Assessing the Potential of Midges as Paleoecological Indicators

by

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Abstract

Three exclusive studies (in-vitro, observational and empirical) comprise this doctorate dissertation aimed at assessing the capacity of midges (Order Diptera: Families Chironomidae, Chaoboridae and Ceratopogonidae) as paleoecological indicators.

In-vitro experiments were conducted to determine the impact that temperature and salinity have on midge development and survival. Results indicate that some taxa may achieve optimal development at cooler temperatures; most taxa are cued for emergence by, and require, warmer temperatures; exposure to temperatures that are too warm may result in developmental stress and sometimes death; midge emergence events appear more or less synchronous; and emergences may be controlled by a threshold temperature as opposed to accumulated degree-days.

Also, in-vitro experiments were conducted to assess larval midge salinity thresholds (LD50s). Dasyhelea (Ceratopogonidae), Cricotopus/Orthocladius, and Cladotanytarsus mancus type appeared to have the highest salinity LD50s while Chironomus anthracinus type and subtribe Tanytarsina displayed the lowest.

In the second study, water chemistry and environmental data were compared with midge assemblage data using multivariate analysis to assess the environmental gradients that limit midge distributions in the Hudson Bay Lowlands (northeastern Manitoba). The results demonstrate the midges’ potential as paleosalinity indicators.

The third study involved extracting sediment cores from four separate lakes within the Hudson Bay Lowlands, each extracted from a pond at a different elevation (range from 127 to 10 m above sea level) and distance from the current Hudson Bay shoreline (range from 104 to 2.5 km). My reconstructions suggest that two inland ponds experienced an initial gradual freshening trend from their inception to <1,000 cal. years BP, followed by more recent rapid freshening. Reconstructions for two ponds situated proximal to Hudson Bay indicate stable salinity through the entirety of the sediment records. Quantitative salinity reconstructions for each of the four sampled ponds were ‘statistically insignificant’ (P ≤ 0.05). Predicted isostatic rebound rates, inferred by linear extrapolation of age depth models constructed for four Hudson Bay Lowland ponds, do not indicate an exponentially declining salinity trend as expected.
Preface

The literature, tables and diagrams presented in this document are of my own making. Dr. Ian Walker contributed, Wizardlike, to theoretical discussions, study design, sampling procedures, and manuscript editing. Marlow Pellatt and Darren Bos contributed data for this project. Nicole Pyett assisted on field excursions. Students Kimberly Loudon, Amber Brown, Matt Meehan, Kelsey Mills, Jordan Wu, Omar Mwangari and Brooke McConnell assisted in the laboratory by picking midge remains.

As is common with scientific work, assumptions based on the results of other researchers are plentiful in my dissertation. Sincerely, it is necessary to acknowledge some contributors to paleoecology and appreciate their input. For example, much of my research is based on ecological philosophies of Doctors Ian Walker and John Birks. Also, as important, I’ve invested in the statistical understanding of data structure, developed by many other great minds. Without the statistical procedures and related computer programs designed by such luminaries as ter Braak (1987), Juggins (2003), Grimm (2011), and Telford and Birks (2011) my work would have been scarcely possible. Thus, to deliver the preface of all prefaces, my results and interpretations can only be as valid as those before me, upon which my work is based.

I’m hopeful that three publications will arise from the work presented here ( Chapters 3, 4 and 5). Content provided in Chapter 4 has been accepted for publication in the Journal of Paleolimnology. Content provided in Chapter 3 has also been submitted to the Journal of Paleolimnology.
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List of Abbreviations

C2 – program used for model execution
Cal. years BP – calibrated years before present (1950)
CANOCO – program used for ordination analysis
CCA – Canonical Correspondence Analysis
CONISS – Constrained Incremental Sums of Squares Cluster Analysis
DCA – Detrended Correspondence Analysis
Dist. Co – distance to coastline
LC1 – Long Core 1
LC2 – Long Core 2
LogCond – log transformed specific conductance
LogDO – log transformed dissolved oxygen
LogElev – log transformed elevation
masl – meters above sea-level
mm a⁻¹ – Millimeters per year
PCA – Principal Correspondence Analysis
PLS – partial least squares
RL – Rocket Lake
RMSEP – root mean square error of prediction
Temp. – temperature
TL – Twin Lakes
µS cm⁻¹ – Micro-Siemens per centimeter (specific conductance)
WA – weighted averaging
WAPLS – weighted averaging partial least squares
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Dedication

To Papa

“I buy you books, I buy you books and all you do is rip out the pages and wipe your butt”.

- Papa
Chapter 1: Introduction

Over the past several decades, naturalists have begun to decipher obscure codes to unlock secrets of past environmental change in hopes of understanding and predicting future change. Today, scientists are building upon previous theories and models to enable more accurate interpretations, predictions and inferences of environmental change through geologic time.

Upon realizing that Earth’s species only occur where habitats are suitable, researchers began measuring species distributions and correlating them with environmental parameters. From these results, scientists began describing species-environmental interactions (e.g., Walker et al. 1997; Woodward and Shulmeister 2006).

Consequential to my own research interests, in order to quantitatively interpret a fossil record to infer paleoenvironments, the associations between the living descendants of fossilized organisms and their habitable environments needed to be established. Here I focus on investigating the relationships of midge taxa (Order: Diptera) with temperature and salinity in order to determine the usefulness of midge remains (subfossils) as paleosalinity and paleotemperature indicators.

This is a feasibility study, which focuses on assessing midges (Chironomidae, Ceratopogonidae and Chaoboridae) as paleoindicators with respect to temperature and salinity. The working hypothesis for this project is that: midge taxonomic assemblages are regulated by physical and chemical properties (here, specifically, temperature and salinity) of lake-water. Thus, changes in midge subfossil remains within lake sediment over time reflect changes in these variables. Here, I attempt to identify midge emergence responses to temperature, and lethal thresholds for salinity. I also attempt to correlate midge taxa within the Hudson Bay Lowlands with their apparently preferred salinity habitats. Finally, based on these findings, I reconstruct salinity changes in the Hudson Bay Lowlands to infer a sea level history for the area.

This is the first study, to my knowledge to test midge subfossils as indicators of sea-level change.
Chapter 2: Literature Review

2.1 Midge biology and life cycle

Midges (here, comprising the dipteran families Chironomidae, Chaoboridae and Ceratopogonidae) are holometabolous aquatic insects whose life cycles include four stages: egg, four larval instars, pupa, and adult (imago). Among nearly 125 chironomid taxa studied, 33%, 44% and 18% proved to be univoltine, bivoltine, and multivoltine, respectively (Tokeshi 1986). Generally, in temperate regions, a life cycle can be completed in one year, whereas in high latitude regions it may take up to several years for a chironomid to fully develop (Tokeshi 1986). Other than food quality and quantity, photoperiod and temperature are two major factors thought to drive midge (and most other insects’) development. Granted this information, it is of no surprise that tropical, low latitude environments tend to yield more generations of midges in a single year than cold arctic regions (e.g., Welch 1976; Aagaard 1982; Butler 1982). Other studies have shown that voltinism is negatively correlated with latitude (Armitage et al. 1995).

Although Chironomidae (“non-biting midges”) are most abundantly represented in my research projects, Ceratopogonidae (“biting-midges”) and Chaoboridae (“phantom midges”) also occur. In many respects, these three aquatic dipteran families share similar biology. Ceratopogonidae differ most notably in the biting habit of the imago. Although chironomid and ceratopogonid larvae are benthic, chaoborids are typically planktonic, at least at night. Paleoecologists note that the chitinous head capsules of Chironomidae and Ceratopogonidae taxa are preserved abundantly in lake sediments whereas mandibles normally are the only structures of Chaoboridae preserved.

2.2 Midges and their use in paleoecology

For the purposes of my research, I am interested in the merits of midges as paleoindicators. The characteristics that make midges suitable for paleoenvironmental studies include their abundance in lakes and ponds (upward to 50,000 m⁻² of sediment), their diversity taxonomically, the stenotopic nature of individual taxa, and the strong sclerotisation of Chironomidae and Ceratopogonidae head capsules and Chaoboridae mandibles, permitting them to preserve in sediment for thousands of years (Hofmann 1988). Furthermore, midges have relatively short life cycles and are very mobile in the adult (fly) stage, enabling their
rapid dispersal to and from other lakes as climate and other aspects of the environment change.

Thanks to early work by scientists such as Ekman (1915), Naumann (1919), Thienemann (1921), Gams (1927), Andersen (1938), Brehm et al. (1948), Brundin (1956), Sæther (1979), and Walker et al. (1991a), midge remains have been commonly used to infer past environmental change. They were first used to describe broad late-glacial climate changes and patterns in lake ontogeny (Thienemann 1921; Andersen 1938), but researchers have now developed intricate models and transfer functions allowing subtle climatic changes, such as those occurring during the Holocene, to be deciphered (e.g., Armitage et al. 1995; Porinchu and MacDonald 2003; Walker and Cwynar 2006).

Researchers, using carefully selected research sites that maximize the gradient of a variable at interest, have also developed modern day calibration data sets which can, in-turn, through a down-core analysis, be used to reconstruct the chronological story of how lake ontogeny/eutrophication (Warwick 1980), surface water temperature (Walker and Cwynar 2006), dissolved organic carbon, nutrient concentrations, pH, lake depth, and/or lake salinity (Heinrichs et al. 1997), amongst other variables, have fluctuated through time (Porinchu and MacDonald 2003; Walker 2006).

2.3 Midges and paleotemperature

Midges have frequently been used as paleotemperature indicators. Lake water and/or ambient air temperature may have direct and indirect influences on midge development and thus fossil assemblages preserved in lake sediment.

Directly, water temperature may affect the rate of egg and larval development through bioenergetic relationships via respiration rates and altered larval feeding patterns (Oliver 1971; Danks and Oliver 1972; MacKey 1977; Anderson and Cummins 1979; Danks 1981; Lee and Baust 1982). Furthermore temperature may drive, in part, pupation and emergence of adults (Danks and Oliver 1972), timing of eclosion (Kureck 1979; Brodersen and Lindegaard 2000), and relative abundance. For instance, although not previously experimentally tested, multivoltine taxa may be limited to only one emergence sequence annually if sufficiently high temperatures are not reached through the course of a year, which
in turn will affect the relative abundance of these taxa in the sediment record (Armitage et al. 1995).

Walker and Mathewes (1989) described the relationship of midge assemblages to altitude such as that observed in surface sediments from thirty lakes in the southern Canadian Cordillera. Climate was the suggested driver for taxa assemblage variations. Several taxa (e.g., *Stempellinella* Brundin, *Parakiefferiella* cf. *bathophila* (Kieffer), and *Zalutschia* Lipina) common at low elevation lakes were rare or absent at higher elevations. They also recognized the correlation between these altitudinal distributions and the midge’s latitudinal distributions from temperate to arctic regions.

Walker and Mathewes (1989) classified midges into three categories based on their altitudinal ranges (low to mid-elevation taxa; high elevation taxa; and widely distributed taxa). Low to mid-elevation taxa included *Cladopelma* Kieffer, *Dicrotendipes* Kieffer, *Stempellinella* Brundin, *Parakiefferiella* cf. *bathophila* (Kieffer), *Zalutschia* Lipina, and members of the tribe Pentaneurini. Along with these taxa were some species common in lower elevation lakes and present, but much less common, in high elevation lakes. These taxa included *Monopsectrocladius* Laville and *Psectrocladius*.

High elevation taxa, such as *Heterotrissocladius* Spärck, *Paracladius*, *Protanypus* Kieffer, and *Parakiefferiella* sp. A, were not exclusively limited to lakes in the alpine, but were also present in the benthos of low elevation arctic lakes or the profundal of deep, stratified lakes in temperate zones.

Taxa included in the ‘widely distributed’ category included *Tanytarsus s.lat*, *Procladius* Skuse, and *Sergentia* Kieffer.

The taxa found in each lake appeared to be regulated by water temperature. Nevertheless, the relationships between midge assemblages and air/water temperature are still debated as midges may be indirectly affected by climate (e.g., via food availability through lake development).

A few publications (Warner and Hann 1987; Warwick 1989; Hann et al. 1992) recognize that climate must have an influence on midge assemblages in lakes, but ask if this connection is direct or indirect. Warner and Hann (1987) and Warwick (1989) suggested that turbidity, substrate composition, water-depth, sedimentation rates, and lake productivity have more bearing on midge assemblages than temperature alone. Warwick (1989) suggested that the
abundance of *Heterotrissocladius* was driven by mineral sediment accumulation and the availability of organic food resources rather than temperature changes, as Walker and Mathewes (1987, 1989) had suggested.

Walker et al. (1991a) employed canonical correspondence analysis (CCA), to reveal that summer surface-water temperature and maximum lake depth had the most statistically significant correlation with midge taxon distributions. Past summer surface-water temperatures for a lake in New Brunswick were then inferred (Walker et al. 1991b) based on a transfer function. The transfer function was derived by sampling many lakes distributed across a north-south climatic transect spanning much of Atlantic Canada. This was the first research to demonstrate that midge taxon distributions could be used to quantitatively predict lake temperatures and eventually be used to reconstruct past (late glacial/Holocene) temperature fluctuations.

Midge paleoenvironmental research from 1990 - 2000s has improved our understanding of the magnitude and timing of temperature change from many parts of the world (Walker et al. 1991a, 1991b; Cwynar and Levesque 1995; Brooks 1997; Levesque et al. 1997; Brooks and Birks 2001). These improvements have led to refined temperature inference models capable of detecting relatively subtle temperature fluctuations, such as those of the Holocene (including ones of anthropogenic origin). For instance, in eastern North America, Levesque et al. (1993) described temperature depressions of about 2-3°C via fossil midge assemblages in sediment cores.

### 2.4 Midges and paleosalinity (specific conductance)

Midges have also been used as paleosalinity indicators. Salinity is a measure of the total mass of different salts such as calcium sulphate, magnesium, bicarbonate, and sodium chloride that are dissolved in water (or soil) (McManus et al. 1992).

Because ions (salts) and other inorganic chemicals conduct an electrical current when dissolved in water, conductivity also increases as salinity increases. Conductivity thus measures the water’s ability to conduct electricity (or, its resistance to conduct), which in turn provides a measure of salinity.

Conductivity is also affected by temperature. To remove the temperature influence, conductivity measurements are commonly corrected to represent the conductivity at 25°C.
These corrected values are referred to as specific conductance. Since I have used specific conductance as a measure of salinity in my research, this document, hereafter, will refer to ‘salinity’ and ‘specific conductance’ interchangeably, however, all measurements will be presented as µS cm⁻¹ or as back-transformed µS cm⁻¹.

As with other aquatic organisms, midges have evolved specific physiological traits enabling them to endure moderate salinities. Some taxa, perhaps owing to osmotic regulation problems, appear to be bound to more extreme saline environments.

Paterson and Walker (1974) noted that midge faunas varied with lake salinity and were correlated with variations in the lake’s evaporation-precipitation balance. Since then, midge-based paleosalinity assessments have successfully been completed in western Canada (Walker et al. 1995; Heinrichs et al. 1997), east Africa (Verschuren et al. 2000), and the Tibetan Plateau (Chen et al. 2009).

Many midge species are restricted to fresh water, however some species (e.g., Cricotopus ornatus and Tanypus nubifer) thrive in more saline environments (Walker 2006). A study of benthic communities in western Victoria, Australia indicated that taxa such as Procladius and Chironomus duplex typified low salinity lakes and Tanytarsus barbitarsus dominated lakes of higher salinity (Timms 1986).

Walker et al. (1995) showed through their survey of eighty-six British Columbia lakes, that Cricotopus/Orthocladius were indicative of salinities exceeding about 10.0 g L⁻¹; less saline waters had abundant Chironomus, Procladius, Psectrocladius, and subtribe Tanytarsina; and freshwater habitats were dominated by Heterotrissocladius, Lauterborniella/Zavreliella, Pagastiella, and Sergentia.

Walker et al. (1995) also employed canonical correspondence analysis to reveal salinity as a principal environmental variable explaining midge distributions among interior British Columbia lakes. A weighted-averaging calibration function was then developed to infer salinity from subfossil midges.

Zhang et al. (2007) constructed analogous models to quantitatively reconstruct paleosalinity from the Tibetan Plateau. The findings of Zhang et al. (2007) were consistent with other paleoclimate studies for the region, including climatic inferences from diatom-based salinity reconstructions (e.g., Yang et al. 2003; Yang et al. 2004).
2.5 Isostatic rebound, salinity and sea-level change

Isostatic rebound is one of the important potential drivers of salinity change in the Hudson Bay Lowlands. My research focuses in part on the potential of using the salinity changes, inferred from fossil midges, as a way to reconstruct sea level changes driven by isostatic rebound.

Glacial isostatic rebound, the rise of landmasses formally depressed by the weight of great ice sheets, has been documented in Europe (Johanson et al. 2002), Siberia, Canada (Rayburn and James 2006), and the United States (Sella et al. 2007). As ice sheets grow they apply pressure to the malleable crust of Earth’s surface, displacing subsurface molten material, causing a depression. Isostatic rebound occurs as the ice sheets decay, removing pressure from the Earth’s surface and allowing the subsurface molten material to be re-injected to areas formerly lying beneath the ice sheet (Figure 2.1) (Sella et al. 2007).

![Figure 2.1](Image)

**Figure 2.1:** Artist’s depiction of isostatic adjustment a) glacial ice-weight displacing mantle and depressing overlying landmass, b) ice-weight lifted causing mantle and landmass to rebound, c) mantle and crust assume original position. (Image reproduced from Pidwirny (n.d.), with permission from Dr. Michael Pidwirny).

Isostatic rebound is known to occur at an exponentially declining rate, ultimately determined by the viscosity of the mantle and elasticity of the lithosphere (Sella et al. 2007). It may take several thousands of years to achieve only half-recovery time, as rebound will slow rapidly following deglaciation.
2.6 Hudson Bay Lowlands (study area)

Isostatic rebound is one of the principal agents of environmental change in my study area, the Hudson Bay Lowlands. During the Wisconsian glaciation, my study area was continually glaciated by Laurentide Ice originating from two centers of outflow, one lying to the north in the Districts of Keewatin-MacKenzie, the other lying to the east in central Quebec or Hudson Bay (Andrews and Short 1983).

Keewatin ice flowed southward and Hudson ice migrated westwards, each transporting distinctive tills (Fulton 1989). The Keewatin tills are very sandy, have low clay contents, are composed of granitic lithologies, and are derived from Shield terrain. Less permeable, silty calcareous till deriving from Paleozoic limestone is the main till type in areas crossed by Hudson-Labradorean ice (Dredge and Nixon 1992).

By 10,000 years ago there had been extensive retreat of Hudson ice, accompanied by an expansion of proglacial lakes (glacial lakes Ojibway and Agassiz, and the Tyrrell Sea – which eventually evolved into present-day Hudson Bay). Lake Agassiz covered the area vacated by the receding ice sheets, as the ice decayed in a north and east direction.

