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Subfossil Chironomids as Indicators of Recent Climate Change in Sierra Nevada, California, Lakes

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Abstract

High-resolution chironomid (Insecta: Diptera) stratigraphies were developed for three subalpine lakes in the Sierra Nevada of California to assess whether these lakes have been impacted by recent climate change evident in regional instrumental records for the 19th and 20th centuries. Detrended correspondence analysis (DCA) of the chironomid fauna indicates that the lakes have experienced similar unidirectional change in community composition over the 20th century, with two of the lakes showing particularly sharp gradients of change since the 1970s. Application of a chironomid-based surface water temperature inference model ($r^2_{\text{jack}} = 0.73$, $\text{RMSEP}_{\text{jack}} = 1.1^\circ\text{C}$, and a maximum bias of 1.24°C) to the subfossil chironomid assemblages preserved in the lake sediment provided quantitative estimates of surface water temperature changes and revealed the existence of similar water temperature trends between the late 19th century and the present. Above average water temperatures characterized the late 20th century and below average surface water temperatures occurred between A.D. 1910 and A.D. 1980. Fluctuations in the surface water temperature of these lakes closely track changes in mean July air temperature as measured in Fresno, California, over the period A.D. 1895–2001. It appears that 20th century climate change has had an overriding influence on the composition of the chironomid communities within these three lakes. This study demonstrates that subfossil chironomid analysis can provide detailed records of community response to local and regional climatic changes at subdecadal time scales. It also suggests that chironomid communities in subalpine lakes in the Sierra Nevada are already recording the impact of recent climate warming.

Introduction

Lakes are extremely sensitive to local and regional environmental change and it is becoming increasingly apparent that climate warming during the latter half of the 20th century is responsible for some of the recent changes that have been evidenced in aquatic ecosystems (Battarbee, 2000; Naiman and Turner, 2000; Schindler, 2001). A number of studies have used the biological, physical, and chemical information preserved within lake sediment to develop records of recent climate change, providing valuable information on past climatic variability and its effects on aquatic ecosystems (Douglas et al., 1994; Finney et al., 2002; Smol et al., 2005). It is important to broaden the analysis of recent changes in lake ecosystems with respect to geography and limnological conditions in order to understand the larger scale impacts of recent climate change and projected future global warming.

Analysis of subfossil chironomid, or midge, (Insecta: Diptera), remains provides an important tool for assessing climate changes and their impacts on lake ecosystems. Over the last decade there has been a dramatic increase in the number of paleolimnological and paleoclimatological studies incorporating analysis of chironomids to describe past climate and limnological conditions (e.g., Levesque et al., 1997; Verschuren et al., 2000; Brooks et al., 2001; Porinchi and Cwynar, 2002; Heiri and Lotter, 2005). The major reason for the increased interest in chironomid analysis relates to the fact that chironomids are extremely sensitive to

environmental factors such as air and water temperature, salinity, oxygen concentration, and lake depth. As a result, there has been an explosion in the use of chironomids to not only reconstruct past climate conditions, but to also study aquatic ecosystem dynamics and assess the impact of pollution on aquatic communities (reviewed in Walker, 2001; Porinchi and MacDonald, 2003). In general, these studies use a calibration data set approach to quantify the nature of the relationship that exists between chironomids and their contemporaneous environment and then apply this knowledge to provide quantitative estimates of past climate conditions.

To date, the vast majority of chironomid-based paleoenvironmental reconstructions focus on millennial- to centennial-scale changes that occurred during the late Pleistocene and early Holocene (Levesque et al., 1997; Brooks and Birks, 2001; Porinchi et al., 2003). However, there has been increasing interest in utilizing the paleoenvironmental archives preserved in lake sediments to detect and reconstruct more recent natural and anthropogenic environmental changes at decadal to subdecadal time scales (Clerk et al., 2000; Brooks et al., 2001; Battarbee et al., 2002; Solovieva et al., 2005).

The research presented in this study uses chironomids to reconstruct the pattern and impact of recent climate change (<150 years) on lake ecosystems in the Sierra Nevada, California. Although instrumental climate records extending back to the late 19th century exist in California, century-long observational records of climate and limnic ecosystems are not available for

the Sierra Nevada, but are crucial for the detection and monitoring of the effects of greenhouse warming or other anthropogenic disturbances on thermal regimes and freshwater availability (Millar and Woolfenden, 1999). Interpreting and providing estimates of past climate conditions from the subfossil chironomid assemblages preserved in recently deposited lake sediments requires an understanding of the sensitivity of chironomids to various climate parameters.

Analysis of both instrumental and proxy temperature records indicates that the late 20th century was characterized by a dramatic increase in global surface temperatures relative to the previous 150 to 1000 years (Mann et al., 1998; Mann and Jones, 2003; Jones and Mann, 2004). One question that has not yet been answered satisfactorily is whether it is possible to use chironomids from climatically sensitive sites, such as subalpine and alpine lakes, to develop high-resolution (decadal to subdecadal time scale) paleolimnological and surface water temperature reconstructions to detect the pattern and impact of these recent climate changes. To address this question we present chironomid stratigraphies spanning between ~100 and 140 years from three subalpine lakes in the Sierra Nevada, California. We evaluate the trajectories of chironomid community change between these lakes using detrended correspondence analysis (DCA). We apply a chironomid-based weighted averaging partial least squares (WA-PLS) inference model for surface water temperature (Porinchu et al., 2002) and compare the temperature inferences between the lakes. To verify the transfer function results, we compare the chironomid-based surface water temperature reconstructions for the uppermost samples from two of the lakes to modern site-specific measurements of air and water temperature. Lastly, we compare the three midge-inferred temperature records to an air temperature time series from Fresno, California, that spans the period from A.D. 1895 to the present.

Study Area

The three study sites are situated in subalpine settings in the Sierra Nevada, California (Fig. 1). The Sierra Nevada is characterized by a Mediterranean climate, with warm, arid summers and cool, moist winters (Major, 1988). Topographic relief greatly affects the distribution of temperature and precipitation in California, with any given elevation on the west side of the Sierra Nevada receiving twice the average yearly precipitation of the east side (Anderson, 1990). Two of the lakes, Rocky Bottom Lake and Moat Lake, are located east of the crest of the Sierra Nevada and one lake, MG-2 (unofficial name), is located just west of the crest.

