



The modern distribution of chironomid sub-fossils (Insecta: Diptera) in the Sierra Nevada, California: Potential for paleoclimatic reconstructions

David F. Porinchi^{1,*}, Glen M. MacDonald^{1,2}, Amy M. Bloom³ and Katrina A. Moser³

¹Department of Geography, University of California at Los Angeles, 1255 Bunche Hall, Los Angeles, CA 90095-1524, USA; ²Department of Organismic Biology, Ecology and Evolution, University of California at Los Angeles, Los Angeles, CA 90095, USA; ³Department of Geography, University of Utah, 260 South Central Campus Drive, Room 270, Salt Lake City, UT 84112-9155, USA; *Author for correspondence (e-mail: porinchi@ucla.edu)

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Abstract

Surface lake sediment was recovered from 57 lakes along an elevation gradient in the central, eastern Sierra Nevada of California. The surface sediment was analysed for subfossil chironomid remains in order to assess the modern distribution of chironomids in the region. The lakes sampled for the calibration dataset were between 2.0 and 40.0 m in depth, spanned an altitudinal gradient of 1360 m and a surface water temperature gradient of approximately 14 °C. Redundancy analysis (RDA) identified that five of the measured environmental variables – surface water temperature, elevation, depth, strontium, particulate organic carbon – accounted for a statistically significant amount of the variance in chironomid community composition. Quantitative transfer functions, based on weighted-averaging (WA), partial least squares (PLS) and weighted-averaging partial least squares (WA-PLS), were developed to estimate surface water temperature from the chironomid assemblages. The best model was a WA model with classical deshrinking, which had a relatively high coefficient of determination ($r^2 = 0.73$), low root mean square error of prediction (RMSEP = 1.2 °C) and a low maximum bias (0.90 °C). The results from this study suggest that robust quantitative estimates of past surface water temperature can be derived from the application of these models to fossil chironomid assemblages preserved in late-Quaternary lake sediment in this region.

Introduction

High frequency, centennial-scale climate oscillations have been identified in the late-glacial and Holocene portions of Greenland ice core and marine sedimentary records (Taylor et al. 1993; Bond et al. 1993; Bond and Lotti 1995; Alley et al. 1997; Bond et al. 2001). Previous research has indicated that California's eastern Sierra Nevada and adjacent portions of the Great Basin have experienced centennial- to millennial-scale changes in temperature and moisture balance during this period (Lamarche Jr. and Mooney 1967; Lamarche Jr. 1974; Scuderi 1993; Graumlich 1993; Stine 1994; Benson et al. 1997, 1998). A

number of researchers have suggested that changes in ocean-atmosphere interactions in the north Pacific are the proximate cause of these millennial-scale climate oscillations (Stine 1994; Benson et al. 1997; Bradbury 1997); and in some cases these changes have been linked to changes in the North Atlantic (Benson et al. 1997). Understanding the nature of past extreme climate events and assessing the linkages of these events to conditions in the north Pacific is essential for improving our insight into the causal mechanisms driving climate change in California. To study the links between climate change in the Sierra Nevada and other parts of the world, a continuous, high-resolution (centennial-scale) record of environmental

change that spans the late-glacial period and Holocene is required. The paleolimnological approach (*sensu* Smol et al. (1995)) can potentially provide such a record.

It is increasingly recognized that high-elevation and high-altitude regions are responsive and extremely sensitive to climate change (Houghton 2001; Sorvari et al. 2002; Battarbee et al. 2002). The increases in surface temperature that are projected to occur as a result of global warming will greatly impact the chemical and physical limnology of high-altitude lakes, as well as the biota currently present in these lakes. However, alpine lakes, due to their remoteness, tend to be poorly monitored with limited faunal distributional data collected and little or no instrumental climate records available. Studying the modern distribution of aquatic fauna in these high-elevation sites will establish 'baseline' conditions against which the effects of projected warming in these regions can be evaluated and will also further refine our understanding of how alpine aquatic ecosystems responded to past periods of climate change. Although continental and regional-scale climate models have been developed for North America (e.g., Thompson et al. (1993)), the spatial resolution of these models is not sufficient to accurately capture the climate dynamics associated with the complex topography of mountainous regions such as the Sierra Nevada. Because a large proportion of California's freshwater emanates from the snow-pack of the Sierra Nevada accurate reconstructions of past climate variability in this region are essential.

In this paper we use the remains of chironomids (non-biting midges), preserved in the surface lake sediment of small, climatically sensitive Sierra Nevada lakes to develop chironomid-based inference models for surface water temperature. This is the first attempt at quantifying the modern relationship between chironomids and surface water temperature in the Sierra Nevada, California. The chironomid-based inference models developed in this study will be applied to subfossil chironomid assemblages preserved in Sierra Nevada lake sediments in order to provide a quantitative estimate of past temperature change and allow for the identification of past extreme climate events.

Chironomids are widely distributed and frequently the most abundant insects found in freshwater ecosystems (Cranston 1995). They are particularly well suited for paleolimnological studies because they have relatively short lifecycles, the larvae possess

chitinous head capsules and the adults are mobile. The larval head capsules of midges tend to be well preserved in lake sediments due to the presence of chitin, and are easily recovered and identified. The mobility of adult midges, along with their short life cycle, allows them to respond to climate change very quickly and as a result, midges are likely to have distributions near equilibrium with climate (Walker and MacDonald 1995; Porinchu and Cwynar 2002). The biotopes occupied by chironomids are extremely varied due to the ability of different chironomid species to tolerate large gradients of pH, salinity, depth, oxygen concentration, temperature and productivity (Armitage 1995). As a result, chironomids have been used to track a number of limnological changes, such as atmospheric contamination (Ilyashuk and Ilyashuk 2001), deepwater oxygen levels (Little and Smol 2001), eutrophication (Clerk et al. 2000) and salinity (Verschuren et al. 2000a, 2000b).

A number of studies in northern temperate and sub-arctic regions – using the calibration dataset approach and multivariate statistical techniques – have demonstrated that mean summer air temperature and/or summer surface water temperature have a statistically significant relationship to the distribution of chironomids and have developed chironomid-based inference models for temperature (Walker et al. 1991a; Lotter et al. 1997; Walker et al. 1997; Olander et al. 1999; Brooks and Birks 2000; Larocque et al. 2001; Brooks and Birks 2001). Researchers have applied these models to sub-fossil chironomid assemblages preserved in lake sediments to quantitatively reconstruct changes in past surface water temperature in Atlantic Canada and the northeastern United States during the late-glacial (Walker et al. 1991b; Levesque et al. 1993; Wilson et al. 1993; Levesque et al. 1994; Cwynar and Levesque 1995; Levesque et al. 1997) and past air temperature in western Norway and southeast Scotland during the late-glacial and the early Holocene (Lotter et al. 1999; Brooks and Birks 2000, 2001).

This study was undertaken, in part, to determine the feasibility of using chironomids to quantitatively reconstruct the paleotemperature regime for the eastern Sierra Nevada during the late-glacial period and Holocene and is part of a larger project that will ultimately determine past temperatures and drought in the Sierra Nevada using chironomids, diatoms, Cladocera, isotopes, pollen and stomates found in Sierra Nevada lake sediment. Application of the diatom-based inference models for temperature and salinity

that have been developed in conjunction with this project will enable independent assessment of past changes in temperature and drought conditions (Bloom et al. (in press)). In this paper, we describe the modern distribution of chironomids along an elevation gradient in the eastern Sierra Nevada and assess the nature of the relationship between chironomids and the contemporaneous environment. We present the results from weighted-averaging (WA), partial least squares (PLS) and weighted-averaging partial least squares (WA-PLS) chironomid-based inference models that were used to quantify the relationship between chironomid distribution and surface water temperature. These models are compared to the existing chironomid-based air- and water-temperature inference models that have been developed in eastern Canada, Fennoscandia and Switzerland.

Study area

The Sierra Nevada extends for approximately 600 km and is a large asymmetric, north-northwest trending, westward-tilting fault block composed primarily of Mesozoic batholithic rocks. The batholith consists largely of coarse-grained granodiorite and quartz monzonite, that intruded into metamorphic Paleozoic and Mesozoic rocks (Unruh 1991). The study area extends from Bishop to Bridgeport, California, and covers approximately 1360 m in elevation (Figure 1). Most of the study area is underlain either by pre-Cretaceous metamorphic rock, Cretaceous granitic rock, mid- to late-Tertiary volcanics, early Quaternary volcanics with Quaternary glacial deposits or Quaternary alluvium present locally (Koenig 1963; Strand 1967) (Table 1).

The study area is characterized by an alpine Mediterranean climate with hot, arid summers and cool, humid winters (Major 1988). The eastern Sierra Nevada experiences a strong rainshadow effect, so that moist alpine ecosystems are found at the crest and semi-arid desert is found near Bishop (Sierra Nevada Ecosystem Project 1996). The effects of elevational differences and the rainshadow effect on climate conditions are illustrated in Table 2. Strong gradients of aridity and temperature also exist from north to south along the Sierra Nevada axis, with warmer and drier sites found in the south, as a result of the location of the jet stream and a subtropical high-pressure cell (Hawaiian High) (Table 2).

