A QUANTITATIVE MIDGE-BASED RECONSTRUCTION OF THERMAL CONDITIONS IN CENTRAL COLORADO DURING MARINE ISOTOPE STAGE 5

by

DANIELLE RENEE HASKETT

(Under the Direction of David Porinchu)

ABSTRACT

Subfossil chironomid analysis was used to establish the efficacy of adding chironomid assemblages from Colorado to the Great Basin (GB) midge calibration set. The most robust inference model was developed using a 2-component weighted averaging-partial least squares and the calibration set was incorporated into the GB training set. It was used to develop a midge-based mean July air temperature (MJAT) inference model with a robust jack-knifed r^2 (0.61) and root mean square error of prediction (0.97°C). This inference model was applied to a midge stratigraphy and enabled the development of a quantitative reconstruction of MJAT from ~70 – 140 ka for the Ziegler Reservoir fossil site near Snowmass Village, Colorado. Reconstructed temperatures ranged from 8.9 – 13.2°C. The transition from MIS 6 to MIS 5e was characterized by an increase in the MJAT of ~1.5°C (9.0-10.5°C). MIS 5 exhibited increasing midge-inferred MJAT, culminating in a MJAT of 13.2°C during MIS 5a.

INDEX WORDS: Chironomid, midge, inference model, calibration set, Ziegler Reservoir Fossil Site, Colorado, Rocky Mountains, Sangamon Interglacial

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DEDICATION

This work is dedicated to my family and friends who have supported me throughout this crazy and wonderful endeavor. The writing group from the cohort of 2011 deserve a big thank you for keeping me constantly on my toes and aware of the next looming deadline. Also, a special thank you to my advisor, Dr. David Porinchu for introducing me to the wonderful world of chironomids.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

In October 2010, the remains of a *Mammuthus columbi* (Columbian mammoth) were discovered during the excavation of the Ziegler Reservoir near Snowmass Village, Colorado. A systematic excavation of the site during the months that followed led to the recovery of over 5,400 fossils of Pleistocene megafauna and microfauna, including *Mammut americanum* (American mastodon), *Bison latifrons* (Giant Ice Age Bison) and a *Megalonyx jeffersonii* (Jefferson's Ground Sloth) as well as smaller vertebrates, invertebrates, insects and plant matter. The locality, which has become known as the Ziegler Reservoir fossil site (ZR), is located at 2,705 m above sea level (asl). The importance of the locality is, in part, due to the diverse Ice Age ecosystem that is captured and documented by the very well-preserved biota. Another notable feature of the site is that it is characterized by a lengthy and relatively complete sediment sequence of fossil bearing strata. The sediment sequence recovered from ZR spans approximately 85.5 ka (55.1 – 140.6 ka). Determination of the age of the ZR sediment sequence is based on optically stimulated luminescence (OSL) dating of eolian deposited fine-grained quartz crystals (Mahan et al. *under review*).

Alpine and sub-alpine environments are particularly sensitive to climate change (Haeberli and Beniston, 1998; Dahe et al., 2006; Chen, et al., 2011; Elliot, 2012). This site offers the opportunity to address how high elevation ecosystems in the western United States responded to past warm periods (Reinemann et al., 2009) and recent warming (Porinchu et al., 2010). The sediment sequence recovered from ZR extends through the previous interglacial, which is known as the Sangamon Interglacial or marine isotope stage 5 (MIS 5). The Sangamon Interglacial was characterized by a climate that was analogous to or even warmer than present (Anklin et al., 1993; Bauch et al., 2011; Goñi et al., 2012). Evidence suggests that global sea-level was between 4 m to 9.4 m higher than the present (Goñi et al., 2012). Glaciological and geomorphological evidence from the Rocky Mountains presents a more complex regional picture (Porter et al., 1983; Pierce, 2003). Although there have been a number of studies conducted on moraines (Licciardi et al., 2001; Gosse and Philips, 2001), hydration rinds in obsidian clasts (Pierce et al., 1976) and river terraces in this region (Pierce, 2003; Sharp et al., 2003), very few of them have documented the nature of climate and environmental conditions that existed during the Sangamon Interglacial. For example, a recent study of loess deposits near Jackson Hole, Wyoming suggest a period of extensive weathering occurred during MIS 5e, correlating to an interval of elevated temperature (Pierce et al., 2011). To date, no studies have directly quantified thermal variability during MIS 5 in the Colorado Rockies (Pierce et al., 2011).

Analyses of the sub-fossil midge remains preserved in the ZR sediment will enable the development of a quantitative reconstruction of past thermal conditions and provide a means to determine the magnitude of temperature change during MIS 5. Collaboration with scientists associated with the larger Snowmastodon research team will also enable a determination of whether midges and vegetation, as inferred from pollen, experience a differential response to environmental or climate forcing. Studies suggest that midge-inferred climatic shifts typically occur near-synchronously with pollen-inferred vegetation change, especially when the ecological responses are driven by “spatially coherent and abrupt climate changes.” (Williams et al., 2011). However, other studies indicate that chironomids respond to climatic warming more quickly than vegetation (Pellatt, et al., 2000; Seppä et al., 2002; Dalton et al., 2005; Velle et al., 2005). For example, Porinchu and Cwynar (2002) identify the existence of an 1800 year lag between when inferred summer temperatures became sufficiently high enough to support coniferous trees and when trees arrived locally in northeast Siberia. Birks and Birks (2008) also found that biotic assemblages responded much quicker to climate amelioration than vegetation. In addition, Velle et al. (2005) and Dalton et al. (2005) identify that the influence of chemical and physical changes in the watershed or catchment on midge community composition leads to a lag in the response of the midge community to changes in vegetation during transitions from warmer to colder conditions. Taken together it is clear that biological proxies such as midges will experience a differential response to climate forcing and that this response depends largely on local conditions and the type of forcing occurring. Paleoenvironmental reconstructions based on pollen and macro-fossil analysis, which are currently underway, are important components of the ZR project (Anderson et al. *under review*). Comparison of the vegetation reconstructions to the observed changes chironomid composition may help identify whether aquatic and terrestrial proxies respond synchronously to external forcing.

PALEOLIMNOLOGY APPROACH

The preservation of physical, geochemical and biotic proxies in lake sediment archives provides researchers with the opportunity to develop detailed, high-resolution reconstructions of past environmental and climatic changes (Walker, 1987; Hofmann, 1988; Battarbee, 2000; Porinchu and MacDonald, 2003; Walker and Cwynar, 2006). Heino et al. (2009), argue that lakes will be the first bodies of water to feel the effects of climate change and this sensitivity may be measured by implementing the use of proxies taken from lacustrine sediments (Dodds and Whiles, 2010). Biological markers such as diatoms, chironomids, ostracods and cladocera are sensitive to chemical, physical and biological changes in a lake system and may be used to qualitatively and quantitatively assess the relationships between environmental and limnological variables and the biological proxy indicator in question (Battarbee, 2000; Porinchu and MacDonald, 2003; Smol, 2010; Batterbee and Bennion, 2012). Quantitative paleolimnological reconstructions are based on four assumptions: 1) a linear relationship exists between the biological proxy of interest and the environment in which it is found, 2) subfossil remains can be recovered in sufficient numbers to enable statistical treatment, 3) the quality of preservation must be sufficient enough that consistent identification is possible and 4) a chronology may be developed for the sediment in order to provide temporal context (Smol et al., 1995; Birks, 1998; Porinchu and MacDonald, 2003).

The paleolimnological approach is predicated on establishing an understanding of the modern relationship that exists between the relevant proxy and the environment. This is accomplished by correlating the relationship between measured environmental variables such as surface water temperature or pH and the modern distribution of the organism in question. A calibration set, or training set, is a collection of modern lakes that have been sampled for a multitude of variables such as elevation, dissolved oxygen, pH, and temperature in order to capture the complexity of the limnological properties that characterize each lake. In addition to the limnological data, surface sediment (uppermost 1 cm) is also collected at each site. The surface sediment is processed and the biotic remains of the organism of interest will be extracted and identified. The surface sediment has typically been deposited over the last 2-8 years and represents the modern lake environment. Relationships between each variable and the proxy are established using multivariate ordination techniques. The inference model that is developed is ultimately applied to subfossil chironomid assemblages from a long sediment core (Moser et al. 1996).

Chironomids (Insecta: Diptera), or midges, are particularly sensitive to thermal conditions and are one of the most promising approaches to reconstructing past thermal regimes (Porinchu and MacDonald, 2003; Eggermont and Heiri, 2012). The life cycle of a chironomid goes through several stages and begins as an egg mass deposited on the surface of the water by an adult chironomid. As the eggs hatch, midges erupt in their first larval state and mainly persist as benthos on the floor of the lake. In this state, the chironomid has a maggot-like form and a chitinous head capsule that is shed three more times (Porinchu and MacDonald, 2003). With each progressive instar stage, the chironomid becomes larger and may reach lengths ranging from 1-20mm. Eventually, the larval chironomid reaches the pupae stage and rises through the water column of the lake. This stage is abrupt and leads to metamorphosis from pupae to an adult fly that emerges from the lake (Figure 1.1). Chironomids are one of the most productive freshwater insects and are comprised of between 8000 to 20000 species (Porinchu and MacDonald, 2003). They are also found in almost every environment on Earth that range from the tropics to the Arctic and Antarctic with three subfamilies particularly ubiquitous: Tanypodinae, Orthocladiinae and Chironominae (Brooks et al., 2007).

Midges have been extensively used as a proxy for past climate and are valuable in paleoclimate studies because they are abundant, well preserved in lake sediment and sensitive to key environmental variables such as air and water temperature (Porinchu and MacDonald, 2003). Inference models relating midges to air and/or water temperature have been developed in North America (Walker et al., 1997; Barley et al. 2006; Porinchu et al., 2009), Eurasia (Olander et al. 1999; Engels et al., 2008; Self et al., 2010; Heiri et al., 2011), Africa (Eggermont et al., 2010) and Australasia (Rees et al., 2008). These inference models have been applied to recently deposited sediment to reconstruct 20th century, Holocene and late Pleistocene climate change in

North America (Levesque et al. 1993; Levesque et al. 1997; Porinchu et al. 2003; Potito et al. 2006; Reinemann et al. 2009; Porinchu et al., 2010; Axford et al., 2011; Medeiros et al. 2012).

Calibration sets typically identify the existence of a strong statistical relationship between modern midge assemblages and some measure of growing season temperature (air and/or water) with a root mean square error of prediction (RMSEP) for summer air temperatures ranging between 1.0ºC and 1.5ºC and a jack-knifed r^2 of 0.80 – 0.90 according to Velle et al. (2010). The jack-knifed r^2 provides a more meaningful estimate of the error associated with an inference model. Jack-knifing is a form of leave-one-out cross-validation that estimates the value of the variable of interest for a site by using all the sites except the test site in the development of the inference model. However, some authors have cautioned that the influence of temperature on midge community composition may be overridden by site-specific biological and ecological processes (Hann et al., 1992; Seppällä, 2001; Velle et al., 2010). While assessing the strength or validity of a paleoenvironmental reconstruction should be done cautiously, the strength of chironomids as an indicator for surface water temperature and air temperature has been established for over twenty years (Walker et al. 1991). The centennial to millennial-scale changes in midge community composition and the associated midge-based temperature reconstructions are reflected in other proxies such as ice cores and pollen records, as well as the instrumental record (Walker et al., 1992; Larocque and Hall, 2003; Larocque et al. 2009; Brooks et al., 2012).

THESIS OBJECTIVES

This manuscript-style thesis contains two chapters that includes two separate manuscripts. One manuscript, submitted to *Quaternary Research*, is currently under review for inclusion in a special issue devoted to the Ziegler Reservoir fossil site. The other manuscript will be submitted in 2014 for peer-review and potential publication at *Arctic, Antarctic and Alpine Research*. The first article established the development of an inference model that establishes a relationship between chironomid assemblages and mean July air temperature in the central Colorado Rocky Mountains. The second article documents chironomid community change and develops a 70 ka record of thermal conditions for the Ziegler Reservoir site. The goals of this thesis research project are two-fold:

1) development of a midge-based inference model for MJAT incorporating midge assemblages from the central Colorado Rockies into the existing Great Basin training set;

2) the application of the newly developed inference model to a long core taken from the Ziegler Reservoir site to document changing thermal conditions during the late Bull Lake Glaciation and into the Sangamon Interglacial for the central Colorado Rockies. Upon completion of this work, the study of a lengthy, well-preserved record of the previous interglacial, a time that was analogous to modern thermal conditions and perhaps warmer (Anklin et al., 1993; Bauch, et al., 2011; Goñi et al., 2012) will provide a context to better understand the contemporaneous changes that are curtly occurring in the Intermountain West of the United States. This research will contribute a quantitative understanding of thermal conditions that existed between ~140 and 70 ka yr BP in central Colorado. This research will also expand the temporal limits and application of sub-fossil midges and has the potential to become amongst the oldest midge-based temperature records in the world (Francis et al. 2006; Engels et al. 2010; Axford et al., 2011).

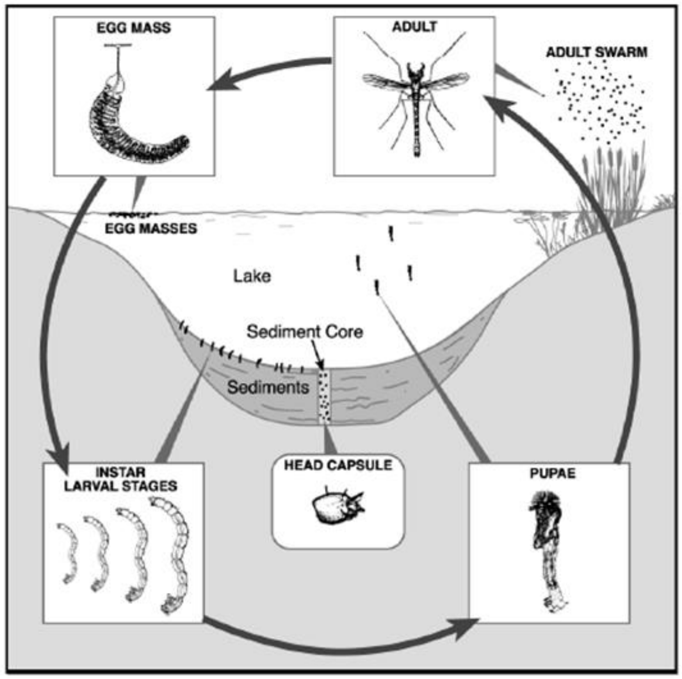

Figure 1.1: The life cycle of a chironomid (Porinchu and MacDonald, 2003).

CHAPTER 2

THE DEVELOPMENT OF A CHIRONOMID-BASED MEAN JULY AIR TEMPERATURE INFERENCE MODEL FOR THE CENTRAL COLORADO ROCKY MOUNTAINS.[1]

[1] Haskett, D.R. and D.F. Porinchu. To be submitted to *Arctic, Antarctic and Alpine Research.*

ABSTRACT

Subfossil chironomid head capsules were collected from the surface sediment of 45 lakes located in the central Colorado Rocky Mountains to develop a midge-based inference model for mean July air temperature (°C). The lakes sampled spanned a 1024 m elevation range and a mean July air temperature (MJAT) range of 5.63°C. The distribution of midge taxa varies by elevation. The midge communities at the highest elevations are characterized by low diversity and eurythermic taxa including *Chironomus, Corynocera oliveri, Cladotanytarsus* and *Diplocladius.* Taxa associated with the subalpine zone include *Corynocera ambigua*, and taxa belonging to the sub-family Chironomini including *Chironomus*, *Dicrotendipes* and *Einfeldia.* The lakes associated with the lowest elevations are located in the montane forest zone and characterized by midge assemblages dominated by taxa belonging to the sub-family Orthocladiinae including *Limnophyes, Brillia,* and *Parakiefferiella bathophila*-type. Canonical correspondence analysis (CCA) identified that MJAT (°C) was the sole measured environmental variable that could account for a statistically significant amount of variance in the distribution of subfossil midges. The most robust midge-based inference model for MJAT (°C) was developed using a 2-component weighted averaging-partial least squares (WA-PLS) approach (r^2_{jack} = 0.47, RMSEP = 0.81°C). This newly developed inference model provides a means to develop quantitative thermal reconstructions for the central Colorado Rockies and expands the existing Great Basin training set for the western United States.

Keywords: Inference model, chironomid, midge, training set, paleolimnology, paleoclimate, Colorado, Rocky Mountains, temperature

INTRODUCTION

The high elevations of the western United States are responding to climate change at a particularly rapid rate (Chen, et al., 2011; Elliot, 2012). Declines in mountain snowpack (Mote et al., 2005; Hidalgo et al, 2009; Pedersen et al. 2011) as well as the changes in the timing of snowfall (Knowles et al., 2006) have been well documented in this area. Also, increases in forest wildfire activity (Westerling et al., 2006) and increased sediment delivery (Goode et al., 2012) have been well documented throughout the Mountain West of the United States and attributed, in large part, to global climate change. The environmental archives preserved in lake sediment may help to elucidate the rate and magnitude of past climatic changes and provide a broader context for understanding contemporaneous climate change. Robust midge-based inference models, developed for surface water temperature (Porinchu et al., 2002; Porinchu et al., 2007a) and air temperature (Porinchu et al., 2010) for the Great Basin of the United States, have proven to be useful in reconstructing changes in thermal conditions in this region during the Holocene (Porinchu et al., 2003; Potito et al., 2006; Porinchu et al., 2007b; MacDonald et. al, 2008; Reinemann et al., 2009; Porinchu et al., 2010).