Lake Agassiz originally formed in North Dakota as ice sheet recession began about 11,700 calibrated years before present (cal. years BP) (Clayton and Moran 1982). During deglaciation, natural drainage towards the east was blocked by Hudson ice. A deep proglacial lake therefore developed and expanded as the ice sheet retreated, and persisted as long as Hudson ice remained grounded in Hudson Bay (Dredge 1983).

The distribution of surface and buried postglacial lacustrine deposits indicates that Lake Agassiz extended northward somewhat beyond North Knife River, as far east as Lofthouse Lake, and, farther south, possibly as far east as the mouth of Nelson River (Figure 2.2). Lake Agassiz eventually drained between 8180 to 8310 cal. years BP (Li et al. 2012; Dredge and Nixon 1992).

The precise time when marine waters entered Hudson Basin and isolated Keewatin Ice from Hudson Ice remains unknown. However, the oldest date obtained from Tyrrell Sea shells is from northern Manitoba (near Churchill), which suggests that the sea had reached this area by 8530±220 cal. years BP (Blake 1970). However, these shells are thought to yield erroneous dates because they date some centuries older than other Tyrrell Sea shells from the region, the shell fragments were well worn, and old shells recycled from Bell Sea sediments.
are fairly abundant in the Hudson Bay Lowlands (Fulton 1989). Other studies suggest that the sea probably occupied the area by 7800-8200 cal. years BP (Dredge and Cowan 1989).

The Tyrrell Sea, the ancient body of water in the Hudson Bay Lowlands, reached levels higher than present owing to glacioisostatic deformation. It began as a high sea and regressed to the present shoreline of Hudson Bay. The Tyrrell Sea flooded the central and southern parts of the study area immediately following break-up of Hudson ice, while Keewatin ice remnants still lay in the northern region (Dredge and Nixon 1992).

Below an elevation of 150 m, the glaciolacustrine sediments of Lake Agassiz are overlain by marine sediments deposited by the Tyrrell Sea. Above that elevation, Lake Agassiz sediments form the principal surficial material over a vast area (Figure 2.2). Since the elevation of this area is gradually inclined along a northeast-southwest axis, a conceptual picture emerges with glaciolacustrine sediments (deposited in glacial Lake Agassiz) exposed on the southwestern portion of the study area and marine sediments (deposited by Tyrrell Sea) overlying the northeastern portion of the area, extending to Hudson Bay. The transition from lacustrine to marine sediments is evident at about 150 m elevation (Dredge and Nixon 1992).

Isostatic adjustment studies for the Churchill region of Hudson Bay have been conducted via shell dates, and indicate the lack of an initial rapid emergence. This is atypical of most deglaciated regions. The shell date studies also indicate lower marine limits for the Churchill area than for other parts of the central Laurentide Ice Sheet. These two aspects suggest that substantial rebound may have occurred beneath Lake Agassiz prior to the marine incursion and may also reveal multiple ice loading centers (Fulton 1989).

Emergence curves (representing isostatic rebound) for Hudson Bay indicate varied times and degrees of rebound near Churchill. These studies also indicate that substantial rebound is still occurring along the south shore of Hudson Bay and that parts of the bay will one day become dry land. Present day rates of emergence as determined by tide gauge and historical records from Churchill indicate an 11.4 ± 0.7 mm a⁻¹ rebound rate (Wolf et al. 2006). In order for isostatic equilibrium to be achieved, Hudson Bay still needs to rebound as much as 150 meters (Barnett 1970).
Given acknowledged discrepancies in the paleo sea level data, it is clear that additional tools for determining the rate and degree of isostatic adjustment and timing of marine inundation for this region need to be identified. This may also lead to further postulations regarding areas of ice loading. Given the glacial history, hydrologic and geographic characteristics of the study area, northeast Manitoba may prove ideal for midge-based salinity reconstructions in relation to sea level history.

2.7 Methodology for paleo-reconstructions

The use of midges as paleoindicators has progressed from subjective interpretations to quantitative reconstructions of environmental variables, using powerful statistical analyses. Initial work by Ekman (1915), Thienemann (1921), Gams (1927), and Andersen (1938), attempting to explain lake types and the conditions accompanying dominant midge communities, paved the way for the climatic interpretation of midge remains.
Although descriptive, subjective classifications greatly enhanced scientists’ understanding of midge ecology, environmental monitoring agencies are more interested in the value of midges as environmental indicators, and a more quantitative, more objective approach is often required.

2.7.1 Environmental indices

The need for less subjective means of assessment has, in part, been fulfilled through the introduction of a variety of environmental indices. Wiederholm (1980), for example, introduced the Benthic Quality Index (BQI), an index of a lake’s overall trophic state as calculated from the dominant elements in a lake’s benthic fauna:

\[ BQI = \sum_{i=0}^{5} \frac{k_i n_i}{N}, \]

Eq. 1

where \( k_i \) represents the indicator score given to species \( i \); \( n_i \) represents the number of individuals of that species; and \( N \) represents the total number of individuals of all indicator species (Wiederholm 1980). Note that the indicator scores are integer constants ranging from 0 to 5 (oligotrophy to eutrophy) subjectively assigned to each indicator species, in accordance with their perceived distributions across the trophic gradient. The BQI was created and used as a modern inference model to reconstruct 150 years of lake productivity for a lake in central Sweden (Wiederholm and Eriksson 1979).

With the BQI index, the occurrences of a few principal midge indicator species are used to assess water quality. Simply, this model takes into account the indicator value of particular species in terms of their relative average ecological valence. Although the method is more quantitative and less subjective than earlier approaches, the index suffers from two obvious deficiencies: 1) the indicator scores are subjectively assigned to each species, and 2) the index is based on a handful of indicator species, not the whole fauna.

Although the BQI method is valuable for defining general shifts in lake type and quality, paleolimnologists have worked to decipher, more quantitatively, shifts in environmental variables. The desire to more definitively understand the environmental shifts that have
occurred through time has led to an array of tools and techniques enabling quantitative reconstructions of past environments.

2.7.2 Quantitative reconstructions

The implementation of modern quantitative reconstruction techniques awaited two further developments: 1) realization that the ecological indicator scores (“environmental optima”) of species should be assessed objectively, in advance, by surveying the present distributions of indicator taxa amongst lakes (i.e., through development of a “training-set”), and 2) the adoption of more sophisticated statistical techniques.

These approaches were widely adopted by paleoecologists working with fossil pollen and diatoms in the 1980s and later by midge researchers. Palynologists used the techniques to infer climatic variables (e.g., Parsons et al. 1980), whereas diatomists focused primarily on reconstructions of salinity and pH (e.g., Battarbee et al. 1986; ter Braak 1987). It should be noted here that some debate exists regarding the validity of the statistical methods to be discussed below (e.g., Pither and Aarssen 2005).

Quantitative paleolimnological reconstructions typically involve two steps. First, a modern calibration training/data-set must be developed. This data set is developed by surveying the fauna, chemistry and other environmental variables across a broad array of lakes. This data set is used to calculate the environmental optima of indicator organisms, and to develop a quantitative model for reconstructing past conditions. This step is referred to as the “regression step”.

The second step applies this model to fossil assemblages to quantitatively reconstruct how the environment has changed through time. This is referred to as the “calibration step” (ter Braak and Juggins 1993).

Although a variety of statistical approaches were first adopted for reconstruction modeling and later dropped (e.g., linear or multiple linear regression on environmental indices, or on ecological groups, or on individual taxa), the weighted averaging approach has been most widely adopted (e.g., Dickson and Walker, in press). Below, this method is illustrated in the development of a midge-temperature reconstruction model, although the same method can be used for reconstructions involving a different proxy (e.g., diatoms or pollen) and different environmental variables (e.g., lake depth, pH, or salinity).
2.7.3 Weighted Averaging – the regression step

The first step, development of a modern training data set, provides basic data from which quantitative estimates of the modern temperature optimum of each taxon can be made (Brooks and Birks 2001). This is done by sampling a series of lakes for their surface midge assemblages while also measuring environmental variables of interest (here, primarily, surface-water temperature). The temperature optimum (O) for each species is then calculated as:

$$O = \frac{\sum_{i=1}^{n} (T_i \times \% A_i)}{\sum_{i=1}^{n} \% A_i}$$

Eq. 2

where $T_i$ is the temperature at lake i and $\% A_i$ is the percent abundance of this midge taxon in lake i.

It is assumed that the temperature optimum for a taxon coincides with the temperature at which that taxon is most abundant (Birks 1995). Furthermore, when using these data for paleoreconstructions, it is also assumed that the temperature optima for these taxa have not changed over time.

These optima are the basis for constructing a transfer function to infer environmental conditions from midge assemblages. Temperature estimates for each lake within the training-set may be calculated from these optimum temperatures and the percent abundance of each taxon within a lake:

$$T_{\text{initial estimate}} = \frac{\sum_{j=1}^{m} (O_j \times \% A_j)}{\sum_{j=1}^{m} \% A_j}$$

Eq. 3
where $O_j$ is the temperature optimum of taxon $j$, and $\%A_j$ is the percent abundance of this taxon.

These initial temperature estimates are then evaluated against the actual measured temperatures ($T_{actual}$) for each lake as determined by linear regression of the measured versus inferred temperatures. This process is necessary as a means to correct for error within the model and will result in an improved temperature estimate for each lake.

The regression yields the equation:

$$T_{initial\_estimate} = mT_{actual} + b,$$

Eq. 4

which may be rearranged algebraically as:

$$T_{actual} = \frac{T_{initial\_estimate} - b}{m},$$

Eq. 5

Using the slope ($m$) and intercept ($b$) obtained via the regression, this equation can then be used to secure improved temperature estimates, by applying it to the temperature estimates initially calculated using Eq 3. This equation:

$$T_{improved\_estimate} = \frac{T_{initial\_estimate} - b}{m},$$

Eq. 6

is referred to as the deshrinking equation.

These calculations (applying Eq.2 through Eq.6) together constitute the “regression step”, and are entirely based on modern assemblages (i.e., the assemblages in the modern training-
These calculations provide the model (i.e., transfer function) used for paleoenvironmental reconstruction.

2.7.4 Weighted Averaging – the calibration step

In the next step, the “calibration step”, this new model is applied to fossil samples and a paleoenvironmental reconstruction is produced. Eq. 3 is used to provide the initial estimates. These initial estimates are corrected for shrinking (overestimation of low temperatures, and underestimation of high temperatures) via Eq.6, the deshrinking equation. Thus, merging Eq. 3 with Eq. 6, the reconstructed temperatures may be calculated as:

\[
T_{reconstructed} = \left( \frac{1}{m} \right) \left[ \frac{\sum_{j=1}^{m} (O_j \times %A_j)}{\sum_{j=1}^{m} %A_j} \right] - b.
\]

Eq. 7

Note that the temperature optima used in Eq.7, are those calculated by applying Eq.2 to the modern “surface sample” training-set. The percent abundances are those obtained from sampling fossils.

The quality of the transfer function can then be determined through error estimation techniques such as jackknifing, bootstrapping, and cross-validation (Birks 1995). A robust quality check involves omitting one or more lake(s) from the model and the remaining lakes are used to predict the midge-inferred temperature (or another variable of interest) for the omitted lake(s). This information can then be applied to a down core biological assemblage to reconstruct past environmental conditions (assuming that species optima have not changed over time).

From this point forward, I wish to explain, in detail, my research projects and results.
Chapter 3: In-vitro temperature and salinity experiments

3.1 Background

A major drawback in the field of paleoecology is the lack of species-specific ecological information. If contemporary species’ ecological preferences are known, their fossil remains can confidently be used to infer past environments (assuming that these species-environment correlations have not changed over time). A common trend in the paleo-community is to identify these species-specific ecological correlations through the use of surface sample training-sets (e.g., Walker et al. 1995; Barley et al. 2006; Zhang et al. 2007). Trends that are observed in these training-sets can be used to construct hypotheses regarding species-environment relationships. Unfortunately, these assumed relationships are seldom tested in-vitro.

In this chapter I discuss the direct impacts of temperature and salinity on midge emergence patterns and survival in laboratory settings. My goal was to elucidate how temperatures directly affect larval development and emergence. I also define larval, midge-salinity thresholds (LD50s) with dose response experiments. Results from such experiments will not only help determine the direct impact these variables have on midge emergence and survival, and provide taxon-specific ecological information, but will also evaluate the calibration/training-set methods currently employed by paleoecologists. Ultimately, these experiments will shed light on the linkages between midges and their environments. This information can be supportive for bio-monitoring and paleoreconstructions alike.

3.2 Methods

3.2.1 Temperature: midge-emergence experiments

To investigate the relationship between temperature and midge emergence three separate experiments were conducted. In each instance, sediments containing living larval midges were collected from sites via an Ekman grab and immediately transported to PaleoLab at the University of British Columbia’s Okanagan (UBCO) campus. Sediment samples from each sampling location were then thoroughly mixed to yield as homogeneous a mud-fauna slurry as possible. The resulting slurry from each location was then divided into nine equal aliquots, and each aliquot was transferred into one of nine individual aquaria. Each experimental aquarium consisted of a 19-litre plastic Sterilite® (Townsend, MA) bin.
These nine sediment-laden aquaria were then divided equally amongst three separate containment rooms held at a different constant temperature (one each at 4, 14, and 24ºC) (Figure 3.1).

The chosen temperatures for these experiments were meant to reflect nature, as these temperatures are frequently observed in temperate-zone lakes. For example, in deep, stratified lakes the bottom waters are nearly constantly 4ºC. In the Okanagan Valley, at the height of summer, surface waters are often as high as 24ºC. The 14ºC temperature was chosen as an intermediate.

As mentioned previously, all experimental aquaria were aerated to achieve 100% oxygen saturation. The aeration provided to each aquarium also induced water circulation in the aquaria, but this was insufficient to cause any perceptible disruption to the sediment-water interface.

Figure 3.1: Photograph of the experimental chambers used for in-vitro temperature experiments to test midge-emergence patterns. The 4ºC containment (left) and 24ºC containment (right) are shown here. The 14ºC containment was not photographed. Photos show three sediment-laden aquaria from each of the sampled lakes (or lake zones) being held at equal temperatures, the lighting and oxygenation systems. These containments were used for all three temperature experiments.

For each experiment, three different sites were sampled; thus, altogether, each experiment consisted of a total of 27 experimental aquaria (3 lakes or zones × 3 temperatures × 3 replicates). Care was taken to ensure that temperature was the sole variable differing amongst the containment rooms and aquaria. Each of the three containment rooms was outfitted with a full spectrum ‘daylight’ lighting system on a 12-hour light cycle.
Furthermore, each aquarium was aerated to 100% oxygen saturation. No food or other energy inputs, other than light, were added to the aquaria. Oxygen, conductivity, and temperature measurements from each aquarium were recorded weekly to facilitate adjustments as necessary. As midges emerged, they were aspirated daily from their respective aquaria and identified with reference to Pinder (1978) and Alexander et al. (1981), and subsequently verified by experts.

Emergence counts for each taxon were noted and compared across temperature treatments, and sampling sites. First, a two-way analysis of variance (ANOVA), Omnibus test, was employed to determine if ‘sample site’ and/or ‘temperature treatment’ are significant (p ≤ 0.05) variables and whether interactions were present in the data. Subsequently, post-hoc TukeyHST tests were utilized to determine if each taxons’ emergence counts were statistically different (p ≤ 0.05) across the three temperature treatments (4, 14, and 24°C).

3.2.1.1 Experiment 1 (Temp 1)

The first temperature experiment (Temp 1) was conducted using littoral zone sediments collected from three lakes (Echo, Wood, and Ellison Lakes) located in the Okanagan Valley of British Columbia, Canada (Table 3.1), sampled on the 14th, 16th, and 17th of September 2009, respectively. Littoral zone sediments consisted of those residing between the shoreline and the maximum depth of macrophyte growth. Homogeneous mud-fauna slurries were made and divided amongst the temperature treatments. After a period of 70 days, temperatures in the 4°C (280 degree-days above 0°C) and 14°C (980 degree-days above 0°C) containments were raised to 24°C to observe any effect. By this time the 24°C aquaria had attained 1680 accumulated degree-days above 0°C. Degree-days were calculated using the experimental start date as ‘day 0’ for all experiments. Taxon-specific emergence rates were then observed and compared among treatments, and before and after the temperature increases.
Table 3.1: Physical data for lakes comprising the temperature experiments

<table>
<thead>
<tr>
<th>Lake</th>
<th>Mean Depth (m)</th>
<th>Max Depth (m)</th>
<th>Surface Area (ha)</th>
<th>Elevation (m)</th>
<th>Volume (km³)</th>
<th>Latitude</th>
<th>Longitude</th>
</tr>
</thead>
<tbody>
<tr>
<td>Echo Lake</td>
<td>16.0</td>
<td>50.0</td>
<td>57</td>
<td>840</td>
<td>0.009</td>
<td>50°12′N</td>
<td>118°42′W</td>
</tr>
<tr>
<td>Wood Lake</td>
<td>21.5</td>
<td>34.0</td>
<td>916</td>
<td>391</td>
<td>0.196</td>
<td>50°06′N</td>
<td>119°02′W</td>
</tr>
<tr>
<td>Ellison Lake</td>
<td>2.5</td>
<td>4.3</td>
<td>209</td>
<td>426</td>
<td>0.005</td>
<td>49°59′N</td>
<td>119°02′W</td>
</tr>
<tr>
<td>Okanagan Lk</td>
<td>75.0</td>
<td>242.0</td>
<td>35,008</td>
<td>349</td>
<td>26.256</td>
<td>49°05′N</td>
<td>119°03′W</td>
</tr>
<tr>
<td>Kalamalka Lk</td>
<td>59.0</td>
<td>142.0</td>
<td>2,574</td>
<td>395</td>
<td>1.519</td>
<td>50°09′N</td>
<td>119°03′W</td>
</tr>
<tr>
<td>Mabel Lake</td>
<td>119.9</td>
<td>200.6</td>
<td>5,942</td>
<td>395</td>
<td>7.124</td>
<td>50°35′N</td>
<td>118°41′W</td>
</tr>
</tbody>
</table>
3.2.1.2 Experiment 2 (Temp 2)

The second temperature experiment (Temp 2) involved profundal sediments and midge fauna collected from Kalamalka, Okanagan, and Mabel Lakes (Table 3.1). These lakes are all large, deep oligotrophic lakes that resemble each other with respect to productivity and size. Profundal sediments are those existing below the thermocline of each lake. Profundal zone sediments for each of these lakes were sampled at an average depth of 50 meters on the 17th, 18th and 19th of February 2010, respectively. Homogeneous mud-fauna slurries were prepared and separated amongst the temperature treatments. After approximately four months (130 days) temperatures in the 4 and 14°C containments were raised to 24°C in order to observe any effect. Taxon-specific emergence rates were then observed and compared among treatments, and before and after the temperature increases.

3.2.1.3 Experiment 3 (Temp 3)

The third temperature experiment (Temp 3) consisted of littoral, sub-littoral, and profundal zone sediments from a meso-eutrophic lake, Wood Lake, collected on March 24, 2011 (Table 3.1). Sediment from each zone was subsequently homogenized and divided amongst the temperature treatments. After 70 days, temperatures in the 4°C containment were raised to 14°C, and temperatures in the 14°C containment were raised to 24°C to observe any effect. Taxon-specific emergence rates were then observed and compared among treatments, and before and after the temperature increases.

