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Late Pleistocene and early Holocene climate and limnological changes in the Sierra Nevada, California, USA inferred from midges (Insecta: Diptera: Chironomidae)

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Abstract

Chironomid and stratigraphic analyses of a lake sediment core recovered from a high-elevation lake in the central Sierra Nevada, California, USA, was undertaken to assess chironomid community development during the Pleistocene–Holocene transition and to quantitatively reconstruct the thermal regime that existed during this interval. Between 14 800 cal yr BP and 13 700 cal yr BP the chironomid community consisted almost exclusively of *Heterotrissocladius*, suggesting this period was characterized by extremely cold climatic conditions. Evidence of post-glacial climatic amelioration, as manifested by increases in thermophilous chironomid taxa, head capsule concentrations, and taxon richness and diversity, commenced at approximately 13 300 cal yr BP. In order to quantify the magnitude of the water temperature changes associated with post-glacial climatic amelioration, a recently developed chironomid-based inference model for surface water temperature was applied to the subfossil chironomid assemblages. The one-component, weighted-averaging partial least squares (WA-PLS) model has an $r^2_{\text{jack}} = 0.72$, $\text{RMSEP}_{\text{jack}} = 1.1$°C and a maximum bias of 1.24°C. The reconstructed surface water temperatures suggest a minimum warming of approximately 4.7°C occurred during the Pleistocene–Holocene transition. However, warming during this interval may not have been monotonic. Evidence of the Younger Dryas has been previously discovered in the study area and adjacent regions; Our research indicates that changes in chironomid community composition and an inferred short-term cooling event occurred between 12 000 cal yr BP and 11 500 cal yr BP, which may represent a local manifestation of the Younger Dryas. Chironomid community development during the Pleistocene–Holocene transition appears to primarily reflect the influence of changing climate conditions.

Keywords: chironomids; paleoclimate; paleolimnology; alpine lakes; Sierra Nevada, California; Younger Dryas

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1. Introduction

It is becoming apparent that high-latitude and high-elevation regions are extremely sensitive to climate change (Douglas et al., 1994; IPCC, 2001; Battarbee et al., 2002). One of the likely effects that projected global warming will have is to raise epilimnetic water temperatures in lakes and reservoirs (Schindler et al., 1990). These higher epilimnetic temperatures will likely affect the structure and function of freshwater ecosystems. Studies of the response of aquatic communities to past periods of climate change will improve our understanding of climate dynamics and our ability to assess the likely response of these communities to projected global warming.

The terrestrial and aquatic ecosystems of the Sierra Nevada, California, USA, appear to have been strongly affected by climate warming during the transition from the late Pleistocene to the early Holocene (14 000 and 9500 cal yr BP; all dates are reported as ^{14}C years before AD 1950 calibrated to calendar years). Available evidence suggests that glacial retreat (Clark and Gillespie, 1997), changes in vegetation structure and composition (Cole, 1983; Davis et al., 1985; Anderson, 1990) and hydrological changes (Benson et al., 1996, 1997) occurred in the Sierra Nevada and adjacent areas during this period. However, quantitative estimates of temperature change and knowledge of the nature and rate of aquatic ecosystem development in the Sierra Nevada during the Pleistocene–Holocene transition are still limited.

In addition to the general trend of unidirectional post-glacial warming, recent work has provided evidence that late Pleistocene climatic oscillations typical of the North Atlantic sector also impacted western North America (Reasoner et al., 1994; Menounos and Reasoner, 1997) including parts of the western USA (Benson et al., 1996, 1997). Work from Great Basin pluvial lakes suggests that Owens Lake, Pyramid Lake and Mono Lake alternated between wet and dry phases during the late Pleistocene and early Holocene (Benson et al., 1996, 1998, 2002). Although dating is problematic, some of these oscillations appear to correspond to previously documented events such as the Younger Dryas stadial (13 000–11 600 cal yr BP). A number of researchers have suggested that changes in ocean–atmosphere interaction in the North Pacific are the proximate cause of the millennial-scale climate oscillations that affected California during this period (Stine, 1994; Benson et al., 1997, 1998; Bradbury, 1997). The hypothesis that changes in ocean–atmosphere interactions in the North Pacific during the late Quaternary impacted climate in California can only be addressed if continuous, high-resolution paleoclimatic reconstructions can be developed for the region.

Unfortunately, detailed, quantitative, high-resolution reconstructions of the thermal regime that existed during the Pleistocene–Holocene transition in the Sierra Nevada are not available. Paleolimnology offers one means of developing these much-needed records. Paleolimnology is a multidisciplinary and integrative science that relies upon the physical, chemical and biological information preserved in lake sediment to reconstruct past environmental conditions in aquatic systems (Battarbee, 2000; Smol and Cumming, 2000). Paleolimnological reconstructions can illuminate aspects of both the structure and development of aquatic ecosystem communities and also provide evidence of the past environmental and climatic conditions that impacted these communities. In this study, we focus on using chironomid (Insecta: Diptera: Chironomidae) remains preserved in the sediments of a small, climatically sensitive Sierra Nevada lake to reconstruct the thermal regime that existed in the region during the Pleistocene–Holocene transition.

Chironomids, which are also known as midge flies, have long been used as biotic indicators to classify lakes in terms of trophic conditions and hypolimnetic oxygen concentration (Thienemann, 1918; Brundin, 1949). They also have a long history of being used to qualitatively interpret late-glacial climatic conditions (Andersen, 1938), and more recently they have been used to develop quantitative paleoclimatic reconstructions (reviewed in Porinchu and MacDonald, 2003). Earlier work in the Sierra Nevada has demonstrated that summer surface lake water temperatures account for a large and statistically significant proportion of the variance present in the modern

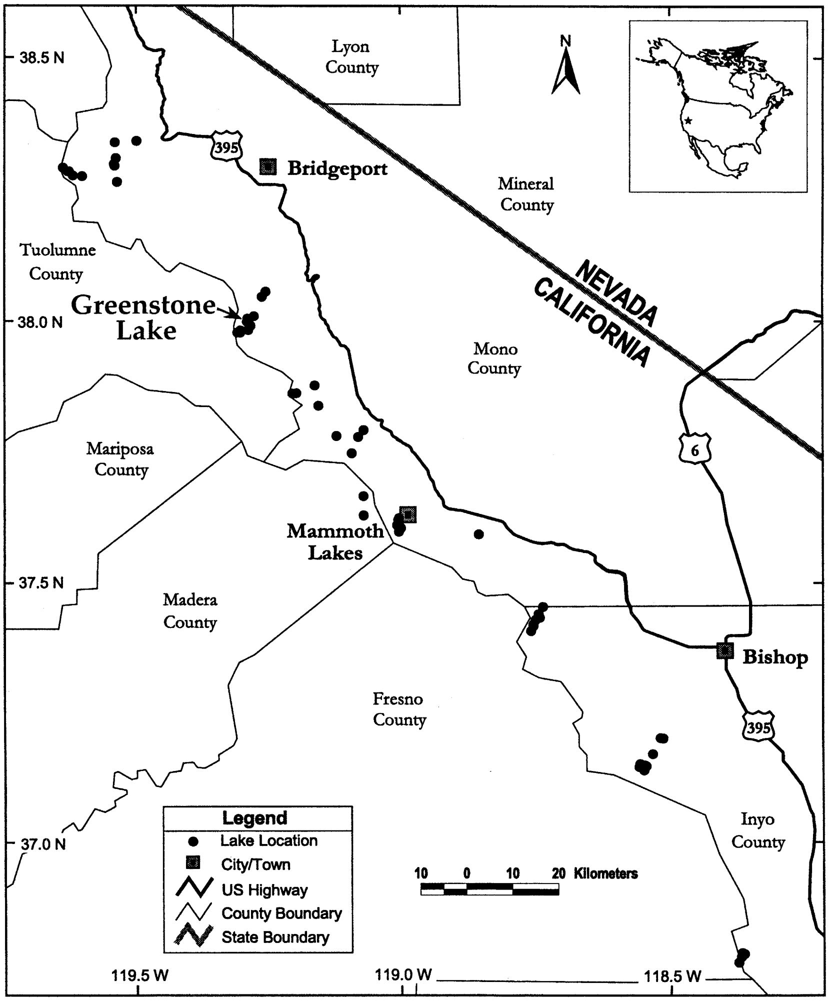

Fig. 1. Map of the study area indicating the distribution of the 56 lakes sampled for inclusion in the modern calibration dataset, including the location of Greenstone Lake.

distribution of chironomids in this region (Porinchu et al., 2002). A number of studies, using the calibration dataset approach and associated multivariate statistical techniques (reviewed in Smol and Cumming, 2000), have demonstrated that summer surface water temperature has a statistically significant relationship to the distribution of chironomids (Walker et al., 1991a, 1997; Olander et al., 1999). Application of quantitative transfer functions, developed from these calibration datasets, to subfossil chironomid assemblages preserved in late Quaternary lake sediment have enabled researchers to quantify changes in past temperature in Atlantic Canada and the northeastern USA during the late Pleistocene (Walker et al., 1991b; Levesque at al., 1993, 1997; Cwynar and Levesque, 1995) and western Norway during the late Pleistocene and early Holocene (Brooks and Birks, 2001).

In this paper we present the first detailed analysis of late Quaternary chironomid community development in the Sierra Nevada of California. We use time-trend analysis to compare late Pleistocene and early Holocene midge community composition and change to the modern distribution of chironomids in this region. Lastly, we apply a recently developed transfer function to the subfossil chironomid assemblages preserved in Greenstone Lake to reconstruct the thermal regime for the central Sierra Nevada during the Pleistocene–Holocene transition. This is the first study to use the remains of subfossil chironomids to reconstruct past temperature regimes in the western USA.

