Diatom-inference models for surface-water temperature and salinity developed from a 57-lake calibration set from the Sierra Nevada, California, USA

Amy M. Bloom[1,*], Katrina A. Moser[1], David F. Porinchu[2] and Glen M. MacDonald[2,3]

[1]*Department of Geography, University of Utah, 260 South Central Campus Drive, Room 270, Salt Lake City, Utah 84112–9155, USA;* [2]*Department of Geography, University of California at Los Angeles, 1255 Bunche Hall, Los Angeles, California 90095–1524, USA;* [3]*Department of Organismic Biology, Ecology and Evolution, University of California at Los Angeles, 405 Hilgard Avenue, Los Angeles, California 90095– 1524, USA;* [*]*Author for correspondence (e-mail: amy.bloom@geog.utah.edu)*

Abstract

Physical, chemical, and biological data were collected from a suite of 57 lakes that span an elevational gradient of 1360 m (2115 to 3475 m a.s.l.) in the eastern Sierra Nevada, California, USA as part of a multiproxy study aimed at developing transfer functions from which to infer past drought events. Multivariate statistical techniques, including canonical correspondence analysis (CCA), were used to determine the main environmental variables influencing diatom distributions in the study lakes. Lakewater depth, surface-water temperature, salinity, total Kjeldahl nitrogen, and total phosphorus were important variables in explaining variance in the diatom distributions. Weighted-averaging (WA) and weighted-averaging partial least squares (WA-PLS) were used to develop diatom-based surface-water temperature and salinity inference models. The two best diatom-inference models for surface-water temperature were developed using simple WA and inverse deshrinking. One model covered a larger surface-water temperature gradient (13.7 °C) and performed slightly poorer ($r^2 = 0.72$, RMSE = 1.4 °C, $RMSEP_{jack}$ = 2.1 °C) than a second model, which covered a smaller gradient (9.5 °C) and performed slightly better ($r^2 = 0.89$, RMSE = 0.7 °C, $RMSEP_{jack}$ = 1.5 °C). The best diatom-inference model for salinity was developed using WA-PLS with three components ($r^2 = 0.96$, RMSE = 4.06 mg L^{-1}, $RMSEP_{jack}$ = 11.13 mg L^{-1}). These are presently the only diatom-based inference models for surface-water temperature and salinity developed for the southwestern United States. Application of these models to fossil-diatom assemblages preserved in Sierra Nevada lake sediments offers great potential for reconstructing a high-resolution time-series of Holocene and late Pleistocene climate and drought for California.

Introduction

As population, irrigation-dependent agriculture, and the need for energy increases in water-limited California, it is essential to know the magnitude and possible recurrence interval of long-term (multidecadal) drought events for successful, long-term, water-resource management. Instrumental records of climate are not available on long time scales (i.e., 100s and 1000s of years), but proxy indicators of climate can be used to document and understand past drought events. Because much of California's freshwater originates in the Sierra Nevada, paleoindicators preserved in Sierra Nevada lake sediments potentially provide such records of paleodrought. Diatoms are one paleoindicator that have been shown to be particularly useful in determining past droughts (reviewed in Fritz et al. (1999), Smol and Cumming (2000)).

Several studies have shown a significant relationship between surface-water temperature and diatom-

community composition (Pienitz et al. 1995; Vyverman and Sabbe 1995; Wunsam et al. 1995; Weckström et al. 1997a, 1997b; Bigler et al. 2000; Joynt and Wolfe 2001), whereas other studies have shown a significant relationship between air temperature and diatom-community composition (Lotter et al. 1997; Korhola et al. 2000; Rosén et al. 2000; Joynt and Wolfe 2001; Bigler and Hall 2002). Diatom distributions have also been shown to vary with physical and chemical limnological changes resulting, in part, due to variations in effective moisture (precipitation minus evaporation). For example, diatom distributions are influenced by lake depth (Gregory-Eaves et al. 1999; Wolin and Duthie 1999; Moser et al. 2000) and salinity (reviewed in Fritz et al. (1999)), which are both a function of effective moisture. Leavitt et al. (1997) showed the sensitivity of alpine lakes in the Canadian Rocky Mountains to climate change and drought by studying fossil ultraviolet-radiation absorbing algal pigments. An increase in the penetration of ultraviolet radiation was seen when dissolved organic carbon (DOC) was reduced due to periods of drought. Sylvestre et al. (2001) have developed diatom-inference models for salinity and ionic concentration using diatoms preserved in lake sediments from alpine lakes in the southern Bolivian Altiplano. Application of these models to a lake-sediment core from the Coipasa basin show that this basin responded dramatically to changes in effective moisture between 21,000–17,500 ^{14}C yr BP (Sylvestre 2002).

In this paper we examine the relationship between modern-diatom distribution and environment and the use of diatoms recovered from modern-surface (0–1 cm) lake sediments from the eastern Sierra Nevada, California, USA to develop inference models to infer past climate conditions (i.e., temperature and effective moisture). This paper is a companion paper to Porinchu et al. (2002), which develops chironomid-based inference models for surface-water temperature from the same study lakes. Ultimately, these diatom- and chironomid-based inference models will be applied to fossil-diatom and fossil-chironomid assemblages preserved in Sierra Nevada lake sediments to reconstruct a paleoclimate time-series of drought for this region.

Alpine lakes are particularly sensitive to climate change (Battarbee et al. 2002), and are a common feature of the Sierra Nevada (Holmes et al. 1989). Sierra Nevada lakes are ideal for use in a lake calibration set from which to develop inference models

for air temperature and effective moisture because they are situated along steep air temperature and effective moisture gradients. Even though considerable research is available on Sierra Nevada lakes and freshwater systems (e.g., Bradford et al. (1981), Landers et al. (1987), Williams and Melack (1991), Leydecker et al. (1999)), relatively few studies have examined diatoms preserved in sediments from Sierra Nevada lakes, and those that have, have focused on using diatoms to reconstruct changes in lakewater pH (Holmes et al. 1989; Whiting et al. 1989). Although previous researchers have used pollen (e.g., Davis et al. (1985), Anderson (1990), Smith and Anderson (1992), Koehler and Anderson (1994)), tree rings (e.g., Graumlich (1993), Scuderi (1993), Lloyd and Graumlich (1997)), and glacial geomorphology (e.g., Clark and Gillespie (1997), Konrad and Clark (1998)) to study climatic change in the Sierra Nevada, the region is a relatively untapped archive of environmental change with respect to paleolimnological research.

Study area

The study area is located in the eastern Sierra Nevada, California, USA, between Bridgeport and Independence (Figure 1). Local topographic relief is large with elevations ranging from 1080 m a.s.l. in Owens Valley on the east side of the study area to Mt. Whitney at 4418 m a.s.l., the highest peak along the crest of the range. Underlying bedrock in the study area is dominated by granitic, volcanic, and metasedimentary lithologies that range in age from Cretaceous to recent. In addition, the study site has been greatly impacted by Pleistocene glaciation and is intermittently covered with glacial and alluvial sediments. Most of the lakes in the Sierra Nevada are of glacial or volcanic origin.

The current climate of the Sierra Nevada region is dominated by warm-dry summers and cool-humid winters (Major 1988). Almost all precipitation occurs in the winter months. Large-scale climatic phenomena are mainly responsible for the seasonal timing of precipitation in the Sierra Nevada. Winter months are characterized by heavy precipitation from eastward moving cyclonic storms brought to California by a southward shift in the position of the jet stream. Storm incidence appears to be influenced by the intensity of the Pacific High and sea surface temperatures (Mitchell 1976; Mock 1996). During summer months, precipitation decreases due to the increased influence
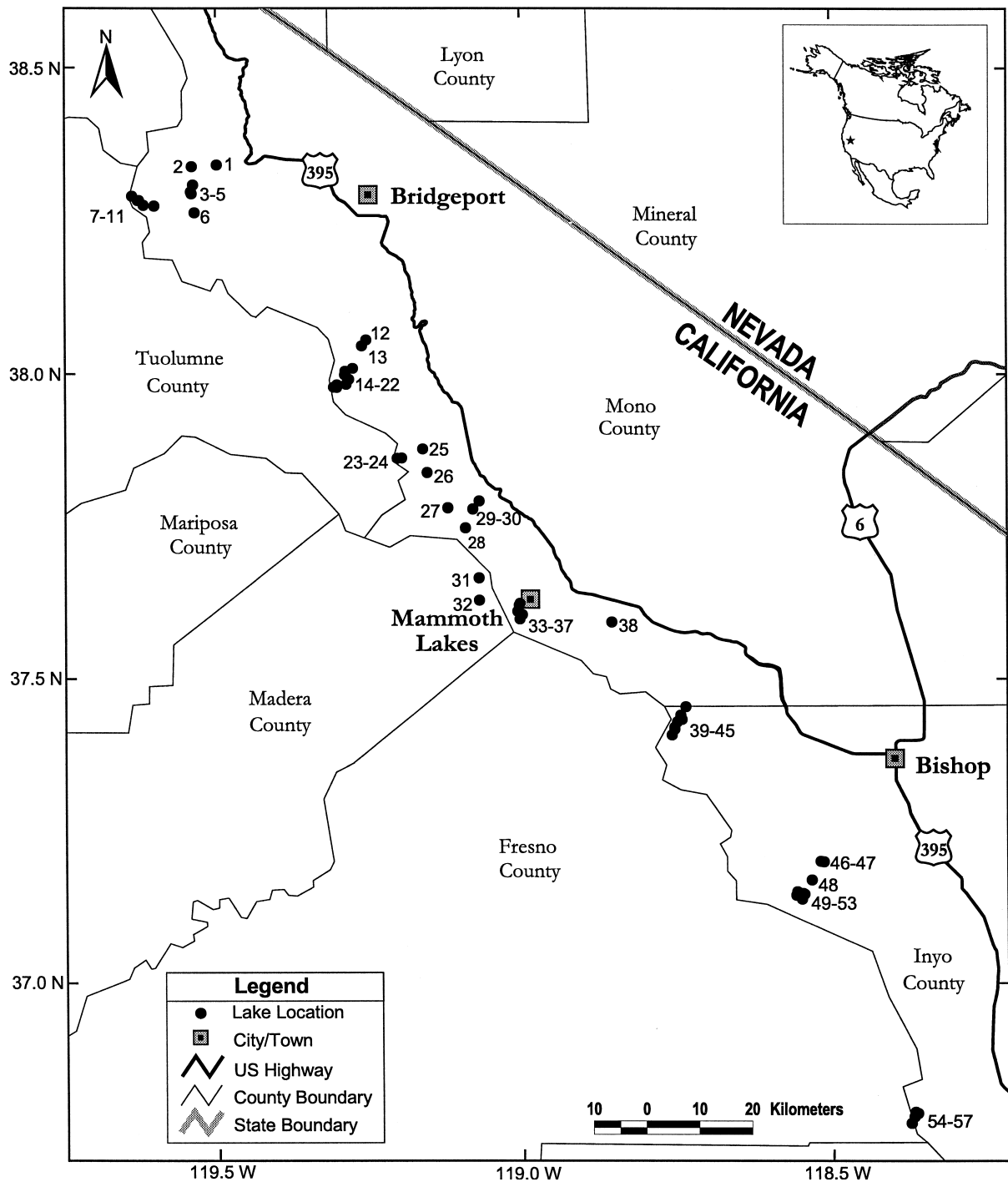
Figure 1. Map of the study area showing the locations of the 57 lakes in the eastern Sierra Nevada, California, USA sampled for this study. Lakes are numerically coded corresponding to Table 1 (e.g., lake 1 on map = lake SN1 in Table 1).

of the Pacific High (Mock 1996). Superimposed on these patterns are the effects of topography, which greatly affect air temperature and the distribution of

precipitation (Anderson et al. 1997). As air masses travel inland from the Pacific Ocean they lose moisture, particularly at high elevations. Because the study

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Table 1. Lake code (corresponding to the study map, Figure 1) and respective lake name (* indicates unofficial name), latitude, longitude, and elevation for the 57 study lakes in the eastern Sierra Nevada, California, USA. A Global Positioning System (GPS) was used to determine the latitude and longitude. The elevation was determined using United States Geological Survey (USGS) 7.5'' quadrangle maps.

