared to be linked to both lake warming and progressive nutrient enrichment (Thackeray et al. 2008). However, in many Ontario temperate lakes, including George Lake, observed increases in *A. formosa* (often as new arrivals) in recent decades have occurred in the absence of nutrient enrichment (Hyatt et al. 2011; Hadley et al. 2013) and therefore may be better explained by lake warming and associated changes in the dynamics of ice break up and thermal stratification.

Longer open water periods and associated water column changes may favour *A. formosa*, even in the absence of external sources of nutrient enrichment (Rühland et al. 2015). For example, *A. formosa* may be exploiting the relatively high nutrients internally available during spring and fall overturn, or alternatively, may utilize the nutrients available near the thermocline in oligo-mesotrophic lakes during summer stratification in strongly thermally stratified lakes (Rühland et al. 2010) such as George Lake. Although the seasonality of *A. formosa* is not known for George Lake, its low sinking velocity as a result of high surface area to volume ratios may favour this taxon during the stratified period, which may occur earlier and may be stronger and longer as a result of warming and changes in ice phenology. These factors may have provided *A. formosa* with a competitive advantage in recent decades across Ontario lakes. The availability of internally available nutrients in the water column combined with the buoyancy of this taxon may explain the recent increase in the relative abundance of *A. formosa* in Ontario lakes.

Finally, although we note that the period of increase in the relative abundance of *A. formosa* overlaps partly with the timing of chemical recovery from lake acidification, this
increase cannot solely be a response to recovery in pH. First, *A. formosa* occurs at very low relative abundances in pre-industrial times, prior to the onset of lake acidification from industrial activities. While the replacement of more acidophilous taxa (*A. ralfsii*) with *A. formosa* is likely in response to increasing lakewater pH, the composition of the modern diatom assemblage is notably dissimilar from the pre-industrial assemblage, suggesting that an additional stressor is affecting limnological conditions (Sivarajah unpublished). Second, similar increases in the relative abundance of *A. formosa* have been recorded in other, non-acidified lakes in Ontario (Rühland et al. 2010; Hyatt et al. 2011; Hadley et al. 2013; Sivarajah unpublished data), and have been linked to warming-related changes in lakes. Thus, chemical recovery does not appear to be a pre-requisite for this observed species change.

### 2.7 Conclusions

Our observation of increases in the relative abundances of *A. formosa* in George Lake as a result of warming is consistent with similar observations from across Ontario (Rühland et al. 2010, 2013; Hyatt et al. 2011; Enache et al. 2011; Hadley et al. 2013; Barrow et al. 2014) and other parts of the world (Solovieva et al. 2005; Stewart et al. 2008; Wang et al. 2012; Berthon et al. 2014). We caution against the interpretation of increases in this taxon as being linked solely to increasing nutrients, as our results demonstrate that additions or increases in nitrogen and/or phosphorus are not necessary pre-conditions for triggering the appearance and increase in the relative abundance of *A. formosa*. Our data, and that of a growing volume of scientific studies, clearly show the opposite. We show that the striking increase in the relative abundance of *A. formosa* occurs during a period of decline in regional nitrogen deposition and lake nitrogen concentrations. Hence, we attribute warming-related changes including longer ice-free periods
and associated changes in lake thermal and mixing properties as the likely causative factors for
the recent increases in the relative abundance of *A. formosa* in Ontario shield lakes.

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2.10 Figures

Figure 2.1 Measured lake-water nutrient concentrations for A) Total Inorganic Nitrogen (µg L\(^{-1}\)), B) Total Nitrogen (µg L\(^{-1}\)), and C) Total Phosphorus (µg L\(^{-1}\)) between 1990 and 2011 from George Lake in Killarney, Ontario. The linear trend line in the plot indicates that the nutrients are generally declining. Lake water nutrient concentrations are point measurements taken in June or July.
Figure 2.2 Regional deposition data: Total Inorganic Nitrogen deposition (kg ha\(^{-1}\) yr\(^{-1}\)) data collected from three bulk precipitation collectors located near Dickie, Plastic, and Harp lakes between 1979 and 2013. Inset shows an image of a bulk precipitation collector.
Figure 2.3 A) Mean annual air temperature (°C) and B) mean winter air temperature (°C) trends recorded at the Sudbury Airport climate station between 1956 and 2012 (thin line). The linear trend line is included in the plot, and the equation of the trend line was used to calculate the change in annual (1.76 °C) and winter (2.58 °C) air temperature over the 57 year period. To improve visualization of trends in the temperature data, a LOESS smoother (sampling proportion 0.1) was applied to the temperature data (thick line).
**Figure 2.4** Relative abundances of the most common taxa present in the sedimentary diatom assemblages of George Lake displayed stratigraphically by depth, with $^{210}$Pb dates provided on the secondary y-axis. To improve the clarity of the stratigraphy, taxa showing similar trends through time are grouped together (all *Eunotia* taxa, *Aulacoseira distans* and *Aulacoseira perglabra*, *Cyclotella tripartita* and *Cyclotella ocellata*). The x-axis is divided into increments of 10% relative abundance.
Figure 2.5 Percent relative abundance of *A. formosa* in the George Lake sediment core. The stars indicate counted samples where *A. formosa* valves were not encountered. Dates for sediment intervals older than A.D. 1844 were extrapolated using a second-order polynomial equation.
Figure 2.6 A) Comparison between increasing sedimentary \textit{A. formosa} percent relative abundance and declining measured lake water Total Inorganic Nitrogen (μg L$^{-1}$). B) Comparison between sedimentary \textit{A. formosa} percent relative abundance and increasing regional mean annual air temperature (°C) (thin line). To improve visualization of trends in the temperature data, a LOESS smoother (sampling proportion 0.1) was applied to the temperature data (thick black line).
supplementary figure 2.1 the $^{210}$Pb activities (solid circles) and estimated $^{210}$Pb dates (open circles) with associated errors for George Lake are plotted against core depth. The average $^{214}$Bi is presented using a vertical dashed line. The calculated CRS dates for the top 14 cm and associated errors are presented in the inset table.
Chapter 3

Are diatoms recovering to pre-acidification assemblages in a warming world? Revisiting Killarney Provincial Park lakes (Sudbury, Canada)
3.1 Abstract

Metal mining and smelting activities since the 1880s have resulted in the acidification of many poorly buffered Canadian Shield lakes in the Sudbury (Ontario) region. Previous paleolimnological assessment of George and Lumsden lakes (Killarney Provincial Park) concluded that these lakes had acidified due to smelting operations in the Sudbury area. In this paper we revisit these lakes after 25 years, a period of chemical recovery from acidification which coincides with regional climate warming, to assess whether recent diatom assemblages share similarities with pre-acidification assemblages. In agreement with the previous study, our results also show that diatoms responded to acidification beginning ~1920/30s, characterized by an increase in the relative abundance of acidobiontic Asterionella ralfsii. Although the most recent diatom assemblages (past ~ 30 years) suggest that pH has returned to pre-acidification levels, the arrival and increases in diatom taxa absent in earlier sedimentary intervals (such as Eunotia exigua, Frustulia magaliesmontana, and Kobayasiella subtilissima) signify the onset of new environmental conditions. The marked difference in composition between recent and pre-acidification diatom assemblages suggests a response to multiple environmental stressors, particularly regional warming, that has likely affected the trajectory of recovery. In these oligotrophic lakes, where long-term monitoring data indicate that nutrients have either declined or not changed in the past ~30 years, the recent increase in the relative abundance of Asterionella formosa and a higher chrysophyte scale : diatom valve index in both lakes suggest that regional warming has influenced the observed algal re-organization. Our paleolimnological investigation shows that the algal communities of these lakes have crossed climate-related ecological thresholds and are not returning to pre-acidification assemblages.
3.2 Introduction

Nickel and copper smelting operations began at the end of the 19th century (Watson & Richardson 1972) and continued into the 20th century in the Sudbury area. These metal mining operations have released excess amounts of $\text{SO}_2$ and $\text{NO}_x$ into the atmosphere resulting in the acidification of many poorly buffered lakes in the region and has been well documented (Beamish 1976; Keller & Pitbaldo 1986; Keller 1992). Decreases in lake water pH and higher metal concentrations ultimately led to the extirpation of fish populations in some of the most affected Sudbury lakes (Beamish & Harvey 1972; Beamish et al. 1975). Furthermore, paleolimnological studies using sedimentary chrysophycean scales and diatom valves have shown that there have been substantial changes in assemblage composition of these important primary producers as a result of acidification and elevated metal concentrations (Dixit et al. 1987, 1992a, 1992b, 1992c; Tropea et al. 2010). More recently, Labaj et al. (2015) have documented the long-term assemblage changes in fossil Cladocera in response to long-term acidification and metal inputs.

Implementation of $\text{SO}_2$ reduction programs in the Sudbury area throughout the 1970s and 1980s led to a substantial decrease in $\text{SO}_2$ emissions (Keller 1992; Keller et al. 2004). As a result, many Sudbury lakes have shown signs of chemical recovery (specifically increases in pH) (Keller et al. 2004, 2006; Keller 2009). However, the biota of these lakes have often shown incomplete biological recovery from acidification (Dixit et al. 2002; Yan et al. 2004; Gray & Arnott 2009; Valois et al. 2010; Gray et al. 2012; Labaj et al. 2015). Similar observations of chemical recovery with a lack of complete biological recovery have been observed in other previously acidified lakes around the world (e.g. Monteith et al. 2005; Layer et al. 2010; Bennion et al. 2011; Hesthagen et al. 2011; Battarbee et al. 2014). It is not surprising that biological
communities have not returned to pre-disturbance assemblages when one considers that these lakes are recovering during a period when many new and emerging environmental stressors, absent during the pre-acidification era, are simultaneously affecting freshwater ecosystems. In particular, the pervasiveness of recent warming has been found to exacerbate the effects of many individual stressors on aquatic ecosystems (Smol 2010).

The first detailed paleolimnological investigation of George and Lumsden lakes from Killarney Provincial Park was conducted by Dixit et al. (1992a), who analyzed compositional changes in sedimentary diatoms and scaled chrysophytes preserved in sediment cores retrieved in 1987. Their study concluded that both lakes have experienced acidification beginning around the 1930s as a result of smelting operations in the Sudbury area, and that both chrysophyte and diatom assemblages were showing early signs of recovery back to pre-acidification assemblages in the top-most intervals of their cores (~1980s). Twenty-five years later (in 2012), Labaj et al. (2015) re-cored these lakes to assess changes in the zooplankton assemblages and whole lake primary production (spectrally inferred chlorophyll $a$ in lake sediments). Labaj et al. (2015) observed subtle changes in sedimentary cladoceran assemblages as a result of acidification in the mid-twentieth century but reported marked increases in primary production starting in the post-1970 sediments in George Lake and post-1990 in Lumsden Lake, and they suggested that recent cladoceran assemblage changes were partially attributed to increased whole lake primary production induced by climate-related changes to the lake thermal properties (such as longer open water season). Both Dixit et al. (1992a) and Labaj et al. (2015) concluded that these lake ecosystems have substantially changed during the twentieth century.

Here we analyze diatom assemblage changes over the past ~200 years from George and Lumsden lakes using the same dated cores collected in 2012 by Labaj et al. (2015) for their
cladoceran study. We focus particularly on changes in sedimentary diatom assemblages over the past ~30 years to determine whether the diatom changes continued along the trajectory of early biological recovery post-1987 that was reported in the Dixit et al. (1992a) study. The last three decades (i.e. post-dating the Dixit et al. (1992a) study) are of particular interest, as we would expect that regional warming and other stressors may be affecting diatom community recovery in these previously acidified lakes.

3.3 Site description

Killarney Provincial Park (KPP) is located on the northern shores of Georgian Bay, Lake Huron, approximately 60 km south-west of Sudbury, Ontario (Canada) (Figure 3.1). Like many lakes located in Ontario Provincial Parks, George and Lumsden lakes at KPP support a wide array of winter and summer recreational activities (OMNR 1985). The park’s proximity to the Sudbury smelters and the poor buffering capacity of the underlying Precambrian Shield bedrock led to the acidification of many lakes in the KPP (Beamish & Harvey 1972). From the onset of lake acidification in the 1920s and 1930s, aquatic biota including fish populations (e.g. Beamish & Harvey 1972; Beamish et al. 1975) and primary producers such as diatoms and chrysophytes (Dixit et al. 1992a) have been adversely affected. However, as a result of the SO₂ emission reduction programs initiated in the 1970s, acid deposition in the region has decreased and many of the lakes have, or are currently recovering chemically in the KPP (Keller et al. 2003, 2006; Gray et al. 2012).