Midges are one of the most productive freshwater insects and are comprised of between 8000 to 20000 species (Porinchu and MacDonald, 2003). They are also found in almost every environment on Earth, ranging from the tropics to the Arctic and Antarctic (Porinchu and MacDonald, 2003). The life cycle of a chironomid (Insecta: Diptera), or non-biting midge, involves several stages. The life cycle begins when an egg mass is deposited on the surface of the water by an adult chironomid. As the eggs hatch, midges erupt into their first larval state and mainly persist as benthos in the sediment–water interface at the bottom of a lake. Chironomid larvae have a maggot-like form and consist of soft-body tissue and a chitinous head capsule

(Walker, 1987). Chironomids become progressively larger through each of four larval instar stages with the chitinous head capsule being shed three more times (Walker, 1987; Porinchu and MacDonald, 2003; Brooks et al., 2007). The fourth instar ranges in length from 1-20 mm (Porinchu and MacDonald, 2003). Eventually, the larval chironomid reaches the pupae stage and rises through the water column of the lake. The pupal stage, which is abrupt, involves the pupae metamorphosing into an adult fly that emerges from the lake (Walker, 1987; Porinchu and MacDonald, 2003). The heavily chitinized head capsule of the 4th instar is resistant to decomposition and tends to be well preserved in lake sediment (Walker et al. 1987). These head capsules, which can be extracted from the lake sediment and identified, provide a means to reconstruct midge community composition through time.

Midges have been extensively used as a proxy for past climate and are valuable in paleoclimate studies because they are abundant, well preserved in lake sediment and sensitive to key environmental variables such as air and water temperature (Porinchu and MacDonald 2003). Chironomids are particularly sensitive to thermal conditions and are one of the most promising approaches to reconstructing past thermal regimes (Eggermont and Heiri, 2012). The remains of three subfamilies of the Chironomidae are typically encountered in temperate lakes in the northern hemisphere: Tanypodinae, Orthocladiinae and Chironominae (Porinchu and MacDonald, 2003; Brooks et al., 2007; Eggermont and Heiri, 2012). The Orthocladiinae are most abundant in the oligotrophic lakes that characterize alpine and arctic environments but have also been described from the sediment of tropical lakes. The Chironominae and Tanypodinae are often associated with warm, eutrophic lakes that are characterized by a greater diversity of midge taxa (Eggermont and Heiri, 2012).

Inference models relating midges to air and/or water temperature have been developed in North America (Walker et al., 1997; Barley et al. 2006; Porinchu et al., 2009), Eurasia (Olander et al. 1999; Self et al. 2010; Heiri et al. 2011), Africa (Eggermont et al., 2010) and Australasia (Rees et al., 2008). These inference models have been applied to recently deposited sediment to reconstruct 20th century, Holocene and late Pleistocene climate change (Porinchu et al., 2007b; Reinemann et al. 2009; Axford et al., 2011). Calibration sets typically identify the existence of a strong statistical relationship between modern midge assemblages and some measure of growing season temperature (air and/or water) with a RMSE of prediction (RMSEP) for summer air temperatures ranging between 1.0ºC and 1.5ºC and a jack-knifed r^2 of 0.80 – 0.90 according to Velle et al. (2010). However, some authors have cautioned that the influence of temperature on midge community composition may be overridden by site-specific biological and ecological processes (Hann et al., 1992; Seppällä, 2001; Velle et al., 2010). While assessing the strength or validity of a paleoenvironmental reconstruction should be done cautiously, the strength of chironomids as an indicator for surface water temperature and air temperature has been established for over twenty years (Walker et al. 1991; Eggermont and Heiri, 2012). The centennial and millennial-scale climate variability captured by variations in midge community composition have been substantiated by the instrumental record and other proxy records such as ice cores and pollen (Walker et al., 1992; Korhola et al., 2001; Larocque and Hall, 2003; Brooks et al., 2012).

The development of a regional midge training set in the Colorado Rockies provides the opportunity to increase the diversity of midge assemblages and expand the temperature range and the geographic extent of the existing Great Basin midge calibration set. The expansion of a training set will improve our ability to quantify the tolerances and optima of individual midge taxa to measured environmental variables, including MJAT (Juggins and Birks, 2012). The addition of the Colorado Rocky training set to the larger Great Basin training set will improve our ability to develop robust quantitative paleotemperature reconstructions for the Intermountain West of the United States.

The relationship between six measured environmental variables and the modern distribution of chironomid taxa from 38 lakes in the central Colorado Rockies are described in this paper. Multivariate statistical approaches, including various forms of ordination analyses, are utilized to establish which of the measured environmental variables could account for the largest and statistically significant amount of variance in the distribution of the midge taxa present in the training set lakes. The results of the ordination analyses indicate that a robust chironomid-based inference model for MJAT can be developed. Application of the midge-based MJAT inference model to chironomid stratigraphies developed for central Colorado Rockies provides the opportunity to document the impact of recent and longer-term climate change in this region.

STUDY AREA

A suite of forty-five lakes were sampled in July 2011 and July 2012 for incorporation in the central Colorado Rocky Mountain midge calibration set (Table 1). The lakes are located in the White River National Forest, which encompasses the Elk Mountains and the Sawatch Range of central Colorado (Figure 2.1). The training set lakes span three vegetation zones: 1) montane forest, which is dominated by Engelmann spruce *(Picea engelmannii*), quaking aspen *(Populus tremuloides*), subalpine fir *(Abies lasiocarpa*) and lodgepole pine *(Pinus contorta*) and found between 2,870 and 3,120 m asl; 2) subalpine forest, which is dominated by a pine forest (*Pinus* spp.) with spruce (*Picea* spp.), and fir (*Abies* spp.) and found between 3,275 and 3705 m asl; 3) timberline which bounds the transition from subalpine forest to alpine tundra, which in this part of the central Colorado Rockies occurs at 3,415 to 3,660 m asl. The alpine zone is characterized by abundant sagebrush (*Artemesia)* and grasses *(Poaceae)* (McMulkin et al., 2010; Anderson et al., *under review*). The sub-surface geology of the area consists primarily of Proterozoic diorites and granites that intrude into Proterozoic biotite gneisses, migmatites and schists (Hopkins and Hopkins, 2000).

The climate of central Colorado is characterized by large seasonal variations consistent with a continental climate and large diurnal variations in temperature (Pepin, 2000). During the spring and winter, upper westerly atmospheric flow facilitates the accumulation of notable precipitation at high elevations. During the spring and fall, easterly winds carry heavy precipitation in the form of snowfall (Barry, 1992). Summer precipitation is derived from localized convective storms that are characterized by strong winds and occasionally hail (Pepin, 2000). The Sunlight weather station (39.43°, -107.38°) is located at 3232 m asl and is characterized by average January temperatures of -7.5°C. This site receives the highest precipitation during the winter months and received 2.88 in of precipitation averaged monthly over a 30-year period (PRISM data group, 2012). Lower elevation sites, such as Aspen (39.23°, -106.87°) at 2384 m asl, are characterized by slightly higher temperatures and less precipitation for both July (MJAT = 17.41°C, average monthly precipitation=1.87 in) and mean January air temperature (MJT = -6.34°C, average monthly precipitation = 1.03 in.)

A suite of limnological variables were sampled at each lake in order to characterize the relationship between chironomid communities and the lake environment. In order to maximize the environmental gradient, the lakes sampled spanned a large elevation range (2869 m - 3893 m asl). The environmental variables sampled included depth, Secchi depth, surface water temperature (1.9 - 20.3ºC), lake depth (0.90 – 25.50 m), pH (5.24 - 9.74), specific conductivity (0.007 - 0.217 $\mu S \cdot cm^{-1)}$ and dissolved oxygen (6.40 - 11.92 mg/L).

METHODS

Field

Surface sediment was recovered from twenty-seven lakes in July 2011 and eighteen lakes in July 2012. Surface water temperature, dissolved oxygen, specific conductivity and pH were measured using an YSI Professional Plus multi-probe. Maximum lake depth and Secchi depth for each lake were calculated using a Secchi disk. A DeGrand maxi-corer was used to collect surface sediment from the center of each lake. Before leaving each site, the upper 1 cm section of the sediment core was sectioned at a 0.25 cm resolution and deposited into Whirlpacks®. The sediment was stored in a cooler for the duration of the fieldwork. The samples were stored in a refrigerator once they arrived at the lab at the University of Georgia.

Instrumental data for air temperature are limited in this region due to the remoteness and elevation of these sites. Two approaches were employed to derive the mean July air temperature (MJAT) estimates that were used in the ordination analyses and inference model development. The estimates of MJAT were initially extracted from the PRISM dataset using GIS and ArcMap10 (PRISM Climate Group, 2012). The PRISM dataset is available at an 800 m grid resolution. Estimates of MJAT for areas below 3000 m asl are well-constrained in the PRISM dataset; however, given the paucity of weather stations above 3000 m asl elevation and the absence of weather stations above 3500 m asl, estimates of MJAT in the subalpine and alpine zones are not as well constrained by observations (Rangwala and Miller, 2012). The PRISM-based estimates of MJAT were not sufficient to resolve the influence of the complex topography and steep relief found in the central Colorado Rockies on air temperature. The second approach used to derive estimates of MJAT for use in the ordination analyses was based on the application of a lapse rate. Pepin and Losleben (2002) calculated an average July environmental lapse rate of 5.5°C/km for this region using yearly and daily seasonal synoptic controls such as synoptic classification systems and daily changes in temperatures. Estimates of MJAT for each of the calibration set lakes were determined applying the Pepin and Losleben (2002) lapse-rate and using a MJAT of 15.47°C calculated for the Sunlight weather station (39.43°, -107.38°), which is located at an elevation of 3232.10 m asl.

Laboratory

The head capsules of chironomids were collected in the laboratory following the procedures described in Walker (2002) and Porinchu and MacDonald (2003). The sediment was soaked in an 8% KOH solution and heated to 35ºC for a minimum of 30 minutes, or until colloidal matter was broken down enough to deflocculate each sample. The solution was sieved through a 95 µm-grade mesh screen using distilled water to eliminate any remaining KOH residue. The material remaining on the screen was backwashed into a beaker with distilled water. The resulting residue was poured into a Bogorov counting tray and sorted using a stereoscope at 40X. Samples collected in 2012 were also treated with a blue cotton stain to aid in increasing the recovery time of the picking process (Larocque-Tobler and Oberli, 2011). The sub-fossil chironomid head capsules extracted from the residue are permanently mounted on glass slides using Entellan®. Identification of the subfossil midge remains was made using a Ziess Axioskop at 400x. The identifications were based primarily on Brooks et al. (2007), an extensive reference collection of sub-fossil midges from the Great Basin and an online chironomid identification key http://chirokey.skullisland.info/). Lakes that contained a minimum of 50 head capsules in the uppermost 1 cm of sediment were included in the statistical analysis (Heiri and Lotter, 2001;

Larocque, 2001; Quinlan and Smol, 2001). Seven lakes did not satisfy this criterion and thus were excluded from further analysis (EMD, GRZ, LMN, PTL, TLN, TLW, and WND), leaving thirty-eight lakes in the training set. A training set typically must contain a minimum of 30 lakes (Hall and Smol, 1993) to satisfy the statistical criteria for ordination analyses and the development of inference models. *Tanytarsus* sub-types were identified and aligned with the existing Great Basin training set. *Tanytarsus* type-G possesses a clearly defined median tooth with two lateral teeth comparable to the *Corynocera oliveri*-type median tooth complex but the six lateral teeth were equal in size and located on the same focal plane. *Tanytarsus* type-H possesses the characteristic "trident-shaped" median tooth complex described in Porinchu et al. (2007a).

STATISTICAL METHODS

Data Screening

Geographic variables that did not influence the limnology of each site were excluded from statistical analyses and include latitude, longitude and elevation. The data collected for pH was incomplete or inaccurate due to a malfunctioning pH sensor and were also removed from further statistical analyses. The variables included in statistical analysis include MJAT (°C), SWT (°C), dissolved oxygen, specific conductivity, lake depth and Secchi depth (n=6). Ordination techniques are used in paleolimnological research to identify a subset of the measured environmental variables that capture the largest, statistically significant amount of variance within the dataset (Maddy and Brew, 1995). Indirect ordination analysis techniques, such as principal components analysis (PCA) and detrended correspondence analysis (DCA) are used for initial data exploration. Statistical analysis begins with screening the training set to determine whether the limnology or the faunal assemblages can be considered outliers. The screening of the dataset is done by undertaking a DCA of the midge assemblage data and a PCA of the environmental data. Any lake with DCA and PCA scores that are greater than one standard deviation from the mean on the first two ordination axes are considered outliers; these lakes are removed from further analyses (terBraak and Verdonschot, 1995). Detrended correspondence analysis is also used to determine whether linear, e.g. redundancy analysis (RDA) or unimodal, e.g. canonical correspondence analysis (CCA), approaches should be implemented for the direct ordination analyses. If the length of DCA axis one is greater than 3 standard deviations then CCA should be utilized; whereas, if the length of DCA axis one is less than 2 standard deviations than RDA should be used. Both RDA and CCA are appropriate when the length of DCA axis one falls between two and three standard deviations (terBraak and Verdonschot, 1995).

Direct Ordination Analyses

The gradient length of DCA axis one was 4.90, indicating that the midges were responding in a unimodal fashion to the underlying environmental gradient. This suggests that canonical correspondence analysis (CCA) is the appropriate form of direct gradient analysis to utilize for further analyses. Direct gradient analysis, or constrained ordination, include the environmental variables in the analyses (Maddy and Brew, 1995), and is used to establish the relationship between modern midge distribution and the measured environmental variables. The site scores or, the axes of the CCA are constrained by the environmental variables that can account for the most “scatter” along the first CCA axis. The second CCA axis is then determined so as to maximize the remaining amount of variance evident in the chironomid assemblages as accounted for by the measured environmental variables (Jongman et al., 1995). The CCA will identify a minimum subset of the environmental variables that are correlated with the distribution of the midge taxa and can account for a maximum amount of variance in midge distribution

(Maddy and Brew, 1995). Forward selection and Monte Carlo permutations (499 unrestricted permutations) were used determine the statistical significance of each environmental variable as well as demonstrating the amount of variance that each variable accounted for (Birks, 1998; ter Braak and Verdonschot, 1995).

Inference Model Development

The CCA identified that of the six environmental variables incorporated in the direct gradient analysis only MJAT could account for a statistically significant amount of variance in the distribution of the subfossil midges. An inference model, or transfer function, relating the distribution of midges to variations in MJAT was developed using various approaches including, Weighted Averaging (WA), Weighted Averaging – Partial Least Squares (WA-PLS) and Partial Least Squares (PLS). WA and WA-PLS are particularly useful models for biological data that have an underlying unimodal distribution. Weighted-averaging assumes that a taxon will be most abundant at a site where the value of a limiting environmental variable is close to the taxon's optima. The taxon's optimum is taken as an average of the possible sites where that taxon occurs. It is then weighted by the relative abundance of that taxon (Birks, 1995). WA-PLS improves upon the WA method and uses the residuals of the regression to create new site scores. WA-PLS is a linear combination of the individual components of the WA of taxa (Birks, 1995). The best model was selected based on the coefficient of determination, the root-mean square error of prediction (RMSEP) and the maximum bias of the model (Birks, 1998). All models used square-root transformed abundance data that were implemented in the program C2 (Juggins, 2003). Leave-one out cross-validation was used in order to evaluate the error estimate of the model. This method is the simplest form of cross-validation and involves resampling from the existing training set and leaving out one site every time an iteration of the model is run in order to derive more meaningful estimates of the error associated with the inferred temperatures (Birks, 1995). The developed model would then use the remaining sites to predict a value. This was done for all of the samples in the training set. The predictions determined for each sample are subtracted from the observed value to calculate the root mean square error of prediction (RMSEP) (Birks, 1995).

RESULTS

The results of the DCA of the chironomid abundance data and the PCA of the environmental variables indicate that none of the thirty-eight lakes in the training set can be considered an outlier. Overall, fifty-seven chironomid taxa were identified in the surface sediment of the thirty-eight lakes incorporated in the central Colorado Rockies training set. A notable relationship exists between the distribution of chironomid taxa and MJAT (°C). For example, the coldest lakes, located in the alpine zone, are characterized by chironomid assemblages with low diversity. These lakes are dominated by taxa such as *Diplocladius*, *Chironomus*, *Cladotanytarsus,* and *Corynocera oliveri*-type. The subalpine zone is the most represented within the training set and include chironomid assemblages that are more diverse. While taxa found in the colder lakes are still evident within the subalpine lake assemblages, Chironomini such as *Cladopelma, Dicrotendipes,* and *Einfeldia* become important constituents of the midge community with smaller percentages of Orthocladiinae taxa such as *Psectrocladius sordidellus*-type, *Chaetocladius,* and *Heterotrissocladius* also present. The presence of *Corynocera ambigua*-type is particularly striking because *C. ambigua*-type is essentially locally extant in sub-alpine lakes. The montane forest zone witnesses a sharp increase in the relative abundances of Orthocladiinae and a decrease in Chironomini and *Corynocera ambigua*-type. The distribution of Pentaneurini is restricted to the warmer, forested sites. Eurythermic taxa such as

Tanytarsus (spp.) and *Corynocera oliveri*-type are represented in all three zones and are evident in lakes that span the entire MJAT (°C) gradient.

Ordination

A series of CCAs with each environmental variable incorporated as the sole predictor variable were run to assess the amount of variance that each of the environmental variables could account for in the distribution of the midge taxa. These constrained ordinations determined that MJAT was the only measured environmental variable that could account for a statistically significant amount of variance ($p \leq 0.05$) (see Table 2.2). Forward selection of the remaining five environmental variables was performed to verify that they did not contribute any significance to the CCA. No other variable was found to be statistically significant. A CCA run with MJAT as the sole predictor variable results in eigenvalues for the first two axes of 0.122 and 0.343 and can account for 5.4% of the variance evident within the chironomid assemblages (Table 2.2). The ratio of the two axes with regard to eigenvalues is relatively high (0.356). The strength of the relationship evident between MJAT and chironomid assemblages substantiated the development of a midge-based inference model for MJAT.

CCA bi-plots were created to illustrate the relationship between the midge assemblages in the 38 lake training set and MJAT (Figure 2.3) as well as the relationship between the individual chironomid taxa and MJAT (Figure 2.4). The sites were categorized into one of three vegetation zones with regard to the constrained MJAT environmental variable. The warmest lakes in the training set, found in the montane forest, load highly on CCA axis 1 on the right hand side of the diagram (Figure 2.3). The chironomid assemblages in these lakes are dominated by taxa such as *Brillia, Polypedilum* and *Paraorthocladius.* The subalpine lakes, located near the centroid of the CCA, represent a wider range of MJAT capture and are dominated by taxa such as *Tanytarsus* spp., *Cricotopus/Orthocladius*, *Psectrocladius* spp. Alpine lakes are plotted on the far left hand side of the ordination diagram. The alpine midge assemblages contain relatively high abundances of taxa such as *Monodiamesa*, *Geoorthocladius, Diplocladius* and *Smittia*.