2. Study area

The study site, Greenstone Lake, California (37°58′47″N, 119°17′24″W), is located in the Hoover Wilderness near Tioga Pass on the east side of the Sierra Nevada crest at an elevation of 3067 m a.s.l. (Fig. 1). At present, Greenstone Lake is a small (8.1 ha), relatively shallow (maximum depth approximately 5.10 m), slightly alkaline (pH = 8.1) lake. Greenstone Lake is located on a contact between metamorphosed sedimentary rocks of Jurassic age and metarhyodacite of Triassic age (Sietz, 1983). Surficial talus and slopewash deposits of Quaternary age are present on the south and southwest sides of the lake. According to D. Clark (Western Washington University, personal communication) the lake is located outside the Recess Peak moraines. The vegetation surrounding Greenstone Lake is typified by sub-alpine boreal vegetation dominated by *Pinus contorta*, *Tsuga mertensiana* and *Pinus flexilis*.

The Sierra Nevada is characterized by a montane, Mediterranean climate, with hot, arid summers and cool, humid winters (Major, 1988). The dominant factor, controlling climate in California, is the presence of a semi-permanent high-pressure system in the north Pacific Ocean (Raphael and Mills, 1996). Topographic relief greatly affects the distribution of temperature and precipitation in the Sierra Nevada. Lee Vining, CA (37°57′N, 119°07′W), situated 15 km east of Greenstone Lake, is located at the base of the eastern flank of the Sierra Nevada at an elevation of 2073 m a.s.l. Over the climate normal period of 1971–2000, Lee Vining has had an average January temperature of −1.28°C, an average July temperature of 21.67°C and an average total precipitation of 33.05 cm (Western Regional Climate Center, 2002). There are no high-elevation meteorological stations in the Sierra Nevada that have records covering the climate normal period (1971–2000). The nearest high-elevation station with comparable records is located approximately 100 km southeast of Lee Vining in the White Mountains (37°35′N, 118°14′W) at an elevation of 3780 m a.s.l. This station has had an average January temperature of −9.03°C, an average July temperature of 7.67°C and an average total precipitation of 51.03 cm during the climate normal period (Western Regional Climate Center, 2002).

Study of the late Quaternary glacial history of the Sierra Nevada began late in the 19th century and has continued to the present (Russell, 1889; Blackwelder, 1931; Matthes, 1939; Birman, 1964; Curry, 1969; Burke and Birkeland, 1983; Phillips et al., 1996; Clark and Gillespie, 1997). Recent work has revised the chronology of late Pleistocene and Holocene glaciations in the Sierra Nevada (Clark and Gillespie, 1997; Konrad and Clark, 1998). Based on detailed mapping of moraine deposits and ^{14}C dating of sediment cores recovered from alpine lakes and meadows in the central Sierra Nevada, Clark and Gillespie (1997) suggest that the last major late Pleistocene glacial advance was the Recess Peak. Clark and Gillespie (1997) obtained dates of 11 190 ± 70^{14}C yr BP (∼13 200 cal yr BP) and 10 880 ± 60^{14}C yr BP (∼13 000 cal yr BP) for basal lake sediments from high-elevation lakes in the eastern Sierra Nevada which are morainally dammed by Recess Peak deposits. They suggest that these dates provide a minimum age estimate for the Recess Peak advance, indicating that the Recess Peak advance likely occurred prior to 12 000 ^{14}C yr BP (∼14 000 cal yr BP) and therefore pre-dates the Younger Dryas event.

3. Methods

3.1. Field

Replicate sediment cores were recovered from Greenstone Lake on 18 July 2001, using a modified Livingstone piston sampler (Wright, 1991) deployed from a platform supported by inflatable rafts. Cores were recovered from the basin located

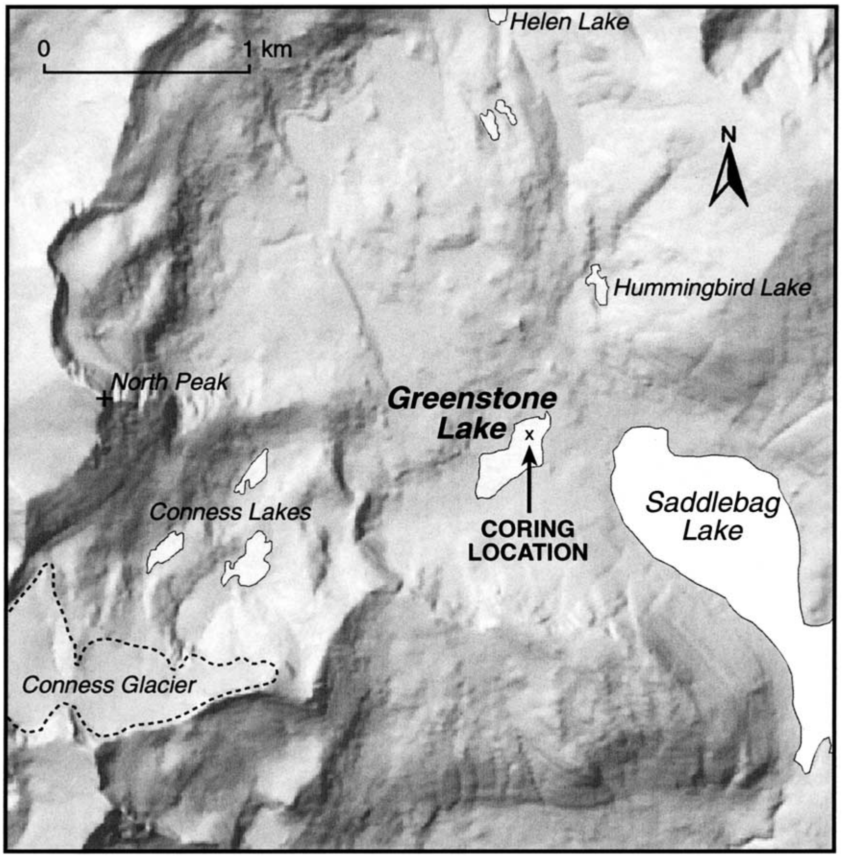

Fig. 2. Map showing the position of Greenstone Lake in relation to the nearby Conness Glacier. Coring location depicted by X.

in the northeast quadrant of the lake in 5.10 m of water (Fig. 2). A plastic tube fitted with a piston was used to recover the flocculent surface sediment and ensure that the sediment–water interface was recovered intact. The sediment recovered with the plastic tube was sub-sampled in the field at 1-cm increments and stored in Whirl-paks®. The remaining lake sediment was extruded in the field, described, wrapped in plastic film and aluminum foil and transported to the laboratory where the cores were stored at 4°C. Measurements of the limnological characteristics of Greenstone Lake were made on 9 August 1999 during an earlier visit to collect surface (0–1 cm) sediment for use in the modern calibration set.

3.2. Laboratory

The amount of organic carbon present in the lake sediment was analyzed using loss-on-ignition (LOI) analysis (Dean, 1974). LOI analysis for the late Pleistocene and early Holocene portion of the Greenstone lake core was undertaken at 0.5-cm resolution, with the analysis based on 1 cm^3 of sediment.

Chironomid analysis follows methods outlined in Walker (1987). A minimum of 45 head capsules were identified and enumerated from 26 of the 29 samples analyzed (range: 45–231 head capsules) (Quinlan and Smol, 2001; Heiri and Lotter, 2001); chironomid analysis was based on 40 head capsules for three samples (231, 234 and 254 cm). The amount of sediment processed and treated to obtain the minimum number of head capsules varied greatly between samples (range: 0.25–6.5 ml). 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 Simpson and Bode (1980), Cranston (1982), Wiederholm (1983), Oliver and Roussel (1983), Walker (1988, 2000) and an extensive University of California at Los Angeles (UCLA) reference collection. In general, identification of subfossil chironomid remains is made at the generic level. However, in certain cases species-type level identifications are possible, e.g., *Corynocera oliveri*-type, while in other cases broader taxonomic grouping are required, e.g., grouping *Hydrobaenus* and *Oliveridia* together. *Corynocera*-type 1 has a mentum intermediate between *Corynocera oliveri* and *Corynocera* nr. *ambigua*, short distally rounded spurs on the antennal pedestal and a large dorsal tooth present on the mandibles. *Tanytarsus* group 3 is characterized by a broad trident-shaped median tooth and lateral teeth arrangement that is similar to *C.* nr. *ambigua*. *Tanytarsus* group 4 is characterized by a mentum very similar to *C.* nr. *ambigua* and a distinctive sharp apical projection on the antennal pedestal. *Micropsectra radialis*-type and *Micropsectra insignilobus*-type were separated based on the presence of a distinct post-occipital plate associated with the *M. insignilobus*-type specimens.

3.3. Statistical analyses

3.3.1. Modern calibration dataset

The modern distribution of chironomids in the eastern Sierra Nevada was established by analyzing the subfossil chironomid remains preserved in the surface sediment of 56 lakes in this region (Porinchu et al., 2002) (Fig. 1). These lakes were sampled during late July and early August 1999, July 2000 and July 2001. Surface sediment was recovered using a mini-Glew gravity corer (Glew, 1991). During surface sediment collection each lake was characterized by a number of physical and limnological variables, e.g., pH, maximum depth, surface water temperature, specific conductivity. At this time water samples were also collected for water chemistry analysis (see Porinchu et al., 2002 for further details). The lakes incorporated in the calibration set spanned an elevation gradient of 1360 m, were generally small (mean surface area = 10 ha), circum-neutral to alkaline (pH range: 6.7–8.8) and relatively shallow (mean maximum depth = 10.50 m). In total each lake was characterized by 31 environmental variables.

Redundancy analysis (RDA) with forward selection of the 56-lake dataset identified that five of the 31 measured environmental variables have a large, independent and statistically significant relationship to the distribution of chironomids in the study lakes (Porinchu et al., 2002). These variables were surface water temperature, depth, elevation, strontium and particulate organic carbon (POC). Surface water temperature accounted for 11.2% of the variance in the chironomid data. A partial RDA with surface water temperature as the sole environmental variable and depth, elevation, Sr and POC as co-variables revealed that surface water temperature independently accounts for 6.8% of the variance present in the calibration dataset.

