J Paleolimnol (2007) 38:477–491
DOI 10.1007/s10933-006-9080-z

ORIGINAL PAPER

A chironomid-based salinity inference model from lakes on the Tibetan Plateau

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Received: 14 September 2006 / Accepted: 1 December 2006 / Published online: 17 July 2007

Abstract Previous studies have shown chironomids to be excellent indicators of environmental change and training sets have been developed in order to allow these changes to be reconstructed quantitatively from subfossil sequences. Here we present the results of an investigation into the relationships between surface sediment subfossil chironomid distribution and lake environmental variables from 42 lakes on the Tibetan Plateau. Canonical correspondence analysis (CCA) revealed that of the 11 measured environmental variables, salinity (measured as total dissolved solids TDS) was most important, accounting for 10.5% of the variance in the chironomid data. This variable was significant enough to allow the development of quantitative inference models. A range of TDS inference models were developed using Weighted Averaging (WA), Partial Least Squares (PLS), Weighted Averaging–Partial Least Squares (WA–PLS), Maximum Likelihood (ML), Modern Analogues Technique (MAT) and Modern Analogues Techniques weighted by similarity (WMAT). Evaluation of the site data indicated that four lakes were major outliers, and after omitting these from the training set the models produced jack-knifed coefficients of determination (r^2) between 0.60 and 0.80, and root-mean-squared errors of prediction (RMSEP) between 0.29 and 0.44 $\log_{10}$ TDS. The best performing model was the two-component WA–PLS model with $r^2_{\text{jack}} = 0.80$ and $\text{RMSEP}_{\text{jack}} = 0.29$ $\log_{10}$ TDS. The model results were similar to other chironomid-salinity models developed in different regions, and they also showed similar ecological groupings along the salinity gradient with respect to freshwater/salinity thresholds and community diversity. These results therefore indicate that similar processes may be controlling chironomid distribution across salinity gradients irrespective of biogeographical constraints. The performance of the transfer functions illustrates that chironomid assemblages from the Tibetan Plateau lakes are clearly sensitive indicators of salinity. The models will therefore allow the quantification of long-term records of past water salinity for lacustrine sites across the Tibetan Plateau, which has important

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implications for future hydrological research in the region.

Keywords Chironomids · Hydrological balance · Lakes · Tibetan Plateau · Transfer functions · Total Dissolved Salts (TDS).

Introduction

Studying past variations in climate change from the Tibetan Plateau is of critical importance for understanding regional and global atmospheric circulation, given the pivotal role that the Plateau plays in shaping circulation patterns (Gasse and Derbyshire, 1996). In recent decades, the warming climate has greatly impacted the hydrological cycle of the Tibetan Plateau (Singh and Kumar, 1997; Singh, 2003; Barnett et al., 2005), which may bring serious consequences to the water supply of western China where glacial melt-water provides the principal dry season water source (Gao and Shi, 1992). In order to assess the impact of past climate changes on the hydrological regime of the Tibetan Plateau, a large number of palaeoclimate studies have been undertaken within the region using a range of archives such as lake sediments, ice cores, and tree rings (e.g., Zhang et al., 2004; Shao et al., 2005; Yao et al., 2006). In particular, fluctuations in both lake level and water chemistry in closed basin lakes in response to climatic changes have attracted much attention in recent years (Gasse and Derbyshire, 1996; Gasse et al., 1996) with a particular focus on diatoms. This group of algal indicators was used successfully to quantitatively reconstruct the palaeosalinity from the Tibetan Plateau (Yang et al., 2003, 2004). Another useful indicator group which can complement and augment data derived from diatom analysis are Chironomidae (Insecta: Diptera), the non-biting midges. Although diatoms are recognized as being more sensitive to salinity changes than chironomids, and are therefore often better indicators of past salinity (Verschuren, 2003), chironomids can be especially useful where diatoms are absent or poorly preserved in saline lake sediments. Until now, however, no chironomid inference models have been previously available from this region.

Previous research on chironomids has shown them to be excellent environmental indicators (Walker, 2001). The heavily chitinised head capsules from the larval stage are well preserved in lacustrine sediments, and their remains have been used to reconstruct a range of environmental parameters, including aspects of climate change, eutrophication, and other forms of ecosystem change and human impacts (e.g. Brooks, 2003; Brooks et al., 2005; Woodward and Shulmeister, 2005; Gandouin et al., 2006; Heegard et al., 2006; Langdon et al., 2006). Reconstructing palaeosalinity from sub-fossil midge assemblages, like other environmental parameters, is based upon sound ecological and empirical observation, and has much potential. Previous applications of quantitative transfer functions to reconstruct palaeosalinity have, however, only been undertaken from western Canada and Africa (e.g., Walker et al., 1995; Heinrichs et al., 2001; Verschuren et al., 2004; Eggermont et al., 2006; Heinrichs and Walker, 2006) and new transfer functions from semi-arid regions worldwide are required in order to test quantitative paleosalinity reconstructions across geographical spaces (Heinrichs and Walker, 2006). Due to the harsh environment of the Tibetan Plateau, only limited chironomid studies have been undertaken in the past and most of these were focused solely on taxonomy (e.g., Academica Sinica, 1979). The aim of our present work is to assess the distribution of chironomid communities in a range of lakes on the Tibetan Plateau and to determine which environmental parameters are most influential on the midge fauna. Subsequently, we aim to stimulate future research interests into Tibetan chironomids, notably regarding taxonomy and the relationships between the fauna and their environment. Based on the high salinity variation present in the lakes from the Tibetan Plateau, it is likely that salinity exerts a strong control on chironomid distribution. The main aim of this research is thus to construct a chironomid-inferred salinity (CI-S) transfer function, which can be applied to reconstruct palaeosalinity quantitatively from midge remains retrieved from lake sediments in this region.

