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Development of a Midge-Based Summer Surface Water Temperature Inference Model for the Great Basin of the Western United States

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Abstract

Surface sediment recovered from 51 lakes in the Uinta Mountains of northeast Utah was analyzed for subfossil chironomid remains, and incorporated in a midge-based inference model for summer surface water temperature (SSWT). The lakes in the calibration set spanned elevation, depth, and summer surface water temperature ranges of 900 m, 12.7 m, and 11.3°C, respectively. Redundancy analysis (RDA) identified four variables, SSWT, depth, specific conductivity, and Al concentration, that could account for a statistically significant amount of variance in the chironomid distribution, with SSWT accounting for the largest amount of variance. The Uinta Mountain calibration set was merged with a previously developed calibration set from the Sierra Nevada, California, in order to develop a midge-based inference model for SSWT applicable to subfossil chironomid stratigraphies from the Great Basin. A variety of statistical approaches, such as weighted averaging (WA), weighted averaging-partial least squares (WA-PLS), and partial least squares (PLS) were used to assess model performance. The best inference model for SSWT, based on a 3-component WA-PLS approach, had robust performance statistics ($r^2_{\text{jack}} = 0.66$, RMSEP = 1.4°C). The newly expanded inference model will enable more accurate estimates of late Pleistocene and Holocene thermal regimes and help address many outstanding questions relating to long-term and recent climate change in this region.

Introduction

A robust midge-based inference model for summer surface water temperature (SSWT) developed (Porinchu et al., 2002) and applied in the Sierra Nevada demonstrated the utility of subfossil midge analysis in providing detailed records of long-term (Porinchu et al., 2003; Potito et al., 2006) and recent climate change (Porinchu et al., 2007). Expansion of the Sierra Nevada calibration set to incorporate sites from the Uinta Mountains of northeastern Utah will increase the diversity of midge communities informing the inference model and improve our knowledge of the tolerances and optima of midge taxa to SSWT in this region. This will increase the utility of the inference model for application to subfossil midge stratigraphies from the Great Basin, which will help answer many outstanding questions relating to the manifestation of specific climate events that may have affected this region during the Holocene and the degree to which this region is experiencing the impact of recent climate change. For example, evidence of high frequency, centennial-scale late Quaternary climate events such as the Younger Dryas (Behl and Kennett, 1996; Benson et al., 1998) and the 4200 year event (Booth et al., 2005) have been discovered in the western United States. However, the spatial imprint of these events in the Intermountain region of the western United States is still poorly known.

The research described here is a part of a larger, multi-proxy study focused on understanding the magnitude and frequency of prolonged drought during the Holocene in the Uinta Mountains (see MacDonald and Tingstad, 2007). The Uinta Mountains contribute approximately 9% of the freshwater supply to the Upper Colorado River Basin (Basin) and serve as a significant source of drinking and irrigation water for Utah. Because the

Basin is vulnerable to periods of sustained drought (Woodhouse et al., 2006), quantifying the magnitude, frequency, and spatial extent of past droughts will help elucidate the forcing mechanisms responsible for past climate variability and monsoon dynamics in this region.

In this paper we describe the modern distribution of subfossil midges from 51 lakes in the Uinta Mountains and discuss the relationship between midge distributions and their contemporaneous environment. Environmental variables that can account for a statistically significant amount of variance in the midge distributions in the Uinta Mountains are identified. Lastly, the development and performance of a midge-based inference model for SSWT, based on a merged data set that incorporates lakes from the Sierra Nevada and the Uinta Mountains, is described. The findings from this research improve our understanding of chironomid ecology and biogeography in the Great Basin of the United States. The development of a midge-based regional inference model for SSWT has the potential to provide much-needed insight into the rate and magnitude of late Pleistocene and Holocene climate change in this region.

Study Area

The Uinta Mountains extend approximately 200 km from the Wasatch Front in northeastern Utah into northwestern Colorado, and are the longest east-west-trending mountain range in the United States outside of Alaska. The core of the Uinta Mountains are a Laramide-age uplift of Precambrian metasedimentary rock, composed primarily of quartzite and slate (Bryant, 1992). The western sector of the study area receives ~30% of its annual

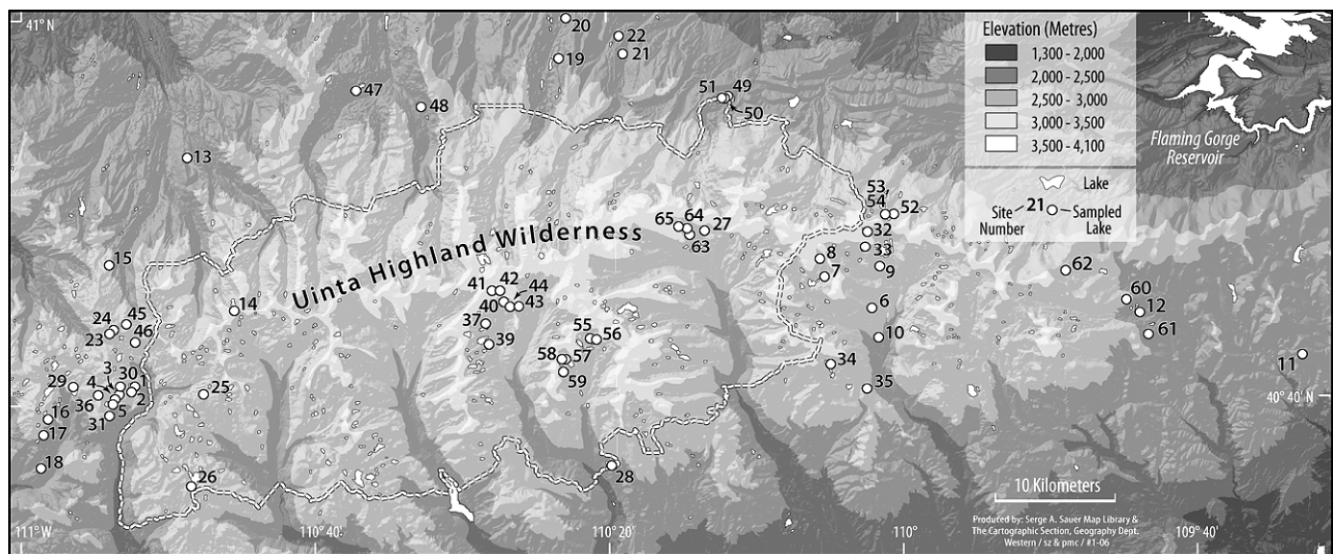


FIGURE 1. Location of study lakes in the Uinta Mountains, Utah. Numbers refer to lakes (see Table 1 for full lake names).

precipitation during the winter (Dec–Feb), and the eastern end of the range receives <20% during these months (MacDonald and Tingstad, 2007). In addition to the influence of the eastern Pacific high-pressure system, the Uinta Mountains lie at the northern edge of the U.S. southwest monsoon, and as a result receive precipitation associated with the northward penetration of the monsoon (Mock, 1996). The broad elevation range and resulting climate gradients affect the distribution of vegetation in the Uinta Mountains. Low elevations (2130–2440 m), typically referred to as the shrub-montane zone, are characterized by *Artemisia tridentata* (sagebrush), *Quercus gambelii* (gambel oak), *Cercocarpus montanus* (mountain mahogany), *Pinus ponderosa* (ponderosa pine), *Pseudotsuga menziesii* (Douglas fir), and *Picea pungens* (blue spruce). Mid-elevations (2740–3050 m) are dominated by *Pinus contorta* (lodgepole pine) and *Populus tremuloides* (aspen). Higher elevations (3050–3350 m) are characterized by *Picea engelmannii* (Engleman spruce), *Abies lasiocarpa* (subalpine fir), and rarely Douglas fir. The alpine zone, located above the spruce-fir zone, is dominated by grasses, lichens, mosses, and sedges (Cronquist et al., 1972). The elevation at which timberline occurs varies through the Uinta Mountains but is generally between 3050 and 3400 m (Goodrich, 2005).