A one-component weighted-averaging partial least squares (WA-PLS) model based on 44 lakes and all taxa present in the calibration set was

Table 1
Details of the radiocarbon dates obtained for Greenstone Lake

Sample	Lab number	Depth (cm)	Material	Age (^{14}C yr BP)	2σ age range (cal yr)	Relative area under distribution	Calibrated age: age–depth model (cal yr BP)
Greenstone Lake	Beta-157868	245–246	bulk	10 700 ± 80	12 980–12 610*	0.855	12 800
					12 490–12 350	0.145	
	Beta-157867	229–231	bulk	9 270 ± 60	10 580–10 360*	0.742	10 470
					10 360–10 240	0.245	

Dates based on AMS analysis carried out by Beta Analytic Incorporated. *These ranges had the highest probability distribution although they were < 95%. The midpoint of these ranges was used in constructing the chronologies.

developed (12 lakes were removed from the training set, including Greenstone Lake, based on screening criteria discussed in Porinchu et al., 2002). 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.

3.3.2. Comparison and model application to subfossil assemblages

Time-trend analysis, which relies on a space-for-time substitution, was used to assess the trajectory of chironomid community development in Greenstone Lake (Porinchu and Cwynar, 2002). Changes in the composition of subfossil chironomid assemblages were compared to the modern distribution of chironomids in this region using correspondence analysis (CA). The composition of the subfossil chironomid communities present in Greenstone Lake during the Pleistocene–Holocene transition was averaged at 250-year intervals and passively ordinated with abundance data describing the contemporaneous distribution of chironomids in the Sierra Nevada. The first two ordination axes were constrained using the 44 lakes that are incorporated in the chironomid-based inference model (Porinchu et al., 2002). All taxa present in both the subfossil assemblages and the calibration set were included in this analysis.

A one-component WA-PLS model was applied to the subfossil chironomid assemblages recovered from Greenstone Lake to develop a quantitative estimate of temperature change during the Pleistocene–Holocene transition. One means of assessing the reliability of a quantitative paleoenvironmental reconstruction is to determine for each subfossil assemblage the total percentage of taxa present that do not appear in the modern calibration dataset. According to Birks (1998) reconstructions that are based on subfossil assemblages that have $>95\%$ of the subfossil taxa present in the calibration set are very reliable. Of the 35 chironomid taxa present in the late Pleistocene–early Holocene portion of Greenstone Lake, 32 (or 91%) are present in the calibration set. The taxa that are not present in the calibration set, *Pseudodiamesa*, *Apedilum* and *Glyptotendipes*, are extremely rare in the Greenstone Lake chironomid stratigraphy and never exceed 5% of the total identifiable chironomids at any level. 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. A LOWESS smoother (span = 0.20) was applied to the reconstruction to highlight the main trends in surface lake water temperature during the Pleistocene–Holocene transition.

All ordinations were implemented by the program CANOCO version 4.0 (ter Braak and Smilauer, 1998). The chironomid percentage diagram was created using TILIA (version b2.0) developed by E. Grimm (Illinois State Museum, Springfield, IL, USA). Zonation of the chironomid percentage diagrams was performed by ZONE version 1.2 and based on optimal sum of squares partitioning (Juggins, 1991). The WA-PLS calibration model and the sample-specific errors associated with the reconstruction were developed using the program WA-PLS version 1.1 (Juggins and ter Braak, 1996). The LOWESS smoother applied to the temperature reconstruction was implemented by MINITAB version 13. The Shannon–Wiener diversity measure, defined by the equation: $H' = -\Sigma(p_i)(\ln p_i)$, where H' is the Shannon–Wiener index of diversity and p_i is the proportion of all individuals in the sample belonging to taxon i, was used as a measure of the diversity of the chironomid assemblages (Levesque et al., 1996). The diversity index was applied to abundance data grouped at the generic level. Assemblages that consist of and/or are dominated by few taxa tend to have a relatively low index of diversity.

4. Results

4.1. Chronology and lake sediment characteristics

A 283-cm core was recovered from Greenstone Lake. The stratigraphy of the early Holocene portion of the core is typified by dark brown, organic-rich gyttja between 225 cm and 232 cm (Fig. 3). Between 232 cm and 247 cm a grading of the gyttja into lighter-colored, less organic sediment

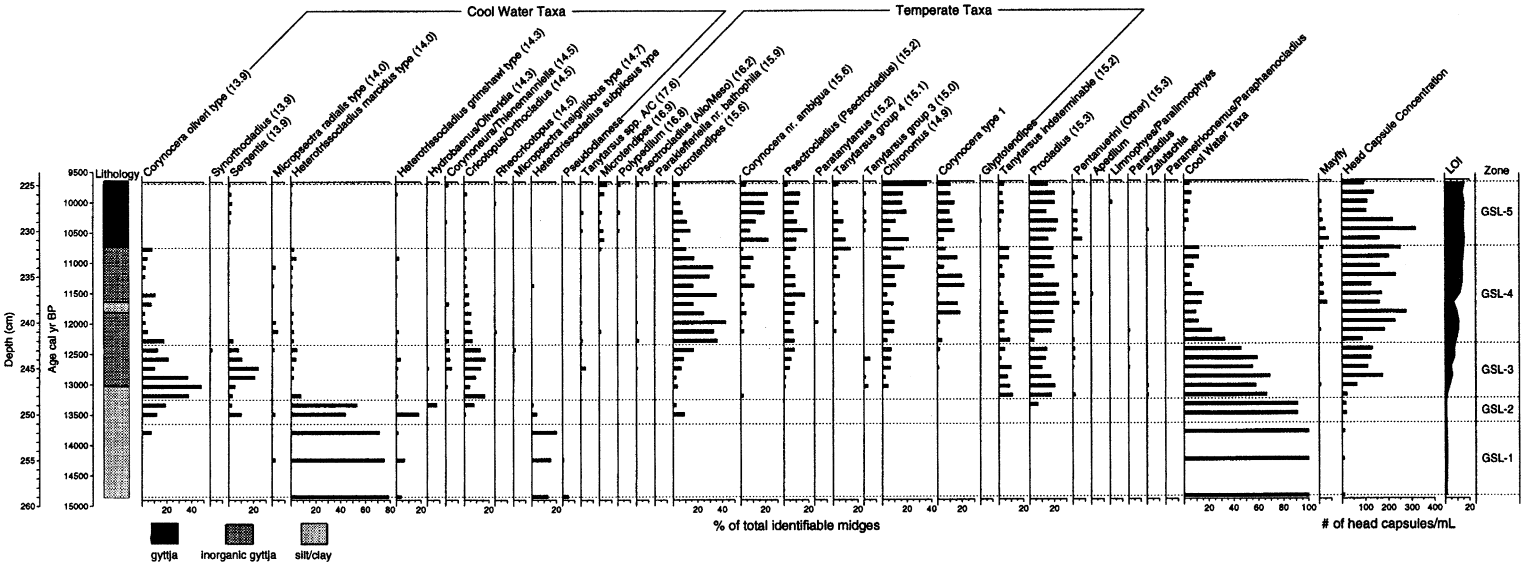

Fig. 3. Chironomid stratigraphy and percent LOI for Greenstone Lake. Abbreviations for chironomid taxa: *Psectrocladius* (*Allo/Meso*) = *Allopsectrocladius/Mesopsectrocladius*. Taxa are grouped into 'Cool-water Taxa' or 'Temperate Taxa' according to their surface water temperature optima (as determined in Porinchu et al., 2002) with the exception of *Heterotrissocladius subpilosus*, *Pseudodiamesa*, *Corynocera*-type 1 and *Glyptotendipes* which are placed into groups based upon their surface water temperature optima as defined in the literature. Surface water temperature optima values listed in parenthesis following each taxon. Optima for the taxa are based on a simple WA regression and calibration model using classical de-shrinking. Optima are provided for the taxa that are present in greater than 20% of the modern calibration dataset lakes. The number of Mayfly (Insecta: Ephemeroptera) mandibles encountered in Sediments also indicated.

occurs with a gray silty clay band occurring between 238 and 239 cm. A distinct transition to silty clay occurs at 247 cm and likely reflects the transport of glacial flour from the nearby Conness Glacier into Greenstone Lake. Application of HCl to the late Pleistocene and early Holocene portion of the core suggests that the sediment does not contain carbonates; carbonates have been shown to adversely affect ^{14}C dating (MacDonald et al., 1991).

The chronology for Greenstone Lake is based on two accelerator mass spectrometer (AMS) radiocarbon dates (Table 1). The age–depth function developed for the core assumed a constant rate of sediment deposition between the ^{14}C radiocarbon dates. The program CALIB version 4.3 (Stuiver et al., 1998) and the atmospheric decadal dataset were used to convert the radiocarbon dates to calibrated ages. The midpoint of the cal BP age range with the highest probability of occurring at the 2σ level was used to create the cal yr BP age scale.

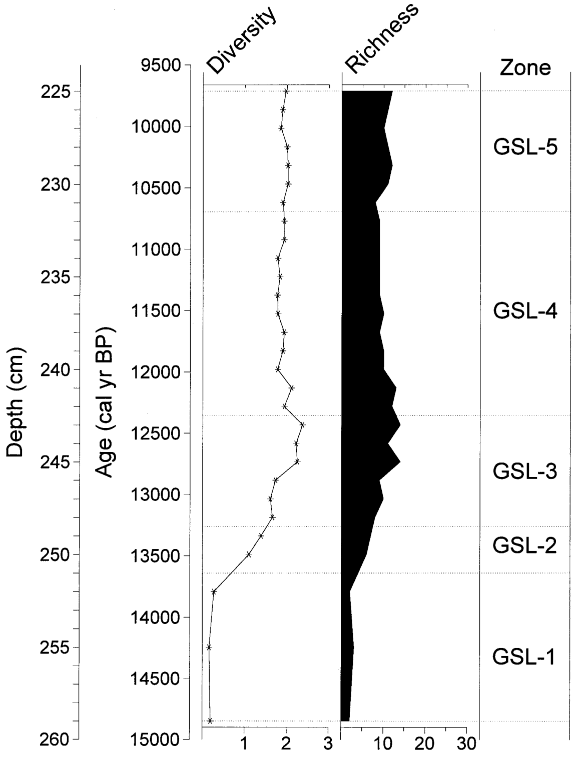

Fig. 4. Richness and diversity measures for the chironomid community from Greenstone Lake.