Methods

Study sites, sampling methods and water chemistry analysis

The Tibetan Plateau (often termed the Tibet-Qinghai Plateau), with an area of nearly 2×10^6 km^2 at an average altitude of over 4000 m a.s.l., exerts an important control on the Asian monsoon circulation pattern (e.g., Flohn, 1968; Hahn and Manabe, 1975; Lau and Li, 1984). As the youngest and highest plateau in the world, the Tibetan Plateau is the origin of many important rivers in Asia, and hence any changes in the physical, chemical and biological regimes within the region will have strong regional and potentially global implications. This makes the Tibetan Plateau an ideal natural laboratory for studies in environmental change at a range of scales.

The present dataset includes 42 lakes which are located on the Tibetan Plateau, spanning from 28.148° to 38.884° N and 84.570° to 100.734° E (Fig. 1). Their altitude ranges from 2797 to 5420 m a.s.l. The catchment of the studied lakes is mostly covered by desert vegetation or high-frigid meadow. The lakes include some sites (15 lakes) sampled by Yang et al. (2003) as well as more recently sampled sites (27 lakes), and the distribution area of the chironomid training set is much larger than the published diatom model of Yang et al. (2003). The lakes were chosen due to their accessibility and range of salinities, but the relative increase in distribution area compared to Yang et al. (2003) also allowed us to increase the temperature gradient, and hence test whether temperature exerts a significant influence in the chironomid distribution in this research area. Surface sediment samples (uppermost 0.5 cm) were collected using a Kajak gravity corer between 1998 and 2003.

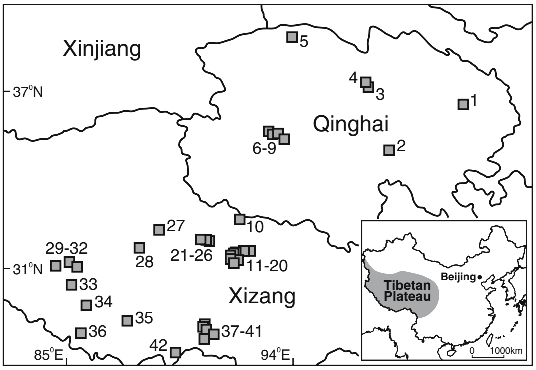

Fig. 1 Location of sampling lake sites on the Tibetan Plateau. (1) Erhai Lake (2) Xingxinghai Lake (3) Tuosuhai Lake (4) Keluke Lake (5) Sugan Lake (6) Kusai Lake (7) Haidingnuoer Lake (8) Yanhubei Lake (9) Qingshui Lake (10) Tanggula Lake (11) Lake C (12) Cuomorong Lake (13) Chuolongcuo Lake (14) Elucuo Lake (15) Pengcuo Lake I (16) Pengcuo Lake II (17) Cuoe Lake (18) Hangcuo Lake (19) Nairipingcuo Lake (20) Lingyangcuo Lake (21) WP I (22) Lake B (23) Lake A (24) WPIII (25) WP II (26) Guojialin Lake (27) Xuguocuo Lake (28) Wurucuo Lake (29) Dawacuoerhu Lake (30) Maiqiongcuo Lake (31) Zharinancuo Gulf (32) Zharinanmucuo Lake (33) Dingnarong Lake (34) Dajiacuo Lake (35) Langcuo Lake (36) Peigucuo Lake (37) Yangzhuoyongcuo Lake (38) Kongmucuo Lake (39) Chencuo Lake (40) Bajiucuo Lake (41) Pumoyongcuo Lake (42) Duoqingcuo Lake

Samples for water chemistry analysis were collected in July and August 1998–2003. Each lake was sampled only once. Samples were collected in 0.5–1 m water depth using polyethylene bottles. pH was measured in the field using a HANNA EC-214 pH-meter. Chemical analyses were determined using standard techniques (Greenberg et al., 1992; Institute of Hydrogeography and Engineering Geology, MGMR 1990) and included measurements of potassium (K^+), sodium (Na^+), calcium (Ca^{2+}), magnesium (Mg^{2+}), chloride (Cl^-), sulphate (SO_4^{2-}), carbonate (CO_3^{2-}), and bicarbonate (HCO_3^-) ions. CO_3^{2-} and HCO_3^- were combined to take into account pH dependent transformations. Salinity (TDS Total Dissolved Solids) was calculated as the sum of concentrations of the eight ions mentioned above expressed in mg/l (Wetzel, 2001). In shallow lakes (<ca. 1.5 m depth) the maximum water depth was measured directly using a weighted rope. In deeper lakes it was measured using a portable echo sounder (SHH type, NAII, China). The mean July air temperature was estimated from limited meteorological station data, using approximately 26 stations. As the study area is relatively large, and the geomorphology varies greatly, it is likely that the accuracy of the temperature data is not very high.

A summary of the main environmental characteristics of the 42 lakes sampled is presented in Table 1. TDS had a range between 242.67 and 56586.06 mg/l, and pH ranged from 7.40 to 10.88.

Table 1 Summary of the measured environmental characteristics for the 42 lakes

Environmental proxy	Value range
TDS (mg/l)	242.67–56586.06
Depth (m)	0.3–48
July temperature (°C)	4.6–20.3
Altitude (m a.s.l)	2797–5420
pH	7.40–10.88
Na^+ (mg/l)	22.00–17839.75
K^+ (mg/l)	0.33–890.93
Ca^{2+} (mg/l)	2.47–209.00
Mg^{2+} (mg/l)	5.22–2987.59
Cl^- (mg/l)	3.00–15763.87
SO_4^{2-} (mg/l)	13.21–13228.41
CO_3^{2-} (mg/l)	0–2429.50
HCO_3^- (mg/l)	0–11958.56

Water depth of the 42 lakes varied from 0.3 to 48 m and 16 of the studied lakes were shallow with depths <1m. The altitudes of the lakes surface varied from 2797 to 5420 m and the mean July air temperature ranged from 4.6 to 20.3°C accordingly. However, the distribution of the 42 lakes on the altitudinal gradient was uneven, and only three sites had an altitude below 4000 m a.s.l. with mean July air temperatures >12°C. The majority of lakes thus had a relatively narrow temperature gradient.

