

Inc., Yellow Springs, OH, USA) with a 600XL probe. Additional chemical variables were measured in the laboratory. Total nitrogen (TN), total phosphorus (TP) and concentration of HCO_3^- and CO_3^{2-} , and Chlorophyll-a (Chl-a) were analysed using Water and Waste water Monitoring Methods (EPA, 2002). Loss-on-ignition (LOI) and grain size of the surface sediment were also calculated.

Chironomid analysis

Surface sediment samples were analysed for chironomids by following standard methods (Brooks *et al.*, 2007). The sediment was deflocculated in 10% caustic potash (KOH) in a water bath at 75°C for 15 min. The samples were then sieved at 212 and 90 μm and the residue was examined under a stereo-zoom microscope at $\times 25$. All the head capsules found were mounted on microscope slides in a solution of Hydromatrix[®]. The chironomid head capsules were identified mainly following Wiederholm (1983), Oliver and Roussel (1983), Rieradevall and Brooks (2001), and Brooks *et al.* (2007).

Numerical and statistical analyses

All taxa recovered from the 46 samples were categorised into three units. A taxon would be defined as rare if it failed to exceed 3 occurrences. In fact, if it exceeded 3 occurrences, the taxon would be identified as either common or uncommon when its mean frequency exceeded or remained below one specimen per sample, respectively (Eggermont *et al.*, 2007). The chironomid diversity was assessed using species richness (calculated as the total number of species), Shannon-Wiener index (Shannon and Weaver, 1963) and Hill's N2 (Hill, 1973).

A range of numerical methods were used to determine the influence of the environmental variables on the chironomids distributions within the lake. Environmental variables – except pH – were $\log_{10}(x+1)$ transformed prior to ordi-

nation analysis. Species with a maximum abundance <1% or an occurrence in only one sample were removed prior to numerical analyses. A detrended correspondence analysis (DCA) (Hill and Gauch, 1980) with detrending by segments and non-linear rescaling was used to identify the gradient length within the chironomid data in order to check whether unimodal analysis was appropriate (ter Braak, 1987). Detrended correspondence analysis results showed that the axis 1 gradient length was 1.815 standard deviations, indicating that linear analysis was suitable. Direct gradient ordination by redundancy analysis (RDA) with automatic selection was used to identify significant ($P \leq 0.05$) explanatory variables that explained the chironomid distribution (ter Braak and Šmilauer, 2002). Monte Carlo permutation tests (499 permutations) were employed to test the significance of each variable. Variance inflation factors (VIFs) were examined via a series of RDAs on all the significant variables, and variables with high VIFs (>20) were excluded from further analysis (Hall *et al.*, 1999). Then, partial RDAs were performed to calculate the explained variance in the chironomid data by the unique effects of the individual variables selected in the forward-selection. All analyses were based on square root transformed percentage data with downweighting of rare taxa, and the program CANOCO version 4.5 was used for ordination analysis (ter Braak and Šmilauer, 2002). Chironomid percentage diagrams were produced with software TILIA and TGView 2.02 (Grimm, 1990, 2004). Midge zones in surface sediments were identified using the constrained incremental sum of squares (CONISS) based on square-root transformation of species data.

RESULTS

Physical and chemical variables in Lugu lake

Bottom water temperature (T) ranged from 7.2 to 22.9°C with a mean and median value of 13.5 and 11.0°C,

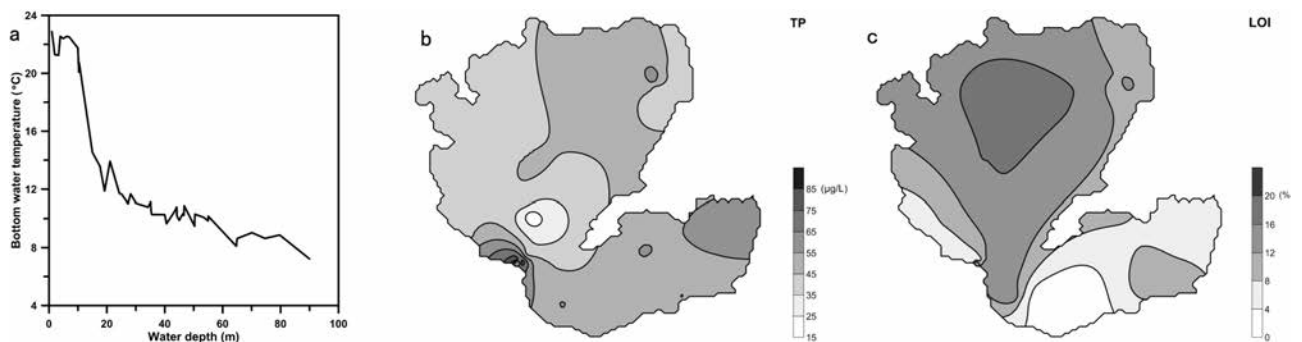


Fig. 2. Selected environmental parameters gradient in Lugu lake: a) bottom temperature vs water depth; b) TP (total phosphorus) concentration; c) LOI (loss-on-ignition) of surface sediment.

