Regional Climate Change Evidenced by Recent Shifts in Chironomid Community Composition in Subalpine and Alpine Lakes in the Great Basin of the United States

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Regional climate change evidenced by recent shifts in chironomid community composition in subalpine and alpine lakes in the Great Basin of the United States

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Abstract

Chironomids (nonbiting midges) are used to develop centennial length temperature reconstructions for six subalpine and alpine lakes in the central Great Basin of the United States. Faunal turnover, assessed by detrended correspondence analysis (DCA), indicate that substantial compositional change in the midge communities has occurred during the past 100 years. Although the changes in composition are site-specific, increases in *Dicrotendipes* and decreases in *Procladius* characterize the late 20th century at a majority of the sites. Notable faunal turnover in midge community composition is observed at five of the six sites beginning at approximately A.D. 1970. Application of a chironomid-based mean July air temperature inference model (r^2_{jack} = 0.55, RMSEP = 0.9 °C) to the subfossil chironomid assemblages provides site-specific quantitative reconstructions of past temperature variability for the 20th and 21st centuries. Midge-inferred temperature estimates indicate that four of the six lakes were characterized by above average air temperatures during the post–A.D. 1980 interval and below average temperatures during the early 20th century. The rate of temperature change between A.D. 1920 and A.D. 2010 for these four lakes are: Smith Lake = 0.6 °C 100 yr^{-1}; Birdeye Lake = 0.7 °C 100 yr^{-1}; Cold Lake = 1.2 °C 100 yr^{-1}; Stella Lake = 0.4 °C 100 yr^{-1}. Correspondence between fluctuations in the midge-inferred temperature and instrumental measures of mean July air temperature for Nevada Climate Division #2 is also documented. This study adds to the growing body of evidence that subalpine and alpine lakes in the Intermountain West of the United States have been and are increasingly being affected by anthropogenic climate change in the early 21st century.

Introduction

The Intermountain West of the United States, home to the fastest growing population in the United States, is increasingly affected by global climate change (Wise, 2012). Much of this region has experienced exceptional drought, among the most severe recorded in the instrumental record, during the late 20th and early 21st centuries (Cayan et al., 2010). Observed changes in regional hydroclimatology include decreased snowpack, earlier spring-melt runoff peaks, altered seasonality of precipitation, and a change in the snow-to-rainfall ratio (Knowles et al., 2006; Westerling et al., 2006; Harpold et al., 2012; Wise, 2012). In the Intermountain West, multiple studies have assessed the response of vegetation to increasing disturbances from climate change, fire, and beetle outbreaks; these studies have determined that forests in the Intermountain West are on a trajectory toward elevated mortality and will likely be more susceptible to future disturbances (Williams et al., 2010; DeRose and Long, 2012; Shriver and Minckley, 2012). In addition, recent work by Kulakowski et al. (2013) suggested that conifer-dominated forests in the western United States will experience reduced regeneration in response to compound disturbances including the direct and indirect effects of climate change. Global climate change has also been implicated in altering alpine aquatic ecosystem structure, composition, and function in western North America (Fenn et al., 2003; Wolfe et al.,

2003; Porter and Johnson, 2007; Baron et al., 2009; Hobbs et al., 2011; Saros et al., 2011).

The impact of local, regional and global drivers of climate and environmental change are recorded in the sedimentary archive preserved in lakes (Smol and Douglas, 2007; Smol, 2008). Paleolimnology focuses on extracting information preserved in lake sediment records, providing a broad time perspective on changes in aquatic ecosystem structure and composition that can help to identify the direct and indirect effects of climate change (Williamson et al., 2008; Adrian et al., 2009; Mladenov et al., 2011) and pollutant loading (Baron et al., 2000; Fenn et al., 2003; Sickman et al., 2003; Wolfe et al., 2003; Neff et al., 2008; Saros et al., 2011; Morris et al., 2013) on aquatic ecosystems. Paleolimnology provides an effective means to monitor changes in faunal distribution in mountain lakes and establish "baseline" conditions against which the effects of projected warming in these regions can be evaluated (Camarero and Catalan, 2012) and assess how the biotic and abiotic components of aquatic ecosystems have responded to anthropogenic and natural forcings. For example, increased levels of nitrogen deposition and algal productivity have been documented in alpine lakes in the Rocky Mountains and southern Utah (Wolfe et al., 2003; Morris et al., 2013). Furthermore, recent work suggests that high elevation lakes in the Intermountain West are experiencing significant amounts of species turnover because of the susceptibility of these lakes to the

direct and indirect effects of increasing water and air temperature (Holzapfel and Vinebrooke, 2005). It is important to note that the changes in biota, nutrients, and geochemical cycles that have been identified in western North America are linked to both natural and anthropogenic climate change (Karst-Riddoch et al., 2005; Parker et al., 2008). Although there are multiple drivers responsible for the recent changes observed in alpine ecosystems in this study we focus on using the remains of subfossil midges to document the influence of temperature on aquatic communities in high elevation lakes. Midges are sensitive to air and water temperature and have been successfully used to reconstruct recent and long-term patterns of climate change throughout the western United States (Porinchu et al., 2003, 2007b; Potito et al., 2006; MacDonald et al., 2008; Reinemann et al., 2009, 2011).

Chironomids, known as nonbiting midges, possess a number of characteristics that make them well-suited as a biological proxy for paleoclimate studies (Porinchu and MacDonald, 2003; Eggermont and Heiri, 2012). One, they have relatively short life cycles. Two, adult midges have the ability to disperse in search of more favorable environmental conditions and habitat. Three, they are sensitive to key environmental variables such as temperature, oxygen concentration, and lake depth. Lastly, the larval remains are abundant and well preserved in lake sediment. We are studying chironomid communities in subalpine and alpine lakes in the western United States to examine the response of midges to recent observed climate change as recorded by the instrumental record (Porinchu et al., 2007a, 2010). Assessing the degree of correspondence between compositional change and climate observations will increase our confidence in quantitative down-core mean July air temperature (MJAT) reconstructions over longer time scales (centuries to millennia) and allow us to examine how climate change has impacted high elevation aquatic ecosystems in the Great Basin during the recent past.

This paper builds on previous studies that have made use of subfossil midge analysis to document the impact of recent natural and anthropogenically induced environmental change on aquatic communities (Porinchu et al., 2007a; Larocque et al., 2009; Larocque-Tobler et al., 2009; Medeiros et al., 2012). Regionally, change in the composition of aquatic ecosystems has been documented in the Sierra Nevada (California), Snake Range (Nevada), and Uinta Mountains (Utah) (Porinchu et al., 2007a, 2010). These and other studies have demonstrated that environmental change has greatly affected subalpine, alpine, and arctic lakes in North America and Eurasia, with aquatic communities experiencing dramatic reorganization in recent decades (Smol et al., 2005; Rühland et al., 2008; Hobbs et al., 2010; Battarbee and Bennion, 2011). The goal of this study is to add to the growing body of evidence documenting the impacts of climate change on alpine and subalpine lake ecosystems in the Great Basin of the United States. This is especially important because alpine and subalpine lakes in the Great Basin are poorly monitored with limited faunal surveys and long-term instrumental climate data available.

Sediment cores from six lakes, dated using ^{210}Pb, and analyzed for sediment organic content (estimated by loss-on-ignition [LOI]) and subfossil midges to document the response of subalpine and alpine lakes in the central Great Basin to recent climate change. The results from this study are compared to existing midge stratigraphies and temperature reconstructions from sites in the Sierra Nevada, California, and the Snake Range, Nevada (Porinchu et al., 2007a, 2010). The chironomid-inferred MJAT reconstructions are also compared to instrumental records from NOAA Climate Division #2 to assess the robustness of the reconstructions.

Study Location

The study sites are located in the Great Basin of the western United States (Fig. 1). The Great Basin is characterized by horst and graben topography. The presence of alternating high mountain ranges and long narrow valleys allow for wide local variations in temperature and precipitation. The mountain ridges experience mean winter (December, January, February) and summer (June, July, August) temperatures of approximately –7 °C and 13.5 °C, respectively. The valley floors experience mean summer temperatures of 22 °C and mean winter temperatures of –1.0 °C (WRCC, 2012). Overall precipitation, which is limited in the Great Basin due to its location on the lee side of the Sierra Nevada, ranges from approximately 100 to 450 mm annually, producing a semi-arid to arid climate. Precipitation maxima vary from winter to spring over the entire Great Basin, with some areas experiencing a summer maximum due to convective storm activity (WRCC, 2012).

