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# A quantitative midge-based reconstruction of mean July air temperature from a high-elevation site in central Colorado, USA, for MIS 6 and 5

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A B S T R A C T

Sediments recovered from the Ziegler Reservoir fossil site (ZRFS) in Snowmass Village, Colorado (USA) were analyzed for subfossil chironomids (or midges). The midge stratigraphy spans ~140–77 ka, which includes the end of Marine Oxygen Isotope Stage (MIS) 6 and all of MIS 5. Notable shifts in midge assemblages occurred during two discrete intervals: the transition from MIS 6 to MIS 5e and midway through MIS 5a. A regional calibration set, incorporating lakes from the Colorado Rockies, Sierra Nevada, and Uinta Mountains, was used to develop a midge-based mean July air temperature (MJAT) inference model ($r^2_{jack} = 0.61$, RMSEP = 0.97°C). Model results indicate that the transition from MIS 6 to MIS 5e at the ZRFS was characterized by an increase in MJAT from ~9.0 to 10.5°C. The results also indicate that temperatures gradually increased through MIS 5 before reaching a maximum of 13.3°C during MIS 5a. This study represents the first set of quantitative, midge-based MJAT estimates in the continental U.S. that spans the entirety of MIS 5. Overall, our results suggest that conditions in the Colorado Rockies throughout MIS 5 were cooler than today, as the upper limit of the reconstructed temperatures is ~2°C below modern July air temperatures.

## Introduction

Developing quantitative estimates of past temperature, with specific reference to past warm intervals such as Marine Oxygen Isotope Stage (MIS) 5, will improve our understanding of the magnitude of variability that exists in the climate system. Although MIS 5 is an imperfect analog of future conditions, improving our understanding of climate variability during this interval will provide valuable insight into the possible nature of future conditions and the potential feedbacks that may be important in future warm climate scenarios.

Chironomids (Insecta: Diptera), or midges, have been used extensively as a proxy for past climate and are one of the most promising approaches to reconstructing past thermal regimes (Battarbee, 2000). Chironomids, which are among 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 much needed, 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; 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; 2010) and long-term regional climate change in the western USA during the latest Pleistocene and Holocene (Porinchu et al., 2003; Potito et al., 2006; Reinemann et al., 2009) as well as the relationship between local thermal conditions and regional and hemispheric climate dynamics (MacDonald et al., 2008). This study is the first attempt to develop a midge-based quantitative reconstruction of MJAT in the continental USA that spans MIS 5.

The recent discovery of a Pleistocene megafauna fossil site, known as the Ziegler Reservoir fossil site (ZRFS), in Snowmass Village, Colorado (CO) provides an exciting opportunity to use chironomids to document climate variability at high elevations for an interval that includes the

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termination of MIS 6, MIS 5, and the onset of MIS 4. The exceptionally well-preserved late Pleistocene ecosystem archived at the ZRFS is significant because it contains a relatively complete sequence of fossil bearing strata spanning approximately 85 kyr (140–55 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) to a midge stratigraphy from the ZRFS and develop a detailed, quantitative reconstruction of thermal conditions for the region that spans portions of MIS 6 and MIS 5.

## Study site

The Rocky Mountains have a rich and diverse geologic history and have been subjected to millions of years of uplift, subsidence and erosion (Epis and Chapin, 1975). The landscape, which has been influenced by these tectonic and geomorphic processes, has also been shaped by repeated glaciations (Porter et al., 1983; Pierce, 2003). The ZRFS (39.2075 °N, 106.9648 °W, 2705 m asl), located near Snowmass Village in the Elk Mountains of central CO, is a small (300 m diameter), perched reservoir. The reservoir is surrounded by moraine deposits comprised of red sandstone clasts originating from the nearby Maroon Bells Formation and underlain by the Mancos Shale (Bryant, 1972). The lake basin associated with the fossil site was initially formed during MIS 6 and subsequent glacial re-advances during MIS 4 and MIS 2 were not expansive enough to override the lake basin. Thus, the sedimentary sequence present in the basin was left undisturbed (Pigati et al., 2014–in this volume).

Snowmass Village is influenced by a continental climate with cold winters and cool moist summers. Mean July temperature at Aspen, CO (2389 m asl) is 17.17°C (Western Regional Climate Center, http://www.wrcc.dri.edu, accessed August 2013). 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 15.43°C for mean July temperature for Snowmass Village. The arboreal vegetation currently surrounding the ZRFS is dominated by quaking aspen (*Populus tremuloides*), sub-alpine fir (*Abies lasiocarpa*) and lesser amounts of scrub oak (*Quercus gambelii*) and sagebrush (*Artemisia*) (Anderson et al., 2014–in this volume).

A number of approaches were used to determine the age of the sedimentary sequence preserved at the ZRFS (Mahan et al., 2014–in this volume). Well-preserved wood and plant macrofossils, as well as collagen from tooth and bone, were dated using AMS radiocarbon dating. The dates obtained for these samples were either near the analytical limit of the approach or the samples yielded infinite ages. Surface exposure dating was undertaken on a single, large boulder located on the moraine deposited during MIS 6. In situ cosmogenic $^{10}$Be dating provided an age of 138 ± 12 ka. Optically stimulated luminescence (OSL) provided a robust chronology for the site that ranged from 55 ± 10 ka at the surface to 141 ± 1 the ZRFS 4 ka for the lowermost sampled unit (Unit 3). Thus, the sediments at t span the end of MIS 6, all of MIS 5 and 4, and the earliest part of MIS 3.

## Methods

### Modern calibration set and inference model development

To characterize the distribution of midges in central CO surface sediment was collected from 20 lakes in the vicinity of Snowmass Village during July 2011 and July 2012 (Table 1). The lakes sampled, which are located in the White River National Forest and within 50 km of the ZRFS (Fig. 1), fall within one of three broad vegetation zones: 1) montane (2440–3050 m asl) which is dominated by pine (*Pinus*) and aspen (*Populus*), with Douglas-fir (*Pseudotsuga menziesii*) present locally; 2) Subalpine (2895–3475 m asl) which is dominated by spruce (*Picea*), sub-alpine fir and pine; and 3) Timberline (3415–3660 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 and air and water temperature ranges of ~1024 m (2869–3893 m asl), 5.6°C (8.24–13.91 °C) and 13.3°C (7.0–20.3 °C), respectively. These lakes also spanned ranges in maximum depth and pH of 23.1 m and 3.24, respectively (Table 1).

A suite of limnological variables was measured in the field during the collection of surface sediment for the calibration set. A YSI Professional Plus probe was used to measure surface water temperature, dissolved oxygen, specific conductivity and pH at a depth of 0.50 m. A Secchi disk was used to estimate optical transparency and determine maximum depth for each lake. The upper 1 cm of sediment was recovered from the center of each lake using a DeGrand corer. This sediment was subdivided into 0.25-cm increments, placed into Whirlpacks® and stored in a cooler until the completion of fieldwork.

The Great Basin midge-based calibration set, initially published by Porinchu et al. (2010), incorporated 79 lakes from the Sierra Nevada, California and Uinta Mountains, Utah. The chironomid-based inference model for mean July air temperature (MJAT) developed using the Great Basin calibration set had an $r^2_{\text{jack}} = 0.55$ and a RMSEP = 0.90°C. The Great Basin midge-based inference model (Porinchu et al., 2010) was complemented with the addition of the 20 lakes from CO sampled in this study. The expanded calibration set and associated inference model will hereafter be referred to as the Intermountain West (IMW) chironomid calibration set and MJAT inference model. The IMW chironomid-based inference model for MJAT was developed using a two-component weighted averaging-partial least squares (WA-PLS) model (Birks, 1995). Mean July air temperature for each lake included in the IMW calibration set was extracted from data made available by the PRISM Climate Group (http://www.prism.oregonstate.edu/, last accessed May 9, 2014) and incorporates MJAT estimates based on the most recent Climate Normal (1981–2010) (PRISM data group, 2012). For the development of the quantitative MJAT inference model, training set samples were considered outliers if they had an absolute residual (predicted–observed) greater than one standard deviation of MJAT (Lotter et al., 1997; Porinchu et al., 2002) (Table 1).