Chironomid analysis

Lake sediment samples were processed for chironomid head capsules following conventional procedures (Walker and Paterson, 1985), and the ultra-sonic washing method was also used as many of the samples contained significant amounts of carbonate (Lang et al., 2003). Samples were treated with hot 10% KOH to deflocculate the organic material. After ultra-sonic treatment, the samples were sieved on 212 µm and 90 µm meshes and the residues were transferred to a sorting tray and examined under a binocular microscope (×25). All chironomid subfossils in both size fractions were picked out and mounted on microscope slides in Berlese solution with a minimum of 50 head capsules yielded per sample. The head capsules were identified with a compound microscope at ×100–400 by reference to published taxonomic keys and photographic guides (Wiederholm, 1983; Oliver and Roussel, 1983; Rieradevall and Brooks, 2001). Two taxa were identified for which head capsule morphologies have not been described previously. *Psectrocladius* sp3 can be identified by the two median teeth of the mentum being far more prominent than that of other *Psectrocladius* spp., and *Chironomus dorsalis* can be differentiated from other *Chironomus* spp. as its 4th lateral teeth on the mentum are much shorter than the adjacent teeth. Criteria for counting fragmentary subfossils followed Walker (1987). To our knowledge, no previous work has been undertaken on the analysis of chironomid head capsules from the Tibetan Plateau, with only little work having been undertaken in nearby regions such as eastern China (e.g., Zhang et al., 2006).

Data transformations

Taxa with a maximum abundance <1% or which occurred in only one lake were eliminated from the subsequent numerical analyses. The environmental indicators were log-transformed ($\log_{10}(x + 1)$) except for pH, in order to reduce the skew error in ordination (ter Braak and Šmilauer, 1998). Rare species were down-weighted in all ordination analyses.

Ordination

Detrended correspondence analysis (DCA; Hill and Gauch, 1980) was used to estimate the amount of compositional change within the chironomid data and to determine whether linear or unimodal based numerical techniques should be used (ter Braak, 1987).

Canonical correspondence analysis (CCA) (ter Braak, 1987) was used to examine the relationships between the chironomid taxa and the environmental parameters. Variance inflation factors (VIF) were used to identify any intercorrelated variables, and hence some of these could be deleted from subsequent analyses. CCA with forward selection (ter Braak, 1990) was performed on all sites using a subset of eleven environmental variables (Table 1: altitude was not included and CO_3^{2-} and HCO_3^- were combined) to identify which of these variables explained a statistically significant ($p \leq 0.05$)

amount of variation in the chironomid data. The significance of each variable was tested using an unrestricted Monte Carlo permutation test (999 permutations).

In addition, a series of constrained, detrended CCA (DCCA) were run with the species data and each environmental variable on its own (e.g., Lotter et al., 1997; Clerk et al., 2000). This was to determine the strength of each variable by its ability to maximize the dispersion of the chironomid taxon scores, expressed as a ratio of the first constrained DCCA eigenvalue to the second unconstrained DCA eigenvalue (ter Braak and Šmilauer, 1998). All the ordinations were undertaken using the program CANOCO for Windows 4.0 (ter Braak and Šmilauer, 1998).

Transfer functions

In order to generate the most reliable transfer function, a range of models were tested, including: Weighted Averaging (WA) with and without tolerance down-weighting, using unweighted classical and inverse deshrinking (Birks et al., 1990a); Partial Least Squares(PLS); Weighted Averaging–Partial Least Squares (WA–PLS) (ter Braak and Juggins, 1993); Maximum Likelihood (ML); the Modern Analogue Technique (MAT); and modern analogues techniques weighted by similarity (WMAT). The minimal adequate model was identified as having a combination of a high coefficient of determination (r^2_{jack}) between observed and predicted values, a low mean and maximum bias, and a low root mean squared error of prediction (RMSEP$_{\text{jack}}$), all assessed by leave-one-out (jack-knifing) cross-validation (Birks, 1995). In WA–PLS only components giving a reduction in RMSEP$_{\text{jack}}$ of 5% or more were retained (Birks, 1998). Model development was undertaken using the program C2 (Juggins, 2003).

Outliers from the calibration set occurred when the samples whose absolute residual exceeded the standard deviation of log-transformed conductivity in all trial models (Martens and Naes, 1989; Birks et al., 1990b; Jones and Juggins, 1995). It is common to delete these outliers from the calibration sets, although in our dataset they were only deleted if their removal reduced the RMSEP by at least 5% (cf. Quinlan and Smol, 2001).

Results

Chironomid taxa

A total of 30 chironomid taxa were identified, of which 24 taxa were retained following the deletion criteria for numerical analyses as described above. Clear patterns in chironomid abundance against TDS levels can be seen (Fig. 2), suggesting that TDS is a strong driver of chironomid distribution from these lakes on the Tibetan Plateau. The surface sediment samples were dominated by Orthocladiinae, presumably a reflection of the relatively cool environmental conditions recorded across the sites. Taxa that inhabit the most saline lakes include *Psectrocladius barbimanus*-type and the *Orthocladius*/*Cricotopus* group, which was also the overwhelmingly dominant taxon in the most saline lakes from the analyses undertaken by Walker et al. (1995) in British Columbia, Canada. The *Orthocladius*/*Cricotopus* group from this study may well comprise a few taxa at most, as one other *Cricotopus* type (*C. sylvestris*-type) has been identified as distinct from the *Orthocladius*/*Cricotopus* group, and occurs in less saline lakes. One other notable trend in chironomid diversity shows that all the Tanytarsini occur at medium to lower levels of TDS, with *Cladotanytarsus mancus*-type restricted to lakes with low levels of TDS.