George Lake has been monitored for lake water quality over three decades (since the 1980s) as part of the Sudbury Environmental Study Extensive Monitoring Programme to assess chemical recovery of acidified lakes in the Sudbury region (Keller et al. 2006). In 1981, the measured pH
at George Lake was ~5.3 (in July) and by 2005 pH had increased to 6.5 (in July) (Keller et al. 2006). Additionally, lake water metal concentrations (aluminum, nickel, copper, zinc), sulphate (SO₄), and calcium have all shown declining trends (Keller et al. 2006). The trends in lake water chemistry observed at George Lake are likely representative of regional post-remediation recovery occurring at other nearby lakes including Lumsden Lake.

3.4 Methods

3.4.1 Field methods

Sediment cores were collected in July 2012 from the deepest basins of Lumsden (coring depth – ~22m; coordinates: 46 01.464 N, 81 25.741 W) and George (coring depth – ~38m; coordinates: 46 01.708 N, 81 24.037 W) lakes using a Glew (1989) gravity corer. The sediment cores were vertically extruded onshore using a Glew (1988) extruder at 0.25 cm increments from 0 to 15 cm and at 0.5 cm increments below 15 cm to the base of the core. Samples were stored in a cooler and transported to Paleoecological Environmental Assessment and Research Laboratory (PEARL), Queen’s University, Kingston, Ontario.

3.4.2 Radioisotopic dating

Gamma spectrometry techniques outlined by Schelske et al. (1994) were used to measure ²¹⁰Pb and ¹³⁷Cs activities at selected intervals from each core at facilities available at PEARL. Unsupported concentrations of ²¹⁰Pb and the constant rate of supply (CRS) model described by Appleby (2001) were used to estimate the ²¹⁰Pb dates for the past ~ 150 years. A second order polynomial function was used to extrapolate sediment age beyond background ²¹⁰Pb levels based on established ²¹⁰Pb chronology.
3.4.3 Diatom analysis

Diatom samples were processed using standard guidelines outlined by Battarbee et al. (2001). Briefly, ~0.02 g of freeze-dried sediment from selected core intervals was treated with a 50:50 molar ratio of sulfuric (H$_2$SO$_4$) and nitric (HNO$_3$) acids to digest the organic material and isolate the siliceous material in the sediment. The samples were placed into a hot-water bath at 80°C for at least 2 hours, after which the resulting slurries were allowed to settle for ~24 hours. The supernatant was removed and de-ionized water was used to rinse the samples. This rinsing procedure was repeated until the samples approached a circumneutral pH. An aliquot of the well-mixed slurries was plated onto glass cover slips and allowed to air dry. The mounting medium Naphrax® (refractive index 1.73) was used to permanently mount the samples onto microscope slides.

For each sample, a minimum of 350 diatom valves were identified and enumerated for both George and Lumsden lakes at 1000X magnification using a Leica DMR light microscope fitted with differential interference contrast optics. Diatoms were identified to the lowest taxonomic level possible (usually variety or strain) using a selection of taxonomic sources (Krammer & Lange-Bertalot 1986-1991; Camburn & Charles 2000). Fragmented diatom valves of pennate diatoms such as *Asterionella formosa* and *Tabellaria flocculosa* str. IIIp were present in the sediment cores from both George and Lumsden lakes. For fragmented *A. formosa* valves the larger terminal ends were enumerated as one valve. However, for fragmented *T. flocculosa* str. IIIp one of the terminal ends were enumerated as half a valve (presence of two terminal ends would constitute as one valve). The number of chrysophycean scales encountered per minimum of 40 diatom valves was enumerated, but were not identified taxonomically. The changes in chrysophyte scale abundance are presented as the index of chrysophyte scales to diatom valves.
(total number of chrysophytes scales / (total number of chrysophytes scales + total number of diatom valves)).

Diatom data are expressed as percent abundance relative to the total number of valves counted per sample. The most common diatom taxa encountered were stratigraphically displayed using the computer program C2. For clarity of display, some diatom taxa from the same genera or varieties of a given species were grouped if they showed similar trends through time. Diatom taxa that occurred in low relative abundances throughout the core were included in the stratigraphy as “all other taxa”. However, for all statistical analyses, the full diatom data set (i.e. no groupings) was used.

3.4.5 Data analysis

All statistical analyses were completed using CANOCO version 5.0 (ter Braak & Šmilauer 2012) and R (version 3.1) (R Core Team 2014) software. The “vegan” package (Oksanen et al. 2012) developed for R software environment was used to both rarefy the diatom data from each lake to a common sum (George = 354; Lumsden = 415), and to calculate species diversity, Hill’s N2 (Hill 1973). Prior to undertaking the ordination analysis, the diatom percent relative abundance data were square-root transformed to equalize the variance among taxa. The detrended correspondence analysis on the diatom species data, revealed gradient lengths < 2 standard deviation units (1.6, 1.1 for George and Lumsden lakes respectively) suggesting that a Principal Components Analysis (PCA covariance matrix) was the appropriate ordination method for summarizing the major patterns of diatom variation in the stratigraphic sequence (Birks 2010). For each sedimentary sequence, PCA axis 1 (PC1) sample scores and diatom relative abundance data were plotted against $^{210}\text{Pb}$ dates to enable comparisons in the timing and magnitude of
diatom changes at each lake. To compare trajectories in diatom assemblages through time between George and Lumsden lakes, PCA axis 1 was plotted against PCA axis 2, with samples from both lakes sharing the same ordination space. This enabled us to assess and compare the similarities and dissimilarities in diatom assemblage composition between the two study lakes along the PCA axis 1 and the magnitude and trajectory of change through time in diatom assemblage composition along the PCA axis 2 (e.g. Faulkenham et al. 2003; Rühland et al. 2010).

3.5 Results

3.5.1 Radiometric dating

The radiometric dating profiles for the two sediment cores followed characteristic exponential declines in $^{210}\text{Pb}$ through depth suggesting sediment mixing is not a concern for these cores. The sediment cores reach background $^{210}\text{Pb}$ levels at a core depth of approximately 14 cm (see Labaj et al. (2015) for details). The dating profiles are attached as supplementary material (Supplementary figure 3.1).

3.5.2 General diatom trends

Diatom valves from both study lakes were present and well preserved in all samples analyzed. We identified 186 diatom taxa across both lakes with many of these taxa occurring in both lakes. Taxa such as *Discostella stelligera*, *Tabellaria flocculosa* str. IIIp (*sensu* Koppen), and taxa from the genera *Aulacoseira* and *Eunotia* were present throughout the cores in both lakes and co-dominated the assemblages (Figures 3.2 & 3.3). Diatom assemblages in both sediment cores have undergone notable changes over the past ~200 years as a result of acidification and climate warming. For example the appearance and increase in relative abundance of acidobiontic
Asterionella ralfsii between ~1920 and ~1980 marks a response to acidification at both lakes. The largest compositional changes of the entire core sequence occur over the past ~30 years at both lakes and was characterized by abrupt increases in the relative abundances of several taxa that were only present in trace abundances in earlier intervals (Figures 3.2 & 3.3). Summarizing these compositional trends, PCA axis one sample scores closely track these assemblage changes throughout the core with gradual changes prior to 1980s and abrupt, higher magnitude changes occurring over the last three decades (Figures 3.2 & 3.3). A separation of sample scores along PCA axis 1 indicates that diatom composition differs between George and Lumsden lakes, whereas the high degree of separation of sample scores along PCA axis 2 track the major assemblage changes in these lakes over the past ~200 years and indicate that the composition of early and modern assemblages share little similarity (Figure 3.4).

3.5.3 George Lake

Pre-acidification era (before ~1920)

The diatom assemblages at George Lake prior to the 1920s were dominated by oligotrophic and circumneutral to slightly acidic taxa typical of relatively deep lakes in this region (Dixit et al. 2002). D. stelligera dominated the assemblages (~37 – 45 % relative abundance) in this earliest part of the record (Figure 3.2). Other taxa that were common during this period include planktonic and tychoplanktonic diatoms such as T. flocculosa str. IIp (Average Relative Abundance (ARA): ~11%), cyclotellloid taxa (Cyclotella ocellata (ARA: ~2%) and C. tripartita (ARA: ~7%)), Aulacoseira distans/perglabra (A. distans (ARA: ~8%), and A. perglabra (ARA: ~3%)), and Fragilaria tenera (ARA: ~2%) (Figure 3.2). Prior to acidification, species diversity was quite low and variable with the number of very abundant taxa in a given sample (i.e. Hill’s
N2) varying between 4 and 6 (Figure 3.2). The down core PCA axis 1 sample scores remained relatively stable for much of the pre-acidification era with subtle changes detected around the turn of the twentieth century, reflecting subtle changes in the diatom assemblages (Figure 3.2). The scale:diatom index showed an overall increasing trend (albeit minor) during this period (Figure 3.2).

Acidification era (between ~1920 - ~1980)

*D. stelligera* continued to dominate the assemblage (ARA: ~41%) during the acidification period. This period (~1920 to ~1980), however, was also characterized by a distinct increase in the relative abundances of acidobiontic *A. ralfsii* (peaking at 10% in ~1978) together with an increase in *T. flocculosa* str. IIIp (increase by 6% from the pre-acidification era) (Figure 3.2). Concurrently, a modest decline in *Aulacoseira distans* / *perglabra* (specifically *A. distans* declined by ~2% relative to pre-acidification era) and a more notable decline in *C. ocellata* / *C. tripartita* (by 6%) were observed. Diatom species diversity was relatively stable during this period (Figure 3.2). Down-core PCA axis 1 sample scores reflect the modest changes in diatom assemblage composition during the acidification era that nevertheless indicates a notable difference from the pre-acidification assemblages. The scale:diatom index continued to gradually increase during this period (Figure 3.2).

Last ~30 years

The highest magnitude diatom compositional changes occurred in the most recent sediments (~post 1980), with planktonic *Asterionella formosa* (ARA: ~7%) and benthic *Psammothidium marginulatum* (ARA: ~2%) occurring in notable abundances for the first time in the core, with corresponding marked declines in *A. ralfsii* and *Achnanthidium minutissimum* to trace
abundances (Figure 3.2). *D. stelligera* continued to be the dominant diatom (ARA: ~37%) during this time. Although not as striking as *A. formosa*, the relative abundance of *T. flocculosa* str. IIIp has also been increasing (increased by ~3% relative to the acidification period) during this period. *Aulacoseira distans/perglabra* (mostly *A. distans* (ARA: ~6%), and *A. perglabra* (ARA: ~4%)) remain prominent throughout the last ~30 years with minimal changes in percent relative abundances. Species diversity remains low but is highly variable during this time (i.e. does not exhibit a directional trend). Consistent with sharp changes in diatom composition, PCA axis 1 sample scores also show a distinct change for the first time in the core beyond background variability. The scale:diatom index likewise exhibited the greatest change in this most recent period, with a doubling of this index compared to that of the pre-acidification era (Figure 3.2).

### 3.5.4 Lumsden Lake

Pre-acidification era (before ~1920)

Similar to George Lake, the Lumsden Lake pre-acidification diatom assemblages were also dominated by oligotrophic and circumneutral to acidic taxa that are typical of relatively deep shield lakes from this region (Dixit et al. 2002). The diatom assemblages from Lumsden Lake were co-dominated by several taxa and the relative abundances remained relatively stable during this period (Figure 3.3). Diatom taxa characterizing the assemblages include planktonic and tychoplanktonic taxa such as *T. flocculosa* str. IIIp (ARA: ~15%), *A. distans* (ARA: ~7%), *D. stelligera* (ARA: ~5%), and *F. tenera* (ARA: ~2%). Unlike George Lake, a greater assortment of benthic species such as the *Brachysira* complex (*B. procera* (ARA: ~4%) and *B. brebissonii* (ARA: ~6%)), *A. minutissimum* (ARA: ~4%), cymbellloid species (mostly *Cymbella gaeumannii, Enysonema gracile, E. silesiacum*), and *Chamaepinnularia mediocris* (ARA: ~3%) were also
present in the pre-acidification assemblage. Consistent with trends in diatom composition, species diversity, as well as the scale:diatom index, remained relatively stable during this pre-disturbance period (Figure 3.3), both of which are considerably higher than what was recorded in George Lake during this period (George Lake: 4-6 Hill’s N2; Lumsden Lake: 14-25 Hill’s N2). The stability of the downcore PCA axis 1 sample scores are indicative of the minimal changes in diatom assemblage composition during the pre-acidification period (Figure 3.3).