Lake code	Lake name	Latitude (North)	Longitude (West)	Elevation (m a.s.l.)
SN1	Kirman Lake	38° 20′ 24″	119° 29′ 59″	2174
SN2	Millie Lake	38° 20′ 14″	119° 32′ 25″	2115
SN3	Secret Lake	38° 18′ 25″	119° 32′ 18″	2272
SN4	Roosevelt Lake	38° 17′ 44″	119° 32′ 31″	2213
SN5	Lane Lake	38° 17′ 33″	119° 32′ 28″	2213
SN6	Hidden Lake	38° 15′ 40″	119° 32′ 10″	2379
SN7	Latopie Lake	38° 17′ 19″	119° 38′ 14″	3145
SN8	Koenig Lake	38° 16′ 53″	119° 37′ 42″	2905
SN9	Koenig Lake 2*	38° 16′ 53″	119° 37′ 35″	2897
SN10	Leavitt Lake	38° 16′ 24″	119° 37′ 08″	2896
SN11	Ski Lake	38° 16′ 21″	119° 36′ 05″	2972
SN12	Trumbull Lake	38° 03′ 12″	119° 15′ 26″	2921
SN13	Red Lake	38° 02′ 35″	119° 15′ 51″	2978
SN14	Moat Lake	38° 03′ 22″	119° 16′ 45″	3197
SN15	Lake Helen	38° 00′ 05″	119° 17′ 30″	3054
SN16	East Twin Lake*	37° 59′ 46″	119° 17′ 31″	3145
SN17	West Twin Lake*	37° 59′ 43″	119° 17′ 32″	3152
SN18	Hummingbird Lake	37° 59′ 16″	119° 17′ 08″	3105
SN19	Greenstone Lake	37° 58′ 47″	119° 17′ 24″	3067
SN20	Upper Conness Lake 1*	37° 58′ 30″	119° 18′ 37″	3280
SN21	Lower Conness Lake*	37° 58′ 28″	119° 18′ 19″	3220
SN22	Upper Conness Lake 2*	37° 58′ 44″	119° 18′ 18″	3251
SN23	Lower Sardine Lake*	37° 51′ 30″	119° 11′ 59″	2996
SN24	Sardine Adjacent Lake*	37° 51′ 29″	119° 12′ 25″	3170
SN25	Walker Lake	37° 52′ 24″	119° 09′ 54″	2405
SN26	Parker Lake	37° 50′ 04″	119° 09′ 29″	2520
SN27	Silver Lake	37° 46′ 37″	119° 07′ 28″	2186
SN28	Yost Lake	37° 44′ 39″	119° 05′ 44″	2756
SN29	June Lake	37° 47′ 17″	119° 04′ 23″	2309
SN30	Gull Lake	37° 46′ 30″	119° 05′ 00″	2303
SN31	Starkweather Lake	37° 39′ 46″	119° 04′ 25″	2424
SN32	Satcher Lake	37° 37′ 35″	119° 04′ 24″	2313
SN33	Twin Lakes 1*	37° 37′ 17″	119° 00′ 24″	2595
SN34	Twin Lakes 2*	37° 37′ 05″	119° 00′ 29″	2595
SN35	Lake Mammie	37° 36′ 29″	119° 00′ 38″	2694
SN36	Lake Mary	37° 36′ 10″	119° 00′ 11″	2714
SN37	Lake Barrett	37° 35′ 44″	119° 00′ 25″	2816
SN38	Convict Lake	37° 35′ 26″	119° 51′ 25″	2309
SN39	Rock Creek Lake	37° 27′ 07″	119° 44′ 11″	2938
SN40	Serene Lake	37° 26′ 18″	119° 44′ 39″	3108
SN41	Eastern Brook Lake	37° 25′ 52″	119° 44′ 32″	3131
SN42	Mack Lake	37° 25′ 38″	119° 34′ 01″	3155
SN43	Heart Lake	37° 25′ 06″	119° 45′ 16″	3160
SN44	Box Lake	37° 24′ 54″	119° 45′ 15″	3178
SN45	Long Lake	37° 24′ 20″	119° 45′ 31″	3194
SN46	Rocky Bottom Lake	37° 12′ 01″	119° 31′ 02″	3180
SN47	Funnel Lake	37° 11′ 59″	119° 30′ 43″	3180
SN48	Green Lake	37° 10′ 10″	119° 31′ 55″	3350
SN49	Bull Lake	37° 09′ 00″	119° 33′ 18″	3268
SN50	Long Lake 2*	37° 09′ 39″	119° 33′ 24″	3258
SN51	Chocolate Lake 2*	37° 08′ 51″	119° 32′ 44″	3355
SN52	Chocolate Lake 1*	37° 08′ 47″	119° 32′ 38″	3355
SN53	Ruwau Lake	37° 08′ 17″	119° 32′ 52″	3347
SN54	Golden Trout Lake 2*	36° 47′ 20″	119° 22′ 00″	3475
SN55	Golden Trout Lake 3*	36° 47′ 13″	119° 21′ 44″	3440
SN56	Golden Trout Lake	36° 46′ 52″	119° 22′ 05″	3463
SN57	Big Pothole Lake	36° 46′ 15″	119° 22′ 22″	3431

area is situated on the leeside of the Sierra Nevada crest, precipitation decreases and air temperature increases with decreasing elevation (Table 2, Porinchu et al. (2002)).

Vegetation in the Sierra Nevada is strongly influenced by climate, and therefore changes with elevation. The study area is comprised of several vegetation zones (Major 1988) including, from low to high elevation: pinyon pine-juniper woodland, jeffrey pine woodland, upper montane forest, subalpine forest, and upper subalpine forest, which are described in more detail in Porinchu et al. (2002).

Fifty-seven lakes were sampled for this study (Figure 1). Table 1 provides a key to the lake codes used in Figure 1, as well as the location and elevation of each study lake. The study lakes are generally small (1–10 ha) and of varying depths (2–40 m), although intermediate depth (4–10 m) lakes were preferentially selected, as they are the most similar to those used for long-coring and paleoenvironmental reconstructions. A majority of the study lakes are located in U.S. National Forests and Wilderness Areas. The lakes span an altitudinal range of 1360 m (2115 to 3475 m a.s.l.), and thus span steep air temperature and effective moisture gradients. They are generally ultra-oligotrophic to oligotrophic and circum-neutral to alkaline. For additional information concerning the study lakes see Porinchu et al. (2002).

Methods

Field methods

During July 21–August 18, 1999, July 15, 2000, and July 20–24, 2001, physical, chemical, and biological data were collected from the 57 lakes. Sampling was performed at this time of year as it was assumed that water temperatures were highest and algal growth was expected to be maximal. Due to logistical restrictions, sampling was done only once at each of the 57 lakes; therefore, all lakewater data collected represent a single-summer measurement for a particular day, not a summer or an annual average. Measurements of physical and chemical variables were taken 0.5 m below the lakewater surface over the deepest part of each lake. Because bathymetric data were unavailable, the depth of the lake at its center was generally assumed to be the deepest and was used to approximate the maximum lake depth (depth). A YSI-M85 meter was used to measure surface-water temperature

(temp) and specific conductivity (spcond). Lakewater pH was measured with both a Corning Checkmate M90 meter and three hand-held Hanna pHep 2 pocket-sized waterproof pH meters. The pH values included in this study are based on an average of the four measurements. Although Secchi depth was measured, this variable was excluded from this study because numerous sites had Secchi depths greater than the lake depth (i.e., the Secchi disk was visible at the bottom of the lake). Surrounding geology and vegetation were also noted at each lake.

A precleaned, 1 L, polyethylene bottle was filled with lakewater from each lake for water chemistry analyses. All 1 L lakewater samples were divided and prepared for various chemical analyses in the field following procedures outlined in the Analytical Methods Manual (Environment Canada, 1996a, 1996b). Samples were kept cool and out of direct sunlight until shipped to the National Environmental Testing Laboratory at the Canada Centre for Inland Waters (C.C.I.W.) in Burlington, Ontario, Canada for analyses of major ions, trace metals, chlorophyll a (Chl a), particulate organic carbon (POC), DOC, and nutrients.

Lake surface-sediment samples were collected using a Glew Mini Corer (Glew 1991). The uppermost 5.0 cm of lake sediment was sectioned at 1.0 cm intervals with a close-interval sectioner (Glew 1988), placed in Whirl-paks®, and kept cool and out of direct sunlight.

A Global Positioning System (GPS) was used to determine the latitude and longitude of each study late. The elevation of each lake was obtained from United States Geological Survey (USGS) 7.5'' quadrangle maps. Lake-surface area was determined using the computer program ArcGIS 8.1 (Environmental Systems Research Institute 2001) and 10 m digital elevation maps (DEMs) obtained from the USGS.

Laboratory methods

For each sample, 36 chemical and nutrient variables were measured by C.C.I.W. Details of these measurements, the salinity calculation (summing Ca, Mg, K, Na, SO_4, dissolved inorganic carbon (DIC), and Cl values), and the measurement of the organic component using loss-on-ignition (LOI) are provided in Porinchu et al. (2002).

Samples from the uppermost 1.0 cm of sediment from each of the 57 study lakes, representing the last few years of sediment accumulation, were prepared

for diatom analysis following standard procedures (Battarbee et al. 2001). Approximately 0.5 g of sediment from each study lake was treated with sulfuric and nitric acids (50:50 molar) to digest organic matter. The samples were then rinsed with distilled water until neutralized (pH = 7). Varying concentrations of the diatom slurries were evaporated onto glass coverslips, which were subsequently mounted onto glass microscope slides using Naphrax®, a medium of high refractive index (refractive index = 1.74). At least 600 diatom valves were identified and enumerated along a minimum of one half of one horizontal transect on each slide using a Nikon Eclipse E6000 microscope equipped with Nomarski differential interference contrast optics and a 100× oil immersion objective (total magnification = 1000×, N.A. = 1.4). Identifications to the lowest taxonomic level (e.g., species or subspecies) were primarily based on Krammer and Lange-Bertalot (1986-1991) and Cumming et al. (1995). Each diatom taxon was photographed with a DAGE MTI video capture camera; plates of the dominant diatom taxa are available in Bloom (2001).

Statistical methods

Diatom and environmental data were screened prior to statistical analysis. In all statistical analyses, a square root transformation was applied to the diatom data and, when the statistical method allowed, rare taxa were downweighted. Ordination was performed to explore the relationships between modern-diatom assemblages and environmental variables, as well as to check the data for outliers. The computer program CANOCO for Windows version 4.02 (ter Braak and Šmilauer 1999) was used for indirect analyses, including principal components analysis (PCA), correspondence analysis (CA), and detrended correspondence analysis (DCA), as well as direct analyses, including redundancy analysis (RDA), canonical correspondence analysis (CCA), and detrended canonical correspondence analysis (DCCA).

In order to develop diatom-inference models, weighted-averaging (WA), partial least squares (PLS), and weighted-averaging partial least squares (WA-PLS) calibration and regression were performed using the computer programs WACALIB version 3.3 (Line et al. 1994) and CALIBRATE version 0.3 (Juggins and ter Braak 1993). The predictive ability of each model developed was evaluated by calculating the coefficient of determination (r^2), the root mean-squared error (RMSE), the root mean-squared error of

prediction (RMSEP) estimated by bootstrapping ($RMSEP_{boot}$) and jackknifing ($RMSEP_{jack}$), the RMSEP as a % of the gradient, and the mean and maximum bias. $RMSEP_{boot}$ was calculated in WACALIB version 3.3 (Line et al. 1994), whereas $RMSEP_{jack}$ and the mean and maximum bias were calculated in CALIBRATE version 0.3 (Juggins and ter Braak 1993). The best models were those with: 1) high r^2-values, 2) low RMSEP-values and RMSEP as a % of the gradient, 3) low mean and maximum bias, and 4) residuals that were random (i.e., no trends) (Birks 1998).