MG-2 (37°09'56"N, 118°44'29"W; 3320 m a.s.l.) is located in northern Kings Canyon National Park. The underlying bedrock in the vicinity consists of alkalsite of Cretaceous age (Bateman and Moore, 1965) with Pleistocene glacial deposits present locally. The vegetation surrounding MG-2 consists predominately of *Pinus albicaulis* (whitebark pine) and *Pinus contorta* (lodgepole pine), with *Salix* (willow) found lakeside. Moat Lake (38°03'22"N, 119°16'45"W; 3197 m a.s.l.) is located west of Conway Summit in the Virginia Lakes region. It is surrounded by *P. albicaulis*, *P. contorta*, and *Salix* and is underlain by Triassic metavolcanic rock, with glacial deposits and talus present in the catchment (Huber et al., 1989). Rocky Bottom Lake (37°12'01"N, 118°31'02"W; 3180 m a.s.l.), located southeast of Bishop, California, is a moraine-dammed lake surrounded by *P. albicaulis* and *P. contorta*. The local geology underlying and surrounding Rocky Bottom Lake is dominated by Quaternary and Tertiary surficial deposits and

unmetamorphosed volcanic rocks (Bateman, 1992). Measurement of bottom water temperature (BWT) and total phosphorus (see Table 1) indicates that Moat Lake and Rocky Bottom Lake stratify during the summer and can be considered oligotrophic; no BWT or water chemistry measurements are available for MG-2.

Methods

FIELD

Two replicate sediment cores were recovered from the approximate center of each lake using a Glew mini-corer (Glew, 1991) deployed from an inflatable raft. The presence of a discrete contact between the lake sediment and the overlying water was observed upon core recovery, suggesting that the flocculent surface sediment was recovered intact. The sediment cores were retrieved in September 1998 (MG-2), June 2004 (Moat Lake), and July 2005 (Rocky Bottom Lake). The sediment cores varied in length: a 9.5 cm core was recovered from Rocky Bottom Lake, a 12 cm core was recovered from MG-2, and a 16.5 cm core was recovered from Moat Lake. Sediment was extruded in the field at 0.5 cm increments using a portable sectioning device (Glew, 1988), stored in Whirl-paks®, and kept cool and dark until transported to the lab. During surface sediment collection, measurements of surface water temperature, maximum depth, and Secchi depth were also made (see Table 1). All analyses were restricted to sediment subsampled from one of the replicate cores to limit errors associated with the cross correlating of cores. Surface water temperature data loggers (Hobo Tidbit, Onset Corporation) were fixed to a float and suspended 50 cm below the surface of the water. Average summer water temperatures for Rocky Bottom and Moat Lakes were based on the average value of hourly measurements taken between June and August, 2002–2005.

LABORATORY

The amount of organic carbon present in the lake sediment was estimated using loss-on-ignition (LOI) analysis, following standard procedures (Heiri et al., 2001). LOI analysis was undertaken at 0.5 cm resolution for Moat and Rocky Bottom Lakes and 1.0 cm resolution for MG-2.

Chironomid analysis follows methods outlined in Walker (2001). Chironomid analysis for the three sites was completed at 0.5 cm resolution, with a minimum of 40 head capsules identified and enumerated for every sample (Quinlan and Smol, 2001). Chironomid remains that consisted of less than half a head capsule were not enumerated, those that consisted of greater than half a head capsule were enumerated as a whole head capsule, while those that were half a head capsule were enumerated as half a head capsule. Identifications were based predominately on Wiederholm (1983), Oliver and Roussel (1983), Walker (1988), and reference collections housed at UCLA and The Ohio State University. The amount of sediment analyzed to obtain the minimum amount of head capsules varied greatly between cores and within cores (0.5–4.5 mL). The average number of head capsules enumerated per sample from each lake varied between 72 and 81, while head capsule concentrations varied between 17 head capsules mL⁻¹ and 335 head capsules mL⁻¹ (see Table 2 for further details).

NUMERICAL AND STATISTICAL ANALYSIS

The relationship between the modern distribution of chironomids in the Sierra Nevada and the contemporaneous

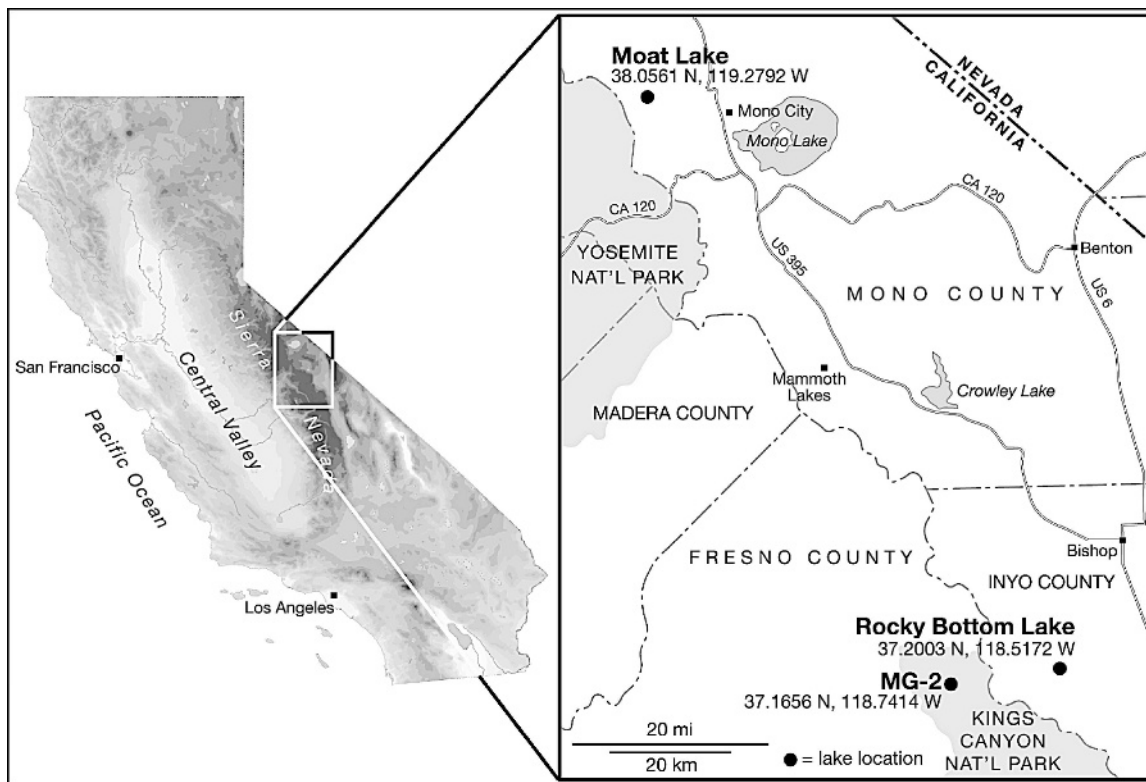


FIGURE 1. Location of study lakes (MG-2, Rocky Bottom Lake, and Moat Lake).