Inference Model Development

The inference model for MJAT was developed by following Birks (1995). Six lakes (WLL, DMR, EGL, TCL, MRL and CRL) were removed from the final 2-component WA-PLS inference model due to the presence of high absolute residuals. Closer examination of these lakes provides some insight for the poor fit between the midge assemblages and MJAT. Weller Lake (WLL), Crater Lake (CRL) and Maroon Lake (MRL) are located close to major roadways, easily accessed by short hiking trails and/or heavily utilized for recreational activities such as fishing. The influence of MJAT on the midge assemblages in these lakes is likely overridden by surface runoff from roadways resulting in changes in lake water chemistry and the introduction of fish. Tabor Creek Lake (TCL), with a depth of 24 m, is amongst the deepest lakes in the training set; the chironomid community in TCL could be responding directly to cold profundal waters. Deimer (DMR) and Eagle (EGL) lakes are the lowest elevations sites included in the training set. These lakes were relatively shallow and the most productive of the study lakes. There was clear indication that Deimer Lake was experiencing seasonal anoxia at the time of sampling. The large abundance of *Chironomus*, a taxa that can survive long periods of anoxia, and the acidophilic *Psectrocladius sordidellus* further substantiate these findings.

The large gradients captured by DCA Axes 1 and 2, which are represented by the eigenvalues of the first two axes (4.99 and 2.70, respectively), indicate that the midge taxa present in the Colorado Rocky mountain training set are broadly distributed and can be represented by a Gaussian distribution (Table 2.3). The underlying unimodal distribution of the midge taxa supported the use of WA and WA-PLS approaches in developing the midge-based inference model for MJAT. The ratio between the first axis and the second axis eigenvalues are used to determine which environmental variables are the best candidates for the development of a quantitative inference models. In this instance, only MJAT was statistically significant and the eigenvalue ratio of the CCA axes 1 and 2 were 0.355 and would suggest that a strong enough relationship exists to create a model (ter Braak, 1986). However, the relatively low ratio of axis 1:axis 2 does indicate that a notable amount of variance is captured by the remaining CCA axes. While WA-PLS typically performs better with datasets possessing longer gradients, it can also outperform other types of regression over shorter gradients as well (Juggins and Birks, 2012). The performance statistics (Table 2.4) for this model indicated that a 2-component WA-PLS model was the most robust option based upon a root mean square error of prediction (RMSEP) of 0.81°C and a jack-knifed co-efficient of determination (r^2_{jack}) of 0.47. The maximum bias evident for the model is 0.94°C. The *jack-knifed* inferred MJAT estimates as compared to the calculated MJAT values are illustrated in Figure 2.5. The calculated 2-component WA-PLS residuals (Figure 2.6) indicate that no additional information is present given the residuals have no discernible pattern.

DISCUSSION

Midges have been extensively used as a proxy for past climate and are valuable in paleoclimate studies because they are abundant, well preserved in lake sediment and sensitive to key environmental variables such as air temperature (Porinchu and MacDonald 2003). Inference models relating midges to air temperatures have been developed in North America (Porinchu et al., 2009), Eurasia (Olander et al. 1999; Heiri et al. 2011), Africa (Eggermont et al., 2010) and Australasia (Rees et al., 2008). These inference models have been applied to recently deposited sediment to reconstruct 20th century, Holocene and late Quaternary climate change in the western United States (Porinchu et al., 2007a; Reinemann et al. 2009; Potito et al. 2006; Porinchu et al. 2003). The development of midge-based MJAT inference models is predicated on the understanding that the distribution of chironomids is directly related to environmental variables, particularly temperature. Chironomid assemblages collected in mountainous regions follow a similar trajectory and distribution as chironomids collected along a latitudinal gradient with arctic assemblages comparable to those collected from lakes located in alpine tundra (Thienemann, 1954; Porinchu et al., 2002). Chironomids such as *C. oliveri*, *Heterotrissocladius* spp. and *Sergentia* have been well documented and are typically associated with cold, oligotrophic lakes in alpine and arctic environments (Porinchu and Cwynar, 2000; Porinchu et al., 2002; Brooks et al., 2007). However, these taxa are much more broadly distributed along the temperature gradient in the Colorado Rocky Mountain training set. This indicates that a greater number of low elevation sites should be incorporated in the training set to further expand the temperature gradient. Studies documenting air temperature variability in the Front Range reveal that the alpine tundra in this region is experiencing deficits in temperature at night that exceed the warming that occurs during the day. This situation is creating a progressively strong heat sink in the Colorado Rocky Mountains (Pepin and Losleben, 2002) and could explain the modern distribution of the cold stenothermic midge taxa. This substantiates the collection of a wider suite of variables in the future in order to determine whether other factors could be influencing the distribution of chironomid communities in the central Colorado Rockies. A recent study which implemented the use of chironomids to infer air temperatures for a high elevation site in Colorado during the Sangamon Interglacial indicated that temperatures were lower than present

(Haskett and Porinchu, *under review).* This situation could potentially explain the cold bias evident in the existing inference model and reflect the complexity of regional climate.

The presence of taxa typically associated with warm, eutrophic lakes demarcates the transition between the alpine and subalpine zones. The dramatic appearance of *C. ambigua* is particularly striking. *Corynocera ambigua* has been used to infer the existence of elevated temperatures and the northward movement of treeline in northeastern Siberia during the mid-Holocene (Porinchu and Cwynar, 2002). The species bi-plot and the relative abundance diagram indicates that *Parakiefferiella bathophila*-type, *Limnophyes*, *Brillia* and *Polypedilum* are associated with the high air temperature and are most abundant in lakes located in the montane forest zone. The high abundance of *Diplocladius* present in the highest and coldest lake measured should be noted. *Diplocladius* is typically found in cold ponds, or in cool springs and are rarely abundant (Brooks et al., 2007). The high relative abundance (66.9%) of this taxon in Seven Sisters West Lake likely reflects the influence of the flux of snowmelt to the lake.

Typically, calibration sets identify the existence of a strong statistical relationship between modern midge assemblages and some measure of growing season temperature (air and/or water) with a RMSE of prediction (RMSEP) for summer air temperatures ranging between 1ºC and 1.5ºC and a jack-knifed r^2 of 0.80 – 0.90 (Velle et al., 2010). Due to the successful application of midge-based inference models to long sediment archives collected in the western United States, an abbreviated suite of limnological variables was collected along an elevation gradient to capture a large MJAT range for the Colorado Rocky Mountain training set. While the model is robust, the RMSEP for the model seems to overestimate and elevate inferred MJAT for the lakes sampled at the colder end of the spectrum. This trend could be attributed to several factors. While MJAT were derived using a linear environmental lapse rate, these are sensitive environments and the lakes evident in the highest elevations are more than likely much colder than the extrapolated temperatures. Other issues arose during fieldwork and could account for errors evident in the model. Air temperature in July 2012 was notably higher than in July 2011. The elevated temperature led to earlier snowmelt and thus could have influenced midge community composition. The inter-annual variability in midge community composition may not be adequately reflected by the midge-based inference model. Future work should attempt to more fully document the modern limnological environment to ensure that the environmental drivers of midge distribution in this region are better characterized.

The midge assemblage data collected for this study increase our understanding of the biogeographic distribution of chironomid taxa in the Rocky Mountains. The inclusion of these assemblages in the existing Great Basin training set will likely decrease the potential for non-analogue conditions in other areas of the western United States. However, expanding the existing Great Basin training set will increase environmental and biological heterogeneity, which may result in "noise" being added to the model and result in the performance being negatively impacted (Porinchu et al., 2002). Additional work is necessary to increase the robustness of the of the current midge-based MJAT inference model developed for the Colorado Rocky Mountain training set. A wider set of limnological variables could potentially explain more variance inherent in this complex system. Also, refining methods to increase the resolution of MJAT is necessary and instrumental data collected from more elevations above 3000 m asl could greatly improve the estimates of site-specific MJAT that are used to calibrate the midge-based MJAT inference model.

CONCLUSION

Chironomid analysis derived from the surface sediment of forty-five lakes along a 1024 m elevation range were assessed and used to develop a midge-based inference model for MJAT. Ordination analyses (CCA) indicated that MJAT was the sole statistically significant variable that captured the greatest amount of variance evident within the chironomid communities. The most robust inference model was developed using a 2-component WA-PLS with a coefficient of determination of r^2_{jack} = 0.47 and a very low RMSEP (0.81°C). This is an exploratory study to establish the efficacy of potentially adding the chironomid assemblages to the existing Great Basin midge training set. It also provided the opportunity to assess the relationships that exist between chironomids and air temperature.

Table 2.1: Table of environmental variables collected for each of the 45 lakes sampled. MJAT = mean July air temperature, SWT = surface water temperature, DO = dissolved oxygen. Highlighted lakes were removed from the training set for insufficient head capsule recovery. ** Refers to lakes that were anomalous or outliers for the inference model and were removed from analyses. **** Indicates missing data.

Lake Name	Code	Latitude	Longitude	Elevation (m)	MJAT (°C)	SWT (°C)	Depth (m)	Secchi Depth (m)	Specific Conductivity ($\mu S \cdot cm^{-1}$)	DO mg/L	pH
American	AML	39.0564	-106.8301	3450.0	14.27	8.20	10.50	3.8 / 3.1/ **3.45m**	0.083	9.41	7.37
Anderson	AND	39.0204	-106.6275	3583.9	13.53	7.49	3.50	2.98 / 2.70 / **2.84m**	0.035	10.26	7.25
Bear	BRL	39.2964	-106.4153	3350.9	14.82	15.15	4.60	3.50 / 2.90 / **3.2m**	0.027	8.05	5.24
Brady	BRD	39.3683	-106.5006	3353.4	14.80	15.10	2.10	*Unlimited*	0.021	8.21	9.36
Cathedral	CAT	39.0278	-106.8429	3597.9	13.46	5.40	6.70	3.97/ 3.40 / **3.69m**	0.160	9.69	7.30
Cleveland	CVL	39.4211	-106.4908	3608.5	13.40	15.80	6.65	3.15 / 3.0 / **3.08m**	0.028	7.48	8.50
Constantine	CNS	39.4503	-106.4550	3471.7	14.15	14.00	3.65	*Unlimited*	0.020	7.73	8.60
Crater	CRL	39.0851	-106.9673	3053.3	16.45	7.20	3.25	*Unlimited*	0.102	10.21	*5.60*
Diemer**	DMR	39.3347	-106.6069	2869.1	17.47	20.30	2.60	2.0 / 1.5 / **1.75m**	0.035	7.31	9.30
Eagle**	EGL	40.2108	-105.6503	3073.9	16.34	13.70	2.00	*Unlimited*	0.026	7.42	8.11
Emerald	**EMD**	**39.0099**	**-107.0425**	**3168.2**	**15.82**	**12.90**	**13.40**	**2.60 / 2.50 / 2.55m**	**0.217**	**7.72**	**7.82**
Galena South	GAL-S	39.2967	-106.4201	3363.9	14.74	15.55	3.10	*Unlimited*	0.018	6.86	6.40
Grizzly	**GRZ**	39.0504	-106.5942	**3788.2**	**12.41**	**1.90**	**13.70**	**10.0 / 9.40 / 9.7m**	**0.067**	**8.86**	**7.20**
Half Moon North	**HFM-N**	**39.1812**	**-106.4962**	**3704.5**	**12.87**	**7.97**	**5.30**	***Unlimited***	**0.025**	**9.95**	********
Half Moon South	HFM-S	39.1782	-106.4929	3647.9	13.18	10.10	5.55	*Unlimited*	0.025	9.08	****
Hard Scrabble	HRD	39.2313	-107.1006	3069.7	16.36	14.82	4.05	2.25 / 2.15 / **2.20m**	0.128	8.69	7.59
Hunky Dory	HDY	39.4217	-106.4836	3452.5	14.26	16.20	2.50	*Unlimited*	0.030	8.15	9.15
Independence	IND	39.1440	-106.5674	3784.8	12.43	10.85	6.90	2.8 / 2.4 / **2.60m**	0.020	8.70	****
Linkin	LNK	39.1285	-106.5884	3638.8	13.23	5.64	9.00	**2.3 / 1.9 / 2.10m**	0.015	7.67	6.55
Lost Man	**LMN**	**39.1531**	**-106.5688**	**3774.8**	**12.48**	**10.02**	**16.70**	**3.6 / 3.4 / 3.5m**	**0.042**	**9.11**	********
Maroon**	MRL	39.0970	-106.9454	2903.0	17.28	5.80	3.10	*Unlimited*	0.120	10.92	7.38
Missouri Adjacent	MLA	39.3992	-106.5154	3524.1	13.86	14.60	2.45	*Unlimited*	0.029	7.70	8.17
Missouri Central	MLC	39.3964	-106.5153	3487.8	14.06	15.90	3.20	1.90 / 0.80 / **1.35m**	0.014	6.85	8.37
Missouri North	MLN	39.3964	-106.5112	3513.1	13.92	15.50	5.90	2.80 / 1.90 / **2.35m**	0.030	7.53	8.49
Missouri South	MLS	39.3871	-106.5155	3476.5	14.13	13.20	3.60	2.90 / 2.10 / **2.50m**	0.034	9.43	8.16
Native	NTV	**39.2253**	**-106.4592**	3403.0	14.53	9.89	0.90	*Unlimited*	0.011	8.56	*2.70*
Petroleum	**PTL**	**39.0263**	**-106.6367**	**3729.1**	**12.74**	**6.81**	**20.00**	**4.9 / 4.45 / 4.68m**	**0.039**	**8.35**	**6.75**
Savage	SVL	39.3595	-106.5203	3377.6	14.67	9.98	3.45	2.4 / 2.2 / **2.3m**	0.010	9.59	6.12
Seller	SLR	39.3236	-106.5847	3119.3	16.09	19.80	3.60	2.0 / 1.85 / **1.93m**	0.026	6.51	8.47
Seven Sisters Central	SSC	39.4365	-106.4831	3707.9	12.85	12.60	1.20	*Unlimited*	0.019	9.15	8.66
Seven Sisters North	SSN	39.4413	-106.4811	3755.4	12.59	15.20	5.80	3.05 / 2.45 / **2.75m**	0.016	7.77	8.79
Seven Sisters South	SSS	39.4319	-106.4873	3612.2	13.38	13.70	5.60	2.00 / 1.80 / **1.90m**	0.017	8.35	9.74
Seven Sisters West	SSW	39.4433	-106.4874	3892.9	11.84	7.00	6.90	2.10 / 0.90 / **1.50m**	0.016	9.38	8.66
Sopris	SOP	39.3711	-106.5025	3364.1	14.74	16.60	5.40	*Unlimited*	0.011	6.40	8.28
St. Kevin	SKL	39.3106	-106.4269	3580.0	13.56	8.39	6.80	4.4 / 3.9 / **4.15m**	0.041	10.38	*0.97*
Tabor Creek**	TCL	39.0539	-106.6475	3588.5	13.51	13.68	24.00	*Unlimited*	0.016	7.78	6.82
Thomas North	TL-N	39.2727	-107.1436	3089.1	16.26	5.69	9.50	2.10 / 2.60 / **2.35m**	0.031	11.92	7.79
Thomas South	TL-S	39.2700	-107.1403	3113.9	16.12	15.17	5.70	1.60 / 1.90 / **1.75**	0.082	7.97	7.69
Timberline	TMB	39.2980	-106.4753	3275.2	15.23	14.50	10.35	4.3 / 4.15 / **4.23m**	0.007	7.70	6.23
Tuhare East	TLE	39.4487	-106.4701	3690.8	12.95	14.10	11.00	2.90 / 1.90 / **2.40m**	0.021	7.76	8.28
Tuhare West	**TLW**	**39.4506**	**-106.4781**	**3774.9**	**12.48**	**12.10**	**25.50**	**1.85 / 1.60 / 1.73m**	**0.021**	**8.30**	**8.81**
Weller**	WLL	39.1151	-106.7209	2893.9	17.33	8.10	8.70	2.30 / 2.60 / **2.45m**	0.019	9.52	6.20
Whitney	WHT	39.4262	-106.4505	3320.9	14.98	15.22	7.80	3.4 / 3.1 / **3.25m**	0.017	6.95	5.80
Williams	WIL	39.2222	-107.1223	3277.3	15.22	7.51	3.60	3.60 / 3.20 **3.35m**	0.114	11.01	7.21
Windsor	**WND**	**39.2421**	**-106.4866**	**3524.2**	**13.86**	**11.59**	**16.90**	**3.9 / 3.7 / 3.8m**	**0.009**	**8.36**	**6.86**

Table 2.2: CCA results for MJAT. λ_1 is the eigenvalue for the first CCA axis. λ_1/λ_2 is the ratio of the first constrained CCA axis to the second unconstrained CCA axis. % Total Variance corresponds to the amount of variance captured by the predictor (MJAT) variable.

Environmental Variable	λ_1	λ_1/λ_2	% Total Variance
MJAT (°C)	0.122	0.355685	5.4

Table 2.3: Summary Statistics for the chironomid MJAT calibration set: sd = standard deviation units; λ = eigenvalue

Number of Samples	38
Number of Species	57
N2 for samples	
mean	9.86
maximum	22.80
minimum	3.74
N2 for species	
mean	8.12
maximum	28.54
minimum	1.00
DCA Axis 1	
λ_1	0.49
gradient length (sd)	4.99
% variance	0.55
sd	0.914
DCA Axis 2	
λ_2	0.3199
gradient length (sd)	2.6976
% variance	0.3326
sd	0.636592
λ_1/λ_2	0.355685
Mean July Air Temperature (°C)	
minimum	11.84
maximum	17.47
range	5.63
mean	14.58
median	14.35
standard deviation	1.37

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Table 2.4: Performance statistics for midge-based inference models for MJAT (°C) with relation to chironomid assemblages. RMSE = root mean square error. RMSEP = root mean square error of predicition. Cross-validation analysis followed leave-one-out sampling.