Ordination

DCA of the chironomid data revealed that the eigenvalues of the first two DCA axes were $\lambda_1 = 0.61$ and $\lambda_2 = 0.41$. The gradient of the first two axes was 4.18 and 3.84 SD units respectively, indicating that a unimodal species response model was appropriate in the two axes and that the data were suitable for CCA analysis (ter Braak, 1987).

The CCA of the chironomid and environmental data showed that the eigenvalues for CCA axis 1 (0.40) and axis 2 (0.30) accounted for 23.6% of

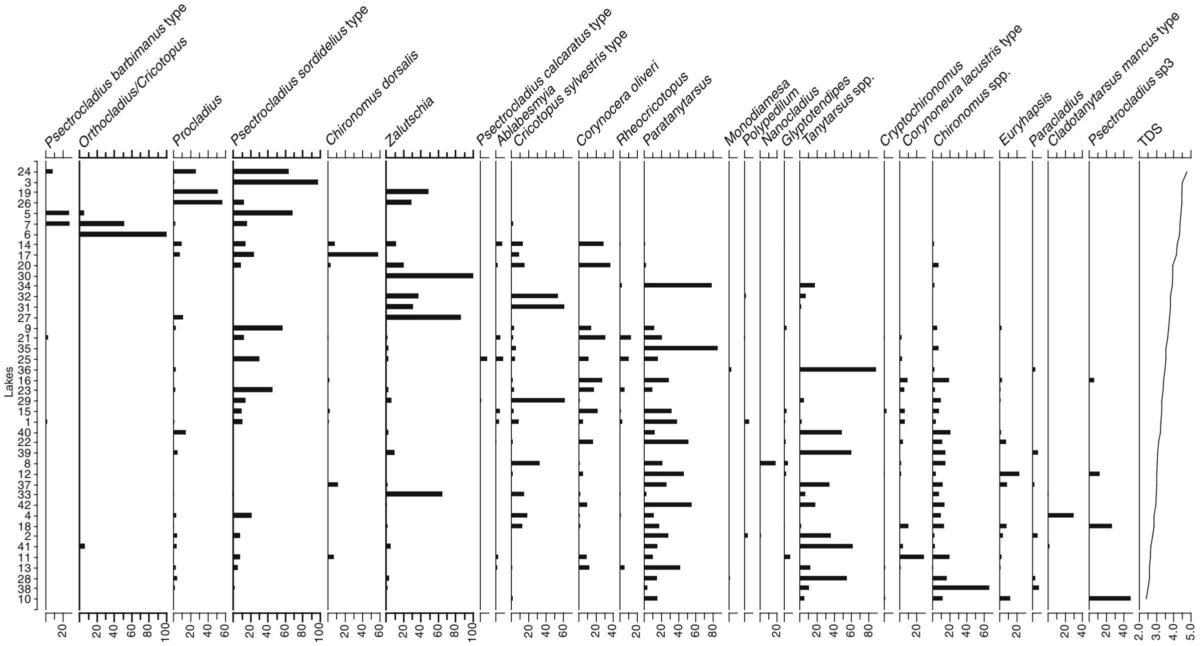

Fig. 2 Percentage chironomid abundance (%) for each lake from the Tibetan Plateau training set, illustrated with TDS (TDS is measured in mg/l and the scale is $\log_{10}$ TDS)

the variance in chironomid taxa. The species-environment correlations for CCA axis 1 and 2 , 0.862 and 0.867 respectively. These high relatively correlation explained 50.0% of the variance in the chironomid-environmental relationship, suggesting there was a strong relationship between the environmental variables and the chironomid taxa in the 42 lakes sampled. CCA with forward selection procedure was re-run after omitting July temperature, K^+ and Ca^{2+} , which did not pass the significance test ($p \geq 0.05$), and two redundant variables i.e. Na^+ and Cl^- (VIF ≥ 20). The result revealed that six environmental variables, namely TDS, depth, pH, Mg^{2+} , SO_4^{2-} and CO_3^{2-} $+HCO_3^-$, were significant ($p \leq 0.05$). The CCA using the six forward-selected significant variables indicated that the eigenvalues for axis 1 (0.398) and axis 2 (0.261) accounted for 22.0% of the cumulative percentage variance in the chironomid data. These values were only slightly lower than those obtained for CCA using all the environmental variables, indicating that these selected variables are the key factors in explaining the variance of the chironomid data (Table 2). Partial CCA suggested that Mg^{2+} did not pass the significance test ($p \geq 0.05$), and that TDS, depth and pH all had similar marginal effects and could effectively explain the variance of the chironomid data. According to the CCA results, TDS and depth had the potential for the establishment of a

Table 2 Comparison of the results in the CCA with 11 and six environmental variables, respectively

CCA axis	1	2	3	4	1	2	3	4
	With 11 environmental variables				With six environmental variables			
Eigenvalues	0.404	0.304	0.219	0.166	0.398	0.261	0.196	0.130
Species-environment correlations	0.862	0.867	0.742	0.765	0.857	0.819	0.735	0.707
Cumulative percentage variance								
-of species data	13.5	23.6	30.9	36.4	13.2	22.0	28.5	32.8
-of species-environment relationship	28.6	50.0	65.6	77.3	37.6	62.4	81.0	93.3

suitable inference model, and as TDS is the most significant variable and can be utilized as a significant climate proxy from closed lake basins, we focus here on mainly developing a chironomid–TDS transfer function but chironomid-depth inference models were also attempted.

The CCA correlation biplots based on the chironomid data from the 42 lakes and 5 significant environmental variables are shown in Fig. 3. These biplots indicate that TDS is closely related to axis 1, highlighting an obvious salinity gradient along the first axis. High salinity lakes, such as Haidingnuoer Lake (7; 23575.9 mg/l), Sugan Lake (5; 25728.0 mg/l), Kusai Lake (6; 21534.6 mg/l) and WPIII Lake (24; 56586.1 mg/l), were positioned on the right with chironomid fauna typical of salinity-resistant conditions (e.g. *Orthocladius/Cricotopus* and *Psectrocladius barbimanus*-type), whereas relatively low salinity lakes such as Pumoyongcuo Lake (41; 452.6 mg/l), Kongmucuo Lake (38; 311 mg/l) and Yangzhuoyong Lake (37; 1025.0 mg/l), were located on the left side dominated by a characteristic chironomid taxa such as *Psectrocladius* sp3 and *Euryhapsis*. CCA axis 2 is more related to depth and pH.