TABLE 1

Selected environmental characteristics of MG-2, Moat Lake, and Rocky Bottom Lake. SWT = surface water temperature, BWT = bottom water temperature. SWT measured on 12 September 1998 for MG-2, 28 June 2004 for Moat Lake, and 7 July 2005 for Rocky Bottom Lake. BTW measured on 12 September 1998 for MG-2, 29 June 2004 for Moat Lake, and 9 July 2005 for Rocky Bottom Lake. Total phosphorus measured in late July 1999 for Moat Lake and for Rocky Bottom Lake.

Environmental variable	MG-2	Moat Lake	Rocky Bottom Lake
Elevation (m a.s.l.)	3320	3197	3180
Depth (m)	7.25	8.00	10.55
Surface area (ha)	3.90	2.43	2.76
Measured SWT (°C)	13.0	11.5	15.4
Measured BWT (°C)	12.0	9.5	7.02
Secchi depth (m)	Extends to bottom	6.10	7.60
pH	NA	7.75	8.11
Total phosphorus ($\mu\text{g L}^{-1}$)	NA	2.90	2.70

TABLE 2

Selected characteristics of chironomid head capsules from MG-2, Moat Lake, and Rocky Bottom Lake.

Variable	MG-2	Moat Lake	Rocky Bottom Lake
Volume of sediment (mL^{-1}) (range)	1.0–2.0	0.50–4.50	1.0–3.0
Head capsule count (range)	42.5–101.5	56.0–167.50	51.5–138.0
Average head capsule count (range)	72	81	79
Head capsule concentration (mL^{-1}) (range)	21.0–51.25	18.0–335.0	17.0–69.0

environment was established by analyzing the subfossil chironomid remains preserved in the surface sediment of 56 lakes in this region (see Porinchi et al., 2002, for further details). A one-component weighted averaging partial least squares (WA-PLS) surface water temperature inference model based on 44 lakes and all taxa present in the calibration set was developed. The r^2_{jack} between measured and predicted surface water temperature was

0.72, the $\text{RMSEP}_{\text{jack}}$ was 1.1°C , and the maximum bias of the WA-PLS model was 1.24°C (Porinchi et al., 2002). This one-component WA-PLS inference model for surface water temperature was applied to the chironomid stratigraphies from MG-2, Moat Lake, and Rocky Bottom Lake to reconstruct the thermal regime for each lake spanning the interval for which a reliable radiometric chronology could be developed.

A form of indirect gradient analysis, detrended correspondence analysis (DCA), was used to assess the nature of the changing trajectories of midge community composition in the lakes. This analysis was based on all taxa that were present in each sample and used square-root transformed chironomid percentage data in order to optimize the “signal-to-noise” ratio and to stabilize variances (Prentice, 1980). DCA was performed using CANOCO version 4.0 (ter Braak and Šmilauer, 1998). Optimal sum of squares partitioning, implemented by the program ZONE version 1.2 (Juggins, 2005), was used to identify zones in the midge stratigraphies.

It is important to evaluate the reliability of any quantitative paleoenvironmental reconstruction, and one method commonly used to do this in paleolimnological research involves determining the total percentage of taxa in each subfossil assemblage (sample) that are not present in the modern calibration data set (Birks, 1998). Reconstructions that incorporate less than 5% novel taxa (i.e., taxa present in the subfossil samples but not present in the calibration set) are considered very reliable, and reconstructions with 5–10% novel taxa can be considered reliable (Birks, 1998). There were 17 chironomid taxa present in MG-2, one of which was not present in the modern calibration set; the missing taxon is the *Cyphomella/Harnischia/Paracladopelma* group, which makes up less than 1% of the total identifiable midge remains. Three taxa were present in each of the stratigraphies from Rocky Bottom (31 total taxa) and Moat Lake (26 total taxa) that were absent from the calibration set. The three taxa in Rocky Bottom Lake absent from the calibration set are *Tanytarsus* type *H*, *Paracladius*, and *Mesocricotopus thienemanni*; these taxa do not exceed 5% in any sample with the exception of *Tanytarsus* type *H*, which comprises 7% of the 3–3.5 cm sample. The three taxa in Moat Lake absent from the calibration set are the *Cyphomella/Harnischia/Paracladopelma* group, *Glyptotendipes*, and *Tanytarsus* type *H*; these taxa do not exceed 3% in any sample with the exception of *Tanytarsus* type *H* which comprises 11.6% of the 5.5–6.0 cm sample. Based on this measure, the surface water temperature estimates for Rocky Bottom Lake can be considered very reliable and the estimates for Moat Lake and MG-2 can be considered reliable. Sample-specific standard errors were estimated for each fossil assemblage by Monte Carlo simulation using leave-one-out cross-validation as implemented by the program WA-PLS version 1.1 (Juggins and ter Braak, 1996). A LOWESS smoother (span = 0.50) was applied to the reconstructions to highlight the main trends in surface lake water temperature. Deviations of the inferred surface water temperatures for each of the lakes from the mean chironomid temperature inferences were calculated as the difference between the inferred surface water temperature for a given sample and the average chironomid-inferred surface water temperature for the period A.D. 1895 to the year the core was collected.

INSTRUMENTAL CLIMATE DATA

The climate data for Fresno, California (the nearest station with a long [>100 year] record), was obtained from the National Climatic Data Center (NCDC) via the World Wide Web (NCDC, 2006). Surface air temperatures were converted from °F to °C, with deviations from the long-term average calculated as the difference between a given year's average summer temperature (June–August) and the average summer temperature for the period A.D. 1895–2005.

²¹⁰PB ANALYSES AND CORE CHRONOLOGIES

To develop chronological control, 12 stratigraphic samples from Moat Lake and MG-2 and 10 stratigraphic samples from

Rocky Bottom Lake were analyzed for ²¹⁰Pb content. A 1 cm sampling interval was used to constrain the chronologies for the MG-2 and Rocky Bottom Lake cores. For the Moat Lake core, the top 5 cm were sampled at 1 cm intervals, and a 2 cm sampling interval was used below this depth. Ages and sedimentation rates ($\text{g cm}^{-2} \text{yr}^{-1}$) were calculated using the constant rate of supply model (CRS), which is most robust in situations where the sediment accumulation rate changes with depth. The ²¹⁰Pb analysis was carried out by MyCore Scientific Incorporated (Dunrobin, Ontario, Canada).

Results

LAKE SEDIMENT CHARACTERISTICS

The cores recovered from MG-2 and Moat Lake were similar in appearance, consisting of very flocculent surficial sediment in the upper 5 cm, and increasingly denser gyttja deeper in the cores. The core recovered from Rocky Bottom Lake was much shorter and interbedded with two distinct sand layers at 2–3 cm and 5–6 cm depth. Results of the LOI analysis for each lake are presented in their respective chironomid percentage diagram (Figs. 3a–3c). The percentage organic matter, as estimated by LOI analysis, is similar for the three lakes, varying between 5 and 25%; however, shifts in the LOI profiles were not synchronous between lakes.