The reliability of the quantitative midge-based reconstruction was evaluated by determining: 1) the total percentage of taxa present down-core that do not appear in the modern calibration data set; 2) the proportion of rare taxa present in the down-core samples; 3) the dissimilarity between each ZRFS midge sample and its closest modern analog using a modern analog technique (MAT) approach based on minimum dissimilarity chord distance; and 4) square residual goodness-of-fit (G-O-F) of each ZRFS midge assemblage to the 1st ordination axis in a canonical correspondence analysis constrained solely by MJAT. Reconstructions that are based on sub-fossil assemblages that have >95% of the sub-fossil taxa present in the calibration set are considered 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). The 2nd and 5th percentiles of the distribution of dissimilarities, based on the IMW calibration set samples, were used to define the cut-off for ‘no close’ and ‘no good’ analogs, respectively (Birks et al., 1990; Heiri et al., 2003; Engels et al., 2008). Samples with a squared residual distance greater than the 90th and 95th percentile of the residual distances of the calibration set samples, were identified as having a ‘poor fit’ or ‘very poor fit’ with temperature, respectively (Birks et al., 1990). In addition, the significance of the reconstruction was assessed using the significance test outlined in Telford and Birks (2011). A reconstruction can be considered statistically significant if it explains more of the variance in the fossil data than 95% of the 999 reconstructions

**Table 1**
Location of the Colorado Rocky Mountain sampled lakes. DO = Dissolved Oxygen, SWT = surface water temperature, MJAT = mean July average temperature. Lakes in bold font were not included in the midge-based MJAT inference model. **** indicates sensor malfunction.

| | Lake name | Code | Elevation (m) | Latitude (°N) | Longitude (°E) | Lake depth (m) | Secchi depth (m) | Specific conductivity ($\mu S \cdot cm^{-1}$) | DO% | DO (mg/L) | pH | SWT (°C) | MJAT (°C) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | **Anderson** | **AND** | **3583.94** | **39.0204** | **−106.6275** | **3.50** | **2.98/2.70/2.84** | **0.035** | **0.856** | **10.26** | **7.25** | **7.49** | **8.68** |
| 2 | Brady | BRD | 3353.41 | 39.3683 | −106.5006 | 2.10 | Unlimited | 0.021 | 0.836 | 8.21 | 9.36 | 15.10 | 11.09 |
| 3 | Cleveland | CVL | 3608.53 | 39.4211 | −106.4908 | 6.65 | 3.15/3.0/3.08 | 0.028 | 0.762 | 7.48 | 8.50 | 15.80 | 9.97 |
| 4 | Constantine | CNS | 3471.67 | 39.4503 | −106.4550 | 3.65 | Unlimited | 0.02 | 0.763 | 7.73 | 8.60 | 14.00 | 10.67 |
| 5 | **Diemer** | **DMR** | **2869.08** | **39.3347** | **−106.6069** | **2.60** | **2.0/1.5/1.75** | **0.035** | **0.822** | **7.31** | **9.30** | **20.30** | **13.69** |
| 6 | Eagle | EGL | 3073.91 | 40.2108 | −105.6503 | 2.00 | Unlimited | 0.026 | 0.716 | 7.42 | 8.11 | 13.70 | 12.76 |
| 7 | Half Moon South | HFM-S | 3647.88 | 39.1782 | −106.4929 | 5.55 | Unlimited | 0.025 | 0.808 | 9.08 | **** | 10.10 | 9.51 |
| 8 | Independence | IND | 3784.85 | 39.1440 | −106.5674 | 6.90 | 2.8/2.4/2.60 | 0.020 | 0.792 | 8.70 | 6.55 | 10.85 | 8.24 |
| 9 | Missouri Adjacent | MLA | 3524.10 | 39.3992 | −106.5154 | 2.45 | Unlimited | 0.029 | 0.757 | 7.70 | 8.17 | 14.60 | 9.96 |
| 10 | Missouri Central | MLC | 3487.83 | 39.3964 | −106.5153 | 3.20 | 1.90/0.80/1.35 | 0.014 | 0.701 | 6.85 | 8.37 | 15.90 | 9.96 |
| 11 | Native | NTV | 3403.03 | 39.2253 | −106.4592 | 0.90 | Unlimited | 0.011 | 0.759 | 8.56 | **** | 9.89 | 11.07 |
| 12 | Savage | SVL | 3377.58 | 39.3595 | −106.5203 | 3.45 | 2.4/2.2/2.3 | 0.010 | 0.851 | 9.59 | 6.12 | 9.98 | 10.98 |
| 13 | Seven Sisters Central | SSC | 3755.44 | 39.4413 | −106.4811 | 5.80 | 3.05/2.45/2.75 | 0.016 | 0.768 | 7.77 | 8.79 | 15.20 | 10.98 |
| 14 | **Seven Sisters West** | **SSW** | **3892.91** | **39.4319** | **−106.4873** | **6.90** | **2.10/0.90/1.50** | **0.016** | **0.779** | **9.38** | **8.66** | **7.00** | **8.55** |
| 15 | **Sopris** | **SOP** | **3364.08** | **39.3711** | **−106.5025** | **5.40** | **Unlimited** | **0.011** | **0.679** | **6.40** | **8.28** | **16.60** | **9.55** |
| 16 | St. Kevin | SKL | 3580.00 | 39.3106 | −106.4269 | 6.80 | 4.4/3.9/4.15 | 0.041 | 0.887 | 10.38 | **** | 8.39 | 11.72 |
| 17 | Tabor Creek | TCL | 3588.48 | 39.0539 | −106.6475 | 24.00 | Unlimited | 0.016 | 0.751 | 7.78 | 6.82 | 13.68 | 10.20 |
| 18 | Tuhare East | TLE | 3690.82 | 39.4487 | −106.4701 | 11.00 | 2.90/1.90/2.40 | 0.021 | 0.779 | 7.76 | 8.28 | 14.10 | 9.19 |
| 19 | Weller | WLL | 2893.94 | 39.1151 | −106.7209 | 8.70 | 2.30/2.60/2.45 | 0.019 | 0.829 | 9.52 | 6.20 | 8.10 | 13.91 |
| 20 | **Williams** | **WIL** | **3277.27** | **39.2222** | **−107.1223** | **3.60** | **3.60/3.20 3.35** | **0.114** | **0.921** | **11.01** | **7.21** | **7.51** | **13.27** |

trained on random environmental data drawn from a uniform distribution (Telford and Birks, 2011).

### Stratigraphic subfossil midge analysis

Sediment samples were collected for sub-fossil midge analysis at fixed intervals using stratigraphic markers present within the relict lake basin at the ZRFS in June 2011. Sediment samples from Locality 43 (units 14–8) and Locality 51 (units 17–15) were collected at 10-cm intervals from the cleaned sediment facies. Sediment was removed and placed into Whirlpacks®. Additional sediments from units 8–3 was collected using a Giddings Soil Probe and sub-sampled from Core Z43C-B in the lab at 5-cm intervals and stored in Whirlpacks®.

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 min, or until colloidal matter was sufficiently deflocculated. Sediment from the calibration set lakes and from the core that did not contain much plant matter was sieved through a 95 μm mesh screen using distilled water. Nested sieving (500, 300 and 95 μm) was implemented for the organic-rich sections from the ZRFS to remove plant fragments and enable more accurate and efficient sorting of midge head capsules. The material remaining on the screen was backwashed into a beaker with distilled water and the resulting residue was poured into a Bogorov counting tray and sorted using a stereoscope at 40× magnification. The sub-fossil chironomid head capsules extracted from the residue were permanently mounted on glass slides using Entellan® mounting medium. A Zeiss Axioskop microscope at 400× magnification was used to identify the midge remains. Taxonomic determination of the remains followed Brooks et al. (2007), an extensive reference collection of sub-fossil midges from the Great Basin housed in the Department of Geography at the University of Georgia, and an online chironomid identification key (http://chirokey.skullisland.info/, last accessed 9 May, 2014).