These strong climate gradients affect the vegetation

of this area. Low elevation sites (2100–2300 m a.s.l.), near valley bottoms, are characterized by a pinyon pine (*Pinus monophylla*) – western juniper (*Juniperus occidentalis*) woodland, manzanitas (*Arctostaphylos* spp.), mountain mahogany (*Cercocarpus* spp.) and scrub oak (*Quercus* spp.). The Jeffrey pine woodland zone (2200–2500 m a.s.l.) is dominated by jeffrey pine (*P. jeffreyi*) and ponderosa pine (*P. ponderosa*). The Upper Montane forest (2300–2900 m a.s.l.) consists of lodgepole pine (*P. contorta* var. *murrayana*), red fir (*Abies magnifica*), sugar pine (*P. lambertiana*) and western white pine (*P. monticola*). The next vegetation zone, the Sub-alpine forest (2750–3475 m a.s.l.), consists of lodgepole pine, mountain hemlock (*Tsuga mertensiana*), and limber pine (*P. flexilis*). In dry, exposed sites in this zone, western juniper may also be found (Anderson 1990). Above the sub-alpine forest is found the alpine tundra vegetation zone. The elevation of the transition from sub-alpine forest to alpine tundra varies through the Sierra Nevada, but generally occurs between 3300 and 3500 m a.s.l. (Lloyd and Graumlich 1997).

Fifty-seven lakes were sampled spanning the steep climate gradients of the study area (Figure 1, Table 1). The lakes sampled are situated from 2115 to 3475 m a.s.l. in elevation, are between 2.0 and 40.0 m in depth, and have surface water temperatures that range from 7.7 to 21.4 °C (Table 1). The majority of lakes sampled are small (1–10 ha), circum-neutral (pH range = 6.7–8.8) and have salinities ranging from 2.20 to 120.28 mg L⁻¹.

Methods

Field

Sampling took place during late-July and early-August, 1999, July 2000 and July 2001. Sediment was recovered from the approximate centre of each lake using a Glew (1991) mini-corer deployed from an inflatable raft. Sediment was extruded using a portable sectioning device (Glew 1988). The top 0–1 cm and 1–2 cm intervals were sampled and stored separately. All samples were immediately placed in Whirl-Paks[®] and kept cool and in the dark until shipped back to the lab. During surface sediment collection, measurements of physical variables, including surface water temperature, specific conductivity, pH and depth were made and epilimnetic water samples were collected (Table 1) (Bloom 2001).

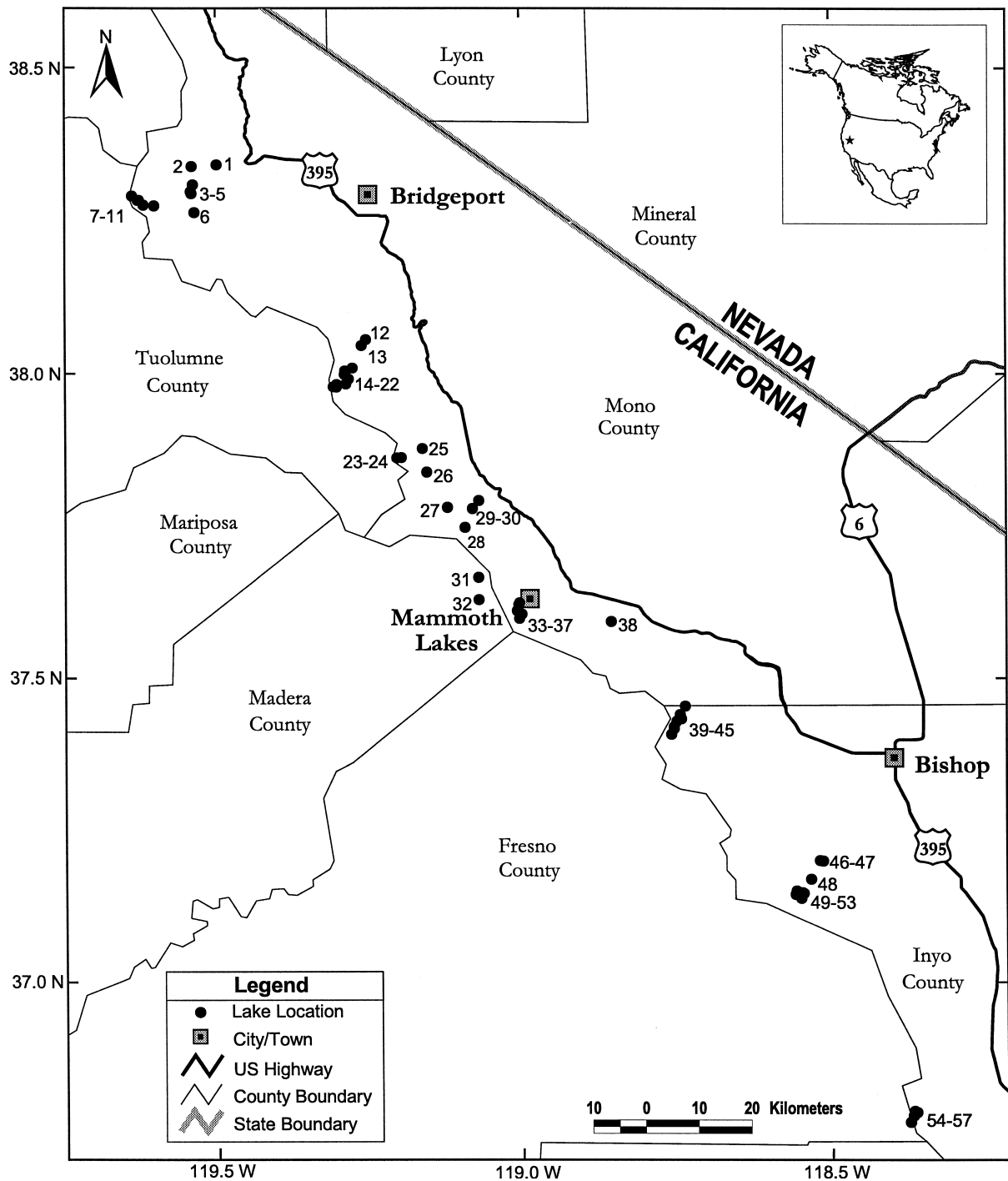


Figure 1. Map of the study area indicating the distribution of the 57 lakes sampled for inclusion in the 'training-set'. Numbers correspond to lakes sampled, with full lake names available in Table 1.

Water samples were collected 0.5 m below the water surface in pre-cleaned polyethylene bottles and immediately treated in the field following the proto-

cols outlined in the Analytic Methods Manual (Environment Canada 1996a, 1996b). Untreated water samples were collected in: one 125 ml glass bottle to

Table 1. Location and selected environmental characteristics of the 57 lakes sampled in the study