Inference Model	Apparent RMSE (°C)	r^2	Cross Validation RMSEP (°C)	r^2_{jack}	Maximum Bias (°C)
WA-PLS 2 Component	0.45	0.83	0.81	0.47	0.94

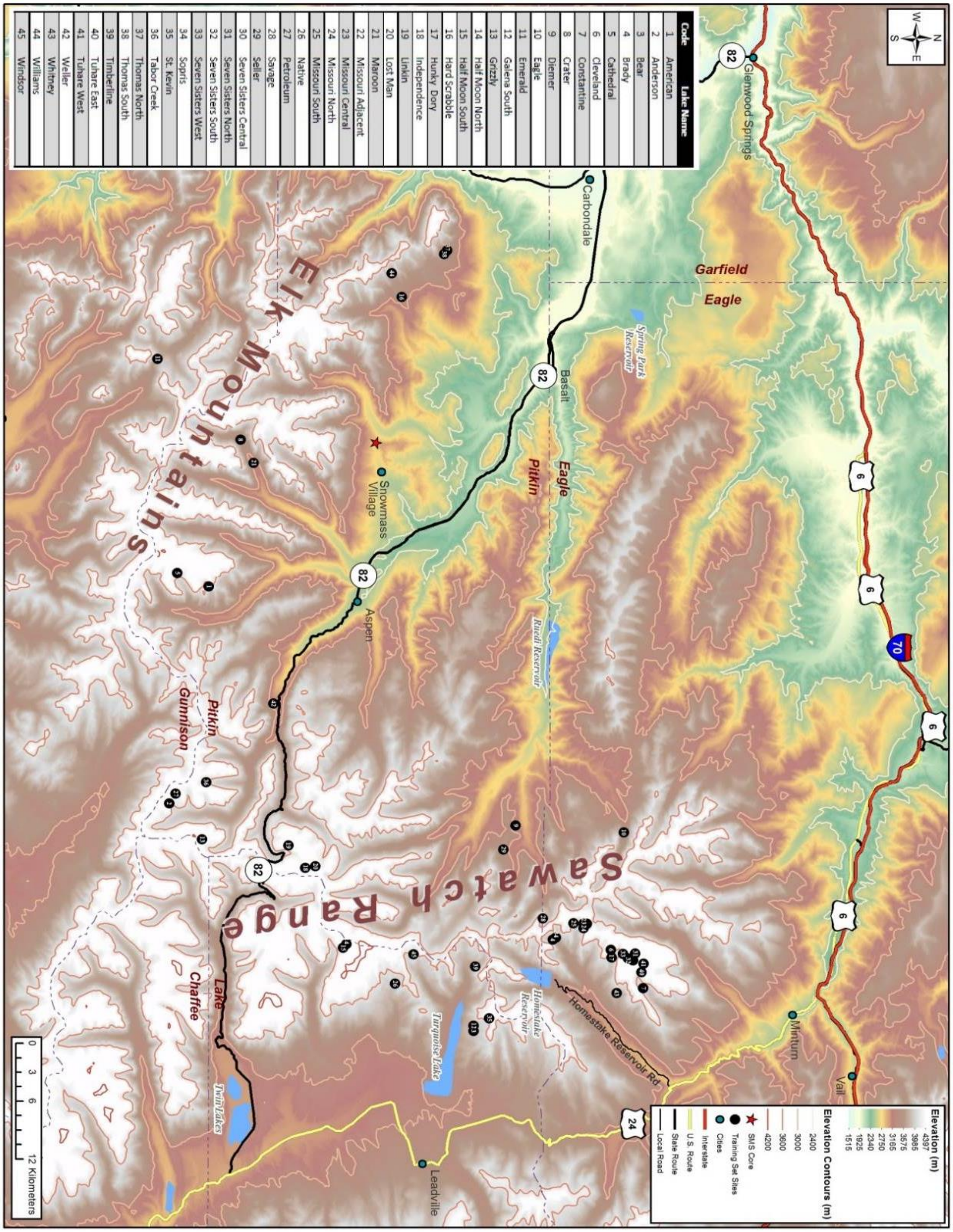


Figure 2.1: Location map of the 45 sampled lakes in the central Colorado Rocky Mountains.

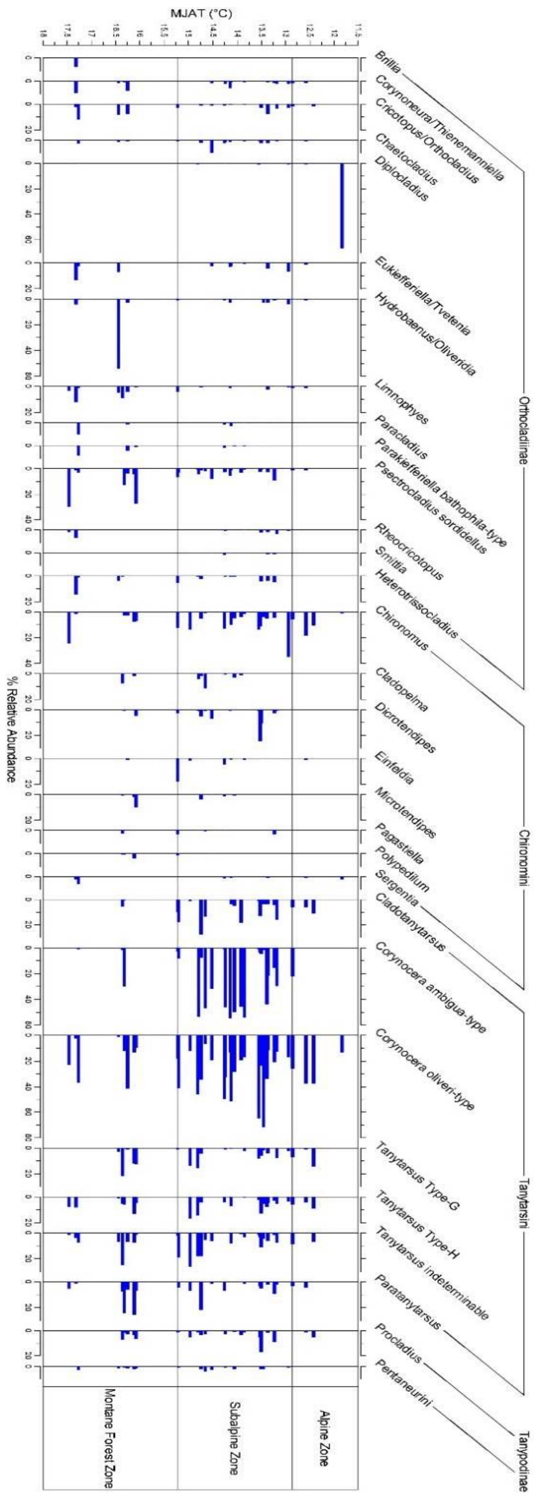


Figure 2.2: Relative abundance (%) curve of chironomid taxa arranged by MJAT. Zones were determined using vegetation zones.

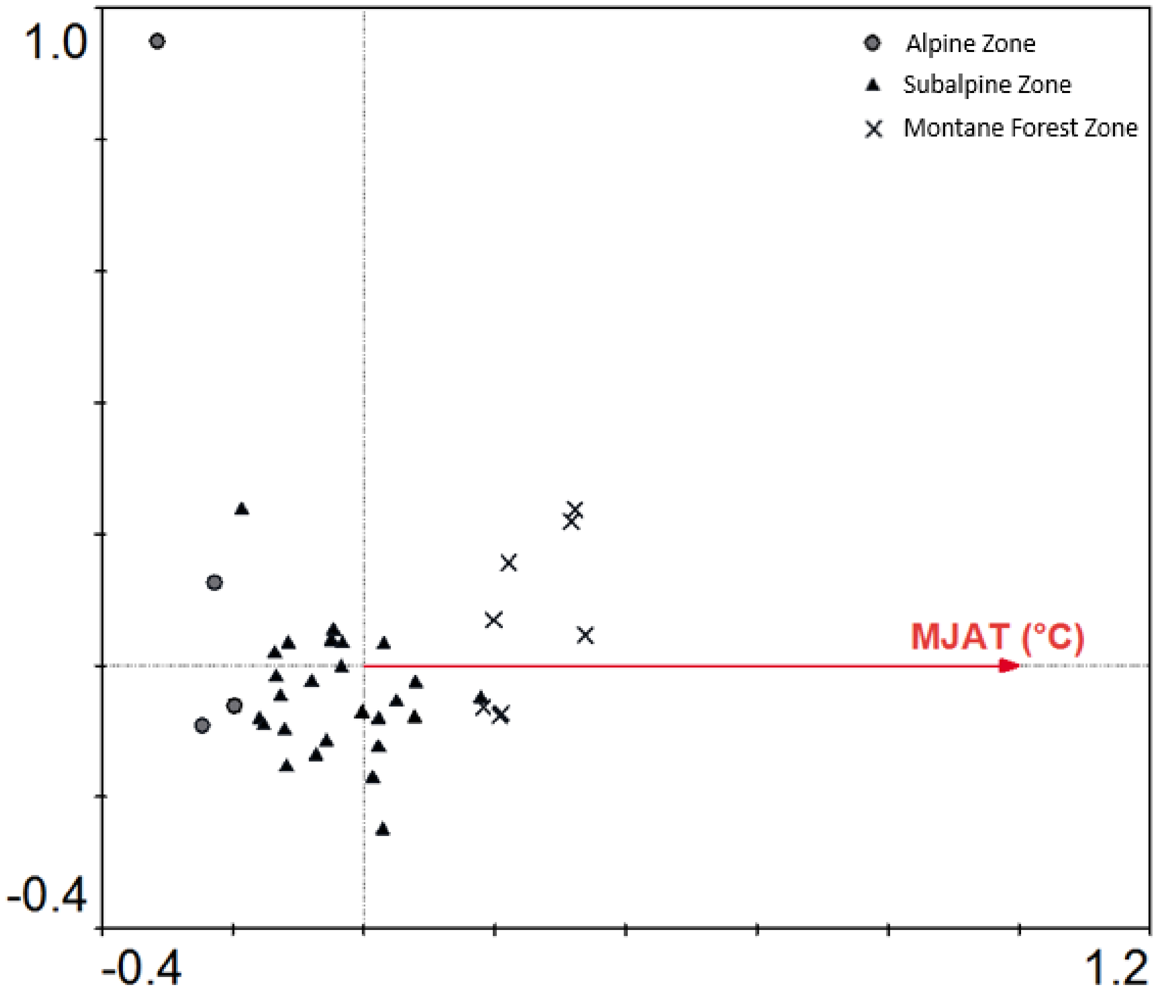


Figure 2.3: CCA bi-plot depicting the relationship between the 38 lakes incorporated in the midge-based MJAT inference model and MJAT (°C).

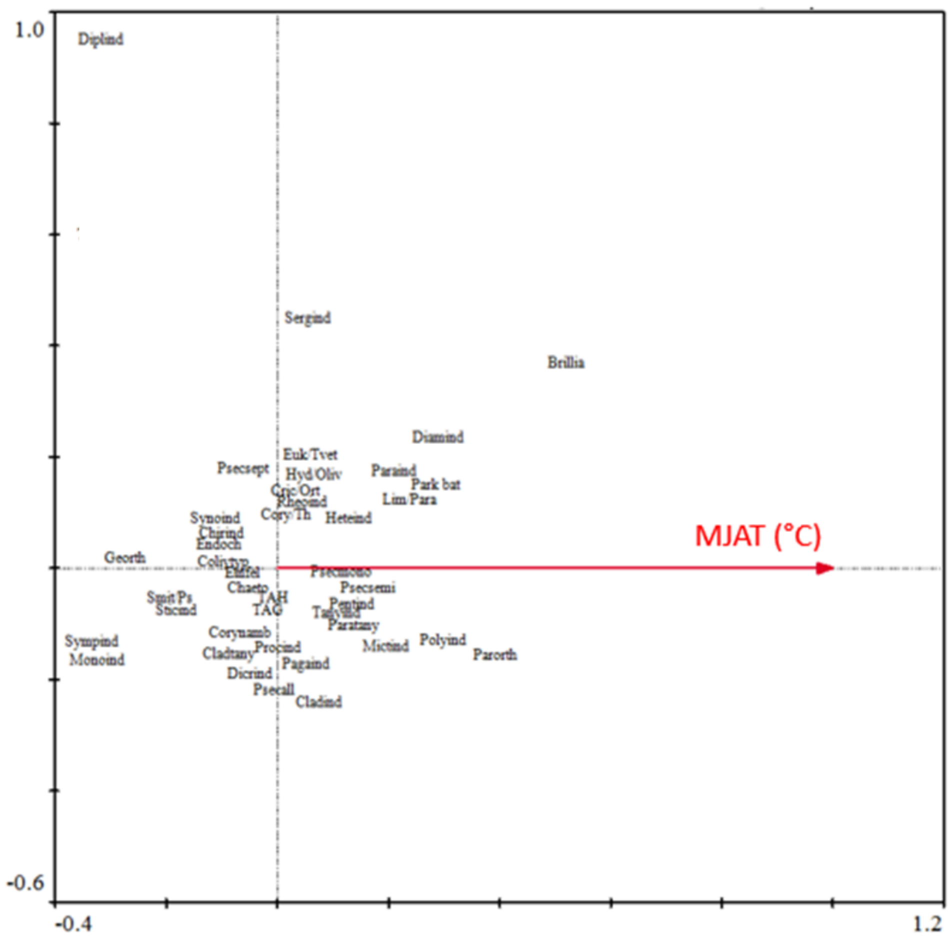


Figure 2.4: CCA bi-plot indicating the relationship between MJAT and the chironomid taxa found in the 38-lake training set. Chaeto = *Chaetocladius*, Chirind = *Chironomus*, Cladtany = *Cladotanytarsus*, Cladind = *Cladopelma*, Colivtyp = *Corynocera oliveri*, Coryamb = *Corynocera ambigua*, Cory/Th = *Corynoneura/Thienemanniella*, Cricort = *Cricotopus/Orthocladius*, Dicrind = *Dicrotendipes*, Dimin = Diamesa, Diplind = *Diplocladius*, Einfel = *Einfeldia*, Endoch = *Endochironomus*, Euk/Tvet = *Eukiefferiella/Tvetenia*, Georth = *Georthocladius*, Heteind = *Heterotrissocladius*, Hyd Oliv = *Hydrobaneous/Oliveridia*, Lim = *Limnophyes*, Mictind = *Microtendipes*, Monoind = *Monodiamesa*, Pagaind = *Pagastiella*, Paraind = *Paratendipes*, Parkbat = *Parakiefferiella bathophila*, Paratany = *Paratanytarsus*, Paroth = *Parorthocladius*, Pentind = *Pentaneurini*, Polyind = *Polypedilum*, Procind = *Procladius*, Psecall = *Psectrocladius*

allopsectrocladius, Psecmono = *Psectrocladius monopsectrocladius,* Psecsemi = *Psectrocladius semisordidellus*, PsecSept = *Psectrocladius septentrionalis*, Rheoind = *Rheocricotopus*, SmitPs = *Smittia*, Synoind = *Synorthocladius*, Tanyind = *Tanytarsus indeterminable*

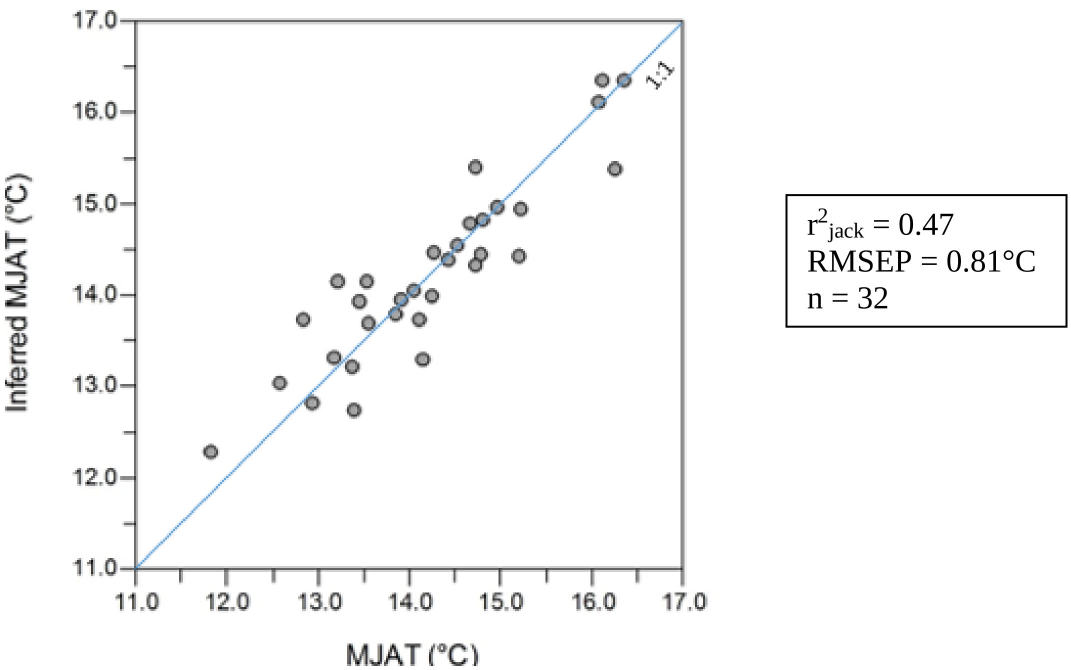
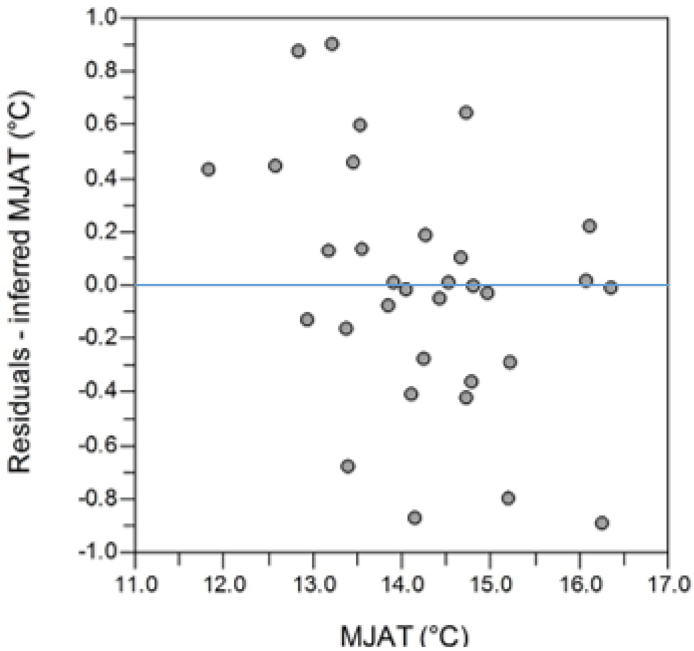


Figure 2.5: Relationship between the lapse rate-derived MJAT and the midge-inferred MJAT based on a 2-component WA-PLS inference model.



r^2_{jack} = 0.47
RMSEP = 0.81°C
n = 32

Figure 2.6: The residuals for MJAT based on a 2-component WA-PLS inference model.