3.2.2 Midge-salinity experiments

In August 2011 nineteen shallow ponds (< 1.5 m) located near Churchill, Manitoba were sampled via Ekman grab for their midge faunas. Sediment from each pond was placed in a bucket and transported to the Churchill Northern Studies Centre for processing. Within one day of collection, sediments were washed on a series of stacked sieves (6.5 mm, 1.0 mm, and 0.8 mm mesh sizes), which were then picked for living midges using a probe and soft forceps under a dissecting microscope at 100× magnification. Midges were then segregated
into a series of Petri dishes containing artificial sea-water (Instant Ocean, Aquarium Systems, Mentor, Ohio) with differing salinity levels (measured as specific conductance).

Ten midges from each sampled pond were placed in each dish, exposing them to specific conductance levels of <1000, 2500, 5500, 10000, 15000, 20000, 25000, 30000, 35000, 40000 and 45000 µS cm⁻¹, and one control dish with a specific conductance equal to the sampled pond. This conductivity range was chosen because it encompasses the variability found among ponds of the Churchill region and also brackets ranges marked by midge assemblage changes evident in a salinity calibration/training-set constructed for the region (Dickson and Walker, in press; see chapter 4 of this dissertation).

Petri dishes were aerated daily to maintain high levels of dissolved oxygen. Petri dishes were splayed on a bench-top and exposed to natural daylight and constant indoor temperatures (≈22°C). Each Petri dish was examined each day and any dead midges were removed from the experiment and placed in a labeled 20 ml vial with ethanol as a preservative. Vials containing ethanol-preserved dead midges were transported to PaleoLab at UBCO for identification. Identifications were conducted with reference to Oliver and Roussel (1983) and Wiederholm (1983). These salinity dose-response experiments were completed within a one month time span (August 2011).

### 3.2.3 Statistics

Salinity survival thresholds (LD50s) for the midge taxa were evaluated with dose-response statistical techniques. Midges were picked from the sediments and placed at random in Petri dishes of varying salinities. As a result, varying numbers of each taxon were subjected to different salinities. Therefore, percent survival rates were calculated for each taxon at each concentration. Of note, a large number of organisms were lost due to predation by other midges within the experimental Petri dishes. Where predation occurred, as indicated by missing or disfigured body parts, dead midges were removed from the Petri dish and excluded from statistical analysis. Dose-response curves for each taxon were then calculated based on the number of dead divided by the total for each concentration.

Of the 53 taxa recorded in Dickson and Walker’s (in press) salinity calibration/training-set for the Hudson Bay Lowlands, 13 taxa were represented in this in-vitro experiment. Here, salinity thresholds (LD50s) observed from this experiment were
compared with the upper salinity tolerances estimated from Dickson and Walker’s (in press) survey data.

3.3 Results

3.3.1 Temperature overview

3.3.1.1 Temp 1 – littoral experiment

Temp 1 comprised littoral zone sediments collected September 2009 from Ellison, Wood, and Echo Lakes (Table 3.1). A total 1,337 individuals comprising 23 midge taxa emerged in this experiment. After 70 days, no adult midges had emerged at 4°C from any of the lakes’ sediments, 59 adults emerged within aquaria at 14°C, and 738 adults emerged at 24°C (Figure 3.2). On December 7, 2009 (after 70 days from the experiment start date) temperatures in the 4 and 14°C containments were raised to 24°C to observe any effect. Thirty days following the temperature increase a total of 201 adults had emerged from aquaria formerly at 4°C and 328 adults had emerged from aquaria formerly at 14°C.
Figure 3.2: Scatter graphs of overall midge emergences from littoral zone sediments collected from Ellison, Wood, and Echo Lakes and incubated at 4, 14, and 24°C, comprising Temp 1. The Y-axes delineate the number of adults emerged and the X-axes represent time (measured in days). The vertical line at day 70 indicates when temperatures in the 4 and 14°C containments were raised to 24°C, thus all emergences after day 70 occurred at 24°C.

3.3.1.2 Temp 2 – Profundal Experiment

The second experiment was designed to evaluate the impact temperature has on profundal midges. Profundal sediments were collected from Kalamalka, Mabel and Okanagan Lakes in February 2010 (Table 3.1). Overall, more adult midges emerged at 14°C (n = 119) than at 4°C (n = 90) and 24°C (n = 15) (Figure 3.3). Midges began to emerge from all three lakes’ sediments at 4°C approximately 40 days after the start date and emergence rates from Kalamalka and Okanagan Lakes’ sediments steadily increased until temperatures were raised to 24°C on day 130. No emergences were observed from these lakes’ sediments after temperatures were raised from 4°C to 24°C. Emergences from sediments at 14°C from Kalamalka Lake occurred at the onset of the experiment and remained steady for
approximately 100 days. Emergences from Okanagan Lake’s sediments at 14°C began on day 20 and peaked on day 60 with 7 individuals. Emergence rates from these sediments rapidly declined thereafter. Emergence rates from all sediments at 24°C and from all Mabel Lake sediments were low with less than 10 individuals emerging, from each, in total, with the exception of Mabel Lake sediments at 14°C (n = 14). All taxa observed in this experiment emerged in greater abundances at 14°C as compared to the other temperatures, with the exception of Parakiefferiella nigra Brundin, which emerged at greater abundances at 4°C.

**Figure 3.3:** Scatter graphs of overall midge emergences from profundal zone sediments collected from Kalamalka, Mabel, and Okanagan Lakes and incubated at 4, 14, and 24°C, comprising Temp 2. The Y-axes delineate the number of adults emerged and the X-axes represent time (measured in days). The vertical line at day 130 indicates when temperatures in the 4 and 14°C containments were raised to 24°C, thus, all emergences after day 130 occurred at 24°C. Note, no midges emerged from Mabel Lake’s sediments originally placed at 24°C.
Midge mortality was noted from nearly all profundal sediments when held at 24°C, including those originally placed within the 24°C containment and those transferred from 4 and 14 to 24°C. This includes sediments from all three of the sampled lakes and in total thirteen dead, larval midges were observed in this experiment.

### 3.3.1.3 Temp 3 – Wood Lake Experiment

The third midge-temperature experiment included sampling the littoral, sub-littoral, and profundal zones of Wood Lake in March 2011 (Table 3.1). Each sediment type had replicate samples (3) held at 4, 14, and 24°C for 70 days. Thereafter aquaria at 4°C were transferred to 14°C, and aquaria at 14°C were transferred to 24°C. The aquaria which started at 24°C were kept at this temperature for the full 97 days. Overall midge emergence trends for Temp 3 are presented in Figure 3.4.

Overall, littoral zone sediments produced low emergences at 4°C (n = 3) and a total of three individuals emerged from profundal sediments for all three temperature treatments (profundal graphs were excluded from Figure 3.4 due to very low emergence). Furthermore, four dead midges were observed from profundal sediments within 24°C containments in this experiment. No emergence was observed from sediments after being transferred from 4 to 14°C. Emergence rates from littoral sediments at 14°C increased at the onset of the experiment, peaked with 21 adults/day between 3 - 4 weeks. Thereafter emergence declined but remained consistent with approximately 5 individuals emerging per day until temperatures in these aquaria were raised to 24°C, at which time another peak occurred. Midges collected from the littoral zone and immediately placed at 24°C responded with a rapid emergence. Emergence peaked with over 30 individuals per day within 3 - 4 weeks of the experiment start date and emergence rates rapidly declined thereafter. Similar emergence rates were observed from sub-littoral sediments as those at the same temperatures from littoral sediments. In total 1,489 individuals representing 15 taxa were observed in Temp 3.
**Figure 3.4:** Scatter graphs of overall midge emergences from littoral and sub-littoral zone sediments collected from Wood Lake and incubated at 4, 14, and 24°C, comprising Temp 3. The Y-axes delineate the number of adults emerged and the X-axes represent time (measured in days). The vertical line at day 70 indicates when temperatures in the 4°C containment were raised to 14°C and temperatures in the 14°C containment were raised to 24°C. Note, profundal sediment emergences are not shown in this graph due to overall low numbers.

### 3.3.1.4 *Polypedilum (Tripodura) simulans*

*Polypedilum simulans* Townes emerged from sediments of all three (Ellison, Wood and Echo) lakes in Temp 1 and from the littoral and sub-littoral sediments of Wood Lake in Temp 3. When *P. simulans*’ emergence counts were pooled for each temperature treatment from all three lakes in Temp 1 and from littoral and sub-littoral sediments in Temp 3, two-way ANOVA analyses indicated that both ‘sample site’ and ‘temperature treatment’ are significant (*p* ≤ 0.05) variables and no interaction effect between the two was present. Post-
hoc TukeyHST analyses indicate that *P. simulans’* emergences were statistically different across all three temperature treatments.

*P. simulans* was the most abundant taxon observed in Temp 1 with 646 emergences, of which, all except one individual emerged at 24ºC (Figure 3.5). On day 4 (96 degree-days above 0ºC), *P. simulans* began to emerge from Wood Lake’s sediments at 24ºC. No *P. simulans* emerged at 4 and 14ºC from Wood Lake’s sediments until day 70 when temperatures in the 4 and 14ºC containments were raised to 24ºC. On day 75 (1,100 degree-days above 0ºC), *P. simulans* began to emerge from aquaria formerly at 14ºC and by the end of the experiment (101 days) 35 *P. simulans* had emerged.

On day 22 (528 degree-days above 0ºC), *P. simulans* began to emerge from Echo Lake’s sediments at 24ºC (n = 460). No emergences were observed at 4 and 14ºC from Echo Lake’s sediments by day 70, at which time these temperatures were raised to 24ºC. Emergences began from the formerly 14ºC aquaria on day 79 (1,196 degree-days above 0ºC; n = 89) and steadily increased until the experiment ended. Sixty-four *P. simulans* emerged from Echo Lake’s sediments formerly held at 4ºC, beginning on day 93 (832 degree-days above 0ºC).

*P. simulans’* emergence trends from Temp 3 are represented in Figure 3.7. *P. simulans* began to emerge from sub-littoral sediments at 24ºC on day 3 (72 degree-days above 0ºC; n = 39, overall). Overall, *P. simulans’* emergence rates from sub-littoral sediments at 24ºC dropped from 0.68 individual per day in the first half of this experiment to 0.1 individual per day in the second half. Twenty-nine *P. simulans* emerged from sub-littoral sediments at 14ºC, beginning on day 18 (252 degree-days above 0ºC). An additional thirty *P. simulans* emerged after temperatures were raised to 24ºC on day 70. *P. simulans’* emergence rates increased from 0.41 individual per day at 14ºC to 1.1 individuals per day after being transferred to 24ºC. In Temp 3, *P. simulans’* emergence trends are similar from littoral and sub-littoral sediments at each respective experimental temperature.

### 3.3.1.5 Tanytarsina

Tanytarsina were observed in all three temperature experiments and difficulty distinguishing morphological dissimilarities has led to the amalgamation of many individuals
within the subtribe Tanytarsina. Despite this, the results were similar across lakes. Two-way ANOVA analyses indicate that temperature treatment is the sole significant \((p \leq 0.05)\) variable. Further, post-hoc TukeyHST analyses indicate that Tanytarsina’s emergences were statistically \((p \leq 0.05)\) different between the 4 and 14ºC, 4 and 24ºC, but not 14 and 24ºC temperature treatments.

In Temp 1, 90% of all Tanytarsina emerged at 24ºC and the remaining 10% emerged at 14ºC \((n = 519, \text{ in total})\) (Figure 3.5). From Wood Lake’s sediments, Tanytarsina began to emerge on day 8 at 24ºC \((192 \text{ degree-days above } 0ºC; n = 60)\). Tanytarsina emergence rates at 14ºC were low and consistent \((0.66 \text{ individual per day})\) until these temperatures were raised to 24ºC on day 70, after which emergence rates steadily increased to 2.5 individuals per day. No Tanytarsina emerged at 4ºC from Wood Lake’s sediments in the first 70 days. Temperatures were then raised to 24ºC and emergences from aquaria formerly at 4ºC began on day 76 \((424 \text{ degree-days above } 0ºC; n = 46)\). Tanytarsina exhibited similar emergence trends from Echo Lake’s sediments as Wood Lake’s at the same temperatures.

Tanytarsina emergence rates for Temp 3 are visually represented in Figure 3.7. One Tanytarsina emerged from profundal sediments at 24ºC. A total 488 and 395 Tanytarsina emerged from sub-littoral and littoral sediments, respectively.

Tanytarsina began to emerge from sub-littoral sediments at 24ºC on day 4 \((96 \text{ degree-days above } 0ºC)\). Tanytarsina emergence declined from 1.88 individuals per day in the first half of this experiment to 0.92 individual per day in the latter half. Tanytarsina emergence rates from sub-littoral sediments at 14ºC were high and constant throughout this experiment. Emergence from sub-littoral sediments at 14ºC began on day 7 \((98 \text{ degree-days above } 0ºC)\), and by day 70 a total 262 individuals had emerged. These temperatures were raised to 24ºC on day 70 and an additional 116 individuals emerged before the experiment ended. Eight individuals emerged from sub-littoral sediments at 4ºC, seven of which emerged on day 65 \((260 \text{ degree-days above } 0ºC)\). No emergences were observed from these sediments after temperatures were increased from 4 to 24ºC on day 70. Tanytarsina demonstrated similar emergence trends between littoral sediments and sub-littoral sediments at the same temperatures.
3.3.1.6 *Procladius (Holotanypus) denticulatus*

*Procladius denticulatus* Sublette emerged in both Temp 1 and Temp 3. Two-way ANOVA analyses indicate that neither the sample site nor temperature treatment are significant (p ≤ 0.05) variables.

One *P. denticulatus* emerged at 14°C in Temp 1, all others emerged at 24°C (n = 89) (Figure 3.5). Emergences at 24°C began on day 31 (744 degree-days above 0°C) from both Echo and Wood Lakes’ sediments and by the end of the experiment, after 101 days, 4 and 11 individuals had emerged from these sediments, respectively. Overall, *P. denticulatus* emergence rates at 24°C for the three lakes were higher in the beginning half of this experiment compared to the latter half.

On day 70, temperatures in the 4 and 14°C containments were raised to 24°C. Emergences were observed from Wood Lake’s sediments on day 80 from both the formerly 4 and 14°C aquaria (520 and 1,220 degree-days above 0°C, respectively) and by the end of the experiment 11 and 13 individuals had emerged, respectively.

Emergences from Echo Lake’s sediments formerly at 4°C began on day 90 (769 degree-days above 0°C) and by day 101, fifteen individuals had emerged. Emergences from the formerly 14°C aquaria began on day 94 (1,316 degree-days above 0°C) and by day 101 five individuals had emerged.

*P. denticulatus* emerged from both littoral and sub-littoral sediments but not from profundal sediments in Temp 3 (Figure 3.7). No *P. denticulatus* emerged at 4°C from any of the sediment zone types and no emergences were observed after temperatures were raised to 14°C. Emergences at 24°C from littoral sediments began at the onset of the experiment and declined from 0.68 individual per day in the first half of this experiment to 0.14 individual per day in the second half (n = 41, in total). A total 28 *P. denticulatus* emerged at 14°C from littoral sediments and the first emergence was observed on day 16 (224 degree-days above 0°C).

3.3.1.7 *Parakiefferiella nigra*

*Parakiefferiella nigra* was the most abundant taxon observed in Temp 2. Two-way ANOVA analyses of *P. nigra’s* emergence data indicate that temperature treatment was the
sole significant (p ≤ 0.05) variable. Post-hoc TukeyHST analyses indicate that *P. nigra* emerged at significantly different abundances between all three temperature treatments. *P. nigra* emerged in greater abundances at 4°C (n = 68) than at 14°C (n = 29) and 24°C (n = 5) (Figure 3.6).

At 14°C, *P. nigra* began to emerge on days 31 and 35 from Okanagan and Kalamalka Lake’s sediments, respectively (434 and 490 degree-days above 0°C, respectively). *P. nigra* emerged from Okanagan and Kalamalka Lake’s sediments at 4°C on days 79 and 83, respectively (316 and 332 degree-days above 0°C, respectively). Overall, *P. nigra* emerged in clustered events from Okanagan and Kalamalka Lakes.

### 3.3.1.8 Corynoneura

*Corynoneura* was observed in Temp 2 (Figure 3.6) and two-way ANOVA analyses indicate that neither the sample site nor temperature treatment are significant variables. No *Corynoneura* emerged from Mabel Lake’s sediments. Two individuals emerged from Kalamalka Lake’s sediments, both at 24°C on day 35. From Okanagan Lake, *Corynoneura* emerged at 14°C on day 29 (406 degree-days above 0°C), peaking with 5 individuals on this day. Emergence rates declined thereafter with no *Corynoneura* emerging after day 59. Three individuals emerged at 4°C one on day 81 (324 degree-days above 0°C), and two on day 86.

### 3.3.1.9 Tanypus punctipennis

*Tanypus punctipennis* Meigen was observed in Temp 1 and Temp 3. Two-way ANOVA analyses indicate that temperature treatment is the sole significant (p ≤ 0.05) variable and post-hoc TukeyHST analyses indicate that *T. punctipennis* emerged at significantly different abundances at 4°C when compared to the other treatments but emergences at 14 and 24°C were not significantly different.

A total 20 *T. punctipennis* emerged in Temp 1 (data not shown in figures), of which, one individual emerged at 14°C and the remaining 19 individuals emerged at 24°C.

In Temp 3, *T. punctipennis* emerged from littoral zone sediments on days 5 and 11 at 24°C and 14°C, respectively (120 and 154 degree-days above 0°C, respectively) (Figure 3.7). Emergence rates from littoral sediments at both temperatures peaked within the first three
weeks of the experiment and declined thereafter. Although low in abundance following the early peaks, *T. punctipennis* consistently emerged at both 14°C (n = 28) and 24°C (n = 79) throughout the experiment. *T. punctipennis*’ emergence rates at 24°C declined from 1.01 individuals per day in the first half to 0.29 individual per day in the latter half. *T. punctipennis*’ emergence rates declined from 0.35 individual per day at 14°C to 0.14 individual per day after temperatures were raised to 24°C, on day 70. One *T. punctipennis* emerged at 4°C from littoral sediments.

**Figure 3.5:** Scatter graphs of selected taxa (*Polypedilum simulans*, Tanytarsina and *Procladius denticulatus*) emergences from littoral zone sediments collected from Echo, Wood, and Ellison Lakes and incubated at 4, 14, and 24°C, comprising Temp 1. The Y-axes delineate the number of adults emerged and the X-axes represent time (measured in days). Circles indicate emergences from Ellison Lake, triangles represent emergences from Wood Lake, and a plus-sign indicates an emergence from Echo Lake. The vertical line at day 70 indicates when temperatures in the 4 and 14°C containments were raised to 24°C, thus, all emergences after day 70 occurred at 24°C.
Figure 3.6: Scatter graphs of selected taxa (*Parakiefferiella nigra*, *Tanytarsina*, and *Corynoneura*) emergences from profundal sediments collected from Kalamalka, Mabel, and Okanagan Lakes and incubated at 4, 14, and 24°C, comprising Temp 2. The Y-axes delineate the number of adults emerged and the X-axes represent time (measured in days). Circles indicate emergences from Okanagan Lake, triangles represent emergences from Kalamalka Lake, and a plus-sign indicates an emergence from Mabel Lake. The vertical line at day 130 indicates when temperatures in the 4 and 14°C containments were raised to 24°C, thus, all emergences after day 130 occurred at 24°C. Note, no Tanytarsina or *Corynoneura* emerged from Mabel Lake’s sediments.