Lake code	Lake name	Latitude (N)	Longitude (W)	Geology	Veg	Elev (m a.s.l.)	Area (ha)	Depth (m)	pH	Temp (°C)	Salinity (mg L ⁻¹)	LOI (%)	PON (µg L ⁻¹)	SR (µg L ⁻¹)
SN1	Kirman (KRL)	38° 20' 24"	119° 29' 59"	Q	PP	2174	11.6	3.80	7.6	18.4	92.66	40.24	335.00	898.00
SN2	Millie (MLL)	38° 20' 14"	119° 32' 25"	V	PP	2115	4.4	3.50	7.2	17.9	120.28	44.03	107.00	287.00
SN3	Secret (SCL)	38° 18' 25"	119° 32' 18"	MG	JP	2272	2.4	11.80	6.8	19.60	58.32	43.63	34.00	354.00
SN4	Roosevelt (RVL)	38° 17' 44"	119° 32' 31"	MG	JP	2213	3.7	7.20	8.2	21.4	80.63	57.37	72.00	619.00
SN5	Lane (LLL)	38° 17' 33"	119° 32' 28"	MG	JP	2213	4.1	11.00	8.5	20.4	46.44	45.72	68.00	304.00
SN6	Hidden (HDL)	38° 15' 40"	119° 32' 10"	MG	JP	2379	2.0	9.70	7.8	19.1	9.81	56.47	108.00	38.50
SN7	Latopie (LPL)	38° 17' 19"	119° 38' 14"	V	US	3145	1.9	6.50	6.9	10.8	5.31	14.12	69.00	10.20
SN8	Koenig (KL)	38° 16' 53"	119° 37' 42"	V	S	2905	3.0	2.90	6.8	12.3	9.36	12.63	53.00	27.60
SN9	Koenig (KL2)*	38° 16' 53"	119° 37' 35"	V	S	2897	1.2	3.50	7.0	15.0	6.64	24.62	34.00	20.50
SN10	Leavitt (LVL)	38° 16' 24"	119° 37' 08"	V	S	2896	21.9	24.50	6.8	11.4	13.80	16.57	55.00	41.50
SN11	Ski (SKL)	38° 16' 21"	119° 36' 05"	V	US	2972	1.9	5.20	7.0	12.4	6.99	17.63	53.00	28.30
SN12	Trumbull (TBL)	38° 03' 12"	119° 15' 26"	Q	S	2921	4.0	6.70	7.8	16.3	18.23	39.69	243.00	17.60
SN13	Red (RDL)	38° 02' 35"	119° 15' 51"	PM	S	2978	2.0	4.70	7.3	13.6	25.52	10.55	61.00	24.23
SN14	Moat (MTL)	38° 03' 22"	119° 16' 45"	PM	US	3197	2.4	8.30	7.1	12.3	3.87	24.39	0.00	4.20
SN15	Helen (HLL)	38° 00' 05"	119° 17' 30"	PM	US	3054	2.6	17.50	8.1	12.6	4.45	22.90	67.00	4.60
SN16	East Twin (ETL)*	37° 59' 46"	119° 17' 31"	PM	US	3145	0.6	8.50	7.6	12.8	6.08	30.57	50.00	4.20
SN17	West Twin (WTL)*	37° 59' 43"	119° 17' 32"	PM	US	3152	0.8	8.10	7.2	13.1	6.03	26.42	47.00	4.20
SN18	Hummingbird (HBL)	37° 59' 16"	119° 17' 08"	PM	US	3105	1.2	5.90	7.0	15.4	17.15	34.22	39.00	15.40
SN19	Greenstone (GSL)	37° 58' 47"	119° 17' 24"	Q	S	3067	8.1	4.30	7.8	11.9	2.92	17.08	77.00	3.40
SN20	Upper Conness 1 (UCL1)*	37° 58' 30"	119° 18' 37"	MG	US	3280	1.9	4.80	7.4	7.7	2.65	4.69	50.00	3.80
SN21	Lower Conness (LCL)*	37° 58' 28"	119° 18' 19"	MG	S	3220	1.6	6.30	6.8	11.7	2.73	6.73	72.00	3.40
SN22	Upper Conness 2 (UCL2)*	37° 58' 44"	119° 18' 18"	MG	US	3251	3.9	4.60	7.4	13.0	2.46	6.23	139.00	2.60
SN23	Lower Sardine (LSL)*	37° 51' 30"	119° 11' 59"	MG	US	2996	7.1	13.50	7.5	14.0	8.30	15.19	51.00	6.90
SN24	Sardine Adjacent (SAL)*	37° 51' 29"	119° 12' 25"	PM	US	3170	0.1	2.00	7.9	18.7	6.00	35.12	350.00	5.90
SN25	Walker (WL)	37° 52' 24"	119° 09' 54"	MG	UM	2405	31.3	3.10	8.0	15.2	12.91	33.70	81.00	11.40
SN26	Parker (PL)	37° 50' 04"	119° 09' 29"	Q	JP	2520	8.9	8.30	7.4	10.2	19.97	7.64	46.00	14.30
SN27	Silver (SVL)	37° 46' 37"	119° 07' 28"	Q	PP	2186	58.4	14.00	7.2	15.4	9.17	15.93	50.00	12.20
SN28	Yost (YL)	37° 44' 39"	119° 05' 44"	Q	S	2756	1.2	2.00	7.4	15.4	24.21	28.68	121.00	25.10
SN29	June (JL)	37° 47' 17"	119° 04' 23"	Q	PP	2309	121.6	28.00	8.6	17.8	99.03	19.55	61.00	255.00
SN30	Gull (GLL)	37° 46' 30"	119° 05' 00"	Q	PP	2303	26.8	19.00	7.9	18.9	62.27	17.22	67.00	65.70
SN31	Starkweather (SWL)	37° 39' 46"	119° 04' 25"	MG	UM	2424	1.1	9.80	7.8	19.0	4.94	38.55	90.00	7.10
SN32	Satcher (SRL)	37° 37' 35"	119° 04' 24"	MG	UM	2313	7.8	9.30	8.8	19.9	27.98	16.52	178.00	77.40
SN33	Twin (TL1)*	37° 37' 17"	119° 00' 24"	Q	UM	2595	2.6	2.00	8.3	15.2	17.36	31.16	93.00	35.50
SN34	Twin (TL2)*	37° 37' 05"	119° 00' 29"	Q	UM	2595	4.7	2.30	8.1	15.7	25.82	38.10	89.00	33.40
SN35	Mamie (MML)	37° 36' 29"	119° 00' 38"	Q	UM	2694	5.5	5.00	7.4	16.1	11.44	28.54	79.00	12.30
SN36	Mary (MYL)	37° 36' 10"	119° 00' 11"	Q	UM	2714	42.9	16.00	7.9	15.8	11.64	21.47	73.00	11.70
SN37	Barrett (BRL)	37° 35' 44"	119° 00' 25"	Q	S	2816	1.8	6.08	6.9	19.4	2.20	33.36	52.00	2.10
SN38	Convict (CL)	37° 35' 26"	119° 51' 25"	Q	PP	2309	66.9	40.00	7.6	16.1	45.38	17.28	63.00	29.00
SN39	Rock Creek (RCL)	37° 27' 07"	119° 44' 11"	MG	UM	2938	20.6	29.50	7.6	15.0	5.95	27.60	51.67	5.07
SN40	Serene (SL)	37° 26' 18"	119° 44' 39"	MG	S	3108	0.9	9.20	6.7	17.8	5.82	37.79	55.00	7.80
SN41	Eastern Brook (EBL)	37° 25' 52"	119° 44' 32"	MG	S	3131	4.4	9.00	7.6	16.7	7.20	32.14	77.00	8.30
SN42	Mack (ML)	37° 25' 38"	119° 34' 01"	MG	S	3155	1.1	6.20	7.2	15.9	3.97	27.51	44.00	3.10
SN43	Heart (HL)	37° 25' 06"	119° 45' 16"	MG	S	3160	2.3	4.30	7.4	14.2	3.55	23.98	42.00	3.00
SN44	Box (BL)	37° 24' 54"	119° 45' 15"	MG	S	3178	4.4	9.30	7.4	14.3	3.90	27.82	42.00	2.60
SN45	Long (LL)	37° 24' 20"	119° 45' 31"	MG	S	3194	7.4	11.60	7.1	12.8	4.18	24.23	40.00	2.90
SN46	Rocky Bottom (RBL)	37° 12' 01"	119° 31' 02"	Q	US	3180	2.8	26.50	7.6	15.4	26.79	22.35	0.00	31.20
SN47	Funnel (FL)	37° 11' 59"	119° 30' 43"	Q	S	3180	1.8	10.20	7.9	15.4	21.08	25.00	95.00	33.70
SN48	Green (GL)	37° 10' 10"	119° 31' 55"	Q	S	3350	6.8	12.50	7.4	12.4	7.39	14.74	51.00	10.00
SN49	Bull (BUL)	37° 09' 00"	119° 33' 18"	MG	S	3268	3.1	5.90	8.5	15.1	12.45	42.65	48.00	12.90
SN50	Long 2 (LL2)*	37° 09' 39"	119° 33' 24"	MG	S	3258	14.9	20.80	8.0	14.3	6.97	32.57	69.00	8.90
SN51	Chocolate 2 (CCL2)*	37° 08' 51"	119° 32' 44"	MG	US	3355	0.7	6.30	8.2	14.3	8.37	46.75	71.00	9.90
SN52	Chocolate 1 (CCL1)*	37° 08' 47"	119° 32' 38"	MG	US	3355	2.4	8.50	8.7	14.0	7.68	28.47	59.00	10.10
SN53	Ruwau (RL)	37° 08' 17"	119° 32' 52"	MG	S	3347	9.6	16.00	7.7	12.7	6.84	33.49	69.00	7.00
SN54	Golden Trout 2 (GTL2)*	36° 47' 20"	119° 22' 00"	MG	S	3475	4.4	18.00	7.5	13.4	6.26	24.44	83.00	6.90

Table 1. (continued)

Lake code	Lake name	Latitude (N)	Longitude (W)	Geology	Veg	Elev (m a.s.l.)	Area (ha)	Depth (m)	pH	Temp (°C)	Salinity (mg L ⁻¹)	LOI (%)	PON (µg L ⁻¹)	SR (µg L ⁻¹)
SN55	Golden Trout 3 (GTL3)*	36° 47' 13"	119° 21' 44"	MG	S	3440	1.6	6.50	7.6	17.2	5.67	25.57	48.00	7.60
SN56	Golden Trout (GTL)	36° 46' 52"	119° 22' 05"	MG	S	3463	3.2	11.50	8.5	15.3	19.15	38.65	56.00	20.20
SN57	Big Pothole (BPL)	36° 46' 15"	119° 22' 22"	MG	US	3431	4.3	26.00	7.9	13.3	5.01	29.02	54.00	5.70
				Mean		2906	10.0	10.48		15.1	19.28	27.36	77.75	61.72
	*unofficial name			Median		3054	3.2	8.30		15.2	8.30	27.51	61.00	11.40
				Maximum		3475	121.6	40.00	8.8	21.4	120.28	57.37	350.00	898.00
				Minimum		2115	0.1	2.00	6.7	7.7	2.20	4.69	0.00	2.10

Lake code refers to numbering on study area map (Figure 1). Lake name includes 3–4 letter code referred to in text. Latitude and longitude reported in degrees, minutes and seconds north and west. Abbreviations for geology: MG = Mesozoic granite; Q = Quaternary alluvial or glacial deposits; PM = Paleozoic marine; V = Pliocene/Miocene volcanics. Abbreviations for vegetation: US = upper subalpine; S = subalpine; UM = upper montane; JP = Jeffery pine woodland; PP = pinyon pine-juniper woodland. Elev = elevation. Veg = surrounding vegetation community; Temp = surface water temperature; LOI = Loss-on-Ignition; Sr = strontium; POC = particulate organic carbon.

analyse total phosphorus and two 125 ml polyethylene bottles for major ions and trace metals analyses. Water samples were filtered for Chl *a* (4.7 cm GF/F filter), POC and PN (2.5 GF/F filter) and total nutrients (4.7 cm 0.45 µm cellulose acetate filter). For each water sample 36 chemical variables were measured following protocols outlined in Analytic Methods Manual (Environment Canada 1996a, 1996b) including, sodium (Na), potassium (K), calcium (Ca), magnesium (Mg), chloride (Cl), sulphate (SO₄), lithium (Li), barium (Ba), strontium (Sr), dissolved silica (SiO₂), iron (Fe), manganese (Mn), zinc (Zn), copper (Cu), aluminum (Al), beryllium (Be), cadmium (Cd), cobalt (Co), chromium (Cr), molybdenum (Mo), nickel (Ni), lead (Pb), vanadium (V), nitrite (NO₂), ammonia (NH₃), nitrate-nitrite (NO₃NO₂), particulate organic nitrogen (PN), soluble reactive phosphorus (SRP), dissolved organic carbon (DOC), dissolved inorganic carbon (DIC), particulate organic carbon (POC), total Kjeldahl nitrogen (TKN), total phosphorus (TP), total 'dissolved' phosphorus (TP-F), and total chlorophyll (Chl *a*). Trace metal analysis was based on the dissolved and extracted portion of the water samples. Water chemistry analyses were carried out under

contract by the National Environmental Testing Laboratory at the Canadian Centre for Inland Waters in Burlington, Canada. The water salinity measure is based on the sum of Ca, Mg, K, Na, SO₄, DIC and Cl (Cumming et al. 1995).