²¹⁰PB ANALYSES AND CORE CHRONOLOGIES

Because of its relatively short half-life of 22.3 years, ²¹⁰Pb dating is only reliable back to ca. A.D. 1850 (Appleby, 2001). Thus, uninterpolated dating on lake sediments terminated at 6 cm in Moat Lake, 7 cm in Rocky Bottom Lake, and 10 cm in MG-2. Sedimentation rates in MG-2 were relatively uniform, apart from a brief episode of rapid accumulation in the late 1890s (Fig. 2a). The mean sediment accumulation rate for MG-2 was $0.006 \text{ g cm}^{-2} \text{yr}^{-1}$. Sediment accumulation in Moat Lake was relatively uniform through the chronology, with a mean sedimentation rate of $0.004 \text{ g cm}^{-2} \text{yr}^{-1}$ (Fig. 2b). Sedimentation rates in Rocky Bottom Lake were more variable, with two brief episodes of rapid accumulation during the 1940s and early 1980s evidenced by sand layers and sedimentation rates of 0.037 and 0.033 $\text{g cm}^{-2} \text{yr}^{-1}$, respectively (Fig. 2c). Sediment accumulation rates for the remainder of the Rocky Bottom Lake chronology averaged $0.012 \text{ g cm}^{-2} \text{yr}^{-1}$. Sediment accumulation within these three lakes is consistent with sedimentation rates documented in previous studies of high-elevation, oligotrophic Sierra Nevada lakes (Shirahata et al., 1980; Holmes et al., 1989). The duration of the well-constrained radiometric chronologies vary for each lake: MG-2 (A.D. 1856–1998), Rocky Bottom Lake (A.D. 1906–2005), and Moat Lake (A.D. 1844–2004).

CHIRONOMID PERCENTAGE DIAGRAMS

The chironomid percentage diagrams for MG-2, Rocky Bottom Lake, and Moat Lake are presented in Figures 3a–3c.

MG-2

The chironomid community in the MG-2 core is dominated by relatively warm-water taxa such as *Dicrortendipes*, *Psectrocladius semicirculatus/sordidellus*, and *Chironomus*. Cold-water midges such as *Heterotrissocladius marcidus* type and *Cricotopus/Orthocladius* appear in contiguous samples, albeit at low levels, beginning ca. A.D. 1880. Also of note is the appearance of the

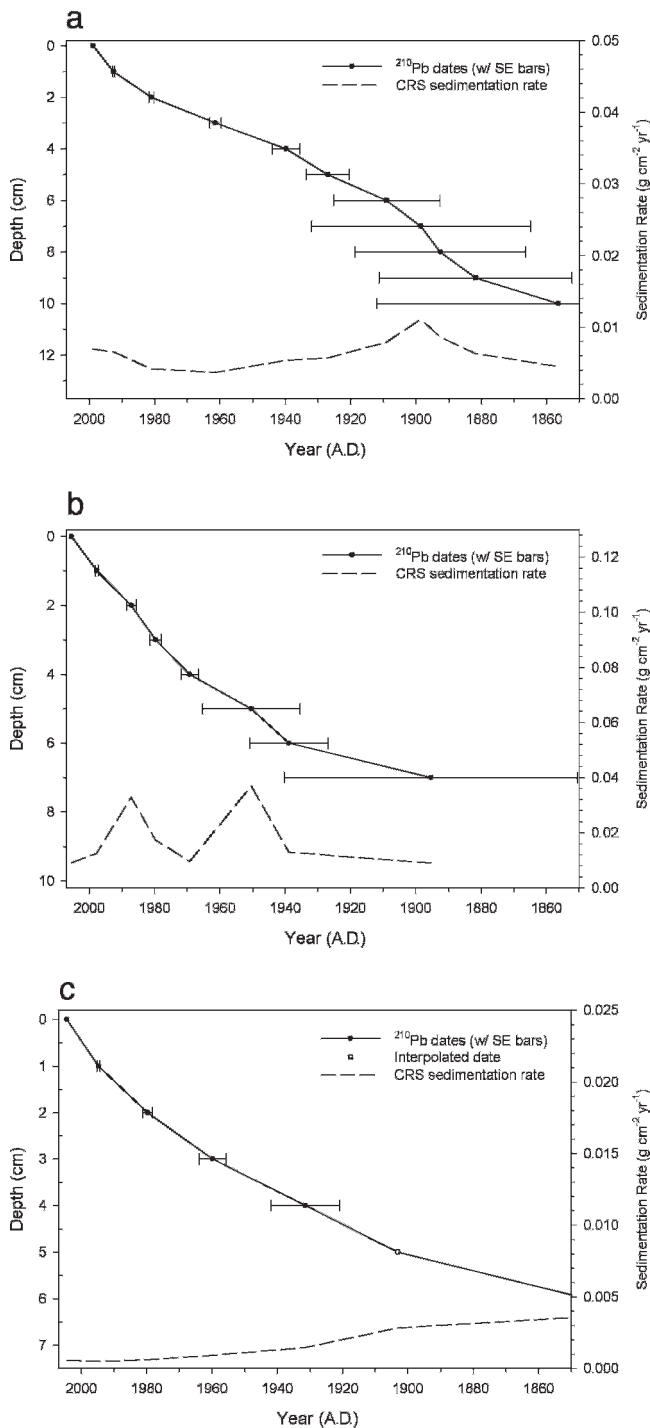


FIGURE 2. (a, b, c) Radiometric chronologies of MG-2, Rocky Bottom and Moat Lake, depicting the constant rate of supply (CRS) model dates and sedimentation rates. SE = standard error.

thermophilous taxon *Microtendipes* at ca. A.D. 1890. Cold-water taxa such as *H. marcidus* type, *Micropsectra*, and *Hydrobaenus/Oliveridia* are extirpated by ca. A.D. 1990. The uppermost sample is dominated by eurythermic taxa *Tanytarsus* (indeterminable),

which nearly doubles its relative abundance, and warm-water taxa such as *Microtendipes*, *Dicrotendipes*, and *Chironomus*.

Rocky Bottom Lake

The lowermost portion of the midge stratigraphy at Rocky Bottom Lake is dominated by a cold-water taxon, *Corynocera oliveri* type, which comprises 30–40% of the midge assemblage. However, the midge community present in the basal portion of the core consists of a mixed assemblage with thermophilous taxa such as *Dicrotendipes*, *Corynocera* nr. *ambigua*, *Psectrocladius semicirculatus/sordidellus*, *Paratanytarsus*, and *Chironomus* present at high levels. At ca. A.D. 1945 a shift in the chironomid community occurs with an increase in many cold-water taxa including *Hydrobaenus/Oliveridia*, *Cricotopus/Orthocladus*, and *Corynoneura/Thienemanniella*, and a decrease in *C. oliveri* type. Also present at high levels are *Chironomus*, *Paratanytarsus*, and *Psectrocladius semicirculatus/sordidellus*. The uppermost zone is characterized by a decrease in the cold-water taxa, *Corynocera oliveri* type, *Hydrobaenus/Oliveridia*, and *Cricotopus/Orthocladus*, and an increase in the warm taxa *Paratanytarsus* and *Dicrotendipes*.