*T. punctipennis* emerged from sub-littoral sediments in low abundances at both 14°C and 24°C (n = 3 and 7, respectively). No *T. punctipennis* emerged at 4°C from sub-littoral sediments and none emerged from profundal sediments in this experiment.
Figure 3.7: Scatter graphs of selected taxa (Polypedilum simulans, Tanypus punctipennis, Tanytarsina and Procladius denticulatus) emergences from littoral, sub-littoral and profundal zone sediments collected from Wood Lake and incubated at 14, and 24°C, comprising Temp 3. The Y-axes delineate the number of adults emerged and the X-axes represent time (measured in days). Circles indicate emergences from littoral sediments, triangles represent emergences from sub-littoral sediments, and a plus-sign indicates an emergence from profundal sediments. The vertical line at day 70 indicates when the temperature in the 4°C containment was raised to 14°C and temperature in the 14°C containment was raised to 24°C.

3.3.2 Salinity: larval midge toxicity experiments

A total 702 individuals representing two Ceratopogonidae taxa and thirteen Chironomidae taxa comprised this experiment (Figure 3.8). Dasyhelea type (Family: Ceratopogonidae) was the most abundant (n = 258) and was subjected to all specific conductance levels chosen for this experiment. Dasyhelea type had the highest salinity LD50 of all taxa. Two individuals died, one at 25,000 µS cm⁻¹ and another at 35,000 µS cm⁻¹. The remaining 256 individuals survived: this included 22 individuals at 35,000 µS cm⁻¹, 34 individuals at 40,000 µS cm⁻¹, and 10 individuals at 45,000 µS cm⁻¹.
Procladius was subjected to nearly all specific conductance levels (n = 75). Overall, low death rates were observed <10,000 µS cm⁻¹. Fifty-percent of Procladius subjected to 10,000 µS cm⁻¹ perished (n = 4) and 75% perished at 15,000 µS cm⁻¹ (n = 4). Only one Procladius survived >15,000 µS cm⁻¹ (n = 52).

Chironomus anthracinus type showed low salinity LD50. Although all four individuals subjected to <1,000 µS cm⁻¹ survived, twenty-percent perished at 2,500 µS cm⁻¹ (n = 10) and 61.5% perished at 5,500 µS cm⁻¹ (n = 13). Only two C. anthracinus type survived >5,500 µS cm⁻¹ (both at 15,000 µS cm⁻¹) (n = 48).

Dicrotendipes revealed low salinity LD50. A total 67 individuals were observed and none survived >10,000 µS cm⁻¹ (n = 27), and 88% perished at 10,000 µS cm⁻¹ (n = 9).

A total 57 subtribe Tanytarsina were observed and none survived >15,000 µS cm⁻¹ (n = 31). Two individuals perished at 2,500 µS cm⁻¹ (n = 4) and 83% perished at both 5,500 µS cm⁻¹ and 10,000 µS cm⁻¹ (n = 6 at both concentrations). Seventy percent of Tanytarsina perished at 15,000 µS cm⁻¹ (n = 10).

A total 43 Glyptotendipes were tested and none died when exposed to <15,000 µS cm⁻¹ (n = 9). Sixty-six percent died at 15,000 µS cm⁻¹ (n = 3) and no Glyptotendipes survived >20,000 µS cm⁻¹ (n = 31).

Thirty-four Psectrocladius sordidellus type were tested, all at <30,000 µS cm⁻¹. Eight individuals survived at 1,000 µS cm⁻¹, one individual perished at 2,500 µS cm⁻¹ (n = 11), and all three P. sordidellus type subjected to 5,500 µS cm⁻¹ survived. No individuals survived >5,500 µS cm⁻¹ (n = 12).

Thirty-three Bezzia type (Family: Ceratopogonidae) were also tested. All seventeen individuals subjected to <20,000 µS cm⁻¹ survived. All four Bezzia type subjected to 20,000 µS cm⁻¹ and 25,000 µS cm⁻¹, each, perished. However, the only individual tested at 30,000 µS cm⁻¹ survived. All Bezzia type subjected to >30,000 µS cm⁻¹ perished (n = 7).

Seventeen Cladopelma were tested and none were subjected to >25,000 µS cm⁻¹. Twenty-five percent perished at 2,500 µS cm⁻¹ (n = 4). One Cladopelma was subjected to 10,000 µS cm⁻¹ and survived. Fifty percent of all Cladopelma at 15,000 µS cm⁻¹ perished (n = 4). All six Cladopelma at 20,000 µS cm⁻¹ and both individuals at 25,000 µS cm⁻¹ perished.
*Polypedilum* (not shown on figures due to low abundances) were subjected to 10,000 µS cm\(^{-1}\) (n = 1), 15,000 µS cm\(^{-1}\) (n = 3), and 20,000 µS cm\(^{-1}\) (n = 5). The individual tested at 10,000 µS cm\(^{-1}\) survived. One individual also survived at 15,000 µS cm\(^{-1}\) however the other two individuals perished. All 5 individuals died at 20,000 µS cm\(^{-1}\).

*Cryptochironomus* (not shown on figures due to low abundances) (n = 7) had low salinity LD50. Only two individuals survived in this experiment, one <1,000 µS cm\(^{-1}\) and another at 5,500 µS cm\(^{-1}\).

**Figure 3.8:** Dose response curves for nine midge taxa represented in this salinity-toxicity experiment, taxa with less than twenty occurrences were not plotted. The Y-axes indicate percent death rate, and the X-axes signify the specific conductance (µS cm\(^{-1}\)).

### 3.4 Discussion

These experiments indicate that temperature and salinity can have an effect on midge emergence patterns and survival rates, respectively. These results suggest that midge-based calibration/training-sets may be accurate but also indicate that caution must be used when interpreting optima and tolerance levels as calculated using the weighted averaging techniques commonly employed for quantitative reconstructions.
3.4.1 Temperature: midge-emergence experiments

Walker and Mathewes (1989) considered in detail the various factors regulating midge distributions, especially in relation to climate. They concluded that “low summer temperatures and short growing seasons probably prevent many temperate species from permanently colonizing arctic and alpine waters”, noting that absolute temperature thresholds must be attained for some taxa to complete pupation and emergence. Walker and Mathewes (1989) also note that the “availability of cold, well-oxygenated profundal environments probably limits the southern and lower [elevation] limits of arctic and alpine lake taxa”. The use of midge fossils as paleotemperature indicators is largely based on these observations and theory.

My experimental results largely conform to this expectation. Emergence trends from the experiments indicate that some midge taxa are cued for emergence by threshold temperatures as opposed to accumulated degree-days. For example, in Temp 1 Polypedilum (Tripodura) simulans began to emerge from Wood Lake’s sediments on day 4 (after the accumulation of just 96 degree-days above 0ºC) at 24ºC. No *P. simulans* emerged from Wood Lake’s sediments held at 4 or 14ºC by day 70 when a total 280 and 980 degree-days above 0ºC had accumulated, respectively. However, on day 70 the temperatures in the 4 and 14ºC containments were warmed to 24ºC and *P. simulans* began to emerge on days 91 and 75, respectively. Comparable emergence trends were observed for other taxa (*Procladius denticulatus*, Tanytarsina, *Cryptochironomus*, *Tanypus*, *Cladopelma*, and *Einfeldia*) in this experiment.

Some midges collected from profundal zones (Temp 2 and Temp 3) responded negatively to 24ºC temperatures. Midge mortality was noted from nearly all profundal sediments when held at 24ºC. This includes those sediments that were initially placed at 24ºC and those which were transferred, after a period of time, from 4 and 14ºC to 24ºC (n = 17, in total). Notable midge mortality was not observed in any of the other experimental scenarios. This includes experiments where littoral midges were collected in winter from Wood Lake and abruptly transferred to 24ºC. In most instances where profundal sediments were tested, midges emerged at greater abundances at 14ºC than at 4 and 24ºC. One exception to these findings occurred in Temp 2 where more adult midges emerged at 4ºC than at 14ºC due to a
high abundance of the cold stenotherm *Parakiefferiella nigra*. Thus, although most midge species respond with higher emergence rates in warmer waters, for some other taxa (e.g., *Parakiefferiella nigra*), exposure to warm waters resulted in stress and sometimes death.

More midges emerged from littoral zone sediments at 24°C (n = 1,852) than at 14°C (n = 319) and 4°C (n = 3) (Temp 1 and Temp 3). Moreover, more midges emerged from profundal zone sediments at 14°C (n = 104) than at 4°C (n = 89) and 24°C (n = 42) (Temp 2 and Temp 3). Midge emergences appeared to be clustered, with peak emergences occurring rather soon after the initial emergence and gradually declined thereafter. These results indicate that most midge taxa respond, via emergences, synchronously to threshold temperatures. In general, midge emergence rates from littoral sediments were higher and more abundant from sediments that were held for a prolonged time at 4 and 14°C before being transferred to warmer (24°C) temperatures when compared to those kept at 24°C for the full experiment. This may indicate that optimal development occurs at lower temperatures, after which time a threshold temperature may cue mass emergence. According to Hågvar and Østbye (1973), many Orthocladiinae larvae grow only at temperatures below 5°C, whereas *Chironomus plumosus* (L.) may not feed below 5°C (Hilsenhoff, 1967).

Overall, results from these three temperature experiments suggest that optimal midge development tends to occur at cooler temperatures, emergences are cued by temperatures higher than what is typically found at each lake-zone, but temperatures that are too high may result in organism stress and death.

In summation, some midge taxa may have relatively narrow optimal temperatures at which development and emergence can occur. My observations indicate that midges collected from littoral zone sediments (e.g., *Polypedilum simulans*) responded in the manner expected for ‘warm-water’ taxa (requiring warm temperatures to complete development), and profundal midges (especially *Parakiefferiella nigra*) responded in a manner expected for ‘cold-stenothermous’ taxa (where temperatures too warm impaired emergence and survival).

### 3.4.2 Salinity: midge-toxicity experiments

A total 702 individuals representing two Ceratopogonidae taxa and thirteen Chironomidae comprised this experiment. Results show that *Dasyhelea* had the highest salinity LD50; *Cricotopus/Orthocladius* and *Cladotanytarsus mancus* type showed 50%
death rates at 25,000 µS cm\(^{-1}\); *Glyptotendipes, Cladopelma, Cricotopus intersectus* type, *Polypedilum* and *Chironomus* exhibited 50% death rates at 15,000 µS cm\(^{-1}\); *Procladius*, *Psectrocladius sordidellus* type, *Cryptochironomus*, and *Dicrotendipes* demonstrated 50% death rates at 10,000 µS cm\(^{-1}\); and *Chironomus anthracinus* type and subtribe Tanytarsina had the lowest salinity LD50s at 5,500 and 2,500 µS cm\(^{-1}\), respectively. There were clear differences in salinity LD50 thresholds amongst taxa. Some taxa are clearly adapted to relatively fresh water. Other taxa are very tolerant across a wide salinity range. Low salinities did not impair the survival of any species. The absence in nature of such species at low salinities and their great abundance at high salinities is likely a reflection of indirect effects (e.g., decreased competition, predation and disease in saline water).

Dickson and Walker (in press) calculated specific conductance optima and tolerances for 13 of the midge taxa I observed in the in-vitro salinity experiments. Their specific conductance optima and tolerances were calculated via weighted averaging (WA) based on a calibration/training-set for the Hudson Bay Lowlands (Table 3.2). *A priori*, it was expected that the Hudson Bay Lowland upper salinity tolerances, calculated via WA, would approximate the LD50s determined in these experiments. However, most of the LD50s determined in my experiment are significantly higher than the upper salinity tolerances calculated via WA (Table 3.2), with the exception of *Dasyhelea, Cryptochironomus, Procladius, Chironomus anthracinus* type, and the subtribe Tanytarsina. Ponds with high specific conductance were underrepresented in Dickson and Walker’s (in press) training-set. The low optima and tolerances calculated from the weighted averages may therefore be an artifact of sampling bias. Differences between these two studies may also be attributed to intrinsically different effects of chronic versus acute salinity exposure.

Furthermore, in-vitro experiments (such as conducted here) are not an accurate representation of nature due to the lack of all cofounding variables that exist in nature and not in the laboratory. Many factors such as seasonality, ice-cover and energy inputs are lacking from the in-vitro experiments and ultimately impact the results.

Further-still, analyses using calibration data work on assumptions themselves. By no means is a calibration data set that was collected over a very short time period, in such localized geographical regions a likely representation of all the organisms occurring over the course of a year or decade across a vast landscape.
Table 3.2: Weighted-averaging optima, upper tolerance, and LD50 data for the 13 midge taxa present in both this study and Dickson and Walker’s (in press; see chapter 4 of this dissertation) training-set constructed for the Hudson Bay Lowlands. I present the optima here as anti-logged values. Similarly the upper tolerances values are presented as the anti-log (optimum + tolerance) of the values reported by Dickson and Walker.

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<td>Dasyhelea type</td>
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Bradley (1987) noted that the physiology of osmoregulation in mosquitoes included the production of a dilute urine to rid the body of water and replace lost salts by active ion uptake in freshwater taxa. He also noted that saline tolerant taxa drink the external medium to maintain body volume and produce a hyperosmotic urine to eliminate ingested ions. It is likely that midges use similar mechanisms for osmoregulation.

Substantial differences are apparent between the surface sample and in-vitro experiment results. For example, the rank order of the upper salinity tolerances (= WA optimum + tolerance) calculated from the Hudson Bay Lowlands training-set are not highly correlated with the ranked LD50s in this experiment (Table 3.2). Spearman’s Rank Correlation analysis indicated overall low correlation between the LD50s and WA-upper tolerance values produced from these two studies (r = -0.205). Of the taxa observed in both
studies, subtribe Tanytarsina had the lowest LD50 (2,500 μS cm⁻¹) but recorded a moderately high upper salinity tolerance at 4,786 μS cm⁻¹; a higher upper-tolerance than seven other taxa observed in both experiments. Similarly, Chironomus anthracinus type recorded the second lowest LD50 (5,500 μS cm⁻¹) but was ranked higher than all but three taxa with respect to its WA upper-tolerance. Cricotopus/Orthocladius and Cladotanytarsus mancus type both had the highest LD50s (25,000 μS cm⁻¹, respectively) after Dasyhelea (>30,000 μS cm⁻¹) but had moderate WA upper-tolerances, 3,326 and 7,499 μS cm⁻¹ respectively. Furthermore, Glyptotendipes and Polypedilum had the two lowest calculated WA upper-tolerances (1,012 and 1,091 μS cm⁻¹, respectively) yet recorded moderately high LD50s (both at 15,000 μS cm⁻¹), higher than both Procladius and Cryptochironomus. Despite these discrepancies, the results are comparable in one important regard; Dasyhelea had both a very high LD50 (>30,000 μS cm⁻¹) and a very high WA upper-tolerance (14,997 μS cm⁻¹); thus, this genus may be one of the most reliable indicators of high salinity environments.

3.5 Implications for Paleoecology

Understanding contemporary species’ ecologies facilitates better interpretation of their fossil remains. Experiments and species-environment surveys, such as presented here, provide data illustrating how living biota respond across environmental gradients; thus, aiding interpretation of fossil remains. And in turn, a paleoecological record can help contemporary ecologists put current phenomena into the context of a longer time-frame and help gauge the importance of past and present cyclic and unusual events (Shoonmaker and Foster 1991). Ultimately, contemporary and paleoecological studies are synergistic, both facilitating a better understanding of midge-environment relationships.

The importance of neolimnological and biological data for paleoecologists is highlighted by the resurrection of the historic debate (e.g., Walker and Mathewes 1989; Hann et al. 1992) over midges as paleoclimatic indicators. Velle et al. (2010, 2012) have criticized the use of midges as Holocene paleotemperature indicators, while Brooks et al. (2012) disagree. Eggermont and Heiri (2012, p 447) concluded that “the temperature response of midge assemblages may be strongly affected by indirect effects of temperature” and further note (p. 450), “In our estimation, the most significant advancement in chironomid-based temperature reconstruction can be achieved by increasing our understanding of the ecological
and eco-physiological mechanism controlling chironomid assemblage structures”. The research presented here addresses this point, demonstrating direct linkages between temperature and salinity, and midge emergence and survival.

The revived and ongoing debate between the two camps (Velle et al. 2012 versus Brooks et al. 2012) comes to a spearhead when considering two very valid points made by both sides; (1) when Holocene temperature reconstructions from different sampling localities are compared there are many instances of strongly mismatching curves (Velle et al. 2010, 2012), and (2) in mountainous areas and at spatial scales of hundreds to thousands of kilometers, changes in climatic forcing factors during the Holocene may well have led to differential regional climatic responses (Brooks et al. 2012). That being said, it is crucial that midge workers acknowledge the correlations observed between modern day midge assemblages and temperature gradients, correlations between midge inferred temperatures and instrumental data, correlations with other proxy data, and now, presented here, in-vitro evidence that midge emergence and survival are directly linked to temperature and salinity. Furthermore, while the pattern of midge emergence in my experiments closely followed expectations, the upper salinity tolerances calculated from Hudson Bay Lowlands surface samples were poor predictors of actual LD50s measured in my in-vitro experiments; thus some caution is warranted when attempting quantitative reconstructions based on Dickson and Walker’s (in press) WA salinity inference models.

My experiments support the use of midge remains as both paleosalinity and paleotemperature indicators. Nevertheless, caution should always be exercised when interpreting such paleoenvironmental reconstructions.
Chapter 4: Midge assemblages from the Hudson Bay Lowlands, Manitoba, Canada: A midge-salinity transfer function for inferring sea level change and landscape evolution

4.1 Background

When inferring past environmental and ecological conditions from fossil assemblages an ideal indicator species is one that only occurs under distinct environmental conditions and nowhere else. However in nature these ‘ideal’ indicator species may be rare, thus community composition analyses (which consider species with both wide and narrow ecological tolerances) can provide valuable information regarding environmental and ecological conditions. Aquatic midges (Chironomidae, Chaoboridae and Ceratopogonidae) have worldwide distributions and their chitinous larval head-capsules and mandibles preserve in sediments for thousands of years. Consequently, they have been used for inferring paleoenvironmental conditions (Walker et al. 1991a; Brooks and Birks 2001; Verschuren et al. 2004; Zhang et al. 2007). Midges are now valued as quantitative indicators of water and air temperature (Walker et al. 1997; Olander et al. 1999; Brooks and Birks 2001), lake depth (Korhola et al. 2000), productivity (Woodward and Shulmeister 2006), water quality (Luoto 2011) and salinity (Walker et al. 1995; Eggermont et al. 2006; Zhang et al. 2007). This study explores the usefulness of midge communities as indicators of salinity, which may enable future explorations of midge community development in response to sea level change, an important variable relevant especially for sea level and climate reconstructions (Heinrichs and Walker 2006).