The six, small, glacially formed lakes incorporated in this study have a mean elevation of 2980 m a.s.l. (see Table 1 for details). Smith Lake (41.033920°N, 115.093674°W) is located in the East Humboldt range in central Nevada at an elevation of 2780 m. The lake covers a surface area of 1.75 ha. Birdeye Lake (40.915728°N, 115.159457°W) is located in the East Humboldt range in central Nevada at an elevation of 2850 m. The lake is positioned on the north side of an arête that extends west from the main divide of the range. The lake has a surface area of 0.60 ha. Cold Lake (40.714761°N, 115.301720°W) is located in the northern Ruby Mountains of central Nevada at an elevation of 2777 m. The lake, which is 0.40 ha, is situated directly below the headwall of the surrounding cirque, on the west side of the main north-south–trending divide. At the time of coring in August 2011, snow was located immediately adjacent to the lake. Stella (39.005332°N, 114.318686°W), Dead (38.935738°N, 114.274232°W), and Teresa (39.003244°N, 114.311286°W) lakes are located in the Snake Range of eastern Nevada. They are found at elevations of 3170, 2916, and 3135 m, respectively. Stella Lake is located in the source area for the Lehman Creek catchment and currently does not have an apparent inflow or outflowing stream. Dead Lake is situated on a large Quaternary Angel Lake moraine (Osborn and Bevis, 2001), and its small volume and catchment area likely result in desiccation during extended droughts (Gretchen Baker, personal communication, 2010). Teresa Lake's catchment area has the largest spatial extent of the six lakes, and the lake is supported by a spring-fed inlet stream with no surface outflow. Teresa Lake experiences large fluctuations in lake level, as observed from repeated trips to the lake between 2005 and 2012; the surface area estimation of Teresa Lake was taken in 2010 during a higher lake level. The surface area for Stella, Dead, and Teresa Lakes is 3.0, 0.10, and 0.70 ha, respectively.

Methods

FIELD

Sediment was recovered from the approximate center of each lake by a messenger-operated, modified Glew gravity corer. The cores recovered varied in diameter, with 5 cm diameter cores recovered in August 2010 and 7.5 cm diameter cores recovered in August 2011. The corer was deployed from an inflatable raft anchored in the deepest portion of the lake. All cores preserved the flocculent surface sediment, evidenced by little to no disturbance of the surface-water interface. Sediment was extruded in the field at 0.25 cm increments
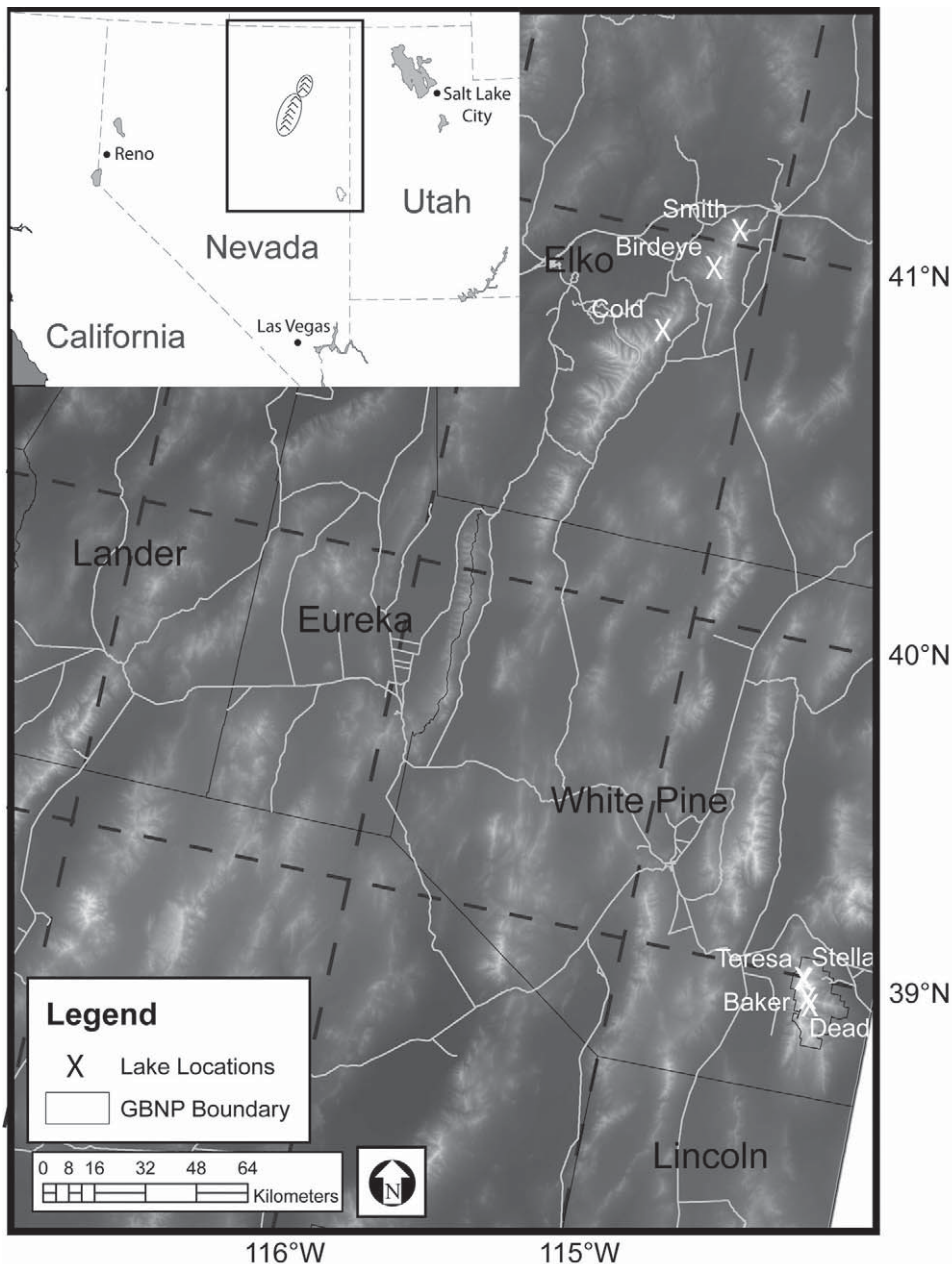
FIGURE 1. Location of study site lakes in the Great Basin of western United States (inset). The six lakes are located within the East Humboldt range, Ruby Mountains, and Great Basin National Park (boundary plotted on map). Nevada counties and major lakes are labeled for reference.

between 0 and 15 cm, 0.5 cm increments between 15 and 20 cm, and at 1.0 cm increments for depths greater than 20 cm. The sediment was stored in Whirl-paks® and kept cool and dark during transport to the Integrated Paleoenvironmental Laboratory (IPL) at the Ohio State University. At the time of collection, measurements of maximum depth, secchi depth and water temperature profiles, conductivity, dissolved oxygen (DO),and pH (using a YSI multimeter; pH sensor malfunctioned in 2010) were made (see Table 1).

LABORATORY

The lake productivity was estimated using loss-on-ignition (LOI) analysis following standard procedure, as outlined by Heiri et al. (2001). LOI analysis was conducted at 0.5 cm resolution for all cores. To develop chronological control, 12 sediment samples from each lake core were analyzed for ^{210}Pb activity using α-spectroscopy. The sampling interval used to

develop the chronologies ranged from 0.25 to 2.0 cm, with the sample interval increasing with depth. An increasing sampling interval is used to capture the exponential decay of unsupported ^{210}Pb in the lengthier sediment cores. Supported levels of ^{210}Pb were determined by examining the exponential decay of ^{210}Pb in the cores until it no longer decayed with depth. Ages and sedimentation rates (g cm^{-2} yr^{-1}) were calculated using a constant rate of supply (CRS) model (Appleby, 2001). The CRS model is appropriate in environments where sediment accumulation rates change with depth (Turner and Delorme, 1996). The ^{210}Pb analysis was carried out by MyCore Scientific Incorporated (Dunrobin, Ontario, Canada). For depths below which a reliable ^{210}Pb age could be estimated, the mean sedimentation rate for each individual lake was used to extrapolate the lake chronology to the base of the core (Mast et al., 2010). As a note, there is a large degree of uncertainty in extrapolating the chronology to the base of the cores.

TABLE 1

TABLE 1

Selected limnological and environmental measurements for the study sites.

Variables	Smith Lake	Birdeye Lake	Cold Lake	Stella Lake	Teresa Lake	Dead Lake
Year cored	2010	2010	2011	2011	2010	2010
Elevation (m)	2780	2854	3015	3175	3135	2916
Depth (m)	3.60	3.85	6.00	1.50	2.00	2.00
Lake volume (m³)	31,460	11,760	12,380	9350	8450	780
Surface area (ha)	1.8	0.6	0.4	1.9	0.7	0.1
Catchment area (ha)	63.9	15.2	40.5	17.0	107.9	5.2
Drainage ratio (catchment:lake surface)	33.6	25.3	101.3	8.9	154.1	52.0
Catchment aspect	NE	NE	N	NE	NE	E
Secchi depth (m)	Unlimited	Unlimited	5.12	Unlimited	Unlimited	Unlimited
Measured SWT (°C)	15.09	17.05	10.07	13.77	*	*

Notes: SWT—surface water temperature. *Sensor malfunction.