CHAPTER 3

A QUANTITATIVE MIDGE-BASED RECONSTRUCTION OF THERMAL CONDITIONS IN CENTRAL COLORADO DURING MARINE ISOTOPE STAGE 5[2]

[2] Haskett, D.R. and D.F. Porinchu. Submitted to *Quaternary Research.*

ABSTRACT

A sediment core recovered from the Ziegler Reservoir fossil site in Snowmass Village, Colorado was analyzed for subfossil midges. The midge stratigraphy spans from ~70 – 140 ka and captures the Bull Lake Glacial, the Sangamon Interglacial and the early Wisconsin Glacial. A regional calibration set, incorporating lakes from the central Colorado Rockies, the Sierra Nevada and the Uinta Mountains, was used to develop a midge-based mean July air temperature inference model with robust performance statistics (2-component WA-PLS; r^2_{jack}=0.61, RMSEP=0.97ºC). Application of this inference model to midge stratigraphy developed for the Ziegler Reservoir fossil site enabled the development of a quantitative reconstruction of MJAT spanning Marine Isotope Stage (MIS) 5 for the central Rockies. Reconstructed temperatures ranged from 8.9 – 13.2°C. The transition from MIS 6 to MIS 5e was characterized by an increase in the MJAT of ~1.5°C (9.0-10.5°C). MIS 5 exhibited gradually increasing midge-inferred MJAT, culminating in a maximum MJAT of 13.2°C midway through MIS 5a (~ 79.6 ka). Fluctuations in lake level and ice cover likely also influenced midge community composition.

Keywords **:** Chironomids; midges; temperature reconstruction; paleoclimate; Sangamon, MIS 5, Colorado Rockies, Snowmastodon Site, paleolimnology

INTRODUCTION

Developing quantitative estimates of past temperature, with specific reference to past warm intervals, e.g. the Sangamon Interglacial, will improve our understanding of the magnitude of variability that exists in the climate system. Although the previous interglacial is an imperfect analogue of future conditions, improving our understanding of climate variability and conditions during this interval will provide valuable insight to the possible nature of future conditions and the potential feedbacks that may be important in warm climate scenarios.

Chironomids (Insecta: Diptera), or midges, have been extensively used as a proxy for past climate and are one of the most promising approaches to reconstructing past thermal regimes (Battarbee, 2000). Chironomids, which are amongst the most productive freshwater insects present in lacustrine environments, are found on every continent, with distributions ranging from the tropics to the high latitudes (Porinchu and MacDonald, 2003). Midges are valuable in paleoclimate studies because they are abundant, well preserved in lake sediment and sensitive to key environmental variables such as air and water temperature (Porinchu and MacDonald, 2003; Walker and Cwynar, 2006; Eggermont and Heiri, 2012). Quantitative temperature reconstructions based on subfossil midge analysis have provided independent estimates of regional climate conditions during intervals of transition in the late Quaternary (Cwynar and Levesque, 1995; Porinchu et al., 2003; Engels et al., 2010).

A number of midge-based calibration sets relating variations in chironomid assemblages to temperature (air and water) have been developed for use in North America (Walker et al., 1997; Barley et al. 2006; Porinchu et al., 2009; Porinchu et al., 2010). Previous research in the Great Basin has led to the development of a robust midge-based inference model for mean July temperature (MJAT) and surface water temperature (SWT) (Porinchu et al., 2007a; Porinchu et al., 2010). Application of the water and air temperature inference models to the sub-fossil midge remains extracted from late Quaternary sediment has improved our understanding of the spatial and temporal patterns of recent (Porinchu et al., 2007b; Porinchu et al., 2010) and long-term regional climate change in the western United States during the latest Pleistocene and Holocene (Porinchu et al., 2003; Potito et al., 2006; Reinemann et al., 2009) and provided insight into the relationship between local thermal conditions and regional and hemispheric climate dynamics (MacDonald et al., 2008). For example, a recent multi-proxy paleolimnological investigation in the eastern Sierra Nevada of California provides evidence of shifts in hydrology and an approximate 3°C depression of lake water temperature during the Younger Dryas chronozone (MacDonald et al., 2008).

The existing midge-based records of past thermal conditions in the western United States do not extend through the Last Glacial Maximum (LGM). However, sub-fossil midge analysis has been used successfully in high northern latitudes to provide quantitative estimates of the thermal conditions that existed during the penultimate interglacial, the Sangamon Interglacial, and the Wisconsin Glacial (Axford et al., 2011; Engels et al., 2010). Engels et al. (2010) reconstructed past changes in climate at Sokli, Finland during MIS 5d and 5c; however, the authors indicate that the midge-based temperature estimates are based on midge assemblages that exhibit poor fit-to-temperature in their model and therefore the temperature estimates need to be viewed with caution. Similar findings are evident in records from Alaska that extend beyond the LGM (~39,000 year record) (Kurek et al., 2009). Axford et al. (2011) have successfully developed a 200,000 year record from Baffin Island, Canada with robust temperature estimates for MIS 5 and MIS 7 (Axford et al., 2011).

The recent discovery of a Pleistocene megafauna fossil site, known as the Ziegler Reservoir fossil site, in Snowmass Village, CO provides an exciting opportunity to use chironomids to document climate variability at high elevation for an interval that includes the early Wisconsin Glacial (MIS 4), the Sangamon Interglacial (MIS 5), and the termination of the Bull Lake glaciation (MIS 6). The exceptionally well-preserved Ice Age ecosystem entombed at the Ziegler Reservoir fossil site is significant because it contains a relatively complete sequence of fossil bearing strata spanning approximately 70 ka (70 – 140 ka). This lengthy record provides an opportunity to develop detailed records of climate and environmental change that span the previous glacial-interglacial transition, an interval characterized by dramatic re-organization of the climate system and biotic communities. In this paper we apply a chironomid-based inference model for mean July air temperature (MJAT) (Porinchu et al., 2010; Porinchu et al., *in prep*) to a midge stratigraphy from the Ziegler Reservoir fossil site and develop a detailed, quantitative reconstruction of thermal conditions for the region that spans portions of MIS 5. The results of the sub-fossil midge analyses are compared to a pollen-based reconstruction of vegetation change (Anderson et al., this issue) to examine how changes in climate may have influenced vegetation response.

STUDY SITE

The Rocky Mountains, and the Basin and Range to their west, cumulatively comprise over 100 individual ranges stretching from Canada to New Mexico in a 2000 km northwest trending belt (Pierce, 2003). These mountains have a rich and diverse geologic history and have been subjected to millions of years of uplift, subsidence and erosion (Pierce, 2003). The landscape, which has been influenced by these processes, has also been shaped by repeated glaciations (Porter et al., 1983). The surficial geology of the area surrounding Snowmass Village has been heavily modified by glacial activity. The Ziegler Reservoir fossil site, situated in the Elk Mountains in central Colorado and located at an elevation of 2705 m asl, was initially formed during the Bull Lake glaciation, which has been correlated with MIS 6 (Johnson and Miller, 2012). It appears that the Pinedale glaciation and any possible MIS 4 glacial advance, which followed the Bull Lake glacial expansion, were not sufficient to overtop the ridge separating Snowmass Creek from Brush Creek, thus the ZR was not overridden and the sediment sequence spanning the Sangamon Interglacial remained undisturbed (Johnson and Miller, 2012). The Ziegler Reservoir fossil site (39º12'29N, 106º57'51W) is a small (300 m diameter), perched reservoir that is surrounded by moraine deposits comprised of red sandstone clasts that originated from the adjacent Maroon Bells Formation. These deposits are underlain by the Mancos Shale (Bruce, 1972). The arboreal vegetation currently surrounding Ziegler Reservoir fossil site is dominated by quaking aspen (*Populus tremuloides*), sub-alpine fir (*Abies lasiocarpa*) and lesser amounts of scrub oak (*Quercus gambelii*) and sagebrush (Artemesia) (see Anderson et al. this volume for further detail). Snowmass Village, CO is influenced by a continental climate with cold winters and cool moist summers (see Anderson et al. this issue for further detail). Mean July temperature at Aspen, CO (2389 m asl) is 17.17ºC. Applying a lapse rate of 5.5°C/km (based on the average of daytime and nighttime lapse rates; Pepin and Losleben, 2002) provides an estimate of 15.43ºC for mean July temperature for Snowmass Village, CO.

To complement the existing Great Basin midge calibration set (Porinchu et al., 2010) additional surface sediment was recovered from twenty lakes in the vicinity of Snowmass Village, CO during July 2011 and July 2012 (see Table 1). The calibration set lakes, which are located within 50 km of the Ziegler Reservoir fossil site, are all located within the White River

National Forest (see Figure 3.1). These lakes fall within one of three broad vegetation zones: 1) Montane (2,440 – 3,050 m asl) which is dominated by pine (*Pinus*), aspen (*Populus*), with Douglas-fir (*Pseudotsuga menziesii*) present locally; 2) Subalpine (2,895 to 3,475 m asl) which is dominated by spruce (*Picea*), sub-alpine fir and pine; 3) Timberline (3,415 to 3,660 m asl) which demarcates the transition from subalpine to alpine tundra, with herbaceous plants and low-lying shrubs dominating this zone (McMulkin et al., 2010). The sub-surface geology of the area consists primarily of Proterozoic diorites and granites (Hopkins and Hopkins, 2000). The lakes sampled spanned elevation, maximum lake depth, pH and air (MJAT) and surface water temperature (SWT) ranges of ~1024 m (2869 – 3893 m asl), ~23.1 m (0.9 – 24 m), 3.24 (6.12 – 9.36), ~5.6^{o}C (8.24 – 13.91^{o}C) and 13.3^{o}C (7.0– 20.3^{o}C) respectively (see Table 3.1).

METHODS

Sediment samples were collected for sub-fossil midge analysis at known intervals using stratigraphic markers present within the relict lake basin at the Ziegler Reservoir fossil site in June 2011 (Pigati et al., 2013). Sediment samples from Locality 43 (Units 14 - 8) and Locality 51 (Units 17 - 15) were collected in 10 cm increments from the cleaned sediment facies. Sediment was removed using a specula and placed into Whirlpacks®. Additional sediment from Units 8 – 3, collected using a Giddings Soil Probe, were sub-sampled in the lab every 5 cm and placed into Whirlpacks®.

A suite of limnological variables were collected in the field during the collection of surface sediment for the modern midge calibration set. A YSI Professional Plus probe was used to measure surface water temperature, dissolved oxygen, specific conductivity and pH. A Secchi disk was used to estimate optical transparency and measure depth for each lake. Water samples were also collected from the surface for stable isotope analysis (^{18}O, D/H) (Street et al., see this issue). Sediment was recovered from the center of each lake using a DeGrand corer. Each core was sectioned in the field with the upper 1 cm sectioned at 0.25 cm resolution and placed into Whirlpacks® and stored in a cooler until the completion of field work. Surface sediment was stored in a refrigerator upon return to the lab at the University of Georgia. Mean July air temperatures (MJAT) were extracted from data made available by the PRISM Climate Group (http://www.prism.oregonstate.edu/).

Procedures described in Walker (2002) were followed for the extraction and mounting of sub-fossil chironomid remains. Sediment samples were soaked in an 8% KOH solution and heated to 35°C for a minimum of 30 minutes, or until colloidal matter was sufficiently deflocculated. Material from the surface sediment and sediment from the core that did not contain much plant matter were sieved through a 95μm-grade mesh screen using distilled water to eliminate any remaining KOH residue. Nested sieving (500μm, 300μm, and 95μm) was implemented for the organic-rich sections from the Ziegler Reservoir fossil site to remove plant fragments and enable more accurate and efficient picking (Walker, 2002). The material remaining on the screen was then backwashed into a beaker with distilled water. The resulting residue was poured into a Bogorov counting tray and sorted using a stereoscope at 40x. The sub-fossil chironomid head capsules extracted from the residue were permanently mounted on glass slides using Entellan®. Taxonomic determination of the midge remains were made using a Ziess Axioskop at 400x and followed Brooks et al., 2007, an extensive reference collection of sub-fossil midges from the Great Basin and an online chironomid identification key (http://chirokey.skullisland.info/).

The chironomid percentage diagram was plotted using C2 (Juggins, 2003) and was based on the relative abundance of all chironomid taxa that were present in two or more samples with a relative abundance of at least 2% in one sample. The relative abundance data used in the ordination analyses and in the development of the MJAT inference model were square-root transformed to maximize the 'signal to noise' ratio (Prentice, 1980). Ordination analyses were implemented using CANOCO version 4.5 (ter Braak and Šmilauer, 2002). All statistical analyses were based on samples with a minimum recovery of 40 head capsules with the exception of a single sample found at 304 cm above glacial till (~ 113.6 ka) for which only 39 head capsules were identified (Heiri and Lotter, 2001). A form of indirect gradient analysis, detrended correspondence analysis (DCA), was used to assess the amount of faunal turnover in the Ziegler Reservoir midge stratigraphy.

The existing Great Basin midge-based inference model for MJAT developed using a 2-component WA-PLS approach, has a RMSEP=0.9^{o}C and a r^2_{jack}=0.66 (Porinchu et al., 2010 Porinchu et al., *in prep*). An additional twenty lakes sampled from Colorado have been incorporated in the existing Great Basin training set. This new training set will be referred to as the Intermountain West (IMW) training set. The expanded midge-based air temperature inference model incorporates MJAT estimates based on the most recent Climate Normal (1981-2010) (PRISM data group, 2012). The inference model applied to the sub-fossil midge assemblages recovered from the Ziegler Reservoir fossil site is based on ninety-one lakes with a RMSEP=0.97^{o}C and a r^2_{jack}=0.61 (Porinchu et al., *in prep*). The reliability of the quantitative midge-based reconstruction was evaluated by: 1) determining for each sub-fossil assemblage the total percentages of taxa present down-core that do not appear in the modern calibration data set; 2) determining the proportion of rare taxa present in the down-core samples. Reconstructions that are based on sub-fossil assemblages that have >95% of the sub-fossil taxa present in the calibration set are considered very reliable (Birks, 1998). Taxa with an effective number of occurrences or Hill's N2 >5 in a training set can be considered well represented and will likely provide reliable estimates of temperature optima (Brooks and Birks, 2001).

RESULTS

Modern Chironomid Assemblages

The addition of the midge assemblages from the twenty lakes sampled in the White River National Forest to the IMW training set expands the elevation gradient captured by the training set by ~ 350 m and has added three new chironomid taxa: *Diplocladius, Chaetocladius*, and *Einfeldia* to the existing Great Basin training set (Porinchu et al. 2007a; Porinchu et al. 2010). *Diplocladius*, which is found in three of the twenty lakes sampled in Colorado, dominates the midge community in Seven Sisters West Lake (SSW) (~ 66%), the highest (~ 3900 m asl) and the coldest lake (7°C) in the IMW calibration set. Seven Sisters West Lake is a relatively deep lake surrounded by talus and located approximately 350 m above the modern timberline. The midge community in SSW is likely influenced by the direct contribution of cold meltwater emanating from the snowfields surrounding the lake. *Chaetocladius* is found in five lakes, which are characterized by wide elevation, lake depth and air (MJAT) and surface water temperature (SWT) ranges. The presence of *Einfeldia* in Seven Sisters Central Lake (SSC) and Missouri Lake Adjacent (MLA) is particularly important because sub-fossil remains of *Einfeldia* are present in the Ziegler Reservoir midge stratigraphy. Seven Sisters Central Lake and MLA are located above timberline with vegetation in both basins consisting of dwarf Picea, Compositae, and Poaceae. Sub-fossil midge remains from an additional twenty-five Colorado lakes will be identified and incorporated into the existing IMW training set; description of the expanded IMW training set will be provide in a future publication (Haskett and Porinchu, *in prep*).

Ziegler Reservoir: Midge Stratigraphy, Community Change and Temperature Reconstruction

A number of approaches were used to determine the age of the sediment sequence preserved at the Ziegler Reservoir fossil site. Well-preserved wood and plant macrofossils, as well as collagen from tooth and bone, were dated using AMS radiocarbon dating. Unfortunately, the dates obtained on these samples were either near the analytical limit of the approach or the samples yielded infinite ages (Mahan et al., this issue). Surface exposure dating was undertaken on a single, large boulder located on the Bull Lake moraine. *In situ* cosmogenic dating based on one ^{10}Be provided an age estimate for the emplacement of the moraine ranging from 138 ± 12 ka (Mahan et al., this issue). Optically stimulated luminescence (OSL) yielded the most robust results and provided a chronology for the site that ranged from 55.1 ± 9.6 ka at the surface to 140.6 ± 14.2 ka for the lowermost sampled unit (Unit 3) (Mahan et al., this issue). The pollen record (Anderson et al., this issue) indicated that the OSL-derived ages toward the top did not change for ~2.5 m in the upper portion of the stratigraphic sequence recovered from the Ziegler fossil site. The presence of three distinct transitions in the pollen record was incorporated in the BACON age model and used to help further constrain the chronology. Further details regarding the development of the age-model for the Ziegler Reservoir fossil site are available in Mahan et al. (this issue).

Unit 3 (0 – 22 cm above glacial till). The sub-fossil chironomid head capsules recovered from the base of the Ziegler Reservoir sediment sequence were obtained from cores ZR-3B and ZR-3C. Glacial till is found below Unit 3. The sediment immediately above the glacial till consists of sticky clay (Pigati et al., 2013). The base of Unit 3 is characterized by high midge head capsule concentration (110 head capsules/mL) and low taxonomic diversity. *Corynocera oliveri*-type is the dominant midge comprising approximately 75% of the assemblage with lesser amounts of *Procladius* (11%) and *Tanytarsus*-type G (12%) and *Tanytarsus*-type H (2%) present (see Figure 3.2).