Laboratory

The amount of organic material present in the lake sediment was determined using loss-on-ignition (LOI) (Dean Jr. 1974; Heiri et al. 2001). Chironomid analysis followed standard procedures, as outlined in Walker (1987). A minimum of 2 ml (range: 2–40 ml) of sediment was deflocculated in a 5% KOH solution and heated at 30 °C for 30 min. The sediment was then sieved through a 95 µm mesh. The material retained on the sieve was rinsed with distilled water, back-washed into a beaker and aliquots were examined in a Bogorov plankton counting tray. Head capsules were hand picked with the aid of a Wild 5×[®] dissection microscope at 50×. The specimens were permanently mounted on slides in Permount[®] for identification and identified at 400×, generally to genus.

Table 2. Climate station details

Climate station	Station ID number	Location (N, W)	Elevation (m a.s.l.)	Average January temperature (°C)	Average July temperature (°C)	Average annual precipitation (cm)
Bridgeport	041072	38°15', 119°14'	1942	-3.83	16.28	25.78
Bishop WSO	040822	37°22', 118°22'	1265	3.22	24.83	13.64
White Mountain	049633	37°35', 118°14'	3780	-8.69	7.36	50.67
Independence	044232	36°48', 118°12'	1192	5.11	27.11	13.87

Climate data obtained from Western Regional Climate Center (2002). Station ID number refers to National Weather Service meteorological station coding system.

Chironomid identifications were based predominantly on Wiederholm (1983), Walker (1988), Oliver and Roussel (1983), Cranston (1982), Simpson and Bode (1980) and the University of California at Los Angeles reference collection. *Psectrocladius*-type 3 is similar to Walker's *Psectrocladius* (*Psectrocladius*) type 3 (Walker 2000), and is characterized by a distinctive pair of raised median teeth. *Tanytarsus* group 1 is characterized by a *Corynocera oliveri* type mentum and short distally rounded spurs on the antennal pedestal. *Tanytarsus* group 2 is characterized by a mentum similar to *Tanytarsus* group 1 and short, distally rounded spurs on the antennal pedestal; however, the mandibles associated with *Tanytarsus* group 2 specimens have a large dorsal tooth present (there are no mandibles associated with *Tanytarsus* group 1). *Tanytarsus* group 3 is characterized by a broad trident-like median tooth with lateral teeth arrangement similar to *Corynocera* nr. *ambigua* (Walker 2000). *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.

A minimum of 50 head capsules were enumerated and identified from the surface sediment (0–1 cm) from each of the lakes with the exception of Secret Lake (SCL), which was excluded from the calibration set due to the lack of a sufficient number of head capsules. A sum of 50 head capsules has been shown to provide representative counts in other paleolimnological studies (Quinlan and Smol 2001; Heiri and Lotter 2001). In some cases the sediment from the 1–2 cm interval was also analysed in order to achieve a minimum head capsule count of 50. Lakes for which the 1–2 cm interval were required are FL, PL, GLL, LVL, ETL, WTL, GL, HLL, SRL, YL, KRL, HDL, LLL, BPL and GTL2 (see Table 1 for full lake names).

Statistical methods

Data screening

Each lake in the calibration dataset was characterized by 48 environmental variables. However, variables such as Ag, Be, Cd, Co, Cr, Cu, Mn, Mo, Ni, Pb, V and Zn were below the detection limit in the majority of

the lakes sampled and were removed from further analysis. Non-limnological environmental variables such as latitude, longitude, geology, vegetation and surface area were not included in the ordination analyses. The remaining 31 environmental variables included in the ordination analyses were lake depth, pH, specific conductivity, elevation, surface water temperature, salinity, LOI, Al, Ba, Ca, Chl *a*, Cl, DIC, DOC, Fe, K, Li, Mg, Na, NH₃, NO₂, NO₃NO₂, POC, PN, SiO₂, SO₄, Sr, SRP, TKN, TP-F and TP.

Calibration datasets can generally be characterized as 'noisy' and redundant and they tend to contain outliers or 'rogue' observations (Lotter et al. 1997; Birks 1998). In this dataset observations were considered outliers if their samples scores fell outside the 95% confidence limits on the first two axes of both a detrended correspondence analysis (DCA) of the species data and a principal components analysis (PCA) of the environmental data (Hall and Smol 1992).

For the development of the quantitative inference model, samples were identified as outliers if they had an absolute residual (predicted–observed) greater than one standard deviation of the variable of interest (Jones and Juggins 1995; Lotter et al. 1997). Cook's 'D', a statistical test that measures the change in the regression coefficient as samples are deleted from the regression, was used to assess the statistical influence of each potential outlier (Lotter et al. 1997). Samples with high Cook's 'D' values have a large influence on the regression coefficient and were generally not removed from the dataset.

Ordination

All numeric analyses (ordination, regression and calibration) were based on taxa that were present in at least two lakes with a relative abundance of 2% in at least one lake, and used square-root transformed chironomid percentage data in order to optimise the 'signal' to 'noise' ratio and to stabilize variances (Prentice 1980). All ordinations, i.e., DCA, PCA, redundancy analysis (RDA), detrended canonical correspondence analysis (DCCA), were performed using CANOCO version 4.0 (ter Braak and Smilauer 1998).

DCA of the chironomid data was used to identify the length of the environmental gradients sampled in order to determine whether linear- or unimodal-based analysis should be used for constrained ordination (Birks 1995). The gradient lengths of DCA axis 1 and axis 2 were 1.98 and 1.90 standard deviation (S.D.)

units respectively, suggesting the use of RDA for constrained ordination (ter Braak 1995). The eigenvalues for the first two DCA axes were 0.25 and 0.17 respectively and together they explained 25% of the variance in the chironomid data. RDA was used to explore the relationships between the chironomid assemblages and the measured environmental variables. A series of RDAs, in which the first axis was constrained to an individual predictor variable, identified which of the measured environmental variables could explain a statistically significant ($P \leq 0.05$) amount of variation in the chironomid dataset. The statistical significance of each environmental variable was assessed using a Monte Carlo permutation test (199 unrestricted permutations). Of the remaining variables, those with high variance inflation factors (VIFs), were removed one at a time until all remaining variables had VIFs below $20\times$. Forward selection was then used to identify a minimal sub-set of the remaining variables that explained the largest statistically significant amount of variation in the dataset. A Monte Carlo permutation test (199 unrestricted permutations) with a Bonferroni-type adjustment for significance levels was used to assess the statistical significance of each variable identified by the forward selection procedure.

As the primary interest of this study is the development of a quantitative inference model for surface water temperature we assessed the proportion of the variance in the chironomid data that water temperature could independently account for using variance partitioning (Borcard et al. 1992). This was done through the use of a series of partial RDAs in which the variance present in the chironomid data was partitioned between water temperature and (1) elevation, (2) all other variables that were selected by forward selection, (3) physical variables present in the screened dataset (elevation, area, depth, surface water temperature and LOI) and (4) lake chemistry variables present in the screened dataset (salinity, Ba, K, Li, NO_3NO_2 , POC, SiO_2 , SO_4 , Sr, TKN, TP-F).

Canonical co-efficients, approximate *t*-tests and the ratio of the eigenvalue from the first constrained axis (λ_1) to the eigenvalue of the second unconstrained axis (λ_2), for each of the variables identified in forward selection, were used to determine which of these variables would be good candidates for the development of quantitative inference models. Environmental variables with high λ_1/λ_2 ratios are considered good candidates for transfer function development (ter Braak 1986).

Model development

Constrained DCCA was used to assess whether the chironomid taxa were responding in a linear or unimodal fashion along the surface water temperature gradient (Birks 1995). If the gradient length in a DCCA constrained solely to the variable of interest is less than two standard deviations then linear-based methods such as partial least squares (PLS) are favoured for model development, whereas if the gradient length is greater than two standard deviations unimodal methods such as WA-PLS should be favoured (Birks 1998). There are theoretical reasons for using either linear-based or unimodal-based regression methods in the development of quantitative inference models; in situations with biological data of low beta-diversity or compositional turnover along the environmental gradient of interest there are strong statistical reasons to use linear methods (ter Braak and Prentice 1988; Birks 1998). However, in some situations unimodal-based methods may outperform the corresponding linear-based methods even when the compositional turnover of taxa along the environmental gradient of interest is low (ter Braak et al. 1993). Therefore, a variety of linear and unimodal methods were tested to determine the best model.

Weighted-averaging (WA), partial least squares (PLS) and weighted-averaging partial least squares (WA-PLS) were all used to develop chironomid-inference models for surface water temperature. Evaluation of model performance was based on: (1) RMSEP of the model; (2) the maximum mean bias along the temperature gradient (ter Braak et al. 1993); and (3) the number of 'useful' components incorporated in the model. A component was considered 'useful' if it reduced the RMSEP by at least 5% with its addition (Olander et al. 1999; Larocque et al. 2001). Calculation of RMSEP, bias statistics and the number of 'useful' components to be incorporated in the model are based on jack-knifing. The program CALIBRATE version 0.3 (Juggins and ter Braak 1993) was used to perform all the analysis based on WA, PLS and WA-PLS.

A hierarchical set of taxon response models was used to assess the statistical relationship of each taxon to surface water temperature (Huisman et al. 1993). This hierarchical set of taxon response models consists of a skewed unimodal response model, a symmetric (Gaussian) unimodal response model, a monotonically increasing or decreasing sigmoidal response model and a null model of no relationship to

the environmental variable of interest. Taxon response models were fitted to taxa present in greater than ten of the samples in the dataset. This analysis was performed by the Huisman-Olff-Fresco (HOF) program version 2.3 (Oksanen, unpublished).