The chironomid percentage diagrams (Figs. 2, 4), plotted using C2 (Juggins, 2003), were 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 Smilauer, 2002). The MAT analysis was executed using the analog package (Simpson, 2007) in R (R Development Core Team, 2010). The significance test outlined in Telford and Birks (2011) was implemented using the palaeoSig package in R (Telford, 2011). All statistical analyses were based on samples with a minimum recovery of 50 head capsules (Heiri and Lotter, 2001) with the exception of seven samples at the following depths 979, 914, 715, 589, 564, 531 and 246 cm. A total of 39, 43.5 and 43 head capsules were recovered from samples at 715, 589 and 564 cm, respectively; an average of 47 head capsules were recovered from the remainder of the samples identified above. A form of indirect gradient analysis, detrended correspondence analysis (DCA), was used to assess the amount of faunal turnover in the ZRFS midge stratigraphy.

## Results

### Modern chironomid assemblages

Incorporating the 20 lakes from the White River National Forest in the IMW training set expands the elevation gradient captured by the training set by ~350 m. In addition, the midge communities in these lakes contain three chironomid taxa: *Diplocladius*, *Chaetocladius*, and *Einfeldia*, not found in the existing Great Basin training set (Porinchu et al., 2007a, 2010). The midge assemblages from the CO lakes sampled for inclusion in the IMW training set are depicted in Fig. 2. The midge

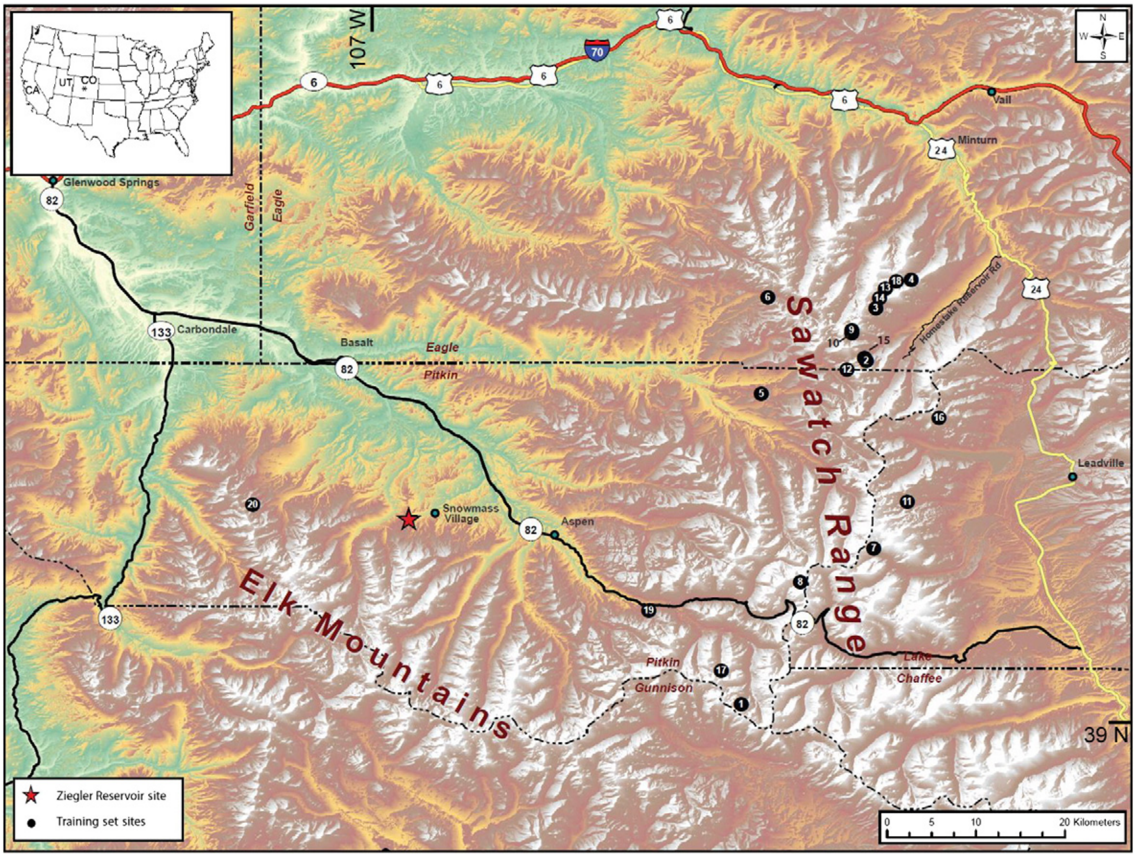

**Figure 1.** Location of the Colorado training set lakes (filled, numbered circles) and the Ziegler Reservoir fossil site (denoted by the red star).

communities in the alpine lakes have the lowest taxonomic richness (number of taxa present in a sample) with the midge assemblages in the sub-alpine and montane lakes characterized by nearly equivalent taxonomic richness. Midges belonging to the sub-tribe Tanytarsini dominate all the lakes with *Tanytarsus* spp. and *Corynocera* spp. most abundant in the alpine and sub-alpine lakes. *Dicrotendipes*, *Microtendipes* and *Cladopelma*, taxa typically associated with warmer, productive lakes (Brooks et al., 2007) are also abundant in the sub-alpine midge community. Taxa such as *Cladotanytarsus*, *Corynocera ambigua*-type and *Tanytarsus type G* are only found in lakes located above the montane-subalpine ecotone.

*Diplocladius*, which is found in three of the 20 lakes sampled in CO, dominates the midge community in Seven Sisters West Lake (SSW) (~66%), the highest (~3900 m asl) and the coldest lake (MJAT = 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 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 characterized by wide elevation, lake depth and 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 ZRFS midge stratigraphy. Seven Sisters Central Lake and MLA are located above timberline with vegetation in both basins consisting of dwarf *Picea*, Compositae, and Poaceae.

The newly developed IMW midge-based inference model applied to the sub-fossil midge assemblages recovered from the ZRFS is based on 91 lakes and has a RMSEP = 0.97°C and a $r^2_{\text{jack}} = 0.61$ (Fig. 3). The diversity and performance statistics associated with the IMW midge-based inference model have been improved relative to the Great Basin inference model. The Great Basin training set had lower taxonomic richness and the MJAT inference model based on the Great Basin training set had a lower $r^2_{\text{jack}}$ (0.55) (Porinchu et al., 2010). In addition, inclusion of the CO lakes increases the climatic gradient captured by the training set lakes. The range of MJAT and SWT captured by the lakes incorporated in the IMW inference model is 9.9°C and 16.4°C, respectively.

### *ZRFS midge stratigraphy*

The sub-fossil midge stratigraphy has been divided into six midge zones (MZ): MZ 6 (Unit 3 and the base of Unit 4); MZ 5e (units 4, 5 and the base of 6); MZ 5d (units 6, 7 and the majority of Unit 8); MZ 5c (the upper portion of Unit 8 through the lower portion of Unit 13); MZ 5b (units 13–14); MZ 5a (units 15–16) and MZ 4 (Unit 17) (Fig. 4; Table 2). The sediment analyzed for midge remains from units 3–8 was obtained from core Z43C-B. The remainder of the sediment was obtained from the cleaned sediment facies at localities 43 and 51. These midge zones, which correspond closely to the pollen zones of Anderson et al. (2014–in this volume) and are approximately equivalent to marine isotope stages, facilitate direct comparison of the midge stratigraphy with the pollen record (Table 2).