Unit 4 (22 – 59 cm above glacial till). The sediment stratigraphy transitioned to an organic-rich silt at the base of Unit 4 (~ 138 ka). This sediment, which was obtained from the cores ZR-3B and ZR-3C (Pigati et al., 2013), contained abundant midge remains. However, the head capsules were disarticulated and heavily degraded, precluding the recovery of a sufficient number of head capsules to permit use of these samples in statistical analyses. The midge remains preserved in Unit 4 are comprised of warm-stenothermic taxa such as *Chironomus, Glyptotendipes* and *Cladopelma*, a genus associated with mesotrophic lakes (Brooks et al., 2007).

Unit 5 (59 – 95 cm above glacial till). A transition to laminated silty clay occurs in Unit 5. This transition is characterized by a significant decrease in midge head capsule concentration. Three head capsules (*Chironomus* and *Procladius*) were recovered from sediment that was deposited at 80 cm above the glacial till (~132.5 ka).

Unit 6 (95 – 147 cm above glacial till). The stratigraphy coarsens to organic-rich silt in Unit 6. The midge community in the uppermost Unit 6 sample at 126 cm above glacial till (~ 128 ka) contains the remains of *Chironomus* and *Glyptotendipes*. A large number of mandibles belonging to Chaoborus (phantom midge), an organism that that can survive long periods of anoxia (Brooks et al., 2007), are also present in the top of Unit 6.

Unit 7 (147 – 223 cm above glacial till). Unit 7 was obtained from cores ZR-3B and ZR-3C. The sediment in Unit 7 consists of organic-rich sand at the base, which coarsens upward into a sandy silt that is interspaced with carbonate lenses. The sub-fossil midge community present during this interval is not well described due to the extremely poor head capsule recovery (0-5 head capsules/mL). However, warm stenothermic midge taxa are present and comparable to those found in Unit 4, albeit at very low numbers.

Unit 8 (223 – 355 cm above glacial till). Organic silt, obtained from cores ZR-3B and ZR-3C, represents the base of Unit 8. Additional sediment samples from Unit 8 were collected from Locality 43 and represent the upper portion of this unit. The base of Unit 8 is dominated by eurytopic taxon, *Cricotopus* (23.1%), which is present at 273 cm (~116.2 ka). Head capsules of the acidophilic *Psectrocladius sordidellus*-type (9.0%) appear in the record at 304 cm (~113.6 ka). The very top of Unit 8 (~109.5 ka) is characterized by a complete absence of midge head capsules.

Unit 9 (355 – 415 cm above glacial till). Sediment representing Unit 9 was sampled from Locality 43 and is characterized by mottled brown silt. Two sections in Unit 9 contain midge remains albeit with extremely low head capsule recovery (~ 4.5 head capsules/mL). The sub-fossil midge remains recovered from Unit 9 consisted entirely of *Glyptotendipes.*

Unit 10 (415 – 438 cm above glacial till). The transition from Unit 9 to Unit 10 is the most abrupt and notable in the Ziegler Reservoir midge stratigraphy. The sediment, which was collected from Locality 43, consists of a yellow-banded silt containing large fragments of organic matter. The base of Unit 10 is characterized by low head capsule abundance. A shift to abundant midge remains occurs at 424 cm above glacial till (~103.6 ka). *Tanytarsus* spp., *Corynocera oliveri-type, Procladius* and *Chironomus* are abundant during the interval represented by Unit 10.

Unit 11 (438 – 457 cm above glacial till). The sediment transitions from the yellow-banded silt of Unit 10 to a weakly banded silt. Unit 11 is characterized by low head capsule recovery at the base of the unit; however, at 453 cm (~101.4 ka) chironomid remains become very abundant (257 head capsules/mL). *Psectrocladius sordidellus*-type, *Chironomus, Dicrotendipes, Cladotanytarsus, Tanytarsus* spp. and *Procladius* dominate the midge community during this interval.

Unit 12 (457 – 463 cm above glacial till). The stratigraphy of Unit 12 is described as an organic mat rich with macroscopic wood and leaf particles and was collected from Locality 43. The chironomid assemblages are composed of *Cricotopus, Psectrocladius sordidellus*-type, *Chironomus, Dicrotendipes, Cladotanytarsus, Tanytarsus* and *Procladius.* The composition of the midge community is comparable to that found in Unit 11.

Unit 13 (463 – 568 cm above glacial till). The sediment for Unit 13 transitions to banded silty clay from the organic-rich sediment of Unit 12. The chironomids sampled for this interval were taken from Locality 43 and are found in banded silty clay. The chironomid counts and assemblages located at the base of this unit are identical to those found in Unit 10. However, a large transition in midge community composition is evident at 512 cm above glacial till (~97.0

ka). Subfossil midges disappear during this interval and remain absent from the uppermost sediment of Unit 13

Unit 14 (568 – 688 cm above glacial till). Unit 14, which transitions to a massive silty clay, was also taken from Locality 43. This unit is unique in that no sub-fossil chironomid head capsules were recovered.

Unit 15 (688 – 727 cm above glacial till). The samples collected for chironomid analysis from the sediment in Unit 15 were collected from Locality 51. The sediment is comprised of peaty silt that includes large organic fragments and macroscopic plant matter. Chironomid head capsule abundance and concentrations are high and range from 45 head capsules/mL to 241 head capsules/mL. Taxa such as *Parakiefferiella bathophila*-type, *Psectrocladius sordidellus*-type, *Chironomus, Dicrotendipes, Glyptotendipes* and *Cladotanytarsus* are the most common constituents of the midge community.

Unit 16 (727 – 802 cm above glacial till). Unit 16 ultimately transitions into dark brown peat with very high concentrations of organic matter. This sediment was collected from Locality 51. A large change in head capsule recovery and midge community composition accompanies the transition between Units 15 and 16. Sediment above the 728 cm section (~83.4 ka) of Unit 16 is characterized by increasingly peaty material and low head capsule recovery. Taxa such as *Limnophyes, Smittia, Paratendipes, Polypedilum, Paratanytarsus* and the cold stenotherm, *Heterotrissocladius*, are relatively abundant in Unit 16. The appearance and high relative abundance of the remains of carnivorous Ceratopogonidae in Unit 16 is notable. No sub-fossil midge remains were recovered from the uppermost portion of this unit.

Unit 17 (802 cm – 860 cm above glacial till) Sediment from Units 17 and 18 were collected at Locality 51. The silt of Unit 17 transitions to a poorly preserved mottled silty clay in Unit 18. Samples were not collected for chironomid analysis from Unit 18. Only one individual head capsule was recovered for Unit 17 sediment. The head capsule belonging to *Zavreliella* was found at 858 cm (~ 71.5 ka). The remainder of the sediment processed from Unit 17 was devoid of sub-fossil midge remains.

De-trended correspondence analysis (DCA) reveals that two intervals of rapid turnover in midge community composition occurred at the Ziegler Reservoir fossil site. The first interval of turnover in the midge community occurs at the base of the Ziegler Reservoir midge stratigraphy with a shift from a *C. oliveri*-type dominated assemblage in Unit 3 to a *Chironomus* and *Glyptotendipes* dominated assemblage at the base of Unit 4. The turnover that occurred at the uppermost portion of Unit 15 (~ 83.4 ka) is more notable. The midge community shifts from a Chironomini-dominated assemblage to an Orthocladiinae-dominated assemblage in the uppermost sediment extracted from Unit 15. The replacement of *Chironomus, Dicrotendipes and Glyptotendipes* by a cool water taxon, *Heterotrissocladius*, and semi-terrestrial taxa such as *Limnophyes/Paralimnophyes* and *Smittia/Parasmittia* characterizes this shift in midge community composition.

The taxa present in the Ziegler Reservoir midge stratigraphy are well-represented and characterized by the Intermountain West calibration set with all twenty five chironomid taxa comprising the chironomid stratigraphy present in the Intermountain West training set (Porinchu et al., 2010; Porinchu et al., *in prep*); therefore, the MJAT reconstructions should be considered reliable (Birks, 1998). The Hill's N2 diversity index values range between 5 and 58 for twenty of the twenty-five taxa present in ZR relative to their distribution in the IMW training set. This provides added support that the quantitative midge-based MJAT reconstructions can be considered robust (Birks, 1998). Five taxa: *Smittia/Psuedosmittia, Einfeldia, Glyptotendipes, Paratendipes* and *Labrundinia* have Hill's N2 values below five; however, these taxa, with the exception of *Glyptotendipes*, are present in five or less samples and do not dominate any of the assemblages in which they are found. The chironomid-inferred MJAT reconstruction for the ZR midge stratigraphy is presented in Figures 3.5 & 3.6. Sample-specific error estimates associated with the midge-based MJAT estimates varied between 1.0°C and 1.4°C. The sample specific error estimates were calculated using the program C2 (Juggins, 2003). The midge-based MJAT inference model, which was applied to samples containing thirty-nine or more identifiable head capsules, provided estimates of MJAT for three discrete intervals: the transition from Unit 3 to Unit 4, the transition from Unit 12 to Unit 13, and the transition between Unit 15 and Unit 16. In addition, a point estimate of MJAT is available for Unit 6. The transition from Unit 3 to Unit 4 is characterized by an increase in MJAT of ~1.5ºC (9.0-10.5ºC). A midge-inferred point estimate of 10.5ºC is available for the upper portion of Unit 6. A midge-inferred MJAT of 10.5ºC, which occurs in Unit 12 (~100.9 ka), is followed by a 2.0ºC decrease in MJAT to 8.9ºC during the transition from Unit 12 to Unit 13. A slight increase in MJAT occurs prior to the disappearance of all sub-fossil midge remains in Unit 14. Mean July air temperature increases through Units 15 and 16. Midge-inferred MJAT, which is 10.1ºC at the base of Unit 15, reaches a maximum value of 13.3ºC in Unit 16 (~79.6 ka). Prior to the transition to Unit 17, the midge-inferred MJAT decreases approximately 2^{o}C. The reconstructed midge-inferred MJAT temperature range captured by variations in the midge community at the ZR was 4.3°C (8.9–13.2°C).

DISCUSSION

The well-dated sediment sequence recovered from the Ziegler Reservoir fossil site has provided an outstanding opportunity to develop detailed paleoenvironmental and paleoclimatic histories spanning the previous interglacial for the Rocky Mountains in central Colorado. The Ziegler Reservoir fossil site is unique, representing the only record in this region extending from the Bull Lake Glacial (MIS 6), through the Sangamon Interglacial (MIS 5) to the early Wisconsin Glacial (MIS 4) and sub-fossil midge analysis provides a means to reconstruct thermal conditions spanning this interval. Changes in midge community composition and head capsule concentration together with the midge-based MJAT estimates provide a means to address questions relating to the role that climate and environmental change played in shaping the structure and composition of this high elevation Ice Age ecosystem. Although the Ziegler Reservoir chironomid stratigraphy is discontinuous, qualitative and quantitative inferences can be made based upon changes in faunal composition and contribute to our understanding of paleoenvironmental change at the site.

The formation of the Ziegler Reservoir fossil site during the Bull Lake glaciation is well established by the robust chronology derived from the bottom-most stratigraphic units deposited directly above glacial till (Mahan et al., this issue). These findings are substantiated by the cosmogenic dating of *in situ* boulders derived from the Bull Lake advance, which surround the site (Pigati et al. this issue).

The chironomid assemblage found in Unit 3 (MIS 6) is low in diversity and composed primarily of *Corynocera oliveri*-type, a species that typically occurs in the profundal zone of cold, oligotrophic lakes (Brooks et al., 2007). The MJAT optimum for *C. oliveri*-type (10.6^{o}C) is amongst the lowest in the IMW training set (Porinchu et al., 2010; Porinchu and Haskett, *in prep*). The presence of disarticulated and degraded head capsules beginning at the base of Unit 4 (~138.4 ka) suggests that deposition of midge capsules may have been occurring in a high-energy environment, potentially reflecting high glacial meltwater influx or increased sedimentation rates. It is important to note that the taxa preserved throughout the core, particularly in MIS 5e and MIS 5d, consist of those that are highly sclerotized and hardy, thus the subfossil midge assemblages could potentially represent a biased sample of the extant midge community at any given interval. In addition, the current IMW midge training set does not contain a large number of lakes located lower in elevation than Ziegler Reservoir. As a result, it is possible that the absolute values of the midge reconstruction have a "cold" bias.

A shift from a profundal dominated midge assemblage to a midge community dominated by littoral taxa occurs at 37 cm above glacial till in Unit 4 (~136.9 ka) and demarcates the transition from MIS 6 to MIS 5e. Increases in taxa such as *Glypotendipes*, *Cladopelma* and *Psectrocladius,* which are often associated with aquatic macrophytes (Brooks et al., 2007), provides evidence for increased lake productivity during the transition from MIS 6 to MIS 5e. An increase in midge-inferred MJAT of ~ 1.5^{o}C (9.0-10.5^{o}C) provides further support for climate amelioration during the MIS 6-MIS 5e transition. Evidence from pollen (Anderson et al., this issue) suggests that the transition from MIS 5e to MIS 5d occurred ~ 128.7 ka. Low chironomid head capsule recovery and the limited change in head capsule concentrations that characterize the interval between the close of MIS 5e and the onset of MIS 5d limits our ability to provide corroboration for this timing of this transition. A lone sample from Unit 6 (MIS 5d) provided a MJAT estimate of 10.5°C, a temperature comparable to those derived for Unit 4 (MIS 5e).

The inception of MIS 5c is evident in Unit 8 (~112.5 ka) in the pollen record. However, low head capsule recovery continues through MIS 5c suggesting that the shift in limnological conditions that drove the initial decline in sub-fossil midge remains midway through MIS 5e persists. The absence of chironomids in the early portion of MIS 5c is particularly striking because the stratigraphic unit spanning this interval is mostly comprised of organic silt, a sediment type that contains high numbers of chironomid head capsules elsewhere in the Ziegler Reservoir stratigraphy. Very few sections contained sub-fossil midge remains; however, those recovered consisted of *Glyptotendipes*, a taxon that is associated with macrophytes and most commonly found in the littoral of warm, productive lakes (Brooks et al., 2007). The inference of low lake level during this interval is supported by the increase in *Pediastrum* and *Botryococcus* that occurs in MIS 5c, which parallel the initial increase in midge head capsule concentration at 426 cm in Unit 10 (~ 103.5 ka). The presence of high amounts of *Botryococcus* and *Pediastrum* suggest that relatively shallow and possibly fluctuating lake levels characterized Ziegler Reservoir between 452 cm in Unit 10 (~103.5) and 493 cm in Unit 13 (~98.3 ka). Midge-based MJAT peaks at 453 cm in Unit 11 (~ 101.4 ka), corresponding to elevated S:P pollen values.

Although midges disappear from the record at 504 cm in Unit 13 (~ 97.5 ka) they provide evidence of relatively warm conditions during early MIS 5b, suggesting that interglacial conditions persisted longer than evidenced in the pollen record. The absence of midges beginning at 504 cm in Unit 13 (~97.5 ka) may be due to the existence of persistent and extensive ice cover through the summer growing season during MIS 5b. A greatly reduced ice-free season would limit aquatic productivity and likely midge survival. Evidence supporting this claim is provided by the low S:P pollen ratio, which suggests the existence of cool and/or dry conditions and a possible depression in timberline of 800-1000 m relative to today during this interval (Anderson et al., this issue).

The chironomid assemblages in Unit 15 are mostly comprised of taxa such as *Chironomus, Dicrotendipes* and *Glyptotendipes,* that are characteristically associated with the littoral of shallow, mesotrophic and eutrophic lakes. The composition of the midge community during the early portion of MIS 5a is indicative of increased lake productivity and elevated temperatures. A notable shift in midge community composition occurs at the transition from Unit 15 to Unit 16 (~83.4 ka) with community increasingly dominated by taxa associated with macrophytes. The presence of *Limnophyes* and *Smittia*, taxa associated with terrestrial and semi-terrestrial environments (Brooks et al., 2007), suggest a continued lowering of lake levels. Ceratopogonidae, which appear for the first time in the record, provide further evidence for the presence of extensive macrophytic cover. The presence of *Heterotrissocladius*, a taxon normally associated with cold, oligotrophic lakes (Brooks et al. 2007), in the latter half of MIS 5a is intriguing; however, *Heterotrissocladius* is also known to prefer acidophilic environments, such as peat bogs. The midge-based temperature estimates suggest that MJAT rises through MIS 5a with the highest midge-inferred temperatures for the entire record evidenced at 773 cm in Unit 16 at approximately 79.6 ka (13.2°C). Evidence from Yellowstone National Park, which indicates that MIS 5a was the warmest interval of the Sangamon Interglacial, corroborates these findings (Baker, 1986). The chironomid record suggests that a limnological threshold is crossed at 793 cm above glacial till in Unit 16 (~77.9 ka), prior to the transition to Unit 17 (MIS 4), with the disappearance of sub-fossil midges from sediment. Deviations of the midge-inferred MJAT from the 78-140 ka midge inferred average (10.4°C), indicates that Units 15 and 16 (MIS 5a), and to a lesser degree, Unit 4 (MIS 5e), were characterized by above average temperatures and that Unit 3 (MIS 6) and the transition between Units 12 and 13 (MIS 5c and MIS 5b) was characterized by below average temperatures (See Figure 3.7).