Acidification era (between ~1920 - ~1980)

Similar to George Lake, during the period of acidification, an increase in the relative abundance of acidobiontic *A. ralfsii* from trace to peak abundances (~16%; ARA: 10%) around the 1970s was also observed at Lumsden Lake (Figure 3.3). Surprisingly, the relative abundances of *T. flocculosa* str. IIIp (ARA: ~17%) and *D. stelligera* (ARA: ~9%) also peaked during this period. A subtle increase in the relative abundances of the *Brachysira* complex occurred at the beginning of this era, however subsequent declines are observed toward the close of this period. Subtle declines in percent abundances of cymbelloid taxa, *A. minutissimum*, *F. tenera*, and *Frustulia saxonica* were also observed (Figure 3.3). A marked decrease in species diversity (Hill’s N2 from 24 at the beginning of the era to 10 by the 1970s), and the scale:diatom index relative to the pre-acidification era is also observed during this period (Figure 3.3). The lowest species diversity and scale:diatom index values throughout the entire cores was observed ~1970. The PCA axis 1 sample scores tracked the changes in diatom assemblages in response to acidification.

Last ~30 years

Similar to George Lake, Lumsden Lake also experienced the greatest degree of species reorganization in the most recent sediments (post ~1980). However, unlike George Lake, several
taxa that were hitherto present in only trace abundances underwent striking increases in the recent sediments (post ~1980) including *Kobayasiella subtilissima* (ARA: ~5%), *Eunotia exigua* (ARA: ~4%), *Frustulia magaliesmontana* (ARA: ~4%), *A. formosa*, (ARA: ~4%) and *P. marginulatum* (ARA: ~2%) (Figure 3.3). The arrival of these taxa occurred concurrently with equally pronounced decreases in the relative abundances of *T. flocculosa* str. IIIp (ARA: ~7%), *D. stelligera* (ARA: ~7%), and *A. ralfsii* (ARA: ~4%). *Aulacoseira distans*, the *Brachysira* complex, and all other *Eunotia* taxa remain prominent over the past ~30 years with minimal changes in relative abundances (Figure 3.3). Both species diversity and the scale:diatom index have been increasing gradually since reaching the lowest values ~1970 (Figure 3.3). On average, Hill’s N2 species diversity over the last ~30 years (average 24 very abundant taxa) is higher than the pre-acidification era (average 20 very abundant taxa) with the highest species diversity recorded ~2000 (31 Hill’s N2). PCA axis 1 sample scores tracked the pronounced shifts in diatom assemblage composition over the past ~ 30 years (Figure 3.3).

3.5.5 *Diatom assemblage composition trends through time at Lumsden and George lakes*

Although sediment cores from both lakes share similar taxa, PCA ordinations (PCA axis 1 versus PCA axis 2 sample scores; Figure 3.4) clearly show that diatom assemblages from George and Lumsden lakes are quite different as indicated by their separation along the first PCA axis. The second PCA axis tracks the main changes in diatom composition over the past ~200 years (Figure 3.4). The large spread of sample scores along PCA axis 2 for the entire core highlights that modern species assemblage composition is markedly different from diatom assemblages in both pre-acidification and acidification eras (Figure 3.4).

3.6 *Discussion*
3.6.1 Algal response to acidification and subsequent pH recovery

Sedimentary diatom assemblages at both of our study lakes show marked and synchronous changes over the past ~200 years. Based on diatom-inferred pH reported by Dixit et al. (1992a), George and Lumsden lakes likely had baseline pH levels (i.e., prior to acidification) of about 5.8 to 6.1 and 5.4 to 5.9, respectively. At the peak of the acidification era, George and Lumsden lakes had diatom-inferred pH levels of ~5.3 and ~4.7 respectively and, as expected, diatom assemblage changes observed in both lakes show a clear response to the onset of acidification (Figures 3.2 & 3.3), consistent with previous observations by Dixit et al. (1992a). The earliest evidence of diatom response to changes in pH in our study lakes occurs as early as ~1920 (Figures 3.2 & 3.3).

Although the floristic changes we report are consistent with the onset of acidification and follow the general patterns reported by Dixit et al. (1992a), the magnitude and species-specific changes we observed in our cores differed somewhat from those reported from cores collected in 1987. For example, at George Lake we did not observe the marked decline in the relative abundance of *Discostella stelligera* during the peak of acidification and the subsequent increase following chemical recovery, as reported by Dixit et al. (1992a). Furthermore Dixit et al. (1992a) did not observe or record the rise and fall of *Asterionella ralfsii* during acidification and recovery periods in their core from George Lake. There are a variety of potential reasons for inter-core variability (Charles et al. 1991). In this study, we suggest that it may be due to differences between coring locations as GPS technology was not available at the time the Dixit et al. (1992a) cores were retrieved, making it difficult to ascertain whether the cores were retrieved from the same location within the lakes. Additionally the sediment cores analyzed in this study were retrieved from deeper sites (coring depths Lumsden - ~22 m; George - ~38 m) at both lakes.
compared to the sediment cores analyzed by Dixit et al. (1992a) (coring depths Lumsden - ~17 m; George - ~22 m). Nevertheless, both diatom records provide a similar ecological and acidification history of the lakes, as outlined below.

Both lakes record increases in the relative abundances of acidobiontic diatoms following regional acid deposition, particularly *A. ralfsii* that has a reported pH optimum in this region of ~5.5 (Dixit et al. 2002). In other regions, this taxon has been observed to occur in considerable abundances at even lower pH (Ginn et al. 2007). Our observation is consistent with other studies which have shown that *A. ralfsii* increases in relative abundance with an initial decline in pH (Dixit et al. 1992a, b; Tropea et al. 2010). Of note is that *A. ralfsii* has been reported to tolerate relatively high aluminum (Al) concentrations, as are often found during the early stages of acidification (Gensemer 1991; Gensemer et al. 1993; Dixit et al. 2002). In addition to the increase in the relative abundance of *A. ralfsii* at Lumsden Lake, relative abundances of *D. stelligera* peaked during the acidification period. Although many limnological and paleolimnological studies have shown that cyclotelloid taxa do not fare well under acidic conditions (Battarbee et al. 1999) and that *D. stelligera* is commonly found in neutral to slightly acidic water (~ pH > 6) (Hall and Smol 1996; Dixit et al. 2002), Taylor et al. (1987) have shown that, at least in the Sudbury region, this taxon occurs in considerable abundances even when pH is lower than 5, suggesting that *D. stelligera* may have a broader tolerance to pH in this part of Ontario.

We observe marked changes in diatom assemblages over the past ~30 years, which post-dates the data available in the Dixit et al. (1992a) study. A change in diatom composition at this time might be expected given that this period corresponds to the timing of environmental mitigation efforts and subsequent chemical recovery of lakes from acidification in the Sudbury region.
Indeed, the reported pH optima of diatom taxa common in the modern assemblages at Lumsden Lake (e.g. *Psammothidium marginulatum*, *Eunotia exigua*, *Frustulia magaliesmontana*, and *Kobayasiella subtilissima*) suggests that it has returned to pre-acidification pH levels (~5.2 to 5.5), and this is consistent with recently measured mid-summer pH readings of ~5.7 in 2013 (Alex Ross pers. comm.). Interestingly, these species were not a prominent component of the pre-acidification nor the acidification era assemblages.

The observed decrease in diatom species diversity (Hill’s N2) between ~1920 and ~1970 at Lumsden Lake is likely a response to acidification and is consistent with the findings of Findlay & Kasian (1996) who have shown that phytoplankton species diversity tends to decrease during low pH conditions. Given that George Lake did not acidify to the same extent as Lumsden Lake (Dixit et al. 1992a), it is not surprising that a clear decline in species diversity was not observed in the former. Furthermore diatom composition at George Lake has been dominated by one taxon (*D. stelligera*) throughout the entire core and therefore diatom species diversity at George Lake has always been lower relative to Lumsden Lake, making interpretations of species diversity difficult (Alatalo 1981), particularly when used as an indicator of environmental stressors such as acidification (Gray and Arnott 2009). The increase in diatom species diversity post ~1970 at Lumsden Lake could suggest that diatom assemblages are recovering from acidification given that these changes occur during the implementation of reduction on sulphur dioxide emissions from the Sudbury smelters and decreased regional acid deposition (Keller et al. 2003). However, the composition of the modern diatom assemblages are notably distinct from all other assemblages in the sedimentary record, even though the diatom assemblages today may be indicative of pH levels similar to pre-acidification conditions (Figure 3.4). Species diversity is
only one aspect of biological recovery hence, it should be used cautiously as a recovery metric from acidification (Gary & Arnott 2009).

3.6.2 Algal response to recent warming

As clearly illustrated by our PCA trajectories through time, the recent diatom assemblages (post ~1980) from both lakes are distinct, relative to pre-acidification or acidification assemblages (Figure 3.4). Although there appears to be a chemical recovery in terms of pH, and the diatoms in recent sediments have similar pH optima, the taxonomic composition of the assemblages are very different. This is consistent with observations from other studies in the Sudbury region (e.g. Dixit et al. 2002; Tropea et al. 2010). The difference in diatom assemblage composition between the recent sediments and pre-acidification sediments is likely a result of several differences in the environment including elevated metal concentrations (relative to the pre-acidification era) as well as the effects of regional warming. Although other stressors, such as changes in dissolved organic carbon, nutrients (phosphorus and nitrogen), and silica could have direct impacts on algal assemblages, a growing number of studies are emphasizing the overarching indirect effects of climate warming on diatom communities in lakes across the world (reviewed by Rühland et al. 2015).

An interesting trend observed at both oligotrophic lakes (point measurements of total phosphorus in 2013 - Lumsden = 2.6 µL\(^{-1}\), George = 3.2 µL\(^{-1}\); Alex Ross pers. comm.) is the establishment and subsequent increase in the relative abundance of Asterionella formosa beginning around the late-1980s. *A. formosa* has been often associated with increased nutrient conditions (e.g. Clerk et al. 2000; Little et al. 2000; Reynolds et al. 2002), and recent increases in the relative abundance of this taxon in the Rocky Mountains region of the USA has been attributed to the increased
delivery of nitrogen to the high elevation lakes proximal to agricultural activities (Wolfe et al. 2003; Saros et al. 2005, 2011; Hundey et al. 2014). Interestingly, in our study region (south central Ontario), direct monitoring data clearly track declines (not increases) in regional aerial deposition of total inorganic nitrogen as well as declines in water column inorganic nitrogen (measured in George Lake) since the 1980s and 1990s, respectively (Sivarajah et al. 2016). In George Lake, no clear relationship has been observed between the recent increase in the relative abundance of this taxon and total inorganic nitrogen availability, and in fact there is instead a clear inverse relationship (Sivarajah et al. 2016). These observations are consistent with previous conclusions from a regional assessment of 53 lakes in south-central Ontario by Hadley et al. (2013), who also recorded increasing A. formosa relative abundances with decreasing nitrogen and phosphorus concentrations. In George Lake, where we have ~20 years of monitoring data, we found no clear relationship between total inorganic nitrogen availability and the relative abundance of A. formosa (Sivarajah et al. 2016). Instead, a positive relationship was observed between the increase in the relative abundance of A. formosa and rising regional air temperatures (Sivarajah et al. 2016). Although unlike George Lake, long-term monitoring data does not exist for Lumsden Lake, the increase in the relative abundance of A. formosa could also be attributed to warming as we proposed for George Lake. A growing number of studies from oligotrophic lakes suggest that the recent increase in A. formosa could be due to changes in lake thermal properties induced by climate warming (Solovieva et al. 2005; Rühland et al. 2010, 2013; Hyatt et al. 2011; Hadley et al. 2013; Barrow et al. 2014; Chen et al. 2014; Sivarajah et al. 2016), rather than nutrient enrichment. For example, the high surface area to volume ratio of A. formosa provides these diatoms with a low sinking velocity and allows them to maintain a favourable
position in the photic zone (Canter & Lund 1948), an advantage under warming-induced strengthening of thermal stratification (Rühland et al. 2015; Sivarajah et al. 2016).