Results and discussion

Data screening

Three hundred and forty-four diatom taxa were identified and enumerated from the 57 study lakes. Initially all taxa were used in the ordination analyses, but a reduced data set (i.e., taxa that occurred in a minimum of three lakes and with a relative abundance of $\geq 1\%$ in at least one lake) was used to simplify biplot construction. Regardless of whether all 344 taxa or the reduced 99-taxa data set was used, ordination results were similar. Appendix A lists the 99 diatom taxa and their respective diatom code used in plots illustrating statistical results. Diatom authorities are also included in Appendix A and, therefore, are not provided in the text. Diatom taxonomy for the Sierra Nevada is problematic and not well documented. Based on our observations, as well as previous diatom research in the Sierra Nevada (e.g., Holmes et al. (1989)), we anticipate documenting new diatom taxa. To date, 36 of the 344 (10.5%) diatom taxa identified are potentially new species; however, detailed taxonomic work, necessary for new classification, is beyond the scope of this paper.

Although a total of 48 physical and chemical environmental variables were measured, 12 variables (Ag, Be, Cd, Co, Cr, Cu, Mn, Mo, Ni, Pb, V, and Zn) were removed because a large number (> 50%) of the study lakes had values below detection limit. Six variables (latitude, longitude, elevation, area, geology, and vegetation) were removed because although they indirectly influence diatom distributions (i.e., they affect factors, such as pH, specific conductivity, nutrients, etc., that are known to affect diatom-community composition), there is no direct link between these variables and diatom distributions. Two vari-

ables, LOI and Chl *a*, were not included because diatoms themselves contribute to these variables. After this preliminary data screening, 28 environmental variables, namely, depth, pH, spcond, temp, salinity, Al, Ba, Ca, Cl, DIC, DOC, Fe, K, Li, Mg, Na, NH_3, NO_2, NO_3NO_2, POC, particulate organic nitrogen (PON), SiO_2, SO_4, Sr, soluble reactive phosphorus (SRP), total Kjeldahl nitrogen (TKN), total phosphorus (TP), and total phosphorus filtered (TPF) remained.

A PCA of the environmental data and a DCA of the diatom data were performed. Samples whose scores for axes 1 and 2 were outside one standard deviation (SD) of the mean for both axes of both the PCA and DCA were considered outliers and were removed from further statistical analyses. Results of the PCA of the 28-variable environmental data and DCA of the 99-diatom taxa showed that one study lake, SN3, was an outlier so this lake was removed, leaving 56 lakes for use in all further analyses. SN3 was an outlier in the PCA due to high values of Al, Li, and Ba. Although the reason for these high values is unclear, it is likely related to a local geologic anomaly. As a result of the unique water chemistry, the diatom-community composition is also distinct and is mainly characterized by *Synedra radians* (43%), *Asterionella formosa* (23%), and *Achnanthes exigua* (5%).

What environmental variables most influence diatom distributions in the Sierra Nevada?

In order to determine a subset of variables that explain a significant amount of the total variance in the data set, a series of ordination analyses was performed. First, DCA with detrending-by-segments was done to check the gradient lengths of each of the first two axes in order to determine which type of direct ordination analysis to use. Axes 1 and 2 of the DCA had eigenvalues of 0.35 and 0.17, respectively, and they accounted for 19.4% of the variance in the diatom data. Axes 1 and 2 had gradient-length values of 3.75

and 2.15, respectively. Gradient-length values < 2 SD suggest the use of RDA while those > 4 SD suggest the use of CCA (ter Braak 1995). Because gradient lengths for axes 1 and 2 fall between the cut-off values suggested by ter Braak (1995), both RDA and CCA methods were tested. Results were similar for both analyses, so only the CCA results are presented here.

A CCA constrained to a single environmental variable with Monte Carlo permutation tests (199 unrestricted permutations) was used to check which of the environmental variables explained a significant amount ($p \leq 0.05$) of variance in the diatom data. Twenty-two of the 28 variables (depth, pH, spcond, temp, salinity, Al, Ba, Ca, Cl, DIC, DOC, K, Li, Mg, Na, NO_3NO_2, SiO_2, SO_4, Sr, TKN, TP, and TPF) had a significant ($p \leq 0.05$) relationship to diatom distributions. Of the 22 significant variables, those with high collinearity, as determined by high variance inflation factors (> 20), (spcond, Li, Ca, DIC, Na, Mg, Cl, and DOC), were removed one at a time starting with the largest value (spcond) until all values were < 20 (ter Braak and Šmilauer 1998). Forward selection, with Monte Carlo permutation tests (199 unrestricted permutations), was used to identify a minimal subset of the remaining explanatory variables that could explain a statistically significant ($p \leq 0.01$) proportion of the variance in the diatom data. Of the remaining 14 environmental variables (depth, pH, temp, salinity, Al, Ba, K, NO_3NO_2, SiO_2, SO_4, Sr, TKN, TP, and TPF), five variables (salinity, depth, temp, TKN, and TP) explained a significant ($p \leq 0.01$) amount of variance in the diatom data. These five environmental variables accounted for 56.4% of the variance explained by the 14 environmental variables included at the beginning of forward selection and were used to construct CCA biplots.

Eigenvalues for each of the four CCA axes were $\lambda_1 = 0.23$, $\lambda_2 = 0.12$, $\lambda_3 = 0.11$, and $\lambda_4 = 0.08$. Because the eigenvalues for axes 2 and 3 are similar, axes 1, 2, and 3 were considered in subsequent

Table 2. Canonical coefficients, *t*-values, and intraset correlations for the five significant environmental variables are shown for CCA axes 1, 2, and 3. * indicates significant at $p \leq 0.05$.

Environmental variable	Canonical coefficient			*t*-value			Intraset correlation		
	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
Salinity	1.16	0.74	0.25	*7.52	*4.80	1.47	0.80	0.45	−0.34
Depth	0.47	−0.67	0.44	*5.07	*−7.30	*4.33	0.55	−0.63	0.41
Temp	0.18	−0.60	−0.60	1.76	*−5.76	*−5.16	0.39	−0.24	−0.82
TKN	−0.61	−0.05	−0.67	*−3.87	−0.31	*−3.81	0.43	0.34	−0.59
TP	0.04	0.18	0.41	0.35	1.69	*3.44	0.18	0.61	0.05

analyses. The first three axes accounted for 17.0% of the cumulative variance of the diatom data and 75.3% of the cumulative variance of the species-environment relation. All four axes accounted for 20.1% of the cumulative variance of the diatom data and 89.1% of the cumulative variance of the species-environment relation. Canonical coefficients, *t*-values, and intraset correlations (the correlation between the environmental variable and the ordination axis) were used to approximate the relative contributions of each of the individual environmental variables to each of the first three ordination axes (Table 2). These values show that axis 1 is largely determined by salinity (r = 0.80); axis 2 is largely determined by depth (r = −0.63); and axis 3 is largely determined by surface-water temperature (r = −0.82) (Table 2). These relationships are also indicated by the significant canonical coefficient of salinity with axis 1, depth with axis 2, and surface-water temperature with axis 3 (Table 2).

How does salinity and temperature in the Sierra Nevada affect diatom-distribution patterns?

Sites were classified based on salinity and surface-water temperature and were plotted on CCA biplots

(Figures 2a and 3a, respectively). Groups of sites defined by salinity are generally distinct from one another, although there is some overlap between sites in the low-and middle-salinity groups (Figure 2a). In general, lakes with low-salinity values plot in the left portion of the biplot, whereas lakes with high-salinity values plot in the right portion. Because axis 3 is largely determined by surface-water temperature, groups of sites defined by surface-water temperature are plotted on axes 1 and 3 (Figure 3a). Cooler lakes are mainly located in the upper-left portion of the biplot, whereas warmer lakes tend to plot in the lower portion. Because site scores are dependent on both the environmental characteristics and the diatom species, Figures 2a and 3a indicate that sites with different salinities and different surface-water temperatures, respectively, have distinct diatom-community compositions (ter Braak 1995).

The projection of the points representing diatom species, including *Amphora inariensis* (18), *A. libyca* (19), *A. pediculus* (20), *Cocconeis placentula* var. *lineata* (32), *Nitzschia amphibia* (79), *N.* cf. *palea* (80), *N. linearis* var. *tenuis* (84), *Rhopalodia gibba* (89), and *Stephanodiscus parvus* (95), onto the arrow representing salinity indicate that these species have
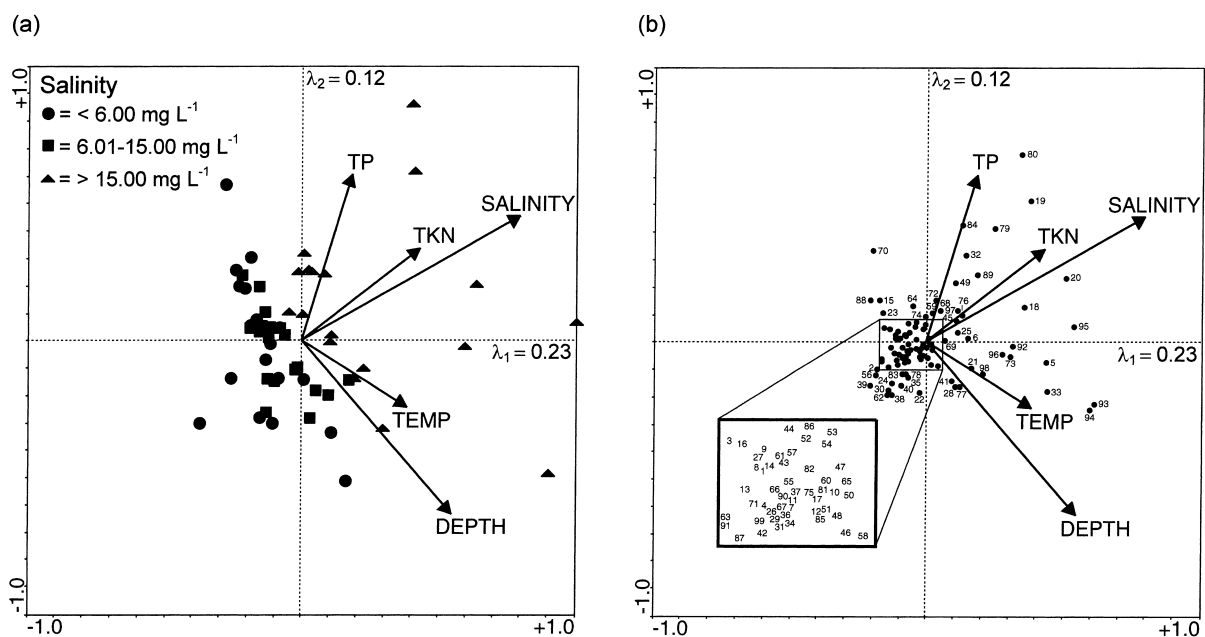

Figure 2. CCA biplots for axis 1 versus axis 2. (a) Environmental variables (arrows) and study lakes (points) are shown; lakes are classified into groups based on salinity. (b) Environmental variables (arrows) and diatom species (points) are shown. Appendix A provides a key to the numerical diatom species codes shown.
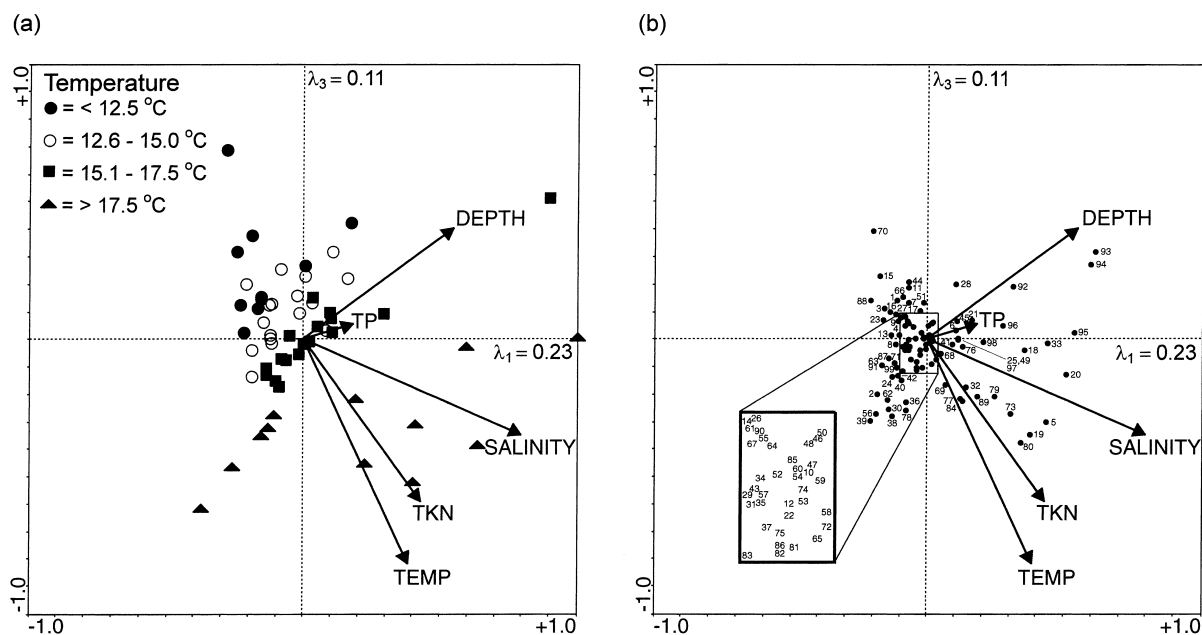
Figure 3. CCA biplots for axis 1 versus axis 3. (a) Environmental variables (arrows) and study lakes (points) are shown; lakes are classified into groups based on surface-water temperature (*sensu* Porinchu et al. (2002)). (b) Environmental variables (arrows) and diatom species (points) are shown. Appendix A provides a key to the numerical diatom species codes shown.