The LOI curve shows a roughly sigmoidal relationship with the immediate late-glacial period characterized by extremely low organic content (~2%) (Fig. 3). At 13 200 cal yr BP an approximately three-fold increase in percent LOI occurs. The monotonic increase in LOI is interrupted only once with a marked drop in LOI occurring centered at 11 700 cal yr BP. The drop in LOI from approximately 12% to 7% at this depth is associated with the presence of a 1 cm thick band of silty clay sediment (238–239 cm) identified in the sediment stratigraphy. This short-term reversal in the amount of organic matter present in the lake sediment is followed by increasing LOI values with a local peak of approximately 15% attained at 10 900 cal yr BP. The modern LOI value for Greenstone Lake is ~17%.

4.2. Chironomid community composition and trajectory

The chironomid percentage diagram is divided into five zones (Fig. 3).

4.2.1. GSL-1 (14 800–13 700 cal yr BP; 259–252 cm)

This zone is dominated by a single cold-water chironomid taxon, *Heterotrissocladius marcidus*-type (~75%). Also present in this zone are other cold-water taxa such as *Heterotrissocladius grimshawi*-type (~5%), *Heterotrissocladius subpilosus*-type (~15%), *Pseudodiamesa* (~3%) and *Micropsectra radialis*-type (~1%), is also present in GSL-1, albeit at extremely low levels. Head capsule concentrations are extremely low throughout GSL-1 averaging less than 10 head capsules/ml. The richness and diversity of the chironomid community during this period are also low; richness fluctuates between 2 and 3, and diversity averages approximately 0.20 (Fig. 4).

4.2.2. GSL-2 (13 700–13 300 cal yr BP; 250–248 cm)

This zone is characterized by a decrease in the relative abundance of the cold-water chironomid taxon, *Heterotrissocladius* (~60%). Other cold-water taxa, such as *Sergentia* (~10%), *Hydrobaenus/Oliveridia* (~5%) and *Corynocera oliveri*-type (~15%), do appear, as does the temperate taxon *Dicrotendipes* (~5%). Appearing for the first time in the chironomid stratigraphy is a member of the Tanypodinae, *Procladius*. Head capsule concentrations approximately double in this zone averaging 16 head capsules/ml. Taxon richness and diversity also increase averaging 7.0 and 1.4 respectively.

4.2.3. GSL-3 (13 300–12 300 cal yr BP; 248–242 cm)

Increases in cold-water taxa such as *Sergentia* (~20%), *Corynocera oliveri*-type (~30%) and *Cricotopus/Orthocladius* (~10%), along with an initial decrease in the dominant warm-water taxon *Dicrotendipes* (~10%), characterize this zone. The appearance of *Chironomus*, Tanytarsina and mayfly (Ephemeroptera) mandibles and an increase in *Procladius* are also observed. Head capsule concentration increases dramatically in this zone, reaching a zonal peak of 174 head capsules/ml at 246 cm. Both the richness and diversity of the chironomid community initially increase, reaching values of 14 and 2.3 respectively at 245 cm.

4.2.4. GSL-4 (12 300–10 700 cal yr BP; 242–231 cm)

GSL-4 is marked by a sharp decrease in the abundance of the Orthocladiinae, which is chiefly comprised of cold-water chironomid taxa. *Sergentia*, *Heterotrissocladius* (~2%) and *Corynocera oliveri*-type (~5%) are dramatically reduced while there is a corresponding increase in the relative abundance of temperate chironomid taxa such as *Dicrotendipes* (~25%), *Psectrocladius* (*Psectrocladius*) (~10%) and *Corynocera* nr. *ambigua* (~5%). Midway through this zone, however, a brief increase in *C. oliveri*-type and total Orthocladiinae head capsules is observed. Also of note is the appearance of *Parametriocnemus/Paraphaenocladius* and the increase and continuous presence of *Corynocera*-type 1 and mayfly mandibles in the sediment. The richness and diversity measures, which are initially high, decrease through the zone. Head capsule concentrations increase dramatically, reaching up to 232 head capsules/ml near the top of the zone.

4.2.5. GSL-5 (10 700–9700 cal yr BP; 225–231 cm)

This zone is characterized by the appearance and/or increase of thermophilous chironomid taxa such as *Psectrocladius* (*Psectrocladius*) (~10%), *Microtendipes* (~3%), *Corynocera* nr. *ambigua* (~15%) and *Polypedilum* (~1%) and a decrease in *Dicrotendipes* (~10%). Some cold-water taxa such as *Heterotrissocladius* and *Corynocera oliveri*-type are essentially extirpated in this zone; *Sergentia* (~1%) remains present, albeit at very low levels. *Tanytarsus* group 4 (~5%) and *Tanytarsus* group 3 (~1%) are also present in this zone at moderate levels. Taxon richness and diversity do not change markedly from the previous zone. Following a peak in head capsule concentration that occurs at the base of GSL-5 (~320 head capsules/ml), a decrease in head capsule concentration to levels similar to GSL-3 occurs (~94 head capsules/ml).

4.3. Time-trend analysis

The ordination diagram based on correspondence analysis (ca) illustrates the trajectory of chironomid community development in Greenstone Lake during the Pleistocene–Holocene transition (Fig. 5). The composition of the initial chironomid community (~14 500–13 700 cal yr BP) is positioned well outside the ordination space that is described by the chironomid communities that are incorporated in the chironomid-based inference model. These initial chironomid assemblages are dominated by the cold-water taxon *Heterotrissocladius* and likely represent colder water conditions than we have been able to capture in our modern calibration set (Porinchu et al., 2002). By 13 500 cal yr BP the chironomid community is increasingly typified by taxa that are commonly associated with the coldest calibration set lakes today. At approximately 12 500 cal yr BP the trajectory of chironomid community development changes dramatically with the presence and relative abundance of thermophilous taxa increasing, suggesting warming climatic conditions. A shift in

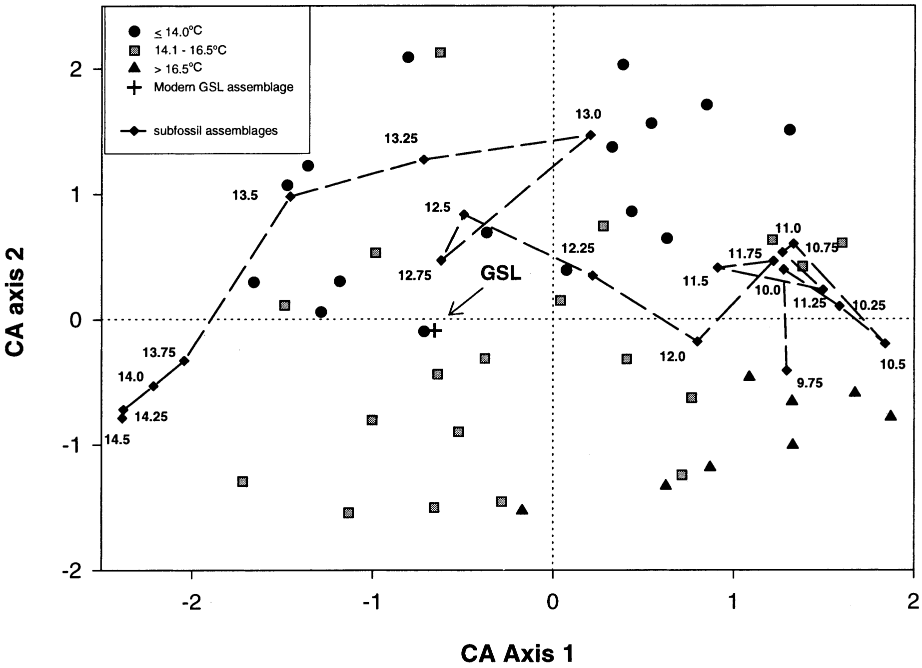

Fig. 5. Time-trend CA bi-plot comparing fossil chironomid assemblages from Greenstone Lake with the 44-lake calibration dataset from the Sierra Nevada, California. Calibration dataset lakes are grouped according to measured surface water temperature. Numeric values represent the fossil chironomid assemblages at 250-year intervals ($\times 10^3$).

chironomid community composition occurs at approximately 12 000 cal yr BP when the trajectory of community development moves away from assemblages associated with the warmest calibration lakes. Of note is the brief reversal in the trajectory between 11 750 cal yr BP and 11 500 cal yr BP when the relative abundance of cold-water chironomid taxa briefly increases. Between 11 500 and 10 000 cal yr BP the composition of the subfossil chironomid community appears to stabilize with little change apparent. However, at 10 000 cal yr BP the chironomid community trajectory moves towards a composition increasingly similar to the warmest lakes in the Sierra Nevada calibration dataset.