The impetus for the research outlined in this chapter comes from the desire to expand our understanding of midge-salinity relationships and the desire for a greater understanding of the landscape evolutionary history of the Hudson Bay Lowlands with respect to sea level change via isostatic rebound. The principal aim of this research is to construct a midge salinity transfer function, which can be applied to quantitatively reconstruct paleosalinities and ultimately infer a sea level history for the Hudson Bay Lowlands. Analyzing the midge assemblages from four sediment long-cores with this training-set may establish inception
times for each pond and provide a framework for reconstructing sea level change and landscape evolution via isostatic rebound (Chapter 5).

4.2 Study area

A training-set comprised of sixty-three ponds located in the Hudson Bay Lowlands (32 in Wapusk National Park), between 58.772°N to 56.330°N latitude, and 94.500°W to 93.011°W longitude, was used in this study (Figure 4.1). Field excursions/sampling conducted in July 2004 and August 2010 yielded surface-sediment samples, and physical and chemical measurements for the 63 ponds. The sampled area extends from Gillam, Manitoba, north to Churchill, Manitoba and east to the Hudson Bay shoreline covering an elevation gradient from 0 m to 128 meters above sea level (masl).

The sixty-three study ponds are distributed among two broad ecozones, Taiga Plains and Hudson Plains, with the majority within the Hudson Plains ecozone (Natural Resources Canada 2007). More specifically, the sixty-three study sites reside within three major vegetation zones identified as: tundra, forest-tundra and open forest (Brook et al. 2002). Catchments for the ponds included open tundra, fen, bog, and forested sites. The region is characterized by very little topographic relief (less than 1 m km⁻¹) (Wolf et al. 2006).

The Hudson Bay Lowlands has experienced relatively recent and ongoing isostatic rebound from submarine conditions, hence proximity to the coast has been found to be a major factor in determining the concentration of dissolved salts and the ages of ponds in the area (Wolf et al. 2006; Bos and Pellatt 2012). Currently, it is estimated that the area encompassing Churchill, Manitoba is rebounding at approximately 11.4 ± 0.7 mm a⁻¹. The highest elevation ponds, located near Gillam are potentially 8500 years old. New ponds are continually being generated by isostatic uplift along the Hudson Bay shoreline (Wolf et al. 2006).

The emergent sea bottom has substrates composed mainly of marine silts/clays (Martini 1989), marine washed tills and subglacial deposits (Lafleur and Rouse 1995). The raised features (areas formerly inundated by glacial Lake Agassiz but not the Tyrrell Sea) consist of glacial deposits and generally have poorly developed soils with very thin (20 mm) organic soil (Martini 1989). At low elevations (below approximately 150 masl) the region is underlain by marine silts and clays where the Tyrrell Sea once resided. Wetlands are
extensive in the region and Bello and Smith (1990) estimated that lakes and ponds comprise over 40% of the surface area of Hudson Bay Lowlands. Peat deposits ranging from 10 – 50 cm thick dominate the landscape (Duguay and Lafleur 2003).

Figure 4.1: Locations of the 63 ponds used for constructing a midge-based salinity training-set for the Hudson Bay Lowlands. Sites with preface ‘CH’ are located along the coast and may not be labeled due to spacing issues. Maps generated using Planiglobe (n.d.) under the Creative Commons Attribution-Share Alike 2.5 license.

The mean annual temperature at Churchill (near many of the sample ponds) is -7.4°C with a mean summer (June – August) temperature of 10.1°C and a mean winter (December – February) temperature of -24.7°C. Annual precipitation is low (411 mm), of which 235 mm fall as rain during May-September and the remaining 43% fall as snow between October and
May (data compiled from 1971 – 2000, National Climate Data and Information Archive (2011)). Most of the study area is underlain by permafrost with active layer depths ranging from 75 to 180 cm (Bello and Smith 1990).

The mean annual temperature at Gillam, Manitoba (the southern limit of the sampled sites) is -4.5ºC with a mean summer (June – August) temperature of 13.5ºC and a mean winter (December – February) temperature of -23.4ºC. Annual precipitation is approximately 499.4 mm a⁻¹, where most precipitation falls as snow from October to April and the remaining precipitation falls as rain (mainly between May and September) (data compiled from 1971 – 2000, National Climate Data and Information Archive (2011)).

Most of the ponds sampled were shallow (depth ranging from 8-200 cm), well oxygenated (86-122 % saturation) water bodies with a pH range from 7.1-9.2 and spanning an elevation gradient from sea level to 128 masl. Specific conductance measurements (a common proxy for salinity) ranged from 45 to 29,000 µS cm⁻¹ (Table 4.1)

4.3 Methods

4.3.1 Midge analysis

Sediments for midge analysis were obtained using a mini-Glew gravity sediment corer (Glew 1991) or via scoop method where a gravity corer proved impractical. The ‘scoop method’ involved scooping surface sediments using a spoon into Whirl-Pak® sampling bags. For each pond sampled, the top 1 or 2 cm of sediment were extruded on site, transferred to Whirl-Pak® sampling bags, and stored until analysis at a later date.
Table 4.1: Environmental and limnological data for the 63 ponds comprising the Hudson Bay Lowlands training-set and descriptive statistics of environmental variables.

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<th>DO (%)</th>
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<th>pH</th>
<th>Depth (cm)</th>
<th>Elevation (m)</th>
<th>Latitude (°N)</th>
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<td>0.2</td>
<td>83.2</td>
<td>18.8</td>
</tr>
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</table>
Sediment processing, picking of midge remains, and midge identifications were performed at the PaleoLab (University of British Columbia, Okanagan Campus). Surface sediments were processed/flushed with 10% hydrochloric acid (HCL) to dissolve any carbonates and warmed in 5% potassium hydroxide (KOH) on a hotplate to deflocculate the sediment. The residual sediment was sieved on a 93 to 95 μm mesh and subsequently picked for midge remains from Bogorov counting trays under 20× and 40× magnification with Nikon SMZ645 dissecting microscopes. Midge remains were picked and transferred to microscope slides, and mounted with Entellan® mounting medium. Midges were identified under 200× and 400× magnification with an Olympus BX51 compound microscope, with reference to Wiederholm (1983), Oliver and Roussel (1983), Walker (1988, 2000), and Brooks et al. (2007).

4.3.2 Taxonomic notes

Midges were identified to the lowest taxonomic group possible. In instances where missing or obscured mouthparts hindered identification to a specific taxon type within a taxon group, the head capsule was tallied as its own type (e.g., a head capsule was tallied as Chironomus if insufficient information enabled the distinction between Chironomus anthracinus type and Chironomus plumosus type).

Due to a lack of distinguishing characteristics most taxa were not identifiable to the species level. Head capsule fragments without the median teeth were not counted. Those with half the mentum intact were counted as half, and those with more than half the mentum were counted as whole. A minimum count of 50 identifiable midge head capsules per sample was used, in accordance with the recommendations of Heiri and Lotter (2001) and Quinlan and Smol (2001).

4.3.3 Environmental variables

Thirty-one ponds (sites 1 – 31, Table 4.1) were sampled for their surface sediments (and midge fauna) in 2010. Elevation, latitude and longitude were obtained at each site using a hand-held geographical positioning system receiver. The depth for each pond was assessed via a weighted tape measure. Specific conductance, pH, dissolved oxygen, and water temperatures were obtained from an YSI meter (YSI® Professional Plus, ©2009 YSI
Incorporated, Yellow Springs, Ohio. Model number 304617). Distance to the coast was determined with the ruler tool in GoogleEarth®. Data for sites 32 - 63 (Table 4.1) were collected in 2004; the data collection methods for these sites are presented in Bos and Pellatt (2012). Descriptive statistics for the environmental variables are presented at the bottom of Table 4.1.

### 4.3.4 Statistical methods

Taxa that were present in fewer than 5% of the sampled ponds were eliminated from analysis. All taxon data were analyzed as relative abundances (calculated as percent of the total identifiable midges for a sample) and analyses were performed with and without square-root transformation of taxon data, and with and without down-weighting of rare taxa. Sites with fewer than the minimum of 50 identifiable midge head capsules were eliminated from the training-set (Walker et al. 1995; Quinlan and Smol 2001). Specific conductance, depth, elevation, and dissolved oxygen measurements were log transformed because of skewed distributions. Latitude and longitude were entered as passive variables in all ordination analyses. Collinearity of environmental variables was determined by inflation factors $\geq 20$ in a series of detrended correspondence analyses (DCAs).

Sites with unusual environmental characteristics and midge assemblages were defined as outliers and eliminated from further analyses if their sample scores fell outside the 95% confidence interval of the sample score mean on axis 1 and axis 2 for both a DCA of the taxon data and a principal components analysis (PCA) of the environmental data.

### 4.3.4.1 Ordinations

Ordinations were performed using the program CANOCO, version 4.5 (ter Braak 1991). Faunistic gradient lengths were calculated from DCA species scores in standard deviation units (SD). The relationships between individual environmental variables and midge distributions were assessed with forward selection in redundancy analyses (RDAs) and canonical correspondence analyses (CCAs). Statistically significant ($P \leq 0.05$) environmental variables were then evaluated in a series of partial RDAs and CCAs (final versions). Selected variables and ordination axes were tested for significance with Monte Carlo permutation tests (using 999 unrestricted permutations, $P \leq 0.05$).
4.3.4.2 Model development

To explore the relationships between midges and salinity (measured as specific conductance), partial CCAs constrained to specific conductance were run and the first to second eigenvalues ($\lambda_1/\lambda_2$) compared. Using the program C2 version 1.4 (Juggins 2003) I developed and assessed midge transfer functions for specific conductance. Weighted Averaging (WA) with classical and inverse deshrinking, Weighted Averaging with tolerance down-weighting (WA$_{tol}$), Weighted Averaging Partial Least Squares (WA-PLS), Partial Least Squares (PLS), and Modern Analogue Techniques (MAT) were assessed to determine the best modeling methods for specific conductance reconstructions. All models were run with 999 Monte Carlo permutations. These models were evaluated by means of the bootstrapped co-efficient of determination ($r^2_{\text{boot}}$), root mean squared error of prediction (RMSEP), and the bootstrapped maximum bias.

4.4 Results

4.4.1 Data screening

Twelve ponds (Pond9, Pond14, Pond15, Pond17, Pond20, Pond22, Pond27, Pond30, CH17.02, CH18.10, CH18.14, and CH18.15) yielded fewer than fifty midge head-capsules and were eliminated from further analyses (Quinlan and Smol 2001). Although some information might be gleaned from their low abundances at these ponds (e.g., environmental characteristics of habitats), the deletions were essential for my statistical treatment of the data. These ponds do not differ notably from the other ponds with respect to their environmental characteristics.

A total of 3,819.5 individuals representing sixty-two midge taxa were identified from the remaining ponds. Fifteen of these taxa were eliminated from further analysis because: (1) they were present in fewer than 5% of the sampled ponds (3 ponds); or (2) missing or damaged parts of the head-capsule hindered identification past the subfamily level (Barley et al. 2006; Eggermont et al. 2006; Woodward and Shulmeister 2006). After initial screening, a total 3,202 midges representing forty-seven taxonomic groups from fifty-one ponds were statistically analyzed for correlations between the measured environmental variables and midge taxon assemblages. All ordination analyses were performed with both square-root
transformed and untransformed taxon data, and with and without down weighting of rare taxa.

Collinearity of environmental variables was assessed using inflation factors in a DCA, detrended with twenty-six segments. No samples produced an inflation factor ≥20 thus there was no strong collinearity among the variables. Site CH16.10 was eliminated from further analyses from both data sets because its sample score fell outside the 95% confidence interval of the sample score mean on axis 1 and axis 2 for both a DCA of the taxon data and a PCA of the environmental data. Site CH16.10 was shallow (33 cm), had a low observed temperature (7.3 °C) and dissolved oxygen saturation (87.6%). CH16.10 also had a relatively high specific conductance (14,210 \( \mu \)S cm\(^{-1} \)) and was overwhelmingly dominated by an unidentified ‘Halophilic Orthocladiniinae’ taxon (86%).

4.4.2 Ordinations

The screened data set comprised fifty ponds and forty-seven midge taxa. A series of ordinations were performed on the screened data sets to determine which environmental variables potentially exerted the strongest influence on the taxon distributions in the Hudson Bay Lowlands datasets. The gradient lengths calculated from DCA species scores (2.96 SD for axis 1 and 2.92 SD for axis 2 in the untransformed data set; and 2.37 SD for axis 1 and 2.11 SD for axis 2 in the square-root transformed data set), indicate that some species turnover occurs in the training-sets (a gradient length of 4 SD units indicates a full species turnover). Gradient lengths such as these imply that both linear (RDA) and unimodal (CCA) relationships between taxa and the observed environmental variables likely occur in the data sets, thus both linear and unimodal methods were explored. Untransformed species data outperformed transformed data for both CCA and RDA analyses, based on the percent variance explained (Table 4.2). Thus, only results from untransformed species data will be discussed further.

In order to determine the extent to which individual environmental variables could account for taxonomic variation in the data sets, forward selection and a series of ordinations constrained to each environmental variable were run in CCA and RDA. Forward selection in CCA identified the following significant (P<0.05) environmental variables, in order of significance: log-transformed specific conductance (LogCond), distance to coast (Dist. Co),
temperature (Temp), and log-transformed dissolved oxygen (LogDO) (Table 4.3). Forward selection in RDA identified LogCond, Dist. Co, log-transformed elevation (LogElev), LogDO and Temp as significant (P<0.05) environmental variables, also presented in order of forward selection (Table 4.3).

Patterns in data structure of the final CCA and RDA restricted to the statistically significant variables were compared with those of unconstrained correspondence analysis (CA) and principal component analysis (PCA), respectively, to explore the ability of the measured environmental data to explain variability in the species data. Correlations between CA and CCA species scores of the first axes ($r^2 = 0.164$) and second axes ($r^2 = 0.181$), and sample scores for the first axes ($r^2 = 0.078$) and second axes ($r^2 = 0.012$) are moderate-poor. Correlations between PCA and RDA species scores of the first axes ($r^2 = 0.403$) and second axes ($r^2 = 0.262$), and sample scores for the first axes ($r^2 = 0.943$) and second axes ($r^2 = 0.497$) were better than those seen between CA and CCA. Forward selection operations in CANOCO indicated that LogCond is responsible for predicting most of the variation captured in this training-set using both linear and unimodal models (Jongman et al. 1987).

The first four axes of the final CCA constrained to the four significant (P $\leq$ 0.05) environmental variables accounted for 21.2% of the species variance (Table 4.3). The first four axes of the final RDA constrained to the five significant (P $\leq$ 0.05) environmental variables accounted for 23.9% of the species variance captured in this data set (Table 4.3). Monte Carlo tests (with 999 unrestricted permutations) confirmed the significance of all four axes (P = 0.002) for both the linear and unimodal ordinations. Relationships between the significant environmental variables and the individual axes were examined through correlation coefficients, t-values and inter set correlations (Table 4.3). Results presented in Table 4.3 indicate that Axis 1 is predominantly determined by LogCond for both the linear and unimodal ordinations. Axis 2 is most correlated with the distance to coast. These findings suggest that the measured environmental variables may influence the present-day midge communities and potentially warrant paleo-reconstruction from fossil assemblages. Because LogCond was the strongest variable linked with midge distributions, as determined by forward selection in both ordinations analyses, a CCA and an RDA constrained to LogCond were run and produced an eigenvalue ratio of 0.60 ($\lambda_1/\lambda_2 = 0.20/0.33$) for the CCA, and 0.45 ($\lambda_1/\lambda_2 = 0.10/0.22$) for the RDA. These results confirm LogCond as a promising variable for
reconstruction and suggests unimodal (CCA) methods may outperform linear (RDA) methods (Jongman et al. 1987)

Table 4.2: Eigenvalues, species-environment correlations, cumulative percent variance of species data and species-environment relation of the first four CCA and RDA axes with untransformed and transformed species data.

<table>
<thead>
<tr>
<th></th>
<th>CCA Axes (Data Untransformed)</th>
<th>CCA Axes (Data Transformed)</th>
<th>RDA Axes (Data Untransformed)</th>
<th>RDA Axes (Data Transformed)</th>
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<td></td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>4</td>
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<td>0.856</td>
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<td></td>
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<tr>
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<tr>
<td>of species-Env relation</td>
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<td>62.7</td>
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Sum of all unconstrained eigenvalues

Sum of all canonical eigenvalues

2.232

1.000

0.981

0.502

0.495
Table 4.3: CCA and RDA (final versions – after excluding the non-descriptive environmental variables) and their associated canonical coefficients, t-values and inter set correlations.