### *ZRFS midge community change and MJAT reconstruction*

#### *MZ 6 (1019–991 cm; 141–138 ka)*

The sub-fossil chironomid head capsules recovered from the base of the ZRFS sedimentary sequence were found in Unit 3 just above the glacial till. The sediment immediately above the till consists of sticky clay (Pigati et al., 2014–in this volume). This zone is characterized by high midge head capsule concentration (110 head capsules/mL) and low taxonomic diversity. *Corynocera oliveri*-type is the dominant

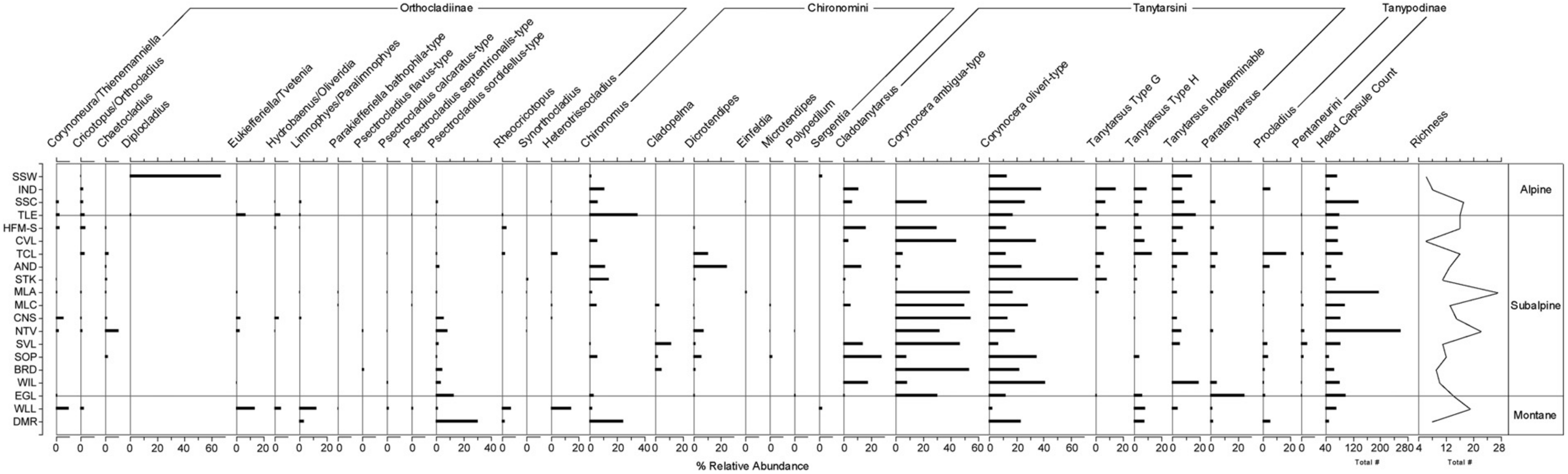

**Figure 2.** Relative abundances of chironomid taxa found in the training set lakes in the Colorado Rocky Mountains. Three zones have been identified (alpine, subalpine, and montane) based on modern plant distributions (McMulkin et al., 2010).

midge comprising approximately 75% of the assemblage, with lesser amounts of *Procladius* (11%), *Tanytarsus*-type G (12%) and *Tanytarsus*-type H (2%) present (Fig. 4). The modern distribution of *Tanytarsus*-type G is restricted to lakes located in upper subalpine and alpine settings in central CO and although widely distributed in the modern training set lakes, *C. oliveri*-type and *Tanytarsus*-type H are also most abundant in sub-alpine and alpine lakes in this region.

### *MZ 5e (991–902 cm; 138–129 ka)*

The sediment stratigraphy transitioned to organic-rich silt at the base of Unit 4 (~138 ka). The sediment at the base of Unit 4 contained abundant midge remains. The midge community at the bottom of MZ 5e consists of thermophilous taxa such as *Chironomus*, *Glyptotendipes* and *Cladopelma*, a genus associated with mesotrophic lakes (Brooks et al., 2007), a cool-water taxon, *C. oliveri*-type and a widely distributed taxon, *Procladius*. Taxon richness increases to 7 at the beginning of MZ 5e. A transition to laminated silty clay occurs midway through MZ 5e. This transition is characterized by a notable decrease in midge head capsule concentration. A total of three head capsules, belonging to *Chironomus* and *Procladius*, were recovered from the sediment spanning the interval between 136 ka and 131 ka. The sediment, which coarsens to organic-rich silt at the top of MZ 5e, contains abundant remains of *Chironomus* and *Glyptotendipes*, taxa that are typically associated with warm, productive lakes (Brooks et al., 2007) and lesser amounts of *Tanytarsus* type G and *Procladius*.

### *MZ 5d (902–704 cm; 129–113 ka)*

The sub-fossil midge community present between 129 ka and 113 ka is not well characterized due to extremely poor head capsule recovery (0–5 head capsules/mL). However, a large number of mandibles belonging to *Chaoborus* (phantom midge), an organism that that can survive long periods of anoxia (Brodersen and Quinlan, 2006), are present at the base of MZ 5d (Fig. 4). Midway through MZ 5d the sediment transitions from organic-rich sand into a sandy silt and is interspaced with carbonate lenses. The taxa that are present during this interval consist of thermophilous taxa comparable to those found at the base of MZ 5e, albeit at very low numbers. The top of MZ 5d, which corresponds to Unit 8, consists of organic silt. The midge community present at the close of MZ 5d is characterized by the appearance of Orthocladiinae such as, *Limnophyes*/*Paralimnophyes* and *Parakiefferiella bathophila*-type and relatively high taxon richness. *Parakiefferiella* and *Limnophyes*/*Paralimnophyes* are often most abundant in the littoral zone of lakes and usually reflect shallow water conditions (Brooks et al., 2007). The relative abundance of the acidophilic *P. sordidellus*-type also increases at the top of MZ 5d (~114 ka).

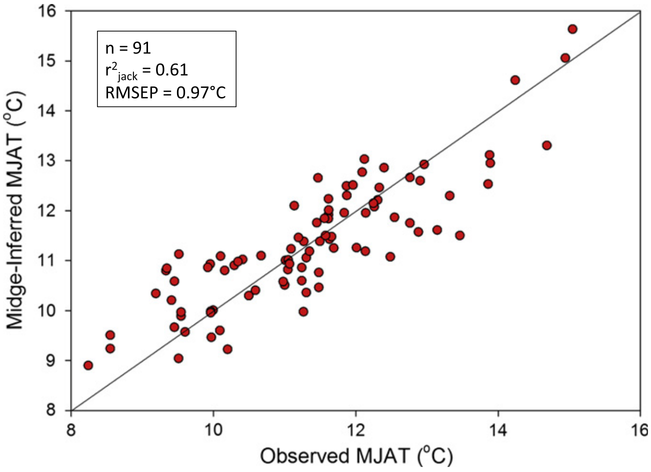

**Figure 3.** Relationship between mean July air temperatures derived using PRISM for the modern calibration set (PRISM data group, 2012) and the midge-inferred mean July air temperature. The solid line represents the 1:1 relationship.

### *MZ 5c (704–543 cm; 113–100 ka)*

Additional sediment samples from Unit 8, collected from Locality 43, represent the lowermost portion of MZ 5c. The basal portion of MZ 5c (Unit 8) is characterized by a complete absence of midge head capsules. The stratigraphy for Unit 9, located midway through MZ 5c, is characterized as mottled brown silt. Two sediment samples in the middle portion of MZ 5c contain midge remains, albeit with extremely low head capsule recovery (~4.5 head capsules/mL). The sub-fossil midge assemblage associated with these samples consists entirely of *Glyptotendipes*. The midge remains in Unit 10 towards the top of MZ 5c were extracted from sediment characterized as a yellowish-brown bedded silt. This sediment contained large fragments of organic matter and was dominated by *Tanytarsus* spp., *C. oliveri*-type, *Procladius* and *Chironomus*. In addition, head capsule recovery and relative abundance of *Paratanytarsus*, a taxon often associated with macrophytes, increases towards the top of MZ 5c. This interval is also characterized by the local extirpation of *Parakiefferiella* and *Limnophyes*/*Paralimnophyes* and a reduction in *P. sordidellus*-type. The sediment transitions from the yellowish-brown bedded silt to a weakly bedded silt in the uppermost portion of MZ 5c. Chironomid remains are very abundant at the top of MZ 5c (257 head capsules/mL). The large increase in littoral taxa such as *P. sordidellus*-type and *Cladotanytarsus* that occurs in the upper portion of this zone likely reflects decreasing lake water pH (Henrikson et al., 1982). The appearance of *Dicrotendipes* and *Einfeldia* characterizes the close of MZ 5c with the relative abundance of *Dicrotendipes* increasing from 0% at ~102 ka to 60% at ~101 ka. *Dicrotendipes* and *Einfeldia*, along with *Cladotanytarsus*, are often found in eutrophic to mesotrophic lakes and where they are associated with aquatic macrophytes in the littoral zone (Brodersen et al., 2001; Langdon et al., 2006).