Detrended CCA with TDS as the constraining variable was used to assess the suitability of TDS in establishing an inference model. The more important an environmental variable is in explaining variance in the species data, the larger the first constrained axis will be in comparison with the second unconstrained axis (ter Braak and Šmilauer, 1998). The DCCA of TDS and chironomid data showed that TDS had a higher statistically significant ($p \leq 0.05$) eigenvalue for DCCA axis 1 relative to the unconstrained DCA axis 2, with a gradient length (SD units) of 2.343, an eigenvalue of 0.315 and ratio of $\lambda1/\lambda2$ of 0.73 (Table 3). This result suggests that a TDS inference model could be established using these data (ter Braak and Prentice, 1988; Birks, 1995). A relatively low $\lambda1/\lambda2$ would have indicated that a potential factor affecting the chironomid assemblage besides the explored variables had not been assessed.

Transfer function

The chironomid–TDS transfer functions were established using WA, PLS, WA–PLS, ML, MAT and WMAT techniques. The results of the models were tested by jack-knifing methods. An optimal two-component WA–PLS model performed best when all the lakes were included, which provided a relatively high jack-knifed coefficient of prediction for conductivity ($r^2_{\text{jack}} = 0.64$), with a low root mean squared error of prediction ($\text{RMSEP}_{\text{jack}} = 0.38$), whereas other inference models yielded relatively poor results with relatively high $\text{RMSEP}_{\text{jack}}$ values. On examining the residuals, four sites were found to be outliers according to the outlier criteria described above: Chuolongcuo Lake (13), Dingnarong Lake (33), Dajiacuo Lake (34) and

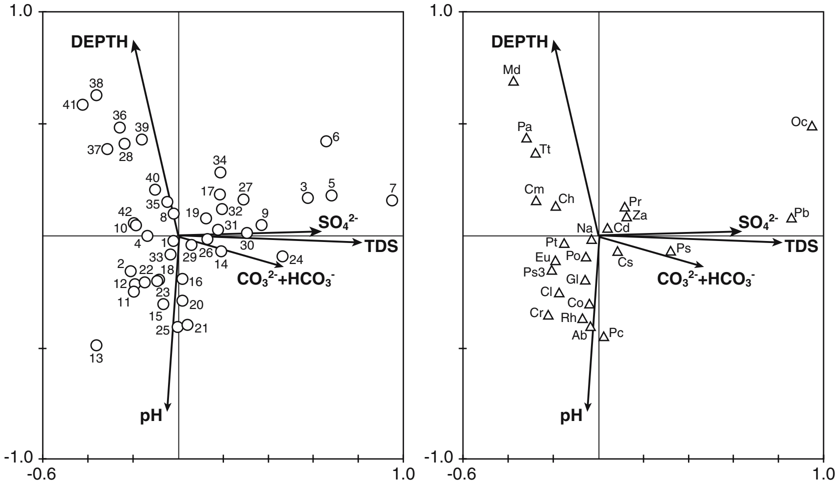

Fig. 3 CCA biplot of axis 1 and axis 2 with sampling sites, chironomid taxa and the five significant environmental variables, (a) sampling sites-environmental variables relationship, (b) chironomid taxa-environmental variables relationship. Taxon codes are listed in Table 5

Table 3 Summary of statistics for the DCCA of chironomid data and TDS

Environment variable	TDS
DCCA axis 1	
λ_1	0.315
Gradient length (SD units)	2.343
Variance explained (%)	10.5
Monte carlo *P* value	0.0001
DCA axis 2	
λ_2	0.413
Gradient length (SD units)	3.462
Variance explained (%)	14.1
λ_1/λ_2	0.73

Peigucuo Lake (36). Referring to the environmental characteristics of these four lakes shows that Chuolongcuo Lake (13) and Dingnarong Lake (33) were quite small and shallow, suggesting that temporary rainfall could desalt the lake greatly and cause a serious salinity underestimation. Dajiacuo Lake (34) and Peigucuo Lake (36), however, were quite deep and the only lakes near a glacier, indicating that the cold melt water inflow and the deep water may result in a salinity overestimation (cf. Brooks and Birks, 2001). These four sites were therefore omitted from the training set and a subsequent set of chironomid–TDS transfer functions were developed and tested by jack-knifing, the results of which are shown in Table 4; Fig. 4. WA without tolerance down-weighting models yielded adequate results (r^2_{jack} = 0.77–0.78, RMSEP$_{\text{jack}}$ = 0.31–0.32, maximum bias = 0.44–0.53, Table 4; Fig. 4); however, WA with tolerance down-weighting models provided relatively poor results (Table 4). The two-component WA–PLS model provided a high jack-knifed coefficient of prediction for conductivity (r^2_{jack} = 0.80), with a low root mean squared error of prediction (RMSEP$_{\text{jack}}$ = 0.29, 6.8% reduction) and low mean (0.0045) and maximum bias (0.36). Omitting the four outliers therefore greatly improved the inference ability of the model. Although the three-component WA–PLS model performed better than two-component WA–PLS, the decrease in RMSEP is 3.7% and hence the two-component WA–PLS was retained as the best model (Table 4; Fig. 4).