Synchronous with the increase in the relative abundance of *A. formosa*, we also observed increases in the scale:diatom index at both lakes in the most recent sediments, which further suggests that regional climate warming is influencing the algal communities. For example, some flagellated scaled chrysophytes thrive under low nutrient (Smol 1985, 1995) and stratified conditions as the flagella allow them to migrate in the water column to efficiently access nutrients and light (Raven 1995). Previous studies by Paterson et al. (2004), and Michelutti et al. (2015), amongst others, have repeatedly shown that there has been a marked increase in the scale:diatom index in lakes with increased thermal stratification. Furthermore, the recent increases in scaled chrysophytes would also be fostered by declining nutrient levels, as these taxa typically thrive under low nutrient conditions (Smol 1985, 1995). Hence, the recent increases in the scale:diatom index further support our interpretations of the diatom changes, concluding that climate-induced changes (and not nutrients) are primarily driving the most recent shifts in diatom assemblages.

### 3.7 Conclusions

The diatom assemblages from both our study lakes tracked the change in pH due to acidification and subsequent chemical recovery. However, the most recent sedimentary diatom assemblages recorded in both lakes are substantially different from pre-acidification assemblages (Figure 3.4), highlighting that modern limnological conditions (despite similar pH levels) are very different from the pre-disturbance environment. These changes in diatom composition together with recent increases in the scale:diatom index suggest that the recent reorganization of algal
communities in Sudbury Ontario lakes is driven by multiple environmental factors including broader regional stressors such as climate warming.

3.8 Acknowledgements

The authors would like to thank Andrew L. Labaj for collecting and radiometrically dating the sediment cores. Thanks to Joshua R. Thienpont for assistance in the field. We also thank Alex Ross for sharing the water chemistry data from George and Lumsden lakes. This project was funded by grants from the Natural Science and Engineering Research Council of Canada to JPS.

3.9 References


Beamish, R.J., 1976: Acidification of lakes in Canada by acid precipitation and the resulting effects of fishes. – Water Air Soil Poll. 6: 501–514.


### 3.10 Tables

**Table 3.1:** Limnological variables of George and Lumsden lakes from Killarney Provincial Park. Dissolved organic carbon (DOC), total phosphorus (TP), and pH were point measurements taken in August 2013 (Alex pers. comm.)\(^a\). Inferred background pH and inferred lowest pH were obtained from Dixit et al. (1992a)*. The 1970s measured pH is from Sprules (1975)\(^b\). Maximum depth (Max. depth) and surfarea were obtained from Beamish et al. (1975)\(^c\), and Beamish and Harvey (1972)\(^d\).

<table>
<thead>
<tr>
<th></th>
<th>George</th>
<th>Lumsden</th>
</tr>
</thead>
<tbody>
<tr>
<td>Max. depth (m)(^{c,d})</td>
<td>39.7</td>
<td>22</td>
</tr>
<tr>
<td>Surface area (ha)(^{c,d})</td>
<td>182</td>
<td>21</td>
</tr>
<tr>
<td>DOC (mg L(^{-1}))(^a)</td>
<td>2.3</td>
<td>2.4</td>
</tr>
<tr>
<td>TP (μg L(^{-1})) (^a)</td>
<td>3.2</td>
<td>2.6</td>
</tr>
<tr>
<td>2013 Surface pH (^a)</td>
<td>6.3</td>
<td>5.7</td>
</tr>
<tr>
<td>1970s Measured pH(^b)</td>
<td>4.9 (1971-3)</td>
<td>4.4 (1971-3)</td>
</tr>
<tr>
<td>Inferred Background pH*</td>
<td>~5.8 - 6.1</td>
<td>~5.4 - 5.9</td>
</tr>
<tr>
<td>Inferred Lowest pH*</td>
<td>~5.3</td>
<td>~4.7</td>
</tr>
</tbody>
</table>
3.11 Figures

Figure 3.1: Location of the study sites, George Lake and Lumsden Lake. Inset (top), map of Canada with the location of Sudbury, Ontario depicted by the open square box. Inset (bottom), map of the study region in relation to Lake Huron and Georgian Bay with the circle representing the location of George and Lumsden lakes and the triangle representing the location of Sudbury, Ontario.
Figure 3.2: Diatom stratigraphic profile showing the relative abundances of the most common diatom taxa from George Lake. For display purposes, select taxa that showed similar trends were grouped including all *Eunotia* taxa, *Aulacoseira distans* and *A. perglabra*, *Cyclotella tripartita* and *C. ocellata*, as well as the sum of all other taxa not specifically included in the stratigraphic profile. Numbers following taxon labels indicate the number of diatom taxa represented by the grouping. Species diversity (Hill’s N2), chrysophyte scale: diatom valve index, and principal components analysis (PCA) axis 1 samples scores are also included. The figure is divided into three time periods differentiating the periods of pre-acidification, acidification, and post-acidification. The x-axis is divided into increments of 10% relative abundance. The pre-acidification and acidification periods were identified using the pH reconstructions by Dixit et al. (1992a)
Figure 3.3: Diatom stratigraphic profile showing the relative abundances of the most common diatom taxa from Lumsden Lake. For display purposes, select taxa that showed similar trends were grouped including all other *Aulacoseira* taxa, *Brachysira brebissonii* and *B. procera*, all other *Eunotia* taxa, as well as the sum of all other species not specifically included in the stratigraphic profile. Numbers following taxon labels indicate the number of diatom taxa represented by the grouping. Species diversity (Hill’s N2), chrysophyte scale: diatom valve index, and principal components analysis (PCA) ordination axis 1 samples scores are also included. The figure is divided into three time periods differentiating the periods of pre-acidification, acidification, and post-acidification. The x-axis is divided into increments of 10% relative abundance. The pre-acidification and acidification periods were identified using the pH reconstructions by Dixit et al. (1992a).
Figure 3.4: Principal Components Analysis (PCA) ordination of axis 1 ($\lambda = 0.40$) and axis 2 ($\lambda = 0.11$) sample scores for George and Lumsden lakes that were calculated and plotted within the same ordination space and based on changes in the percent relative abundances of diatom assemblage composition throughout the two cores. The $^{210}$Pb estimated ages of select intervals are included so as to highlight the history of acidification (pre-acidification, acidification, post-acidification eras) and to follow the main changes in diatom composition over the past ~ 200 years.
Supplementary figure 3.1: Radiometric dating analysis showing $^{210}\text{Pb}$, $^{214}\text{Bi}$ and $^{137}\text{Cs}$ activity in selected sedimentary intervals (Becquerels per kilogram) plotted against core depth for George and Lumsden lakes. For full dating details, refer to Labaj et al. (2015)
Chapter 4

Long-term diatom responses to shoreline development and climate warming in three large embayments of Georgian Bay, Lake Huron
4.1 Abstract

Diatom-based paleolimnological techniques were used to assess whether there is evidence for the effects of shoreline development and recent warming on three large embayments (two impacted and one minimally impacted by shoreline development) of Georgian Bay, Lake Huron. Based on the qualitative assessment of diatom assemblage shifts, shoreline development such as permanent settlements and recreational resorts around the turn of the 20th century has only resulted in modest increases in nutrient conditions at North and South bays. However, no major shifts in diatom assemblages were observed at the unimpacted site (Tadenac Bay). The diatom assemblage of the shallower site, South Bay, records an abrupt shift around the 1950s with an increase in epiphytic Cocconeis placentula coinciding with the timing of increases in Cladophora macro-alga in the Laurentian Great Lakes. All three embayments record pronounced diatom assemblage changes in the mid to late-20th and early 21st centuries, where shifts toward higher abundances of pennate (Asterionella formosa and Fragilaria crotonensis) and/or small centric (Cyclotella ocellata, C. comensis, and C. gordonensis) planktonic diatoms were observed. The observations are consistent with similar trends observed across Ontario, where warming and associated changes in thermal and other physical properties often favor smaller and/or lightly silicified diatoms. Lower water levels in Georgian Bay since the mid-1980s are also tracked by the diatom assemblages at the shallower South Bay as clear increases in benthic taxa are observed during this period. Diverse diatom response among the three embayments to similar environmental stressors highlights the importance of contextually interpreting changes in diatom assemblages in paleolimnological records.
4.2 Introduction

Over the last ~ 200 years, anthropogenic activities such as deforestation, agriculture, urbanization, the introduction of non-native species, and the deposition of contaminants have substantially altered the water quality of the ecologically and economically important Laurentian Great Lakes. In addition to human activities, recent climate warming has also been affecting the Laurentian Great Lakes resulting in longer ice free periods, an increase in mean water temperatures, and longer stratification periods (Magnuson et al., 1997; Austin and Colman, 2007; Jensen et al., 2007). In response to these rapid changes, the governments of the United States and Canada have implemented intensive monitoring programs to track water quality and quantity changes in the Laurentian Great Lakes. However, most monitoring programs only span the last ~ 50 years, and longer records may be needed to understand ecosystem changes prior to the onset of key environmental stressors. In lieu of long term water quality monitoring data, paleolimnology, the science of reconstructing past environmental conditions using biological, chemical and physical information archived in lake sediments, can be used to bridge these knowledge gaps and provide a holistic overview of the ecosystem change over long temporal periods (Smol, 2008). Paleolimnology has proven to be a useful tool to establish pre-disturbance conditions prior to anthropogenic stressors, to assess natural variability, and to evaluate the effects of various stressors, such as cultural eutrophication, pollutant contamination, and climate warming, among others, on aquatic ecosystems around the world (Smol, 2008). We use diatom-based paleolimnological methods to assess the potential effects of shoreline development and recent regional climate warming on three large embayments of Georgian Bay, Lake Huron over the past ~ 200 years.
Georgian Bay, the largest bay of Lake Huron, is partially separated from the main basin by the Bruce Peninsula and Manitoulin Island (Fig. 4.1). In 2004, the Georgian Bay Littoral was designated as one of 16 Biosphere Reserves in Canada by the United Nations Educational, Scientific and Cultural Organization (UNESCO) as it contains the largest freshwater island archipelago in the Laurentian Great Lakes (UNESCO, 2010 Georgian Bay Littoral accessed on January 28th 2016 http://www.unesco.org/mabdb/br/brdir/directory/biores.asp?code=CAN+13&mode=all), and likely in the world (Clark et al., 2015). Unlike other parts of the Great Lakes, Georgian Bay is completely contained within the province of Ontario and contributes strongly to the provincial economy by supporting a substantial tourism industry. The presence of road accessible embayments and islands makes southeastern Georgian Bay an ideal location for permanent residences, cottage development, and seasonal recreational activities. However, limnological surveys and anecdotal observations from recent decades have indicated that the water quality in embayments within southeastern Georgian Bay has changed substantially as a result of anthropogenic activities such as cottage development (HESL, 2014; Clark et al., 2015). Common concerns in the embayments include continuous low water levels, increases in macrophyte growth, declines in deep-water oxygen, higher nutrient levels relative to the open waters of Georgian Bay, and loss of cold-water fish habitat (Schiefer, 2003; Schiefer et al., 2007; Chiaandet and Sherman, 2010). In 2012, the Government of Canada granted $29 million to the Lake Simcoe clean-up fund to, in part, improve the water quality and protect the vulnerable aquatic ecosystems of Georgian Bay (Environment Canada, 2015 accessed on January 28th 2016 http://www.ec.gc.ca/eau-water/default.asp?lang=En&n=85C54DAE-1#Figure4).

Existing monitoring programs in Georgian Bay, while extremely important and necessary for providing valuable water quality and ecological information, does not extend beyond ~ 3
decades, and many do not provide continuous records. To better determine baseline (pre-disturbance) conditions and to assess the long-term influence of humans on the embayments of Georgian Bay, longer records of environmental information are needed. Here we utilize paleolimnological approaches to provide the much needed long-term ecological context to the growing knowledge about Georgian Bay. Diatoms and spectrally inferred sedimentary chlorophyll $a$ in dated sediment cores from three embayments in Georgian Bay are used to assess past trends in water quality and whole-lake primary production, respectively.