Results

A total of 68 taxa were identified in the dataset with 44 taxa meeting the initial screening criteria. The results of a PCA of the environmental data and a DCA of the chironomid abundance data indicated that none of the 56 lakes were outliers based on the screening criteria.

The chironomid percentage diagram reveals that the distribution of several chironomid taxa are related to water temperature (Figure 2). For example, *Corynocera oliveri* type, *Rheocricotopus*, *Heterotrissocladius grimshawi* type, *H. marcidus* type, *Synorthocladius*, *Sergentia* and *Hydrobaenus/Oliveridia* are most common and most abundant at sites with surface water temperature less than 15 °C, whereas *Pagastiella*, *Polypedilum* and *Tanytarsus* spp. A/C are most abundant at sites with surface water temperatures in excess of 17.5 °C. As well, *Micropsectra insignilobus* type has a broader temperature tolerance than *Micropsectra radialis* type. Also, the distribution of *Tanytarsina* group 1 is limited to the warmest lakes.

Ordination

RDA constrained to individual environmental variables identified 22 of the 31 environmental variables as having a statistically significant relationship ($P \leq 0.05$) to the distribution of chironomids within the dataset. Of these 22 variables, seven were removed due to high collinearity. The explanatory variables remaining in the analysis were: maximum depth, surface water temperature, salinity, elevation, organic content (as determined by LOI analysis), Ba, K, Li, NO_3NO_2 , POC, SiO_2 , SO_4 , Sr, TKN and TP-F. The eigenvalues for the first two axes from RDA using these 15 variables were 0.14 and 0.10 respectively. These two axes captured 24.0% of the variance in the dataset. Forward selection was used to identify a subset of five variables – surface water temperature, depth, elevation, Sr and POC – that accounted for nearly the same amount of variance that the 15 environmental variables could. RDA using these five

variables provided eigenvalues of 0.14 for axis 1 and 0.08 for axis 2 and these two axes captured 22.0% of the variance in the chironomid data (Figure 3). This indicates that the remaining five environmental variables still capture the majority of the variance present in the dataset. The species-environment correlations for the first two axes were 0.81 and 0.85, respectively. Monte Carlo permutation tests (199 unrestricted permutations) indicated that both axes were significant ($P \leq 0.05$).

Correlation co-efficients, intra-set correlations and approximate *t*-tests indicate that elevation and surface water temperature are strongly related to RDA axis 1; depth and elevation are important components of RDA axis 2; and Sr is strongly related to axis 3 (Table 3). Surface water temperature and elevation also have high ratios of the eigenvalues from the first constrained axis (λ_1) to the eigenvalue of the second unconstrained axis (λ_2) capturing 11.2 and 11.0% of the variance, respectively (Table 4), indicating that from a statistical standpoint, both of these variables are good candidates for developing chironomid-inference models. However, as we are primarily interested in the relationship between chironomid distribution and temperature we choose to focus our efforts solely on developing a quantitative inference model for surface water temperature.

The RDA bi-plots clearly illustrate that the chironomid taxa are well separated along the water temperature axis and that sites, which are positioned in ordination space on the basis of their chironomid assemblages, can be distinguished from one another based on water temperature. The sites, in the site-environment bi-plot, are classified into four categories based on surface water temperature (Figure 3a). This ordination diagram separates out lakes along the surface water temperature gradient with the warmest lakes (> 17.5 °C) positioned high on the temperature axis in the lower right quadrant, the coldest lakes (< 12.5 °C) found in the upper left quadrant and the lakes with intermediate water temperatures positioned in between. The species-environment bi-plot (Figure 3b) also separates the taxa along the surface water temperature gradient. Cold-water taxa, such as *Heterotrissocladius grimshawi* type, *H. marcidus* type, *Sergentia*, *Micropsectra radialis* type and *Hydrobaenus/Oliveridia*, are found with their highest abundances in the coldest lakes, whereas thermophilous taxa, such as *Polypedilum*, *Dicrotendipes*, *Cladotanytarsus mancus* group and *Pagastiella*, are associated with the warm water sites.

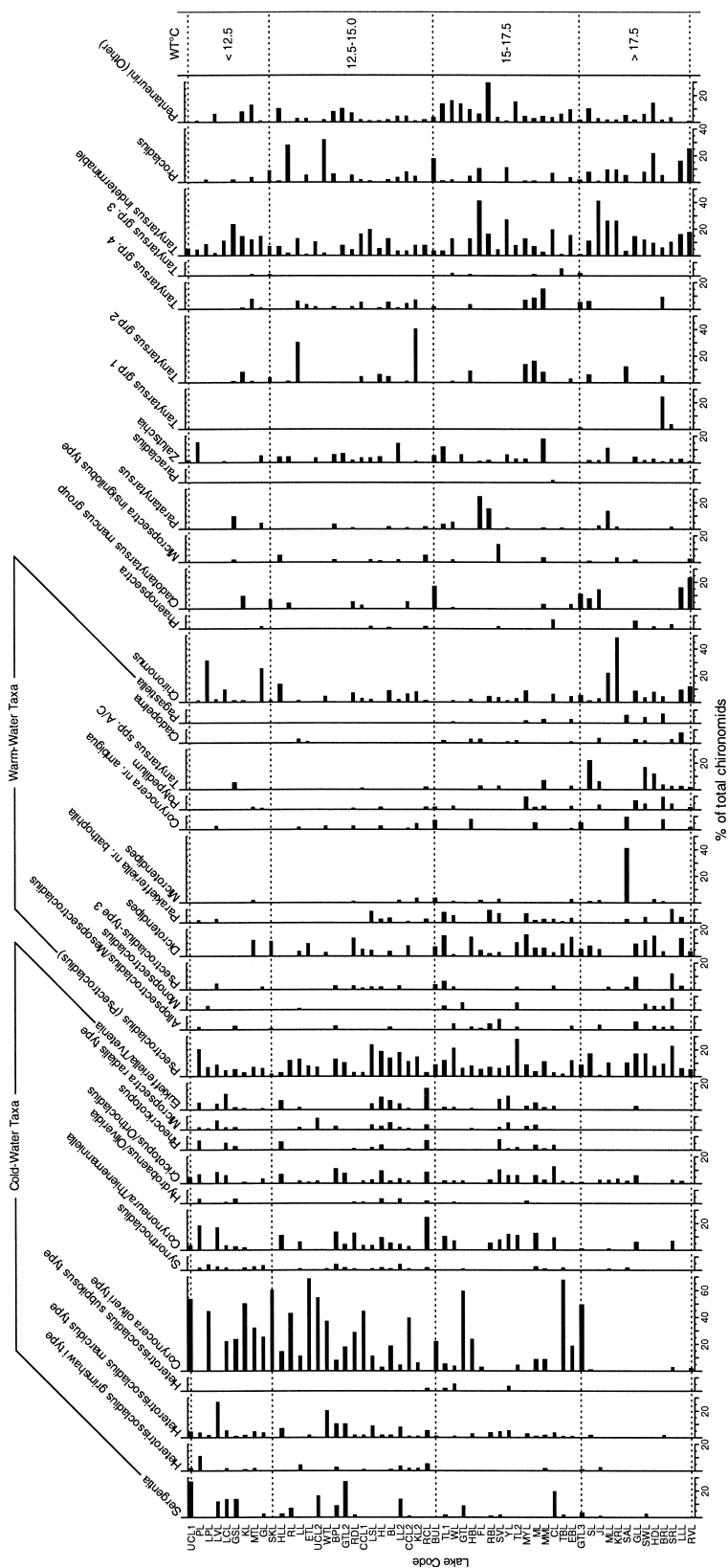


Figure 2. Distribution along a surface water temperature gradient of the most common chironomids found in the 56-lake dataset with the coldest lakes found at the top of the diagram. Full lake names available in Table 1. WT = surface water temperature.