Linear-based PLS models yielded relatively poor results, most likely due to the long compositional gradient of TDS within the Tibetan chironomid dataset, suggesting unimodal species response models are more suitable. ML-based models provided the equal highest r^2_{jack}(0.80), and equal lowest RMSEP (0.29) with lowest maximum bias (0.33). However, ML models over-estimate TDS both at the low and high end

Table 4 Summary of statistics for the chironomid–TDS inference models from 38 lakes

Model	r^2_{jack}	RMSEP$_{\text{jack}}$	Mean bias$_{\text{jack}}$	Max bias$_{\text{jack}}$	(%)RMSEP change
Inverse					
WA	0.7722	0.3080	0.0169	0.5317	
WA$_{\text{tol}}$	0.5943	0.4154	–0.0254	0.5736	
Classical					
WA	0.7781	0.3153	0.0185	0.4405	
WA$_{\text{tol}}$	0.5971	0.4350	–0.0314	0.5506	
WA–PLS(1)	0.7719	0.3082	0.0167	0.5317	
WA–PLS (2)	0.8010	0.2873	0.0045	0.3600	6.8
WA–PLS (3)	0.8159	0.2767	–0.0097	0.3434	3.7
WA–PLS (4)	0.7989	0.2899	0.0042	0.3648	–4.8
WA–PLS (5)	0.7574	0.3276	0.0190	0.3948	–13.0
PLS (1)	0.6020	0.4077	0.0274	0.5447	
PLS (2)	0.6729	0.3708	–0.0075	0.4288	9.1
PLS (3)	0.7380	0.3303	0.0190	0.4938	10.9
PLS (4)	0.7502	0.3226	–0.0089	0.3613	2.3
PLS (5)	0.7484	0.3243	0.0005	0.4013	–0.5
ML	0.8025	0.2875	–0.0167	0.3297	
MAT-4	0.7414	0.3353	0.0116	0.7554	
WMAT-4	0.7821	0.3061	–0.0069	0.6247	

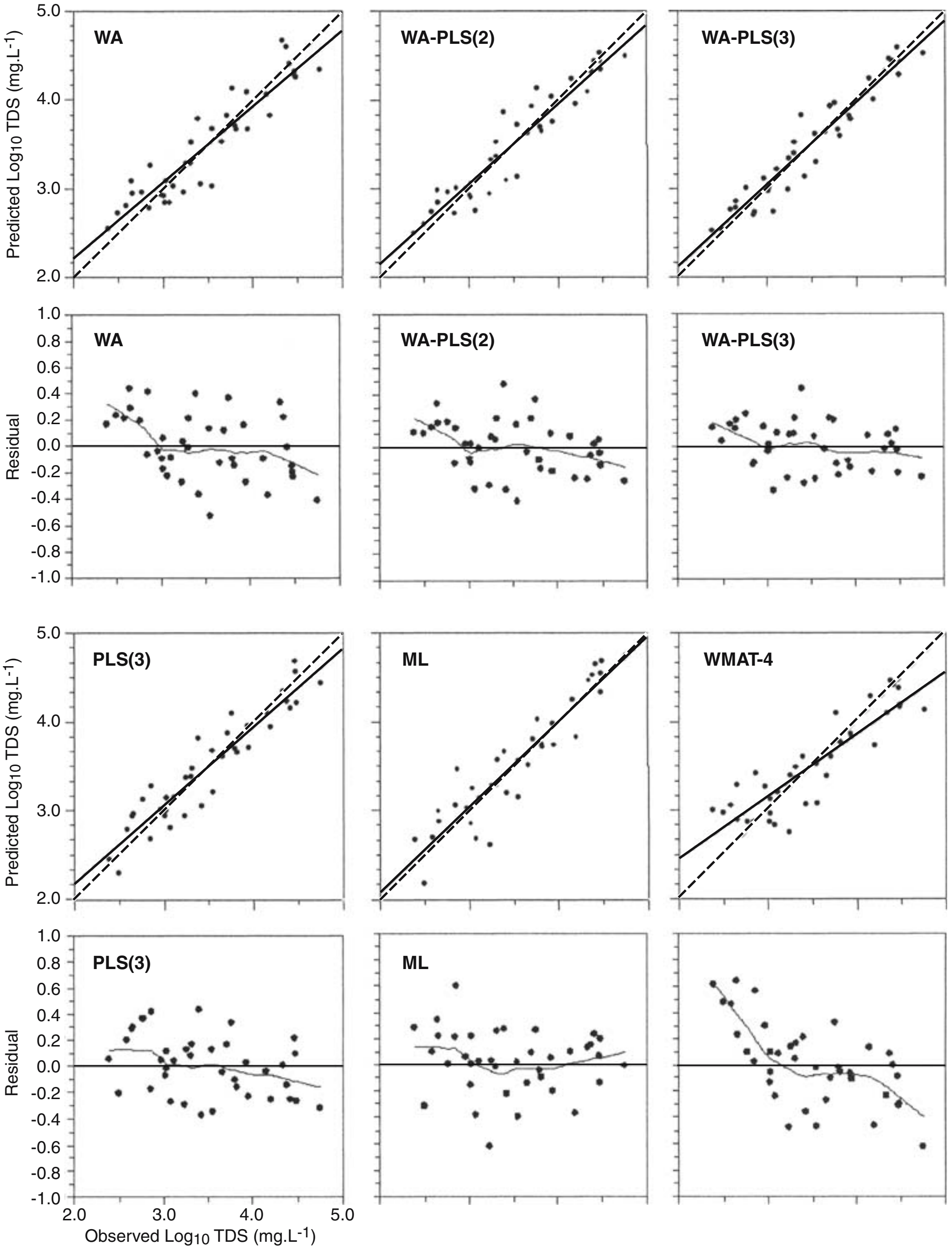

Fig. 4 Plots showing the observed versus predicted $\log_{10}$ TDS, and the residuals (inferred-observed) of the chironomid-inferred TDS models

of the gradient (Fig. 4). MAT with a mean of the four closest analogues (MAT-4) and with a weighted mean of the four closest analogues (WMAT-4) also yielded similar results ($r^2_{\text{jack}} = 0.74$ and 0.78, $\text{RMSEP}_{\text{jack}} = 0.34$ and 0.31 respectively; Table 4; Fig. 4)

Although our goal was to generate chironomid–TDS transfer functions, as depth was also a significant predictor of chironomid distribution we also attempted to develop chironomid-depth inference models using the range of techniques that were used for TDS inference models. The models for depth, however, provided relatively poor results. Among the depth inference models, the best results were from a classical WA with tolerance down-weighting model which had a low coefficient of correlation ($r^2_{\mathrm{jack}} = 0.46$, $\mathrm{RMSEP}_{\mathrm{jack}} = 0.37\ \log_{10}\mathrm{Depth}$).