4.4. Temperature reconstruction

Application of a one-component WA-PLS model to the subfossil chironomid assemblages preserved in the Greenstone Lake sediment suggests that surface water temperatures during the immediate post-glacial interval (14 830 cal yr BP–12 570 cal yr BP) ranged between 12.0°C and 13.5°C (Fig. 6). However, it is important to recognize that the chironomid-based inferences for the period between 14 800 and 13 500 cal yr BP are poorly constrained by the existing Sierra Nevada calibration dataset and that the chironomid-inferred temperatures are likely significantly overestimated. This initial period of low water temperature was followed by fluctuating, upward-trending surface water temperatures. Post-glacial climatic amelioration was possibly interrupted between approximately 12 000 cal yr BP and 11 500 cal yr BP when surface water temperature dropped to 14.9°C from 15.5°C. The LOWESS smoother indicates that that post-glacial warming was essentially monotonic with a brief interruption occurring between 11 000 cal yr BP and 12 000 cal yr BP. However, it is important to note that the decrease in surface water temperature that is inferred to have occurred between 12 000 and 11 500 cal yr BP cannot be considered

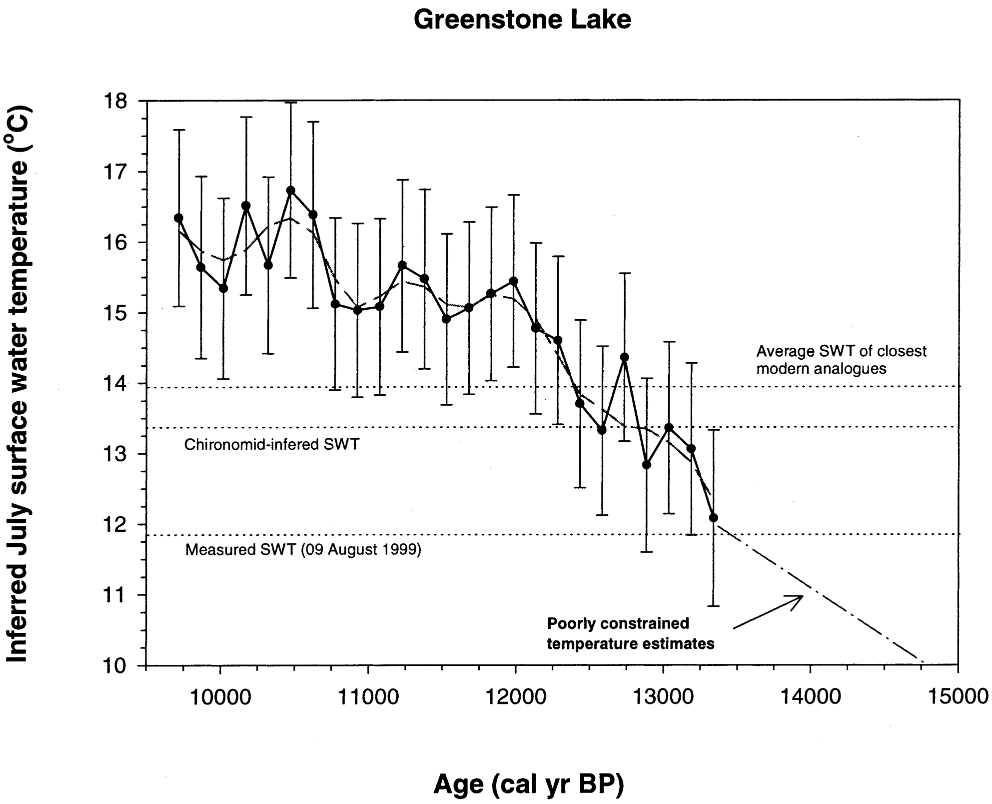

Fig. 6. Chironomid-based surface water temperature reconstruction for Greenstone Lake during the late-glacial and early Holocene. Points represent actual temperature inferences with error bars and dark continuous line represents a LOWESS smoother (span = 0.20) has been superimposed on the chironomid-inferred values.

statistically significant as the sample-specific errors, which varied between 1.2°C and 1.4°C, and the root mean square error of prediction (RMSEP) of the WA-PLS model are larger than the drop in surface water temperature that occurred during this period (Fig. 6).

5. Discussion

5.1. Chironomid community development

The chironomid percentage diagram (Fig. 3) indicates that the initial post-glacial chironomid community in Greenstone Lake is dominated by one taxon, *Heterotrissocladius*. *Heterotrissocladius* is commonly found at high abundances in the late-glacial sediment of temperate North American and northern European lakes (Levesque et al., 1993; Cwynar and Levesque, 1995; Smith et al., 1998; Brooks and Birks, 2000). Today, in the Palearctic and Nearctic, *Heterotrissocladius* is generally associated with arctic and alpine lakes with high oxygen concentrations and deep, thermally stratified, oligotrophic temperate lakes (Walker and Mathewes, 1989a; Walker et al., 1991a; Lotter et al., 1997; Olander et al., 1999; Larocque et al., 2001). In the eastern Sierra Nevada *Heterotrissocladius grimshawi*-type is restricted almost entirely to cold, high-elevation lakes and has a surface water temperature optimum of 14.3°C. *Heterotrissocladius marcidus*-type, although not restricted to cold, high-elevation lakes, has a surface water temperature optimum of 14.0°C, and is most common in these lakes (Porinchu et al., 2002). The dominance of *Heterotrissocladius* in the post-glacial chironomid assemblages indicates that it was present not only in the profundal zone but also in the littoral zone of Greenstone Lake. This suggests that *Heterotrissocladius* was likely responding to cold lake water conditions rather than deep-water oxygen concentration. Also present in zone GSL-1 is *Pseudodiamesa*, a taxon that is associated with cold flowing water and the profundal of still water and can be considered a cold stenotherm (Wiederholm, 1983; Walker et al., 1997; Brooks and Birks, 2001; Larocque et al., 2001). In an eastern Canada calibration set *Pseudodiamesa* has the second lowest surface water temperature optimum (6.7°C) of all the taxa identified (Walker et al., 1997). *Pseudodiamesa* was likely deposited in Greenstone Lake by inflowing streams carrying meltwater from the nearby Conness glaciers; and its presence further substantiates the inference of cold conditions during this interval. The LOI values indicate that lake productivity was low during this period and that the surrounding catchment was poorly vegetated, resulting in high amounts of minerogenic material being deposited within the lake. The low head capsule concentrations and diversity values are typical of late-glacial conditions and sustained periods of climatic deterioration such as the Younger Dryas (Walker and Mathewes, 1989b; Levesque et al., 1996; Brooks and Birks, 2001; Palmer et al., 2002). Low water temperatures, depressed lake productivity and limited amounts of potentially available habitat, i.e., rooted macrophytes and other aquatic vegetation, are likely responsible for the depauperate chironomid community present in GSL-1.

The next zone, GSL-2 (13 700–13 300 cal yr BP), continues to be dominated by *Heterotrissocladius*, however the community diversity increases as other cold-water taxa such as *Corynocera oliveri*-type, *Sergentia* and *Micropsectra radialis*-type appear, as does a temperate taxon, *Dicrotendipes*. *Corynocera oliveri*-type has been associated with tundra lakes in northeast Siberia where its modern distribution is delineated by latitudinal treeline (Porinchu and Cwynar, 2000). In the Sierra Nevada, *C. oliveri*-type, while broadly distributed, is most abundant in colder lakes and has a surface water temperature optimum of 13.9°C (Porinchu et al., 2002). It has also been identified as the dominant taxon in many coastal subalpine lakes in British Columbia, Canada (Walker, 1988) and appears to show preference for tundra sites in northern Fennoscandia (Olander et al., 1999; Seppä et al., 2001). *Sergentia* is a taxon that is commonly found in arctic and alpine lakes (Lotter et al., 1997; Walker et al., 1997; Olander et al., 1999; Larocque et al., 2001), but it is also found in the profundal of deep lakes (Korhola et al., 2000). Its modern distribution in the Sierra Nevada indicates that it is most abundant and most consistently found in cold, high-elevation lakes (Porinchu et al., 2002). The appearance of *Dicrotendipes*, albeit at low levels, suggests that the littoral zone of Greenstone Lake had warmed sufficiently to support its presence. *Dicrotendipes* is considered a littoral, warm-water taxon, and is generally associated with low-elevation lakes and lakes found south of latitudinal treeline (Wiederholm, 1983; Walker and MacDonald, 1995; Porinchu and Cwynar, 2000; Brooks, 2000). Head capsule concentrations and LOI remained low in this zone suggesting that lake water temperatures had not yet sufficiently warmed to greatly impact lake productivity.

Dramatic changes in the aquatic ecosystem occurred in zone GSL-3 (13 300–12 300 cal yr BP). In conjunction with the abrupt decrease in the cold-water stenotherm, *Heterotrissocladius*, is the appearance of warm-water taxa such as *Psectrocladius (Psectrocladius)*, *Psectrocladius* (*Allopsectrocladius/Mesopsectrocladius*) and *Corynocera* nr. *ambigua*, and an increase in *Dicrotendipes*. However, there is also a corresponding increase in cool-water taxa such as *Corynocera oliveri*-type, *Sergentia*, *Cricotopus/Orthocladius* and *Paracladius* and the appearance of a cold stenothermic taxon, *Synorthocladius*. *Paracladius*, which has been identified as a common constituent of cold tundra lakes and flowing water (Porinchu and Cwynar, 2000; Oliver and Roussel, 1983), and the presence of *C. oliveri*-type and *Synorthocladius*, both of which have the coldest temperature optima in the Sierra Nevada calibration dataset, indicate that water temperatures continue to be cool throughout this zone. The relative proportion of the Tanypodinae also increases, with *Procladius* and members of the tribe Pentaneurini present, both of which have temperature optima of 15.3°C. The presence of *Procladius* in this zone is difficult to interpret; it has been identified as a common constituent of late-glacial chironomid communities in western North America (Smith et al., 1998), but it is broadly distributed over a large range of trophic conditions and altitude and temperature gradients (Lotter et al., 1998; Porinchu et al., 2002). The appearance of *Chironomus* and *Sergentia* together with some warm-water taxa suggests that lake stratification and an increase in lake productivity may have occurred resulting in a reduction in hypolimnetic oxygen concentration. *Sergentia*, which is generally associated with cold arctic/alpine lakes, possesses hemoglobin and can tolerate moderate oxygen depletion (Walker, 1990). *Chironomus*, commonly referred to as bloodworm due to the presence of hemoglobin, is often found at high levels in the littoral habitats of shallow, warm, low-elevation lakes and it is often used as a bioindicator of eutrophication. The increase in head capsule concentrations midway through the zone and the increase in taxon diversity towards the top of this zone suggest that an expansion of available habitat likely occurred, enabling the colonization of the littoral zone by an increasingly diverse, thermophilous chironomid community.