Moat Lake

The lowermost portion of the Moat Lake core is dominated by *C. oliveri* type, *H. marcidus* type, *C. nr. ambigua*, and *Procladius*. The next zone, which likely extends from the early 1800s to 1980, is characterized by a decrease in many cold-water taxa including *C. oliveri* type and *Heterotrissocladus marcidus* type, an increase in temperature taxa such as *Psectrocladius semicirculatus/sordidellus* and *Chironomus*, and the appearance of thermophilous taxa such as *Dicrotendipes*. The uppermost zone is characterized by a dramatic reduction in *C. oliveri* type, the extirpation of any remaining cold-water taxa, and large increase in *Dicrotendipes* and *C. nr. ambigua*.

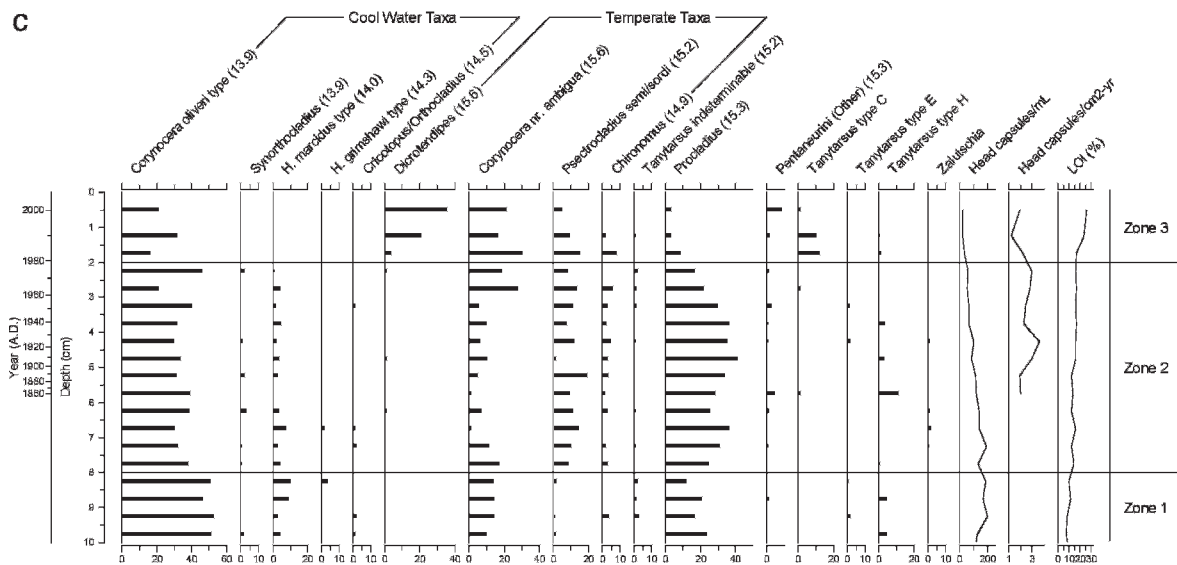
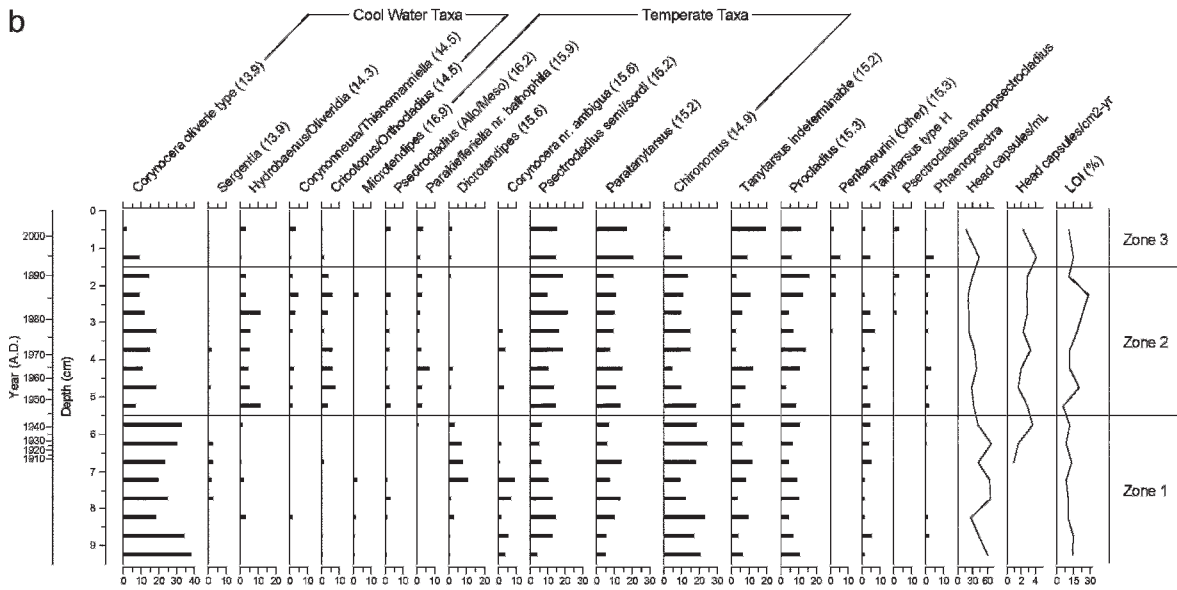
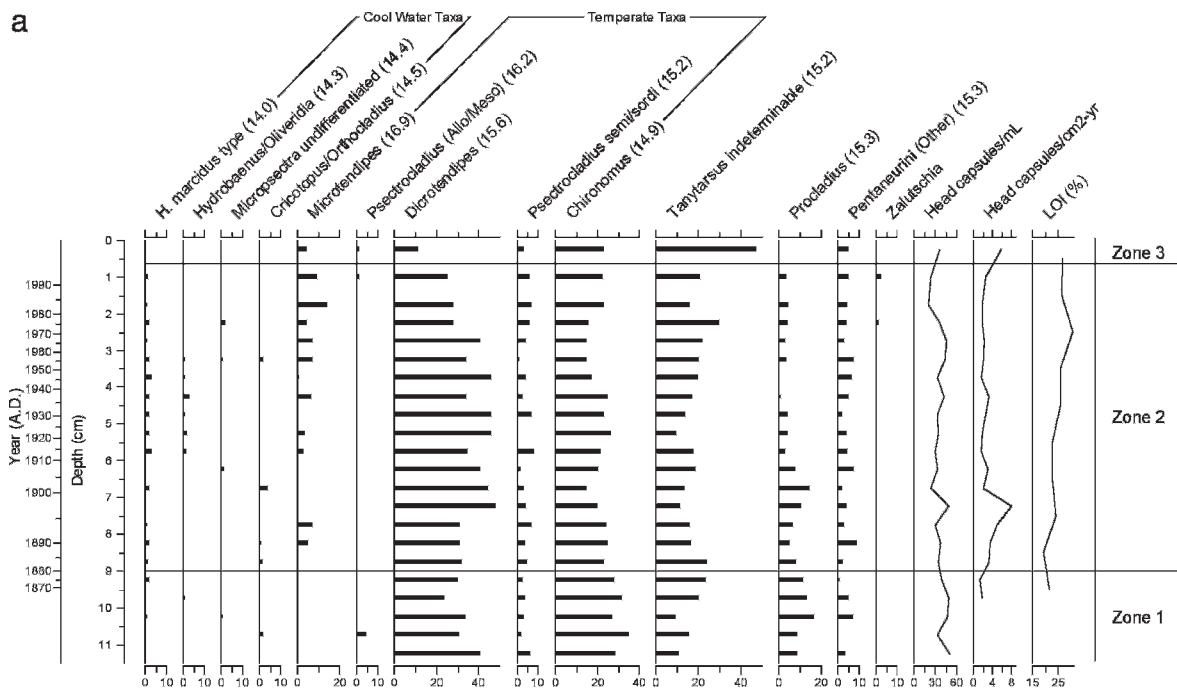
COMMUNITY COMPOSITIONAL CHANGE