### *MZ 5b (543–338 cm; 100–87 ka)*

The sediment represented by MZ 5b was collected from Locality 43. The stratigraphy of the upper portion of Unit 13, which is found at the base of MZ 5b, transitions to bedded silty clay from the organic-rich sediment of Unit 12. A notable decrease in taxon richness and head capsule concentration occurs during the transition between MZ 5c and MZ 5b. A large decrease in *Dicrotendipes* and the local extirpation of all Orthocladiinae taxa including *P. sordidellus*-type and *Einfeldia* characterizes the onset of MZ 5b. Subfossil midges disappear from the sediment at ~97 ka and remain absent throughout the remainder of MZ 5b. Maximum taxon richness increases from nine in MZ 5c to twelve in MZ 5b.

### *MZ 5a (338–215 cm; 87–77 ka)*

The samples spanning MZ 5a were collected from Locality 51. The sediment is comprised of peaty silt (Unit 15) and peat (Unit 16) that includes large organic fragments and macroscopic plant matter. A dramatic increase in chironomid head capsule concentration occurs in the basal portion of MZ 5a with concentrations reaching 241 head capsules/mL. The midge community at the base of MZ 5a is dominated by *Dicrotendipes*, which reaches a relative abundance of ~70% at ~86 ka. Other taxa present at the base of MZ 5a include *Chironomus*, *Glyptotendipes*, *Cladotanytarsus* and *P. bathophila*-type. The transition in the sediment to dark brown peat with very high concentrations of organic matter that occurs at ~84 ka is associated with a notable decrease in head capsule recovery, a major shift in the midge assemblages from a Chironomini-dominated assemblage to an Orthocladiinae-dominated assemblage, and a core maximum in taxon richness. Taxa such as *Limnophyes*, *Smittia*, *Paratendipes*, *Polypedilum*, *Paratanytarsus* and *Heterotrissocladius* are relatively abundant in the upper portion of MZ 5a. The increase in *Limnophyes*/*Paralimnophyes* and the appearance of *Smittia*/*Pseudosmittia*, *Paratendipes* and *Polypedilum* may reflect a lowering of lake level and continued eutrophication of the lake. Many *Limnophyes*/*Paralimnophyes* and *Smittia*/*Pseudosmittia* species are semi-

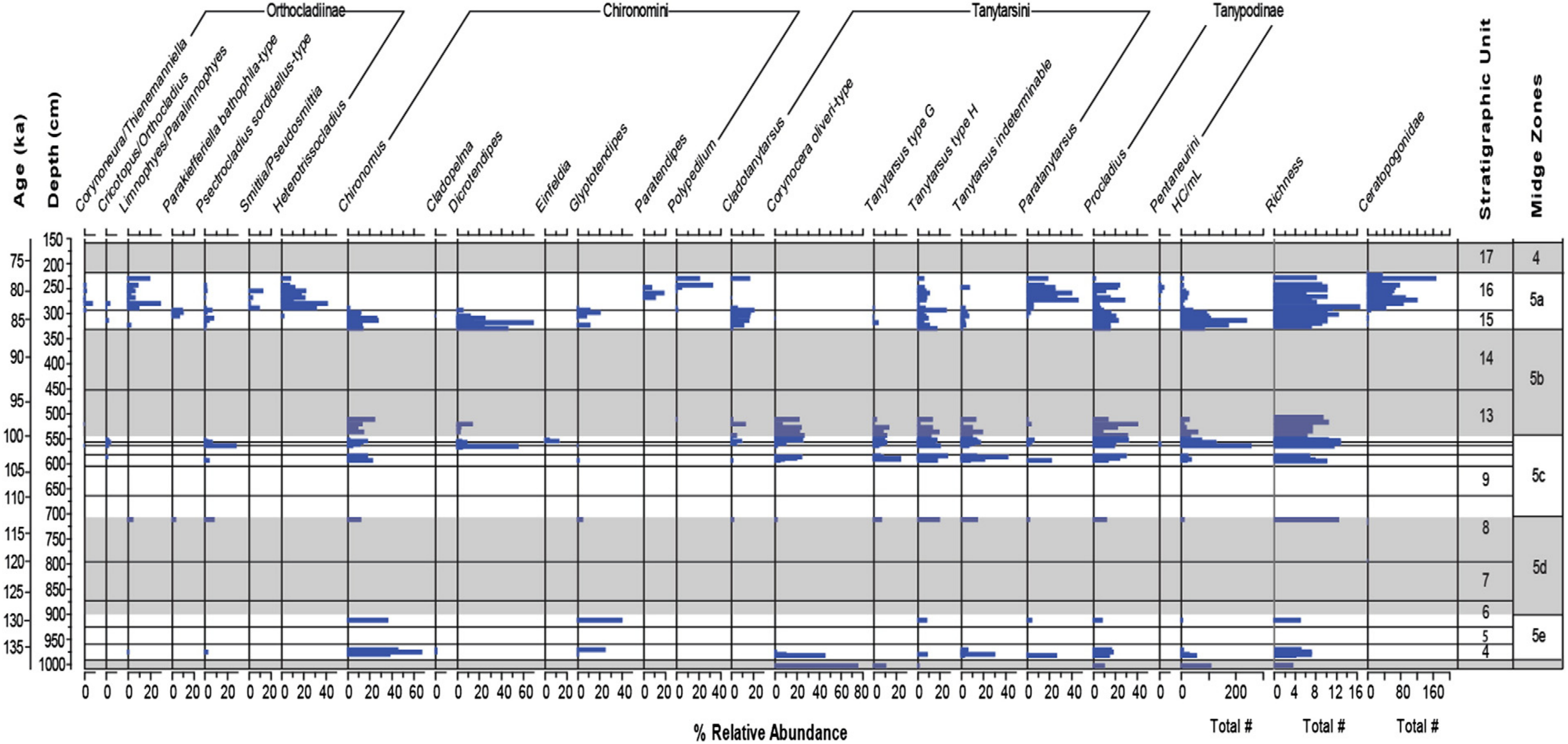

**Figure 4.** Relative abundances of chironomid taxa found in sediments at the Ziegler Reservoir fossil site.

**Table 2**
Classification of zones based on the changes within midge communities. MIS equivalents, the pollen zones identified by Anderson et al. (in this volume), stratigraphic units, depths and ages are provided to aid in comparison.

| Midge zone (Haskett/Porinchu) | Pollen zone (Anderson et al) | Stratigraphic units | Lower depth (cm) | Upper depth (cm) | ZRFS ages (ka) | MIS equivalent |
|---|---|---|---|---|---|---|
| 4 | 4 | 17, 18 | 215 | 0 | 77 ± 4 to 55 ± 10 | 4 |
| 5a | 5a | 15, 16 | 338 | 215 | 87 ± 3 to 77 ± 4 | 5a |
| 5b | 5b | 13, 14 | 543 | 338 | 100 ± 3 to 87 ± 3 | 5b |
| 5c | 5c | 8 (upper), 9–12, 13 (lower) | 704 | 543 | 113 ± 8 to 100 ± 3 | 5c |
| 5d | 5d | 6 (upper), 7, 8 | 902 | 704 | 129 ± 10 to 113 ± 8 | 5d |
| 5e | 5e | 4, 5, 6 (lower) | 991 | 902 | 138 ± 13 to 129 ± 10 | 5e |
| 6 | 6 | 3, 4 (base) | 1019 | 991 | 141 ± 14 to 138 ± 13 | 6 |

terrestrial (Cranston et al., 1983) and *Paratendipes* and *Polypedilum* are often associated with aquatic macrophytes in mesotrophic and eutrophic lakes (Brodin, 1986). The appearance and high relative abundance of Ceratopogonidae towards the top of MZ 5a in Unit 16 may also indicate an increase in the availability of semi-aquatic habitat at the close of MZ 5a.

### *MZ 4 (215–0 cm; 77–55 ka)*

The uppermost zone includes sediment from units 17 and 18, collected at Locality 51, which consists of a silt that transitions to a mottled silty clay. Only one individual head capsule was recovered, midway through MZ 4. A head capsule belonging to *Zavreliella*, a taxon intimately associated with aquatic vegetation (Pinder and Reiss, 1983), was extracted from sediment at 161 cm (~72 ka). The remainder of the sediment processed from the MZ 4 was devoid of sub-fossil midge remains.