salinity optima greater than other species in this data set (Figure 2b). Similarly, the projection of the points representing species characteristic of low-salinity sites, including *Achnanthes* cf. *stolida* (2), *Aulacoseira ambigua* (22), *A. distans* (24), *Brachysira brebissonii* (30), *Cymbella falaisensis* (38), *C. gracilis* (39), *C. incerta* (40), *Fragilaria exigua* (56), and *Frustulia rhomboides* (62), onto the salinity arrow indicate that these species have lower salinity optima than other species in this data set (Figure 2b). Because the salinity gradient in the Sierra Nevada is relatively small (2.20-99.03 mg L^{-1}), it is difficult to make direct comparisons between species' salinity optima determined here to those determined in other studies (e.g., Fritz et al. (1993), Wilson et al. (1994, 1996), Cumming et al. (1995), Roberts and McMinn (1998)). For example, in a study from British Columbia, Canada, 111 lakes were sampled whose salinity ranged from 30–3,690 mg L^{-1}. Salinity optima and tolerances are listed for 107 species, but none of the low-salinity diatoms from our Sierra Nevada study are included, probably because they are restricted to fresher conditions than those that were sampled in the British Columbia study (Cumming et al. 1995). Of the nine high-salinity diatoms listed from the Sierra

Nevada, seven are included in the Cumming et al. (1995) study. These seven have optima that range from 120–880 mg L^{-1}, which is low to mid range for the optima of all 107 species (total range of optima = 70–100,690 mg L^{-1}) listed in Cumming et al. (1995).

The projection of points representing diatom species, including a number of small *Achnanthes* species, namely, *Achnanthes carissima* (1), *A. chlidanos* (3), *A. nodosa* (11), *A. stolida* (15), along with *Aulacoseira* cf. *alpigena* (23), *Diatoma mesodon* (44), *Gomphonema gracile* (64), *Navicula* cf. *minima* (66), *N. difficillima* (70), and *Pinnularia microstauron* (88), onto the arrow representing surface-water temperature indicate that these species have lower-temperature optima than other species in this data set (Figure 3b). Similarly, the projection of points representing species characteristic of high surface-water temperature sites, including *Achnanthes exigua* (5), *Amphora libyca* (19), *Cocconeis placentula* var. *lineata* (32), *Navicula pseudoscutiformis* (73), *N. subtilissima* (77), *Nitzschia amphibia* (79), *N.* cf. *palea* (80), *N. linearis* var. *tenuis* (84), and *Rhopalodia gibba* (89), indicate that these species have higher-temperature optima than other species in this data set (Figure 3b). Similar to cold-water species

reported in Weckström et al. (1997b), cold-water species from the Sierra Nevada include *Aulacoseira* and small *Achnanthes* species. Three of the ten species found to have relatively low-temperature optima in the Sierra Nevada were similarly listed as cold-water species in other studies. The optima reported in Weckström et al. (1997b) for *Aulacoseira alpigena* and *Navicula minima* are relatively low (11.86 °C and 12.12 °C, respectively) and the optimum reported for *Gomphonema gracile* is the third coldest optimum (16.4 °C) of the 126 species listed in Pienitz et al. (1995). Similarly, two of the eight warm-water species identified in the Sierra Nevada study have been listed as warm-water species in Pienitz et al. (1995), namely *Amphora libyca* (optimum = 18.4 °C) and *Navicula pseudoscutiformis* (optimum = 18.1 °C) (Pienitz et al. 1995).

Can reliable diatom-inference models for salinity and temperature be developed from the Sierra Nevada calibration set?

Although the exact eco-physiological factors responsible for the patterns and relationships between diatoms and surface-water temperature and diatoms and salinity in the Sierra Nevada are unknown, it should be possible to develop diatom-based inference models for these variables, given that surface-water temperature and salinity explain independent and statistically significant amounts of variation in the diatom data (Pienitz et al. 1995; Joynt and Wolfe 2001). As well as considering canonical coefficients, *t*-values, and intraset correlations (Table 2), constrained CCAs were run with only one variable (surface-water temperature or salinity) selected at a time. If λ_1/λ_2 is large and the p-value is significant (p $\leq$ 0.01) in a CCA constrained to the individual environmental variable, it should be possible to develop reliable diatom-inference models for that selected variable (Hall and Smol 1992). The first eigenvalue of

the CCA constrained to salinity ($\lambda_1 = 0.19$) was significant (p $\leq$ 0.01), and the value of λ_1/λ_2 (0.67) was high, indicating that salinity explained significant variation in the species data (Table 3). As well, salinity accounted for the largest portion of the total variance explained by the 14 variables included prior to forward selection (17.7%) (Table 3). The first eigenvalue of the CCA constrained to surface-water temperature ($\lambda_1 = 0.12$) was also significant (p $\leq$ 0.01), but λ_1/λ_2 (0.36) and the portion of the total variance explained by the 14 variables included prior to forward selection (11.2%) was comparatively low (Table 3), indicating that other variables, namely salinity and depth, explain more of the variation in the diatom data. Although the λ_1/λ_2 value for surface-water temperature in this study is relatively low, other studies with similarly low λ_1/λ_2 values (< 0.40) have developed robust models for mean July air temperature (e.g., Rosén et al. (2000)). While the statistics presented here (Table 3) indicate that reliable diatom-inference models for depth and TKN are possible, such models were not included in this paper. Previous studies have shown that lake-depth models can be problematic (Wolin and Duthie 1999; Moser et al. 2000); and TKN models are not directly relevant to this paper, as the main goal here is to develop models that can be used to infer past drought and climate conditions.

Individual partial CCAs constrained to salinity and surface-water temperature were run with selected covariables to ensure that the given environmental variable independently explained a significant amount of variation in the diatom data (Table 4). Each of the other forward-selected variables was selected independently and as a group as covariables. In all cases, the first eigenvalue was significant (p $\leq$ 0.01). For both salinity and surface-water temperature, the value of λ_1/λ_2 and the amount of variance explained was not greatly altered after removing the effects of other variables (i.e., covariables) (Table 4). These results

Table 3. Results of constrained CCAs for each environmental variable selected for inclusion in the final CCA. Environmental variables are presented with their respective values of λ_1 (constrained axis) and λ_1/λ_2 (constrained axis/unconstrained axis). In all cases, the eigenvalue for axis 1 (λ_1) is significant at p $\leq$ 0.01. The % variance is the proportion that each variable independently explains of the total variance (unconstrained) and variance explained by the 14 environmental variables included in forward selection.

Environmental variable	λ_1	λ_1/λ_2	% total variance	% 14 variance
Salinity	0.19	0.67	7.0	17.7
Depth	0.14	0.45	5.4	13.0
Temp	0.12	0.36	4.5	11.2
TKN	0.12	0.36	4.5	11.1
TP	0.10	0.29	3.7	9.3

indicate that both salinity and surface-water temperature independently explained a significant amount of variance in the diatom data, suggesting that it should be possible to develop reliable models for the reconstruction of salinity and surface-water temperature from the Sierra Nevada calibration set.

CCA was used to identify all variables with extreme influence ($> 8X$) as measured by the leverage diagnostic; these variables have an unduly large influence on the ordination results. Surface-water temperature did not have extreme influence on any sites, but salinity had extreme influence on one site, namely SN2 (13.2X). As a result, diatom-inference models developed for salinity excluded SN2. Gradient lengths for the first axis in a DCCA constrained first to salinity and then to surface-water temperature were used to determine whether to use linear (e.g., PLS) or unimodal (e.g., WA) modeling methods (Birks 1995, 1998). The gradient lengths determined by DCCA with axis 1 constrained first to salinity (gradient length for axis $1 = 1.98$, $n = 55$) and then to surface-water temperature (gradient length for axis $1 = 1.72$, $n = 56$) suggest the use of linear (PLS) models; however, because ter Braak and Juggins (1993) demonstrate that with short gradient lengths (< 2 SD) unimodal models may outperform linear models, both linear and unimodal models were tested. For both surface-water temperature and salinity, unimodal models performed better (i.e., higher r^2-values and lower RMSEP and RMSEP as a % of the gradient values), so these results are presented here.

Estimated optimum and tolerance values of surface-water temperature and salinity for all diatom taxa were determined in WACALIB version 3.3 (Line et al. 1994). These values were used in WA regression to develop diatom-inference models for surface-water temperature and salinity. For each method used, models were developed that included all diatom taxa, as well as only those taxa that occurred in at least three sites and in $\geq 1\%$ in a minimum of one site. When simple WA models were developed using classical deshrinking, trends were noted in the residuals (inferred minus observed). These models underestimated low values and overestimated high values. No apparent trends were seen in the residuals for models developed with simple WA using inverse deshrinking (Figure 4b and 4d). Therefore, all simple WA models from herein use inverse deshrinking.

The diatom-inference models for surface-water temperature were developed for the 56-lake calibration set (SN3 removed), as well as a reduced 41-lake calibration set, in which samples from the 56-lake set were removed if their residual value fell outside one SD of the mean (Jones and Juggins 1995). The best models for surface-water temperature were constructed using simple WA, rather than WA-PLS; and the best simple WA model included 41 lakes and 286 diatom taxa ($r^2 = 0.89$; RMSE = 0.7 °C; $RMSEP_{boot} = 1.7$ °C; $RMSEP_{jack} = 1.5$ °C; RMSEP as a % of the gradient = $17.9\%_{(boot)}$ and $15.8\%_{(jack)}$; mean bias = -0.09 °C; maximum bias = 1.7 °C) (Table 5; Figures 4a and 4b). By reducing the number of lakes from 56 to 41, however, the temperature gradient was reduced from 13.7 °C to 9.5 °C. The best model developed for the larger gradient (i.e., 56-lake set) included 342 diatom taxa ($r^2 = 0.72$; RMSE = 1.4 °C; $RMSEP_{boot} = 2.3$ °C; $RMSEP_{jack} = 2.1$ °C; RMSEP as a % of the gradient = $16.8\%_{(boot)}$ and $15.3\%_{(jack)}$; mean bias = -0.05 °C; maximum bias = 2.6 °C) (Table 5; Figures 4c and 4d).

The WA diatom-inference salinity models were first developed from a 55-lake calibration set (SN2 and

Table 4. Individual partial CCA results showing the contribution of surface-water temperature and salinity to explaining the total variance (unconstrained) and variance explained by the 14 environmental variables included in forward selection in the diatom data independent of their respective covariables. "All 4" includes the four variables (depth, temp, TKN, and TP) that were each used independently as covariables. All variables are significant at $p \leq 0.01$.