An ordination diagram, based on DCA, depicting the trajectories of recent midge community change for the lakes, is presented in Figure 4. DCA indicates that all three lakes have experienced a generally unidirectional pattern of species composition turnover during the 20th century, with Moat Lake and Rocky Bottom Lake experiencing markedly increased rates of turnover in the post-1980 period. The more muted change in MG-2 may be due, in part, to the lower temporal resolution of the subfossil analysis.

CHIRONOMID-BASED TEMPERATURE RECONSTRUCTION

The chironomid-based temperature inferences for MG-2, Moat, and Rocky Bottom Lakes are depicted in Figure 5. The three lakes show similar trends in surface water temperature during the 20th century, although the absolute values differ. The sample specific error estimates of the water temperature inferences varied between 1.2 and 1.4°C for the lakes (see Table 3). The chironomid-inferred surface water temperature for MG-2 ranges

FIGURE 3. (a, b, c) Chironomid stratigraphies for MG-2, Rocky Bottom Lake, and Moat Lake. Abbreviations for chironomid taxa: *Psectrocladius (AllolMeso)* = *Allopsectrocladius/Mesopsectrocladius*, *Psectrocladius semilsordidellus* = *Psectrocladius semicirculatus/sordidellus*. Values in parenthesis are optimum surface water temperatures for each taxon generated during transfer function development (Porinchu et al., 2002).



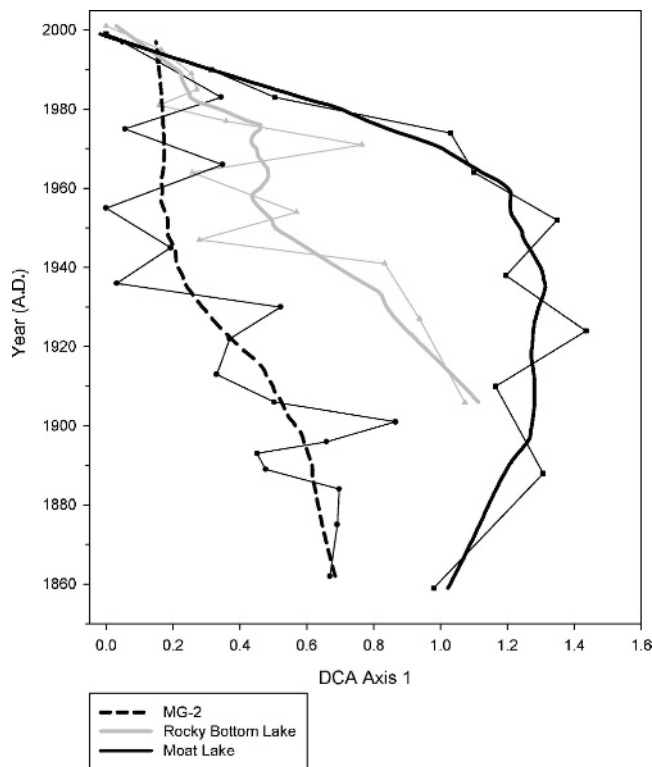


FIGURE 4. DCA Axis 1 plotted against age for MG-2, Rocky Bottom Lake, and Moat Lake (dotted lines). Heavy lines represent a LOWESS smoother (span = 0.50).

from $\sim 15.4^{\circ}\text{C}$, which occurs at A.D. 1900 and A.D. 1930, to 16.6°C , which occurs at A.D. 1983. The inferred surface water temperatures for Rocky Bottom Lake range from 14.5°C at A.D. 1906 to 16.1°C at A.D. 2001. The inferred surface water temperatures for Moat Lake range from 14.1°C at A.D. 1888 to 15.8°C at A.D. 1983. There is a decrease in the offset for the chironomid inferred surface water temperatures between Moat and Rocky Bottom Lakes following ca. A.D. 1970, with the inferred surface water temperatures for all three lakes converging on their highest values post-1980. The average surface water temperature during the well-constrained interval for MG-2 (A.D. 1860–1998), Rocky Bottom (A.D. 1906–2005), and Moat (A.D. 1860–2004) Lakes were 15.9 , 15.2 , and 14.7°C , respectively. The post-1980 average inferred surface water temperature for MG-2, Rocky Bottom, and Moat Lakes was 16.5 , 15.6 , and 15.6°C , respectively. A LOWESS smoother (span = 0.50) was applied to the reconstructions to highlight the main trends in surface water temperature over the interval for which we had a well-constrained chronology (Fig. 5). The smoothed data indicates that surface water temperatures were lower than the long-term average prior to A.D. 1950 for MG-2, A.D. 1980 for Rocky Bottom Lake, and A.D. 1970 for Moat Lake. All three lakes experienced warming in the latter half of the 20th century, with