Sixty-four lakes, spanning the broad climate and elevation range in the Uinta Mountains, were sampled for this study (Fig. 1). The lakes sampled range in elevation from 2640 m to 3540 m a.s.l., are between 1.1 m and 22.3 m in maximum depth, and spanned a SSWT range of 16.4°C. The majority of lakes are small (1–10 ha), circum-neutral to alkaline (pH range = 6.8–9.5), with specific conductivity ranging between 4.10 and 236.50 μ S (Table 1).

Methods

FIELD

Sediment samples were collected during July–August 2000, July–August 2004, and July 2005 from the approximate center of each lake using a mini-Glew gravity corer (Glew, 1991) or in some cases a modified Kajak-Brinkhurst (Glew et al., 2001). The upper 0–1 cm and 1–2 cm intervals were extruded on shore using a portable sectioning device (Glew, 1988), were stored individually in Whirl-paks®, and kept cool and dark until reaching the lab.

During surface sediment collection, measurements and notations were made of: vegetation, depth (maximum), Secchi depth, SSWT, specific conductivity, and pH. Epilimnetic water samples were also collected at this time to enable determination of alkalinity, F, Cl, NO₂, Br, NO₃, PO₄, SO₄, Na, Mg, Al, Si, P, K, Ca, Fe, Mn, Sr, Ba, Li, B, Cr, Co, Ni, Cu, Zn, As, Se, Rb, Cd, Cs, Ti, Pb, U, and dissolved organic carbon (DOC). Each lake was typically characterized by a total of 42 environmental variables. Water chemistry analyses were conducted at the University of Minnesota Analytical Geochemistry Lab (R. Knurr) and the University of Ottawa (D. Lean).

LABORATORY

Processing and sorting of subfossil chironomid remains followed standard procedures outlined in Walker (2001) and Porinchu and MacDonald (2003). Chironomid identifications were based on Wiederholm (1983), Walker (1988), Oliver and Roussel (1983), a Web-based field guide to subfossil midges (Walker, 2007), and an extensive reference collection of subfossil midges from the Intermountain region of the western United States, housed in the Department of Geography at The Ohio State University. A number of distinctive *Tanytarsus* types were identified in the Uinta Mountain sediment (Fig. 2). *Tanytarsus* type A is characterized by a broad, possibly worn mentum, similar in appearance to *Tanytarsus* spp. *Tanytarsus* type D is characterized by a *Corynocera*-type mentum with a broad apical tooth present on the mandible. *Tanytarsus* type H is characterized by four lateral teeth and a trident-shaped median tooth complex. *Tanytarsus* type K is characterized by four lateral teeth and a raised *Corynocera*-type median tooth complex.

A minimum of 45 head capsules were enumerated from the uppermost sediment sample (0–1 cm) for the majority of lakes incorporated in the calibration set, with the exception of five lakes for which 40 head capsules were enumerated (UN-2, UN-33, UN-41, UN-49 and UN-53). Heiri and Lotter (2001) suggested that a sum of 45–50 head capsules is generally sufficient to provide consistent inferences for SSWT. The mean, mode, and median number of head capsules enumerated were 86, 50.5, and 64, respectively. Lakes that did not have a sufficient number of head capsules in the 0–1 cm interval were eliminated from further

TABLE 1

Location and selected environmental characteristics of the 64 lakes sampled in the Uinta Mountains. SSWT = summer surface water temperature, SpCond = specific conductivity, LAT = latitude, LONG = longitude.

Lake Code	Lake Name	Lat (°N)	Long (°W)	Elevation (m asl)	Depth (m)	SSWT(°C)	SpCond (uS)	Al (mg/L)
01-UN-01	Hoover	40.68	110.87	3003	8.1	16.9	16.4	49.19
01-UN-02	Marshall	40.68	110.87	3030	10.7	16.3	15.4	13.63
01-UN-03	No name	40.67	110.89	3115	1.8	16.2	12.0	60.34
01-UN-04	No name	40.67	110.89	3069	2.0	17.0	14.8	65.44
01-UN-05	Echo	40.66	110.90	2958	11.6	18.5	14.5	47.53
01-UN-06	Hidden	40.74	110.03	3139	15.7	16.6	14.9	87.76
01-UN-07	Unnamed	40.77	110.09	3379	2.4	13.6	10.4	13.66
01-UN-08	Taylor	40.79	110.09	3394	9.7	13.5	10.2	13.58
01-UN-09	No name	40.78	110.02	3212	1.1	16.4	13.3	43.09
01-UN-10	No name	40.72	110.03	2972	2.7	18.8	21.5	93.97
01-UN-11	Big	40.70	109.54	2636	1.5	19.1	160.8	2.69
01-UN-12	Lilly Pad	40.74	109.73	2921	1.6	21.0	19.7	93.51
01-UN-13	Lilly	40.88	110.81	2703	1.5	18.3	49.5	49.21
01-UN-14	Amethyst	40.75	110.76	3261	16.2	13.7	31.1	2.38
01-UN-15	Bourbon	40.79	110.90	2970	2.3	18.7	23.7	62.79
01-UN-16	Beth	40.65	110.97	2970	2.3	17.5	16.5	59.44
01-UN-17	Buckeye	40.64	110.97	2933	2.1	18.0	16.0	62.26
01-UN-18	Alexander	40.61	110.98	2833	9.0	19.1	22.1	27.21
01-UN-19	Bridger	40.96	110.39	2824	4.0	16.0	112.4	3.51
01-UN-20	No name	41.00	110.38	2762	5.0	16.9	236.5	2.33
01-UN-21	Quarter Corner	40.97	110.31	2701	1.7	16.4	172.7	6.96
01-UN-22	No name	40.98	110.32	2721	2.0	17.2	56.3	33.42
01-UN-23	Lofty	40.73	110.89	3285	7.1	14.3	12.2	10.25
01-UN-24	Kamas	40.73	110.90	3179	4.0	15.7	13.3	9.10
02-UN-25	Betsy	40.67	110.79	3139	11.7	17.6	14.1	15.01
02-UN-26	Heart	40.59	110.81	3188	4.1	18.0	11.3	9.69
02-UN-27	Davis	40.81	110.22	3356	1.7	13.7	20.9	7.25
03-UN-28	Water Lilly	40.61	110.33	2832	10.0	18.7	116.0	0.99
04-UN-29	Teapot	40.68	110.93	3015	13.0	15.0	21.5	21.89
04-UN-30	Fehr	40.68	110.89	3017	8.0	11.8	13.5	87.11
04-UN-31	Pyramid	40.65	110.90	2943	10.2	14.7	18.2	55.57
04-UN-32	Walk-up	40.82	110.04	3373	22.3	4.6	4.1	5.78
04-UN-33	Elbow	40.79	110.03	3335	10.7	10.1	10.1	28.58
04-UN-34	Upper Rock	40.70	110.08	3220	5.4	9.7	14.4	6.75
04-UN-35	Larvae	40.68	110.04	3055	8.2	13.2	18.2	117.80
04-UN-36	Dead	40.67	109.91	3053	6.5	13.9	13.4	16.78
04-UN-37	Little Superior	40.73	110.47	3396	6.9	11.9	12.8	13.13
04-UN-39	No name	40.43	110.47	3303	1.8	17.7	16.1	7.64
04-UN-40	North Star	40.69	110.45	3453	5.8	12.3	14.6	8.02
04-UN-41	No name	40.76	110.46	3531	3.1	11.3	14.0	1.03
04-UN-42	No name	40.76	110.45	3539	2.4	15.1	14.3	9.48
04-UN-43	Tungsten	40.75	110.45	3438	3.6	13.8	14.1	6.76
04-UN-44	No name	40.75	110.43	3426	4.5	14.6	12.2	19.72
04-UN-45	Ruth	40.73	110.88	3145	8.2	16.2	11.5	28.54
04-UN-46	Bud	40.72	110.87	3097	3.1	17.6	68.9	66.21
04-UN-47	Little Lyman	40.94	110.62	2811	7.3	19.0	200.2	5.98
04-UN-48	Dave	40.92	110.54	2795	1.1	20.8	86.8	51.18
04-UN-49	No name	40.93	110.19	2797	13.8	17.6	206.9	1.75
04-UN-50	No name	40.93	110.20	2788	10.5	17.9	82.0	13.23
04-UN-51	No name	40.93	110.20	2832	4.6	17.8	126.0	5.08
04-UN-52	Summit	40.83	110.00	3182	2.6	11.1	17.7	13.77
04-UN-53	Gail	40.83	110.02	3169	6.2	10.0	188.0	11.71
04-UN-54	Jessen	40.83	110.02	3168	16.8	13.5	18.9	22.97
04-UN-55	Upper Carrol	40.72	110.35	3376	13.8	12.9	12.5	12.88
04-UN-56	East Carrol	40.72	110.35	3403	5.3	12.9	15.1	8.78
04-UN-57	No name	40.71	110.38	3336	5.2	13.6	12.4	9.93
04-UN-58	No name	40.70	110.39	3323	7.7	13.1	12.6	11.95
04-UN-59	Twin	40.69	110.38	3278	4.7	10.0	14.4	11.88
04-UN-60	No name	40.75	109.74	3000	6.4	15.4	25.4	101.90
04-UN-61	No name	40.71	109.72	2933	12.1	16.0	26.8	68.69
04-UN-62	Hacking	40.77	109.81	3220	4.9	12.7	18.1	26.65
04-UN-63	Rainbow	40.81	110.24	3373	7.0	12.8	21.9	10.68