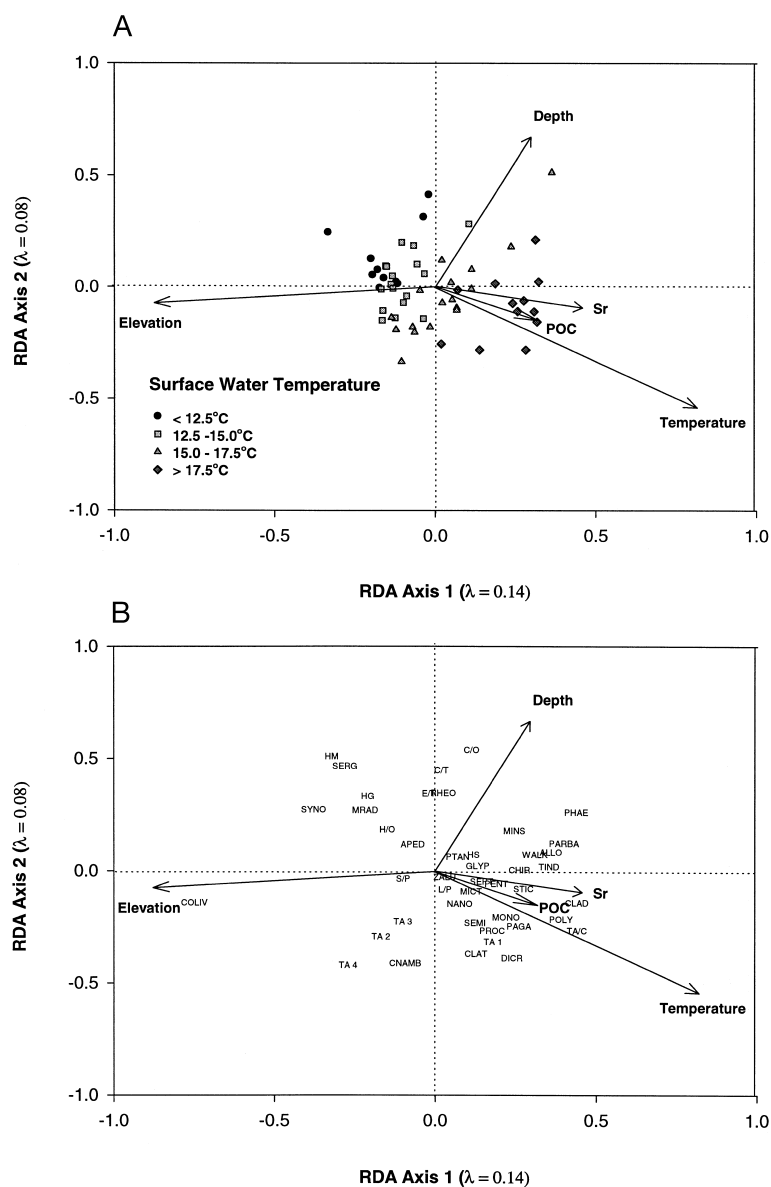


Figure 3. RDA correlation bi-plots illustrating the relationships between (a) the 56 sites classified by surface water temperature, and (b) the 44 chironomid taxa, and the five forward selected variables (elevation, depth, temperature, Sr and POC). POC = particulate organic carbon; Sr = strontium. Abbreviations for chironomid taxa: ALLO = *Allopsectrocladius/Mesopsectrocladius*; APED = *Apedilum*; CHIR = *Chironomus*; CLAD = *Cladopelma*; CLAT = *Cladotanytarsus mancus* group; CNAMB = *Corynocera nr. ambigua*; COLIV = *Corynocera oliveri* type; C/T = *Corynoneura/Thienemanniella*; C/O = *Cricotopus/Orthocladius*; DICR = *Dicrotendipes*; E/T = *Eukiefferiella/Tvetenia*; GLYP = *Glyptotendipes*; HG = *Heterotrissocladius grimshawi* type; HM = *Heterotrissocladius marcidus* type; HS = *Heterotrissocladius subpilosus* type; H/O = *Hydrobaenus/Oliveridia*; L/P = *Limnophyes/Paralimnophyes*; MINS = *Micropsectra insignilobus* type; MONO = *Monopsectrocladius*; MRAD = *Micropsectra radialis* type; MICT = *Microtendipes*; NANO = *Nanocladius*; PAGA = *Pagastiella*; PARBA = *Parakiefferiella nr. bathophila*; PTAN = *Paratanytarsus*; PENT = *Pentaneurini* (Other); PHAE = *Phaenopsectra*; POLY = *Polypedilum*; PROC = *Procladius*; RHEO = *Rheocricotopus*; SEMI = *Psectrocladius (Psectrocladius)*; SEPT = *Psectrocladius septentrionalis* type; SERG = *Sergentia*; S/P = *Smittia/Pseudosmittia*; STIC = *Stictochironomus*; SYNO = *Synorthocladius*; TIND = *Tanytarsus* indeterminate; TAC = *Tanytarsus* spp. A/C; TA1 = *Tanytarsus* group 1; TA2 = *Tanytarsus* group 2; TA3 = *Tanytarsus* group 3; TA4 = *Tanytarsus* group 4; WALK = *Psectrocladius* group 3; ZALU = *Zalutschia*.

Table 3. Canonical co-efficients, approximate *t*-test values and intra-set correlations for the five forward selected variables for the first three RDA axes

	Elevation	Water temperature	Depth	POC	Sr
Canonical co-efficients					
Axis 1	-0.67	0.46	0.26	0.08	-0.13
Axis 2	-0.56	-0.98	0.74	0.42	-0.09
Axis 3	0.26	-0.33	-0.29	-0.12	1.21
Approximate <i>t</i> -values					
Axis 1	-5.55*	3.84*	2.77*	0.76	-1.19
Axis 2	-3.25*	-5.48*	5.39*	2.69*	-0.56
Axis 3	1.37	-1.80	-0.20	-0.71	6.94*
Intra-set correlations					
Axis 1	-0.88	0.82	0.27	0.31	0.45
Axis 2	-0.08	-0.51	0.67	-0.09	-0.12
Axis 3	-0.18	-0.02	-0.09	0.15	0.88

*Statistical significance at $P < 0.05$, based on approximate *t*-tests.

Table 4. The ratios of the eigenvalues (λ) of the 1st (constrained) RDA axis to the eigenvalues of the 2nd (unconstrained) RDA axis

Environmental variable	λ_1	λ_2	λ_1/λ_2	% variance	P
Water temperature	0.112	0.197	0.57	11.2	0.01
Elevation	0.110	0.173	0.64	11.0	0.01
Sr	0.062	0.206	0.31	6.2	0.01
Depth	0.051	0.195	0.26	5.1	0.05
POC	0.035	0.207	0.17	3.5	0.04

Percentage variance explained by each variable and results of Monte Carlo permutation tests (199 unrestricted permutations) based on RDA of the 56 lake 'training set', in which each variable was used as the sole constraining variable. P = significance level of Monte Carlo permutation test.

The results of the partial RDAs indicate that there is a relationship between surface water temperature and chironomid distribution independent of elevation and the other forward selected variables, with temperature accounting for 6.2 and 8.2% of the variance respectively (Table 5). A relationship also exists between the chironomid data and surface water temperature independent of variables related to the physical or chemical conditions of the aquatic environment. The amount of variance accounted for by surface water temperature with 'other physical' variables co-vary-

ing was 4.4%, while the amount of variance explained by water temperature with the 'lake chemistry' variables co-varying was 6.9%.

Regression and calibration

For the development of the temperature inference model 12 lakes (RVL, UCL1, LLL, LPL, PL, MLL, KRL, GTL3, GLL, MTL, GSL and TBL) were deleted due to their high absolute residuals under a WA model with tolerance down-weighting. Only one of

Table 5. Summary of partial RDAs based on chironomid assemblages from the 56 lake 'training set'

Environmental variable	Co-variable(s)	λ_1	λ_2	% variance	P
Water temperature	None	0.112	0.197	11.2	0.005
	Elevation	0.061	0.165	6.8	0.005
	All	0.064	0.126	8.2	0.005
	Lake chemistry	0.050	0.173	6.9	0.005
	Other physical	0.034	0.129	4.4	0.005

P = significance level of Monte Carlo permutation test (199 unrestricted permutations); All = remaining forward selected variables; Other Physical = elevation, area, depth, surface water temperature and LOI; Lake Chemistry = salinity, Ba, K, Li, NO_3NO_2 , POC, SiO_2 , SO_4 , Sr, TKN and TP-F.

these lakes (RVL) had a high Cook's 'D' value, however, it was still removed from the dataset as it had the highest absolute residual (Lotter et al. 1997). The mean, maximum and minimum values of the effective number of taxa in the screened dataset were determined by Hill's N2-diversity measure (Table Hill 1973, Table 6). The presence of large primary and secondary gradients are indicated by the eigenvalues, gradient lengths and percentage variance of the chironomid data captured by DCCA axis 1 (constrained to surface water temperature) and the gradient length of the of the second unconstrained axis (Table 6). The gradient length of a DCCA of the chironomid species data constrained to surface water temperature was 1.77 S.D. units. Taxon response modelling indicated that nine taxa have a statistically significant sigmoidal response and five taxa have a

statistically significant unimodal response to surface water temperature (Table 6). The short gradient length and the results of the taxon response modelling suggest the use of linear-based regression and calibration methods for inference model development. The range, mean, median and standard deviation of surface water temperature for the screened (44 lake) dataset are also summarized (Table 6).

The full results from these models in terms of taxon WA optima and tolerances, WA deshrinking equations, PLS and WA-PLS taxon beta-coefficients are available from D.F.P. upon request. The results from the WA-PLS model indicate that a 1-component WA-PLS model serves as the minimum adequate model (*sensu* Birks (1998)); however, because a 1-component WA-PLS model is equivalent to simple WA with inverse deshrinking (Birks 1998) the results from the WA-PLS model are not reported. The two 'best' models in terms of low RMSEP and maximum bias are: (1) simple WA with inverse deshrinking and, (2) simple WA with classical deshrinking (Table 7). The RMSEP and the maximum bias for the WA model with classical deshrinking are 1.2 °C and 0.90 °C, respectively, while the same statistical measures for the WA model with inverse deshrinking are 1.1°C and 1.20 °C, respectively. The r^2 value for both models was essentially the same, with a value of 0.72 for the WA model based on inverse deshrinking, and a value of 0.73 for the WA model based on classical deshrinking (Table 7). Plots of the observed water temperatures against the predicted water temperatures (jackknifed) for both models are depicted in Figures 4a and 4b. Graphs of the residuals (predicted-observed surface water temperatures) indicate that there is a trend in the residuals of the WA model based on inverse deshrinking ($r^2 = 0.34$) with temperatures overestimated at colder lakes and underestimated at warmer lakes. No trend is apparent in the residuals of the WA model based on classical deshrinking ($r^2 = 0.07$) (Figures 5a and 5b).

Table 6. Summary statistics for the chironomid surface-water temperature calibration set

Number of samples	44
Number of taxa	43
N2 for samples	
mean	12.64
maximum	19.53
minimum	5.54
N2 for taxa	
mean	14.21
maximum	37.90
minimum	1.69
DCCA axis 1 (constrained to surface water temperature)	
λ_1	0.17
Gradient length (S.D.)	1.77
% variance	10.7
DCA axis 2	
λ_2	0.19
Gradient length (S.D.)	2.07
% variance	12.2
$\lambda_{1>}/\lambda_2$	0.87
Surface water temperature (°C)	
minimum	11.4
mean	15.0
median	15.1
maximum	19.9
standard deviation	2.1
range	8.5
Taxon response model	
(maximum likelihood; taxa present in ≥ 10 samples)	
Symmetric unimodal model	3
Skewed unimodal model	2
Sigmoidal model – increasing	4
Sigmoidal model – decreasing	5
Null model	17

S.D. = standard deviation units of compositional turnover. λ = eigenvalue.