Environmental variable	Covariable(s)	λ_1	λ_1/λ_2	% total variance	% 14 variance
Salinity	Depth	0.18	0.67	7.1	16.7
	Temp	0.17	0.60	6.6	15.8
	TKN	0.18	0.65	6.8	16.7
	TP	0.18	0.73	7.1	16.7
	All 4	0.15	0.64	6.8	14.0
Temp	Depth	0.12	0.40	4.9	11.2
	Salinity	0.10	0.36	4.1	9.3
	TKN	0.10	0.30	3.9	9.3
	TP	0.12	0.36	4.7	11.2
	All 4	0.09	0.39	4.3	8.4

(a)
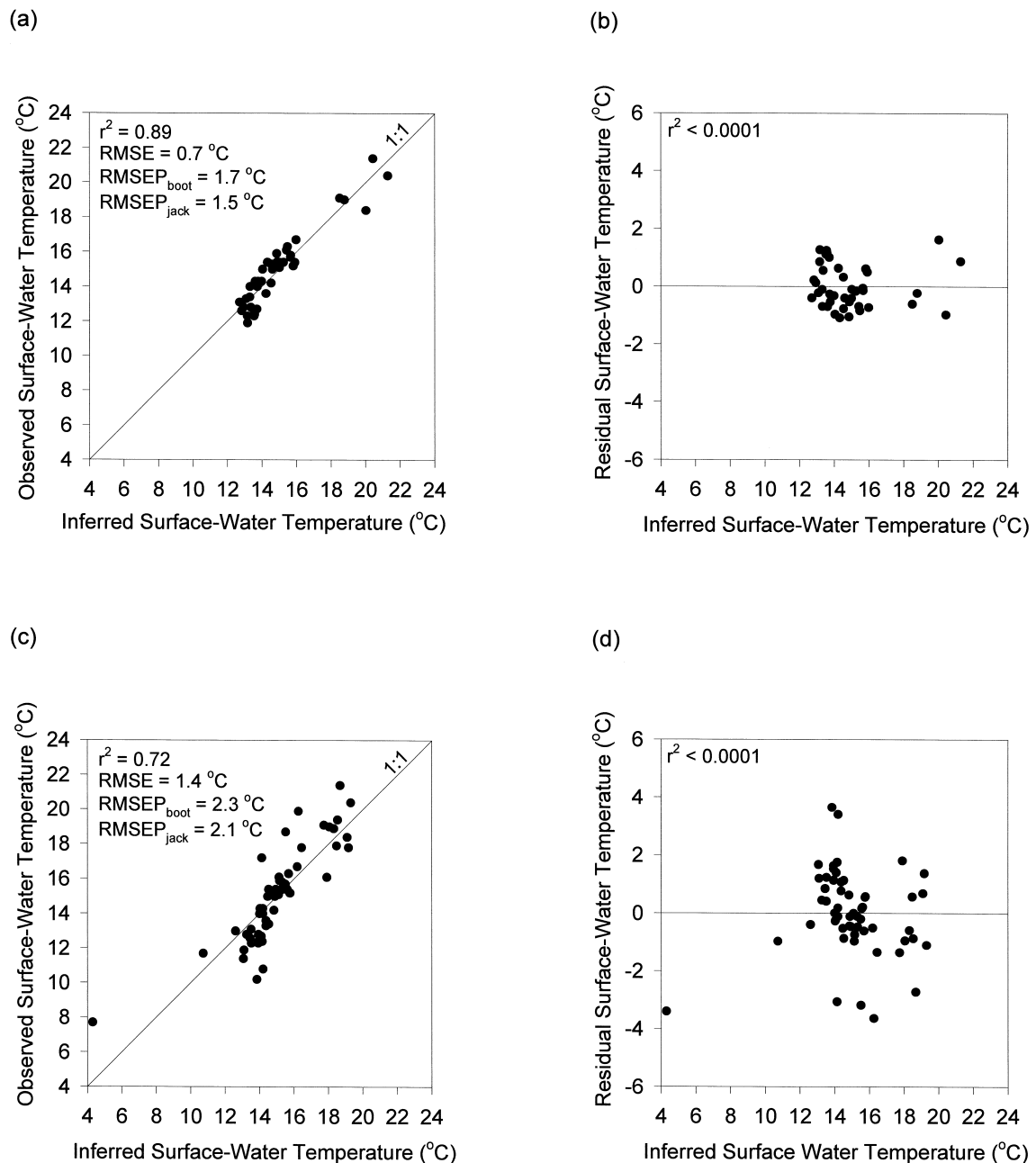

(b)

(c)

(d)

Figure 4. (a) Plot of diatom-inferred versus observed surface-water temperature and (b) inferred versus residual (diatom-inferred minus observed) surface-water temperature using weighted averaging with inverse deshrinking based on the 41-lake, 286-diatom taxa calibration set. (c) Plot of diatom-inferred surface-water temperature versus observed and (d) inferred versus residual surface-water temperature using weighted averaging with inverse deshrinking based on the 56-lake, 342-diatom taxa calibration set.

SN3 removed). When samples whose residual value fell outside one SD of the mean were excluded, the salinity gradient covered was so small (25.25 mg L^{-1}) as to make the model impractical. Therefore, the best model developed for salinity used WA-PLS with three components and the 55-lake calibration set with 94 diatom taxa ($r^2 = 0.96$; RMSE $= 4.06$ mg L^{-1}; RMSEP$_{jack} = 11.13$ mg L^{-1}; RMSEP$_{jack}$ as a % of the gradient $= 11.49\%$; mean bias $= -1.35$ mg L^{-1}; maximum bias $= 8.96$ mg L^{-1}) (Table 5; Figure 5).

Table 5. Comparison of several diatom-inference models for surface-water temperature (temp) and salinity for the eastern Sierra Nevada, California calibration set. Abbreviations include: comp. = component and max. = maximum. The "best" models are in bold.

| Environmental variable	Model type	Type of deshrinking	Study lakes	Diatom taxa	r^2	RMSE	Trend in residuals	RMSEP_boot	RMSEP_jack	Mean bias	Max. bias	Gradient	Gradient length	RMSEP as % of gradient
Temp (°C)	**Simple WA**	**Inverse**	**56**	**342**	**0.72**	**1.4**	**No**	**2.3**	**2.1**	**-0.05**	**2.6**	**7.7–21.4**	**13.7**	**16.8(boot), 15.3(jack)**
	Simple WA	Classical	56	342	0.72	1.7	Yes	2.3	2.0	-0.07	2.2	7.7–21.4	13.7	16.8(boot), 14.6(jack)
	Simple WA	Inverse	56	99	0.67	1.6	No	2.4	2.1	-0.05	2.6	7.7–21.4	13.7	17.5(boot), 15.3(jack)
	Simple WA	Classical	56	99	0.67	1.9	Yes	2.5	2.2	-0.08	2.0	7.7–21.4	13.7	18.2(boot), 16.1(jack)
	Simple WA	**Inverse**	**41**	**286**	**0.89**	**0.7**	**No**	**1.7**	**1.5**	**-0.09**	**1.7**	**7.7–21.4**	**9.5**	**17.9(boot), 15.8(jack)**
	Simple WA	Classical	41	286	0.89	0.9	Yes	2.0	1.4	-0.09	1.5	11.9–21.4	9.5	21.1(boot), 14.7(jack)
	Simple WA	Inverse	41	80	0.81	1.0	No	1.8	1.4	-0.02	2.6	11.9–21.4	9.5	18.9(boot), 14.7(jack)
	Simple WA	Classical	41	80	0.81	1.1	Yes	1.8	1.6	-0.05	1.3	11.9–21.4	9.5	18.9(boot), 16.8(jack)
Salinity (mg L⁻¹)	Simple WA	Inverse	55	333	0.91	6.53	No	15.88	14.94	-1.74	14.14	2.20–99.03	96.83	16.40(boot), 15.43(jack)
	Simple WA	Inverse	55	94	0.73	11.16	No	15.68	14.31	-0.37	8.86	2.20–99.03	96.83	16.19(boot), 14.78(jack)
	Simple WA	Classical	55	333	0.81	10.38	Yes	15.97	14.59	-1.96	12.66	2.20–99.03	96.83	16.49(boot), 15.07(jack)
	Simple WA	Classical	55	94	0.73	13.09	Yes	15.92	15.11	-0.57	9.40	2.20–99.03	96.83	16.44(boot), 15.60(jack)
	WA-PLS 3 comp.		55	333	0.99	2.23	No		14.08	-2.17	13.88	2.20–99.03	96.83	14.54(jack)
	WA-PLS 3 comp.		**55**	**94**	**0.96**	**4.06**	**No**		**11.13**	**-1.35**	**8.96**	**2.20–99.03**	**96.83**	**11.49(jack)**

(a)

(b)
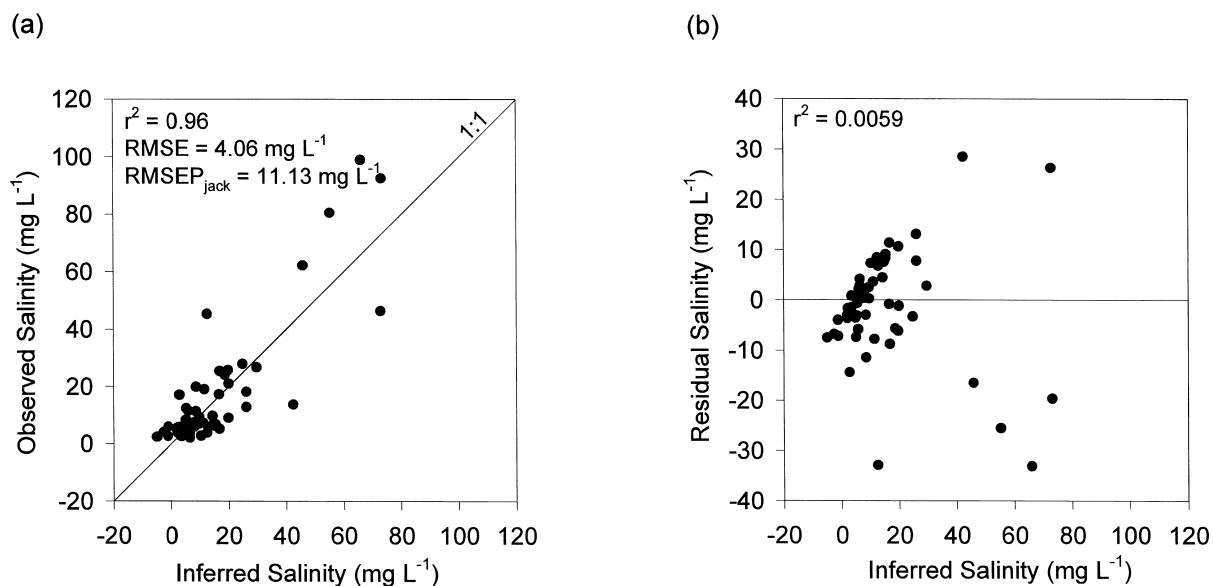
Figure 5. (a) Plot of diatom-inferred versus observed salinity and (b) inferred versus residual (diatom-inferred minus observed) salinity using weighted averaging partial least squares with three components based on the 55-lake, 94-diatom taxa calibration set.

No apparent trends were seen in the residuals (Figure 5b).

How do Sierra Nevada temperature and salinity models compare to other diatom-based inference models?

Numerous diatom-based surface-water temperature models (Pienitz et al. 1995; Vyverman and Sabbe 1995; Wunsam et al. 1995; Weckström et al. 1997b; Bigler et al. 2000; Joynt and Wolfe 2001) and air-temperature models (Lotter et al. 1997; Korhola et al. 2000; Rosén et al. 2000; Joynt and Wolfe 2001; Bigler and Hall 2002) have been developed (Table 6). Although comparing statistics for models inferring surface-water temperatures to air-temperature models should be done cautiously, the summer-air temperature models appear to perform better than the surface-water temperature models (Table 6). The average RMSEP and RMSEP as a % of the gradient for all four summer air-temperature models were 1.08 °C and 12.4%, respectively; whereas, the average RMSEP and RMSEP as a % of the gradient for all eight water-temperature models were 1.96 °C and 16.0%, respectively. Models developed for surface-water temperature and air temperature, from the same training set, also suggest that air-temperature models are more robust than water-temperature models (Joynt and Wolfe 2001) (Table 6). This is to be expected

because summer-air temperature measurements are average values for the entire diatom-growing season, whereas the surface-water temperatures are typically based on a single measurement or a mean of several temperatures taken on a single day in July or August (Lotter et al. 1997; Rosén et al. 2000). Although surface-water temperature was modeled in this study, better inferences of past climate conditions may be possible using diatom-inference models for summer-air temperature. So far we have been unable to develop such models from this calibration set because of the paucity of weather stations with sufficiently long records in and near the study area, particularly at high elevations.