Chironomid analysis followed standard procedures (Walker, 2001). To obtain a consistent temporal resolution, based on the ^{210}Pb chronologies, chironomids were identified in sediment sampled from the cores at varying resolutions for the lakes that ranged from 0.5 cm to 1.0 cm. A minimum of 45 head capsules were enumerated and identified from each sample (Quinlan and Smol, 2001). Identifications were based on Wiederholm (1983), Brooks et al. (2007), and an extensive reference collection housed at the Ohio State University. For a more thorough description of the taxonomy, the reader is directed to Porinchu et al. (2007b) and Porinchu et al. (2002). The volume of wet sediment needed to achieve the minimum number of head capsules varied between 0.25 mL and 3.0 mL.

STATISTICS, MODEL DEVELOPMENT, AND APPLICATION

The relative abundance of midge taxa at each site was plotted stratigraphically using the program C2 (Juggins, 2003). Zones were identified using optimal sum of squares partitioning as implemented by the program ZONE version 1.2 (Juggins, 1992). The statistical significance of the zonation was assessed with a broken stick model using the unpublished program BSTICK (Bennett, 1996). The timing, magnitude, and rate of compositional change in taxa were assessed using detrended correspondence analysis (DCA) and correspondence analysis (CA) and implemented using the program CANOCO version 4.5 (ter Braak and Šmilauer, 2002).

The chironomid-based inference model for mean July air temperature (MJAT) was applied to the square-root transformed midge percent data for all the lakes. The chironomid-based inference model for MJAT was designed specifically for use in the Intermountain West (Porinchu et al., 2010). The chironomid-based inference model is based on 79 lakes and 54 midge taxa and makes use of a weighted averaging–partial least squares (WA-PLS) approach (ter Braak et al., 1993). The performance statistics for the two-component WA-PLS inference model, had an r^2_{jack} = 0.55 °C, root-mean-square error of prediction (RMSEP) = 0.9 °C, and a maximum bias of 1.66 °C. Further detail on the training set lakes and model performance are available in Porinchu et al. (2007b, 2010). The program C2 (Juggins, 2003) was used to develop the WA-PLS inference models and estimate sample-specific error (SSE).

Results

CORE CHRONOLOGIES

Profiles of the ^{210}Pb age to depth relationship, along with sedimentation rates, are presented in Figure 2. The depth at which supported ^{210}Pb reaches background levels varied among the lakes (Smith, 8 cm; Birdeye, 9 cm; Cold, 10 cm; Stella, 21 cm; Dead, 6.5 cm; Teresa, 5.5 cm), with the well-resolved section of each record spanning the following intervals: Smith Lake (A.D. 2010–1905), Birdeye Lake (A.D. 2010–1935), Cold Lake (A.D. 2011–1900), Stella Lake (A.D. 2011–1900), Dead Lake (A.D. 2010–1905), and Teresa Lake (A.D. 2010–1915) (Fig. 2). The sedimentation rates, within the well-constrained sections identified above, display a coefficient of variation of between 2% and 17%. Overall the relatively uniform sedimentation rates and the existence of exponential ^{210}Pb decay profiles (Fig. 2) in six of the lake cores suggest that these chronologies should be considered reliable.

LOSS-ON-IGNITION

The LOI analysis indicates that all six lakes exhibited similar trends in the percent loss-on-ignition (Fig. 3). The study lakes are characterized by relatively small catchment areas, with the exception of Teresa Lake (Table 1). Stella Lake was the most productive lake with LOI values ranging between 30% and 55%, far exceeding the LOI values of the other study sites. The drainage ratio (catchment area: lake surface area) indicates a large difference between Stella Lake (5.7) and the remainder of the lakes (25–154). The LOI values for the sediment in the lowest portion of the cores from Cold, Dead, Teresa, Birdeye, and Smith Lakes vary between 10% and 20%, increasing to 20% to 40% in the upper sediment. The LOI profiles indicate that Cold and Smith Lakes were the least productive of all the lakes, with LOI values fluctuating around 10% through much of the 20th century.

MIDGE PERCENTAGE DIAGRAMS

Fluctuations in midge community composition are presented in Figure 4, parts a–f.
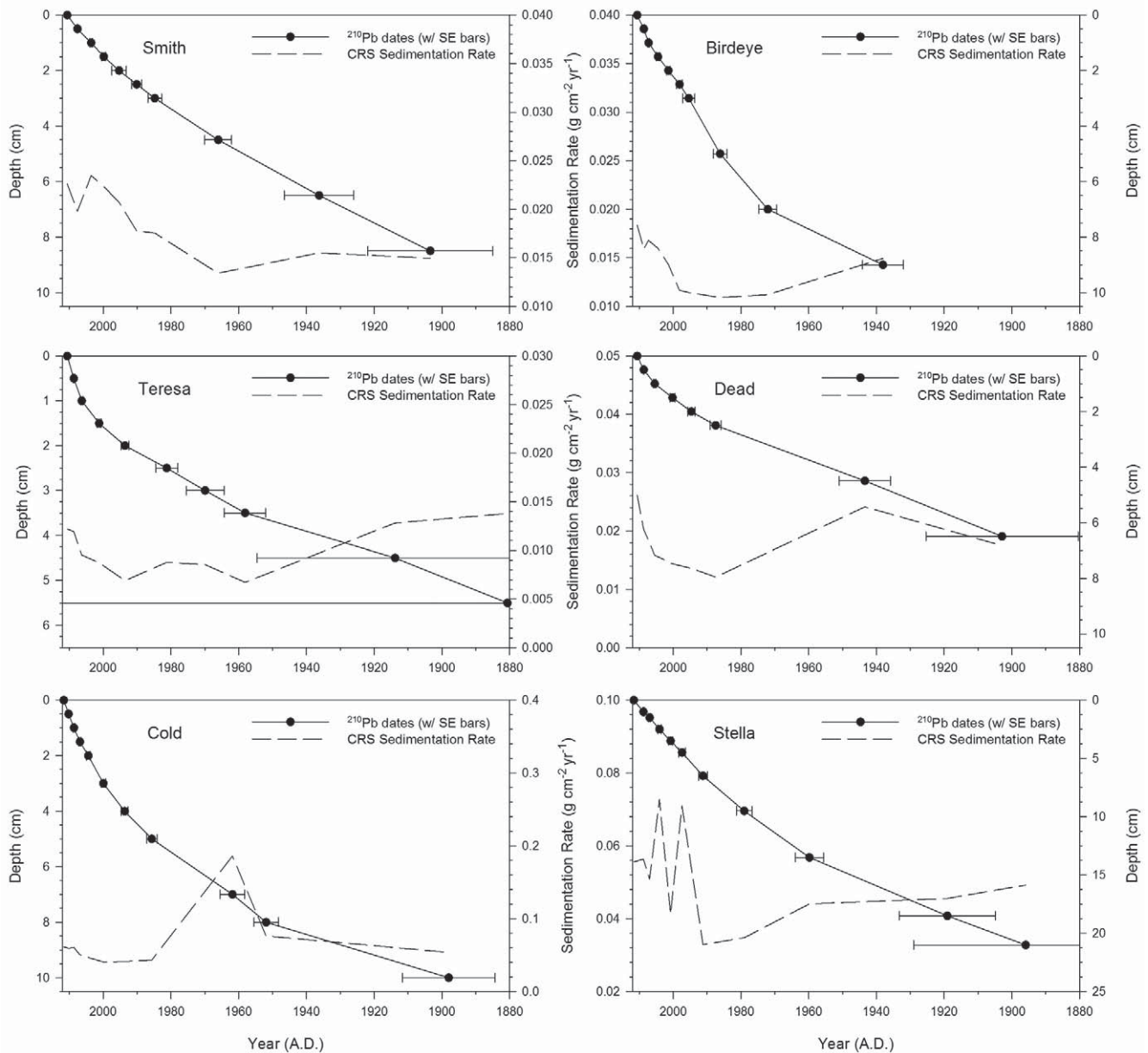
FIGURE 2. Radiometric chronologies for Smith, Birdeye, Teresa, Dead, Cold, and Stella Lakes depicting the constant rate of supply model and sedimentation rates. Note the different vertical axes for depth and sedimentation rates.