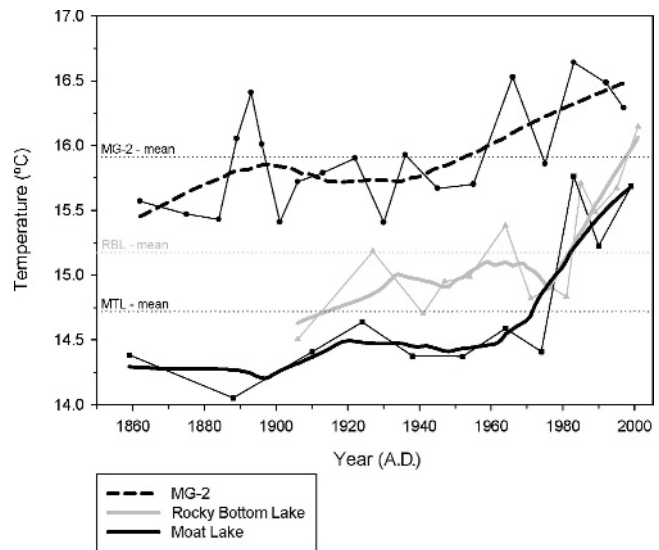


FIGURE 5. Chironomid-based surface water temperature reconstruction for MG-2, Rocky Bottom Lake, and Moat Lake spanning the interval for which each lake has a well-constrained radiometric chronology. Points represent chironomid-based surface water temperature inferences. The dotted line is average chironomid inferred surface water temperature for the well-constrained radiometric interval for each lake. The heavy line represents a LOWESS smoother (span = 0.50).

Rocky Bottom and Moat Lakes experiencing dramatic warming post-A.D. 1970. Regression analysis of the chironomid-based temperature estimates indicates that all three lakes experienced a statistically significant warming trend during the 20th century ($p \leq 0.05$), with the rate of warming varying between $1.3^{\circ}\text{C}/100$ years for Moat Lake and $0.7^{\circ}\text{C}/100$ years for MG-2. It is notable that the rate of warming for all three lakes increased dramatically post-1970, with Rocky Bottom and Moat Lakes warming at a rate of $4.5^{\circ}\text{C}/100$ years and $4.2^{\circ}\text{C}/100$ years, respectively, and MG-2 warming at a rate of $1.7^{\circ}\text{C}/100$ years. A plot of the deviations of surface water temperature from the average chironomid-inferred surface water temperatures for all three lakes for the period A.D. 1895–2005 is depicted in Figure 6. As well, deviations of summer air temperature data from Fresno, California, are shown in Figure 6. This diagram illustrates that the average surface water temperatures for the early to mid-20th century were characterized by an extended period of below-average temperature and that the last two decades have seen a dramatic warming in the surface water temperatures of MG-2, Rocky Bottom, and Moat Lakes. For Fresno, the period between A.D. 1895 and 1910 was typified by higher than average air temperatures. In general, the interval between A.D. 1910 and 1980 was characterized by below-average temperatures, although multi-year periods of warming did occur through this interval, e.g., A.D. 1959–1961. Following A.D. 1980, above average air temperatures were observed at Fresno. In

TABLE 3

Measured surface water temperature (SWT), air temperature, and model results for MG-2, Moat Lake, and Rocky Bottom Lake.

Variable	MG-2	Moat Lake	Rocky Bottom Lake
Measured SWT ($^{\circ}\text{C}$)	13.0	11.5	14.0
Average summer SWT (July–August) ($^{\circ}\text{C}$)	NA	14.6	16.4
Average summer air temperature (July–August) ($^{\circ}\text{C}$)	NA	12.4	14.6
Chironomid inferred temperature ($^{\circ}\text{C}$)	16.3	12.4	15.4
Sample specific error ($^{\circ}\text{C}$)	1.2–1.3	1.3–1.4	1.2–1.3

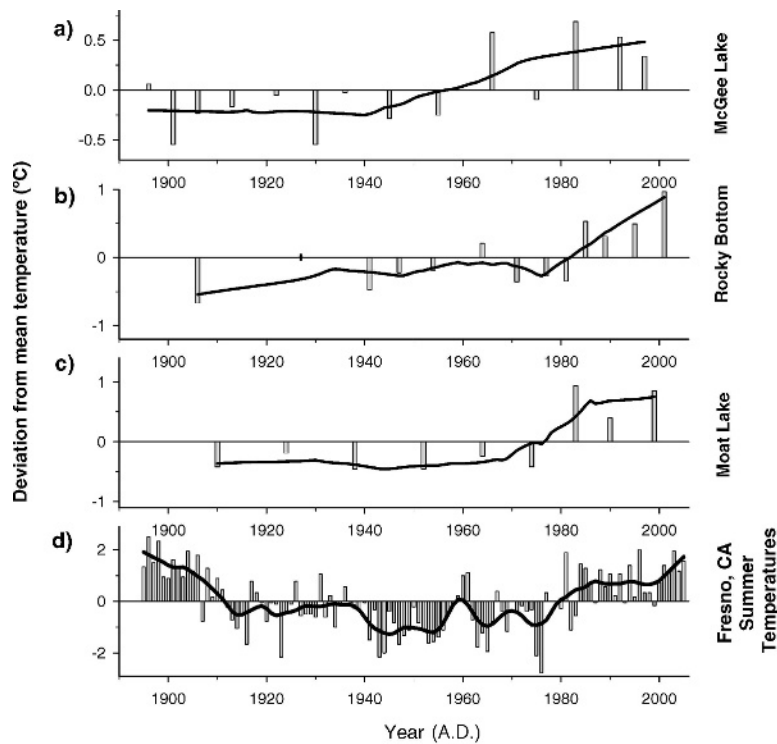


FIGURE 6. (a, b, c) Deviations of the chironomid-based surface water temperature from the average surface water temperature from A.D. 1895 to 2005. (d) Deviations of air temperature from long-term average air temperature over the period A.D. 1895–2005 for Fresno, California (NCDC, 2006).

general, the fidelity of the reconstructed deviations in lake water temperature at MG-2, Rocky Bottom, and Moat Lakes to the observed deviations in air temperature in Fresno is strong, both in terms of general long-term trends and at the decadal to subdecadal time scale.

Discussion

Over the next century, California's climate is predicted to warm dramatically. Recent modeling efforts indicate that California will experience an increase in summer temperature of 1.2–3.1°C by the mid-21st century and 2.2–8.3°C by the end of the 21st century (Hayhoe et al., 2004). This warming is expected to heavily impact subalpine and alpine aquatic ecosystems through alterations in physico-chemical conditions, such as temperature and water column stratification, duration of ice cover and growing season, hydrology, and nutrient cycling (Battarbee et al., 2002; Beniston, 2005). In addition, warming is expected to stress cold-water zooplankton species, influence life-cycle characteristics, and likely enable zooplankton from warmer low-elevation, montane lakes to invade and alter ecosystem structure in subalpine lakes (Holzapfel and Vinebrooke, 2005). The results from this study suggest that increasing summer temperatures have already begun to alter the composition of aquatic communities in the Sierra Nevada. Subalpine midge communities have experienced substantial compositional turnover during the 20th century, with the most dramatic compositional changes occurring post-1970.