Discussion and conclusions

The environmental variables revealed that there was an obvious salinity gradient across the 42 lakes sampled from the Tibetan Plateau. CCA analysis of the chironomid data and environmental variables further indicated that TDS and depth were the two most significant environmental variables accounting for the variance of the chironomid data (Fig. 3). TDS explained 10.5% of the variance recorded in the chironomid assemblages, a figure which compares well with other primary environmental drivers of chironomid inference models (e.g., Brooks et al., 2001; Heiri et al., 2003), although clearly there are still other environmental and ecological factors that influence chironomid distribution within these lakes.

This is the first chironomid-inferred salinity model to be developed outside of Canada and Eastern Africa, and comparisons can be undertaken between the model performances and ecological groupings of the chironomids between each region. When the taxa are arranged with respect to their TDS optima (Fig. 2; Table 5) clear ecological groups can be distinguished. The most salt-tolerant taxa are *Psectrocladius barbimanus*-type, the *Orthocladius/Cricotopus* group, *Procladius* and *Psectrocladius sordidellus*-type which are highly dominant in lakes with TDS >10,000 mg/l (~17,000 µS/cm); the lakes with highest TDS were dominated by either *Psectrocladius sordidellus*-type or *Procladius* with very low taxon diversity. A second clear group of halophytic chironomids with TDS optima between ~3000–10,000 mg/l (~5000–17,000 µS/cm) occurred in more mesosaline lakes (Table 5; Fig. 2), and a third group occurred in more freshwater lakes with TDS values <~2500 mg/l (~4000 µS/cm). The change in fauna between more freshwater and saline lakes is fairly distinct, and in East African lakes a similar change

Table 5 Lists of Chironomidae taxa in 38 lakes and their codes showing the number of occurrences (*N*0), effective number of occurrences (*N*2) and WA optimum values TDS (mg/l). The taxa are arranged in sequence of their TDS optima.

Taxon code	Taxon name	*N*0	*N*2	TDS WA optimum (mg/l)
Pb	*Psectrocladius barbimanus*-type	6	2.96625	22588.68
Oc	*Orthocladius/Cricotopus*	5	2.12027	19229.92
Pr	*Procladius*	21	6.17679	13809.84
Ps	*Psectrocladius sordidellus*-type	20	10.4026	10008.21
Za	*Zalutschia*	23	7.08664	7851.36
Cd	*Chironomus dorsalis*	11	2.4505	6821.44
Ab	*Ablabesmyia*	8	5.93833	3819.85
Co	*Corynocera oliveri*	17	10.3079	3514.36
Cs	*Cricotopus sylvestris*-type	23	7.98875	3318.17
Rh	*Rheocricotopus*	7	3.624	3248.00
Pc	*Psectrocladius calcaratus*-type	2	1.30224	3216.07
Po	*Polypedilum*	4	2.50703	1428.22
Pt	*Paratanytarsus*	24	14.7736	1409.85
Cr	*Cryptochironomus*	5	2.55398	1283.64
Na	*Nanocladius*	4	1.2401	1168.93
Gl	*Glyptotendipes*	10	5.34744	1114.66
Cl	*Corynoneura lacustris*-type	12	5.58829	989.06
Eu	*Euryhapsis*	14	6.21979	860.83
Ch	*Chironomus* spp.	25	11.4094	842.22
Tt	*Tanytarsus* spp.	17	7.73835	780.54
Cm	*Cladotanytarsus mancus*-type	2	1.1155	695.03
Pa	*Paracladius*	7	4.50082	626.13
Ps3	*Psectrocladius* sp3	4	2.68204	466.11

occurred with a clear difference in faunal diversity around the saline-freshwater boundary ~3000 µS/cm (~1800 mg/l TDS) (Eggermont et al., 2006). Walker et al. (1995) and Heinrichs et al. (2001) also observed a similar change in chironomid faunal diversity from a calibration set of lakes in Canada along a salinity gradient, but at a higher conductivity of ~10,000 µS/cm (~6000 mg/l TDS), which is a similar value to the loss of diversity in the Tibetan data (Fig. 2). These results therefore suggest that similar processes may be controlling chironomid distribution across salinity gradients irrespective of biogeographical constraints. Previous studies have suggested that these boundaries may reflect the tolerance limit of key aquatic macrophytes that stabilize shallow lake bottoms and create a range of specialized microhabitats rather than a physiological tolerance limit to osmotic stress in the chironomids themselves (Williams et al., 1990; Verschuren et al., 2000). No taxa appeared to be completely restricted to solely freshwater with very low TDS levels, but the taxa with the lowest TDS optima were *Cladotanytarsus mancus*-type, *Paracladius* and *Psectrocladius* sp3. As the genus *Psectrocladius* has morphotypes that occur at the extreme ends of the salinity gradient within the Tibetan Plateau, it is clear that developing and using the highest taxonomic resolution possible for training sets and subfossil reconstructions is vital for developing model inferences and implementing environmental reconstructions (cf. Eggermont et al., 2006).