(continued)

TABLE 1
(continued)

Lake Code	Lake Name	Lat (°N)	Long (°W)	Elevation (m asl)	Depth (m)	SSWT(°C)	SpCond (uS)	Al (mg/L)
04-UN-64	No name	40.81	110.24	3399	4.9	12.4	16.9	12.87
04-UN-65	No name	40.82	110.25	3436	3.6	12.9	10.3	16.60
	average			3116	6.49	15.15	41.46	29.15
	max			3539	22.33	21.00	236.50	117.80
	min			2636	1.10	4.60	4.10	0.99
	std. dev.			238.57	4.61	3.08	56.35	29.58
	range			903	21.23	16.40	232.40	116.81

statistical analyses (UN-6, UN-7, UN-14, UN-18, UN-19, UN-20, UN-25, UN-28, UN-29, UN-32, UN-50 and UN-54) ($n = 52$).

Statistical Methods

DATA SCREENING OF UINTA MOUNTAIN SAMPLES

A number of lakes lacked values for Li, B, Cr, Co, Ni, Cu, Zn, As, Se, Rb, Cd, Cs, Ti, Pb, and U; these variables, along with Secchi depth, were eliminated from further analyses. Non-limnological variables such as latitude, longitude, vegetation, and elevation were also removed from ordination analyses. The environmental variables active in the ordination analyses were depth (maximum), SSWT, specific conductivity, pH, alkalinity, F, Cl, NO₂, Br, NO₃, PO₄, SO₄, Na, Mg, Al, Si, P, K, Ca, Fe, Mn, Sr, Ba, and DOC ($n = 24$). Calibration data sets typically are 'noisy' and contain many redundant environmental variables and 'outlying' samples (Birks, 1998). A principal components analysis (PCA) of the environmental data and a detrended correspondence analysis (DCA) of the assemblage data were performed to identify outlying samples. A sample was considered an outlier and removed from further analyses if its sample score was greater than 1 standard deviation (S.D.) unit from the mean sample score for axis 1 and 2 of both the PCA and DCA.

ORDINATION

Statistical analyses (ordination and inference model development) were based on all taxa present and used square-root transformed taxa percentage data to optimize the 'signal' to 'noise' ratio and stabilize variances (Prentice, 1980). All ordinations were implemented with CANOCO version 4.5 (ter Braak and Smilauer, 2002).

Detrended correspondence analysis (DCA) of the chironomid percentage data, with down-weighting of rare taxa and detrending by segments, was used to determine the length of the gradients of variation in chironomid distribution, i.e., compositional turnover (Birks, 1995). Compositional turnover, as expressed in S.D. units, identifies whether unimodal or linear approaches are suitable for constrained ordination analyses. Redundancy analysis (RDA) is appropriate when short gradient lengths (S.D. < 2) have been sampled (Birks, 1998). The gradient lengths of DCA axis 1 and axis 2 were 2.44 and 1.40 S.D. units, respectively, and they accounted for 21.5% of the total variance in the midge data. The gradient length of the first two axes suggested the use of linear methods, such as RDA for direct gradient analyses (Birks, 1995). A series of RDAs constrained to the 24 individual predictor (environmental) variables with Monte Carlo permutations (199 unrestricted permutations) were implemented in order to determine which of the predictor variables could account for a statistically significant amount of the variance in the Uinta

Mountain midge data. The collinearity of the remaining environmental variables was assessed using variance inflation factors (VIFs). Forward selection, with Monte Carlo permutation tests (199 unrestricted permutations), was used to identify a minimal subset of the remaining predictor variables that could account for a statistically significant amount of variance in the midge data ($p \leq 0.05$). The purpose of the ordination analyses was twofold: to facilitate exploratory data analyses and to identify which of the measured environmental variables could account for a significant amount of the variance in midge distribution. The amount of variance that SSWT could account for independent of the contribution of the other forward selected variables was assessed using variance partitioning (Borcard et al., 1992). Variance partitioning was implemented using a series of partial RDAs in which the variance present in the midge distribution was partitioned between SSWT and the environmental variables identified in the forward selection procedure.

INFERENCE MODEL DEVELOPMENT

The development of the quantitative Great Basin inference model for SSWT was based on a data set consisting of 51 lakes from the Uinta Mountains and 56 lakes from the Sierra Nevada ($n = 107$). The taxonomy of both data sets was harmonized to facilitate the merging of these two data sets. *Heterotrissocladius grimshawi* type, *Heterotrissocladius marcidus* type, and *Heterotrissocladius subpilosus* type were identified in the Sierra Nevada calibration set; however, due to the difficulty in ensuring consistent identifications, these *Heterotrissocladius* types were combined as *Heterotrissocladius* spp. *Micropsectra radialis* type and *Micropsectra insignilobus* type were identified in the Sierra Nevada calibration set and combined in the merged Sierra Nevada–Uinta Mountains data set. Samples in the merged calibration were considered outliers if they had an absolute residual (observed–predicted) greater than one standard deviation of SSWT (Jones and Juggins, 1995; Lotter et al., 1997; Porinchu et al., 2002). Constrained detrended canonical correspondence analysis (DCCA) was used to assess whether midge taxa were responding to the underlying SSWT gradient in a unimodal or linear fashion (Birks, 1995). When the gradient length of the variable of interest is less than two standard deviation units, linear methods such as partial least squares (PLS) should outperform unimodal methods such as weighted averaging–partial least squares (WA-PLS) (Birks, 1998). However, a variety of WA, PLS, and WA-PLS models were all used to develop transfer functions for SSWT. Model performance was evaluated based upon (1) the root mean square error of prediction (RMSEP); (2) the maximum bias of the model; and (3) the number of components incorporated in the model (*sensu* Birks, 1998). Inference models were developed using the program C2 (Juggins, 2005).