Discussion

Factors affecting chironomid distributions

Published studies relating the distribution of chironomids to the physical and chemical limnology of lakes in the western United States are limited. This is the first attempt at quantifying the modern relationship between chironomids and lake water temperature

Table 7. Performance statistics for the five different inference models relating summer surface water temperature to chironomid distribution

Inference model	Apparent		Cross-validation		Maximum bias (°C)
	RMSE (°C)	r^2	RMSEP (°C)	r^2	
WA (inverse)	0.9	0.82	1.1	0.72	1.20
WA _{tot} (inverse)	1.3	0.64	1.5	0.55	1.71
WA (classical)	1.0	0.82	1.2	0.73	0.90
WA _{tot} (classical)	1.6	0.64	1.3	0.61	1.37
PLS (1 component)	1.0	0.77	1.2	0.66	1.38

RMSE = root mean square error; RMSEP = root mean square error of prediction. Cross-validation statistics based on jack-knifing.

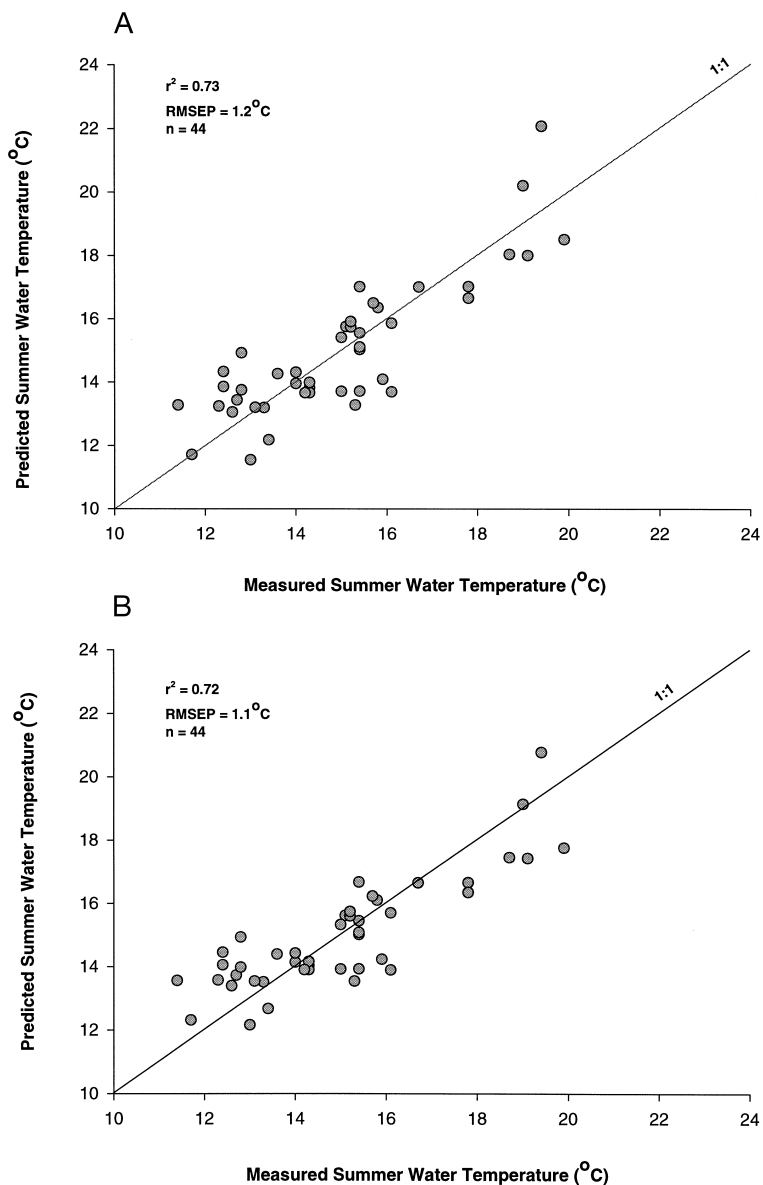


Figure 4. Relationship between observed and predicted (jack-knifed) summer water temperature based on (a) WA with classical deshrinking, and (b) WA with inverse deshrinking.

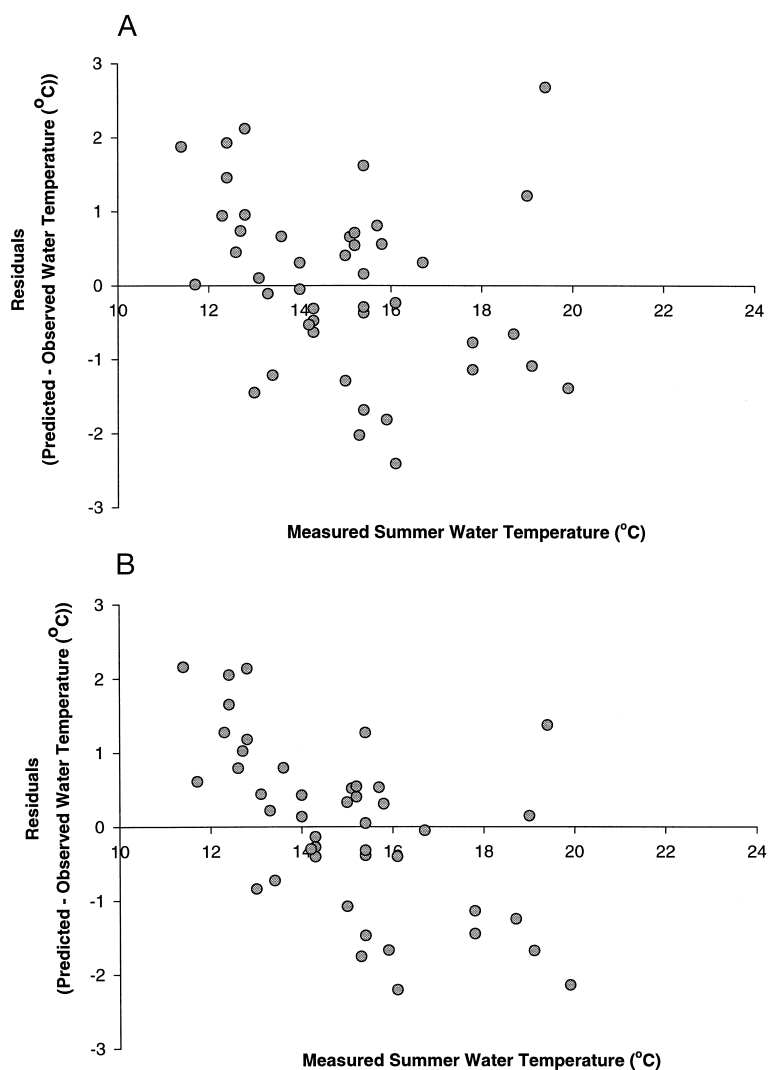


Figure 5. Residuals (predicted–observed) for surface water temperature based on (a) WA with classical deshrinking, and (b) WA with inverse deshrinking.

in California's Sierra Nevada. RDA indicated that five of the measured environmental variables – surface water temperature, lake depth, elevation, Sr and POC – have a statistically significant relationship to the distribution of chironomids in this calibration set and captured the majority of the variance that the measured environmental variables could account for. Of these five variables, surface water temperature explained the greatest amount of variance in the chironomid communities.

The role of water temperature in influencing the composition of chironomid communities has been recognized for some time (Brundin 1949, 1956). Recent work in eastern Canada, Fennoscandia and

Italy has demonstrated that surface water temperature has a strong and statistically significant influence on the composition of chironomid communities in lakes and streams (Rossaro 1991; Walker et al. 1997; Olander et al. 1999). Water temperature has been shown to directly affect larval developmental rates, emergence and voltinism (Brundin 1949; Mackay 1977; Ward and Cummings 1978; Titmus 1979; Menzie 1981). As well, the emergence of chironomids is highly dependent on surface water temperature as demonstrated by a study of the timing of the main emergence of adult chironomids in a shallow Danish lake (Lake Stigsholm) (Lindegaard and Brodersen 2000).

Thienemann (1954) recognized the similarities in

the chironomid communities of high-latitude Scandinavian lakes and alpine lakes. He attributed the similarities in chironomid community composition of these lakes to the influence of their respective, comparable climates. Changes in chironomid faunal composition along an elevational transect of lakes in the Sierra Nevada are similar to the known distribution of chironomids across elevational gradients from other alpine areas, as well as latitudinal transects at northern latitudes. *Heterotrissocladius marcidus* type, *H. grimshawi* type, *Sergentia* and *Corynocera oliveri* type are common and found in relatively high abundances in cold, oligotrophic, high-elevation lakes in the Sierra Nevada. *Heterotrissocladius* is known to be a common constituent of Holarctic lakes (Oliver 1976), whereas *C. oliveri* has been associated with cold, northern lakes and ponds (Oliver and Roussel 1983; Olander et al. 1999; Porinchu and Cwynar 2000). Another study found that coastal, upper subalpine lakes and ponds of British Columbia are dominated by head capsules resembling those attributed in Wiederholm (1983) to *C. oliveri* (Walker and Mathewes 1989). Moreover, it has been suggested *Corynocera* spp. can serve as a proxy for climate, with *C. oliveri* indicative of cold conditions and *C. ambigua* suggestive of warmer climatic conditions (Porinchu and Cwynar 2002). *Sergentia* has also been associated with cold waters (Walker and Mathewes 1989; Walker et al. 1997) and identified as a cold-stenothermic taxon (Brooks and Birks 2000). The chironomid percentage diagram and the species bi-plot suggest that *Parakiefferiella* cf. *bathophila*, *Microtendipes*, *Pagastiella* and *Tanytarsus* spp. A/C are associated with warm surface waters because they are most abundant in lakes with water temperatures greater than 17.5 °C. *Microtendipes* has a limited distribution in arctic environments and has been identified as a thermophilous, littoral genus (Oliver and Roussel 1983; Walker and Mathewes 1989; Walker and MacDonald 1995).