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<tr>
<th>RDA Axes (final version)</th>
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<th>Axis 3</th>
<th>Axis 4</th>
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<td>0.552</td>
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<th>Axis 4</th>
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<th>t-value</th>
<th>Inter set correlations</th>
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<td>Axis 3</td>
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<td>0.071</td>
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<td>Dist. Co</td>
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<td>0.132</td>
<td>0.058</td>
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<td>LogElev</td>
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<td>-0.937</td>
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<td>0.618</td>
<td>0.148</td>
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<tr>
<td>Temp</td>
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<td>0.627</td>
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</table>
CCA (final version)

<table>
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<th>Variable</th>
<th>Canonical coefficients</th>
<th>t-value</th>
<th>Inter set correlations</th>
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<td>Axis 3</td>
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<td>0.471</td>
<td>0.561</td>
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<tr>
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<td>1.123</td>
<td>0.0513</td>
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<tr>
<td>Temp</td>
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<tr>
<td>LogDo</td>
<td>-0.111</td>
<td>-0.394</td>
<td>0.375</td>
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A triplot of the final CCA species scores reflects correlations of individual taxa included in the Hudson Bay Lowlands data set to the significant environmental variables and the sampled sites (Figure 4.2). Taxa situated on the two right-side quadrants are correlated with highly saline ponds in the Hudson Bay Lowlands. These taxa include the Ceratopogonidae member *Dasyhelea*, the unidentified ‘Halophilic Orthocladiinae’ taxon, *Chironomus, Procladius, Metriocnemus,* and *Eukiefferiella.* Taxa situated within the two left-side quadrants are typical in sites with lower salinities and higher temperatures. These taxa include *Constempellina, Paratendipes, Stictochironomus, Zalutschia, Paralimnophyes, Microtendipes,* and *Chaetocladius.* Taxa clustered in the central part of the CCA triplot are found in intermediate salinities or have broad distributions in respect to salinity. Summary statistics from this CCA indicate that Axis 1 is largely correlated with ‘LogCond’ and Axis 2 is mainly correlated with ‘Dist. Co’ (Table 4.3).
Figure 4.2: Final canonical correspondence analysis ordination (triplet) showing the dispersions of taxa and sampled sites relative to the four significant ($P \leq 0.05$) environmental variables: log-transformed specific conductance (LogCond), distance to coast (Dist. Co), temperature (Temp), and log-transformed dissolved oxygen (LogDO). Taxon codes correspond with full taxon names listed in Table 4.5. (Note, some repositioning of sites was necessary to aid presentation).
Table 4.4: Model performances for WA, WA-PLS, PLS, and MAT for reconstructing LogCond, using untransformed and square-root transformed taxon data.

| Untransformed Data | Apparent | | | Bootstrapped | | | |
|---|---|---|---|---|---|---|---|---|
| Model | $r^2$ | RMSE | Max Bias | $r^2_{boot}$ | RMSEP | Max Bias$_{boot}$ | |
| WA | Inverse | 0.778 | 0.363 | 0.402 | 0.659 | 0.495 | 0.853 |
| Classical | 0.778 | 0.412 | 0.476 | 0.664 | 0.502 | 0.706 |
| WA$_{tol}$ | Inverse | 0.741 | 0.393 | 0.587 | 0.571 | 0.594 | 0.967 |
| Classical | 0.741 | 0.457 | 0.428 | 0.579 | 0.613 | 0.848 |
| WA-PLS | 1 Component | 0.778 | 0.363 | 0.402 | 0.652 | 0.497 | 0.852 |
| 2 Component | 0.846 | 0.303 | 0.304 | **0.682** | **0.482** | **0.684** |
| 3 Component | 0.866 | 0.282 | 0.288 | 0.653 | 0.525 | 0.679 |
| 4 Component | 0.911 | 0.232 | 0.298 | 0.613 | 0.595 | 0.513 |
| PLS | 1 Component | 0.426 | 0.586 | 1.29 | 0.281 | 0.692 | 1.494 |
| 2 Component | 0.695 | 0.427 | 0.658 | 0.479 | 0.611 | 1.251 |
| 3 Component | 0.783 | 0.361 | 0.564 | 0.559 | 0.563 | 1.246 |
| 4 Component | 0.814 | 0.333 | 0.357 | 0.576 | 0.556 | 1.165 |
| MAT | 0.532 | 0.555 | 1.275 | 0.563 | 0.593 | 1.255 |

| Square-root Transformed Taxon Data | Apparent | | | Bootstrapped | | | |
|---|---|---|---|---|---|---|---|---|
| Model | $r^2$ | RMSE | Max Bias | $r^2_{boot}$ | RMSEP | Max Bias$_{boot}$ | |
| WA | Inverse | 0.806 | 0.341 | 0.414 | 0.654 | 0.509 | 0.808 |
| Classical | 0.806 | 0.379 | 0.325 | 0.658 | 0.508 | 0.679 |
| WA$_{tol}$ | Inverse | 0.672 | 0.443 | 0.599 | 0.389 | 0.695 | 0.992 |
| Classical | 0.672 | 0.541 | 0.395 | 0.401 | 0.753 | 0.932 |
| WA-PLS | 1 Component | 0.806 | 0.341 | 0.422 | 0.654 | 0.508 | 0.827 |
| 2 Component | 0.886 | 0.298 | 0.362 | 0.637 | 0.509 | 0.891 |
| 3 Component | 0.901 | 0.244 | 0.229 | 0.587 | 0.561 | 0.939 |
| 4 Component | 0.921 | 0.216 | 0.157 | 0.552 | 0.598 | 0.992 |
| PLS | 1 Component | 0.693 | 0.428 | 0.925 | 0.527 | 0.574 | 1.286 |
| 2 Component | 0.799 | 0.346 | 0.509 | 0.621 | 0.515 | 1.555 |
| 3 Component | 0.843 | 0.306 | 0.449 | 0.616 | 0.522 | 1.555 |
| 4 Component | 0.892 | 0.253 | 0.24 | 0.606 | 0.542 | 0.987 |
| MAT | 0.492 | 0.593 | 1.186 | 0.546 | 0.607 | 1.177 |
Table 4.5: Taxon codes, names, and their Weighted Average LogCond optima, tolerances, back-transformed optima and tolerances for all taxa comprising the Hudson Bay Lowlands training-set. Taxa with lowest optima are arranged at the top. Taxon codes correspond with those used in Figure 4.2.

<table>
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Cha Chaoborus americanus 3.50 1.18 3,160 15.23
Eu fi Eukiefferiella fittkaui 3.53 0.80 3,377 6.33
Eu de Eukiefferiella devonica 3.56 0.81 3,625 6.46
Cerato type Ceratopogonidae Dasyhela
Me te Metriocnemus terrester type 3.76 1.09 5,754 12.30
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Chi pl Chironomus plumosus type 3.79 0.71 6,026 5.12
Pseudsm Pseudosmittia 4.23 0.67 16,596 4.71
Halo Orth Halophilic Orthocladiinae 4.23 0.61 16,984 4.04

### 4.4.3 Model development

Weighted Averaging (WA), Weighted Averaging-Partial Least Squares (WA-PLS), Partial Least Squares (PLS), and Modern Analogue Technique (MAT) models were constructed using the screened data sets to determine the best model for robust LogCond reconstructions (Table 4.4). Here, both linear and unimodal models were constructed with and without square-root taxon data transformations for comparative purposes.

The untransformed taxon data set produced the strongest correlation coefficient ($r^2_{boot} = 0.68$), low error of prediction (RMSEP = 0.482) and relatively low bootstrapped maximum bias (Max Bias$_{boot} = 0.684$) indicating a 2 component WA-PLS model as the best for quantitative LogCond reconstructions (Table 4.4). All further analyses were run with the untransformed data. Taxon specific LogCond optima and tolerance ranges (and back-transformed optima and ranges) were generated using WA techniques (Table 4.5) but should be considered with caution as these estimates are limited by the range of measured conductivities within this training-set. Taxa with the lowest specific conductance optima included Paralimnophyes (44.67 μS cm$^{-1}$), Zalutschia group (85.11 μS cm$^{-1}$) and Stempellina (93.32 μS cm$^{-1}$). Taxa with high specific conductance optima include the unidentified ‘Halophilic Orthocladiinae’ taxon (16,983.44 μS cm$^{-1}$), *Pseudosmittia* (16,595.87 μS cm$^{-1}$),
*Chironomus plumosus* type (6,025.59 μS cm⁻¹), *Metriocnemus* (5,754.39 μS cm⁻¹), and a member of the Ceratopogonidae family, *Dasyhelea* (4,466.83 μS cm⁻¹).

Comparison of the observed versus inferred log-transformed specific conductance values and their residuals (Figure 4.3) reveals that the model has little bias and does well at reconstructing the known values for specific conductance. However, trends present in this figure indicate that low levels of salinity may be overestimated and higher salinity levels may be underestimated, which is common with the training-set method. Figure 4.4 shows selected taxa arranged by their calculated LogCond optima (taxa with highest conductance optima on the right) and sites arranged by their observed specific conductance values (along the Y-axis, with higher LogCond sites at the bottom). This figure reveals patterns in taxon distributions in the Hudson Bay Lowlands training-set. Sites with the highest LogCond values were characterized by abundant salt tolerant taxa including the Halophilic Orthocladiinae, *Dasyhelea, Procladius*, and *Chironomus*, and virtually no occurrences of freshwater taxa such as *Paralimnophyes, Constempellina, Microtendipes, Limnophyes*, and *Stictochironomus*. At the other end of the LogCond gradient, only low abundances of saline tolerant taxa were found at fresh-water sites.

![Figure 4.3: Predicted versus observed values for LogCond (left) and residuals of predicted versus observed LogCond (right) for the WA-PLS (2 component) model are shown. X and Y-axes are scaled to log-transformed specific conductance (μS cm⁻¹).](image-url)
Figure 4.4: Relative abundances of selected taxa recovered from surface samples of the Hudson Bay Lowlands data set. Taxa are arranged according to their LogCond weighted averages with saline tolerant taxa on the right-hand side of the graph. Sites are arranged by their observed specific conductance: fresh (top) to more saline (bottom).
4.5 Discussion

Statistical analyses indicated that LogCond explained the highest proportion of taxon variation captured in this training-set. Ultimately, results from this study demonstrate a correlation between midge assemblages and specific conductance in the Hudson Bay Lowlands and support the use of midges as paleosalinity indicators. This conclusion is not unexpected given the importance of osmotic regulation for aquatic organisms and the broad specific conductance (salinity) gradient sampled (Walker et al. 1995). However, the skewed distribution of specific conductance (toward the fresher end of the gradient) from the sampled ponds may hinder accurate quantitative salinity inferences, based on midge assemblages, for times of high salinity. The presence of an unidentified taxon, ‘Halophilic Orthocladiinae’, and a member of the Ceratopogonidae family, *Dasyhelea*, in down-core analysis should, however, indicate saline environments, such as those observed along the current shoreline of Hudson Bay.

Photographs of the Halophilic Orthocladiinae taxon are presented in Figure 4.5 (photos show two individuals at differing focus depths). This taxon was observed to have a single, broad median tooth, often striped and with a nipple-like projection, and with five lateral teeth. The fourth and fifth lateral teeth appear reduced and grouped together. The ventromental plate is weak and appears forked. The mandible has a long apical tooth and three inner teeth. I am not aware of any described midge species that match these characters. This taxon was most abundant in ponds with the highest measured specific conductance, was only found in ponds <20 km from Hudson Bay, and had the highest calculated LogCond optimum (based on weighted averages) in this training-set. This taxon may prove to be extremely valuable for reconstructing paleosalinities and sea level in the Hudson Bay Lowlands. For example, occurrences of this taxon when performing down-core analysis may indicate periods of high salinity before ponds were significantly uplifted from Hudson Bay. Subsequently, the disappearance of this taxon from a sediment core may indicate the emergence of these ponds as Hudson Bay’s shoreline receded in response to isostatic adjustment following deglaciation.
Figure 4.5: Diagnostic images for the unidentified ‘Halophilic Orthocladiinae’ taxon found in the Hudson Bay Lowlands training-set. Each photo represents an individual at different focus depths. All photos were taken at 400X magnification.

A gradual distribution from freshwater to salt tolerant taxa is evident in this training-set (Figure 4.4). Fresh-water taxa are situated on the left-side of Figure 4.4 and include *Polypedilum* group, *Limnophyes*, *Stictochironomus*, and *Microtendipes pedellus* type, to name a few. Intermediate salt tolerant taxa are common across a broad range of salinities in this training-set which include *Psectrocladius*, other *Cricotopus/Orthocladius*, the subtribe Tanytarsina, *Chironomus anthracinus* type, *Paratanytarsus*, and *Procladius*. Salt tolerant taxa are situated on the right-side of Figure 4.4 and include *Eukiefferiella devonica* type, *Dasyhelea* type, *Metriocnemus eurynotus* type, *Chironomus plumosus* type, and the Halophilic Orthocladiinae taxon. These taxa were most abundant in ponds with the highest observed salinities.

I compared specific conductance optima and tolerances for midges from my current study with midge-salinity dose response curves produced in earlier in-vitro experiments (see Chapter 3 of this dissertation) (Table 3.2). Unfortunately only 13 taxa were present in both studies: *Polypedilum*, *Glyptotendipes*, *Psectrocladius sordidellus* group, *Cladopelma lateralis* type, other *Cricotopus/Orthocladius*, *Chironomus* group, *Dicrotendipes*, the subtribe

Substantial differences are apparent between the surface sample and in-vitro experiment results. For example, the rank order of the upper salinity tolerances (= WA optimum + tolerance, calculated from the Hudson Bay Lowlands training-set) are not highly correlated with the ranked LD50s observed (Chapter 3). Spearman’s Rank Correlation analysis indicated overall low correlation between the LD50s and WA-upper tolerance values \( r = -0.205 \). Of the taxa observed in both studies, subtribe Tanytarsina had the lowest LD50 \( (2,500 \, \mu S \, cm^{-1}) \) but recorded a moderately high upper salinity tolerance, \( 4,786 \, \mu S \, cm^{-1} \); a higher upper-tolerance than seven other taxa observed in both experiments. Similarly, *Chironomus anthracinus* type recorded the second lowest LD50 \( (5,500 \, \mu S \, cm^{-1}) \) in the in-vitro salinity experiment (see Chapter 3 of this dissertation), but was ranked higher than all but three taxa with respect to its WA upper-tolerance. *Cricotopus/Orthocladius* and *Cladotanytarsus mancus* both had the highest LD50s (both at \( 25,000 \, \mu S \, cm^{-1} \)) after *Dasyhelea* \( (>30,000) \) but had moderate WA upper-tolerances, \( 3,326 \) and \( 7,499 \, \mu S \, cm^{-1} \) respectively. Furthermore, *Glyptotendipes* and *Polypedilum* had the two lowest calculated WA upper-tolerances \( (1,012 \) and \( 1,091 \, \mu S \, cm^{-1}, \) respectively) yet recorded moderately high LD50s (both at \( 15,000 \, \mu S \, cm^{-1} \)), higher than both *Procladius* and *Cryptochironomus*. Despite these discrepancies, the results are comparable in one important regard. *Dasyhelea* had both a very high LD50 \( (>30,000 \, \mu S \, cm^{-1}) \) and a very high WA upper-tolerance \( (14,997 \, \mu S \, cm^{-1}) \); thus, this species may be one of the most reliable indicators of high salinity environments.

Another trend was observed when comparing these two studies. Most taxa had WA upper-tolerance values, as determined by this study, much lower than the observed LD50s (Chapter 3). This trend is expected given the skewed conductivity distributions (toward the fresh end) of the sampled Hudson Bay Lowlands ponds used in this training-set. Another possible explanation for these differences is the differences between acute versus chronic effects of salinity on midges. In-vitro experiments (Chapter 3) effectively measured acute effects and the surface sample data may be a reflection of the chronic exposure effects.

Comparisons between this study and other projects investigating midge-salinity interactions were also made. This study found similarities with Walker et al.’s (1995) British Columbia study regarding the apparent salinity habitat of several taxa. Both this study and
Walker et al. (1995) indicate that *Stempellina* and *Microtendipes* have low salinity thresholds. My findings also indicate that *Procladius*, the subtribe Tanytarsina, *Chironomus*, and *Psectrocladius*, have broad salinity ranges. One major discrepancy between this study and that of Walker et al. (1995) is with regard to *Cricotopus/Orthocladius*. It overwhelmingly dominated the midge fauna (>75% of all midges) at sites with salinities >10 g L<sup>-1</sup> in British Columbia (roughly translating to ≈10,000 μS cm<sup>-1</sup>). Walker et al.’s (1995) result was similar to other observations of midge distributions in Canada (Hammer et al. 1990) and the northwestern United States (Wiederholm 1980). In my study of the Hudson Bay Lowlands, *Cricotopus/Orthocladius* was observed at sites with the highest specific conductance levels (including the highest observed; @ 29,000 μS cm<sup>-1</sup>), but was never dominant. Zhang et al. (2007) also found the *Cricotopus/Orthocladius* group to be dominant in saline waters of the Tibetan Plateau and concluded that midge distribution is largely dictated by environmental factors as opposed to biogeographic constraints.

Because detailed water chemistry analyses were not conducted in this study, caution must be exercised when considering these results. For example, some midge distributions may be dictated by environmental variables not measured in this study, such as DOC and DIC (Langdon et al. 2008). Langdon et al. (2008) suggest that total organic carbon is a major determinant for *Tanytarsus lugens*’ distribution. Medeiros and Quinlan (2011) also found that *Cricotopus intersectus* type, *Endochironomus*, *Cladopelma*, and *Tanytarsus lugens/Corynocera oliveri* gr. were positively correlated with lakes with higher DOC and DIC in a data set composed of 63 ponds of the eastern Canadian Arctic. Furthermore, oligotrophic lakes with low DOC/DIC contents in arctic environments may allow a more intense ultra violet-B penetration, which could effectively limit zoobenthos of these water bodies (Pienitz and Vincent 2000). Medeiros and Quinlan (2011) also found midge community assemblage differences within localized lakes with similar geographic and climatic regimes. One notable difference between lakes with differing midge communities in Medeiros and Quinlan’s (2011) study was nutrient loading by migrating goose populations. These results may emphasize the influence that nutrient availability has on midge assemblages.

Results presented in Figure 4.4 indicate taxon assemblage changes across a salinity gradient. This study, as well as Bos and Pellatt (2012), found that proximity to the Hudson
Bay coast was a major determinant of pond salinity. Considering the ongoing isostatic rebound for the area (Wolf et al. 2006), it is assumed that the saline ponds closer in proximity to Hudson Bay are younger than the freshwater ponds residing farther from the shoreline. Thus, the midge-salinity trends evident in Figure 4.4 portray a hypothetical midge successional pathway for communities as new ponds are generated and uplifted from the sea. I therefore expect that down-core analyses of pond cores in the Hudson Bay Lowlands should reveal a gradual succession of midge communities from halophilous (e.g. *Dasyhelea* and the unidentified ‘Halophilic Orthocladiinae’ taxon) to halophobous taxa (e.g. *Stictochironomus* and *Glyptotendipes*) with rebound and decreasing age. This hypothetical succession will be tested via subsequent down-core analyses: this model will be used in conjunction with four long-sediment cores extracted from the Hudson Bay Lowland, each extracted from ponds at different elevations and distances from the current shoreline. Using this model, abundance analyses of midge remains from the four long-sediment cores should provide a signal of changing sea level (via isostatic rebound) and a landscape evolutionary history of the Hudson Bay Lowlands over the past ≈7,750 years before present.

My results support the use of midges as paleosalinity indicators for the Hudson Bay Lowlands. Although the sampled ponds of this training-set exhibited a skewed distribution toward the fresher end of the gradient, which may result in inferences that are lower than actual, the presence of the unidentified ‘Halophilic Orthocladiinae’ and *Dasyhelea* taxa should indicate highly saline environments in down-core analysis and provide a signal for inferring sea level change in the Hudson Bay Lowlands. This model should provide strong evidence of transitions from saline to freshwater environments and changing sea level in the Hudson Bay Lowlands.

These results are directly applicable to long-term monitoring and the management for ecological integrity of aquatic ecosystems in Wapusk National Park and surrounding lands of the Hudson Bay Lowlands. Understanding how midge communities respond to salinity changes will help conservation practitioners understand the condition of ponds in the region and discriminate between the impacts of relative sea level change as opposed to other environmental stressors. This information will assist better management and monitoring of aquatic resources in the Hudson Bay Lowlands.
Chapter 5: Midge-based reconstructions of salinity and sea-level change for the Hudson Bay Lowlands, Manitoba, Canada

5.1 Background

Since the 1980s, midges (Chironomidae, Ceratopogonidae and Chaoboridae) have been used, perhaps over-confidently, as quantitative paleoclimatic indicators. Surface sample training-sets spanning broad environmental gradients have clearly revealed correlations between midge community composition and temperature, and other environmental variables (e.g., Walker et al. 1997; Olander et al. 1999; Korhola et al. 2000; Brooks and Birks 2001; Dickson and Walker, in press). However, ongoing and more recent scientific endeavours have demonstrated potential pitfalls in the use of transfer function methods (Telford and Birks 2011).