Diatoms (Bacillariophyceae) are siliceous algae that can respond rapidly to various natural and anthropogenic environmental stressors, and hence they are widely used to monitor the health of aquatic ecosystems. In paleolimnology, diatoms are useful bio-indicators as they have well defined ecological optima and the siliceous cell walls (frustules) preserve well in most sediment, allowing the reconstruction of past changes in environmental conditions. Diatom assemblage change through time can provide powerful qualitative assessments of lake ecosystems and diatoms have been extensively used in southern Ontario to understand the effects of shoreline development and associated changes in nutrients (Hall and Smol, 1996; Hawryshyn et al., 2012; Nelligan et al., accepted). In addition to tracking changes in nutrient levels, diatoms can also be used to track the effects of climate-induced changes on lake thermal properties in southern Ontario (Hawryshyn et al., 2012; Hadley et al. 2013; Barrow et al. 2014). The response of diatoms to warming is complex and is often site-specific, varying with differences in location and the physical-chemical characteristics of individual lakes (Rühland et al., 2015). Diatoms do not necessarily need to respond directly to increases in air temperatures to be useful indicators. Instead they tend to respond indirectly to warming through changes in lake physical properties and associated changes in resources (light and nutrients). Since climatic variables, such as air
temperature and wind, directly influence lake physical processes, such as the length of the ice-free and ice-on seasons, the timing, strength, and duration of thermal stratification, and water levels (Adrian et al., 2009), diatoms can be used to indirectly track past climatic conditions. Changes in the aforementioned lake physical processes directly impact and alter light, nutrient, and habitat availability for algae (Winder and Schindler, 2004; Winder and Sommer, 2012), resulting in certain taxa being favored over others (Rühland et al., 2008; 2015; Winder et al., 2009). Furthermore, diatoms do not necessarily respond to warming-related changes in lakes linearly; rather, critical limnological thresholds need to be crossed for threshold type responses in diatom assemblages to occur (Rühland et al., 2013). Therefore, in this study, we use diatoms to better understand the effects of recent climate warming on two embayments with shoreline development and an embayment with no shoreline development in southeastern Georgian Bay.

4.3 Study site description and design

We assess the limnological changes of three embayments located in southeastern Georgian Bay that have limited exchange with the open waters of Georgian Bay. Honey Harbour is a recreational hub in Georgian Bay that supports seasonal cottages, permanent residences, marinas, and campground facilities, all easily accessed via roads (Chiandet and Sherman, 2010). Most monitoring programs only encompass the last ~30 years at most and do not include limnological data from earlier shoreline disturbances including European settlement (post-1800) and increased disturbances (e.g., cottage development) following the Second World War (post-1950).

In this study, we are employing the impact-unimpacted system approach to assess the effects of shoreline development on the embayments. The North and South bays of Honey Harbour represent our two impact sites as they are easily accessible via roads and have shoreline
development. Shoreline development in North and South bay includes, permanent residences, recreational resorts, and marinas (Murdoch, 1999). Initial (minor) development occurred around the late-19th century in the Honey Harbour area (Murdoch, 1999). During the early to mid-20th century the number of cottages and resorts gradually increased (Murdoch, 1999). However, following the Second World War the amount of shoreline development increased around the Honey Harbour area (Murdoch, 1999). In comparison, our reference site, Tadenac Bay, is fairly isolated with no road access and has experienced little to no shoreline development. Tadenac Bay (adjacent to Tadenac Lake) exists within a pristine refuge managed by a private fishing club since the late-1800s and at any given time only ten club members are allowed to stay in the lodge during the open water season (Croft and Chow-Fraser, 2009). Hence, Tadenac Bay is considered one of the most pristine sites in the Great Lakes.

The three embayments are located within the Great Lakes-St. Lawrence Forest Region and are underlain by the Canadian Shield. Both North and South bays are fairly isolated from the open waters of Georgian Bay by the presence of islands, channels, and smaller bays (Schiefer et al., 2007), while Tadenac Bay is connected to Georgian Bay via a wide and deep channel on the western side (Johnston et al., 2014) (Fig. 4.1). North Bay is located in a small isolated watershed and does not receive substantial inflow from tributaries and has a low natural flushing rate (Schiefer and Schiefer, 2005). In contrast, South Bay has a larger watershed and receives inflow from a tributary of Severn River via Baxter Lake, which has higher conductivity waters and higher natural flushing rates (Schiefer et al., 2006).

Limnological characteristics of the three embayments are provided in Table 4.1. Although South Bay is relatively shallow (11 m), it stratifies during summer, as do deeper North Bay (22 m) and Tadenac Bay (29 m) (Chiandet and Sherman, 2010; Johnston et al., 2014). Based
on recent monitoring data, all three embayments experience end-of-summer oxygen depletion in the hypolimnion (Chiandet and Sherman, 2014; Johnston et al., 2014), however, the severity of the depletion varies from year to year (Schiefer et al., 2006). Dissolved oxygen (DO) is also depleted near the thermocline of North Bay (Schiefer et al., 2007; Chiandet and Sherman, 2014) and in Tadenac Bay (Johnston et al., 2014) near the end of summer. The low levels of DO can have serious consequences on cold water fish species such as lake trout which have shown signs of population decline in Georgian Bay (Bywater et al., 2013). Although cold water fish species are present at the beginning of the open water period in North and South bays, they tend to decline in population by the end of the summer, coinciding with the decline in hypolimnetic DO (Schiefer et al., 2006; 2007). Total phosphorus in the euphotic zones of North and South bays range between 12 - 16 µg/L and remain consistent throughout the open-water period (Chiandet and Sherman, 2014). However, around mid-summer, high phosphorus concentrations (> 100 µg/L) are often recorded in the bottom waters (< 1 m from sediment-water interface) of North and South bays, which undoubtedly are released from the sediments as a result of reduced conditions prompted by hypolimnetic anoxia (< 1 mg/L of DO) (Schiefer et al., 2007; Chiandet and Sherman, 2014). Similar to many other parts of the Laurentian Great Lakes, North and South bays contain invasive dreissenid mussel species such as zebra (*Dreissena polymorpha*) and quagga (*Dreissena bugensis*) mussels since the 1990s (Kathy Kay pers. comm. 2016). However, Tadenac Bay seems to have avoided this fate as recent limnological survey did not observe the presence of dreissenid species (Johnston et al., 2014). Round goby (*Neogobius melanostomus*), an invasive fish species in the Great Lakes, has also been observed at North and South bays (Ontario.ca, 2015 [https://www.ontario.ca/environment-and-energy/round-goby-0](https://www.ontario.ca/environment-and-energy/round-goby-0)) and in the recent fish survey at Tadenac Bay.
4.4 Materials and Methods

4.4.1 Sediment core collection and radioisotopic dating

In February of 2015, sediment cores were retrieved from North (coring depth – ~20 m; coordinates: 44.89° N, 79.79° W) and South (coring depth – ~12 m; coordinates: 44.87° N, 79.79° W) bays (Honey Harbour, Georgian Bay, Lake Huron) using a gravity Uwitec corer (bathymetric maps were used to select coring sites). The sediment cores from North and South bays were 40 cm and 44 cm, respectively. The sediment cores were vertically extruded at 0.5 cm to the base of the core using Uwitec extruding apparatus. In June 2015, a 24.5 cm sediment core was collected from Tadenac Bay (coring depth – ~26 m; coordinates: 45.059° N, 79.975° W) using a Glew (1989) gravity corer and vertically extruded using a Glew (1988) extruder at 0.5 cm intervals to the base of the core (bathymetric map was used to select coring site). Extruded sediment samples were stored in a cooler and transported to the Paleoecological Environmental Assessment and Research Laboratory (PEARL), Queen’s University, Kingston, Ontario for analysis and archiving.

Freeze-dried sediment samples from select intervals were analyzed for $^{210}$Pb, $^{137}$Cs, and $^{214}$Bi activity using gamma spectrometry (EG&G Ortec germanium detector) at PEARL, following standard procedures outlined by Schelske et al. (1994). Sediment core chronologies for approximately the past 150 years were calculated using the unsupported concentrations of $^{210}$Pb and the constant rate of supply (CRS) model (Appleby, 2001). The distinct $^{137}$Cs peak from the atomic bomb testing around the 1960s was used as an independent dating marker to corroborate the $^{210}$Pb dates estimated using the CRS model.

4.4.2 Diatom analysis
Sediment samples were processed for diatom analysis following standard procedures outlined by Battarbee et al. (2001). Approximately 0.05 g of freeze dried sediments or 0.5 g of wet sediments from selected samples were treated with a 50:50 molar mixture of sulphuric (H₂SO₄) and nitric (HNO₃) acids to isolate the siliceous biological indicators from the organic sediment matrix. The samples were then placed in a hot water bath at 80°C for at least 2 hours to speed up the acid digestion process. Subsequent to the acid digestion process, the sediments with the acid mixture were allowed to settle for ~ 24 hours and then rinsed several times with de-ionized water until the slurries approached the pH of de-ionized water (litmus test). Aliquots of the circumneutral slurries were plated onto glass cover slips and allowed to air dry on a slide warmer. The cover slips were permanently mounted onto microscope slides using Naphrax® (refractive index 1.73).

A minimum of 400 diatom valves were identified and enumerated per sample using a Leica DMR light microscope fitted with differential interference contrast optics under 1000X magnification. Diatoms were identified using an assortment of taxonomic guides including, Krammer and Lange-Bertalot (1986, 1988, 1991a, 1991b), Camburn and Charles (2000), and Reavie and Kireta (2015). Diatom data are expressed as relative abundance of total diatom valves enumerated in each sample and the most common diatom species are stratigraphically presented (Figs. 4.3, 4.4, 4.5). For visual clarity, some taxa from the same genera or varieties of the same species were grouped together if they showed similar trends through time. However, for all statistical analyses, the complete diatom data (i.e. no groupings) were used.

4.4.3 Sedimentary chlorophyll-a

Visible reflectance spectroscopy of chlorophyll a (VRS Chl a) was used to assess whole lake primary production over the past ~200 years. VRS Chl a is a non-destructive method to
reliably assess the past trophic statuses of lakes (Michelutti et al., 2010). Briefly, a selection of samples from each core were freeze-dried and the sediments were sieved through a 125 µm mesh sieve (to prevent the influence of particle size) and then transferred to a glass cuvette and the samples were analyzed on a FOSS NIR System model 6500 rapid content analyzer, operating over the range of 400 - 2500 nm. Spectral signatures between 650 and 700 nm wavelengths were analyzed to infer past trends in VRS Chl \( \alpha \) – including all of its isomers and phaeopigments (Michelutti et al. 2010). This method has been used effectively to track whole lake production across many Boreal Shield lakes (e.g. Michulutti et al., 2010; Hawryshyn et al., 2012; Labaj et al., 2015). However, it is important to note that the purpose of this technique is to assess the past trends in whole lake production and not to infer absolute values (Michulutti et al., 2010).

4.4.4 Diatom data analysis

Cluster analysis identified diatom stratigraphical zones for each core using constrained incremental sum of squares (CONISS) using ‘rioja’ (Juggins, 2014) and ‘vegan’ (Oksanen et al., 2015) packages developed for the R software environment (R Core Team, 2015). CANOCO version 5.0 (ter Braak and Šmilauer, 2012) was used to perform all ordination analyses. The detrended correspondence analysis showed that the diatom species data across all three embayments had a gradient length < 2 standard deviation units, hence the linear regression technique, principal components analysis (PCA), was deemed to be an appropriate ordination method to summarize the variation in the diatom data (Birks, 2010). Prior to ordination analyses, the diatom percent relative abundance data were square-root transformed to equalize the variance among taxa. PCA axis 1 sample scores were plotted against depth and time for each sedimentary sequence along with the diatom relative abundance data to compare the timing of shifts in diatom assemblages across the three embayments. Summarizing the data in this way allowed
comparisons in the timing, and magnitude of diatom changes with historical activities in the catchment such as early settlement, resort development and warming related changes. In addition, a separate PCA was conducted where diatom data from all three embayments were assessed within the same ordination space. This provided an opportunity to assess differences in diatom assemblage composition among the three embayments along PCA axis 1 and trajectories through time along PCA axis 2 (e.g. Faulkenham et al., 2003; Rühland et al. 2010; Sivarajah Chapter 3 of this thesis).