Because of the apparent difference in the performance of air-temperature models relative to surface-water temperature models, we have restricted comparisons of our model to surface-water temperature models. RMSEP-values for surface-water temperature models range from 0.88 °C (Weckström et al. 1997b) to 3.21 °C (Vyverman and Sabbe 1995) (Table 6). The RMSEP of our best models, both the 41-lake and the 56-lake model (1.5 °C$_{(jack)}$, 1.7 °C$_{(boot)}$ and 2.1 °C$_{(jack)}$, 2.3 °C$_{(boot)}$, respectively), falls within this range (Table 6). The RMSEP as a % of the gradient for our 41-lake calibration set (15.8%$_{(jack)}$, 17.9%$_{(boot)}$) also falls within the range of RMSEP as a % of the gradient values from other studies (8.1%$_{(boot)}$-32.4%$_{(boot)}$, Wunsam et al. (1995), Joynt

Table 6. Comparison of previously developed diatom-inference models for surface-water temperature (°C), air temperature (°C), and salinity (mg L⁻¹)) to the models developed here for the eastern Sierra Nevada, California (shown in bold) (modified from Rosén et al. (2000)). Abbreviations include: M = mean, WT = water temperature, AT = air temperature, tol = tolerance downweighting, and comp. = component. The Wunsam et al. (1995) study only includes *Cyclotella* taxa. * indicates that all statistical analyses were carried out using salinities that were log transformed.

Environmental variable	Authors	Study area	Model type	Study lakes	Diatom taxa	r^2	RMSE	RMSEP	Gradient	Gradient length	RMSEP as % of gradient
WT	Wunsam et al. (1995)	European Alps (excluding Switzerland)	WA$_{tol}$ classical	85	26	0.62	1.15	1.32$_{(boot)}$	8.1 to 24.5	16.4	8.1$_{(boot)}$
July-August WT	**Bloom et al.**	**Sierra Nevada, California, USA**	**WA inverse**	**56**	**342**	**0.72**	**1.4**	**2.1$_{(jack)}$, 2.3$_{(boot)}$**	**7.7 to 21.4**	**13.7**	**15.3$_{(jack)}$, 16.8$_{(boot)}$**
Summer WT	Bigler et al. (2000)	Northern Sweden	WA-PLS 2 comp.	42	115	0.86	0.11	1.87$_{(jack)}$	2.4 to 14.5	12.1	15.5$_{(jack)}$
July-August WT	**Bloom et al.**	**Sierra Nevada, California, USA**	**WA inverse**	**41**	**286**	**0.89**	**0.7**	**1.5$_{(jack)}$, 17$_{(boot)}$**	**11.9 to 21.4**	**9.5**	**15.8$_{(jack)}$, 17.9$_{(boot)}$**
July WT	Weckström et al. (1997b)	Northern Finland	WA inverse	34	118	N.A.	N.A.	0.88$_{(jack)}$	9.3 to 14.5	5.2	16.9$_{(jack)}$
July WT	Pienitz et al. (1995)	Yukon and NWT, Canada	WA classical	56	126	0.63	1.84	2.00$_{(boot)}$	12.0 to 23.0	11.0	18.2$_{(boot)}$
M WT	Vyverman and Sabbe (1995)	Papua New Guinea	WA classical	171	287	0.86	N.A.	3.21$_{(boot)}$	N.A.	N.A.	21.4$_{(boot)}$
July-August WT	Joynt and Wolfe (2001)	Baffin Island, Nunavut, Canada	WA classical	61	107	0.48	1.94	2.79$_{(boot)}$	2.3 to 10.9	8.6	32.4$_{(boot)}$
M summer AT	Lotter et al. (1997)	Alps, Switzerland	WA-PLS 2 comp.	64	345	0.96	0.69	1.62$_{(jack)}$	7.0 to 20.6	13.6	11.9$_{(jack)}$
M July AT	Bigler and Hall (2002)	Northern Sweden	WA-PLS 2 comp.	100	157	0.86	0.67	0.96$_{(jack)}$	7.0 to 14.7	7.7	12.5$_{(jack)}$
M July AT	Korhola et al. (2000)	Northern Fennoscandia	WA-PLS 2 comp.	38	324	0.96	0.34	0.89$_{(jack)}$	7.9 to 14.9	7.0	12.6$_{(jack)}$
M July AT	Rosén et al. (2000)	Northern Sweden	WA-PLS 3 comp.	52	157	0.92	0.40	0.86$_{(jack)}$	7.5 to 14.3	6.8	12.6$_{(jack)}$
M annual AT	Joynt and Wolfe (2001)	Baffin Island, Nunavut, Canada	WA classical	61	107	0.43	1.81	2.46$_{(boot)}$	−15.5 to −6.9	8.6	28.6$_{(boot)}$
Salinity	Wilson et al. (1996)*	Western North America	WA inverse	219	204	0.87	N.A.	370$_{(boot)}$	20 to 620,000	619,980	0.06$_{(boot)}$
Salinity	Wilson et al. (1994)*	Interior Plateau of B.C., Canada	WA inverse	102	107	0.89	300	420$_{(boot)}$	430 to 369,310	369,270	0.11$_{(boot)}$
Salinity	Roberts and McMinn (1998)*	Antarctica	WA classical	33	47	0.80	330	370$_{(jack)}$	500 to 165,000	164,000	0.22$_{(jack)}$
Salinity	**Bloom et al.**	**Sierra Nevada, California, USA**	**WA-PLS 3 comp.**	**55**	**94**	**0.96**	**4.06**	**11.13$_{(jack)}$**	**2.20 to 99.03**	**96.83**	**11.49$_{(jack)}$**

and Wolfe (2001), respectively), and the RMSEP as a % of the gradient of our 56-lake calibration set ($15.3\%_{(jack)}$, $16.8\%_{(boot)}$) is only surpassed by the Wunsam et al. (1995) model.

Several diatom-based salinity models have also been developed (reviewed in Fritz et al. (1999), Smol and Cumming (2000)); results from Wilson et al. (1994, 1996) and Roberts and McMinn (1998) are presented in Table 6. Published $RMSEP_{boot}$-values for log salinity ranged from 370 to 420 mg L^{-1}, and the $RMSEP_{boot}$ as a % of the gradient ranged from 0.06% to 0.22% (Wilson et al. (1994), Roberts and McMinn (1998), respectively). The $RMSEP_{jack}$ for the best Sierra Nevada model is much smaller than those from previously published models (11.13 mg L^{-1}), but this is because the gradient covered is much shorter, as evidenced by the much higher $RMSEP_{jack}$ as a % of the gradient value (11.49%). Despite the fact that the RMSEP as a % of the gradient is higher for our salinity model than previous models, it is still low.

Various factors will affect how well a model performs (i.e., r^2, RMSEP, and RMSEP as a % of the gradient), including the number of species and sites included in the model (Birks 1994; Wilson et al. 1996), the gradient length, and how well sites are distributed over the gradient. It has been suggested that models based on more diatom taxa and larger calibration sets will perform better (lower RMSEP) than those based on fewer taxa and smaller calibration sets for variables such as pH and salinity (Birks (1994), Wilson et al. (1996), respectively). The best models developed from the Sierra Nevada data set for surface-water temperature show no change or only slight improvement (RMSEP is reduced by $< 6\%$) when the number of diatom taxa are increased (Table 5). In contrast, the best salinity model becomes worse (RMSEP is increased by 21%) when additional diatom taxa are added (Table 5). Reducing the number of sites in the surface-water temperature models reduces the values of RMSEP and increases the r^2-values. In addition, the gradients covered are reduced, and consequently the values of RMSEP as a % of the gradient are increased (Table 5). In the case of salinity, the gradient is reduced to the point of being ineffectual. When applying the diatom-inference models for surface-water temperature developed from the Sierra Nevada calibration set, it is important to consider the questions being addressed and the time interval covered by the fossil-diatom assemblages to which the model will be applied. For example, during the last 2,000 years temperatures likely fluctuated less

than during the entire Holocene, so the ''best'' model to use to infer recent changes in temperature might be the one covering the shorter gradient (41 lakes), but having lower values of RMSEP and maximum bias, whereas the ''best'' model to use to infer temperature variation over the entire Holocene and late Pleistocene might be the model covering the larger gradient (56 lakes), despite having larger values of RMSEP and maximum bias.

These findings suggest that increasing the size of the calibration set could improve the models developed here. Although the surface-water temperature gradient covered by the Sierra Nevada calibration set is the second largest (13.7 °C) of the studies listed in Table 6, the distribution of sites is uneven with more sites being located in the middle of the gradient than at the ends (Figure 6a). The salinity gradient covered by the Sierra Nevada calibration set is orders of magnitude shorter than those covered by the other models listed in Table 6, and the distribution of sites is skewed to the low end of the gradient (Figure 6b). At present, the study lakes span an elevational gradient of 1360 m (2115 to 3475 m a.s.l.); however, the total elevation range of the Sierra Nevada is more than three times this amount. With the addition of more low-elevation lakes (which are typically warmer and more saline) and more high-elevation lakes (which are typically colder and fresher) there would be a more even distribution of lakes over a larger temperature and salinity gradient. Due to the limited number of low-elevation sites and the logistical difficulties of accessing high-elevation sites, increasing the gradient has proven difficult.

How do the diatom-inference temperature models compare with a chironomid-inference temperature model based on the same Sierra Nevada lake-calibration set?

A chironomid-inference model developed by Porinchu et al. (2002) based on the same 57-lake calibration set, included 44 lakes that spanned a gradient of 8.5 °C, performed slightly better ($r^2 = 0.73$, RMSE=1.0 °C, $RMSEP_{jack} = 1.2$ °C, $RMSEP_{jack}$ as a % of the gradient = 14.1%, and maximum bias = 0.9 °C) than the best diatom-inference models for surface-water temperature presented here (Table 5). This suggests that in the Sierra Nevada chironomids are more sensitive to surface-water temperature than diatoms, which is supported by ordination analyses. The RDA of the chironomid data indicates that sur-
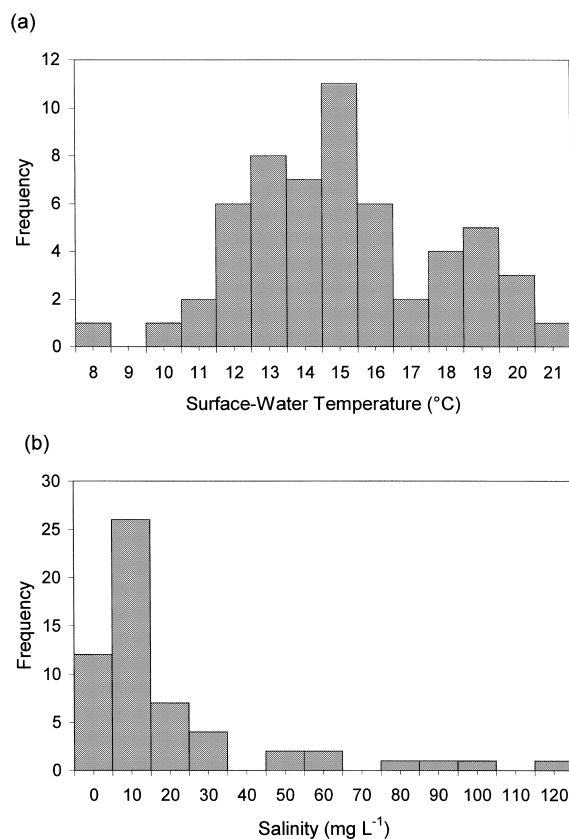
Figure 6. Histograms showing the distribution of (a) surface-water temperature and (b) salinity for the 57-lake calibration set.

face-water temperature explains more of the total variance in the chironomid-species data than any other variable (temp = 11.2% versus elevation = 11.0%, Sr = 6.2%, depth = 5.1%, and POC = 3.5%) (Porinchu et al. 2002), whereas a CCA of the diatom data indicates that salinity and depth both explain more of the variance in the diatom data than surface-water temperature (temp = 4.5% versus salinity = 7.0% and depth = 5.4%) (Table 3). Groups of sites based on surface-water temperature, however, are distinct in both the RDA of the chironomid data (Figure 3a, Porinchu et al. (2002)) and the CCA of the diatom data (Figure 3a), indicating that both chironomid- and diatom-community composition are influenced by surface-water temperature.