In addition to the close ecological agreement between the Tibetan training set and other chironomid-inferred salinity datasets from East Africa and Canada, the model performance statistics also compare well between the different regions. The inference model presented in this study has a higher r^2_{jack} (0.80) and lower RMSEP (0.29) than those quoted by Heinrichs et al. (2001) ($r^2 = 0.755$ and RMSEP = 0.439) for the Canadian model, although the performance statistics of our dataset are a little weaker than those of the chironomid salinity transfer functions for African lakes (Eggermont et al., 2006). It is important to note, however, that evaluating the performance of an inference model should not only rely on the statistical results but also the ecological aspects of the chironomid fauna, which we have shown to compare well between the different regional models. While the number of lakes for the Tibetan inference model ($n = 38$) is lower than for the other two training sets (Canadian = 87; East African = 67), which may lead to improved model statistics, it is more likely that detailed taxonomy most aids good model performance as of the 69 taxa in the East African dataset most were identified to species or species group level (Eggermont et al., 2006). Unfortunately the taxonomy of our Tibetan dataset (only 24 taxa included) failed to identify chironomids to the species level, and the Tibetan taxonomic resolution is currently restricted to genera and species morphotypes, a similar problem that affects most other chironomid inference models (Brooks, 2003). The performance statistics do, however, suggest that our model should be able to reconstruct past changes in salinity from the Tibetan Plateau with some degree of confidence. Eggermont et al. (2006) used their new model to compare chironomid-inferred conductivity estimates with corresponding diatom-inferred estimates from two sediment sequences. Their results showed that the different numerical techniques yielded significantly different results, due to their different sensitivity to the presence or relative abundance of certain key taxa combined with the threshold faunal response to salinity change, but when the most appropriate chironomid inference models were used, a high degree of correlation between the chironomid and diatom records occurred, indicating that chironomids are valuable salinity indicators, and can be used with confidence when, for example, diatoms are not preserved.

Depth was also important in explaining chironomid distribution, with values ranging from 0.3 to 48 m and explaining 7.5% of the variance in the chironomid data. The significance of depth in influencing the distribution and abundance of chironomid assemblages has been found in other chironomid training sets from different regions (e.g., Walker et al., 1991; Walker and MacDonald, 1995; Korhola et al., 2000), and some studies have generated quantitative lake depth reconstructions using subfossil chironomids (Korhola et al., 2000) although problems do exists using this approach (Hofmann, 1998; Walker, 2001). While the low coefficient of depth inference models obtained in this study does not indicate that the models would be significant, the importance of depth in explaining the distribution of chironomids should still be considered when interpreting TDS reconstructions, especially if the community changes involved fluctuations in taxa which are likely to be sensitive to depth.

Perhaps the most dramatic advances in midge palaeoecology over the last decade have been in the area of palaeotemperature inferences (Walker, 2001; Brooks, 2003; 2006; Walker and Cwynar, 2006). Quantitative palaeotemperature reconstructions are obtained by applying inference models to fossil stratigraphies, and these have provided clear evidence for late glacial and Holocene climatic change (e.g., Walker, 2001; Heiri et al., 2003; Langdon et al., 2004; Velle et al., 2005). However, the temperature gradient in our training sets was relatively small (with the exception of three lakes with July temperature >12°C), and temperature was not significant in explaining chironomid distribution within CCA. In order to maximize the temperature gradient within this region, with a view to creating a temperature inference model on the Tibetan Plateau, a greater number of lakes with similar salinities along the temperature gradient should be sampled. However, as the salinity gradient is so large across this region it is likely that a salinity signal will dominate any training set developed in this region. Many other factors also have a significant influence on chironomid distribution and abundance, and have the potential for the establishment of a transfer function (Pinder and Morley, 1995; Walker, 2001), but unfortunately few other environmental variables were measured for this training set (e.g., bottom dissolved oxygen, quantity of aquatic macrophytes) and hence we were unavailable to assess what other factors might drive chironomid distribution on the Tibetan Plateau.

Diatom research in the study area indicates that salinity and depth were also the two major factors constraining diatom distribution and a corresponding diatom-conductivity transfer function with low RMSEP (0.22) and high r^2_{jack} (0.92) has also been established (Yang, 2003, 2004). The diatom-conductivity model and the chironomid–TDS model both have high inference abilities, indicating the reliability of biological transfer functions in the study area. The inference ability of the diatom-conductivity model is slightly better than that of chironomid–TDS model, which might be because the diatoms could be identified to species or subspecies, as well as the greater species diversity and narrower tolerances of the diatoms, and more continuous replacement of diatom species along the salinity gradient. It is useful, however, to have two models based on different biota, in order to: (a) compare quantitative reconstructions from the same sequence using different proxies, which can be important if, for example, non-analogue conditions were ever present in the past; and (b) have more than one means of reconstructing salinity when one proxy is not preserved, for example diatoms can often be destroyed by dissolution in saline lake sediments.

In conclusion, our results indicate that there is a strong relationship between TDS and the chironomid distribution in our Tibetan training set. The aim of this paper was to develop inference models for TDS using chironomids, and the performance statistics of these models suggest they can be used to provide accurate reconstructions of TDS in the study area. However, future improvements are still required for the model, notably improved taxonomic resolution where possible, detailed studies of chironomid community ecology in the Tibetan region, and an enlargement of the number of lakes in the training set in order to maximize the relevant environmental gradients.

Acknowledgements We gratefully acknowledge Prof. Xiangdong Yang for the samples and providing the chemistry data as well as constructive suggestions regarding this paper. Prof. Ji Shen, Prof. John Dearing, Prof. Wang Sumin, Dr. Enfeng Liu, Mr. Xuhui Dong, Dr. Barbara Lang, Prof. Houyuan Lü and Prof. Xinhua Wang, are also acknowledged for their help during the preparation of this paper. Prof. Ian Walker is acknowledged for providing references and Bob Smith of the Southampton University Geography Cartographic Department is thanked for preparing the figures. We are very grateful to Drs Hilde Eggermont and Markus Heinrichs whose comments greatly improved the manuscript. This study is supported by the State Key Basic Research and Development Plan of China (2005CB422002), NSFC (Grant No.:40402015), and the Knowledge Innovation Program of the CAS (KZCX3-SW-339).

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