4.4.5 *Instrumental meteorological records*

Long-term air temperature records from Parry Sound, Ontario (Climate Station ID: 6116254, 6116255, 6116257) and Beatrice, Ontario (Climate Station ID: 6110607) climate stations were obtained from Environment Canada Historical Climate Record ([http://climate.weather.gc.ca/](http://climate.weather.gc.ca/)) and from the Adjusted and Homogenized Canadian Climate Data ([http://www.ec.gc.ca/dccha-ahccd/](http://www.ec.gc.ca/dccha-ahccd/)). The two long-term records are used individually to assess regional trends in air temperature. The air temperature records from Beatrice and Parry Sound contained more than 120 years of temperature data between 1876 and 2015. These two climate stations were less than 60 km from at least one of the three embayments. The trends in seasonal and annual air temperatures through time were assessed using Mann-Kendall trend tests using the Kendall package (McLeod, 2011), developed for the R software environment (R Core Team, 2015). Continuous mean observed water level records between 1962 and 2015 for Parry Sound, Ontario (Station ID: 11375) and Collingwood, Ontario (Climate Station ID: 11500) were obtained from Fisheries and Oceans Canada ([http://tides.gc.ca/eng/data](http://tides.gc.ca/eng/data)). Both these sites are located in Georgian Bay and are less than 60 km to at least one of the three embayments.
4.5 Results

4.5.1 Radiometric dating

Sediment cores from all three embayments exhibited an exponential decline in $^{210}$Pb activity with depth, suggesting sediment mixing is not a concern for these cores (Fig. 4.2). The $^{210}$Pb activities of North Bay and Tadenac Bay sediment cores reached background activities around 35 cm and 10 cm, respectively (based on average $^{214}$Bi activities). However, the $^{210}$Pb activities of the South Bay sediment core did not reach background levels (based on average $^{214}$Bi activities used as a proxy for unsupported $^{210}$Pb), and it plateaued around 20 cm. South Bay is a relatively shallower embayment and has ~64% littoral zone (Chiandet and Sherman, 2014) suggesting it is more productive hence could have had higher sedimentation rates. The CRS model was used to establish the sediment chronology for the past ~150 years and second order polynomial equations (based on established $^{210}$Pb chronologies) were used to extrapolate dates beyond background $^{210}$Pb levels for North and Tadenac bays. All cores exhibited a well-defined $^{137}$Cs peak (Fig. 4.2) that $^{210}$Pb dates estimated to occur ~1960 establishing confidence that our $^{210}$Pb dates are reliable.

4.5.2 Diatom trends across the bays

Diatom valves were present and well-preserved in samples from the three embayments and were dominated by planktonic taxa. The diatom taxa from each bay were plotted stratigraphically (Figs. 4.3, 4.4, 4.5). Diatom assemblages at all three bays have undergone marked shifts over the past ~120 - 200 years.

At North Bay, CONISS identified the first major diatom shift at approximately 1970 that was characterized by marked declines in the relative abundances of planktonic Discostella stelligera (although D. stelligera has been gradually decreasing in relative abundance since the late 1800s), Stephanodiscus species and Aulacoseira subarctica and concurrent increases in
Fragilaria crotonensis and Fragilaria capucina (Fig. 4.3). One of the more notable post-1970s compositional shifts was the arrival and increase in the relative abundances of small Cyclotella species (C. ocellata, C. comensis/gordonensis complex). In the most recent sediments (post-2005), D. stelligera and A. subarctica return to notable relative abundances.

Diatom assemblage shifts in South Bay were somewhat different than what was observed in North Bay, in terms of species composition. For example, the first major shift in diatom assemblage in South Bay occurred earlier, around the 1950s, and was marked by declines in the relative abundances of A. subarctica and D. stelligera and increases in the relative abundances of benthic fragilarioid species (Staurosira construens, Staurosira construens var. venter, Pseudostaurosira brevstriata, Staurosirella pinnata, Fragilaria constricta, Staurosirella leptostauron), Cocconeis placentula, as well as planktonic F. crotonensis, Fragilaria tenera (Fig. 4.4). In the post-1990 sediments, declines in the relative abundances of Aulacoseira ambigua and Fragilaria tenera were observed. In the most recent sediments (~ post-2010), increases in the relative abundances of planktonic Cyclotella ocellata, and Asterionella formosa were observed.

Tadenac Bay, the reference site, displayed a shift in diatom assemblage that was distinct from the two impact sites with only one major shift identified in the sediment core (other changes identified by CONISS are subtle) (Fig. 4.5). Around the late-1970s, an almost complete compositional turnover is observed with the marked increase in the relative abundances of small Cyclotella species (C. ocellata, C. comensis, and C. gordonensis) which occurred in trace abundances in previous sediments. Concomitant decreases in the relative abundances of A. subarctica, Cyclotella michiganiana, D. stelligera, and benthic fragilarioid species (Staurosira construens, Staurosira construens var. venter, Pseudostaurosira brevstriata, Staurosirella pinnata) were also observed.
4.5.3 Diatom assemblage composition change through time (PCA)

In all 3 cores, PCA axis 1 sample scores generally tracked compositional shifts among dominant diatom taxa. At North Bay the PCA axis 1 sample scores ($\lambda = 0.47$) tracked the changes in the dominant diatom species (*F. crotonensis* - *D. stelligera* - *A. subarctica*) (Fig. 4.3). Similarly, at South Bay, the PCA axis 1 sample scores ($\lambda = 0.37$) were tracking shifts in dominant species such as benthic fragilarioid taxa and *A. subarctica* (Fig. 4.4). At Tadenac Bay, the PCA axis 1 sample scores ($\lambda = 0.52$) were tracking the recent arrival and increase in the relative abundances of small *Cyclotella* taxa (*C. ocellata*, *C. comensis*, and *C. gordonensis*) and the concomitant decrease in the relative abundances of *A. subarctica*, *C. michiganiana*, *D. stelligera*, and benthic fragilarioid taxa (Fig. 4.5).

PCA axis 1 versus PCA axis 2 for all three embayments plotted within the same ordination space highlighted that there were distinct differences in assemblage composition across the three sites as samples were well separated along axis 1 ($\lambda = 0.24$) (Fig. 4.6). Temporally coherent changes in diatom assemblages through time were observed at all three sites as suggested by the spread in sample scores along PCA axis 2 ($\lambda = 0.22$) (Fig. 4.6). At both impacted systems (North and South bays), the PCA analysis shows that the first major shift in diatom assemblages occurred between the 1950s and 1970s, which led to a series of novel assemblages in the subsequent decades (Fig. 4.6). The next major shift in diatom assemblages from North and South bays occurred in the mid to late-2000s (Fig. 4.6). In the unimpacted system (Tadenac Bay), consistent with the individual PCA, only one major shift in diatom composition occurred around the late-1970s (Fig. 4.6).

4.5.4 VRS Chl a trends
Sedimentary VRS Chl a showed an increasing trend at all three study sites, however the timing and magnitude of change varied among the three sites (Figs. 4.3, 4.4, 4.5). At North Bay VRS Chl a began to increase at the turn of the 20th century; however, more rapid increases occurred after the 1970s that continued to the top of the core (Fig. 4.3). At South Bay, subtle increases in VRS Chl a were observed around the 1950s followed by a more rapid increase after 1965 (Fig. 4.4). At Tadenac Bay VRS Chl a was stable and low for most of the core with a marked increase around the 1970s, consistent with an almost complete shift in diatom composition (Fig. 4.5).

4.5.5 Instrumental meteorological data

Air temperature data from Beatrice and Parry Sound climate stations exhibit an increasing trend for annual and seasonal temperatures (Fig. 4.7; Table 4.2). The annual, spring and autumn air temperatures present a significant increasing trend across both climate stations (Table 4.2). Increasing trends are observed for winter air temperatures at the Beatrice and Parry Sound climate stations, and summer air temperatures at Beatrice however, these trends are not statistically significant (Table 4.2). The water level data from Parry Sound and Collingwood exhibit synchronous changes (Fig. 4.8). Marked declines in water level began around 1985, however, persistent low water levels were observed between 2000 - 2013 (Fig. 4.8).

4.6 Discussion

Diatom assemblages across all three embayments have recorded pronounced shifts in response to the mid-late 20th century climate warming. However, subtle changes in diatom assemblages are observed in response to shoreline development at both impacted sites in the late-19th century and early 20th century. Furthermore, the differences in the magnitude and species-specific floristic changes suggest that the diatoms were influenced by site specific limnological
characteristics of the embayments. In complex aquatic systems, such as Georgian Bay, untangling the effects of climate warming and shoreline development can be challenging as these stressors can be simultaneously driving changes in diatom assemblages. However, by carefully choosing the study sites, the floristic changes in the unimpacted system clearly demonstrated the effects of warming in the absence of shoreline development, beginning in the 1970s. The impacted-unimpacted study design helps us tease apart the effects of local shoreline development and regional climate warming on the embayments of Georgian Bay.

Diatom response to climate warming is complex as it is influenced by a multitude of factors including geographic location, the morphometry of the lake or bay, and the presence or absence of other stressors (Rühland et al., 2015). This is clearly evident in our study sites as marked differences in diatom assemblage composition are observed in response to warming among the three sites (Fig. 4.6). We first discuss the effects of warming on the diatom assemblages at the unimpacted system (Tadenac Bay) and diatom assemblage shifts in North and South bays are discussed separately.

4.6.1 Diatom response to climate warming at Tadenac Bay

An almost complete turnover in diatom species occurred around the late-1970s at the control site, Tadenac Bay. This shift is characterized by an abrupt and sharp increase in the relative abundances of small Cyclotella species (C. ocellata, C. comensis, C. gordonensis) as these taxa were occurring in very low to trace abundances in the previous sedimentary intervals. While the aforementioned small Cyclotella taxa have been increasing in relative abundance during the warmest period in the meteorological record (Fig. 4.7), other cyclotelloid taxa such as Discostella stelligera and Cyclotella michiganiana have been declining in relative abundance. Many paleolimnological studies from around the world have reported an increase in
Discostella/Cyclotella species, specifically *D. stelligera*, during recent warming (e.g. Rühland et al., 2008; Hadley et al., 2013). However, in deep oligotrophic systems where *D. stelligera* has been the dominant species, newly arrived planktonic diatoms may be favored under warming conditions (e.g. Sivarajah Chapter 3 this thesis). The switch among small cyclotelloid taxa warrants further investigation. The probable mechanisms that need to be explored include, but not limited to, seasonality of blooms for these taxa in southern Ontario, diatom valve size variability among different cyclotelloid taxa, and resource availability.

Increases in the relative abundances of small *Cyclotella* taxa, with concomitant decreases in benthic fragilarioid species and heavily silicified *Aulacoseira* species, have been reported from other lakes in Ontario (Rühland et al., 2010; Hawryshyn et al., 2012; Hadley et al., 2013; Nelligan et al., accepted), the Laurentian Great Lakes (Chraïbi et al., 2014; Reavie et al., 2014) and around the world (Rühland et al., 2008; 2015) in response to warming-related changes to lake thermal properties. Our air temperature records and other climate records from the region show notable increases in seasonal and annual air temperatures over the past century (Fig. 4.7, Hawryshyn et al., 2012). The timing of increases in small *Cyclotella* taxa around the late-1970s closely match substantial increases in annual air temperature records. Recent warming have resulted in longer ice-free periods (Futter, 2003), earlier onset and later breakdown of thermal stratification (Cahill et al., 2005; Stainsby et al., 2011), stronger thermal stability (Hadley et al., 2014), and higher epilimnetic temperatures (Keller, 2007) across Ontario lakes. Alterations of these factors have led to novel diatom assemblages in lakes across Ontario and the Laurentian Great Lakes, where increases in the relative abundances of small centric planktonic diatoms (such as small *Cyclotella* taxa) are observed (Rühland et al., 2010; Hawryshyn et al., 2012; Hadley et al., 2013; Chraïbi et al., 2014; Reavie et al., 2014).
Paleoecological and empirical studies show that the recent increase in the small *Cyclotella* species is likely a response to warming related changes to lake thermal properties (Rühland et al., 2008; 2015; Winder et al., 2009). The small *Cyclotella* taxa have one of the lowest sinking velocities of all diatoms (Diehl et al., 2002; Ptacnik et al., 2003); hence, during long thermally stratified periods (induced by warming), they are able to remain in the photic zone and thrive (Winder and Hunter, 2008). Furthermore, small *Cyclotella* taxa have high surface area to volume ratios, making them effective competitors for nutrients and light under strongly stratified conditions relative to heavily silicified taxa such as *Aulacoseira* that sink faster (Winder and Hunter, 2008; Winder et al., 2009; Rühland et al., 2008). The regional increase in spring temperatures (Fig. 4.7) may also contribute to the recent increase in small *Cyclotella* taxa as spring peak in *Cyclotella* species has been associated with the earlier onset of thermal stratification (Thackeray et al., 2008).