There are many factors that directly and indirectly influence chironomid-community composition; variables such as depth, air and water temperature, trophic conditions, sediment characteristics, habitat availability, and oxygen concentration have all been identified as having a statistically significant relationship to the faunal composition of subfossil-chironomid communities (Porinchu and MacDonald (in press)). However, many studies identify that of these variables, air and/or water temperature can explain the largest amount of variance in the chironomid distributions (Walker et al. 1997; Olander et al. 1999; Larocque et al. 2001; Porinchu et al. 2002). Water temperature directly affects the rate of egg and larval development (Konstantinove 1958; MacKey 1977), timing of pupation (Danks and Oliver 1972), and the emergence of chironomid adults (Danks and Oliver 1972; Butler 1980). Brodersen and Lindegaard (2000) have documented that the emergence of chironomids from a shallow Danish lake is temperature dependent and that most chironomids required water temperatures in excess of 18 °C to initiate emergence. It is during the adult stage that chironomids disperse to more suitable environments, and as result, they may be sensitive to ambient air temperatures (Brooks and Birks 2000).

The degree to which temperature influences diatoms and diatom-community composition has been controversial (Anderson 2000). Temperature is an important factor controlling the rate of metabolic processes, such as photosynthesis and respiration, of algae. Algal growth rate is directly related to these processes (Patrick 1971, 1977; Hartig and Wallen 1986; Dauta et al. 1990). In addition, temperature directly influences cell division (cell division increases with increased temperatures and is highest at optimal temperatures), mobility, and the distributions of diatoms present in different lakes (reviewed in Weckström et al. (1997a)). It has been suggested, however, that temperature has limited direct influence on diatom-community structure, and that temperature more likely affects other limnological variables, such as nutrients, salinity, or pH, and that these variables in turn affect diatoms (Kilham et al. 1996; Anderson 2000). These indirect relationships do not preclude the development of diatom transfer functions for temperature, as long as temperature independently explains variance in the diatom data (Pienitz et al. 1995). Despite the fact that the chironomid model performs better than the diatom models, applying both models to the same long core should provide a better understanding of past temperature as opposed to using a single model (Smol and Cumming 2000). For example, it is possible that when applied to long-core sediments, there may be intervals for which the diatom models provide "more reliable" (*sensu* Bradshaw et al. (2000)) reconstructions than the chironomid model or vice versa.

Conclusions

This study demonstrates the great potential of using diatoms preserved in alpine lake sediments in the western United States to better understand past climates and, in particular, past drought occurrence. The diatom-inference models developed for surface-water temperature and salinity in our study are the only such models presently available from the southwestern United States. The best surface-water temperature models developed here have some of the lowest RMSEP as a % of the gradient values of all models published to date. The salinity models we have developed clearly demonstrate the potential to track even small variations of effective moisture that may have occurred in the past in the mountainous areas of the southwestern United States, which are critical sources of freshwater for the populations living in this region. As water resources become increasingly limited, as a result of greater demands, and perhaps the effects of future climate change, this information will become increasingly important.

Acknowledgements

Appendix A.

Diatom taxa and their respective code used in Figures 2 and 3. * indicates potentially new diatom taxon, and SN denotes Sierra Nevada.

Diatom taxon	Code
Achnanthes carissima Lange-Bertalot	1
Achnanthes cf. *stolida* (Krasske) Krasske	2
Achnanthes chlidanos Hohn & Hellermann	3
Achnanthes didyma Hustedt	4
Achnanthes exigua Grunow	5
Achnanthes lanceolata ssp. *frequentissima* Lange-Bertalot	6
Achnanthes laterostrata Hustedt	7
Achnanthes levanderi Hustedt	8
Achnanthes microscopica (Cholnoky) Lange-Bertalot & Krammer	9
Achnanthes minutissima Kützing	10
Achnanthes nodosa Cleve	11
Achnanthes pusilla (Grunow) De Toni	12
Achnanthes saccula Carter	13
Achnanthes sp. 1 SN*	14
Achnanthes stolida (Krasske) Krasske	15
Achnanthes subatomoides (Hustedt) Lange-Bertalot & Archibald	16
Achnanthes suchlandtii Hustedt	17
Amphora inariensis Krammer	18
Amphora libyca Ehrenberg	19
Amphora pediculus (Kützing) Grunow	20
Asterionella formosa Hassall	21
Aulacoseira ambigua (Grunow) Simonsen	22
Aulacoseira cf. *alpigena* (Grunow) Krammer	23
Aulacoseira distans (Ehrenberg) Simonsen	24
Aulacoseira italica (Ehrenberg) Simonsen	25
Aulacoseira lirata var. *biseriata* (Grunow) Haworth	26
Aulacoseira sp. 4 SN*	27
Aulacoseira sp. 5 SN*	28
Aulacoseira valida (Grunow) Krammer	29
Brachysira brebissonii Ross in Hartley	30
Brachysira vitrea (Grunow) Ross in Hartley	31
Cocconeis placentula var. *lineata* (Ehrenberg) Van Heurck	32
Cyclotella bodanica var. *lemanica* (O. Müller) Bachmann	33
Cyclotella pseudostelligera Hustedt	34
Cyclotella stelligera Cleve & Grunow	35
Cymbella cesatii (Rabenhorst) Grunow	36
Cymbella descripta (Hustedt) Krammer & Lange-Bertalot	37
Cymbella falaisensis (Grunow) Krammer & Lange-Bertalot	38
Cymbella gracilis (Ehrenberg) Kützing	39
Cymbella incerta (Grunow) Cleve	40
Cymbella muellerii Hustedt	41
Cymbella naviculiformis Auerswald	42
Cymbella silesiaca Bleisch	43
Diatoma mesodon (Ehrenberg) Kützing	44
Epithemia sorex Kützing	45
Fragilaria arcus (Ehrenberg) Cleve	46
Fragilaria brevistriata Grunow	47
Fragilaria capucina var. *gracilis* (Oestrup) Hustedt	48
Fragilaria capucina var. *mesolepta* (Rabenhorst) Rabenhorst	49
Fragilaria capucina var. *rumpens* (Kützing) Lange-Bertalot	50
Fragilaria capucina var. *vaucheriae* (Kützing) Lange-Bertalot	51
Fragilaria cf. *robusta* (Fusey) Manguin	52
Fragilaria construens (Ehrenberg) Grunow	53

Appendix A. (continued)

Diatom taxon	Code
Fragilaria construens var. *venter* (Ehrenberg) Grunow	54
Fragilaria elliptica Schumann	55
Fragilaria exigua Grunow	56
Fragilaria lapponica Grunow	57
Fragilaria nanana Lange-Bertalot	58
Fragilaria pinnata Ehrenberg	59
Fragilaria pseudoconstruens Marciniak	60
Fragilaria tenera (W. Smith) Lange-Bertalot	61
Frustulia rhomboides (Ehrenberg) De Toni	62
Frustulia rhomboides var. *crassinervia* (Brébisson) Ross	63
Gomphonema gracile Ehrenberg	64
Gomphonema parvulum (Kützing) Kützing	65
Navicula cf. *minima* Grunow	66
Navicula cf. *seminulum* Grunow	67
Navicula cryptocephala Kützing	68
Navicula cryptotenella fo. 1 PISCES (in Cumming et al. (1995))	69
Navicula difficillima Hustedt	70
Navicula halophila (Grunow) Cleve	71
Navicula laevissima Kützing	72
Navicula pseudoscutiformis Hustedt	73
Navicula pupula Kützing	74
Navicula radiosa Kützing	75
Navicula rhynchocephala Kützing	76
Navicula subtilissima Cleve	77
Neidium ampliatum (Ehrenberg) Krammer	78
Nitzschia amphibia Grunow	79
Nitzschia cf. *palea* (Kützing) W. Smith	80
Nitzschia fonticola Grunow	81
Nitzschia gracilis (Hantzsch)	82
Nitzschia linearis var. *subtilis* (Grunow) Hustedt	83
Nitzschia linearis var. *tenuis* (W. Smith) Grunow	84
Nitzschia palea (Kützing) W. Smith	85
Nitzschia perminuta (Grunow) M. Peragallo	86
Pinnularia interrupta W. Smith	87
Pinnularia microstauron (Ehrenberg) Cleve	88
Rhopalodia gibba (Ehrenberg) O. Müller	89
Stauroneis anceps Ehrenberg	90
Stenopterobia delicatissima (Lewis) Brébisson	91
Stephanodiscus hantzschii Grunow	92
Stephanodiscus medius Håkansson	93
Stephanodiscus minutulus (Kützing) Cleve & Möller	94
Stephanodiscus parvus Stoermer & Håkansson	95
Synedra radians Kützing	96
Synedra ulna (Nitzsch) Ehrenberg	97
Tabellaria flocculosa (Roth) Kützing	98
Tabellaria ventricosa Kützing	99

References

Anderson N.J. 2000. Miniview: diatoms, temperature and climate change. Eur. J. Phycol. 35: 307–314.

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. and Koehler P.A. 1997. Distribution of sites and radiocarbon dates in the Sierra Nevada: implications for paleoecological prospecting. Radiocarbon 39: 121–137.

Battarbee R.W., Jones V.J., Flower R.J., Cameron N.G., Bennion H., Carvalho L. et al. 2001. Diatoms. In: Birks H.J.B., Last W.M. and Smol J.P. (eds), Tracking Environmental Change Using Lake Sediments. Volume 3: Terrestrial, Algal, and Silicious Indicators. Kluwer Academic Publishers, Dordrecht, pp. 155–202.

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

Bigler C., Hall R.I. and Renberg I. 2000. A diatom training set for paleoclimatic inferences from lakes in northern Sweden. Verh. int. Ver. Limnol. 27: 1174–1182.

Bigler C. and Hall R.I. 2002. Diatoms as indicators of climatic and limnological change in Swedish Lapland: a 100-lake calibration set and its validation for paleoecological reconstructions. J. Paleolim. 27: 97–115.

Birks H.J.B. 1994. The importance of pollen and diatom taxonomic precision in quantitative palaeoenvironmental reconstructions. Rev. Palaeobot. Palynol. 83: 107–117.

Birks H.J.B. 1995. Quantitative paleoenvironmental reconstructions. In: Maddy D. and Brew J.S. (eds), Statistical Modelling of Quaternary Science Data. Quaternary Research Association, Cambridge Technical Guide 5., pp. 161–254.

Birks H.J.B. 1998. Numerical tools in palaeolimnology—progress, potentialities, and problems. J. Paleolim. 20: 307–332.

Bloom A.M. 2001. Diatoms in eastern Sierra Nevada lake sediments: quantitative indicators of temperature and salinity, M.Sc. Thesis, University of Utah, Department of Geography, Salt Lake City, 128 pp.

Bradford G.R., Page A.L. and Straughan I.R. 1981. Are Sierra lakes becoming more acidic? Calif. Ag. May-June: 6–7.

Bradshaw E.G., Jones V.J., Birks H.J.B. and Birks H.H. 2000. Diatom response to late-glacial and early Holocene environmental changes at Kråkenes, western Norway. J. Paleolim. 23: 21–34.

Brodersen K.P. and Lindegaard C. 2000. The influence of temperature on emergence periods of Chironomidae (Diptera) from a shallow Danish Lake. In: Hoffrichter O. (ed.), Late 20th Century Research on Chironomidae: An Anthology from the 13th International Symposium on Chironomidae. Shaker Verlag, Aachen, pp. 313–324.