In the time period represented by GSL-4 (12 300–10 700 cal yr BP) the chironomid community becomes increasingly dominated by warm-water taxa such as *Dicrotendipes*, *Corynocera* nr. *ambigua*, *Psectrocladius* (*Psectrocladius*) and *Corynocera*-type 1. Cold-water taxa, with the exception of *Corynocera oliveri*-type and *Cricotopus*/*Orthocladius*, are present at levels less than 5%. The presence of *C.* nr. *ambigua* and *Corynocera*-type 1 is significant as they are most abundant in the warmest lakes of the modern calibration set. *Corynocera*-type 1 is an unidentified *Corynocera* that is intermediate in appearance between *Corynocera oliveri* and *C.* nr. *ambigua*. Remains similar to *Corynocera*-type 1 have been identified as an unknown *Corynocera* in the remains of late-glacial sediment from southern British Columbia, Canada (Palmer et al., 2002). *Corynocera* nr. *ambigua*, typified by a dark and variable mentum, has been identified in the cold, oligotrophic coastal lakes and ponds of British Columbia; however, in the Sierra Nevada it is most commonly associated with warm, low-elevation lakes (Porinchu et al., 2002). It is possible that a number of previously unidentified *Corynocera* species or types may be present in both the late Quaternary sediment from Greenstone Lake and the modern calibration dataset. Although *Psectrocladius* (*Psectrocladius*) and *Psectrocladius* (*Allopsectrocladius*/*Mesopsectrocladius*) are eurythermic, the genus *Psectrocladius* has been identified as a common constituent of low-elevation lakes in British Columbia (Walker and Mathewes, 1989a) and has also been used to distinguish forested lakes from tundra lakes in Siberia (Porinchu and Cwynar, 2000). Midway through this zone there is also a slight increase in the proportion of cool-water taxa present.

The proportion of temperate chironomid taxa including *Microtendipes*, *Polypedilum*, *Tanytarsus* spp. A/C and *Parakiefferiella* cf. *bathophila* continue to increase in GSL-5 (10 700–9700 cal yr BP). Thermophilous taxa such as *Microtendipes*, *Glyptotendipes* and *Polypedilum*, generally associated with the littoral zone of warm, mid- and low-elevation sites, have a limited distribution in arctic and alpine lakes (Walker and Mathewes, 1989a; Walker and MacDonald, 1995; Porinchu and Cwynar, 2000; Olander et al., 1999; Brooks and Birks, 2001; Larocque et al., 2001; Porinchu et al., 2002). *Tanytarsina* spp. A/C, *Microtendipes* and *Polypedilum* have the highest temperature optima of all taxa that appear in greater than 20% of the Sierra Nevada calibration lakes. *Corynocera*-type 1, which is only present in two of the calibration dataset lakes, has an extremely high temperature optimum (19.5°C) and its presence in GSL-5 in relatively high amounts suggests continued climatic amelioration. However, it is interesting to note that the uppermost samples in this zone see the disappearance of mayfly remains, a decrease in head capsule concentration and the reappearance of cold-water taxa such as *Sergentia*, *Heterotrissocladius* spp. and *Corynoneura*/*Thienemanniella*. The reappearance of cold-water taxa at approximately 9500 cal yr BP has been documented elsewhere in the Sierra Nevada (Porinchu and MacDonald, unpublished).

5.2. Paleoclimatic reconstruction and implications

The date 10 700 ± 80 ^{14}C yr BP (12 800 cal yr BP) that we obtained on basal organic sediments from Greenstone Lake provides a minimum date for the deglaciation of this area. Clark and Gillespie (1997) have obtained similar dates from other high-elevation lakes in the Sierra Nevada and have suggested that the Sierra Nevada was essentially deglaciated between 14 000 and 15 000 cal yr BP. The basal date we obtained for Greenstone Lake is slightly younger than this. However, this date is consistent with the chronology of late Pleistocene deglaciation proposed by Clark and Gillespie (1997), given that it is based on a sample located ~40 cm above the bottom-most sediment in the core and that Greenstone Lake is a high-elevation lake, located near a modern glacier (Conness Glacier) which was much larger during the late Pleistocene, as evidenced by the nearby Recess Peak deposits.

The modern chironomid assemblage found in Greenstone Lake was not incorporated in the inference model that was applied in this study due to its high absolute residual (predicted water temperature minus measured water temperature) (see Porinchu et al., 2002 for further details). The measured surface water temperature for Greenstone Lake at the time of surface sediment collection was 11.9°C while measured ambient air temperature was 15.0°C. When the 44-lake chironomid-based inference model is applied to the modern chironomid assemblage found in Greenstone Lake a surface water temperature of 13.3°C is inferred with a sample-specific error estimate of 1.2°C. The difference between the model-inferred surface water temperature and the measured water temperature is slightly greater than the sample specific error estimate. A number of authors have pointed out that a single measurement of surface water temperature does not adequately characterize the mean surface water temperature at a given site (Hann et al., 1992; Brooks and Birks, 2001). Recent work has demonstrated that chironomid-based inference models for mean summer or mean July air temperature often outperform chironomid-based inference models for surface lake water temperature. However, the highly complex and varied topography of the Sierra Nevada and the paucity of high-elevation meteorological stations with adequately long records in this region have limited our ability to make meaningful estimates of mean July air temperature and hence develop a chironomid-based inference model for air temperature (Porinchu et al., 2002). The closest modern analogues currently found in the Sierra Nevada for the surface sample recovered from Greenstone Lake are from Box Lake, Long Lake 2 (unofficial name, Porinchu et al., 2002), Lower Sardine Lake and Big Pothole Lake; these lakes have measured surface water temperatures of 14.3°C, 14.3°C, 14.0°C and 13.3°C, respectively (Porinchu et al., 2002). We suggest that based on its modern chironomid assemblage, the surface water temperature measured at Greenstone Lake on 9 August 1999 is likely an underestimate of the mean July surface water temperature.

The time-trend analysis reveals that the composition of the chironomid community at Greenstone Lake between 14 500 cal yr BP and ~13 700 cal yr BP is not encompassed by the modern calibration dataset. Currently, there are no lakes in the Sierra Nevada calibration set in which the proportional representation of *Heterotrissocladius* taxa exceeds 30%. Late-glacial sediments from northern European lakes are commonly characterized by high levels of *Heterotrissocladius*, as well as other cold stenothermous taxa such as *Sergentia coracina* and *Tanytarsus lugens* (Brundin, 1949). However, contiguous subfossil chironomid assemblages exclusively consisting of *Heterotrissocladius* have yet to be documented. As far as we are aware the only modern analogue for the chironomid assemblage in GSL-1 comes from Chlorine Lake, a high-elevation lake located in southwestern British Columbia, Canada (Walker and Mathewes, 1989a). A surface sample collected from this lake consists almost entirely of *Heterotrissocladius*. The measured surface water temperature of Chlorine Lake was 2°C (Walker and Mathewes, 1989a). *Pseudodiamesa*, which is also present in GSL-1, has a surface water temperature optimum of approximately 7°C in both eastern North America and northwestern Europe (Walker et al., 1997;

Brooks and Birks, 2001). Given the poor calibration of the late-glacial samples in GSL-1, it is quite likely, based on the limited ecological data available from Chlorine Lake and the presence of *Pseudodiamesa*, that any chironomid-inferred temperatures using the current Sierra Nevada calibration dataset are significantly overestimated prior to 13 700 cal yr BP. It is for this reason that no quantitative chironomid-based temperature reconstruction is available for the interval between 14 800 cal yr BP and 13 700 cal yr BP. Expansion of the modern calibration dataset will enable us to incorporate colder lakes into the calibration set, which should improve the accuracy of the chironomid-based temperature inferences for the immediate post-glacial period.

Much of what is known about late Pleistocene and early Holocene environments and climate in the central Sierra Nevada is based upon macrofossil and pollen analyses of packrat middens and lake and meadow sediment. Based on packrat evidence Cole (1983) suggests that the late Pleistocene and early Holocene in the western Sierra Nevada was characterized by an increasingly continental climate that was colder and drier than at present. In general, the palynological research carried out in the central Sierra Nevada illustrates a similar trend of late Pleistocene and early Holocene aridity (Adam, 1967; Davis et al., 1985; Davis and Moratto, 1988; Anderson, 1990; Anderson and Smith, 1994). Based on palynological studies of sediment recovered from lakes located in the sub-alpine and upper montane forest of the eastern Sierra Nevada, Anderson (1990) determined that prior to 10 000 ^{14}C yr BP trees were absent or sparsely established around these sites. Open ground vegetation, such as *Chrysolepis sempervirens*, *Cercocarpus*, *Arctostaphylos* and other Compositae, was more abundant during the late Pleistocene and early Holocene further substantiating the existence of xerothermic conditions during this interval. However, little is still known about the specifics in terms of the magnitude and rate of change of the thermal regime during the Pleistocene–Holocene transition period.

The chironomid-based quantitative surface water temperature reconstruction (Fig. 6) suggests that post-glacial climatic amelioration in the vicinity of Greenstone Lake was essentially sigmoidal rising from approximately 12°C to approximately 17°C between 13 400 cal yr BP and 10 600 cal yr BP. However, the immediate post-glacial period (14 800–13 700 cal yr BP) was characterized by extremely low lake water temperatures, which were likely < 5°C. Glacial meltwater from the nearby Conness Glacier was likely flowing into Greenstone Lake during this period depressing lake water temperatures. Between 13 300 cal yr BP and 12 700 cal yr BP an approximately 1°C increase in lake water temperature occurred with surface water temperatures reaching 13.4°C by 12 700 cal yr BP. This warming trend continued to approximately 12 000 cal yr BP at which time surface water temperatures had reached a post-glacial high of 15.5°C. However, the interval between 12 000 cal yr BP and 11 500 cal yr BP may have been characterized by decreasing surface water temperatures, with chironomid-inferred water temperatures dropping to 14.9°C by 11 500 cal yr BP. A brief increase in lake water temperature was followed by another short-term cooling event, which ended at 11 000 cal yr BP. By 10 500 cal yr BP surface water temperatures at Greenstone Lake had reached 16.7°C.