Smith Lake

A total of 15 midge taxa were identified in Smith Lake (SMT), clustered in three zones: SMT-I spans A.D. 1900 to A.D. 1959; SMT-II spans A.D. 1959 to A.D. 1990; and SMT-III spans A.D. 1990 to the present. *Procladius* and *Chironomus* dominate SMT-I, with this zone also characterized by a slight decrease in *Psectrocladius semicirculatus/sordidellus* and *Tanytarsus* indeterminable. SMT-II is a transition zone with *Tanytarsus* indeterminable rising to a relative abundance of approximately 40% and *Dicrotendipes* appearing and increasing to a relative abundance of approximately 10% toward the top of this zone. Taxa that dominate the basal part of the core (*Chironomus* and *P. semicirculatus/sordidellus*) decrease to below 5% in SMT-II. In SMT-III, many taxa present in the basal sediment are nearly extirpated and replaced with thermophilous taxa such

as *Cladopelma* and *Dicrotendipes*, with the latter continuing to increase through SMT-III and reaching a relative abundance of over 40% in A.D. 2000. Head capsule concentrations vary by zone in Smith Lake: SMT-I has the lowest values of ~100 mL^{-1}; SMT-II has the highest values reaching near 280 head capsules mL^{-1}; and SMT-III features slightly lower values of ~160 head capsules mL^{-1}. Taxon richness for Smith Lake varies between 7.0 and 12.0 with a mean value of 9.5, with the SMT-II exhibiting the highest taxonomic richness.

Birdeye Lake

Birdeye Lake (BDY) contains a total of 12 midge taxa assembled into two zones: BDY-I (A.D. 1940–1970); and BDY-II (A.D. 1970–2010). The principal midge taxon in BDY-I is
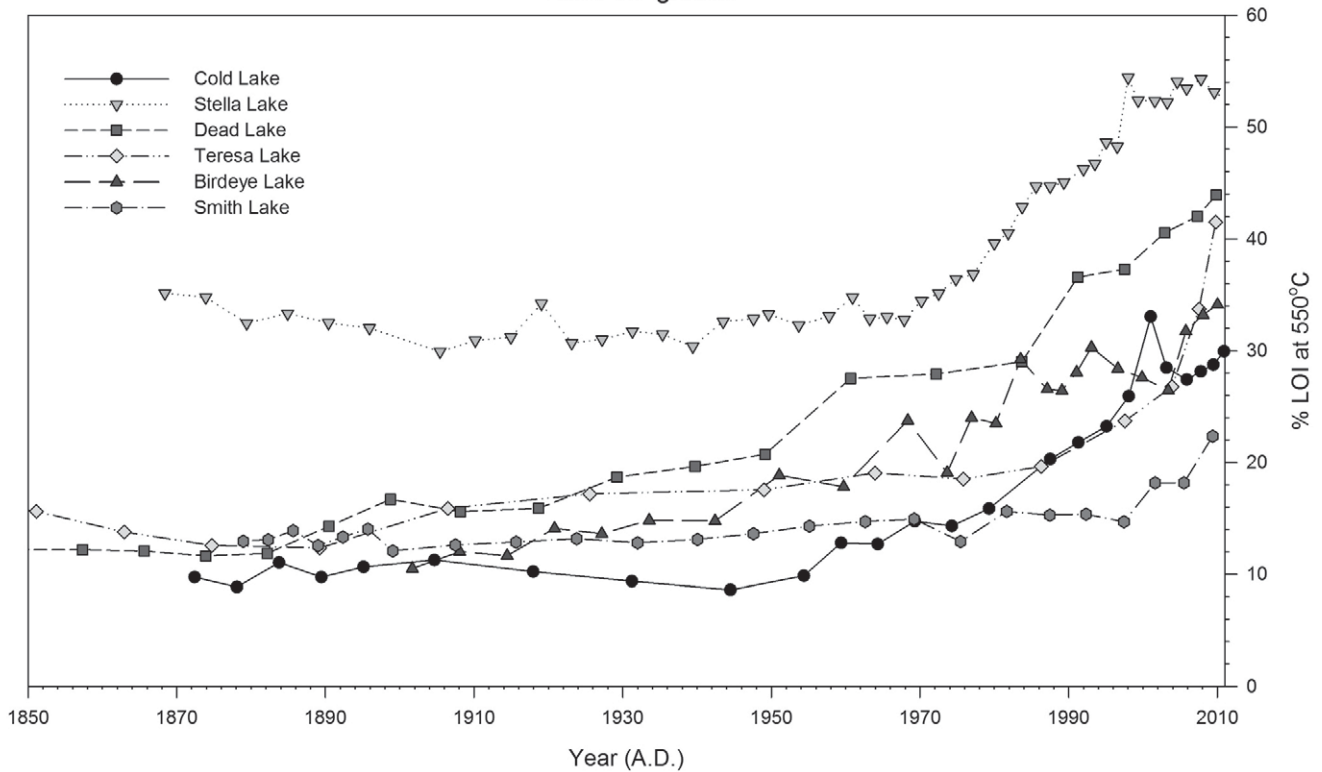
FIGURE 3. Loss-on-ignition (%) conducted at 550 °C from Cold (black circle), Stella (gray downward triangle), Dead (gray square), Teresa (gray diamond), Birdeye (gray upward triangle), and Smith (light gray circle) Lakes graphed with respect to time.

Cladotanytarsus mancus-group, comprising approximately 40% of the samples in this zone. The relative abundance of *Procladius* remains fairly consistent in Birdeye Lake, fluctuating around 10% through both zones. The major shift in midge composition between BDY-I and BDY-II involves *C. mancus*-group and *Tanytarsus* type-G. The increased abundance of *Tanytarsus* indeterminable and *Dicrotendipes* in BDY-II relative to BDY-I is another distinguishing characteristic of BDY-II. Head capsule concentrations in Birdeye Lake remain fairly constant around 120 head capsules mL^{-1}, with the exception of two samples between 3 and 4 cm where head capsule concentrations increase to ~320 head capsules mL^{-1}. The taxon richness in Birdeye Lake varies from 5.0 to 12.0, with a mean value of 8.8.

Cold Lake

Cold Lake (CLD) features the greatest diversity of the lakes in this study with a total of 18 identifiable midge taxa. There are two zones demarcated by a notable shift in the midge community at A.D. 1970. The older zone, CLD-I, is characterized by a high relative abundance of *Procladius* and *Sergentia*, with the latter reaching upward of 35% of the total enumerated subfossils in this zone. CLD-I also contains low percentages of *Cricotopus/Orthocladius* and *Micropsectra.* A significant shift in community composition occurs at A.D. 1970, with *Procladius* and *Sergentia* greatly reduced in abundance. Taxa that continue to increase or appear for the first time in CLD-II include *C. mancus*-group, *Dicrotendipes*, *P. semicirculatus/sordidellus,* and *Corynoneura/Thienemanniella.*

Head capsule concentration also varies throughout the core with basal sediments containing approximately 50 head capsules mL^{-1} and a core maximum of 200 head capsules mL^{-1} at approximately 5 cm. The upper sediment is characterized by very low head capsule concentrations, most likely due to the increased pore water and flocculent surface sediment. Taxon richness for Cold Lake varies between 8.0 and 14.0, with a mean value of 10.9.

Stella Lake

Stella Lake (SL) has a total of 12 identifiable midge taxa, although the diversity is fairly low with only seven taxa reaching above 5% abundance in the core. The first zone, SL-I, encompasses the lowest portion of the core and is very similar in midge composition to SL-II, with a few exceptions. *Corynoneura/ Thienemanniella* reaches its maximum, albeit a low relative abundance, and *Tanytarsus* indeterminable also has its maximum abundance in SL-I. SL-II spans most of the core, extending from ca. A.D. 1925 to the present. SL-II is dominated by several taxa including *Tanytarsus, P. semicirculatus/sordidellus,* and *Procladius.* Head capsule concentration is fairly uniform throughout the core, averaging around 130 head capsules mL^{-1}. The taxon richness from Stella Lake varies between 6.0 and 10.0, with a mean value of 8.1.