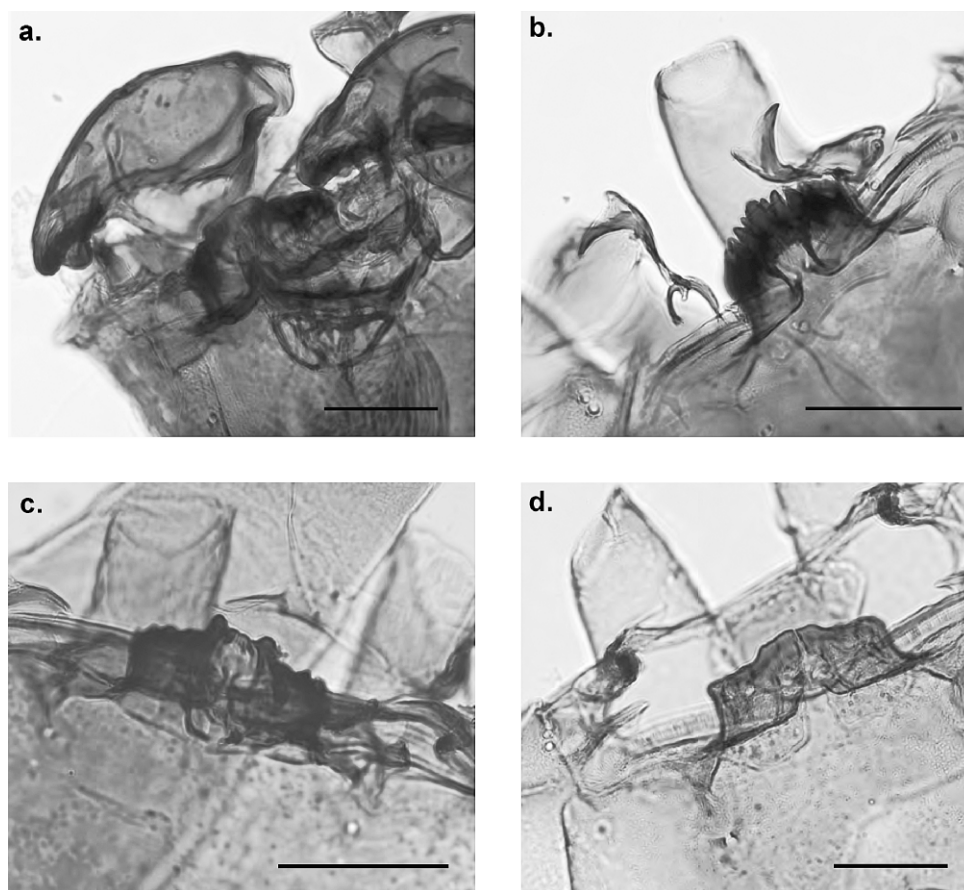


FIGURE 2. Photomicrographs of (a) *Tanytarsus* type D, (b) *Tanytarsus* type H, (c) *Tanytarsus* type K, and (d) *Tanytarsus* type A. See text for description of diagnostic characteristics. The scale bar = 100 μm .

Results

The results of the PCA of the environmental data and the DCA of the midge abundance data from the Uinta Mountains identified one outlier, UN-49, which was removed from the SSWT inference model. Lake UN-49 has the highest specific conductivity (206 μS) in the Uinta Mountains training set, as well as high alkalinity and cation concentrations, which are likely due to the lake's low elevation (2800 m a.s.l.) and location in limestone. These limnological conditions are probably responsible for the distinct midge community found in this lake, which is dominated by a relatively high abundance of *Pentaneurini*.

A total of 41 midge taxa were identified in the Uinta Mountains data set; the distribution and abundances of the common chironomid taxa are depicted in Figure 3. This diagram illustrates that the distribution of many chironomid taxa in Uinta Mountains are related to SSWT; the zones were determined so as to have an approximate equal number of sites in each zone. Taxa such as *Heterotrissocladius*, *Synorthocladoidius*, and *Sergentia* appear to be cold stenothermic and are most abundant and most commonly found in lakes with SSWT $< 13^{\circ}\text{C}$, whereas taxa such as *Cladopelma*, *Polypedilum*, *Pagastiella*, and *Parakiefferiella* nr. *bathophila* are most abundant in lakes that have SSWT $> 17.5^{\circ}\text{C}$. Eurythermic taxa such as *Chironomus* and *Zalutschia* are found in lakes spanning the entire SSWT range.

ORDINATION

RDAs constrained to individual predictor variables ($n = 24$) identified that the following variables contributed significantly (p

≤ 0.05) to the variance present in the midge assemblages in the Uinta Mountains: depth, SSWT, specific conductivity, pH, alkalinity, F, NO_3 , Mg, Al, Si, K, Ca, Fe, Mn, Sr, and dissolved organic carbon (DOC). Those variables with high VIFs ($> 20\times$), Ca and Mg respectively, were eliminated one at a time until the VIFs of the remaining variables were < 20 ($n = 14$). The eigenvalues of the first two axes of a RDA restricted to these 14 variables were 0.123 and 0.093, respectively. These 14 explanatory variables captured 21.7% of the variance in the midge data set. Of the remaining predictor variables (depth, SSWT, specific conductivity, pH, alkalinity, F, NO_3 , Al, Si, K, Fe, Mn, Sr, and DOC), forward selection identified four variables (SSWT, specific conductivity, Al, and depth) that account for a significant and large proportion of the variance present in the midge data. These four variables captured 70.6% of the variance in the midge data accounted for by the 14 predictor variables included in the forward selection procedure, and were used to construct the RDA bi-plots (Figs. 4a, 4b). The eigenvalues for the four RDA axes constrained to the four explanatory variables were $\lambda_1 = 9.2$, $\lambda_2 = 8.5$, $\lambda_3 = 2.6$, and $\lambda_4 = 1.8$, suggesting that the first two axes capture the majority of the variance present in the Uinta Mountains training set. The first two axes account for 17.7% of the variance present in midge data and 80.1% of the cumulative variance of the species-environment relation. Correlation coefficients, intra-set correlations, and approximate t -tests indicate that specific conductivity is strongly related to RDA axis 1 and SSWT to RDA axis 2 (Table 2). When SSWT is used to constrain the first axis (λ_1), the ratio of the eigenvalue of the first constrained axis to the eigenvalue of the second unconstrained axis (λ_2) is high, with SSWT capturing 7.9% of the variance present in the midge data