CONCLUSION

Analysis of subfossil chironomids extracted from sediment recovered from the Ziegler Reservoir fossil site has provided an opportunity to develop a quantitative reconstruction of thermal conditions for a ~70 kyr record that spans the interval between the Bull Lake glaciation (~ 140 ka) and the early Wisconsin glaciation (~ 70 ka). The midge-based inferred MJAT showed surprisingly little variation between MIS 5e and MIS 5d (10.3 and 10.5°C respectively), a trend that was further substantiated by the presence of comparable chironomid assemblages and similar head capsule concentrations in these sediments. Although many studies indicate that MIS 5e was the warmest stage of the Sangamon Interval (Shackleton, 1969; Goñi et al., 2012) our record suggests that alpine environments in the central Colorado Rockies became progressively warmer through MIS 5 with a maximum midge-inferred MJAT of 13.2^{o}C occurring during MIS 5a at ~79.6 ka. The coldest inferred temperatures occur at the onset of MIS 5a and MIS 5e. Midge analysis also provided a means to qualitatively document changes in trophic conditions, lake levels and possibly ice cover. The large change in midge community composition that occurred midway through MIS 5a likely reflects a significant lowering of lake level at ~ 83.4 ka. The absence of midges from sediment deposited during MIS 5b has been inferred to reflect the presence of extensive year round ice cover between 99.0 ka and 87.6 ka. The chironomid stratigraphy corroborates the detailed pollen record produced for the site, which indicates that notable changes in local and regional environmental conditions occurred during the transition from MIS 6 to MIS 5e and from MIS 5b to MIS 5a.

Table 3.1: Location of the Colorado Rocky Mountain sampled lakes. DO = Dissolved Oxygen, SWT = surface water temperature, MJAT = mean July average temperature. Highlighted lakes did not satisfy the screening process and were not included in the midge-based MJAT inference model **** indicates sensor malfunction.

Lake Name	Code	Elevation (m)	Latitude	Longitude	Lake Depth (m)	Secchi Depth (m)	Specific Conductivity (µS•cm-1)	DO%	DO (mg/L)	pH	SWT (°C)	MJAT (˚C)
Anderson	**AND**	**3583.9**	39.0204	-106.6275	**3.5**	**2.98 / 2.70 / 2.84m**	**0.035**	**0.856**	**10.26**	**7.25**	**7.49**	**8.68**
Brady	BRD	3353.4	39.3683	-106.5006	2.1	Unlimited	0.021	0.836	8.21	9.36	15.1	11.09
Cleveland	CVL	3608.5	39.4211	-106.4908	6.65	3.15 / 3.0 / 3.08m	0.028	0.762	7.48	8.5	15.8	9.97
Constantine	CNS	3471.7	39.4503	-106.4550	3.65	Unlimited	0.02	0.763	7.73	8.6	14	10.67
Diemer	**DMR**	**2869.1**	**39.3347**	**-106.6069**	**2.6**	**2.0 / 1.5 / 1.75m**	**0.035**	**0.822**	**7.31**	**9.3**	**20.3**	**13.69**
Eagle	EGL	3073.9	40.2108	-105.6503	2	Unlimited	0.026	0.716	7.42	8.11	13.7	12.76
Half Moon South	HFM-S	3647.9	39.1782	-106.4929	5.55	Unlimited	0.025	0.808	9.08	****	10.1	9.51
Independence	IND	3784.8	39.1440	-106.5674	6.9	2.8 / 2.4 / 2.60m	0.02	0.792	8.7	6.55	10.85	8.24
Missouri Adjacent	MLA	3524.1	39.3992	-106.5154	2.45	Unlimited	0.029	0.757	7.7	8.17	14.6	9.96
Missouri Central	MLC	3487.8	39.3964	-106.5153	3.2	1.90 / 0.80 / 1.35m	0.014	0.701	6.85	8.37	15.9	9.96
Native	NTV	3403.0	39.2253	-106.4592	0.9	Unlimited	0.011	0.759	8.56	****	9.89	11.07
Savage	SVL	3377.6	39.3595	-106.5203	3.45	2.4 / 2.2 / 2.3m	0.01	0.851	9.59	6.12	9.98	10.98
Seven Sisters Central	SSC	3755.4	39.4413	-106.4811	5.8	3.05 / 2.45 / 2.75m	0.016	0.768	7.77	8.79	15.2	10.98
Seven Sisters West	**SSW**	**3892.9**	**39.4433**	**-106.4874**	**6.90**	**2.10 / 0.90 / 1.50m**	**0.016**	**0.779**	**9.38**	**8.66**	**7**	**8.55**
Sopris	**SOP**	**3364.1**	**39.3711**	**-106.5025**	**5.4**	**Unlimited**	**0.011**	**0.679**	**6.4**	**8.28**	**16.6**	**9.55**
St. Kevin	SKL	3580.0	39.3106	-106.4269	6.8	4.4 / 3.9 / 4.15m	0.041	0.887	10.38	****	8.39	11.72
Tabor Creek	TCL	3588.5	39.0539	-106.6475	24	Unlimited	0.016	0.751	7.78	6.82	13.68	10.2
Tuhare East	TLE	3690.8	39.4487	-106.4701	11	2.90 / 1.90 / 2.40m	0.021	0.779	7.76	8.28	14.1	9.19
Weller	WLL	2893.9	39.1151	-106.7209	8.7	2.30 / 2.60 / 2.45m	0.019	0.829	9.52	6.2	8.1	13.91
Williams	**WIL**	**3277.3**	**39.2222**	**-107.1223**	**3.6**	**3.60 / 3.20 3.35m**	**0.114**	**92.1**	**11.01**	**7.21**	**7.51**	**13.27**

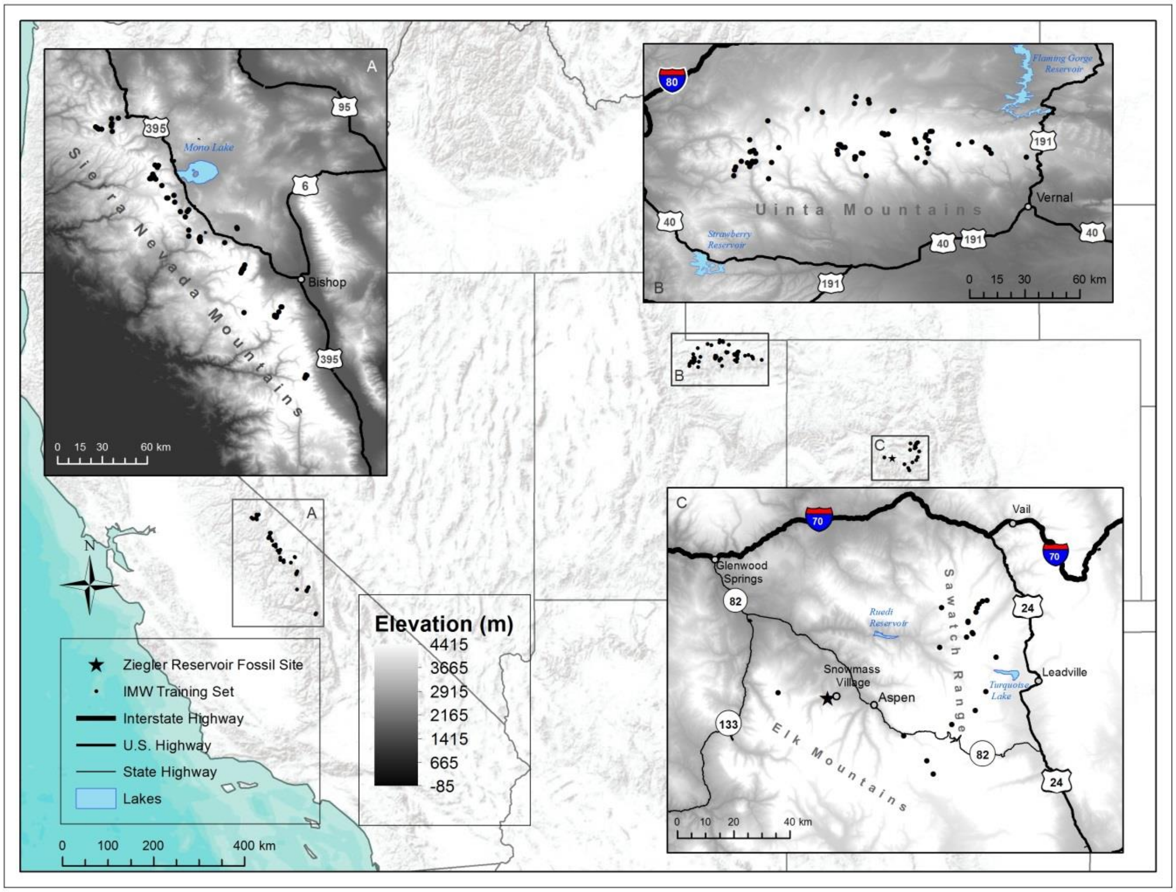


Figure 3.1: Location of the Intermountain West (IMW) training set lakes. A) Lakes sampled in the Sierra Nevada, CA (Porinchu et al., 2002); B) Lakes sampled in the Uinta Mountains, UT (Porinchu et al., 2007a); C) Lakes sampled in the Rocky Mountains, CO (this study).

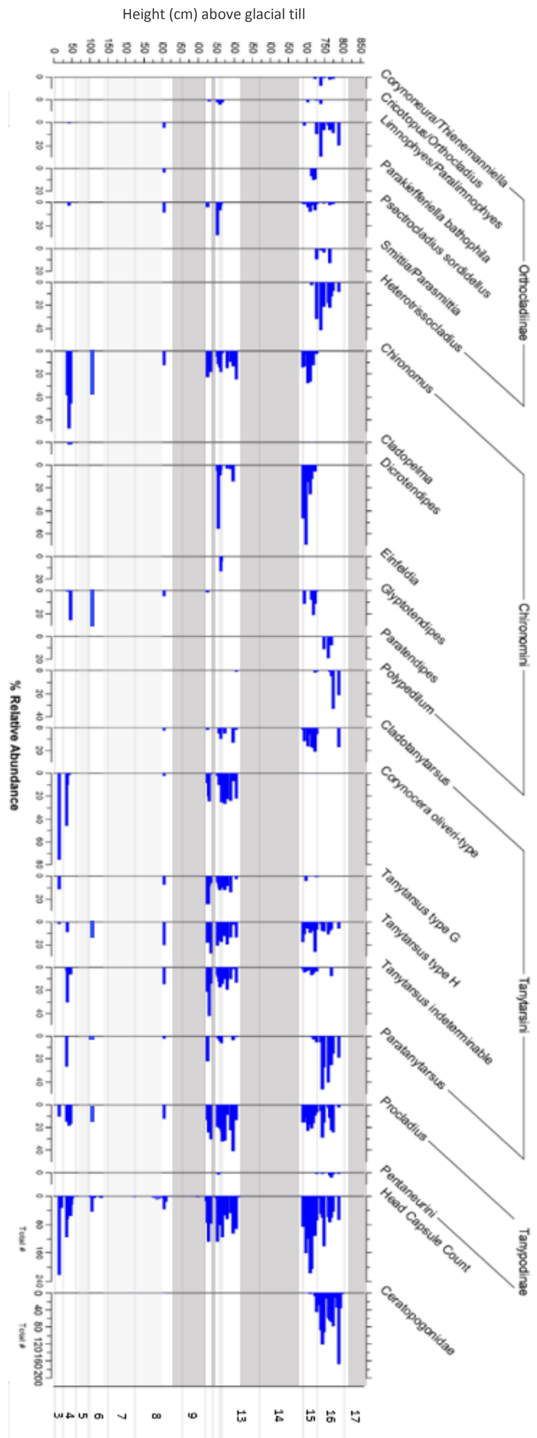


Figure 3.2: Relative abundance diagram of chironomid taxa found in the Ziegler Reservoir fossil site. Dark gray zones indicate no head capsule recovery. The light gray zones indicate low head capsule recovery. The right-hand column corresponds to the stratigraphic units identified at the site.

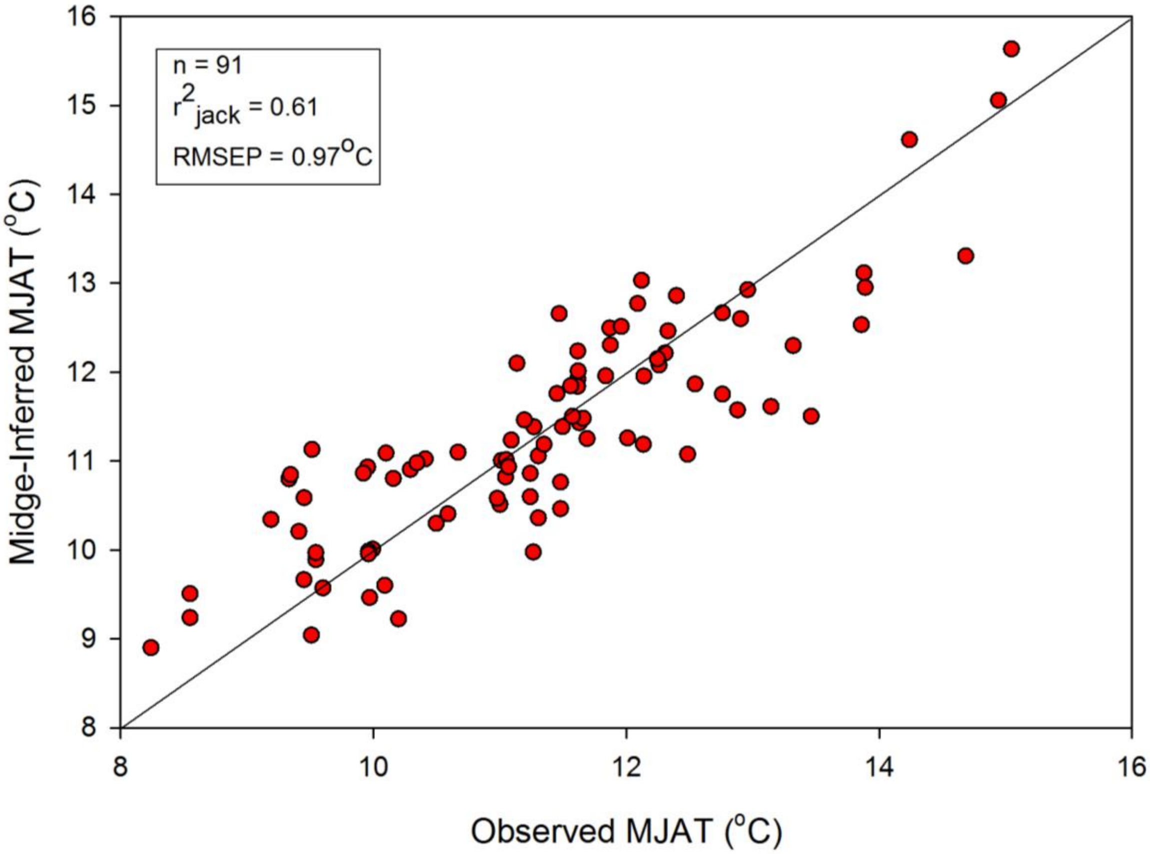


Figure 3.3: Midge assemblages from the Zeigler Reservoir fossil site (green circles) plotted against the Intermountain West training set (red circles) using correspondence analysis (CA). (r^2_{jack}= jack-knifed r^2, RMSEP = root mean-square error of prediction)

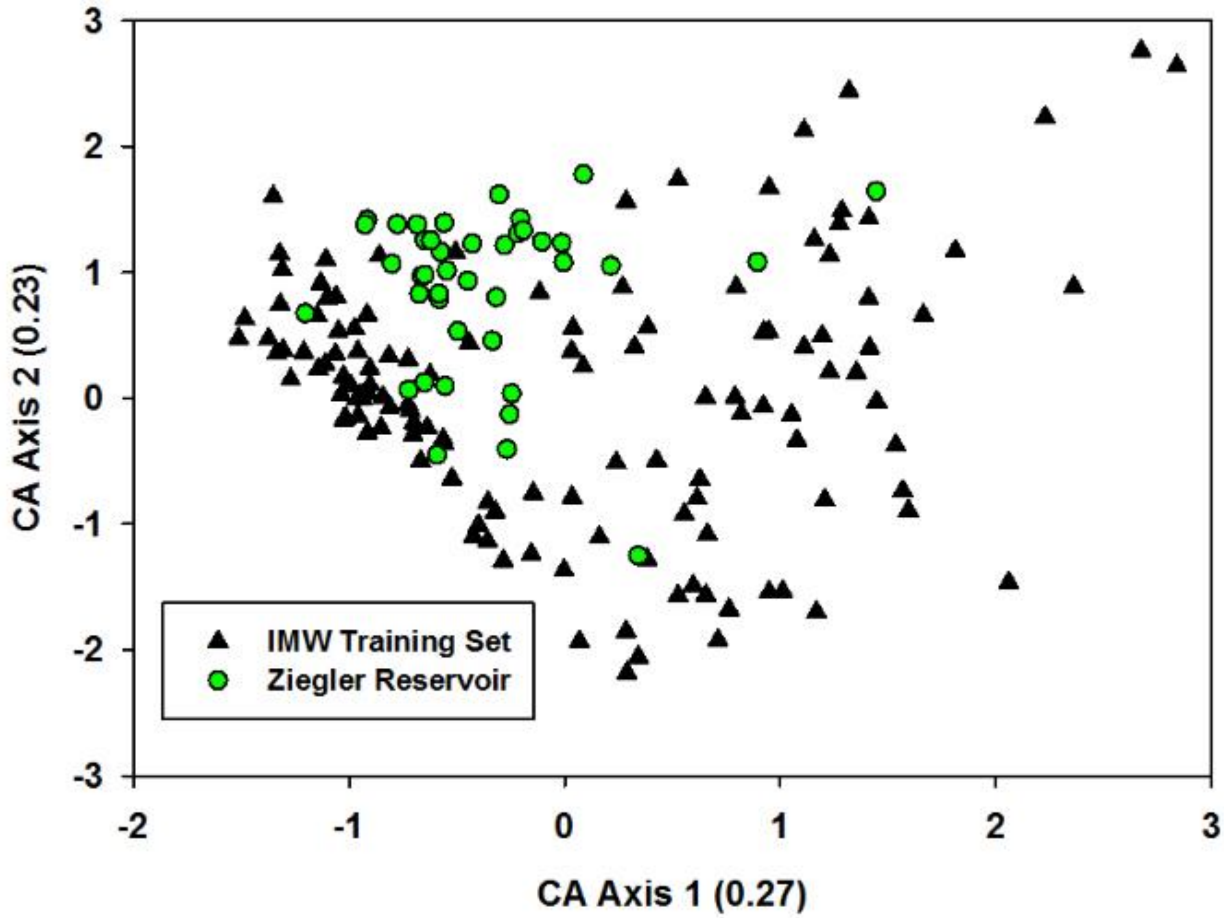


Figure 3.4: Relationship between observed mean July air temperature (derived from the PRISM dataset) and midge-inferred mean July air temperature. The solid line represents the 1:1 relationship.