Teresa Lake

Teresa Lake (TL) is the least diverse of all the lakes in this study with 10 identifiable taxa, and only four of these
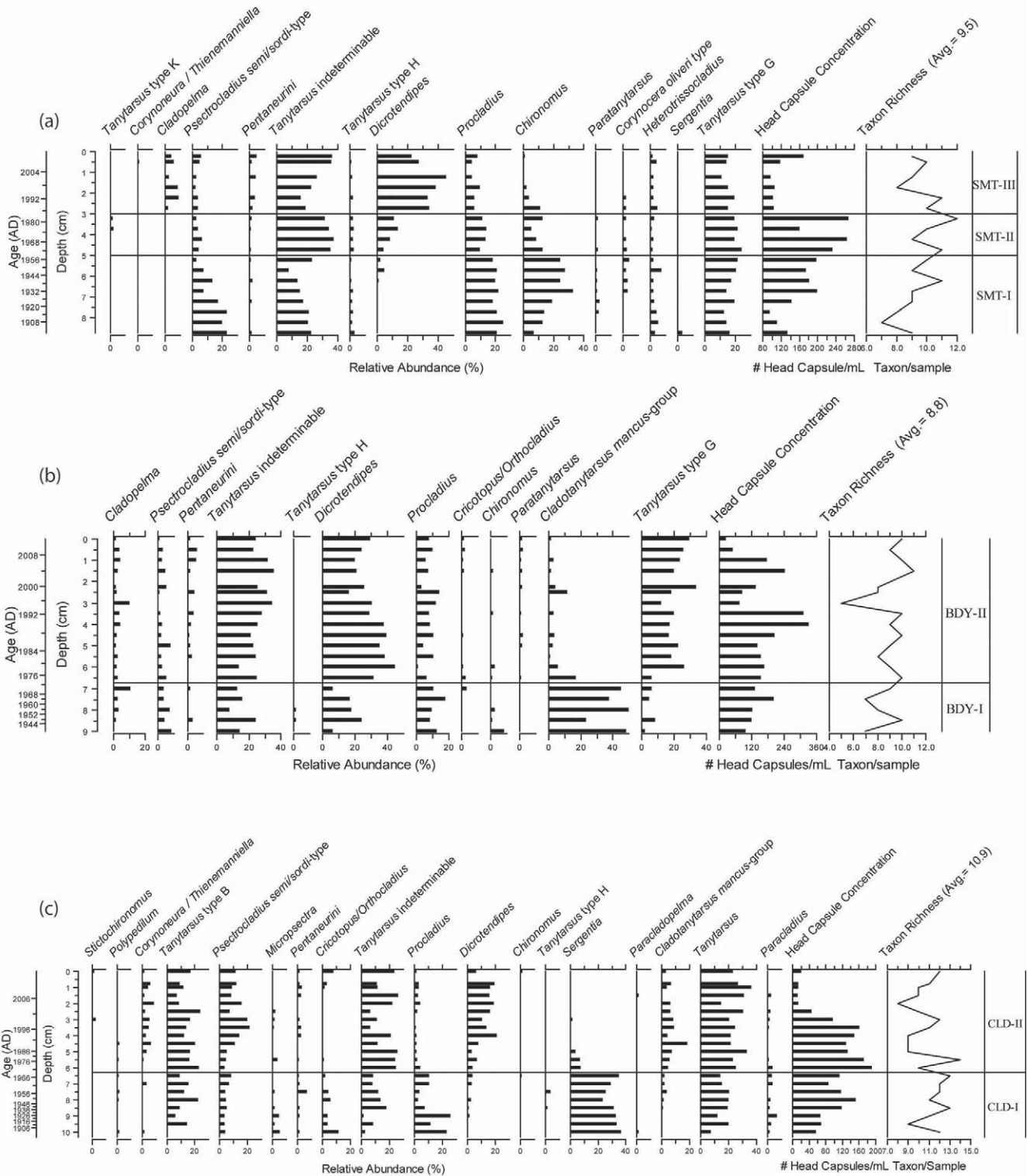
FIGURE 4. Chironomid stratigraphies for (a) Smith, (b) Birdeye, and (c) Cold Lakes. The order is based on the lakes' location from north to south (matching Fig. 7). Taxa have been arranged according to their mean July air temperature (MJAT) optima from the chironomid-based inference model, with decreasing optima temperature from left to right. Horizontal lines divide chronozones, as identified in the text. Abbreviations for chironomid taxa: *Psectrocladius semi/sordi*-type = *Psectrocladius semicirculatus/sordidellus*.

taxa have a relative abundance of >5%. Taxon richness is also lowest among the lakes, varying between 4.0 and 8.0 with a mean value of 5.9. The core is dominated by the presence of

P. semicirculatus/sordidellus, and *Chironomus,* with the former composing greater than 50% of the remains enumerated in any given sample. Variations in the abundance of *P. semicirculatus/*
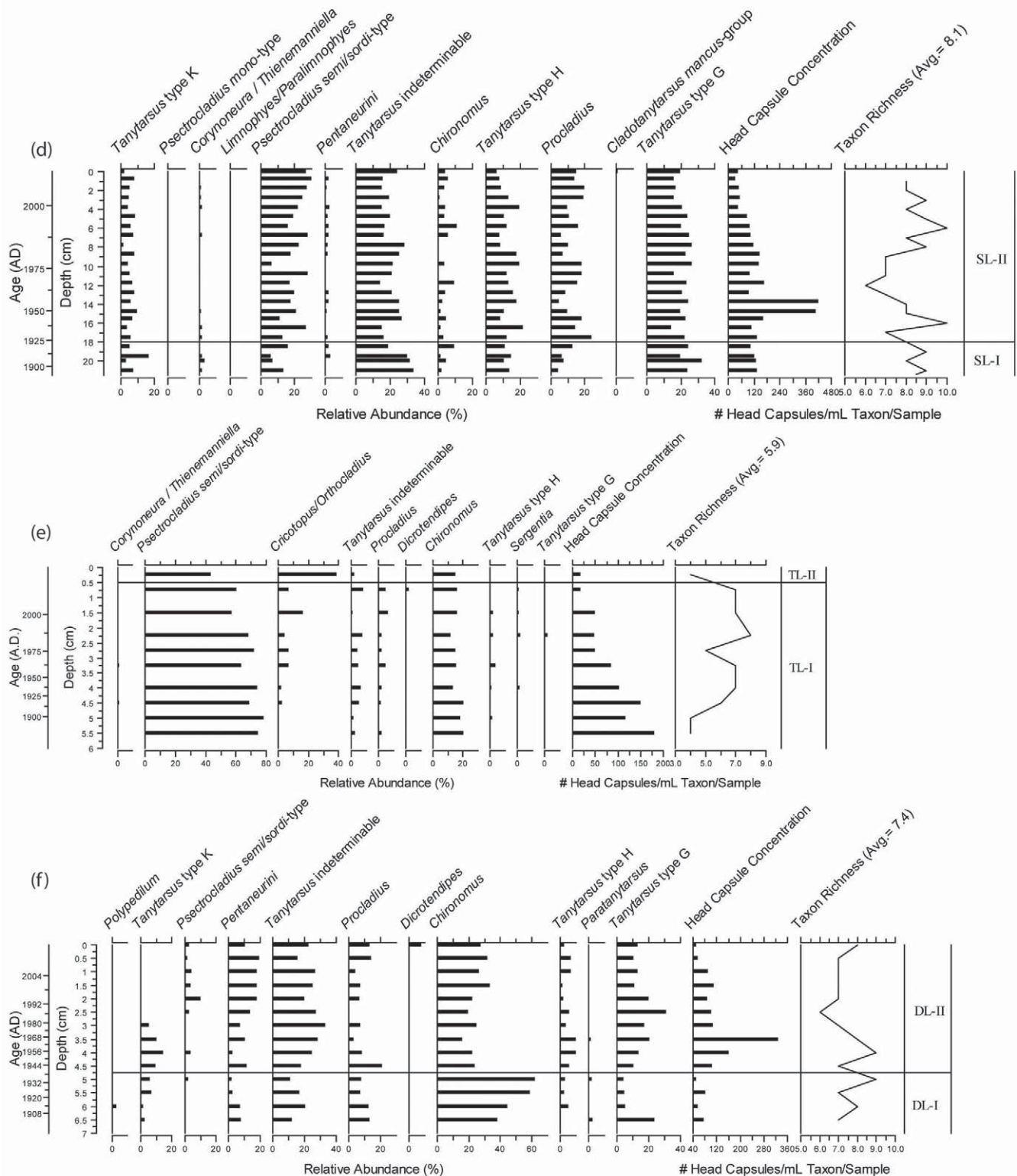
FIGURE 4 (continued). (d–f) Chironomid stratigraphies for (d) Stella, (e) Teresa, and (f) Dead Lakes.

sordidellus and *Cricotopus/Orthocladius* largely drive the zonation; a large increase in *Cricotopus/Orthocladius* in the upper sediment sample defines a statistically significant zone, TL-II. A large decrease in head capsule concentration and taxon richness is also notable in TL-II. The head capsule concentrations in Teresa Lake steadily decline from 175 head capsules mL^{-1} in the basal sediment to approximately 25 head capsules mL^{-1} in the surface sediment.

Dead Lake

Dead Lake (DL) consists of 11 identifiable midge taxa and was split into two significant zones. DL-I spans from approximately A.D. 1900 to A.D. 1940 and is dominated by a single taxon, *Chironomus,* composing 50% of the midge community. DL-II spans from A.D. 1940 to the present and is dominated by three taxa; *Pentaneurini, Tanytarsus* indeterminable, and *Tanytarsus* type-G. Near the base of DL-II, *Tanytarsus* type-K rises to ~18% relative abundance then declines quickly and is extirpated from the core. *P. semicirculatus/sordidellus*, a temperate taxon, increases in abundance through DL-II. *Pentaneurini* and *Tanytarsus* type-G, which are present at relatively low abundances in DL-I, increase in DL-II. The head capsule concentrations average 100 head capsules mL^{-1}, with only one sample exceeding the average concentration, reaching a value of 300 head capsules mL^{-1}. The taxon richness from Dead Lake varies between 6.0 and 9.0 with a mean value of 7.4.