The work presented here assesses the feasibility of using midges as paleosalinity indicators over the past \( \approx 8,000 \) cal. years BP in the Hudson Bay Lowlands. The Hudson Bay Lowlands should provide an ideal location to assess the utility of midges as indicators of paleosalinity and sea level change because the Lowlands have a long and ongoing history of isostatic rebound from submarine conditions.

In this chapter, to make this assessment, I reconstruct salinity change in four Hudson Bay Lowland ponds using a midge-salinity transfer function (presented in Chapter 4) and subsequently test the significance of these reconstructions using newly developed procedures outlined by Telford and Birks (2011).

5.2 Study area

This study was conducted between Churchill and Gillam, Manitoba at sites ranging from 127 masl in the west, to ponds in the east lying adjacent to the current Hudson Bay shoreline (Figure 5.1).

During the Wisconsinan glaciation, the Hudson Bay Lowlands were inundated by Laurentide Ice derived from two separate lobes, the Keewatin and Hudson Lobes (Andrews and Short 1983; Dredge and Nixon 1992). Through the glacial and deglacial phases, natural
Drainage towards the northeast was blocked by Hudson Ice. By \( \approx 10,000 \) cal. years BP, Laurentide Ice was shrinking rapidly and the melt-waters fed a succession of expansive proglacial lakes. Lake Agassiz, the largest of these proglacial lakes, flooded most of Manitoba, and much of Ontario and Saskatchewan as well. The ice sheets decayed in a northerly and easterly direction; thus, this deep proglacial lake persisted as long as Hudson Ice remained grounded in Hudson Bay (Dredge 1983). Lake Agassiz eventually drained between 8,180 to 8,310 cal. years BP (Dredge 1983; Li et al. 2012).

As ice dams failed and glacial melt-water drained from the area to the Atlantic Ocean, marine waters entered the Hudson Basin, creating the Tyrrell Sea. The precise time when marine waters entered Hudson Basin remains unknown, however, the oldest Tyrrell Sea date is derived from shells collected in northern Manitoba (near Churchill), and suggests that the sea had reached the area by 8,530 \( \pm \) 220 cal. years BP (Blake 1970). These shells are thought, however, to yield erroneous dates because the dates are centuries older than other Tyrrell Sea shells in the region, the shell fragments were well worn, and old shells recycled from Bell Sea sediments are fairly abundant in the Hudson Bay Lowlands (Fulton 1989). Other studies suggest that the sea probably occupied the area by 7,800-8,200 cal. years BP (Dredge and Cowan 1989; Li et al. 2012).

The Tyrrell Sea, the ancient predecessor of Hudson Bay, inundated terrain much higher than the present Hudson Bay shoreline owing to glacioisostatic deformation. With isostatic rebound, this high sea regressed to the current bounds of Hudson Bay. Below an elevation of 150 m, the glaciolacustrine sediments of Lake Agassiz are overlain by marine, Tyrrell Sea sediments. Above that elevation, glaciolacustrine sediments form the principal surficial material. Since this northern Manitoba landscape is gradually inclined along the east-west axis, the glaciolacustrine sediments (deposited in glacial Lake Agassiz) are exposed in the western portion of the study area whereas marine sediments (deposited by Tyrrell Sea) overlie the eastern portion below \( \approx 150 \) m elevation (Dredge and Nixon 1992).

Present day rates of emergence for areas near Churchill, Manitoba, as determined by tide gauge, gravimetric evidence and historical records, indicate an 11.4 \( \pm \) 0.7 mm a\(^{-1}\) rebound rate. In order for isostatic equilibrium to be achieved, Hudson Bay still needs to rebound as much as 150 meters (Barnett 1970; Wolf et al. 2006).
Four sediment cores were extracted from four different ponds within the Hudson Bay Lowlands (Figure 5.1). Ponds one and two (yielding Long Core 1 and Long Core 2, respectively) are located at approximately 127 and 60 masl and are 104 and 40 kilometers from the current shoreline of Hudson Bay, respectively. Vegetation around these ponds consists of white and black spruce trees, cotton-grass, lichen and sphagnum mosses.

Twin Lakes Pond and Rocket Lake (yielding the Twin Lakes Pond Core and Rocket Lake Core, respectively) are located at approximately 40 and 10 masl and are 18 and 2.5 kilometers from the current Hudson Bay shoreline, respectively. Twin Lakes Pond is surrounded by spruce forest. The vegetation around Rocket Lake consists of open coastal tundra with stunted white and black spruce trees, willows, cotton-grass, lichen and sphagnum mosses.

Permafrost is almost continuous in this ecodistrict with depths ranging up to 30 m. Polygonal peat plateau bogs covered with sphagnum moss, lichens and low ericaceous shrubs are also abundant in this region. Fens are common throughout. Thermokarst and other ponds are abundant here and Bello and Smith (1990) estimated that >40% of this region is covered with water.

Table 5.1 provides descriptive statistics for the four ponds. Photographs representative of the coring locations are presented in Figure 5.2.
Table 5.1: Descriptive statistics for the four sampled ponds used for reconstructing salinity for the Hudson Bay Lowlands.

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<th>Core Length (cm)</th>
<th>Pond Depth (cm)</th>
<th>Distance to Coast (km)</th>
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<td>1,174.89</td>
<td>10</td>
<td>22</td>
<td>14</td>
<td>2.5</td>
<td>58.75</td>
<td>-93.85</td>
</tr>
</tbody>
</table>
Figure 5.1: Sample locations of four ponds used for quantitatively reconstructing salinity in the Hudson Bay Lowlands. Maps generated using Planiglobe (n.d.) under the Creative Commons Attribution-Share Alike 2.5 license.

Figure 5.2: Photographs of coring locations yielding LC1 and LC2, and representative terrain for TL and RL, respectively.
5.3 Methods
5.3.1 Sediment coring and midge analyses

Sediment cores were collected in four ponds (Table 5.1), mid-basin in 2010. A Brown corer and Livingstone piston corer were used to obtain LC1 and LC2. An HTH corer was used at the other two ponds.

The extracted cores were sectioned into 1 cm intervals in the field, stored in labeled Whirl-Pak® sampling bags, shipped to PaleoLab at the University of British Columbia’s Okanagan (UBCO) campus and stored in a 4°C cold room until analyses were conducted at a later date.

Selected sediment subsamples from each pond were flushed with 10% hydrochloric acid (HCl) to dissolve any carbonates and warmed in 5% potassium hydroxide (KOH) on a hotplate to deflocculate the sediment (Walker et al. 1991a). The residual sediment was sieved on a 93 – 95 µm mesh and subsequently picked for midge remains from Bogorov counting trays under 20× and 40× magnification with Nikon SMZ645 dissection microscopes.

Midge remains were transferred to microscope slides and mounted with Entellan® mounting medium. Midges were identified under 200× and 400× magnification with an Olympus BX51 compound microscope, with reference to Wiederholm (1983), Oliver and Roussel (1983), Walker (1988, 2000), and Brooks et al. (2007).

Midges were identified to the lowest taxonomic group possible and identifications were standardized to those used by Dickson and Walker (in press) for their Hudson Bay Lowland training-set. Due to a lack of distinguishing characteristics most taxa were not identifiable to the species level.

Head capsule fragments without, or less than half, the median teeth were not counted. Those with half the mentum intact were counted as half, and those with more than half the mentum were counted as whole. A minimum of fifty head capsules was counted per interval of sediment (Walker et al. 1995; Quinlan and Smol 2001) and taxon data were analyzed as percent abundances, without square-root transformations, in all analyses.

For salinity reconstructions I employed the midge-specific-conductance transfer function developed in the preceding chapter.

Midge stratigraphic diagrams and salinity reconstructions were plotted using TILIA version 1.7.16 (Grimm 2011). The significance of each salinity reconstruction was assessed
using methods outlined by Telford and Birks (2011). Briefly, this method uses constrained ordinations to determine the proportion of variance in the subfossil data explained by a single reconstruction. Then, using the biotic data from the same training-set, a series of mock reconstructions were inferred using transfer functions trained on randomly generated “environmental variables” with permutation methods (999 permutations). The proportion of variance explained by these mock reconstructions is compared to that explained by the actual reconstructions. Reconstructions were deemed ‘statistically significant’ if the actual reconstructions explained more variance than 95% of the mock reconstructions. Significance testing was performed using the statistical language ‘R’ version 2.11.1 (R Development Core Team 2010).

5.3.2 Chronology

For all cores, surface sediments were assumed to be of modern age. Eight down-core samples were submitted to PALEOTEC Services for macrofossil identification and later submitted for AMS $^{14}$C dating at the Keck Carbon Cycle AMS Facility at the University of California, Irvine. Ages were calibrated to ‘calibrated years before present’ (cal. years BP) using the software CALIB 5.0.2, available online at http://radiocarbon.pa.qub.ac.uk/calib (Stuiver and Reimer 1993). All materials were dated using standard AMS $^{14}$C procedures.

These dates were considered in combination with other dates derived from tide-gauge, GPS and gravimetric evidence compiled in earlier studies near Churchill, Manitoba (Wolf et al. 2006). Thus, these data provided a basis for age-depth modeling within each core and contribute data relevant to age-elevation modeling (a sea level curve) for the study region.

Elevation data for my ponds was acquired using a GPS receiver (reported as meters above sea level (masl)) and the basal age of each core was estimated by linear or curvilinear regression, with extrapolation to the core base. The distances from each sampled pond to the current Hudson Bay shoreline were estimated using the ruler tool in Google Earth®.

One AMS $^{14}$C date (obtained from a wood stem in LC2 at 108-109 cm depth indicating an age of 42,520 cal. years BP) was omitted from these analyses because the age was much older than would be expected for this region. One other date was eliminated
(obtained on a spruce needle from the TL core at 28 – 29 cm depth) because it yielded a modern (post-1950) age.

5.4 Results

Midge stratigraphic diagrams and sediment lithologies for the four cores (LC1, LC2, TL and RL) are presented in Figures 5.3, 5.4, 5.5 and 5.6, respectively.

5.4.1 Long Core 1 (LC1)

Core LC1 was 132 cm long. From 132 to 106 cm depth the sediments consist of grey, silt-sand sediment and progressively become more organic upwards, transitioning into peaty-gyttja at about 100 cm. Another organic rich, silt-sand interval is present from 92 to 90 cm. From 89 to 64 cm the core is again comprised of grey, silt-sand and becomes progressively enriched with organics upwards to 60 cm. Above 60 cm the core largely consists of peaty-gyttja.

Two AMS $^{14}$C dates were obtained from LC1 (Table 5.2). The oldest date (7,310 cal. years BP) was derived from moss at the bottom of the core (129 – 130 cm). In addition, a larch needle at 15 cm depth was dated at 1,010 cal. years BP and the surface sediment is assumed to be modern.

An age depth model fitted to the assumed surface age and the radiocarbon dates for this core projects a basal age of approximately 7,420 cal. years BP (Figure 5.7). Results of Wolf et al. (2006) suggest that the LC1 coring location (127 masl) was at, or near, sea level $\approx$7,750 cal. years BP.

Table 5.2: AMS $^{14}$C dates from four sediment cores extracted from Hudson Bay Lowlands.

<table>
<thead>
<tr>
<th>Core Code</th>
<th>Sample Depth (cm)</th>
<th>AMS $^{14}$C age</th>
<th>Calibrated (year BP)</th>
<th>Material</th>
</tr>
</thead>
<tbody>
<tr>
<td>LC1</td>
<td>15-16</td>
<td>1,100</td>
<td>15</td>
<td>1,010 Larch needle</td>
</tr>
<tr>
<td>LC1</td>
<td>129-130</td>
<td>6,380</td>
<td>50</td>
<td>7,310 Moss</td>
</tr>
<tr>
<td>LC2</td>
<td>0-1</td>
<td>-1,260</td>
<td>15</td>
<td>0 Spruce needle</td>
</tr>
<tr>
<td>LC2</td>
<td>47-48</td>
<td>3,540</td>
<td>30</td>
<td>3,830 Spruce needle</td>
</tr>
<tr>
<td>LC2</td>
<td>108-109</td>
<td>38,250</td>
<td>700</td>
<td>42,520 Woody stem</td>
</tr>
<tr>
<td>TL</td>
<td>12-13</td>
<td>535</td>
<td>15</td>
<td>540 Wood fragment</td>
</tr>
<tr>
<td>TL</td>
<td>28-29</td>
<td>-615</td>
<td>15</td>
<td>0 Spruce needle</td>
</tr>
<tr>
<td>RL</td>
<td>9-10</td>
<td>230</td>
<td>15</td>
<td>280 Spruce needle</td>
</tr>
</tbody>
</table>
Twenty-nine subsamples were analyzed for midge remains. In total thirty-seven taxa were identified. Of the twenty-nine subsamples analyzed, four subsamples (123 – 124, 119 – 120, 115 – 116, and 110 – 111 cm) yielded no midge remains. Subsamples 129 – 130, 130 – 131, and 131 – 132 cm were combined into one interval (129 – 132 cm) due to overall low subfossil counts. Similarly, subsamples 105 – 106, 106 – 107, and 107 – 108 cm and subsamples 91 – 92 and 92 – 93 cm were also amalgamated to form larger samples (105-108 cm and 91 – 93 cm, respectively). The sediments comprising these intervals largely consisted of silt-sand (Figure 5.3).

Midge assemblages for LC1 are shown in Figure 5.3 together with lithology and calibrated AMS ¹⁴C dates. Midge remains were present in the basal sediments of this core (129 - 132 cm), however none were found between that interval and 108 cm depth. The most salt tolerant taxon in the Hudson Bay Lowlands training-set (Dickson and Walker, in press), Halophilic Orthocladiinae, was most abundant in the basal sediment of LC1. Only low abundances of freshwater taxa were counted in the basal portion of this core. The middle portion of the core appears to be dominated by taxa with wide salinity tolerances. A freshwater taxon, Polypedilum was observed at 60 cm depth and became increasingly abundant in the upper portion of the core.

Generally, there appears to be a shift in the midge fauna from the bottom to the top of the core suggesting a gradual salinity change. The quantitative salinity reconstruction infers relatively high salinity in the bottom portion of the core and the lowest salinity at the top (decreasing from 2,400 to 60 μS cm⁻¹; Figure 5.8). The salinity decrease appears slight through most of the core, with an abrupt decrease since 563 cal. years BP, near the core top (salinity decreases from 1,700 to 60 μS cm⁻¹ in the upper most 10 cm). Significance testing indicated that the reconstruction is not statistically significant (α=0.05).

At the time of sampling, the specific conductance was measured as 200 μS cm⁻¹, higher than the salinity (≈60 μS cm⁻¹) inferred from the core top (Figure 5.8). The highest salinity (6,000 μS cm⁻¹) was inferred for the 93-94 cm interval, dating approximately 5,230 cal. years BP.
Figure 5.3: Midge percentage diagram for Long Core 1. Freshwater taxa are situated on the left and salt tolerant taxa are on the right-hand side of the figure. Depth bars indicate the relative abundances of each taxon for the specified interval (depth) of the sediment core. Calibrated AMS $^{14}$C dates, depth (cm) and lithology indicators are presented on the left and a CONISS (total sum of squares) diagram is situated on the right side of the figure.
5.4.2 Long Core 2 (LC2)

LC2 is 112 cm long. Silt-clay dominates the basal portion from 112 to 95 cm depth. This is overlain by a grey silt layer (94 and 95 cm) and by silty-gyttja above 54 cm. Clam shells are present in the peat-gyttja above 10 cm in LC2 (Figure 5.4).

Three radiocarbon dates provide the basis for the LC2 chronology (Table 5.2). Unfortunately, a date obtained from a woody stem at 108 – 109 cm provided a date of 42,520 cal. years BP; much older than could reasonably be expected. Two dates from spruce needles were obtained at 0-1 and 47-48 cm depth, respectively yielding a modern age and ≈3,830 cal. years BP. Discarding the 42,520 cal. years BP date, the remaining two dates were used to construct a linear age-depth model. Extrapolation of this model yields a basal age of approximately 9,105 cal. years BP (Figure 5.7). Results of Wolf et al. (2006) suggest that the LC2 coring location (60 masl) was at, or near, sea level about 5,400 cal. years BP.

Fifty subsamples were analyzed yielding a total thirty-two midge taxa. Only seven midge subfossils were extracted from the bottom-most 57 cm. Therefore, no reconstructions were possible for the bottom half of this core.

Midge assemblage changes for LC2 appear to be congruent with those from LC1 in several portions of the core. The midge stratigraphy (Figure 5.4) indicates little change in the midge fauna. The reconstructed salinity (Figure 5.8) suggests a freshening trend from 650 to 350 μS cm⁻¹ from 53 cm depth to the top sediments. Salinity inferences remained near 500 μS cm⁻¹ from 53 to 10 cm depth, then increased to 1370 and subsequently declined to 350 μS cm⁻¹ at the core surface (Figure 5.8). The uppermost salinity inference (350 μS cm⁻¹) is higher than that measured during core collection (250 μS cm⁻¹). Significance testing indicated that this reconstruction is not statistically significant (α=0.05).

5.4.3 Twin Lakes Pond (TL)

This core is 35 cm long. Coarse sand and fine-grained pebbles comprise the bottom-most sediments from 35 to 28 cm. A gradual change to more organics and angular pebbles is observed from 27 to 20 cm. At 19 cm depth, a rock layer was present. Thereafter the sediment consists of gyttja with small pebbles transitioning first to light brown gyttja at 14 cm and dark brown gyttja at the core top (Figure 5.5).
Figure 5.4: Midge percentage diagram for Long Core 2. Freshwater taxa are situated on the left and salt tolerant taxa are on the right-hand side of the figure. Depth bars indicate the relative abundances of each taxon for the specified interval (depth) of the sediment core. Calibrated AMS $^{14}$C dates, depth (cm) and lithology indicators are presented on the left and a CONISS (total sum of squares) diagram is situated on the right side of the figure. Note, no midges were observed from 55 to 112 cm depth, thus, no reconstructions are shown for the bottom half of this core.
Figure 5.5: Midge percentage diagram for the TL core. Freshwater taxa are situated on the left and salt tolerant taxa are on the right-hand side of the figure. Depth bars indicate the relative abundances of each taxon for the specified interval (depth) of the sediment core. Calibrated AMS $^{14}$C dates, depth (cm) and lithology indicators are presented on the left and a CONISS (total sum of squares) diagram is situated on the right side of the figure.
Two AMS $^{14}$C dates were obtained for this core (Table 5.2). A wood fragment at 12 – 13 cm depth indicated an age of 540 cal. years BP. A spruce needle at 28 – 29 cm indicated a modern age, suggesting that this sample may have been contaminated during core collection or extraction. The modern date was discarded from further consideration.

A linear age depth model for this core was constructed using the assumed modern age of the surface mud and the 540 cal. years BP date at 12 -13 cm. Extrapolation of this model yields a basal age of approximately 1,580 cal. years BP (Figure 5.7). Results of Wolf et al. (2006) suggest that the TL coring location (40 masl) was at, or near, sea level ≈3,600 cal. years BP.

Thirteen midge subsamples were analyzed, and twenty midge taxa identified. No midges were observed in the basal 5 cm, which consisted largely of sand. Ceratopogonid remains were confined to the two basal samples. *Cricotopus/Orthocladius* remains decline markedly in abundance through the core, whereas *Dictrotendipes* and Tanytarsina increase (Figure 5.5).