In addition to increases in small *Cyclotella* taxa, we also observe marked increase in whole lake primary production (i.e. spectrally inferred sedimentary chlorophyll *a*) at Tadenac Bay. The increase in whole lake primary production is likely resulting from a longer growing season. The timing of increases is consistent with similar observations from southern Ontario where whole lake primary production has increased with the lengthening of open-water season (Labaj et al., 2015; Nelligan et al., accepted). The lack of shoreline activities over the past ~ 200 years at Tadenac Bay suggests that the increase in whole lake primary production is occurring independent of external nutrient loading to the embayment.

4.6.2 Diatom response to shoreline development and climate warming at North and South bays

The presence of relatively higher nutrient optima diatom taxa across both embayments suggests that these systems have been moderately influenced by initial shoreline developments
such as permanent residences and recreational resorts at the turn of the twentieth century.

Sedimentary diatom assemblages from North and South bays record a major shift between the 1950s and 1970s. The timing of this shift overlaps with regional climate warming and other limnological changes as described below. However, there are differences in species-specific shifts between these two impact sites, likely resulting from the differences in the morphometry of the bays. South Bay is shallower (11 m) and more macrophyte dominated relative to the deeper North Bay (22 m) (Chiandet and Sherman, 2014). Diatom response to shoreline development and climate warming at North and South bays are discussed separately.

North Bay

The presence of higher nutrient optima *Aulacoseira subarctica* (dominant species) and *Stephanodiscus* species (in notable relative abundances) (Hall and Smol, 1996; Reavie and Smol, 2001) suggests that North Bay has been a mesotrophic system prior to the development around Honey Harbour area. The first major shift in diatom assemblages at North Bay is recorded around the 1970s. However, gradual declines in the relative abundances of *Discostella stelligera* have been occurring since ~1875. The decline in *D. stelligera* ~1875 corresponds to the timing of (minor) initial shoreline developments, such as development of permanent settlements and resorts, in the Honey Harbour area. The subtle increase in VRS Chl *a* suggests that slightly higher nutrient concentrations from the aforementioned shoreline development may have contributed to minor increases in whole lake primary production.

The abrupt increase to dominance in the relative abundance of *F. crotonensis* between the 1970s and 2005 at North Bay occurred with concomitant declines in *A. subarctica, D. stelligera* and *Stephanodiscus* species (Fig. 4.3). The decline in *A. subarctica* and *Stephanodiscus* species may suggest that nutrients have slightly decreased because these species are key indicators of
relatively higher nutrient conditions in Ontario (Hall and Smol, 1996; Hawryshyn et al., 2012). Increases in the relative abundances of *F. crotonensis* have been widely reported from culturally eutrophied Ontario lakes (Clerk et al., 2000; 2004). However, recently *F. crotonensis* has also been observed in low nutrient lakes and lakes with no changes in nutrients over time (Hadley et al., 2013). Although mesotrophic conditions are likely favoring *F. crotonensis*, it may not be the primary driver for the increase in the relative abundance of this taxon at North Bay as changes in assemblage composition at this time also includes the notable arrival of other planktonic taxa that commonly occur in nutrient-poor systems. For example, the recent arrival and increases in the relative abundances of small *Cyclotella* taxa (*C. ocellata, C. comensis/gordonensis* complex) may also suggest a subtle decrease in nutrients as these taxa are known to thrive in relatively low nutrient conditions in Ontario (Werner and Smol, 2005). However, the *C. comensis/gordonensis* complex has been observed in notable relative abundances in mesotrophic systems such as Lake Simcoe in recent decades (Hawryshyn et al., 2012).

We suggest that the recent increase in the relative abundance of *F. crotonensis* and small *Cyclotella* taxa beginning around the 1970s and continuing into the mid-2000s is likely a response to regional climate warming as we clearly observe an increase in the air temperature records presented in this study (Fig. 7) and that of other studies from the region (Hawryshyn et al., 2012). Similar shifts observed from other complex waterbodies such as the Lake of the Woods (Rühland et al., 2010) and Lake Simcoe (Hawryshyn et al., 2012) have been inferred to be a response to warming. In addition to increases in the relative abundance of *F. crotonensis* and small *Cyclotella* taxa, we also observe a marked increase in VRS Chl *a* suggesting longer ice-free periods superimposed on a mesotrophic system may have led to increases in whole lake primary production (Michelutti et al., 2010).
The relative abundances of *D. stelligera* and *A. subarctica* show signs of recovery in the post ~2005 sediments, while subtle declines in the relative abundances of *F. crotonensis* and small *Cyclotella* taxa were observed. Paleolimnological studies from Ontario, including our unimpacted system, have shown decreases in the relative abundance of *A. subarctica* in response to warming (Rühland et al., 2010; Hyatt et al., 2011). However, recent observations from Saidenbach Reservoir, a dimictic reservoir in Germany, show that *A. subarctica* are favored after milder winters (often resulting from warming) (Horn et al., 2011). The authors suggested that *A. subarctica* are likely able to withstand the low light conditions during short winters and start off with a relatively larger initial population size during the spring bloom compared to other diatoms (Horn et al., 2011). Although the ice records are not available for North Bay, the recovery of *A. subarctica* coincides with the warmest winters in the regional meteorological record (Fig. 4.7).

The recovery of *A. subarctica* at North Bay in the recent sediments warrants further exploration, as many paleolimnological studies have shown clear declines in a variety of *Aulacoseira* species in response to declines in nutrients and/or warming (e.g. Rühland et al., 2010; Hawryshyn et al. 2012; Reavie et al. 2014).

**South Bay**

The diatom assemblage of the shallower impacted site, South Bay, responds differently to shoreline development and climate warming compared to the diatom assemblages of North Bay. Based on the $^{210}$Pb dates, this core only contains sedimentary diatom assemblages since the 1890s and therefore the sediment core does not contain diatom assemblages from the same baseline period as the other cores. The diatom assemblage of South Bay prior to the 1950s were dominated by higher nutrient indicating taxa such as *A. subarctica* and *A. ambigua*, suggesting this was a mesotrophic system. This would be expected as shoreline activities such as permanent
residences, and recreational resorts around the Honey Harbour area were developed as early the
1870s resulting in higher nutrients entering the aquatic systems.

The first major shift in the diatom assemblages at South Bay occurs around the 1950s
when the relative abundances of *A. subarctica* gradually decreases while the relative abundances
of *Cocconeis placentula* abruptly increases along with subtle increases in benthic fragilarioid
taxa. Previous paleolimnological and neolimnological surveys from St. Lawrence River have
reported close relationships between ephiphytic *Cocconeis* taxa and its common substrate
*Cladophora* (O’Connell et al., 1997; Reavie et al., 1998). Furthermore, increases in the relative
abundance of *C. placentula* occurred around the late-1950s and early-1960s when increases in
*Cladophora* in the Laurentian Great Lakes were also reported in response to nutrient enrichment
(Higgins et al., 2008). The presence of ephiphytic *C. placentula* in notable abundances at South
Bay in the post ~1965 diatom assemblages is likely an indication of the increases in *Cladophora*
macro-alga. Concurrently, we are also observing an increase in whole lake primary production,
assessed by VRS Chl *a*, likely due to the higher habitat availability provided by the macrophytes.

Benthic fragilarioid taxa have also been associated with *Cladophora* in Lake Huron
(Stevenson and Stoermer, 1982). The initial increases in the relative abundances of benthic
fragilarioid taxa could be attributed to increase in *Cladophora* and macrophytes; however,
subsequent increases between ~1985 and ~2005 closely track the water level changes (likely
induced by climate warming) in the region. The water levels in the Laurentian Great Lakes,
specifically in the Lake Huron-Michigan basin, have greatly fluctuated over the 20th and early-
21st centuries. In our water-level record from Georgian Bay, we are observing a marked decrease
since the mid-1980s and persistent low levels in the 2000s (Fig. 4.8). The effects of water level
drops on diatom communities might not be clearly evident in deep systems like North and
Tadenac bays. However, in a relatively shallower system, like South Bay, the effects low water levels on diatom communities may be more pronounced as changes in habitat availability and light availability may favor certain taxa over others. At South Bay, we observe the combined effects of low water levels and the increased proliferation of macrophytes that may explain the increase in benthic fragilarioid taxa. Additionally, we also observe increases in benthic *Achnanthes sensu lato* species (*Psammothidium curtissimum*, *Planothidium lanceolata*, and *Karayevia clevei*) likely a response to increase in habitat availability provided by the macrophytes while the low water levels may be providing increased light availability to these benthic taxa. These benthic taxa are favored over planktonic taxa such as *Asterionella*, cyclotellloid taxa and *Aulacoseira* taxa during periods of low water levels.

In the most recent sediments (post-2010) a new assemblage of planktonic diatoms dominate, with marked increases in the relative abundances of *A. formosa* and *C. ocellata*, and subtle increases in the relative abundances of *D. stelligera* and *Tabellaria flocculosa* str. IIIp. These changes are consistent with other observations from southern Ontario and the Laurentian Great Lakes where increases in centric and pennate planktonic diatoms have been reported in the most recent sediments (Hadley et al., 2013; Chraïbi et al., 2014). The increase in the relative abundances of *C. ocellata* and other small *Cyclotella* species in response to recent warming have been discussed in detail in the previous sections. Recent increases in the relative abundances of *A. formosa* has been reported in many lakes across Ontario are related to warming and associated limnological changes (Hadley et al., 2013; Barrow et al., 2014; Sivarajah et al., 2016). At South Bay *Asterionella* is known to bloom in late spring and fall (Chiandet and Sherman, 2014). The high surface area to volume ratio (Round et al., 1990) and one of the lowest sinking velocities of all diatoms (Spaulding and Edlund, 2009 Diatoms of the United States.
External phosphorus loading is not a major concern at South Bay; however, end-of-summer internal phosphorus loading is indeed a concern (Chiandet and Sherman, 2014). The high nutrient availability throughout the water column after fall mixing events could explain the fall bloom of *A. formosa* at South Bay. The diatom shifts, specifically *A. formosa*, at South Bay are likely driven by both nutrient availability in the water column and strong thermal stratification.

**4.6.3 Can atmospheric nitrogen deposition influence diatom changes in these embayments?**

Increased atmospheric nitrogen deposition has been suggested as a potential cause for recent shifts in diatom assemblages in so-called “nitrogen hotspots” (e.g. western United States; Wolfe et al., 2003; Saros et al., 2011; Sheibly et al., 2014) and elsewhere (Wolfe et al., 2006; Saulnier-Talbot et al., 2015). Although globally atmospheric nitrogen deposition has increased since the industrial revolution, in our study region (southern Ontario), atmospheric nitrogen deposition (measured at nearby lakes around Dorset, Ontario) has been on the decline over the past three decades (Vet et al., 2014; Sivarajah et al., 2016) when marked changes in diatom assemblages are observed at our impacted and un-impacted sites (i.e. increases in the relative abundances of small *Cyclotella* taxa and pennate planktonic *A. formosa*). No clear relationships are observed between nitrogen availability and shifts in diatom assemblages in southern Ontario (Hadley et al., 2013 Sivarajah et al., 2016). Recent shifts in diatom assemblages in the three embayments and in other southern Ontario lakes are likely response to regional climate warming and not atmospheric nitrogen deposition (Hadley et al., 2013; Sivarajah et al., 2016).

**4.7 Conclusions**
Based on the qualitative assessment of the diatom assemblages, we conclude that the two impacted systems have been mesotrophic since shoreline development that began around the late-1800s in the Honey Harbour area where as the unimpacted site, Tadenac Bay, has been an oligotrophic system. Furthermore, the diatom assemblage changes do not indicate major changes or fluctuations in total phosphorus concentrations at the two impacted sites.