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

Butler M.G. 1980. Emergence phenologies of some arctic Alaskan Chironomidae. In: Murray D.A. (ed.), Chironomidae. Ecology, Systematics, Cytology and Physiology. Pergamon Press, New York, pp. 307–314.

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

Cumming B.F., Wilson S.E., Hall R.I. and Smol J.P. 1995. Diatoms from British Columbia (Canada) lakes and their relationship to salinity, nutrients and other limnological variables. Bibliotheca Diatomologica 31. J. Cramer, Stuttgart.

Danks H.V. and Oliver D.R. 1972. Seasonal emergence of some high arctic Chironomidae (Diptera). Can. Ent. 104: 661–86.

Dauta A., Devaux J., Piquemal F. and Boumnich L. 1990. Growth rate of four freshwater algae in relation to light and temperature. Hydrobiologia 207: 221–226.

Davis O.K., Anderson R.S., Fall P.L., O'Rourke M.K. and Thompson R.S. 1985. Palynological evidence for early Holocene aridity

in the southern Sierra Nevada, California. Quat. Res. 24: 322–332.

Environment Canada 1996a. Manual of analytical methods. Volume 1: Major ions and nutrients. The National Laboratory of Environmental Testing, Canada Centre for Inland Waters, Burlington, 661 pp.

Environment Canada 1996b. Manual of analytical methods. Volume 2: Trace metals. The National Laboratory of Environmental Testing, Canada Centre for Inland Waters, Burlington, 446 pp.

Environmental Systems Research Institute 2001. ArcGIS 8.1 computer software. Environmental Systems Research Institute, Redlands.

Fritz S.C., Juggins S. and Battarbee R.W. 1993. Diatom assemblages and ionic characterization of lakes in the northern Great Plains, North America: a tool for reconstructing past salinity and climate fluctuations. Can. J. Fish. aquat. Sci. 50: 1844–1856.

Fritz S.C., Cumming B.F., Gasse F. and Laird K.R. 1999. Diatoms as indicators of hydrologic and climatic change in saline lakes. In: Stoermer E.F. and Smol J.P. (eds), The Diatoms: Applications for the Environmental and Earth Sciences. Cambridge University Press, Cambridge, pp. 41–72.

Glew J.R. 1988. A portable extruding device for close interval sectioning of unconsolidated core samples. J. Paleolim. 1: 235–239.

Glew J.R. 1991. Miniature gravity corer for recovering short sediment cores. J. Paleolim. 5: 285–287.

Graumlich L.J. 1993. A 1000-year record of temperature and precipitation in the Sierra Nevada. Quat. Res. 39: 249–255.

Gregory-Eaves I., Smol J.P., Finney B.P. and Edwards M.E. 1999. Diatom-based transfer functions for inferring past climate and environmental changes in Alaska, U.S.A. Arct. Antarct. Alp. Res. 31: 353–365.

Hall R.I. and Smol J.P. 1992. A weighted-averaging regression and calibration model for inferring total phosphorus concentration from diatoms in British Columbia (Canada) lakes. Freshwat. Biol. 27: 417–434.

Hartig J.H. and Wallen D.G. 1986. The influence of light and temperature on growth and photosynthesis of *Fragilaria crotonensis* Kitton. J. freshwat. Ecol. 3: 371–382.

Holmes R.W., Whiting M.C. and Stoddard J.L. 1989. Changes in diatom-inferred pH and acid neutralizing capacity in a dilute, high elevation, Sierra Nevada lake since A.D. 1825. Freshwat. Biol. 21: 295–310.

Jones V.J. and Juggins S. 1995. The construction of a diatom-based chlorophyll *a* transfer function and its application at three lakes on Signy Island (maritime Antarctic) subject to differing degrees of nutrient enrichment. Freshwat. Biol. 34: 433–445.

Joynt E.H. III and Wolfe A.P. 2001. Paleoenvironmental inference models from sediment diatom assemblages in Baffin Island lakes (Nunavut, Canada) and reconstruction of summer water temperature. Can. J. Aquat. Sci. 58: 1222–1243.

Juggins S. and ter Braak C.J.F. 1993. CALIBRATE version 0.3: a program for species environment calibration by (weighted averaging) partial least squares regression. Environmental Change Research Centre, University College London, London.

Kilham S.S., Theriot E.C. and Fritz S.C. 1996. Linking planktonic diatoms and climate change in the large lakes of the Yellowstone ecosystem using resource theory. Limnol. Oceanogr. 41: 1052–1062.

Koehler P.A. and Anderson R.S. 1994. The paleoecology and stratigraphy of Nicholas Meadow, Sierra Nevada National Forest, California, USA. Palaeogeogr. Palaeoclim. Palaeoecol. 122: 1–17.

Konrad S.K. and 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.

Konstantinove A.S. 1958. Influence of temperature on the rate of development and growth of chironomids. Doklady Akadamii Nauk SSSR 120: 1362–1365.

Korhola A., Weckström J., Holström L. and Erästö P. 2000. A quantitative Holocene climate record from diatoms in northern Fennoscandia. Quat. Res. 54: 284–294.

Krammer K. and Lange-Bertalot H. 1986-1991. Bacillariophyceae. In: Ettl H., Gerloff J., Heynig H. and Mollenhauer D. (eds), Süβwasserflora von Mitteleuropa. Gustav Fisher Verlag, Stuttgart/Jena Band 2 (1–4).

Landers D.H., Eilers J.M., Brakke D.F., Overton W.S., Kellar P.E., Silverstein M.E. et al. 1987. Western lake survey, phase 1. Characteristics of lakes in western United States: Vol. I. Population descriptions and physico-chemical relationships. U.S. Environmental Protection Agency, Washington D.C., EPA-600/3-86/054a.

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

Leavitt P.R., Vinebrooke R.D., Donald D.B., Smol J.P. and Schindler D.W. 1997. Past ultraviolet radiation environments in lakes derived from fossil pigments. Nature 388: 457–459.

Leydecker A., Sickman J.O. and Melack J.M. 1999. Episodic lake acidification in the Sierra Nevada, California. Water Resour. Res. 35: 2793–2804.

Line J.M., ter Braak C.J.F. and Birks H.J.B. 1994. WACALIB version 3.3—a computer program to reconstruct environmental variables from fossil assemblages by weighted averaging and to derive sample-specific errors of prediction. J. Paleolim. 10: 147–152.

Lloyd A.H. and Graumlich L.J. 1997. Holocene dynamics of treeline forests in the Sierra Nevada. Ecology 78: 1199–1210.

Lotter A.F., Birks H.J.B., Hofmann W. and 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. Paleolim. 18: 395–420.

MacKey A.P. 1977. Growth and development of larval Chironomidae. Oikos 28: 270–275.

Major J. 1988. California climate in relation to vegetation. In: Barbour M.J. and Major J. (eds), Terrestrial Vegetation of California. Special Publication 9. California Native Plant Society, Davis, pp. 11–74.

Mitchell V.L. 1976. The regionalization of climate in the western United States. J. Appl. Meteorol. 15: 920–927.

Mock C.J. 1996. Climate controls and spatial variations of precipitation in the western United States. J. Clim. 9: 1111–1125.

Moser K.A., Korhola A., Weckström J., Blom T., Pienitz R., Smol J.P. et al. 2000. Paleohydrology inferred from diatoms in northern latitude regions. J. Paleolim. 24: 93–107.

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

Patrick R. 1971. The effects of increasing light and temperature on

the structure of diatom communities. Limnol. Oceanogr. 16: 405–21.

Patrick R. 1977. Ecology of freshwater diatoms and diatom communities. In: Werner D. (ed.), The Biology of Diatoms, Botanical Monographs Vol. 13. Blackwell, Oxford, pp. 284–332.

Pienitz R., Smol J.P. and Birks H.J.B. 1995. Assessment of freshwater diatoms as quantitative indicators of past climatic change in the Yukon and Northwest Territories, Canada. J. Paleolim. 13: 21–49.

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

Porinchu D.F. and MacDonald G.M. The use and application of freshwater midges (Chironomidae: Insecta: Diptera) in geographical research. Prog. Phys. Geogr. (in press).

Roberts D. and McMinn A. 1998. A weighted-averaging regression and calibration model for inferring lakewater salinity from fossil diatom assemblages in saline lakes of the Vestfold Hills: a new tool for interpreting Holocene lake histories in Antarctica. J. Paleolim. 19: 99–113.

Rosén P., Hall R., Korsman T. and Renberg I. 2000. Diatom transfer-functions for quantifying past air temperature, pH and total organic carbon concentration from lakes in northern Sweden. J. Paleolim. 24: 109–123.

Scuderi L.A. 1993. A 2000-year tree ring record of annual temperatures in the Sierra Nevada Mountains. Science 259: 1433–1436.

Smith S.J. and Anderson R.S. 1992. Late Wisconsin paleoecological record from Swamp Lake, Yosemite National Park, California. Quat. Res. 38: 91–102.

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

Sylvestre F. 2002. A high-resolution diatom reconstruction between 21,000 and 17,000 ^{14}C yr BP from the southern Bolivian Antiplano (18–23 °S). J. Paleolim. 27: 45–57.

Sylvestre F., Servant-Vildary S. and Roux M. 2001. Diatom-based ionic concentration and salinity models from then south Bolivian Altiplano (15–23 °S). J. Paleolim. 25: 279–295.

ter Braak C.J.F. 1995. Non-linear methods for multivariate statistical calibration and their use in palaeoecology: a comparison of inverse (k-nearest neighbours, partial least squares and weighted averaging partial least squares) and classical approaches. Chemometrics and Intelligent Laboratory Systems 28: 165–180.

ter Braak C.J.F. and Juggins S. 1993. Weighted averaging partial least squares regression (WA-PLS): an improved method for reconstructing environmental variables from species assemblages. Hydrobiologia 269: 485–502.

ter Braak C.J.F. and Šmilauer P. 1998. CANOCO Reference Manual and User's Guide to CANOCO for Windows: Software for Canonical Community Ordination Version 4. Microcomputer-Power, Ithaca, 351 pp.

ter Braak C.J.F. and Šmilauer P. 1999. CANOCO for Windows Version 4.02. Center for Biometry Wageningen, CPRO-DLO, Wageningen.

Vyverman W. and Sabbe K. 1995. Diatom-temperature transfer functions based on the altitudinal zonation of diatom assemblages in Papua New Guinea: a possible tool in the reconstruction of regional palaeoclimatic changes. J. Paleolim. 13: 65–77.

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

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

Weckström J., Korhola A. and Blom T. 1997a. The relationship between diatoms and water temperature in thirty subarctic Fennoscandian lakes. Arct. Alp. Res. 29: 75–92.

Weckström J., Korhola A. and Blom T. 1997b. Diatoms as quantitative indicators of pH and water temperature in subarctic Fennoscandian lakes. Hydrobiologia 347: 171–184.

Whiting M.C., Whitehead D.R., Holmes R.W. and Norton S.A. 1989. Paleolimnological reconstruction of recent acidity changes in four Sierra Nevada lakes. J. Paleolim. 2: 285–304.

Williams M.W. and Melack J.M. 1991. Precipitation chemistry in and ionic loading to an alpine basin, Sierra Nevada. Water Resour. Res. 27: 1563–1574.

Wilson S.E., Cumming B.F. and Smol J.P. 1994. Diatom-salinity relationships in 111 lakes from the Interior Plateau of British Columbia, Canada: the development of diatom-based models for paleosalinity and paleoclimatic reconstructions. J. Paleolim. 12: 197–221.

Wilson S.E., Cumming B.F. and Smol J.P. 1996. Assessing the reliability of salinity inference models from diatom assemblages: an examination of a 219-lake data set from western North America. Can. J. Fish. Aquat. Sci. 53: 1580–1594.

Wolin J.A. and Duthie H.C. 1999. Diatoms as indicators of water level change in freshwater lakes. In: Stoermer E.F. and Smol J.P. (eds), The Diatoms: Applications for the Environmental and Earth Sciences. Cambridge University Press, Cambridge, pp. 183–202.

Wunsam S., Schmidt R. and Klee R. 1995. *Cyclotella*-taxa (Bacillariophyceae) in lakes of the alpine region and their relationship to environmental variables. Aquat. Sci. 57: 360–386.