The slight decline in surface water temperature between 12 000 cal yr BP and 11 500 cal yr BP, during which time surface water temperature dropped from 15.5°C to 14.9°C, is potentially important. It is possible that this chironomid-inferred cooling is a manifestation of the Younger Dryas. Recent work has provided evidence that the Younger Dryas climatic oscillation impacted western North America (Reasoner et al., 1994; Menounos and Reasoner, 1997), eastern California (Benson et al., 1996, 1997) and coastal California (Kennett and Ingram, 1995). However, Benson's work has not resolved whether the negative hydrologic balance that Owens Lake experienced during this period was a result of reduced runoff from the Sierra Nevada or increased evaporation attributable to higher summer temperatures, or some combination of both of these factors.

It is difficult to make any definitive conclusions about the cause and significance of the cooling that is inferred to have occurred between 11 200 and 10 700 cal yr BP; the timing of this event does not correspond well to any known climatic events in the Sierra Nevada. The pause in post-glacial climatic amelioration that may have occurred between 12 000 cal yr BP and 11 500 cal yr BP may be correlative to the Younger Dryas. However, it is equally likely that this event may simply be a result of localized changes in climate or an increase in glacial meltwater inputs from the nearby Conness Glacier to Greenstone Lake. Although the evidence from Greenstone Lake in terms of sediment lithology and faunal changes does not unambiguously support the presence of an extended period of cooling during the Younger Dryas, it is also interesting to note that a similar low-amplitude change in water temperature during the Younger Dryas chronozone has been reported from high-elevation lakes in eastern North America. Cwynar and Spear (2001) have determined that high-elevation sites in the White Mountains of New Hampshire, USA, did not register a strong Younger Dryas signal, while mid-elevation sites, which had experienced significant warming prior to the Younger Dryas, did register a cooling of approximately 5°C. Further work is required on a variety of sites at different elevations in the Sierra Nevada to determine if late Pleistocene climatic oscillations similar to those detected in the circum-North Atlantic and elsewhere are unequivocally present in California.

6. Conclusion

This is the first quantitative chironomid-based reconstruction of late Pleistocene and early Holocene surface water temperatures for the western USA. The chironomid-based temperature reconstruction suggests that the immediate post-glacial period (14 800–13 700 cal yr BP) was characterized by extremely cold surface water temperatures, which were likely < 5°C. Between 13 700 and 12 000 cal yr BP surface water temperatures rose approximately 2°C reaching a post-glacial high of 15.5°C at 12 000 cal yr BP. This was followed by a 500-year period of depressed water temperatures, which may be correlative with the Younger Dryas. The early Holocene was characterized by warmer conditions with surface water temperatures fluctuating between 15.5°C and 16.5°C. Expansion of the modern calibration dataset, to include additional lakes with lower surface water temperatures than currently exist in dataset, should enable us to make more accurate, quantitative inferences of water temperature during the immediate post-glacial period. However, this study does substantiate the use of chironomids in deriving quantitative estimates of past thermal regimes, which should prove quite valuable in improving our understanding of late Quaternary environments and climate in the Sierra Nevada and the surrounding region.

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References

Adam, D.P., 1967. Late-Pleistocene and recent palynology in the central Sierra Nevada, California. In: Cushing, E.J., Wright, H.E. (Eds.), Quaternary Paleoecology. Yale University Press, New Haven, CT, pp. 275–301.

Andersen, F.S., 1938. Spätglaciale Chironomiden. Medd. Dansk Geol. Fören. 9, 320–326.

Anderson, R.S., 1990. Holocene forest development and paleoclimates within the central Sierra Nevada, California. J. Ecol. 78, 470–489.

Anderson, R.S., Smith, S., 1994. Paleoclimatic interpretations of meadow sediment and pollen stratigraphies from California. Geology 22, 723–726.

Battarbee, R.W., 2000. Paleolimnological approaches to climate change, with special regard to the biological record. Quat. Sci. Rev. 19, 107–124.

Battarbee, R.W., Thompson, R., Catalan, J., Grytnes, J.A., Birks, H.J.B., 2002. Climate variability and ecosystem dynamics of remote alpine arctic lakes: the MOLAR project. J. Paleolimnol. 28, 1–6.

Benson, L.V., Burdett, J.W., Kashgarian, M., Lund, S.P., Phillips, F., Rye, R., 1996. Climate and hydrologic oscillations in the Owens Lake basin and adjacent Sierra Nevada, California. Science 274, 746–749.

Benson, L.V., Burdett, J.W., Lund, S.P., Kashgarian, M., Mensing, S., 1997. Nearly synchronous climate change in the Northern Hemisphere during the last glacial termination. Nature 388, 263–265.

Benson, L.V., Lund, S.P., Burdett, J.W., Kashgarian, M., Rose, T.P., Smoot, J.P., Schwartz, M., 1998. Correlation of late-Pleistocene lake-level oscillations in Mono lake California, with north Atlantic climate events. Quat. Res. 49, 1–10.

Benson, L., Kashgarian, M., Rye, R., Lund, S.P., Paillet, F., Smoot, J., Kester, C., Mensing, S., Meko, D., Lindström, S., 2002. Holocene multidecadal and multicentennial droughts affecting Northern California and Nevada. Quat. Sci. Rev. 21, 659–682.

Birks, H.J.B., 1998. Numerical tools in paleolimnology – Progress, potentialities, and problems. J. Paleolimnol. 20, 307–322.

Birman, J.H., 1964. Glacial geology across the crest of the Sierra Nevada, California. Geol. Soc. Am. Spec. Pap. 75, 1–80.

Blackwelder, E., 1931. Pleistocene glaciation in the Sierra Nevada and Basin Ranges. Geol. Soc. Am. Bull. 42, 865–922.

Bradbury, J.P., 1997. A diatom record of climate and hydrology for the past 200 ka from Owens Lake, California, with comparison to other Great Basin records. Quat. Sci. Rev. 16, 203–219.

Brooks, S.J., 2000. Late-glacial fossil midge stratigraphies (Insecta: Diptera: Chironomidae) from the Swiss Alps. Palaeogeogr. Palaeoclimatol. Palaeoecol. 159, 261–279.

Brooks, S.J., Birks, H.J.B., 2000. Chironomid-inferred late-glacial and early-Holocene mean July air temperatures for Kråkenes lake, western Norway. J. Paleolimnol. 23, 77–89.

Brooks, S.J., Birks, H.J.B., 2001. Chironomid-inferred air temperatures from Lateglacial and Holocene sites in north-west Europe: progress and problems. Quat. Sci. Rev. 20, 1723–1741.

Brundin, L., 1949. Chironomiden und andere Bodentiere der südschwedischen Urgebirgsseen. Rep. Inst. Freshwater Res. Drottningholm 30, 1–914.

Burke, R., Birkeland, P., 1983. Holocene glaciation in the mountain ranges of western United States. Holocene 2, 3–11.

Clark, D., Gillespie, A., 1997. Timing and significance of late-glacial and Holocene cirque glaciation in the Sierra Nevada, California. Quat. Int. 38/39, 21–38.

Cole, K.L., 1983. Late Pleistocene vegetation of Kings Canyon, Sierra Nevada, California. Quat. Res. 19, 117–129.

Cranston, P.S., 1982. A key to the larvae of the British Orthocladiinae (Chironomidae). Sci. Publ. Freshwater Biol. Assoc. 45, 1–152.

Curry, R.R., 1969. Holocene climatic and glacial history of the central Sierra Nevada, California. In: Schumm, S.A., Bradley, W.C. (Eds.), United States Contributions to Quaternary Research. Geol. Soc. Am. Spec. Pap. 123, 1–47.

Cwynar, L.C., Levesque, A.J., 1995. Chironomid evidence for late-glacial climatic reversals in Maine. Quat. Res. 43, 405–413.

Cwynar, L.C., Spear, R.W., 2001. Lateglacial climate change in the White Mountains of New Hampshire. Quat. Sci. Rev. 20, 1265–1274.

Davis, O.K., Anderson, R.S., Fall, P., O'Rourke, M., Thompson, R.S., 1985. Palynological evidence for early Holocene aridity in the southern Sierra Nevada, California. Quat. Res. 24, 322–332.

Davis, O.K., Moratto, M.J., 1988. Evidence for a warm dry early Holocene in the western Sierra Nevada of California: pollen and macrofossil analysis of Dinkey and Exchequer Meadows. Madrono 35, 132–149.

Dean, W.E., Jr., 1974. Determination of carbonate and organic matter in calcareous sediments and sedimentary rock by loss-on-ignition: comparison with other methods. J. Sediment. Petrol. 44, 242–248.

Douglas, M.S.V., Smol, J.P., Blake, W., 1994. Marked post-18th century environmental change in high-arctic ecosystems. Science 266, 416–419.

Glew, J., 1991. Miniature gravity corer for recovering short sediment cores. J. Paleolimnol. 5, 285–287.

Hann, B.J., Warner, B.G., Warwick, W.F., 1992. Aquatic invertebrates climate change: a comment on Walker et al. (1991). Can. J. Fish. Aquat. Sci. 49, 1274–1276.

Heiri, O., Lotter, A.F., 2001. Effect of low count sums on quantitative environmental reconstructions: an example using subfossil chironomids. J. Paleolimnol. 26, 343–350.

IPCC, 2001. Climate Change 2001: The Scientific Basis. Summary for Policymakers: A Report of Working Group I of the Intergovernmental Panel on Climate Change. http://www.ipcc.ch/pub.spm22-01.pdf.

Juggins, S., 1991. ZONE, version 1.2 (unpublished). University of Newcastle.

Juggins, S., ter Braak, C.F.J., 1996. WA-PLS, version 1.1. (unpublished).