### *ZRFS midge community change and MJAT reconstruction*

Rapid compositional change often reflects the occurrence of notable fluctuations in limnological and/or environmental conditions (Battarbee, 2000; Smol and Douglas, 2007; Rühland et al., 2008). Detrended correspondence analysis (DCA) reveals that two intervals of rapid turnover in the midge assemblages occurred at the ZRFS (Fig. 5). The first interval of turnover in the midge community occurs at the base of the ZRFS midge stratigraphy with a shift from a *C. oliveri*-type dominated assemblage in MZ 6 to a *Chironomus* and *Glyptotendipes* dominated assemblage at the base of MZ 5e. The taxonomic richness of the midge assemblage increases from 4 in Unit 3 to 7 in Unit 4. The turnover that occurred midway through MZ 5a (~84 ka), which is characterized by a shift from a Chironomini-dominated assemblage to an Orthocladiinae-dominated assemblage, is larger in magnitude, with an increase in taxon richness from 11 to 16 at ~84 ka.

The chironomid-inferred MJAT reconstruction for the ZRFS midge stratigraphy is presented in Fig. 5. 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 provided estimates of MJAT for four discrete intervals: the MZ 6–5e transition, late MZ 5d, the MZ 5c–5b transition and MZ 5a. The MZ 6/5e transition is characterized by an increase in midge-inferred MJAT of ~1.5°C (9.0–10.5°C). The midge-inferred MJAT estimate of 10.4°C at ~137 ka can be considered very reliable according to the G-O-F, MAT and % absent taxa analyses. The midge-inferred point estimate of 9.9°C, available for the upper portion of MZ 5d, is robust according to the G-O-F analysis. The latter portion of MZ 5c is characterized by MJAT that fluctuates between 9.7°C and 10.7°C. The estimate of 10.0°C at ~103 ka can be considered very reliable according to the G-O-F, MAT and % absent taxa analyses. The MZ 5c/5b transition is characterized by decreasing MJAT, reaching a zone minimum of 9.7°C at ~100 ka. The majority of midge-inferred MJAT estimates, which fluctuate between 9.7°C and 10.7°C in MZ 5b, can be considered robust according to the various statistical tests. Mean July air temperature increases through MZ 5a. Midge-inferred MJAT, which is 10.7°C at the base of MZ 5a, reaches a maximum value of 13.3°C at ~80 ka. The MJAT inference of 10.4°C at ~86 ka can be considered robust. The reconstructed midge-inferred MJAT temperature range captured by variations in the midge community at the ZRFS fossil site was 4.3°C (9.0–13.3°C). It is important to note that a plot of observed MJAT versus midge-inferred MJAT (not shown) indicates that the midge-based MJAT model appears to underestimate inferred temperature at the high end of the temperature range captured by the model (<13°C) and overestimate MJAT at the low end of the temperature range captured by the model (>9°C).

The reliability of the quantitative midge-based temperature reconstructions was evaluated using a number of approaches (Fig. 5). An assessment of the total percentage of taxa present down-core that do not appear in the modern calibration data set indicated that the taxa found at the ZRFS are well-represented and characterized, with all 25 chironomid taxa comprising the ZRFS chironomid stratigraphy present in the Intermountain West calibration set. The proportion of rare taxa present in the down-core samples was low as reflected by the Hill's N2 diversity index values, which ranged between 5 and 58 for 20 of the 25 taxa present in the ZRFS. Five taxa: *Smittia*/*Pseudosmittia*, *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. Based on these two measures the midge-based MJAT reconstruction can be considered reliable (Birks, 1998). According to the G-O-F analysis fossil samples in MZ 5b, MZ 5c, MZ 5d and portions of MZ 5a and MZ 5e have a good fit to temperature with the sample scores fluctuating around the 90th and 95th percentile cut-levels. However, the MAT analysis indicates that the fossil samples in MZ 5a, MZ 5d and portions of MZ 5c and MZ 5e do not have good analogs in the IMW training set with close analogs limited to the fossil samples in MZ 5b. The temperature reconstruction is significant when compared to random variables (Telford and Birks, 2011) (Fig. 6).

## Discussion

The midge stratigraphy developed at the ZRFS documents the changing environmental conditions that characterize high elevations in central CO between ~140 and 77 ka. Detrended correspondence analysis identified that the midge community experienced two discrete intervals of notable faunal turnover (Fig. 5). The first interval occurred during the transition between MZ 6 and MZ 5e with a shift in the midge community from a Tanytarsini-dominated assemblage to a Chironomini-dominated assemblage. The decrease in the relative abundance of *C. oliveri*-type, a cool-water taxon, and the increase in *Chironomus* and *Glyptotendipes*, taxa associated with mesotrophic and eutrophic waters (Brooks et al., 2007), that characterizes this transition is suggestive of climatic amelioration. The appearance of *Chironomus*, which has been documented as an early colonizer of lakes during glacial–interglacial transitions (Brooks et al., 1997), supports the interpretation that this interval was characterized by an increase in lake productivity. An increase in midge-inferred MJAT of ~1.5°C (9.0–10.5°C) provides further support for climate amelioration during the MIS 6–MIS 5e transition. The second notable shift in the midge community occurs midway through MZ 5a (~84 ka) when taxa such as *Chironomus*, *Dicrotendipes* and *Glyptotendipes*, which are typically associated with warm, highly productive lakes are replaced by taxa