ORDINATION ANALYSES

DCA of the subfossil midge assemblages reveals that a large amount of compositional turnover characterizes the late 20th and early 21st centuries in four of the six lakes: Smith, Dead, Cold, and Birdeye (Fig. 5). A striking feature is the unidirectional compositional change that occurs post–A.D. 1970. However, Stella and Teresa Lakes display very little species turnover throughout the 20th and 21st centuries. This is most likely the result of the low alpha diversity and the dominance of few taxa in the Stella Lake and Teresa Lake midge communities. The subfossil midge assemblages from all lakes were also plotted passively against the assemblages in the Intermountain West training set using CA to determine the degree to which the lakes are represented in the regional training set (analysis not shown). The CA bi-plot indicates that midge communities in all lakes are located within the ordination space captured by the Intermountain West calibration set.
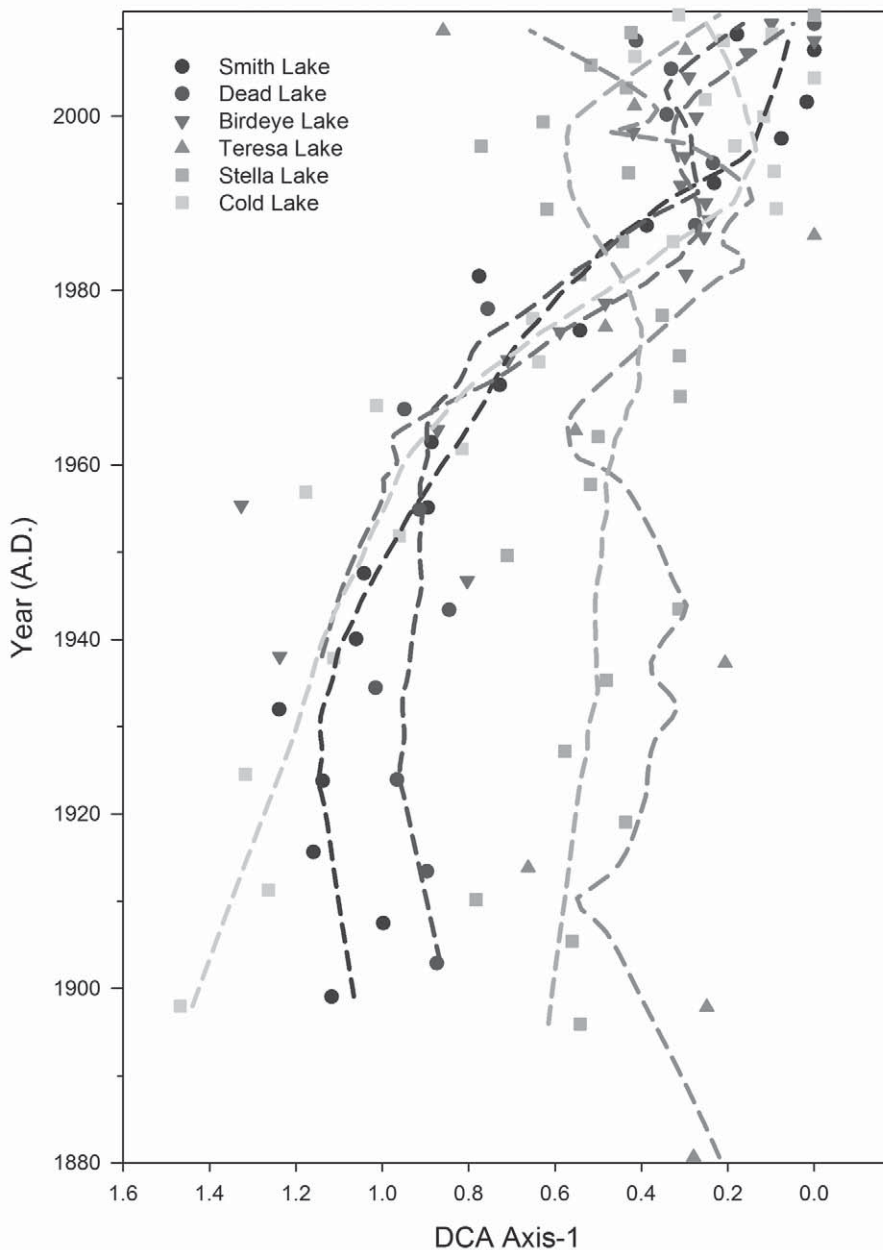

FIGURE 5. Detrended correspondence analysis (DCA) Axis 1 plotted against age for Smith, Birdeye, Teresa, Dead, Cold, and Stella Lakes. Heavy dashed lines represent a LOWESS smoother (span = 0.40).

CHIRONOMID-BASED TEMPERATURE RECONSTRUCTIONS

The taxa present are well-represented and characterized by the Intermountain West calibration set (Porinchu et al., 2010). Since all 18 of the chironomid taxa composing the chironomid stratigraphies reported in this study are present in the training set, the MJAT reconstructions can be considered reliable. Values ranging between 2 and 23 for Hill's N2 diversity index (Hill, 1973) provide added support that the quantitative chironomid-based MJAT reconstructions can be considered reliable (Birks, 1998).

The chironomid-based MJAT reconstructions are illustrated in Figure 6. The inferences for Cold Lake, Birdeye Lake, and Smith Lake show similar trends in the MJAT during the 20th century. Stella Lake also shows very similar trends to Cold, Birdeye, and Smith Lakes, however, the MJAT for Stella Lake is characterized by a large sample-to-sample variability. Teresa Lake and Dead Lake exhibit highly variable MJAT throughout the 20th century. The average chironomid-inferred MJAT and range in MJAT for the lakes are illustrated in Table 2. The SSE estimates associated with the MJAT inferences varied between 1.0 and 1.9 °C. All of the lakes experience their highest chironomid-inferred MJAT in the post–A.D. 1980 interval, with the exception of Teresa and Dead Lakes. A LOWESS (locally weighted scatterplot smoother) (span = 0.4) was applied to the reconstructions from all the lakes to highlight the main trends in MJAT over the entire record (Fig. 6). The large increase in MJAT in the post–A.D. 1980 interval in four of the lakes (Smith, Cold, Birdeye, and Stella) is the most notable feature of the reconstructions, with the expectation of the slight cooling in the uppermost samples of Stella Lake. The rate of temperature change between A.D. 1920 and A.D. 2010 for Smith Lake = 0.6 °C 100 yr^{-1}; Birdeye Lake = 0.7 °C 100 yr^{-1}; Cold Lake = 1.2 °C 100 yr^{-1}; Stella Lake = 0.4 °C 100 yr^{-1}. The rate of warming increased slightly in the post–A.D. 1970 interval, with Smith Lake = 1.5 °C 100 yr^{-1}; Birdeye Lake = 1.6 °C 100 yr^{-1}; Cold Lake = 1.4 °C 100 yr^{-1}; Stella Lake = 0.8 °C 100 yr^{-1}.

A plot of deviations of MJAT from the long-term average for all the lakes for the period A.D. 1895–2012 is depicted in Figure 7. The deviation of July air temperature from Nevada Climate Division #2 (NV#2), which encompasses the region, is also illustrated in Figure 7. For the early 20th century, the northeast portion of Nevada was characterized by average or below average chironomid-inferred temperature. Nevada Climate Division #2 with the exception of the 1930s also experiences an average or below average air temperature during the early 20th century. Starting around A.D. 1950 and extending to A.D. 1990, the lake and the climate division data exhibit similar temperature trends. Post–A.D. 1990, Cold Lake, Birdeye Lake, Smith Lake, and Nevada Climate Division #2 all experienced above average chironomid-inferred MJAT and air temperatures. The