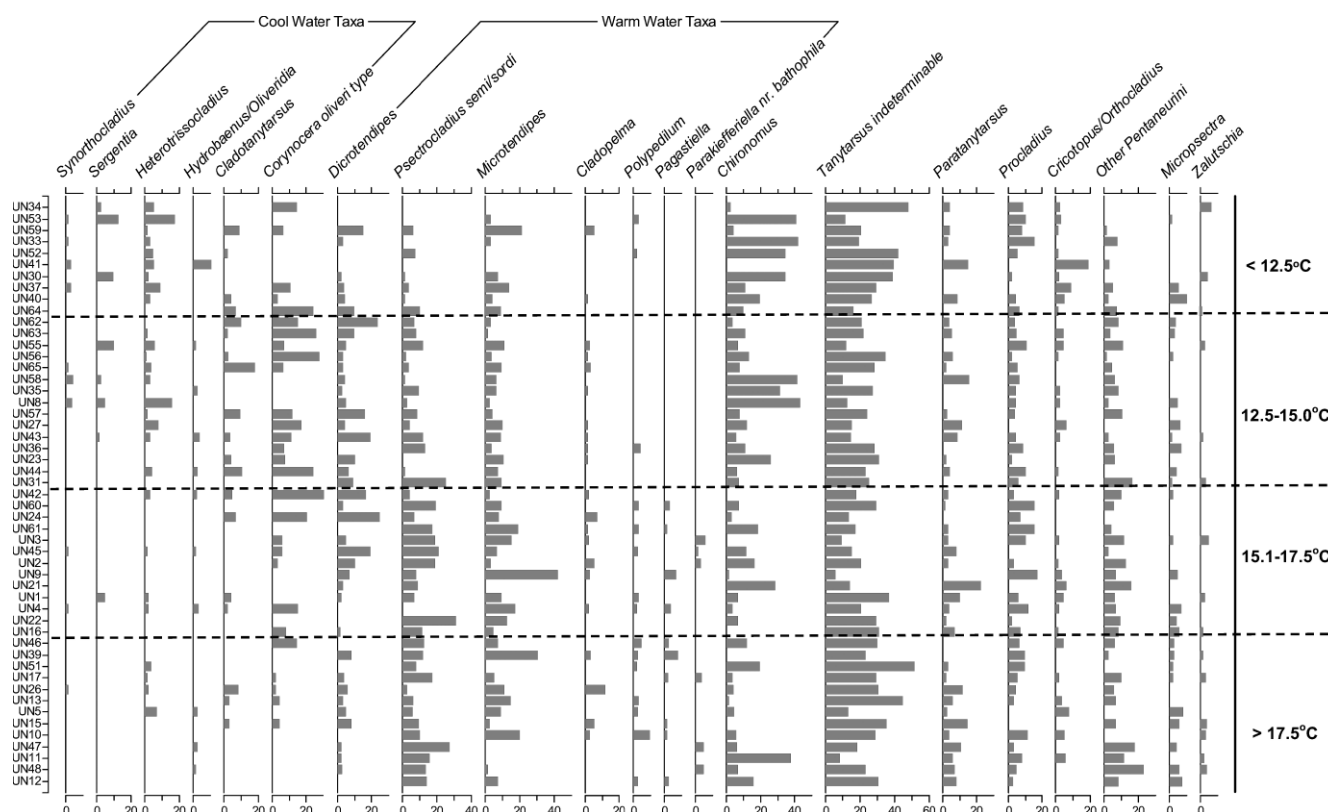


FIGURE 3. Distribution along a summer surface water temperature gradient of the most common chironomids found in the 51-lake data set, with the coldest lakes found at the top of the diagram. The zones were determined so as to have an approximately similar number of sites in each zone.

(Table 3). The strong relationship between SSWT and midge distribution in the Uinta Mountains indicates that from a statistical standpoint, SSWT is a good candidate for the development of a chironomid-based inference model.

The RDA bi-plots clearly separate sites along the SSWT axis and midge assemblages along the SSWT and depth axes (Figs. 4a, 4b). The sites are classified into four categories based on SSWT and an approximately equal number of lakes in each category (Fig. 4a). The site-environment bi-plot separates out the lakes along the SSWT gradient with the coldest lakes (<13°C) positioned low along the SSWT axis, the warmest lakes positioned high on the SSWT axis, and the intermediate lakes positioned in between. The species-environment bi-plot (Fig. 4b) separates taxa along the SSWT gradient with cold stenothermic taxa such as *Heterotrissocladius* and *Synorthocladus* associated with the coldest lakes, while thermophilous taxa such as *Pagestiella*, *Parakiefferiella* nr. *bathophila*, and *Polypedilum* taxa are associated with the warmest lakes. Additionally, taxa typically associated with deep lakes, such as *Sergentia* and *Chironomus*, are positioned high on the depth arrow, whereas taxa that are most abundant in littoral environments, such as *Cladopelma* and *Dicrotendipes*, are most abundant in the shallowest lakes.

The partial RDAs indicate that SSWT can account for a statistically significant amount of variance in the distribution of midges in the Uinta Mountains, independent of the other forward selected variables (depth, specific conductivity, AI) and the larger subset of 14 explanatory variables (Table 4). SSWT can account for 6.6% of the explained variance when all 14 explanatory variables are considered as co-variables and 6.4% of the explained variance when depth, specific conductivity and AI are considered as co-variables.

INFERENCE MODEL DEVELOPMENT

The initial SSWT inference model was based on 107 lakes with 51 lakes from the Uinta Mountains and 56 lakes from the Sierra Nevada. For the development of the summer surface water temperature inference model, following Jones and Juggins (1995), Lotter et al (1997), and Porinchu et al. (2002), 17 lakes were deleted (UN-5, UN-12, UN-13, UN-16, UN-26, UN-45, UN-48, UN-52, UN-59, GTL, GTL3, UCL1, WTL, TBL, LVL, PL, RVL) (see Table 1 in Porinchu et al., 2002, for full Sierra Nevada lake names) from the merged data set ($n = 90$) due to their high absolute residuals as determined by a 2-component WA-PLS model. The mean, maximum, and minimum values of the effective number of taxa in the data, as determined by Hill's N2-diversity measure (Hill, 1973), are presented in Table 5. The presence of a large primary gradient, as well as a large secondary gradient, is indicated by the eigenvalues, gradient lengths and the percent variance captured by DCCA axis 1 (constrained to summer surface water temperature) and unconstrained DCCA axis 2 (Table 5). The ratio of λ_1/λ_2 is 0.50, indicating that a significant secondary gradient exists in the calibration set. This suggests that a WA-PLS model that incorporates additional components will provide a more robust inference model for SSWT.

The performance statistics for nine different inference models are presented in Table 6. A 1-component WA-PLS approach is equivalent to simple WA and therefore, the results for a 1-component WA-PLS model are not shown. The two *best* models, as determined by root mean square error of prediction (RMSEP), *jack-knifed* co-efficient of determination (r^2_{jack}), and maximum bias are (1) 2-component WA-PLS, and (2) 3-component WA-PLS (Table 6). The RMSEP and the r^2_{jack} for the 2-component WA-PLS model are 1.5°C and 0.62, respectively, and 1.4°C and 0.66 for