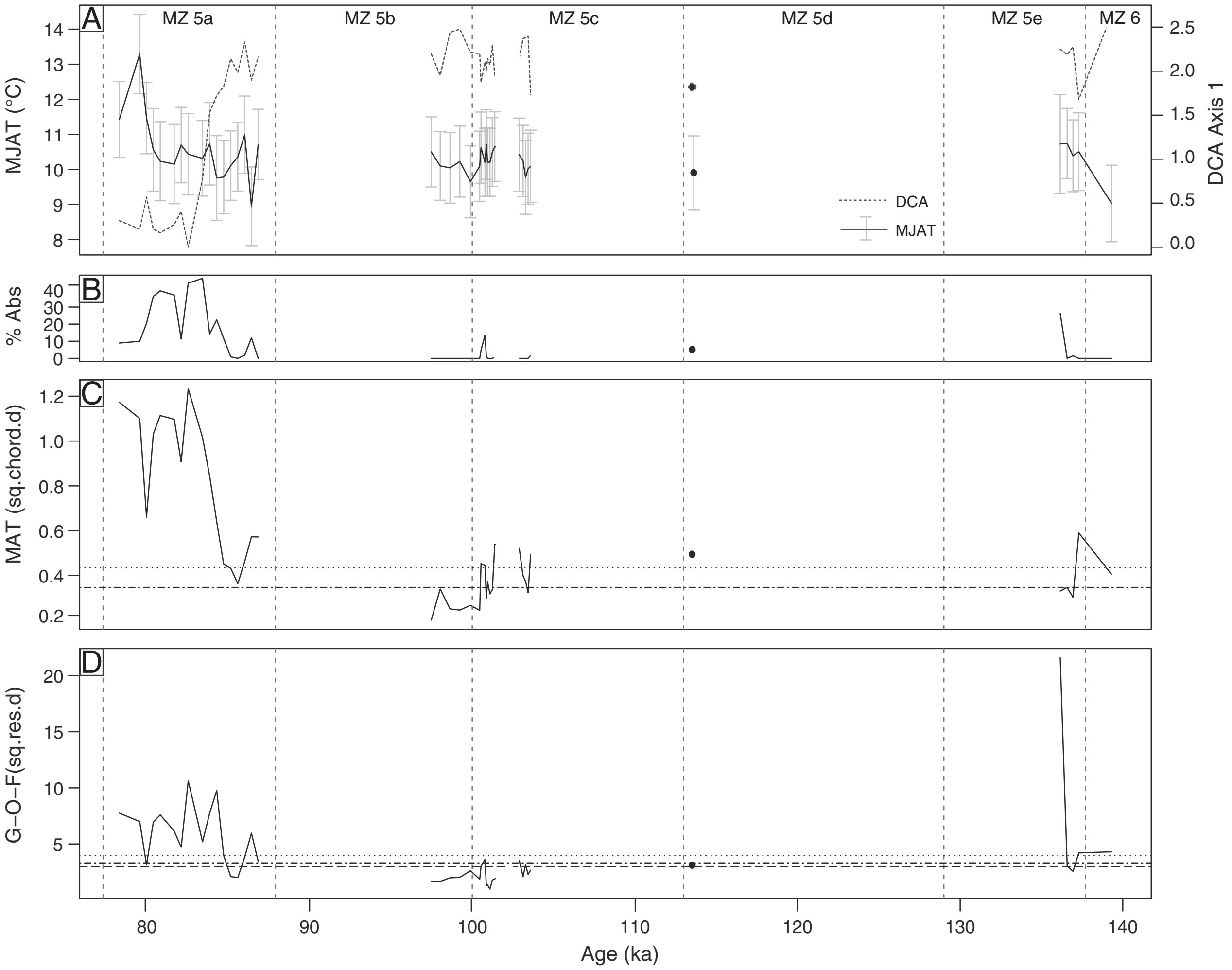

**Figure 5.** (A) Chironomid-inferred mean July air temperature reconstructions for the Ziegler Reservoir fossil site (solid line with error bars) are plotted along with the DCA Axis 1 scores (detrended correspondence analysis; dashed line) for all midge zones. Horizontal lines in the MAT-curves indicate 'no close' (dashed line) and 'no good' (dotted line) analogs, respectively. (B) Percentage of fossil chironomids that are absent from the modern calibration set (% Abs). (C) Square chord dissimilarity distance (sq.chord.d) to the nearest modern analogs (MAT) in the calibration set. (D) The goodness-of fit (G-O-F; sq.res.d.) of the fossil samples to a canonical correspondence analysis constrained solely to temperature. Horizontal lines in the G-O-F curves indicate the 90th (poorly fitted), 95th (very poorly fitted), and 99th (extremely poorly fitted) percentiles in residual distances of the modern samples to the first axis in a constrained CCA and are defined as a 'poorly fitted' (long-dashed line) and 'very poorly fitted' (dashed line) and 'extremely poorly fitted' (dotted line) fit respectively (Birks et al., 1990).

associated with aquatic macrophytes, e.g. *Paratendipes*, *Polypedilum* and *Paratanytarsus*, and semi-terrestrial conditions, e.g. *Limnophyes* and *Smittia*/*Pseudosmittia*. High-elevation lakes in the Intermountain West have experienced large increases in the relative abundance of *Dicrotendipes* in recent decades (post-1980 AD). The change in the abundance of *Dicrotendipes* is inferred to be a response to the elevated temperatures that have characterized this region during the late 20th century (Porinchu et al., 2007b; Reinemann et al., in press). This interval is also characterized by the appearance of Ceratopogonidae. Ceratopogonidae commonly inhabit the transitional zone between fully aquatic and terrestrial habitats (Szadziewski et al., 1997) and its appearance in sediment sequences has been associated with falling lake levels (Hofmann, 1983). Taken together, the change in midge assemblages and the arrival of Ceratopogonidae midway through MZ 5a are suggestive of continued infilling and shallowing of the lake basin. This interpretation is further supported by the appearance of an acidophilic taxon, *Heterotrissocladius*, which may reflect the encroachment by peat of the lake basin.

Also of note was the presence of four intervals in the midge stratigraphy where the sub-fossil midge remains were either highly degraded or absent. The presence of disarticulated head capsules, beginning at the base of Unit 3 (~138 ka) and extending through to the lower portion of Unit 6 (~129 ka), suggests that the deposition of midge capsules during this time span may have been occurring in a high-energy environment, potentially reflecting high glacial meltwater influx and/or increased sedimentation. The diversity of the community is relatively low during the 6/5e transition; however, this often the case during glacial/interglacial transitions (e.g. Porinchu et al., 2003). Low head capsule recovery continued through much of MZ 5d and the early portion of MIS 5c suggesting that the shift in limnological conditions that drove the initial decline in sub-fossil midges persisted until midway through MIS 5e. 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 ZRFS stratigraphy. It is possible that taphonomic processes are affecting the preservation of subfossil midge head capsules; however, the presence of *Procladius*, which has been identified as under-represented in sub-fossil assemblages (Walker et al., 1984), throughout the core suggests that differential preservation may not be a factor. The complete absence of midges between the middle portion of MZ 5b (~97 ka) and the onset of MZ 5a (~87 ka) is puzzling. We speculate that the presence of persistent and/or extensive ice cover through the summer growing season may have limited midge reproduction and survival during this interval. Alternatively, if the lake was sufficiently shallow, transport and re-deposition of midge head capsules from the lake margin to the coring location at the center of the lake may have been restricted.

The reliability of the midge-based temperature inferences, which was assessed using various statistical approaches indicate that the temperature estimates for four intervals can be considered robust: early MZ 5e (~137 ka), late MZ 5c (~101 ka), early MZ 5b (~100–97 ka) and early MZ 5a (~86 ka). The midge-inferred MJAT at the onset of MZ 5e is 10.4°C, which is the same as the average midge-inferred temperatures for MZ 5c and MZ 5a. The lowest robust temperature estimate for the entire core occurs in MZ 5b. The midge-inferred temperature of 9.6°C, which occurs at ~100 ka, is approximately 1.0°C lower than the reconstructed MJAT that characterizes the beginning of MZ 5e and MZ 5a. However, it is worth noting that the lowest midge-inferred MJAT occurs at the base of the midge stratigraphy in MZ 6. The reconstructed MJAT for MZ 6, which is 9.0°C, is nearly 1.5°C lower than the MJAT estimate for MZ 5a, 5c and 5e, although, according to the MAT and GOF analyses, this estimate cannot be considered robust.

Sub-fossil midge analysis has been used successfully in high northern latitudes to provide quantitative estimates of the thermal conditions that existed during MIS 7, 6, 5 and 4 (Engels et al., 2010; Axford et al., 2011). For example, Axford et al. (2011) successfully developed a 200 ka record from Baffin Island, Canada with robust temperature estimates for MIS 7 and MIS 5. 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 for MIS 5d and therefore the quantitative temperature estimates for this interval should be viewed with caution. Similar findings are evident in records from Alaska that extend beyond the Last Glacial Maximum (Kurek et al., 2009). The midge stratigraphy developed for the ZRFS indicates that the later interval during MZ 5a, in particular, was characterized by the majority of sub-fossil midge samples identified as having 'no good' analogs (Birks et al., 1990) and/or a 'very poor fit' (Birks et al., 1990), relative to the midge assemblages in the IMW calibration set. The shift in midge assemblages from a Chironomini-dominated assemblage to an assemblage dominated by semi-terrestrial midge taxa such as *Limnophyes* and *Smittia*/*Pseudosmittia* and Ceratopogonidae that occurs at ~84 ka is likely driven by lake-level changes in habitat availability and limnological conditions, rather than MJAT. This interpretation is further supported by the observed change in the sediment stratigraphy from a peaty silt to peat and an increase in Cyperaceae pollen, which is inferred to suggest a transition to a shallow-water marsh (Anderson et al., 2014–in this volume). The midge stratigraphy developed in this study reveals that quantitative midge-based inference models for MJAT can provide robust estimates of MJAT extending into the previous interglacial; however, estimates of MJAT will be poorly constrained if the modern training set does not include midge assemblages that are associated with shallow water or marsh-like conditions.

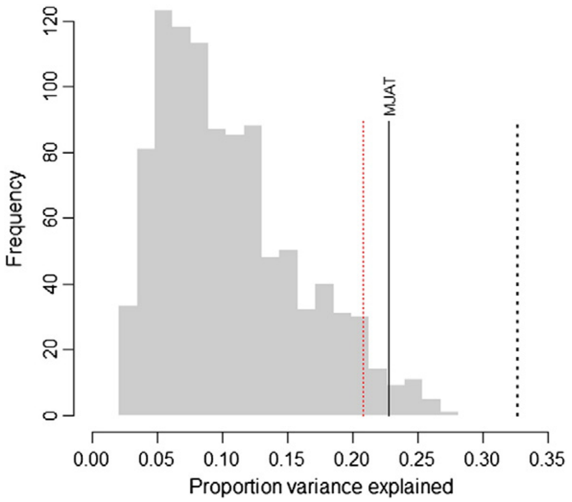

**Figure 6.** The results of the Telford and Birks (2011) significance test. The histogram indicates the proportion of variance in the Ziegler Reservoir fossil site record explained by 999 transfer functions. Random data was used to train the function. The MJAT line shows the proportion of the variance in the fossil data explained by each reconstruction ($n = 999$, $p = 0.026$). The thin dashed line indicates the 95th confidence interval. The thick dashed line shows the proportion explained by the first axis of a PCA (0.327).