Our observations of increases in small *Cyclotella* taxa and pennate planktonic diatoms, such as *A. formosa* and *F. crotonensis* in the most recent sediments, are consistent with observations from other southern Ontario lakes (Hadley et al., 2013; Nelligan et al., accepted; Sivarajah et al., 2016) and the Laurentian Great Lakes (Chraïbi et al., 2014; Reavie et al., 2014). Changes in lake thermal properties in response to regional warming are correlated with the increase in the relative abundances small *Cyclotella* taxa and pennate planktonic diatoms in the most recent sediments. A growing number of studies, including ours, are providing evidence of relationship between rising regional air temperatures and novel diatom assemblage shifts in southern Ontario (Rühland et al., 2010; Hawryshyn et al., 2012; Hadley et al., 2013; Nelligan et al., accepted; Sivarajah et al., 2016).

Marked changes are observed in the sedimentary diatom records in all three embayments in response to local nutrient enrichment and regional climate warming. However, as described above, the diatom responses to shoreline development and climate warming substantially differ among the embayments, suggesting local limnological factors, such as depth and macrophyte growth, may be playing an important role. Our observation of diverse diatom response to similar environmental stressors is consistent with other regional studies and we emphasize the importance of contextually interpreting the changes in diatom assemblages.

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4.9 References


Juggins, S., 2014. Rioja: analysis of quaternary science data, R package version (0.9-3).


4.10 Tables

**Table 4.1:** Limnological characteristics of North Bay, South Bay and Tadenac Bay. Total phosphorus (TP) data for North and South Bay are mean values from surface water samples collected biweekly during the ice free season between 2011 and 2012 (Chiandet and Sherman, 2014). TP data for Tadenac Bay are a mean of surface water samples collected in June 2013 (Johnston et al., 2014).

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<td>Area (km²)</td>
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**Table 4.2:** Mann-Kendall test results on the annual and seasonal temperature data from the Beatrice and Parry Sound climate stations. The bolded values indicate a significant increase in temperature (p < 0.05).

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<td>Autumn</td>
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4.11 Figures

Figure 4.1: Location of the study sites (North Bay, South Bay and Tadenac Bay are indicated by circles) in Georgian Bay, Ontario, Canada.
Figure 4.2: Top panel - Radiometric dating analysis showing $^{210}$Pb (black circles), $^{137}$Cs (white circles) and average $^{214}$Bi (grey vertical line) activities from selected sedimentary intervals (Becquerels per kilogram) plotted against core depth for North, South and Tadenac bays. Bottom panel – Estimated $^{210}$Pb ages (using Constant Rate of Supply model) with associated error (using horizontal error bars) plotted against core depth for North, South and Tadenac bays.
Figure 4.3: Diatom stratigraphic profile scaled by depth (with $^{210}\text{Pb}$ estimated years plotted secondarily) showing relative abundances of the most common diatom taxa from North Bay, Honey Harbour (Georgian Bay). For clarity of display species from the same genera that exhibited similar trends through time were grouped together. Taxa that occurred in trace abundances that did not show any trends were included in all other taxa. Numbers following taxon labels indicate the number of diatom taxa represented by the grouping. Principal components analysis axis 1 (PCA axis 1) samples scores (summarizing changes in diatom assemblage composition), and sedimentary inferred chlorophyll a (Inferred Chl a) are also included. Major CONISS zones are delineated by horizontal broken lines. The x-axis is divided into increments of 10% relative abundance.
Figure 4.4: Diatom stratigraphic profile scaled by depth (with $^{210}$Pb estimated years plotted secondarily) showing relative abundances of the most common diatom taxa from South Bay, Honey Harbour (Georgian Bay). For clarity of display species from the same genera that exhibited similar trends through time were grouped together. Taxa that occurred in trace abundances that did not show any trends were included in all other taxa. Numbers following taxon labels indicate the number of diatom taxa represented by the grouping. Principal components analysis axis 1 (PCA axis 1) samples scores (summarizing changes in diatom assemblage composition), and sedimentary inferred chlorophyll a (Inferred Chl a) are also included. Major CONISS zones are delineated by horizontal broken lines. The x-axis is divided into increments of 10% relative abundance.
Figure 4.5: Diatom stratigraphic profile scaled by depth (with $^{210}$Pb estimated years plotted secondarily) showing relative abundances of the most common diatom taxa from Tadenac Bay (Georgian Bay). For clarity of display species from the same genera that exhibited similar trends through time were grouped together. Taxa that occurred in trace abundances that did not show any trends were included in all other taxa. Numbers following taxon labels indicate the number of diatom taxa represented by the grouping. Principal components analysis axis 1 (PCA axis 1) samples scores (summarizing changes in diatom assemblage composition), and sedimentary inferred chlorophyll a (Inferred Chl a) are also included. Major CONISS zones are delineated by horizontal broken lines. The x-axis is divided into increments of 10% relative abundance.
Figure 4.6: Principal components analysis (PCA) ordination of axis 1 ($\lambda = 0.24$) and axis 2 ($\lambda = 0.22$) sample scores for the three embayments (North Bay, South Bay and Tadenac Bay) that were calculated and plotted within the same ordination space (based on changes in the percent relative abundances of diatom assemblage composition throughout the three cores). The $^{210}$Pb estimated ages of select intervals are included to highlight the major shifts in diatom composition over the past ~ 200 years.
Figure 4.7: Mean annual and seasonal (spring, autumn, winter) air temperatures measured at Beatrice, Ontario and Parry Sound, Ontario climate stations. Data from the Environment Canada Historical Climate Record the Adjusted and Homogenized Canadian Climate Data.
Figure 4.8: Continuous mean observed water level records measured at Parry Sound, Ontario and Collingwood, Ontario between 1962 and 2015. Data were obtained from Fisheries and Oceans Canada.
Chapter 5

General conclusions

Multiple environmental stressors have substantially altered global freshwater systems, including lakes across Ontario. However, the lack of long-term monitoring data poses challenges to understanding the long-term effects of anthropogenic disturbances on aquatic ecosystems. Such information is important for implementing achievable and realistic remediation targets. In this thesis, paleolimnological methods were utilized to assess long-term environmental changes in embayments and lakes in and around Georgian Bay, Lake Huron. The main purpose of this project was to assess the effects of multiple stressors, with a focus on acidification, nutrient enrichment, and climate warming, on freshwater systems over the past ~200 years. In large, complex waterbodies such as Georgian Bay, the response to multiple stressors may be diverse and site-specific; therefore several sites across the region were assessed to provide a more comprehensive overview of ecosystem change. The projects in this thesis were inspired by previous paleolimnological analyses exploring the impacts of multiple stressors in southern and south-central Ontario (e.g., Hawryshyn et al. 2012; Hadley et al. 2013; Labaj et al. 2015).

Chapter 2 explores the relative importance of the aerial deposition of nutrients (specifically nitrogen) and climate warming on the recent increase in the relative abundance of sedimentary Asterionella formosa in George Lake. Similar increases of this taxon are reported across many Boreal Shield lakes in south-central Ontario. In this chapter, the overarching question was:

1) Is nitrogen (N) deposition playing a role in diatom assemblage changes across freshwater systems around Georgian Bay and southern Ontario?
Chapter 2 provides clear evidence that total inorganic nitrogen (TIN) deposition has significantly declined in southern Ontario over the past 3 decades (Sivarajah et al. 2016). *A. formosa* has commonly been reported to occur in more nutrient-enriched lakes and researchers in the US Rocky Mountains have argued that its recent and widespread occurrence has been triggered by increased nitrogen availability, with recent warming exacerbating this trend. Many lakes that report increases in *A. formosa* are affected by multiple environmental stressors including recent warming, and it is plausible that these stressors may work together in some regions to elicit the recent increase in *A. formosa* relative abundances. However, studies that allude N deposition is resulting in an increase in the relative abundance of *A. formosa*, and other planktonic diatoms suggest that N deposition is likely increasing. However, the N deposition data are rarely presented in these studies. In this chapter we provide 20 years of annually measured lake water nutrients and 30 years of regional atmospherically deposited nitrogen to show that *A. formosa* increases have occurred during a period of significant decline in N deposition in southern Ontario. Our results suggest that increased nutrients is not a pre-condition for the success of this taxon and other factors, particularly recent warming, may be influencing the recent shifts in diatom assemblages in this region. In all three chapters diatom assemblages’ show the greatest change during the warmest periods in the climate record (i.e. increase in the relative abundances of *A. formosa*, and other planktonic diatoms coincide with the warmest periods in the meteorological records). Results from this thesis and a growing number of other studies from southern Ontario show that the rising regional temperatures during the 20th and 21st centuries have contributed to changes in lake thermal properties, which may have triggered shifts in diatom assemblages.
Chapters 3 and 4 examine the responses of lakes and embayments in the Georgian Bay area to recent and historical anthropogenic stressors. Chapter 3 details the recovery trajectories of diatoms in previously acidified lakes in the context of a warming world. Meanwhile Chapter 4 contrasts the effects of shoreline development and climate change on Georgian Bay embayments, - two with shoreline development, and one without. Overall, Chapters 3 and 4 address the second and third overarching research themes of this thesis, which can be summarized as:

2) Does the diatom response to warming and other stressors result in similar assemblage shifts across all embayments and lakes in and around the Georgian Bay?

The diatom assemblage changes in Chapters 3 and 4 show clear responses to multiple environmental stressors. However, there are differences in species-specific shifts and the timing of the shifts, as these are influenced by local limnological factors. First, diatoms (and other algae) often cross ecological thresholds in response to stressors such as acidification, eutrophication and climate change. For example, deposition of sulphur dioxide (SO$_2$) into aquatic systems began around the 1880s in the Sudbury region. However, as shown in Chapter 3 and other paleolimnological analyses from the region, a clear response in diatom assemblages were not observed until the early-1900s, when smelting activities in the region increased resulting in substantial changes in lake water pH (i.e., diatom threshold exceeded). In Chapter 4, we show that the diatom response to warming is diverse and may be influenced by local limnological characteristics such as pre-existing nutrient conditions and lake morphometry. Furthermore, diatoms (including $A. \textit{formosa}$ and other planktonic diatoms) do not respond linearly to changes in lake thermal properties induced by rising temperatures, but rather to critical, temperature-related thresholds that must be crossed before marked shifts in diatom assemblages occur.
3) *Have diatom assemblages “recovered” to pre-disturbance assemblages around the Georgian Bay area?*

We show that diatom assemblages have clearly responded to multiple stressors, including recent climate warming, in all the data chapters of this thesis. However, the recent assemblages observed across the lakes and embayments in and around Georgian Bay are substantially different from pre-disturbance assemblages, suggesting that these freshwater ecosystems are either heading towards, or have already entered, new ecological regimes. With marked increases in temperature across Ontario, it is unlikely that these diatom assemblages will return to their pre-disturbance assemblages.

5.1 *Future opportunities*

The Killarney Provincial Park lakes, specifically George Lake, have an exceptionally good long-term monitoring data set. Hence, the addition of seasonal phytoplankton sampling may allow the future comparison of phytoplankton blooms with nutrient availability. Combining seasonal phytoplankton data and paleo-diatom data will undoubtedly provide a more comprehensive overview of diatom ecology. Understanding the ecology of algae (specifically diatoms) in the context of a warming world is crucial, as phytoplankton blooms can be influenced by changes in lake thermal properties and ice phenology, both governed by climate. There is also a need to better understand the nutrient requirements for various diatoms. Diatoms previously linked to higher nutrient conditions (i.e., *Asterionella formosa* and *Fragilaria crotonensis*) in Ontario are now occurring in lakes where nutrients are declining or have not changed, and are currently extremely low (e.g. ultra-oligotrophic George Lake). Therefore, revisiting the resource requirements of these diatom taxon would be prudent for future paleolimnological studies and interpretations. Furthermore, analyses of paleo-zoological
indicators such as Chironomidae and Cladocera can provide information on past hypolimnetic oxygen concentrations, changes in trophic stressors, as well as other important limnological and ecological variables from the three embayments of Georgian Bay (Chapter 4). As freshwater systems in southern Ontario are entering new ecological regimes in response to climate warming and other stressors, there is need for detailed monitoring programs and multi-proxy paleolimnological studies to track biological responses to multiple stressors.

5.2 References


## Appendix A

### Diatom counts from the Killarney Provincial Park Lakes

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# Appendix B

### Diatom counts from the three embayments of Georgian Bay

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