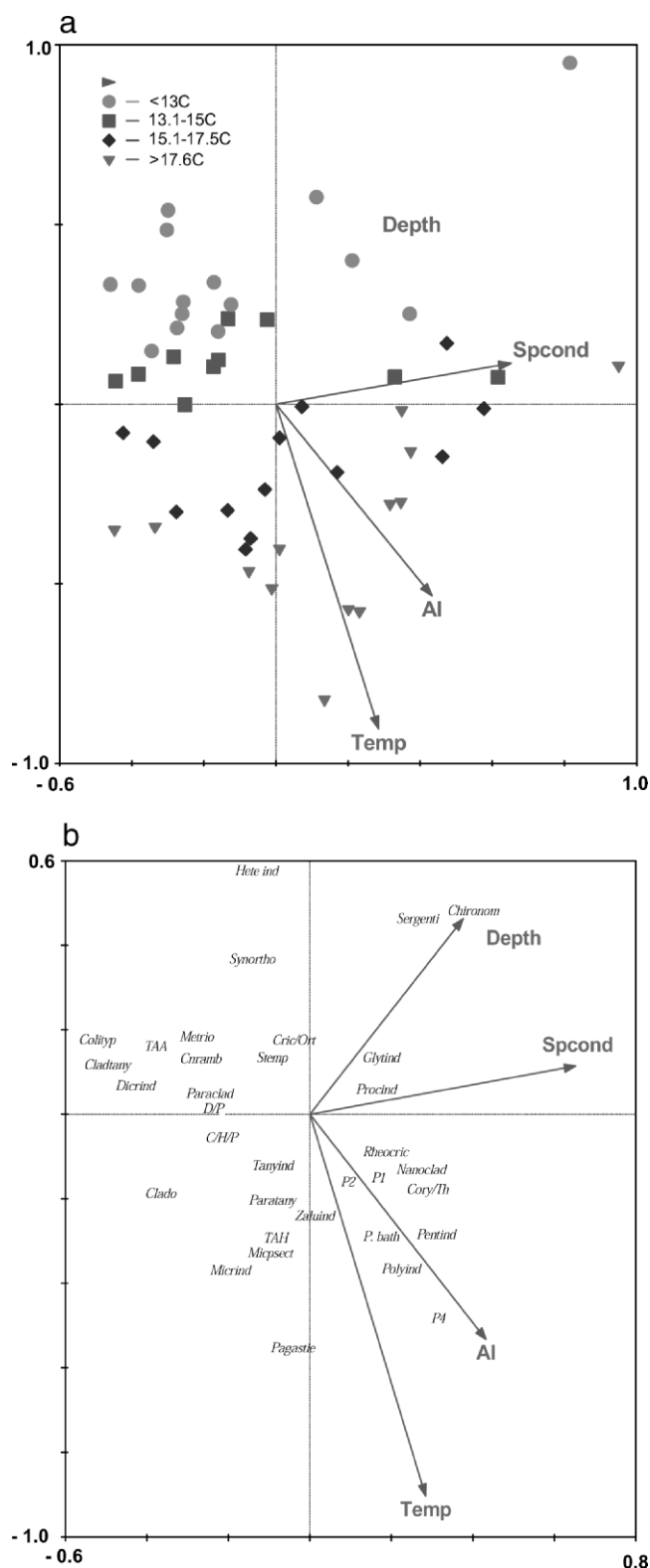


FIGURE 4. (a, b) RDA correlation bi-plots illustrating the relationships between (a) the 51 sites classified by summer surface water temperature, and (b) the chironomid taxa, and the four forward-selected variables (SSWT, depth, specific conductivity, and Al). Abbreviations for chironomid taxa: Chironom = *Chironomus*, Clado = *Cladopelma*, Cladotany = *Cladotanytarsus*, Cnramb = *Corynocera* nr. *ambigua*, Colivtyp = *Corynocera oliveri* type, Coryl Th = *Corynoneural/Thienemanniella*, Cric/Ort = *Cricotopus/Orthocladius*, C/H/P = *Cyphomellal/Harnischial/Paracladopelma*, Dicrind = *Dicrotendipes*, D/P = *Dothrix/Pseudorthocladius*, Glytind =

the 3-component WA-PLS model. The model results suggest that a 3-component WA-PLS model is the minimum adequate model (*sensu* Birks, 1998) as it provides a reduction of ~7% in the RMSEP compared to the 2-component WA-PLS. The beta coefficients used in the 3-component WA-PLS inference model are presented in Table 7. Plots of the *jack-knifed* inferred SSWT against the observed SSWT and the residuals for the 3-component WA-PLS model are depicted in Figure 5a, with no trend apparent in the residuals ($r^2 = 0.0002$) (Fig. 5b).

Discussion and Conclusions

This is the second study to use a calibration set approach to elucidate the relationship between subfossil midge distributions and the contemporaneous environment in the Great Basin of the western United States. The previous study, based on 44 lakes and 43 taxa (Porinchu et al., 2002), identified five variables (SSWT, elevation, Sr, depth, and particulate organic carbon) that account for a statistically significant amount of variance in midge distributions in the Sierra Nevada, California, with SSWT accounting for the greatest amount of variance (Porinchu et al., 2002). In the Uinta Mountains the environmental variables identified as having a statistically significant relationship with chironomid distribution are SSWT, depth, Al, and specific conductivity. The relationship of SSWT, depth, and various measures of ionic concentration to midge distributions has been well documented in northern, eastern, and western Canada, the circum-North Atlantic, and central Europe (Olander et al., 1999; Lotter et al., 1999; Brooks and Birks, 2001; Heinrichs et al., 2001; Porinchu et al., 2002; Barley et al., 2006). The role of these variables in influencing midge distributions is discussed extensively in Walker (2001) and Porinchu and MacDonald (2003).

The chironomid percentage diagram (Fig. 3) reveals that taxa such as *Heterotrissocladius*, *Sergentia*, *Synorthocladius*, and *Corynocera oliveri* type are associated with the coldest lakes in the Uinta Mountains, which is similar to their distribution in the Sierra Nevada. Taxa such as *Polypedilum*, *Pagastiella*, *Cladopelma*, and *Parakiefferiella* nr. *bathophila* are associated with the warmest lakes in the Uinta Mountains (Fig. 3) and the Sierra Nevada (see Fig. 2 in Porinchu et al., 2002). There is only one relatively common taxon (Hill's N2 > 15) in Uinta Mountain lakes, *Tanytarsus* type H, that is absent from the Sierra Nevada, and one relatively common taxon in Sierra Nevada lakes (Hill's N2 > 15), *Tanytarsus* type C, not present in the Uinta Mountain sites. However, the merged calibration set has incorporated four additional taxa, *Metriocnemus*, *Tanytarsus* type A, *Tanytarsus* type H, and *Tanytarsus* type K, that were not present in the Sierra Nevada calibration set. The overall correspondence of midge

Glyptotendipes, Hete ind = *Heterotrissocladius*, Metrio = *Metriocnemus*, Micpsect = *Micropsectra*, Micrind = *Microtendipes*, Nanoclad = *Nanocladius*, Pagastie = *Pagastiella*, Paraclad = *Paracladius*, P.bath = *Parakiefferiella* nr. *bathophila*, Paratany = *Paratanytarsus*, Pentind = *Pentaneurini* (other), Polyind = *Polytendipes*, Procind = *Procladius*, P1 = *Allopsectrocladius/Mesopsectrocladius*, P2 = *Psectrocladius (monopsectrocladius)*, P4 = *Psectrocladius semicirculatus/sordidellus*, Rheocric = *Rheocricotopus*, Sergenti = *Sergentia*, Stemp = *Stempellina*, Synortho = *Synorthocladius*, Tanyind = *Tanytarsus* indeterminate, TAA = *Tanytarsus* type A, TAH = *Tanytarsus* type H, Zaluind = *Zalutisia*.

TABLE 2

Canonical coefficients, intra-set correlations, and approximate *t*-test values for the four predictor variables identified in forward selection for the first two RDA axes. SSWT = summer surface water temperature. Sp. Cond = specific conductivity. *Significant at $p < 0.05$, based on approximate *t*-tests.

	Depth	SSWT	Sp. Cond	Al
Canonical Coefficients				
Axis 1	0.27	0.21	0.47	0.31
Axis 2	0.35	-0.69	0.08	-0.41
Intra-set Correlations				
Axis 1	0.49	0.03	0.76	0.50
Axis 2	0.21	-0.70	0.32	-0.13
Approximate <i>t</i> -value				
Axis 1	3.52*	0.21	5.48*	3.61*
Axis 2	1.66	-5.62*	2.53*	-1.03

assemblages between the Sierra Nevada and Uinta Mountain data sets supports the potential use of the merged data set and the application of the associated inference model for SSWT in the Great Basin of United States.