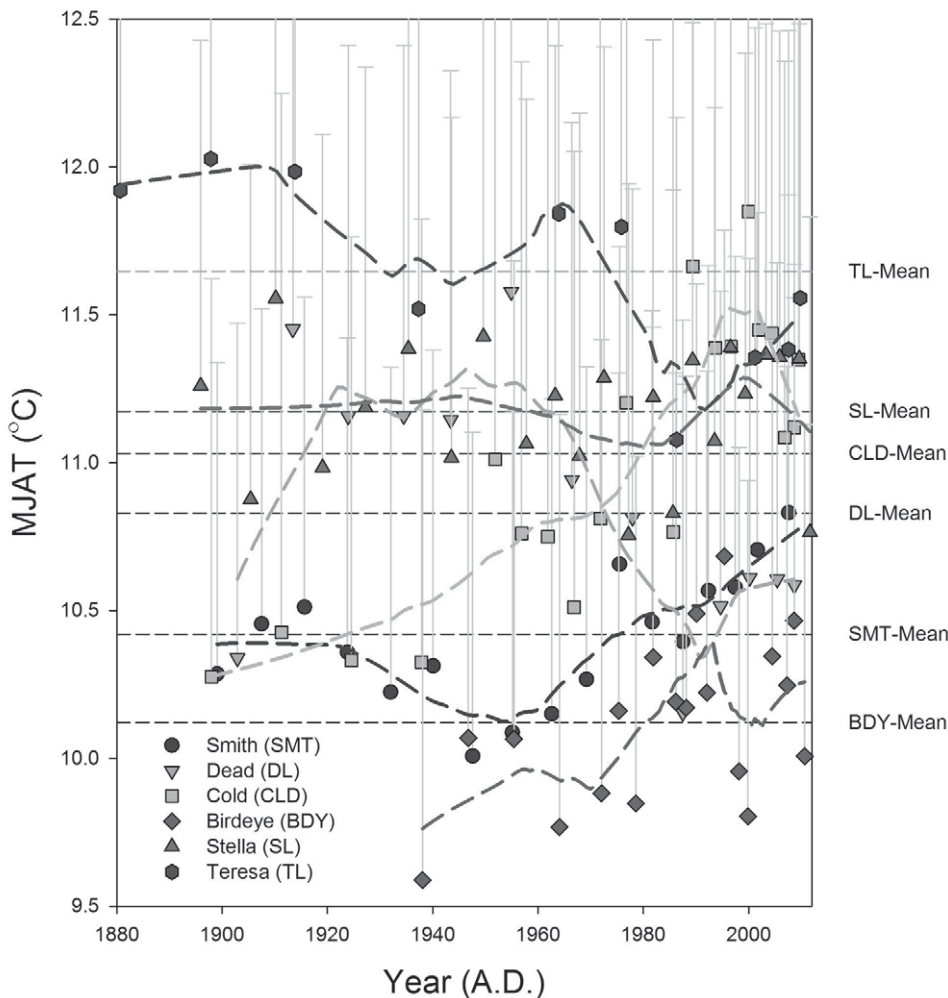FIGURE 6. **Chironomid-based mean July air temperature (MJAT) reconstruction for Smith, Birdeye, Teresa, Dead, Cold, and Stella Lakes. Points represent chironomid-based MJAT inferences, with positive sample specific error (SSE) plotted in light gray. The dotted line is the average chironomid inferred temperature for the entire interval of each lake. The heavy dashed line represents a LOWESS smoother (span = 0.40).**

TABLE 2

Average MJAT and range in chironomid-inferred MJAT for the study sites.

Variables	Smith Lake	Birdeye Lake	Cold Lake	Stella Lake	Teresa Lake	Dead Lake
Average MJAT (°C)	10.4	10.1	11.0	11.2	11.6	10.8
MJAT range (°C)	0.8	1.0	1.6	0.7	1.0	1.0

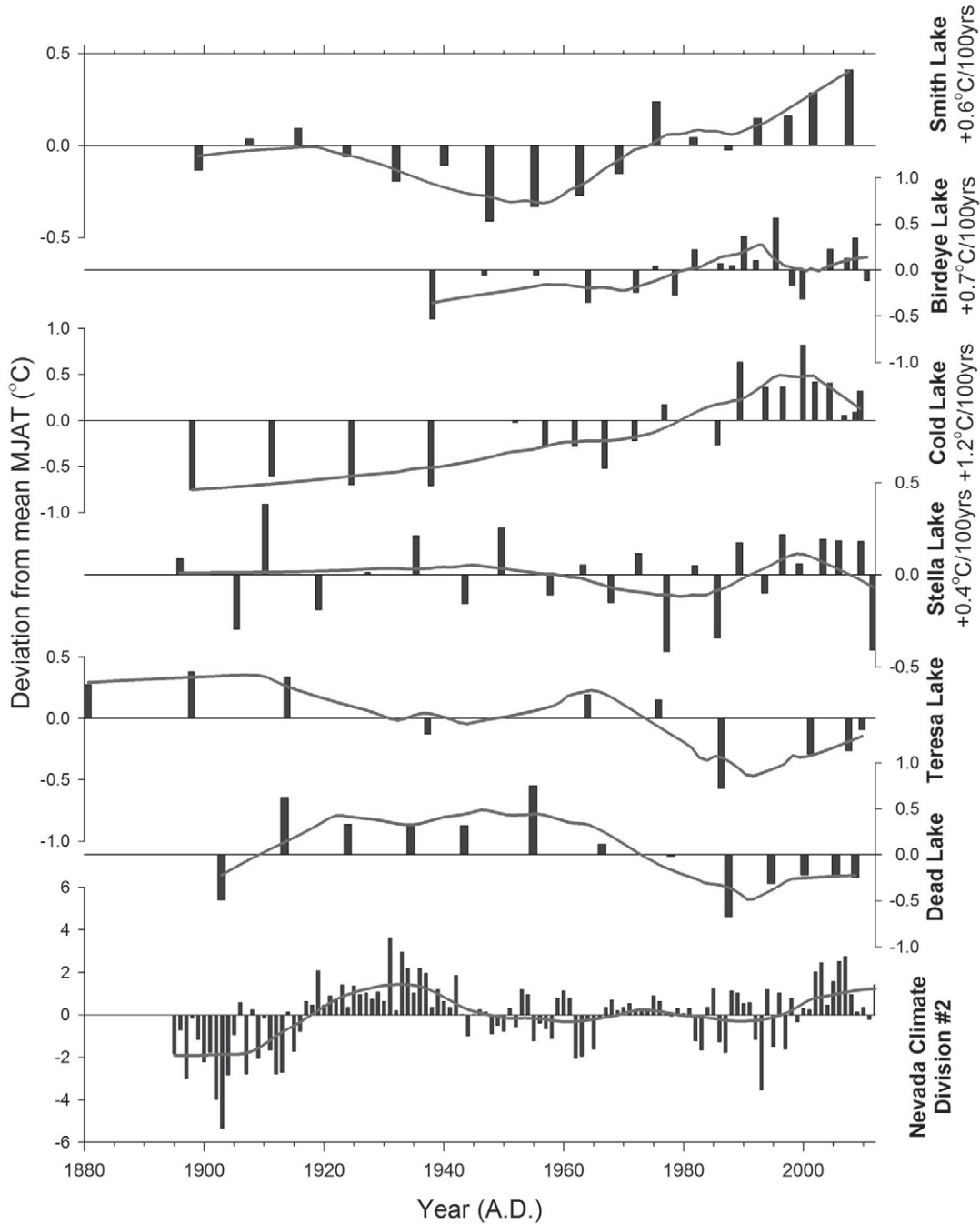Note: MJAT—mean July air temperature.

FIGURE 7. Deviations of the chironomid-based MJAT from the long-term mean of each lake ordered based on the lakes' location (Fig. 1) from north (Smith Lake) to south (Dead Lake). Deviations of air temperature over the period from AD 1895 to 2012 for Nevada Climate Division #2, which encompasses all the lake sites. Thick line represents a LOWESS smoother (span = 0.4).

long-term trends of chironomid-inferred MJAT and Nevada Climate Division #2 air temperatures display a strong correspondence throughout most of the 20th and 21st centuries.

Discussion

Chironomid-based inference models were first used to examine the large swings in temperature, on the order of 10 °C, that characterized the circum–North Atlantic region during the Pleistocene-Holocene transition (Walker et al., 1991; Cwynar and Levesque, 1995; Brooks and Birks, 2001). Reconstruction of late-glacial climate conditions using subfossil midge analysis worked extremely well, in part, because the magnitude of temperature change was much larger than the RMSEP and maximum bias of the inference models and the estimated SSE of the reconstructions. Follow-up studies have extended high-resolution subfossil midge analysis to the recent past by successfully demonstrating that midges are sensitive to the smaller magnitude changes in temperature that characterize much of the Holocene (Larocque and Hall, 2003; Solovieva et al., 2005; Porinchu et al., 2007a). These studies have demonstrated, through comparison to observational data gathered during the 20th century, that the midges are capable of resolving changes in air and surface water temperature on the order of 1–2 °C. However, it is important to note that recent work has highlighted the potential confounding influence that changing lake depth, nutrient availability, and vegetation development may have on midge community composition during the Holocene. Further assessing the ability of subfossil midge analysis to resolve the muted temperature change that characterizes the last century through comparison with instrumental climate data will refine our understanding of the sensitivity of midges to changing thermal conditions. Chironomid-based quantitative temperature reconstructions that incorporate inferences of climate and environmental change available from other proxy sources result in an improved understanding of overall environmental change during the Holocene (Battarbee et al., 2002; Smol et al., 2005; Birks and Birks, 2006; Larocque-Tobler et al., 2012).

In this study, the results of a multi-proxy examination of six lakes located along a 300 km north-south transect in the central Great Basin are presented (Figs. 6 and 7). The environmental change evidenced by the LOI data and the subfossil midge assemblages is consistent among the majority of sites, but notable site-specific differences do exist. Examination of the biotic and geochemical properties of the lake sediment records, together with knowledge of the local catchment conditions and characteristics, provides insight into the relative importance of temperature in influencing midge community composition during the 20th century. Productivity, as estimated by LOI, remains relatively constant in all lakes prior to about A.D. 1970, after which it begins to rise (Fig. 3). It is important to note that LOI can be influenced by (1) sediment composition through changes in lake productivity (autochthonous inputs) and catchment conditions (allochthonous inputs), and (2) sediment accumulation through changes in basin morphology and lake level. Therefore, LOI values reported from a single core must be interpreted with caution (Shuman, 2003). The increase in LOI in the upper sediment likely reflects the differing degrees of decomposition and sediment composition in the surface. A similar trend of increasing LOI is observed in the recently deposited sediment from lakes in arctic, alpine, and subalpine settings (Landers et al., 2008; Porinchu et al., 2009; Mast et al., 2010; Hobbs et al., 2011; Medeiros et al., 2012).