respectively. The lake is alkaline, with pH values changing in the spectrum from 8.5 to 9.3. A large conductivity gradient was measured and varied from 109 to 210 $\mu\text{S cm}^{-1}$, with an average value of 206 $\mu\text{S cm}^{-1}$ [there was an abnormally low value (2 $\mu\text{S cm}^{-1}$) in site 41]. The lake is oligotrophic, with relatively low nutrient concentrations; TP ranged between 18.5 and 87.4 $\mu\text{g L}^{-1}$, with a mean value of 50.8 $\mu\text{g L}^{-1}$. The distribution of the water TP concentration within the lake shows that high TP values is only limited to the lake edge (Fig. 2b). Total nitrogen ranged from 80.4 to 318 $\mu\text{g L}^{-1}$ (with average of 164.8 $\mu\text{g L}^{-1}$), and Chl-a from 0 to 707.3 $\mu\text{g L}^{-1}$ (with average of 20.6 $\mu\text{g L}^{-1}$). The macrophytes were distributed on the edge of the lake in water depth <11 m, which is similar to a previous study (Wang and Dou, 1998).

Chironomid assemblages and species diversity

Forty-one chironomid taxa were identified from the samples. Among them, 21 chironomid taxa had a maximum relative abundance >1% and occurred in more than two samples from 46 sites. The relative abundance and concentration of 21 principle chironomid taxa are presented along the depth gradient in Figs. 3a and b. According to the criteria for judging chironomid appearance frequency (Eggermont *et al.*, 2007), of the total taxa, 12 common types together accounted for 97% of the total number of chironomid head capsules extracted from all samples and the average abundances across the whole lake ranged from 1.0 to 29.6%. The abundance of *Tanytarsus mendax*-type (29.6%), *Procladius* (19.5%), *Polypedilum nubeculosum*-type (13.3%), and *Paratanytarsus penicillatus*-type (10.8%) exceeded 10% of the total chironomid head capsules, respectively. Only 6 taxa were classified as uncommon, which together made up 2% of the total number of chironomid head capsules. The remaining 22 taxa were rare and only occupied less than 1% of the total head capsules in all.

Chironomid assemblages showed an obvious change from the near-shore to offshore. *P. penicillatus*-type, *Chironomus anthracinus*-type and *Paramerina* were the dominant taxa in samples in the near-shore area with water depth <10 m (Zone 2). These littoral sediments also contained relatively high chironomids head capsules (11-33 head capsules per gram of wet sediments) (Fig. 4) and high richness of species (12-20 taxa) (Fig. 5). Species' evenness (Hill's N2) was the highest (5.4-9.1) and had a similar pattern to species diversity.

An obvious assemblage change was apparent at the boundary depth of 10 m. Zone 1d (from 10 to 17 m) comprised a few samples with a high relative abundance of *Microchironomus*, differing from other chironomid communities. *T. mendax*-type and *Procladius* taxa replaced the dominance of *P. penicillatus*-type and *C. anthracinus*-type in zone 1c (from 17 to 33 m), and their abundances rose with increases in water depth. The percentage of *P.*

nubeculosum-type maintained a steady amount in this mid-depth area. Particularly, the development of *Monodiamesa* was limited to this depth spectrum. As the water depth increased, the abundance of chironomids, species diversity and evenness all declined.

The chironomid composition in zone 1b (from 33 to 73 m) appeared to be similar to zone 1c. *T. mendax*-type showed a slight decline after its peak around 45-50 m, while *Procladius* displayed a converse trend. There was no obvious change between these two mid-depth areas in chironomid concentration and species richness.

Three samples from deepest water (>70 m) comprised zone 1a, which possessed relatively low species diversity (4-7) and evenness (2.2-2.5). Several chironomid species were absent in this zone, such as *Ablabesmyia* and *C. anthracinus*-type.

Additionally, as mentioned above, the concentration of head capsule and species diversity combined with Hill's N2 were negatively correlated with water depth, with the correlation coefficients -0.62, -0.74 and -0.72 ($P < 0.001$), respectively. The chironomid diversity (Shannon-Wiener index) was low, with an average diversity of 1.51 in the sites, and none of the sites exceeded 2.4 (Fig. 4). A similar pattern is observed between diversity (Shannon-Wiener index) (Fig. 4) and species richness (Fig. 5), with higher values in the littoral area and lower values in the deep area.