Chironomids are known to be sensitive to a number of different limnological variables, e.g., temperature, depth and substrate (Warner and Hann 1987; Warwick 1989; Hann et al. 1992; Korhola et al. 2000; Verschuren et al. 2000b). Several studies of chironomid ecology have suggested correlations between chironomid taxa and substrate (McGarrigle 1980; Winnell and White 1985; Pinder 1986). Recent calibration datasets from Sweden (Larocque et al. 2001) and Finland (Olander et al. 1999) demonstrate that organic content has a statistically significant relationship to chironomid community composition. Surpris-

ingly, we found that sediment organic content, as measured by LOI, does not account for a statistically significant amount of the variance of the chironomid fauna in Sierra Nevada lakes; however, we did find that POC has a statistically significant relationship to chironomid distribution. The existence of a statistically significant relationship between POC and chironomid distributions has been identified elsewhere (Porinchu and Cwynar 2000). It is likely that the chironomids are responding, at least in part, to the productivity of the lakes, as they appear to be more strongly affected by autochthonous organic matter (measured by POC) than allochthonous matter (comprised of autochthonous and allochthonous carbon) (Wetzel 2002). Walker et al. (1991a) suggest a number of reasons for the poor correlation between LOI and the chironomid taxa that they observed in eastern Canadian lakes. The LOI gradient spanned by the eastern Canadian dataset is relatively short (range of 34%) as is the LOI gradient present in this study (range of 53%), whereas the Finnish and Swedish datasets have longer LOI gradients of 71 and 84%, respectively. The larger range in sediment organic content captured by the Finnish and Swedish datasets may help to differentiate the chironomid communities between lakes (Olander et al. 1999; Larocque et al. 2001).

Strontium concentration also captures a relatively large amount of variance in chironomid distribution in this dataset, accounting for 6.2% of the variance (Table 4). The high canonical coefficient, approximate *t*-value and intra-set correlation for Sr on RDA axis 3 suggest that it is strongly related to this axis. Although Sr captures a large and statistically significant amount of the variance in the chironomid dataset, the manner in which it influences chironomid fauna and community composition is not known. However, it is possible that the chironomids are responding to an underlying salinity gradient which is represented by Sr. The measure of water salinity used in the ordination analyses was based on the sum Ca, Mg, K, Na, SO₄, DIC and Cl (Cumming et al. 1995); it excluded Sr. The effect of salinity on the distribution of midge fauna has been previously noted (Paterson and Walker 1974; Timms 1983). However, it is only fairly recently that chironomid-based inference models have been developed to infer salinity (Verschuren 1994; Walker et al. 1995; Verschuren et al. 2000a; Heinrichs et al. 2001). Attempts to model the response of chironomids to Sr did not provide strong results. However, expansion of the salinity gradient in this dataset may enable the development of robust

chironomid-based inference models for salinity in the future.

Another limnological factor that has been identified in a number of 'training sets', including this study, as having a statistically significant influence on chironomid faunal composition is lake depth (Walker et al. 1991a; Olander et al. 1999; Larocque et al. 2001). A number of inference models for reconstructing lake depth have been developed using various aquatic organisms, including chironomids (Korhola 1999; Korhola et al. 2000). However, some authors caution that faunal assemblages preserved in deep-water cores may not be sensitive to changes in lake level (Frey 1988; Hofmann 1998), while others suggest that reconstructing variables, such as depth, which are intrinsically related to lake morphometry may result in estimates of past hydrologic conditions that are bathymetrically impossible (Birks 1998). Preliminary attempts at modelling depth in this dataset revealed large RMSEP and maximum bias and low r^2 values.

A statistically significant amount of the variance in the chironomid dataset can be explained by elevation (Tables 3 and 4). Partial RDAs demonstrate that the relationship between temperature and chironomid distribution is independent of elevation, however, they also demonstrate that a component of the relationship that exists between temperature and chironomid distribution is not independent of elevation. A simple linear regression of water temperature and elevation indicates that a statistically significant correlation does exist between water temperature and elevation ($r^2 = 0.33$). Elevation itself does not directly affect the distribution of chironomids in the dataset, however, it does affect other physical and chemical variables such as water temperature, ambient air temperature, lake productivity and water chemistry. It is likely that a proportion of the sum of the individual variances that each of the measured environmental variables accounts for in terms of chironomid distribution is captured by elevation. While elevation appears to be strongly related to chironomid distribution in this dataset, from an ecological and paleoecological standpoint, its effects on chironomid community composition is not sufficiently understood to warrant the development of a transfer function quantifying this relationship.

Chironomid inference models

The difference between the WA models using inverse or classical deshrinking is most evident in the esti-

mates of maximum bias. In WA methods, averages are computed twice, once in WA regression and once in WA calibration (Birks 1995). In order to correct for the resulting shrinkage in the inferred values a simple linear 'deshrinking' can be applied. In classical deshrinking values are pulled further from the mean of the calibration set, whereas, inverse deshrinking pulls the inferred values closer to the mean of the dataset (Birks 1995). As a result, WA inference models based on inverse regression tend to have higher residuals at the ends of the gradient of the environmental variable being reconstructed. Selecting between the different deshrinking methods is largely dependent on the part of the gradient that one is interested in reconstructing; classical deshrinking should be used when edges of the gradient are being reconstructed, but inverse deshrinking is appropriate when the central part of the gradient is being reconstructed (Birks et al. 1990; Birks 1995). As there is a trend apparent in the residuals of the WA model with inverse deshrinking, and it has a larger maximum bias (1.20 °C) than the WA model based on classical deshrinking (0.90 °C) the WA model with classical deshrinking appears to be the stronger model. However, the application of a particular model to late-glacial and Holocene chironomid assemblages preserved in Sierra Nevada sediment will be heavily dependent on the part of the temperature gradient being reconstructed.

The results from our inference model for surface water temperature compare favourably to existing inference models for surface water temperature (Walker et al. 1997; Olander et al. 1999; Brooks and Birks 2000, 2001) (Table 8). Currently the coldest lake in the screened 'training set' is 11.4 °C; the possibility exists to expand the surface water temperature gradient by increasing the number of high elevation sites incorporated in the dataset. Expanding the gradient may help to further differentiate the sites based on the faunal composition of the chironomid assemblages and improve the predictive abilities of inference models. Expanding the training set, however, may also increase the biological and environmental heterogeneity that the training set encompasses which may outweigh the potential benefits of improved estimates of taxon optima and tolerances (Olander et al. 1999).

From a paleoclimatological standpoint it would be useful if air temperature could also be directly estimated from sub-fossil chironomid assemblages as opposed to indirectly estimating it by extrapolating from chironomid-inferred surface water temperatures. The highly complex and varied topography of the

Table 8. Comparison of the existing chironomid-based inference models for surface lake-water temperature

Study	Study area	# of lakes	# of taxa	Model	r_{jack}^2	RMSEP (°C)	Range of gradient (°C)	RMSEP as % of gradient	Max bias (°C)
Walker et al. (1997)	Eastern Canada	39	34	WA-PLS (2 component)	0.88	2.26	21	10.76	2.40
Olander et al. (1999)	Northern Finland	53	38	MAT (6 matches)	0.43	1.48	9.3	15.91	1.90
Brooks and Birks (2000)	Western Norway	44	81	WA-PLS (1 component)	0.30	2.22	12.4	17.90	5.29
Brooks and Birks (2001)	Svalbard, Norway	111	119	WA-PLS (3 component)	0.86	2.13	22.7	9.83	2.84
Porinchi et al. (this study)	Sierra Nevada, USA	44	44	WA (classical)	0.73	1.2	8.5	14.1	0.90

The number of lakes (# of lakes) and the number of taxa (# of taxa) included in each study, the jack-knifed values of the coefficient of determination (r_{jack}^2) and the root mean square error of prediction (RMSEP) from each study as well as the range of summer surface water temperature encompassed by the studies (range of gradient), the RMSEP expressed as a percentage of the gradient length and the maximum bias (maximum bias) of each of the models are indicated. The type of model used in each study is also indicated: WA-PLS (weighted averaging partial least-squares), MAT (modern analogue technique), WA (weighted averaging).

eastern Sierra Nevada and the limited number of high elevation meteorological stations with sufficiently long records makes estimating mean summer or July air temperatures difficult. In this dataset, however, it is clear that summer surface water temperature, which is known to co-vary with air temperature (Livingstone and Lotter 1998), accounts for the largest amount of the variance present in the chironomid community. Although chironomid-based air temperature inference models are presently stronger than the existing surface water temperature models (Lotter et al. 1999; Olander et al. 1999; Brooks and Birks 2000), we suggest that incorporating more accurate estimates of surface water temperature, possibly based on seasonal averages, into calibration datasets would greatly improve model performance.

Conclusion

Surface sediment was recovered from 57 lakes along an elevation gradient in the central, eastern Sierra Nevada of California and the chironomid remains preserved in the sediments were analyzed. Ordination analyses indicated that of the measured environmental variables surface water temperature explained the greatest amount of variance in the chironomid data. The relationship between chironomid distributions and surface water temperature was quantified using a number of different inference models. The best of all the models, in terms of a high coefficient of determination ($r^2 = 0.73$), low RMSEP (1.2 °C) and low maximum bias (0.90 °C) was based on simple WA with classical deshrinking. This is the first study in the western United States to establish a quantitative relationship between the distribution of sub-fossil chironomids and surface water temperature. The

strong performance of the inference model suggests that it can be applied to the chironomid assemblages preserved in late-glacial and Holocene lake sediment from this region to provide quantitative estimates of past climate conditions, which should ultimately provide insights into the causal mechanisms of climate change in this area.

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