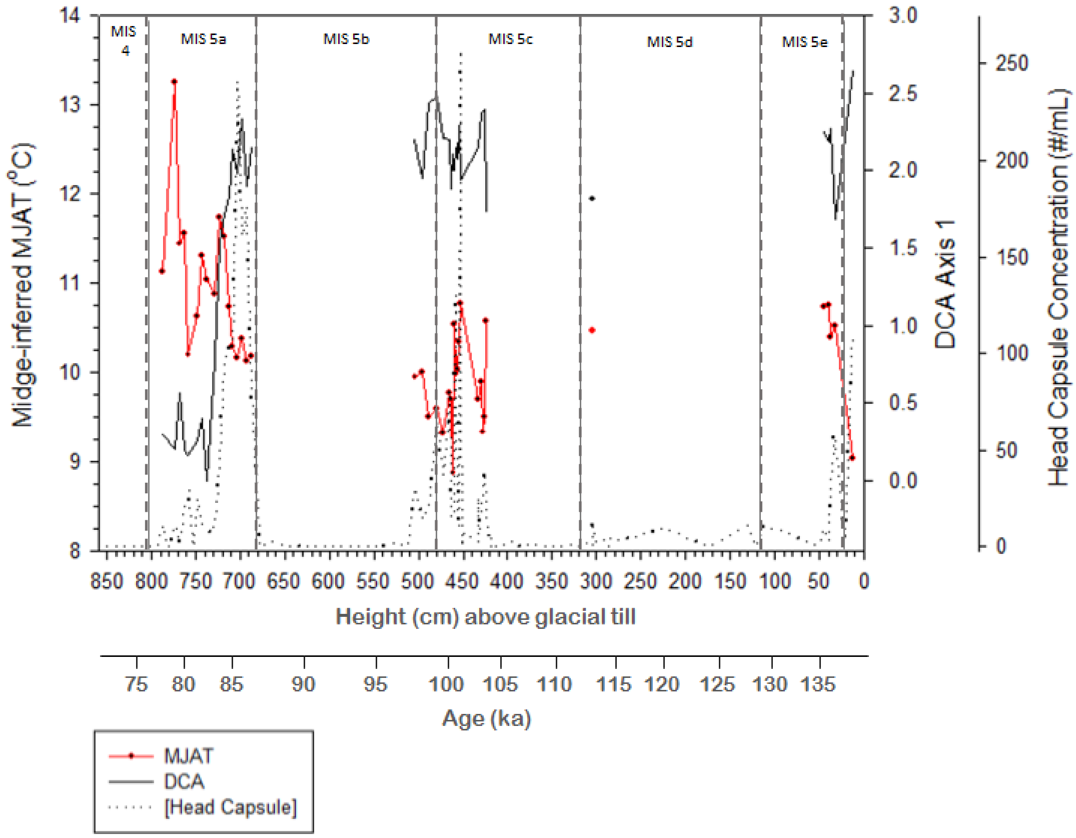


Figure 3.5: Chironomid-based reconstruction of mean July air temperature (MJAT) for the Ziegler Reservoir fossil site plotted by depth (cm) above glacial till and by age (ka). Points indicate the derived MJAT from the chironomid-based reconstruction. The solid line represents DCA axis and the dashed line denotes head capsule concentration (#/mL).

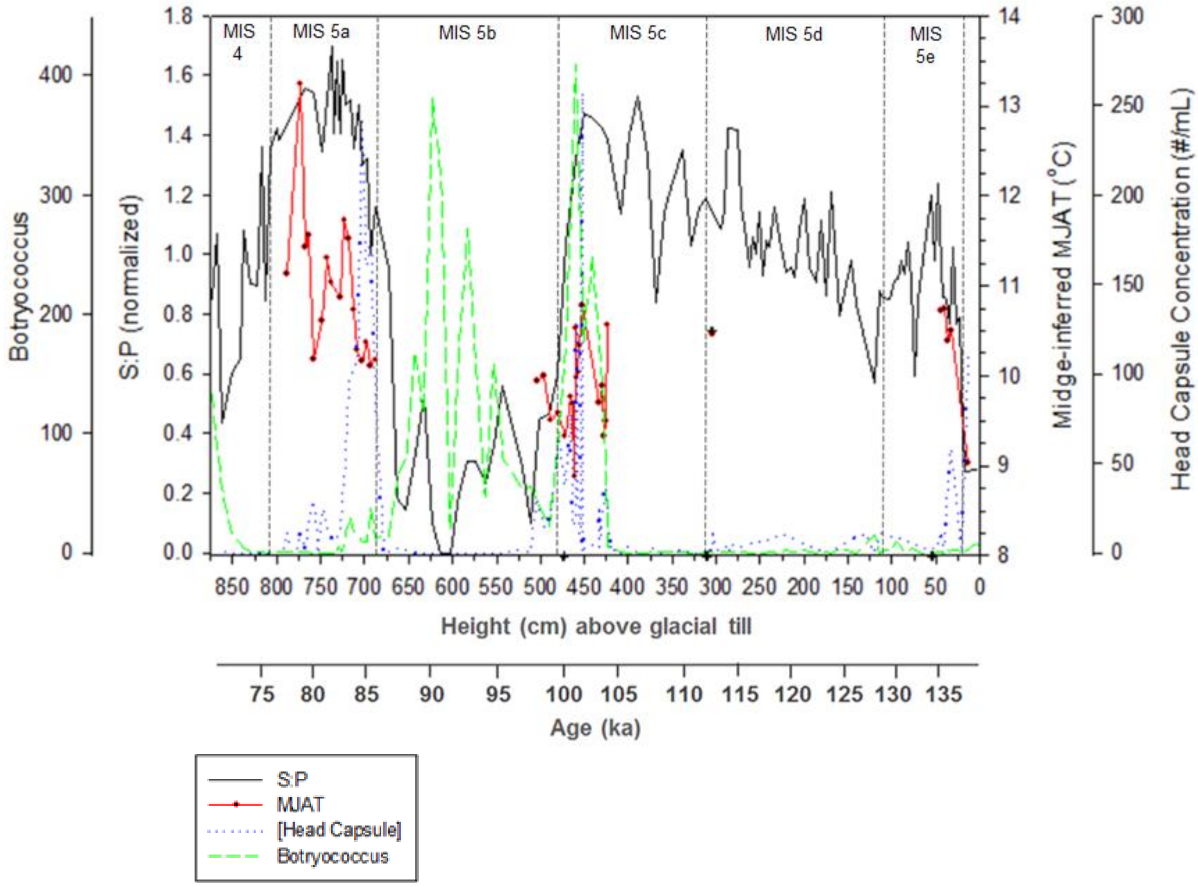


Figure 3.6: Chironomid-based reconstructed mean July air temperatures (ºC) are plotted as data points by depth (cm) above glacial till. MJAT is also plotted by age (ka). Head capsule concentration (#/mL) are represented by the dashed line. The S:P ratio and abundance of *Botryococcus* (green algae) are also depicted (from Anderson et al., this volume).

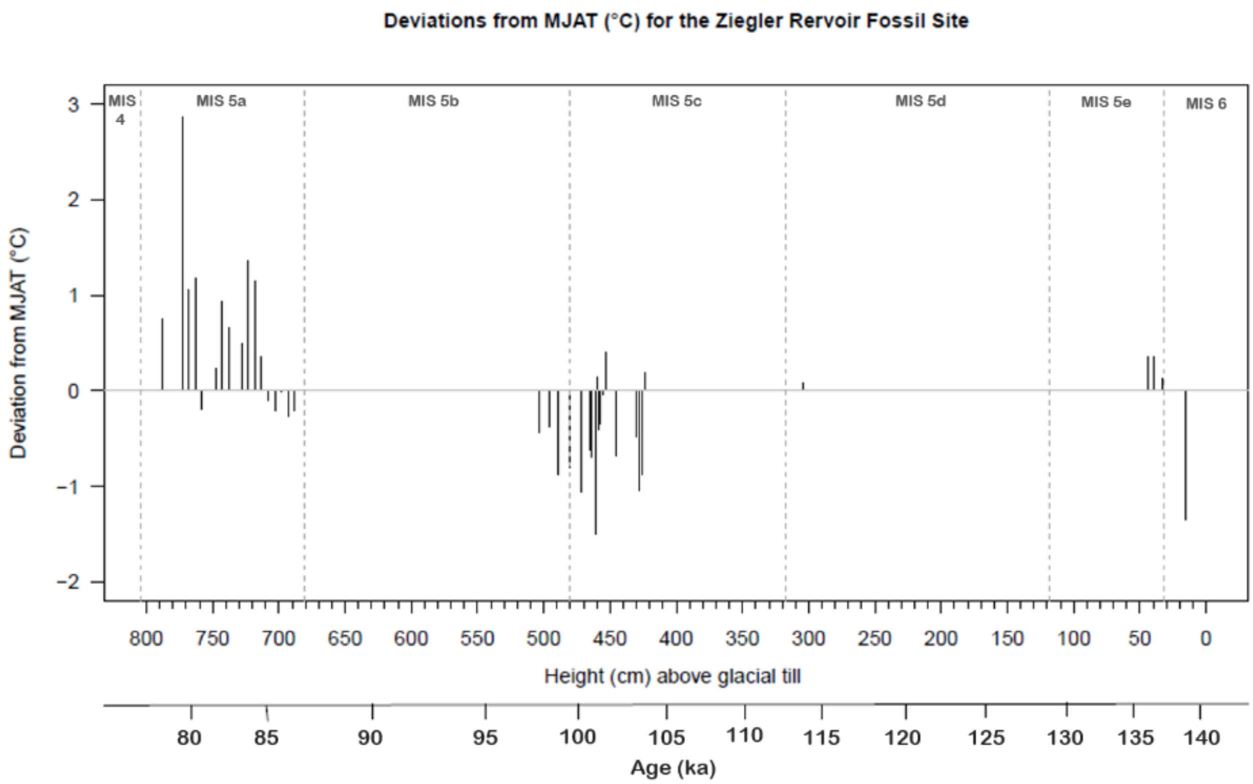


Figure 3.7: Deviations from the chironomid-inferred MJAT (10.38°C) for the ZR site.

CHAPTER 4

CONCLUSIONS

Calibration Set

Major Findings

Chironomid analysis of surface sediment recovered from forty-five lakes in central Colorado Rockies was used to document the modern distribution of subfossil midges in this region. High elevation lakes were characterized by distinct midge assemblages which were dominated by taxa such as *Corynocera oliveri*, *Chironomus* and *Diplocladius.* The midge assemblages found in low elevation lakes were dominated by taxa commonly associated with warm, productive lakes such as *Limnophyes*, *Brillia*, *Parakiefferiella bathophila*-type and *Polypedilum.* Ordination analyses (CCA) indicated that MJAT was the only measured limnological variable that could account for a statistically significant amount of the variance present in the distribution of the midge taxa. A transfer function relating midge taxon abundance and distribution to MJAT was developed using weighted averaging and weighted averaging-partial least squares approaches. The strongest inference model, developed using a 2-component WA-PLS, had a coefficient of determination (r^2_{jack}) = 0.47 and a very low RMSEP (0.81°C). This exploratory study established the efficacy of adding the chironomid assemblages from the central Colorado Rockies to the larger Great Basin training set. It also provided the opportunity to assess the nature and strength of the chironomid-air temperature relationship.

Uncertainties

Although the results did suggest that MJAT is significantly correlated to the distribution of midges in the central Colorado Rockies, it is important to note that MJAT accounted for less of the variance present in the midge dataset than the existing GB training set. Further refinement of the model will require: 1) inclusion of a larger number of limnological variables, including: trace metals, major ions, nutrients, dissolved and particulate carbon and pH, to better characterize the modern conditions of the training set lakes; and 2) developing better estimates of MJAT to constrain the inference model, given the limited observational data that are currently available for lakes located above 3500 m asl. The paucity of instrumental data available in the Colorado Rockies at elevations between 3000 m asl and 3500 m asl and the complete absence of instrumental data above 3500 m asl results in temperatures often being extrapolated from weather stations that are not typical for the site of interest (Rangwala et al., 2012). This, together with the existence of complex topography, which is poorly resolved at the 800 m spatial resolution of the PRISM model, limits the applicability of the PRISM-derived temperature estimates for sites located above 3500 m asl. Daly et al. (2008) identify that the mountainous western United States is the region most prone to error. The cross-validation errors associated with the PRISM-derived temperature estimates for the Colorado Rocky Mountains often exceed 1.5°C and are among the largest errors recorded for the contiguous United States (Daly et al., 2008). During the development of the Colorado Rocky Mountain training set, a large discrepancy in PRISM-derived air temperature was noted between lakes located at similar elevations. For example, Anderson Lake (39.0204, -106.6275) lies at an elevation of 3584 m asl and is located above treeline. Tabor Creek Lake (39.0539, -106.6475) lies at 3589 m and is also present in alpine tundra and located in a cirque with the peak of the mountain to the south. A difference of 1.52°C (8.68°C and 10.2°C respectively) exists over a vertical difference of 5 m.

Ziegler Reservoir fossil site

Major Findings

The third chapter explored the analysis of subfossil chironomids extracted from sediment recovered from a ~70 kyr record that represents the transition from the Bull Lake glaciation (~140 ka) to the Sangamon Interglacial and terminates in the early Wisconsin glaciation (~70 ka). The record, collected from the Ziegler Reservoir fossil site, has allowed for the development of a quantitative midge-based reconstruction of thermal conditions for this region. The inferred MJAT showed little variation between MIS 5e and MIS 5d (10.3°C and 10.5°C respectively). This inference was qualitatively substantiated by the presence of chironomid assemblages experiencing muted compositional change during this interval. The Ziegler Reservoir midge stratigraphy indicates that alpine environments in the central Colorado Rockies became progressively warmer through MIS 5 with a maximum midge-inferred MJAT of 13.2ºC occurring during MIS 5a at ~79.6 ka. This finding is in contrast to the studies that indicate that MIS 5e was the warmest stage of the Sangamon Interglacial (Shackleton, 1969; Goñi et al., 2012). However, evidence from Yellowstone National Park, which indicates that MIS 5a was the warmest interval of the Sangamon Interglacial in this region, corroborates our findings (Baker, 1986). The coldest midge-inferred temperatures occur at the onset of MIS 5a and MIS 5e. Midge analysis also provided a means to qualitatively document changes in trophic conditions, lake levels and possibly ice cover. The large change in midge community composition that occurred midway through MIS 5a likely reflects a significant lowering of lake level at ~83.4 ka. The faunal turnover during this time indicates the increased abundance of acidiphilic, thermophilous taxa that are typically associated with bogs. The absence of midges from sediment deposited during MIS 5b has been inferred to reflect the presence of extensive year round ice cover between 99.0 ka and 87.6 ka. The chironomid stratigraphy corroborates the detailed pollen record produced for the site, which indicates that notable changes in local and regional environmental conditions occurred during the transition from MIS 6 to MIS 5e and from MIS 5b to MIS 5a.

Uncertainties

There are a number of issues related to the paleoenvironmental record developed from the sediment sequence recovered from the Ziegler Reservoir fossil site that require additional discussion. Of the various approaches utilized to develop a chronology for the site, optically stimulated luminescence (OSL) of quartz grains provided the most robust results. Uncertainty associated with OSL dating include issues related to provenance of source material, preservation, and methods of transport. For instance, fluvial transport of quartz grains could potentially cause grains to be repeatedly reset, i.e. become bleached. However, grain size and geochemical analyses indicate that the grains present in the basin, which are primarily aeolian, were unlikely mixed or bleached and as a result conditions were conducive for OSL dating (Mahan et al., *under review).* It is important to note that error estimates for the OSL ages are typically ~10% and caution should be exercised in the interpretation with regard to assigning ages to marine isotope stages.

The taxa preserved in the older sediment at the base of the core possess highly sclerotized and hardy head capsules that were heavily degraded and/or disarticulated; whereas, chironomid communities become more diverse as the sediment becomes younger, with chironomid assemblages well preserved at the top of the stratigraphy. Future research is necessary to elucidate the preservation of chitinous head capsules of chironomids to establish that taphonomic issues are not affecting the midge-based MJAT reconstruction. It should be noted that the chironomid assemblage found in the uppermost portion of the core are atypical in modern assemblages and could alter the interpretation. The presence of semi-terrestrial and terrestrial taxa such as *Limnophyes* and *Smittia* indicate a lowering of lake levels during MIS 5a; however, the presence of *Heterotrissocladius* is confounding. *Heterotrissoclasius* is typically found in the profundal of deep and cold lakes in arctic, sub-arctic and alpine settings and thus caution should be used when interpreting the midge-inferred temperatures for the uppermost units at the site.

At the inception of the Ziegler Reservoir Fossil Site project, evidence indicated that this lake was extant during glacial conditions. Lakes targeted for incorporation in the Colorado calibration set were located above 3000 m asl to fully capture conditions and midge assemblages most closely related to conditions and assemblages associated with the penultimate glacial maxima. The current GB and expanded IMW training sets do not contain a large number of lakes located lower in elevation than Ziegler Reservoir, i.e. lakes with higher MJAT. This is evident by the discrepancy between modern measured mean July air temperature (~15.5°C) at Snowmass Village, CO and the much colder midge-inferred temperatures from the core (8.9 – 13.2°C). While the trends do seem to be correct (see Figure 3.7), it is possible that the absolute values of the midge reconstruction have a "cold" bias. Future field work should address these inconsistencies by incorporating lakes lower in elevation in the IMW training set. Also, due to the nature of the sediment, chironomid head capsule extraction was a tedious and time consuming process. Sediment is still available and the record could be made more robust by increasing head capsule recovery for the core.

Chironomids may be used as a proxy to reconstruct past thermal changes in some of the most remote areas in the world, including the isolated alpine tundra of the Colorado Rocky Mountains. Understanding the ecology of these insects may also help to qualitatively elucidate paleoenvironmental changes as well and may address changes in lake depth, or the trophic status of the lake. By understanding past changes in this region in Colorado, the opportunity to understand the magnitude and rate of change that these sensitive ecosystems may put into perspective rates and magnitude of contemporaneous climate change.

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