A correspondence exists between the chironomid-inferred MJAT reconstructions for Cold, Smith, Birdeye, and Stella Lakes and observed MJAT for Nevada Climate Division #2 for the late 20th century (Fig. 7). All four of these lakes experienced above average temperatures in the post–A.D. 1980 interval, with the instrumental data displaying similar elevated temperatures during the past three decades. The persistent above average chironomid-inferred temperatures that characterize the past three decades are evident in other regional records from the Great Basin (Porinchu et al., 2007a, 2010). Midge communities in the Sierra Nevada (Porinchu et al., 2007a); Snake Range (Porinchu et al., 2010), and the Uinta Mountains (Porinchu, unpublished data) have been documented as responding to elevated air and water temperature during the late 20th century. The rates of warming reported in this study are similar to those from around the region (Porinchu et al., 2007a, 2010). The response of midge communities to radiative forcing of temperature is consistent with studies that have identified the importance of local climatology in influencing the physical, chemical, and biological character of lakes (Parker et al., 2008; Hobbs et al., 2011; Garcia-Jurado et al., 2012; Saros et al., 2012). The elevated temperatures characterizing the post–A.D. 1980 interval identified in four of the lakes in this study also correspond to studies documenting recent changes in hydroclimate in the western United States (Cayan et al., 2001; McCabe and Clark, 2005; Rauscher et al., 2008; Saunders et al., 2008; Brown and Kipfmueller, 2012).

The chironomid-based temperature reconstructions from Teresa and Dead Lakes do not correspond to the reconstructions for the other four lakes in this study or the climate data from Nevada Climate Division #2. The discrepancy between the Teresa Lake and Dead Lake reconstructions and the instrumental record may be related to site-specific catchment or limnological conditions. Examination of DCA axis-1, which in the other four lakes corresponds well to chironomid-inferred MJAT, underscores the potential influence of site-specific or catchment conditions on midge community composition and turnover. Dead Lake is the smallest and shallowest lake in this study. Given the relatively small volume of the lake (see Table 1), Dead Lake would be highly susceptible to lake drawdown and possibly desiccation during sustained intervals of decreased effective moisture. Lake drawdown would significantly alter limnological conditions and thereby affect midge community composition in a manner independent of temperature. Teresa Lake is fed largely by groundwater, some of which emanates as melt from the Wheeler Peak rock glacier. Repeat measurement indicates that the temperature of inflowing groundwater remains constant at ~1.5 °C throughout the summer, before drying/freezing in the late fall–early winter (Mark, unpublished data). Although lake water temperatures do co-vary with air temperature (Larocque et al., 2001), the influence of elevated air temperature on the midge community at Teresa Lake may be mediated by the groundwater influx. The input of cold groundwater may lead to the midge community being decoupled from fluctuations in air temperature.

If Teresa Lake and Dead Lake are removed from the comparison, a coherent regional picture emerges. Subalpine and alpine lakes in the central Great Basin have experienced above average temperatures, relative to the entire 20th century, in the post–A.D. 1980 interval (Fig. 7). Interestingly, a spatial pattern appears to be evident in the magnitude and timing of the response of the midge communities to the elevated temperatures that characterize this region during the late 20th century and early 21st century. The northern sites appear to respond more strongly to the

warming (Figs. 6 and 7), while the southern sites, Stella Lake (this study), and Baker Lake (Porinchu et al., 2010) do not appear to be responding as quickly or as strongly to the change in observed air temperatures. This is evident in the rates of warming over the past 100 years, on average 0.9 °C for the northern sites and 0.5 °C for the southern sites (Porinchu et al., 2010) and during the post–A.D. 1970 interval. This observed spatial variability in midge community response to the elevated temperatures that characterize the central Great Basin during recent decades could be due to (1) complex interactions that exist between hydroclimate, catchment processes, and limnology, or (2) the lower elevation of the northern sites compared to the southern sites, especially in the Great Basin where topography can greatly influence the local environmental conditions (Wise, 2012).

It is important to note that midge communities can be influenced by factors other than temperature. Other studies have identified food and habitat availability, nutrient loading, and lake level fluctuations as factors influencing midge community composition. Some of the earliest studies involving chironomid communities involve lake trophic status classification schemes based on the distribution of taxa, as reviewed by Lindegaard (1995). More recently, Brodersen and Quinlan (2006) demonstrated the influence of lake trophic status and hypolimnetic oxygen conditions on chironomid communities. Adaptations have allowed some chironomid species to survive in low oxygen concentrations, and these adaptations can influence chironomid distribution (Brodersen and Quinlan, 2006). Many studies have also demonstrated the importance of lake level on the distribution of chironomid communities, through its effect on water temperature, oxygen availability, and food quantity (Kurek and Cwynar, 2009; Engels and Cwynar, 2011; Cwynar et al., 2012). Another factor that could be influencing faunal composition is the documented increase in lake productivity, as estimated by LOI, during recent decades (Fig. 4) (Velle et al., 2010). Nitrogen deposition to high-elevation lakes in the Rocky Mountains and elsewhere in the region, which has increased in recent decades, may also be influencing midge community composition (Sickman et al., 2003; Wolfe et al., 2003; Moser et al., 2010; Saros et al., 2011). As mentioned above, LOI, although a crude approximation for lake productivity, exhibits an increase in all lakes post–A.D. 1970. However, the lake productivity does not appear to be influencing the midge communities in this study. For example, Smith Lake and Birdeye Lake exhibit the largest increase in chironomid-inferred MJAT post–A.D. 1970, coincident with the smallest increase in LOI (Figs. 4 and 6). Further confidence in the chironomid-inferred MJAT is gained from the correspondence between the instrumental records and DCA axis-1, representing faunal turnover, and the inferred temperatures.

The varied characteristics of the lakes incorporated in this study provided an opportunity to identify criteria that can be used to improve site-selection for longer-term temperature reconstructions in the Intermountain West. Site-selection criteria have been identified elsewhere (Smol et al., 2001); however, some of the criteria we identify as significant are specific to the Great Basin region. In arid and semi-arid environments, such as those that characterize much of the Great Basin, lakes are typically only found in the upper reaches of a drainage basin near the headwalls of glacial cirques. From the results of this study, it is clear that lakes with highly fluctuating lake levels should be avoided when conducting chironomid reconstructions because of the potential overriding influence on midge community composition (e.g., Dead Lake). In addition, the contribution of cold, glacial meltwater or spring water must be minimized, especially if

attempting to solely develop air temperature reconstructions. For example, the midge community in Teresa Lake is characterized by low taxonomic diversity and is most likely responding to the principal control of a melt water spring that keeps the lake a uniform temperature through the summer months and allows for cold water pooling in the benthic zone of the lake. A more detailed study of the thermal characteristics of a potential study site would be beneficial before selecting it for use in a long-term temperature reconstruction (Smol and Last, 2001). However, this study also suggests that application of surface water temperature and air temperature inference models, to midge stratigraphies from carefully selected sites, may provide a means to quantify the varying influence of glacial meltwater flux to alpine and subalpine lakes through the Holocene.

This study further supports earlier research from western United States and other regions, mainly Europe, documenting recent changes in midge communities in subalpine and alpine lakes (Battarbee et al., 2002; Solovieva et al., 2005; Porinchu et al., 2007a, 2010). Changing thermal conditions, due to radiative forcing, has been implicated in numerous studies as a driver of the observed shift in midge community composition (Solovieva et al., 2005; Porinchu et al., 2010; Larocque-Tobler et al., 2011). Correspondingly, when comparison to independent records are possible, a better understanding of the chironomid-temperature relationship can be gained (Eggermont and Heiri, 2012) and greater confidence can be placed in chironomid-based Holocene temperature reconstructions (Porinchu et al., 2007a). Specifically, the results from this study further reinforce the link between the anthropogenic modification of climate change (i.e., increasing temperatures) and midge communities, thus supporting the continued use of midges in developing longer-term paleotemperature reconstructions. This work also establishes a regional limnological baseline of chironomid communities' composition throughout the 20th and 21st century. This baseline will both help to identify the degree to which aquatic ecosystems in these vulnerable regions have been or are being impacted by anthropogenic activities (Wolfe et al., 2003; Karst-Riddoch et al., 2005), and provide a long-term context to evaluate future changes in aquatic ecosystem structure and function (Swetnam et al., 1999; Smol, 2008).

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