The quantitative salinity reconstruction indicates that salinity was more or less stable for the entire record, fluctuating only from 430 $\mu$S cm$^{-1}$ at 29.5 cm depth to 910 $\mu$S cm$^{-1}$ at 0.5 cm depth (Figure 5.8), with a slight salinity increase from bottom to top. The salinity measured at this pond during core collection was 240 $\mu$S cm$^{-1}$, lower than the uppermost inferred value (910 $\mu$S cm$^{-1}$ at 0 to 0.5 cm depth).

Significance testing indicated that this reconstruction is not statistically significant ($\alpha=0.05$).

### 5.4.4 Rocket Lake (RL)

The RL core was 22 cm long, with coarse sand comprising the bottom 3 cm (from 22 to 19 cm depth). Sandy-silt occurs from 19 to 15 cm depth, and mollusc shells, possibly of marine origin, were noted at 18 to 17 cm depth. At 15 cm a rock layer is present. Peat-gyttja was evident from 15 to 9 cm, where another rock layer was found. Peat-gyttja with shells, possibly of marine origin, formed the top 8.5 cm (Figure 5.6).
Figure 5.6: Midge percentage diagram for the RL core. Freshwater taxa are situated on the left and salt tolerant taxa are on the right-hand side of the figure. Depth bars indicate the relative abundances of each taxon for the specified interval (depth) of the sediment core. Calibrated AMS $^{14}$C dates, depth (cm) and lithology indicators are presented on the left and a CONISS (total sum of squares) diagram is situated on the right side of the figure.
One AMS $^{14}$C date (280 cal. years BP) was obtained at 9 – 10 cm depth. This date was used together with the assumed modern age of the surface sediment to construct a linear age depth model (Figure 5.7). Extrapolation of this model yields a basal age of approximately 685 cal. years BP (Figure 5.7). Results of Wolf et al. (2006) suggest that the RL coring location (10 masl) was at, or near, sea level about 1,000 cal. years BP.

A total twenty-five midge taxa were identified from eleven intervals in the RL sediment core. No midges were obtained from the bottom 2 cm of the RL core. The bottom half of the core appears to contain more mesohaline to freshwater taxa. From 8 to 3 cm, freshwater taxa gradually decline as a slight increase in salt tolerant taxa occurs.

The quantitative salinity reconstruction indicates a stable salinity environment with the largest difference noted from 10.5 to 2.5 cm depth when inferred salinity decreased from 1,620 to 340 μS cm$^{-1}$ (Figure 5.8). The inferred salinity for the uppermost sediments (550 μS cm$^{-1}$) was lower than that measured at the time of sampling (1,170 μS cm$^{-1}$).

Significance testing indicated that this reconstruction is not statistically significant ($\alpha=0.05$).

### 5.4.5 Age-elevation model

The absence of datable organic matter in the bottom portions of most of the sampled ponds hindered the construction of reliable age-depth models for each core and an age-elevation model for the area. Ideally, to produce an accurate age-elevation model, AMS $^{14}$C dates would be obtained from the bottom sediments of each core, providing a basis for estimating the time of its inception from Hudson Bay.

Linear extrapolations of each age-depth model (based on very limited data for each) suggest that ponds LC1, LC2, TL and RL were at, or near, sea level approximately 7420, 9105, 1580 and 685 cal. years BP, respectively. These inferred ages of basal sediments provide estimated times for each pond’s inception from the sea. Rebound rates were then estimated by dividing the elevation difference between two ponds by the estimated time-difference between each pond’s inception (mm a$^{-1}$). My age-elevation model suggests that rebound rates (via isostatic rebound) for the Hudson Bay Lowlands were approximately -39.9 (note the negative number), 2.9, 31.3, and 13.4 mm a$^{-1}$ from approximately 9100 to 7420,
7420 to 1580, 1580 to 685 and 685 cal. years BP to present, respectively. These suggested rebound rates are not consistent with the expectation that isostatic rebound occurs at an exponentially declining rate. The rate of sea level rise since inception of Rocket Lake (685 cal. years BP: 13.4 mm a\(^{-1}\)) approximates the current rebound rate, 11.4 mm a\(^{-1}\), estimated by Wolf et al. (2006).

Data compiled by Wolf et al. (2006), suggest that ponds yielding cores LC1, LC2, TL, and RL were at, or near, sea level approximately 7750, 5400, 3600 and 1000 cal. years BP, respectively (Figure 5.9). Given these assumed dates of inception, isostatic rebound rates can be estimated for the area as 28.5, 12.2, 10.7 and 9.4 mm a\(^{-1}\) from 7750 to 5400, 5400 to 3600, 3600 to 1000, and 1000 cal. years BP to present, respectively. These rates, estimated from the Wolf et al. (2006) data, do not correspond well with estimates derived from my own data.

**Figure 5.7:** Age-depth models for LC1, LC2, TL, and RL cores. X-axes depict age (calibrated years before present). Y-axes depict depth (cm) of core. Blue diamonds indicate ages obtained from this study. Red squares indicate ages adopted from Wolf et al. (2006).
**Figure 5.8:** Quantitative salinity reconstructions for LC1, LC2, TL, and RL cores. X-axes depict reconstructed specific conductance values (back-transformed $\mu$S cm$^{-1}$). Y-axes depict depth (cm) of core and associated ages (cal. years BP) obtained by AMS $^{14}$C dating.
Figure 5.9: Relative sea-level diagram for the Hudson Bay Lowlands reproduced from Wolf et al. (2006). A black trend-line has been added to portray approximately how sea level is likely to have changed based on the Wolf et al. (2006) data. Red dotted lines have also been added indicating elevations of the four long-core study sites and the expected ages for these ponds’ inception, based on the trend line.

Regression analysis of the estimated basal ages of the four long-cores (my data) against ages for each pond’s inception, as estimated using Wolf et al.’s (2006) data, yields an \( r^2 = 0.68 \) (Figure 5.10). Fitting a 1:1 line through these data, reveals that both studies yield similar ages for both LC1 and RL: however, the estimated ages for TL and LC2 differ greatly. The Wolf et al. (2006) data implies that site TL rose above sea level earlier than my data. In contrast, my data suggest that LC2 formed earlier than what the Wolf et al. (2006) data would imply.
5.5 Discussion

Although none of the reconstructions were deemed ‘statistically significant’ ($\alpha = 0.05$), this most likely reflects problems inherent principally to site selection for core extraction, not the midge-salinity inference model. Provided the right circumstance, the training-set method should yield inferences valuable for interpreting salinity change and isostatic adjustments in the Hudson Bay Lowlands. Nevertheless caution is essential when interpreting the quantitative results.

The midge-salinity transfer function constructed for the Hudson Bay Lowlands (see Chapter 4 of this dissertation) and employed for these reconstructions has one notable deficiency. Few ponds with high specific conductance were included in the training-set; thus, large errors accompany high salinity inferences, hindering accurate reconstructions. Interpretations of the quantitative reconstructions should be conducted in this light.

A particularly vexing problem is the open landscape and very low topographic relief of the Hudson Bay Lowlands, enabling un-impeded windstorms. Severe storm conditions...
were noted during coastal field excursions. Given the frequency of extreme storms in this environment and the characteristic shallow bathymetry of Lowland lakes and ponds, these basins are typically polymictic, allowing flocculent surficial sediments to be re-suspended, leading to loss of temporal resolution. Furthermore, many of the coastal ponds are heavily used by wildlife, ranging from waterfowl (e.g., Canada Geese and Snow geese) to caribou and polar bear. Thus, pond sediments are subject to greater mixing potential, and the temporal resolution of their records may be compromised. Given these shortcomings the quantitative salinity reconstructions are likely to yield an imperfect representation of salinity changes through time. Nevertheless, the general salinity trends reconstructed for each pond may still be informative.

Although not statistically significant, the salinity reconstruction trends for the two inland ponds (LC1 and LC2) are consistent with my hypothesis that ponds in the Hudson Bay Lowlands contained more dissolved salts during their inception and became fresher over time as isostatic rebound uplifted them from the sea. Overall, these ponds exhibited freshening trends (ranging from 6000 to 60 μS cm\(^{-1}\) for LC1 and from 650 to 350 μS cm\(^{-1}\) for LC2) (Figure 5.8). However, the largest inferred change in both cores was not at pond inception, as expected, but rather only since 500-800 cal. years BP (ranging from 2400 to 60 μS cm\(^{-1}\) for LC1 and ranging from 1370 to 350 μS cm\(^{-1}\) for LC2). The inferred change over the past 500-800 cal. years BP does not correlate with any documented wet periods for the area. Thus, it is not obvious to me what the driving force for freshening could be.

Quantitative salinity reconstructions for the two coastal ponds (TL and RL) indicate overall stable salinities (ranging from 430 to 910 μS cm\(^{-1}\) for TL and from 760 to 570 μS cm\(^{-1}\) for RL) for the entire sediment records. Overall, relatively low salinities (compared to Hudson Bay; @ ~ 40,000 μS cm\(^{-1}\)) were inferred for the bottom portions of each core. Of note, thermokarst activity is common in the area (Bello and Smith 1990) and may be responsible for the creation of many Hudson Bay Lowland ponds.

The dearth of radiocarbon dateable organic matter in the bottom portions of most cores hinders the construction of reliable age-depth models at each of my sampled sites, and an age-elevation model (sea level curve) for the area. Ideally, to produce accurate age-depth models, AMS \(^{14}\)C dates would be obtained from the bottom sediments of each core; thus, providing a strong basis for estimating the time of pond inception.
Linear extrapolation of my age-depth model (based on limited data) suggests that bottom sediments of LC1, LC2, TL and RL were deposited approximately 7420, 9100, 1580 and 685 cal. years BP, respectively. The LC2 age-depth model implies LC2’s inception prior to LC1’s. These theoretical dates of inception for each pond are not consistent with my hypothesis, which assumes that ponds at higher elevations, and farther from Hudson Bay were uplifted prior to those in closer proximity to the coast. The large gaps in the dated sequences, especially regarding LC2, are clearly a problem, since sedimentation rates, especially in the early phases of pond development, are unlikely to be linear. Consequently, the dearth of AMS ¹⁴C dateable material in each core, and potential sediment mixing in the sampled ponds are important sources of error. Based on my age-elevation model, isostatic rebound rates are calculated as -39.9, 2.9, 31.3 and 13.4 mm a⁻¹ from approximately 9100 to 7420, 7420 to 1580, from 1580 to 685 and 685 cal. years BP to present, respectively.

Although no comparable sea level studies have been conducted using midge fossils, similar studies have been completed using diatoms. For example, a diatom study aimed at reconstructing sea level and isostatic rebound rates for areas encompassing Kuujjuaq, northern Québec, Canada indicated that deglaciation occurred approximately 7000 cal. years BP. The area experienced continuous and rapid emergence in the order of 57 - 58 mm a⁻¹ until 4800 – 4300 cal. years BP. Thereafter, emergence slowed to a rate of approximately 9 mm a⁻¹ (Pienitz et al. 1991).

Pienitz et al’s (1991) study included the extraction of two sediment cores, both of which contained a sediment sequence indicative of marine sediments overlain by lacustrine sediments, suggesting emergence of the basins from a postglacial sea. The rapid transition from marine to freshwater conditions was readily apparent in the diatom stratigraphies. I had expected to find similar results in the Hudson Bay Lowlands using midges.

Pienitz et al. (1991) also implicate unstable depositional conditions and mechanical reworking of sediment in their study area. Further, Lauriol (1982) suggested that isostatic rebound in the Rivi ère B é rard Valley near Tasiujaq (120 km west of Kuujjuiq) reached about 56 mm a⁻¹ between 7000 and 5000 cal. years BP.

In general, the emergence curves constructed by Lauriol (1982), Pienitz et al. (1991) and Wolf et al. (2006) resemble each other, portraying rapid emergence after
deglaciation, followed by a subsequent decreased rate of isostatic rebound. Although the rate of change for these relative sea level curves varies geographically due to proximity to the main ice loading centre of the Laurentide ice sheet and viscosity of subsurface materials of each study area, the drastic differences between my calculated rebound rates and the other studies mentioned here demonstrate a major incongruity.

Evaluating the estimated ages of bottom sediments for the four long-cores produced via my data and with those of Wolf et al. (2006) reveals incongruity between the two studies. Although basal age estimates derived from the two studies’ data for LC1 and RL compare favourably, my age estimates are younger than those estimated using Wolf et al.’s (2006) results for TL and older than those predicted by Wolf et al. (2006) for LC2. These results also suggest that my data may predict an age much too old for bottom sediment of LC2, when compared to those predicted by Wolf et al. (2006). This is likely an artifact of the lack of datable material from bottom portions of the LC2 sediment core and an inaccurate age-depth model.

5.6 Summary

The main purpose of this study was to examine the usefulness of midges as indicators of sea-level change and isostatic rebound in the Hudson Bay Lowlands. Paleosalinity reconstructions for four Hudson Bay Lowland ponds suggest that the extracted sediment cores did not capture the expected transition from marine to freshwater environments associated with isostatic rebound and pond inception. Thermokarst pond generation and wind induced sediment reworking may have generated unfavourable conditions for such reconstructions. Further, the lack of $^{14}$C datable materials in each core hindered good reconstructions.

Significance testing of the quantitative salinity reconstructions for four ponds in the Hudson Bay Lowland indicates that the reconstructed values are not statistically significant ($\alpha=0.05$). Although these results are not significant ($p \leq 0.05$), this likely reflects the problem of identifying suitable coring locations, rather than deficiencies with the midge-salinity inference model or, more generally, the calibration function approach currently employed by paleoecologists.
Estimated ages of basal sediments produced from my data for LC1 and RL were approximated the expected ages of these ponds’ inception as estimated using Wolf et al. (2006) data; a relative sea level study for the Hudson Bay Lowlands utilizing tide-gauge, GPS and gravimetric evidence. Salinity reconstructions for LC1 and RL are similar for corresponding times, generally, indicating overall freshening.

My findings demonstrate the importance of careful site selection during training-set design and long-core extraction. Although it is important to maximize the gradient of the variable of interest, I also sense that equal importance should be granted to evenly sampling across the gradient to avoid training-sets with skewed distributions. Also, most importantly, sample sites must be chosen for their undisturbed sediment records. Diligent sample site selection for long core extraction may prove beneficial for obtaining complete and undisturbed reconstructions.
Chapter 6. Conclusions

The research comprising this dissertation has assessed midges as paleotemperature and paleosalinity indicators from three distinct projects.

In-vitro experiments have demonstrated that midge taxa are directly influenced by both temperature and salinity. Temperature experiments suggest that midge taxa separate themselves within lake environments (littoral, sub-littoral or profundal zones), potentially based on their affinities for cooler or warmer temperatures and that temperature variability, with respect to their chosen habitat, may impact their development, survival, and emergence. My temperature experiments suggest that most taxa achieve optimal development at cooler temperatures and are cued for emergence by, and require, warming temperatures. My results also indicate that threshold temperatures may cue emergences rather than accumulated degree-days. Exposure to temperatures that are too warm may also result in developmental stress and sometimes death of some midge taxa. Emergence events from each experimental aquarium appeared synchronous. Finally, my results indicate that midge taxa may have relatively narrow optimal temperatures at which development and emergence can occur.

Further, in-vitro midge-salinity LD50s were assessed. The results suggest that high salinity environments are lethal for some taxa but not others. These results support my hypothesis: midge taxonomic assemblages are regulated by physical and chemical properties (i.e., temperature and salinity) of lake-water, thus, midge subfossil remains will likely reflect changes in these variables. These results suggest that salinity and temperature, perhaps in combination with other variables, dictate midge assemblages in lakes.

Through the use of multivariate statistical methods, including ordination, log-transformed specific conductance (a function of salinity) was determined to be an environmental variable strongly and significantly influencing midge communities in the Hudson Bay Lowlands. This finding further supports my hypothesis and the continued use of midges as paleosalinity indicators. Weighted Averaging Partial Least Squares modeling provided the most effective means for developing a salinity transfer function based on subfossil midge remains (WA-PLS 2 component: $r^2_{\text{boot}} = 0.682$; RMSEP$_{\text{boot}} = 0.482$; Max Bias$_{\text{boot}} = 0.684$). Although the model appears to be robust, the addition of more ponds to the training-set, particularly those with elevated salinities, could have a beneficial impact on
model performance and thus on the confidence with which salinity levels can be reconstructed. The addition of more high salinity ponds to the data-set could address the biased composition of the 63-pond training-set which currently exhibits a strongly skewed distribution. Freshwater ponds are over-represented in the training-set; thus the model may greatly underestimate specific conductance during the most saline phases of pond development.

Further, this training-set demonstrated midge taxon segregations across a broad salinity gradient, yielding a ‘space for time’ representation of pond development following progressive isostatic uplift and isolation from the sea. The apparent succession across this salinity gradient is associated with elevation and proximity to Hudson Bay (space). This successional pattern, as perceived spatially, can potentially be tested via down-core analysis where actual midge assemblage and salinity changes are recorded as subfossil remains in sediments (time).

Together, these in-vitro experiments and the surface sediment survey demonstrate the potential of midges as paleosalinity indicators.

The midge-salinity inference model was applied to subfossil midge assemblages from four sediment cores collected from Hudson Bay Lowland ponds. The history of midge community composition and salinity change for all four ponds was then quantitatively reconstructed. These salinity reconstructions, potentially, provide the basis for inferring sea level history and isostatic rebound rates for the Hudson Bay Lowlands.

Unfortunately, quantitative salinity reconstructions for LC1, LC2, TL, and RL did not capture the highly saline phase expected during each pond’s initial formation. Although quantitative salinity reconstructions for LC1 and LC2 suggest freshening trends, the salinity reconstructions lack statistical significance, and the largest decrease in the salinity inferences is recent, long after the basins’ catchments were likely uplifted from the Bay. These ponds were possibly formed via other processes, perhaps through thermokarst action.

Results such as these emphasize the importance of thoughtful site selection with respect to both training-set development and long-core analyses. Although maximizing training-set gradient length for variables is extremely important, the entire gradient should be uniformly sampled to facilitate accurate quantitative reconstructions.
Although we never know with certainty what to expect when extracting long sediment cores, diligent advance planning for field work, including consultation with local experts, perusal of aerial photography (e.g., via Google Earth), and experience, are invaluable for success in these challenging landscapes. Long cores from deeper, more sheltered basins are likely to yield better results, if such sites can be identified.

Significance testing of the quantitative salinity inferences indicates that my reconstructed values are not statistically significant ($\alpha=0.05$). Although these results are not significant ($p \leq 0.05$) the issue is most likely a reflection of long core site selection, not the midge-salinity inference model or, more generally, the calibration function methods currently employed by paleoecologists.

Important issues to address in future work are deficiencies in sample site selection, inadequate dating chronologies (a dearth of dateable materials), and model improvements (expansion of the training-set to include more sites from highly saline environments). My results are informative and provide a starting point for future subfossil midge analyses in the Hudson Bay Lowlands.
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