Merging regional training sets may provide more accurate estimates of the tolerances and optima of taxa and increase the number of modern analogs. The performance statistics for the 3-component WA-PLS inference model based on the merged Sierra Nevada and Uinta Mountain data set indicate that this model is more robust than the previous inference model consisting solely of lakes from the Sierra Nevada (Porinchu et al., 2002). The SSWT

TABLE 3

The ratios of the eigenvalues of the first (constrained) RDA axis to the eigenvalues of the second (unconstrained) RDA axis. Percent total variance depicts the amount of variance captured by the each of the predictor variables identified in the forward selection procedure relative to the full set of environmental variables. Percent 14 variance depicts the amount of variance captured by the each of the predictor variables identified in the forward selection procedure relative to the reduced set of environmental variables. In all cases the eigenvalue for axis 1 (λ_1) is significant at $p < 0.01$. SSWT = summer surface water temperature. Sp. Cond. = specific conductivity.

Environmental Variable	λ_1	λ_1/λ_2	% total variance	% 14 variance
SWT	0.079	0.42	7.9	11.0
Sp. Cond.	0.053	0.32	5.3	9.5
Al	0.055	0.29	5.5	8.7
Depth	0.044	0.25	4.4	16.8

TABLE 4

Summary of partial RDAs based on chironomid assemblages from the 51 lake 'training set.' All = set of 14 environmental variables used in forward selection procedure.

Environmental Variable	Co-variable(s)	λ_1	λ_2	% variance
Surface water temperature	None	0.079	0.190	7.9
	All	0.028	0.058	6.6
	Depth	0.075	0.175	7.8
	Specific Conductivity	0.082	0.158	8.6
	Al	0.061	0.184	6.5
	Al, Specific Conductivity and Depth	0.053	0.122	6.4

TABLE 5

Summary statistics for the chironomid summer surface water temperature calibration set. SD = standard deviation units of compositional turnover, λ = eigenvalue.

Number of samples	90
Number of taxa	57
N2 for samples	
mean	11.59
maximum	19.05
minimum	5.37
N2 for taxa	
mean	20.34
maximum	79.89
minimum	1.00
DCCA Axis 1 (constrained to surface water temperature)	
λ_1	0.10
gradient length (SD)	1.32
% variance	4.6
DCA Axis 2	
λ_2	0.20
gradient length (SD)	2.43
% variance	13.6
λ_1/λ_2	0.50
Summer Surface Water Temperature (°C)	
minimum	9.7
mean	14.96
median	14.98
maximum	20.4
standard deviation	2.50
range	10.7

gradient is 2.2°C larger in the merged data set, and as a result, the RMSEP as a percentage of the SSWT gradient is reduced (Table 8). However, the expansion of the training set may also lead to increasing biological and environmental heterogeneity, multiple analogue scenarios and differences in the biogeographical distribution of taxa which can affect their optima and tolerances (Lotter et al., 1997, Olander et al., 1999, Brooks and Birks, 2001). These factors may account for the slightly better r^2_{jack} and RMSEP values for the smaller Sierra Nevada calibration set ($n = 44$) and the larger maximum bias in the merged data set. Nevertheless, the benefits of the expanded SSWT gradient in the merged Great Basin training set outweighs the slight decrease in the performance statistics of the inference model because it will likely improve the applicability of the inference model to down-core midge stratigraphies.

Previous research in the western Great Basin (Porinchu et al., 2003) revealed that midge communities present during the immediate post-glacial interval (15.0–13.5 ka BP) are poorly represented in the Sierra Nevada calibration set. The midge assemblages preserved in the basal sediment of Greenstone Lake, a subalpine lake located at 3067 m a.s.l., are dominated by a cold stenothermic taxon, *Heterotrissocladius* (~95% relative abundance). The composition of the initial midge community at Greenstone Lake fell well outside the ordination space captured by the 44-lake Sierra Nevada calibration set (see Fig. 5 in Porinchu et al., 2003) suggesting the lack of a close modern analog in the existing Sierra Nevada data set. As a result, the SSWT estimates for this interval are poorly constrained, and the chironomid-inferred temperatures are likely significantly over-estimated. The merged Uinta Mountain–Sierra Nevada training set would likely not provide an accurate estimate of SSWT for the midge

TABLE 6

Performance statistics for the different models relating SSWT to chironomid variance. RMSE = root mean square error. RMSEP = root mean square error of prediction. Cross-validation statistics based on jack-knifing.

Inference Model	Apparent	r^2	Cross Validation	r^2	Maximum Bias	% improvement of RMSEP
	RMSE (°C)		RMSEP (°C)			
WA (inverse)	1.4	0.68	1.6	0.57	3.57	
WA (classical)	1.7	0.68	1.8	0.57	2.84	
WA _{tol} (inverse)	1.4	0.69	1.9	0.42	2.54	
WA _{tol} (classical)	1.7	0.69	2.5	0.34	2.56	
WA-PLS 2 Component	1.1	0.81	1.5	0.62	2.95	6.30
WA-PLS 3 Component	0.9	0.86	1.4	0.66	2.61	6.70
PLS 1 Component	1.7	0.53	1.9	0.41	4.47	
PLS 2 Component	1.5	0.63	1.8	0.49	3.19	5.30
PLS 3 Component	1.3	0.73	1.8	0.50	3.70	0.00

TABLE 7

Values for non-rare taxa (i.e. taxa present in >5% of training set lakes) for: taxon occurrence (percent of lakes in which taxon was present), the minimum SSWT taxon was associated with (T-Min), maximum SSWT taxon was associated with (T-Max), beta coefficient values based on square-root transformed data (WA-PLS Beta transformed), and untransformed percentage data (WA-PLS Beta untransformed) used in the 3-component WA-PLS model.