Subfossil midge analysis has been used to reconstruct late Pleistocene climate fluctuations for many regions in North America and Europe with great success (Levesque et al., 1997; Lotter et al., 1999; Brooks and Birks, 2001; Porinchu et al., 2003; Heiri and Lotter, 2005; Velle et al., 2005). Increasingly, attention has been focused on determining whether chironomids can resolve the muted trends that occur during Holocene climate change. Compositional changes in Holocene chironomid fauna reflect high and low frequency temperature variations, and application of regional transfer functions have been used to provide quantitative

reconstructions of such variations (e.g., Seppä et al., 2002; Rosén et al., 2003; Larocque and Hall, 2004; Rosenberg et al., 2004; Heiri and Lotter, 2005; Solovieva et al., 2005). Additionally, work by Larocque and Hall (2003) revealed that 20th century variations in midge community composition closely track changes in mean July air temperature in northern Sweden. A high resolution midge-based study has also demonstrated that Russian arctic lakes had warmed 0.7°C during the 20th century (Solovieva et al., 2005). These studies demonstrate that midges are sufficiently sensitive to detect the subtle temperature changes that have occurred during the Holocene and can be used to provide quantitative reconstructions of these variations, especially when these midge-based paleotemperature reconstructions incorporate other proxy sources of paleoenvironmental information (Birks et al., 2000; Batterbee et al., 2002; Smol et al., 2005).

Midges track changes in temperature due to the sensitivity of the larval, pupal, and adult life-cycle stages to water and/or air temperature. Water temperature directly influences the rate of egg and larval development and affects the timing of eclosion and emergence, thereby affecting ecological functioning (refer to Porinchu and MacDonald, 2003) and response of taxa (see Porinchu and MacDonald, 2003, for references). However, temperature can also indirectly influence midge communities. Higher water temperatures can result in increased lake productivity, changes in food quality and quantity, and decreased hypolimnetic oxygen concentrations; all of these factors have been implicated in influencing midge communities (Quinlan et al., 1998; Brooks et al., 2001; Brodersen et al., 2004; Langdon et al., 2006).

It is important to determine whether the changes seen in these midge stratigraphies are coincident with changing land use or nutrient loading via atmospheric deposition of nitrogen. There has been no logging activity within the catchments of these lakes; MG-2 is located within Kings Canyon National Park and is protected from logging, and Moat and Rocky Bottom Lakes are situated in areas of high relief that are not suitable for logging. Although Wolfe et al. (2002) determined that changes in the algal productivity of lakes in the Colorado Front Range could be

attributed to nutrient enrichment resulting from anthropogenic N emission, this study cannot definitely eliminate nutrient enrichment as a factor influencing 20th century midge community development at these sites. However, previous work relating the modern distribution of chironomids in the Sierra Nevada to various limnological variables did not identify any measures of nutrient availability or oxygen concentration that could account for a significant amount of variance in midge distribution, and the estimates of organic content of the lake sediment (see Figs. 3a and 3b) indicate that LOI for two of the three lakes (MG-2 and Rocky Bottom) either decreased or remained relatively constant post-1980. It appears that climate change, specifically increases in air temperature, is responsible for the shifts that have occurred in the midge communities during the 20th century.

It is difficult to assess the statistical significance of the chironomid-based temperature reconstructions due to temporal autocorrelation; as a result, we have not reported any p-values or confidence intervals for the temperature profiles. Nevertheless, the trajectories of the faunal assemblages, the similarities of the respective temperature profiles for each of the lakes, and the striking correspondence between the chironomid-inferred surface water temperatures and the Fresno climate data appear to indicate a common climate forcing during the 20th century. The strength of the chironomid-based temperature inferences can be further substantiated by comparison to seasonal temperature records available from data loggers placed at Moat and Rocky Bottom Lakes. Rocky Bottom and Moat Lakes have average summer surface water temperatures of 15.5 and 13.9°C, respectively. The midge-based surface water temperature inference for Rocky Bottom Lake, 15.4°C, compares very favorably with the measured temperature. The inferred temperature for Moat Lake is 1.5°C lower than the measured temperature; the relatively high abundance of *C. oliveri* type is likely responsible for this discrepancy.

Although the resolution of the subfossil chironomid analysis is subdecadal and not as high as the yearly climate data, a comparison of the deviations of the chironomid-based surface water temperatures from MG-2, Rocky Bottom, and Moat Lakes (Fig. 6) to the air temperature data from Fresno shows striking similarities. During the 20th century, the average temperature in Fresno has increased from 16.0°C (A.D. 1901–1930 average) to 17.0°C (A.D. 1976–2005 average). The recent warming trend (A.D. 1980–2005) present in the Fresno climate data is apparent in the MG-2, Rocky Bottom, and Moat lake records. The rates of warming that occurred at these lakes post-1970 range from 0.2°C/decade at MG-2 to 0.5°C/decade at Rocky Bottom Lake; these rates fall well within the projected range of warming predicted to occur during the 21st century (Hayhoe et al., 2004). The changes evident in these subalpine lakes also correspond to a broader regional warming with widespread and regionally coherent trends toward earlier onsets of springtime snowmelt and stream flow evidenced across most of western North America (Stewart et al., 2005).

Applied historical limnology, or neo-limnology, is increasingly being used to document the impacts that recent anthropogenic disturbance has had on the structure, function, and composition of aquatic communities and improve our understanding of past environmental conditions. In order to improve our ability to forecast the future behavior and response of aquatic and terrestrial ecosystems to predicted global warming and other natural and anthropogenic perturbations, it is critical that we understand the historical development of these ecosystems (Millar and Woolfenden, 1999; Naiman and Turner, 2000). High resolution analyses of recently deposited, massive lake sediment cores recovered from subalpine lakes can be used to not only monitor the effects of climate change on aquatic ecosystems, but

to also establish “baseline” conditions against which future biotic changes can be compared.

The results from this study substantiate the use of chironomid analysis to develop high resolution reconstructions of recent temperature change in the Sierra Nevada and potentially elsewhere in the intermountain region of the western United States. This technique can be extended further into the past to reconstruct high resolution records of the thermal regimes that existed in the Sierra Nevada during the Little Ice Age and Medieval Warm Period. This will improve our understanding of past climate change, which in turn may help in interpreting historical variability (Millar and Woolfenden, 1999) and more precisely define the limits of the “natural” variability of these aquatic ecosystems (Swetnam et al., 1999).

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