Evidence from the pollen and spruce-to-pine (S:P) ratio (Anderson et al., 2014–in this volume), which document that the transition from MIS 6 to MIS 5e (~138 ka) was characterized by a shift from steppe-like vegetation to a moderately dense Picea forest, is suggestive of climate amelioration (Fig. 7). The appearance of *Glyptotendipes* and *Chironomus*, taxa associated with mesotrophic and eutrophic waters, and the increase in the midge-based estimate of MJAT from 9.0°C in MIS 6 to 10.5°C at the onset of MIS 5e is consistent with this interpretation. Low chironomid head capsule recovery through much of MIS 5d limits our ability to provide strong corroboration of the pollen-based inference that MIS 5d was slightly cooler than MIS 5e; however, the one quantitative midge-based estimate of MJAT available for this interval, which is 9.9°C, is lower than the average midge-based MJAT reconstruction for MIS 5e. The inception of MIS 5c, evidenced by a continued increase in the S:P ratio, is suggestive of an increasingly dense *Picea* forest. Midge-based MJAT peaks at ~101 ka, corresponding to elevated S:P pollen values. The presence of *Dicrotendipes*, *P. sordidellus*-type and *Cladotanytarsus* towards the close of MIS 5c is suggestive of increasing lake productivity, expansion of macrophytic vegetation and decreasing pH. These changes in the midge assemblages are consistent with a lowering of lake level. The inference that the ZRFS was characterized by relatively shallow and possibly fluctuating lake levels at the close of MIS 5c is supported by the large increase in *Botryococcus* that occurs at this time (Anderson et al., 2014–in this volume) (Fig. 7). The lowest S:P ratios documented in the core, elevated amounts of *Botryococcus* and a near absence of midge remains characterizes the sediment deposited during MIS 5b. We do not have a definitive explanation for the absence of midges during MIS 5b. The decrease in the S:P ratio suggests that local timberline dropped 800–1000 m, supporting the assertion that climate deterioration during MIS 5b may have been sufficiently large enough to reduce the summer growing season, which in turn may have affected midge productivity. The increase in midge head capsule concentration and MJAT estimates as well as shifts in the midge assemblages, correspond to changes in the S:P ratio, and are consistent with the inference that MIS 5a was characterized by elevated temperatures and increased lake productivity.

The chironomid stratigraphy supports the detailed pollen record produced for the site, which indicates that notable changes in local and regional environmental conditions occurred during the transitions from MIS 6 to MIS 5e, MIS 5b to MIS 5a, and midway through MIS 5a. Deviations of the midge-inferred MJAT from the 140–77 ka midge-inferred average (10.4°C), indicates that MIS 5e and MIS 5a, were characterized by above average temperatures and that MIS 6, MIS 5d and MIS 5b were characterized by below average temperatures with the lowest inferred temperature, 9.0°C, occurring during MIS 6. Although many studies indicate that MIS 5e was the warmest stage of MIS 5 (Shackleton, 1969; Sanchez-Goñi et al., 2012) our record suggests that alpine environments in the central CO Rockies became progressively warmer through MIS 5 with a maximum midge-inferred MJAT of 13.3°C occurring during MIS 5a at ~80 ka. Evidence from Yellowstone National Park, which indicates that MIS 5a was the warmest interval of MIS 5, corroborates these findings (Baker, 1986).

## Conclusion

The multiproxy paleolimnological and paleoecological studies undertaken at the ZRFS, which incorporate various proxies, including pollen, invertebrates, ostracods and snails and macrofossils, together with sub-fossil midge analysis will help further our understanding of the

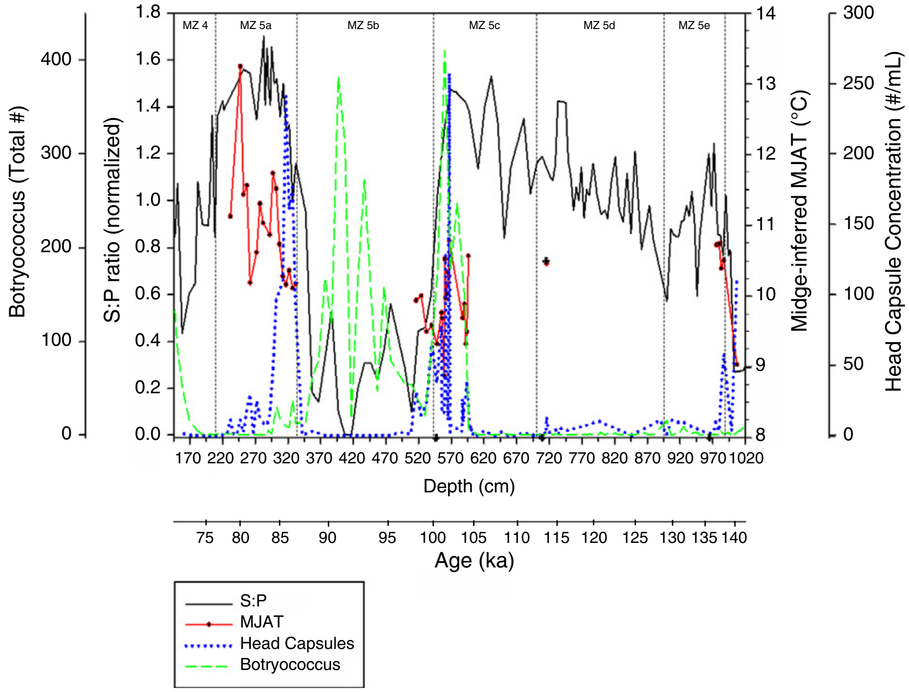

**Figure 7.** Chironomid-based reconstructed mean July air temperatures (ºC) and head capsule concentration (#/mL) from this study compared to spruce/pine ratio and abundance of *Botryococcus* (green algae) (Anderson et al., in this volume).

role that climate and environmental change played in shaping the structure and composition of a high elevation late Pleistocene ecosystem. Analysis of subfossil chironomids extracted from sediment recovered from the ZRFS provided an opportunity to qualitatively document environmental change at the site and develop a quantitative reconstruction of thermal conditions for the region spanning the interval from ~140 to 77 ka, which covers the end of MIS 6 and all of MIS 5. Notable shifts in midge assemblages occurred during two discrete intervals: the transition from MIS 6 to MIS 5e and midway through MIS 5a. The first shift, which was characterized by a replacement of *C. oliveri*-type by *Chironomus* and *Glyptotendipes*, was inferred to reflect climate amelioration during the MIS 6–MIS 5e transition. The midge-based MJAT reconstruction indicates that this interval was characterized by an increase in midge-inferred MJAT of ~1.5°C (from 9.0 to 10.5°C). The second notable shift occurred midway through MIS 5a at ~84 ka when Ceratopogonidae and semi-terrestrial midge taxa such as *Limnophyes* and *Smittia*/*Pseudosmittia* increased in relative abundance. The change in midge assemblages that occurred at this time is inferred to represent a lowering of lake level and changing habitat availability. The reliability of the midge-based MJAT reconstruction, assessed using various statistical tests, indicate that the estimates of MJAT available for the MIS 6–5e transition, late MIS 5d, the MIS 5c–5b transition and MIS 5a can be considered robust. Overall, the midge-based reconstruction indicates that the highest temperature in MIS 5 occurs during MIS 5a. The midge-based reconstruction suggests that MIS 5a and MIS 5e, were characterized by above average relatively warmer temperatures and that MIS 6, MIS 5d and MIS 5b were characterized by relatively cooler temperatures.

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