Taxa	Occurrence (%)	T-Min	T-Max	WA-PLS Beta (transformed)	WA-PLS Beta (not transformed)
<i>Corynoneural/Thienemanniella</i>	46	11.7	19.9	16.2	16.42
<i>Cricotopus/Orthocladius</i>	67	9.7	20.4	18.8	16.34
<i>Doithrix/Pseudoorthocladius</i>	6	11.3	17.8	-1.7	-15.10
<i>Eukiefferiella/Tvetenia</i>	31	11.7	19.1	12.6	14.39
<i>Hydrobaenus/Oliveridia</i>	22	11.3	19.1	14.8	0.77
<i>Limnophyes/Paralimnophyes</i>	14	12.3	19.1	13.9	3.97
<i>Nanocladius</i>	11	11.9	20.4	28.1	33.92
<i>Parakiefferiella bathophila</i>	24	14.0	20.4	25.7	21.50
<i>Alopsectrocladius/Mesopsectrocladius</i>	27	10.1	19.9	14.4	15.52
<i>Psectrocladius (Monopsectrocladius)</i>	16	10.8	19.9	-5.3	-7.32
<i>Psectrocladius semicirculatus/sordidellus</i>	93	10.8	20.4	21.1	21.26
<i>Psectrocladius Walker type</i>	19	12.4	20.4	28.0	30.88
<i>Rheocricotopus</i>	19	11.7	16.1	5.3	9.56
<i>Synorthocladius</i>	32	10.0	18.7	-1.9	-7.11
<i>Zalutschia</i>	63	9.7	20.4	19.1	17.28
<i>Heterotrissocladius</i>	63	9.7	19.4	1.4	-3.72
<i>Apedilum</i>	8	12.6	15.4	-7.1	-19.40
<i>Chironomus</i>	83	9.7	20.4	11.9	13.84
<i>Cladopelma</i>	38	12.3	20.4	22.7	35.75
<i>Dicrotendipes</i>	69	10.1	20.4	11.7	11.17
<i>Glyptotendipes</i>	10	12.8	19.1	52.7	80.43
<i>Microtendipes</i>	57	10.0	19.4	13.4	15.45
<i>Pagastia</i>	19	15.2	19.4	37.0	33.88
<i>Phaenopsectra</i>	16	12.4	19.9	25.3	41.77
<i>Polypedilum</i>	29	10.0	4.0	26.1	32.16
<i>Sergentia</i>	28	9.7	19.0	3.0	8.34
<i>Cladotanytarsus</i>	32	12.3	20.4	16.3	14.44
<i>Corynocera near ambigua</i>	16	12.4	19.4	22.6	23.20
<i>Corynocera oliveri type</i>	66	9.7	19.4	6.3	10.33
<i>Micropsectra</i>	52	1.2	19.0	17.7	16.94
<i>Tanytarsus (spp. A/C)</i>	16	11.9	20.4	27.6	25.80
<i>Tanytarsus type A</i>	8	9.7	13.8	-25.3	-43.10
<i>Tanytarsus type C</i>	24	12.3	19.4	17.4	19.75
<i>Tanytarsus type E</i>	8	12.3	12.3	10.3	11.17
<i>Tanytarsus type H</i>	28	9.7	19.0	12.5	1.59
<i>Tanytarsus</i>	99	9.7	20.4	15.0	14.69
<i>Paratanytarsus</i>	56	9.7	19.9	20.0	21.24
<i>Procladius</i>	80	9.7	20.4	16.7	18.27
<i>Pentaneurini (other)</i>	84	10.1	19.9	16.9	14.50

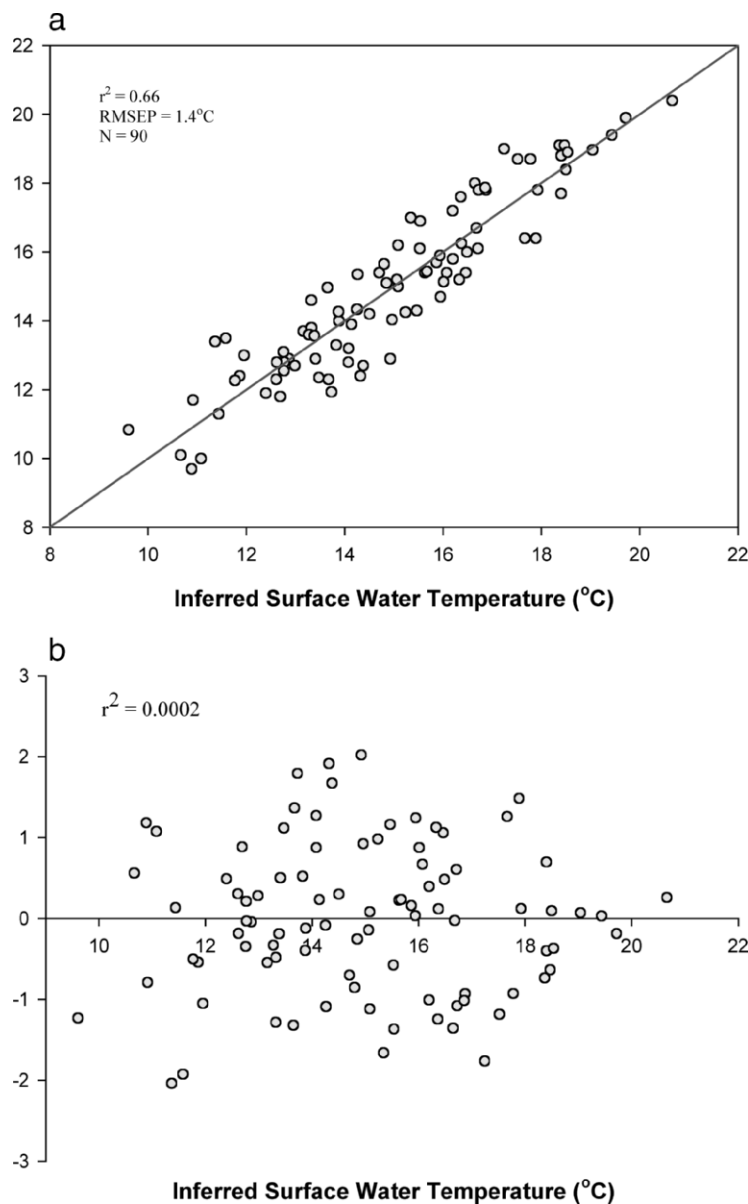


FIGURE 5. (a, b) Relationship between inferred (jack-knifed) and (a) observed summer water temperature, and (b) residuals (inferred-observed) for summer surface water temperature based on 3-component WA-PLS inference model.

assemblages in the immediate post-glacial interval at Greenstone Lake; however, continued expansion of this regional training set may do so. For example, expansion of the calibration set from 44 lakes to 90 lakes has increased the SSWT gradient by 2.2°C (9.7–20.4°C), with the majority of this increase due to the inclusion of Uinta lakes with relatively low SSWT.

Subfossil midge analysis has been used to successfully develop high-resolution (sub-decadal) reconstructions of 20th century

temperature change in the Sierra Nevada (Porinchu et al., 2007). Application of the Great Basin midge-based SSWT inference model to other intact, late Quaternary sedimentary sequences found in subalpine and alpine lakes in the Great Basin will help resolve the impact of late Quaternary and recent climate change in this region, improve our understanding of regional climate and aquatic ecosystem variability, and may help identify the causal forcing mechanisms responsible for these changes.

TABLE 8

Comparison of the Sierra Nevada (Porinchu et al., 2002) and merged Sierra Nevada and Uinta Mountains (this study) chironomid-based inference models for surface water temperature. 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^2_{jack}), 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), WA (weighted averaging).

Study	Study Area	# of lakes	# of taxa	Model	r^2_{jack}	RMSEP (°C)	Range of gradient (°C)	RMSEP as % of gradient	Max Bias (°C)
Porinchu et al. (2002)	Sierra Nevada	44	43	WA (classical)	0.73	1.2	8.5	14.1	0.90
This study	Sierra Nevada and Uinta Mountains	90	57	WA-PLS (3comp)	0.66	1.4	10.7	13.1	2.61

In summary, the modern distribution of chironomids in the Uinta Mountains, Utah, was determined through the analysis of subfossil remains preserved in the sediment of 51 small lakes. The relationship between midge distributions and the modern environment was assessed using ordination analyses. RDA identified that four predictor variables—SSWT, depth, specific conductivity, and Al—could explain a statistically significant amount of variance in the midge distributions. In addition, SSWT could explain the largest proportion of variance, independent of all other measured environmental variables. Inference models for SSWT were developed combining midge abundance data from 56 lakes in the eastern Sierra Nevada, California, with subfossil midge remains from the Uinta Mountain. The most robust inference model (3-component WA-PLS), based on 90 lakes, had a high coefficient of determination ($r^2_{\text{jack}} = 0.66$) and a low RMSEP (1.4°C). The newly merged Sierra Nevada–Uinta Mountains calibration set has a greater diversity of chironomid assemblages, spans a wider SSWT range than the previously published Sierra Nevada calibration set (Porinchu et al., 2002), and will likely provide more accurate quantitative estimates of recent and long-term climate change in the Great Basin.

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