Kennett, J.P., Ingram, B.L., 1995. A 20,000-year record of ocean circulation and climate change from the Santa Barbara basin. Nature 377, 510–514.

Konrad, S.K., Clark, D.H., 1998. Evidence for an early Neoglacial glacier advance from rock glaciers and lake sediments in the Sierra Nevada, California, U.S.A. Arct. Alp. Res. 30, 272–284.

Korhola, A., Olander, H., Blom, T., 2000. Cladoceran and chironomid assemblages as qualitative indicators of water depth in subarctic Fennoscandian lakes. J. Paleolimnol. 24, 43–54.

Larocque, I., Hall, R.I., Grahn, E., 2001. Chironomids as indicators of climate change: a 100-lake training set from a subarctic region of northern Sweden (Lapland). J. Paleolimnol. 26, 307–322.

Levesque, A.J., Mayle, F.E., Walker, I.R., Cwynar, L.C., 1993. A previously unrecognized late-glacial cold event in eastern North America. Nature 361, 623–626.

Levesque, A.J., Cwynar, L.C., Walker, I.R., 1996. Richness, diversity and succession of late-glacial chironomid assemblages in New Brunswick, Canada. J. Paleolimnol. 16, 257–274.

Levesque, A.J., Cwynar, L.C., Walker, I.R., 1997. Exceptionally steep north-south gradients in lake temperatures during the last deglaciation. Nature 385, 423–426.

Lotter, A.F., Birks, H.J.B., Hofmann, W., Marchetto, A., 1997. Modern diatom, cladocera, chironomid, and chrysophyte cyst assemblages as quantitative indicators for the reconstruction of past environmental conditions in the Alps. I. Climate. J. Paleolimnol. 18, 395–420.

Lotter, A.F., Birks, H.J.B., Hofmann, W., Marchetto, A., 1998. Modern diatom, Cladocera, chironomid, and chrysophyte cyst assemblages as quantitative indicators for the reconstruction of past environmental conditions in the Alps. II Nutrients. J. Paleolimnol. 19, 443–463.

MacDonald, G.M., Beukens, R.P., Kieser, W.E., 1991. Radiocarbon dating of limnic sediments: a comparative analysis and discussion. Ecology 72, 1150–1155.

Major, J., 1988. California climate in relation to vegetation. In: Barbour, M., Major, J. (Eds.), Terrestrial Vegetation of California. California Native Plant Soc. Spec. Publ. 9, 11–74.

Matthes, F.E., 1939. Report of Committee on Glaciers, April 1939. AGU Trans., 518–523.

Menounos, B., Reasoner, M.A., 1997. Evidence for cirque glaciation in the Colorado Front Range during the Younger Dryas chronozone. Quat. Res. 48, 38–47.

Olander, H., Birks, H.J.B., Korhola, A., Blom, T., 1999. An expanded calibration model for inferring lakewater and air temperatures from fossil chironomid assemblages in northern Fennoscandia. Holocene 9, 279–294.

Oliver, D.R., Roussel, M.E., 1983. The insects and arachnids of Canada, Part II: The genera of larval midges of Canada-Diptera: Chironomidae. Agric. Can. Publ. 1746, 1–263.

Palmer, S.L., Walker, I.R., Heinrichs, M.L., Hebda, R.J., Scudder, G.G., 2002. Postglacial midge community change and Holocene paleotemperature reconstructions near treeline, southern British Columbia (Canada). J. Paleolimnol. 28, 469–490.

Phillips, F., Zreda, M.G., Benson, L., Plummer, M., Elmore, D., Sharma, P., 1996. Chronology for fluctuations in Late-Pleistocene Sierra Nevada glaciers and lakes. Science 274, 749–751.

Porinchu, D.F., Cwynar, L.C., 2000. The distribution of freshwater Chironomidae (Insecta: Diptera) across treeline near the lower Lena River, northeast Siberia. Arct. Antarct. Alp. Res. 32, 429–437.

Porinchu, D.F., Cwynar, L.C., 2002. Late-Quaternary history of midge communities and climate from a tundra site near the lower Lena River, northeast Siberia. J. Paleolimnol. 27, 59–69.

Porinchu, D.F., MacDonald, G.M., Bloom, A.M., Moser, K.A., 2002. The modern distribution of chironomid sub-fossils (Insecta: Diptera) in the Sierra Nevada, California: Potential for paleoclimatic reconstructions. J. Paleolimnol. 28, 355–375.

Porinchu, D.F., MacDonald, G.M., 2003. The use and application of freshwater midges (Insecta: Diptera: Chironomidae) in geographical research. Prog. Phys. Geogr. 27, 409–453.

Quinlan, R., Smol, J.P., 2001. Setting minimum head capsule abundance and taxa criteria in chironomid-based inference models. J. Paleolimnol. 26, 327–342.

Raphael, M., Mills, G., 1996. The role of mid-latitude Pacific cyclones in the winter precipitation of California. Prof. Geogr. 48, 251–262.

Reasoner, M.A., Osborn, G., Rutter, N.W., 1994. Age of the Crowfoot advance in the Canadian Rockies: A glacial advance coeval with the Younger Dryas oscillation. Geology 22, 439–442.

Russell, I.C., 1889. Geological History of Mono Valley, California. United States Geological Survey Eight Annual Report, Part I, pp. 261–394.

Schindler, D.W., Beaty, K.G., Fee, E.J., Cruikshank, D.R., DeBuryn, E.R., Findlay, D.L., Linsey, G.A., Shearer, J.A., Stainton, M.P., Turner, M.A., 1990. Effects of climatic warming on lakes of the central boreal forest. Science 250, 967–970.

Seppä, H., Nyman, M., Korhola, A., Weckström, J., 2001. Changes of treelines and alpine vegetation in relation to post-glacial climate dynamics in northern Fennoscandia based on pollen and chironomid records. J. Quat. Sci. 17, 287–301.

Sietz, J.F., 1983. Geologic Map of the Tioga Lake, Hall Natural Area, Log-Cabin Saddlebag, and Horse Meadows Roadless Areas, Mono County. United States Geological Survey, MF-1453-A, scale 1:62 500.

Simpson, K.W., Bode, R.W., 1980. Common larvae of Chironomidae (Diptera) from New York State streams and rivers with particular reference to the fauna of artificial substrates. Bull. New York State Mus. 439, 1–105.

Smith, M.J., Pellatt, M.G., Walker, I.R., Mathewes, R.W., 1998. Postgalcial changes in chironomid communities and inferred climate near treeline at Mount Stoyoma, Cascade Mountains, southwestern British Columbia Canada. J. Paleolimnol. 20, 277–293.

Smol, J.P.S., Cumming, B.F., 2000. Tracking long-term changes in climate using algal indicators in lake sediments. J. Phycol. 36, 986–1011.

Stine, S., 1994. Extreme and persistent drought in California and Patagonia during mediaeval time. Nature 369, 546–549.

Stuiver, M., Reimer, P.J., Bard, E., Beck, J.W., Burr, G.S., Hughen, K.A., Kromer, B., McCormac, F.G., van der Plicht, J., Spurk, M., 1998. INTCAL 98 radiocarboncalibration, 24,000–0 cal B.P. Radiocarbon 40, 1041–1083.

ter Braak, C.J.F., Smilauer, P., 1998. CANOCO Reference Manual and User's Guide to CANOCO for Windows: Software for Canonical Community Ordination (version 4). Microcomputer Power, Ithaca, NY, 352 pp.

Thienemann, A., 1918. Untersuchungen über die Beziehungen zwischen dem Sauerstoffgehalt des Wassers und der Zusammensetzung der fauna in Norddeutschen Seen. Arch. Hydrobiol. 82, 316–346.

Walker, I.R., 1987. Chironomidae (Diptera) in paleoecology. Quat. Sci. Rev. 6, 29–40.

Walker, I.R., 1988. Late-Quaternary Paleoecology of Chironomidae (Diptera: Insecta) from Lake Sediments in British Columbia. Ph.D. Dissertation, Simon Fraser University, Burnaby, BC. 204 pp.

Walker, I.R., 1990. Modern assemblages of arctic and alpine Chironomidae as analogues for late-glacial communities. Hydrobiologia 214, 223–227.

Walker, I.R., 2000. The WWW Field Guide to Subfossil Midges. http://www.ouc.bc.ca/eesc/iwalker/wwwguide/.

Walker, I.R., MacDonald, G.M., 1995. Distributions of Chironomidae (Insecta: Diptera) and other freshwater midges with respect to treeline, Northwest Territories, Canada. Arct. Antarct. Alp. Res. 27, 258–263.

Walker, I.R., Mathewes, R.W., 1989a. Chironomidae (Diptera) remains in surficial lake sediments from the Canadian Cordillera: analysis of the fauna across an altitudinal gradient. J. Paleolimnol. 2, 61–80.

Walker, I.R., Mathewes, R.W., 1989b. Early postglacial chironomid succession in southwestern British Columbia, and its paleoenvironmental significance. J. Paleolimnol. 2, 1–14.

Walker, I.R., Smol, J.P., Engstrom, D.R., Birks, H.J.B., 1991a. An assessment of Chironomidae as quantitative indicators of past climate change. Can. J. Fish. Aquat. Sci. 48, 975–987.

Walker, I.R., Mott, R.J., Smol, J.P., 1991b. Allerød-Younger Dryas lake temperatures from midge fossils in Atlantic Canada. Science 253, 1010–1012.

Walker, I.R., Levesque, A.F., Cwynar, L.C., Lotter, A.F., 1997. An expanded surface-water paleotemperature inference model for use with fossil midges in eastern Canada. J. Paleolimnol. 18, 165–178.

Western Regional Climate Center, 2002. http://www.wrcc.dri.edu. Retrieved from the World Wide Web July 15, 2002.

Wiederholm, T. (Ed.), 1983. Chironomidae of the Holarctic region. Keys and diagnoses. Part I – Larvae. Entomol. Scand. Suppl. 19, 1–457.

Wright, H.E., 1991. Coring tips. J. Paleolimnol. 6, 37–50.