Ordinations

The final calibration data set consisted of 13 measured environmental variables and 21 chironomid taxa with a maximum abundance >1% and occurred in more than two samples from 46 sites. An initial RDA with all 13 environment variables explained 56.3% of total variance in the chironomid data. Of the variations in the chironomid assemblages, 45.4% were explained by the first two RDA axes (Fig. 6). Bottom temperature (10.8% of the explained variance), water depth (3.3% of the explained variance), LOI (3.0% of the explained variance) and water TP (2.6% of the explained variance) comprised the minimum subset of significant environmental factors ($P < 0.05$) explaining 47.7% of the cumulative chironomid variances (Tab. 1). Bottom temperature was negatively correlated with water depth, ($r = -0.86$, $P < 0.001$) (Figs. 2a and 6) after removal from the RDA analyses, then the water depth was more significant with both improved P values and the unique explained variance percentage (Tab. 1).

DISCUSSION

Chironomid larval head capsule concentrations were higher in samples from near-shore shallow sites. This phenomenon was also found in other studies, and the reasons are usually attributed to sediment winnowing and focusing, as well as physiological gradients related to water

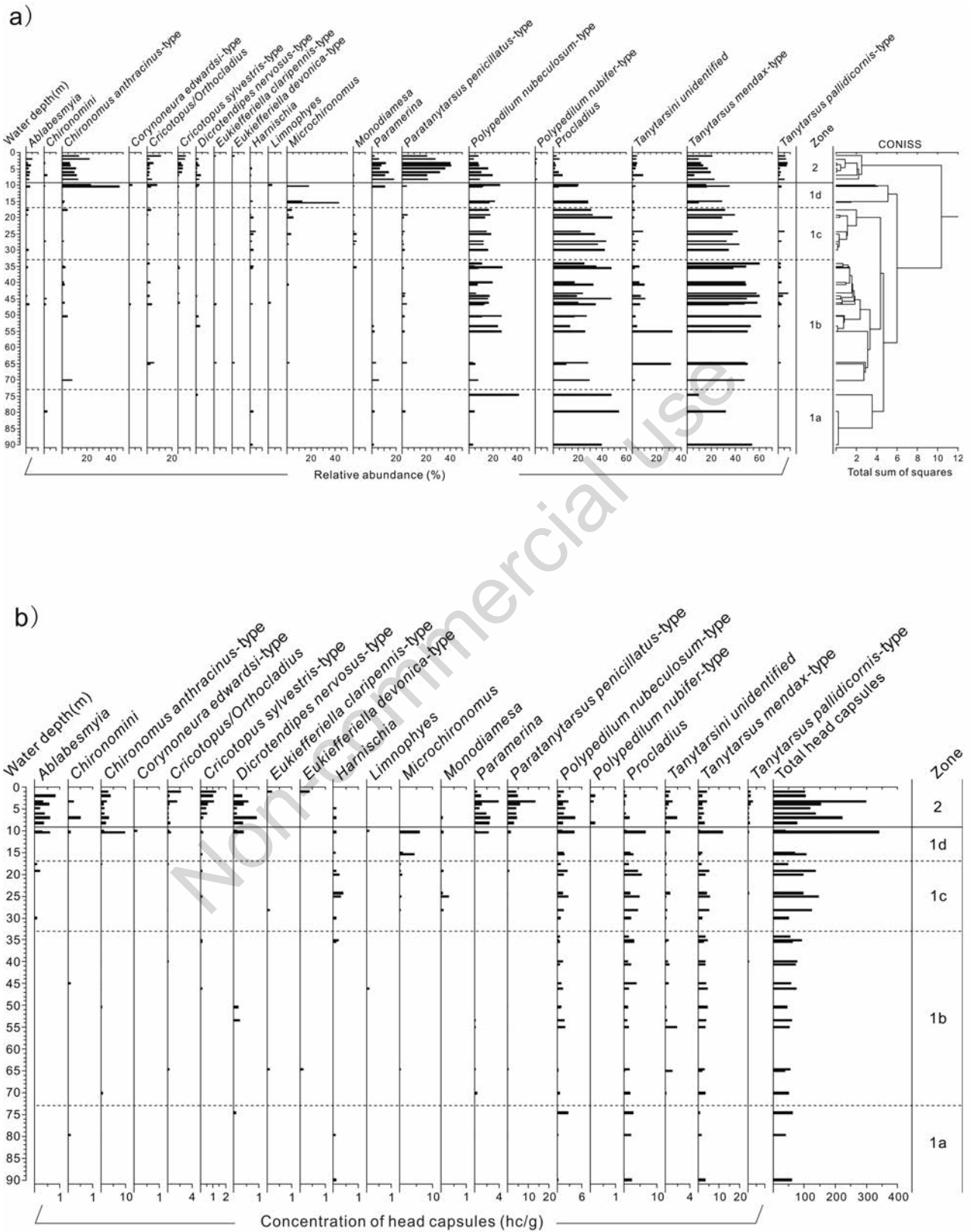


Fig. 3. Distribution of main chironomid taxa in surface-sediment assemblages from Lugu lake. Zones were identified by CONISS analysis along the water depth of sampling sites. a) relative abundance; b) concentration of head capsules.

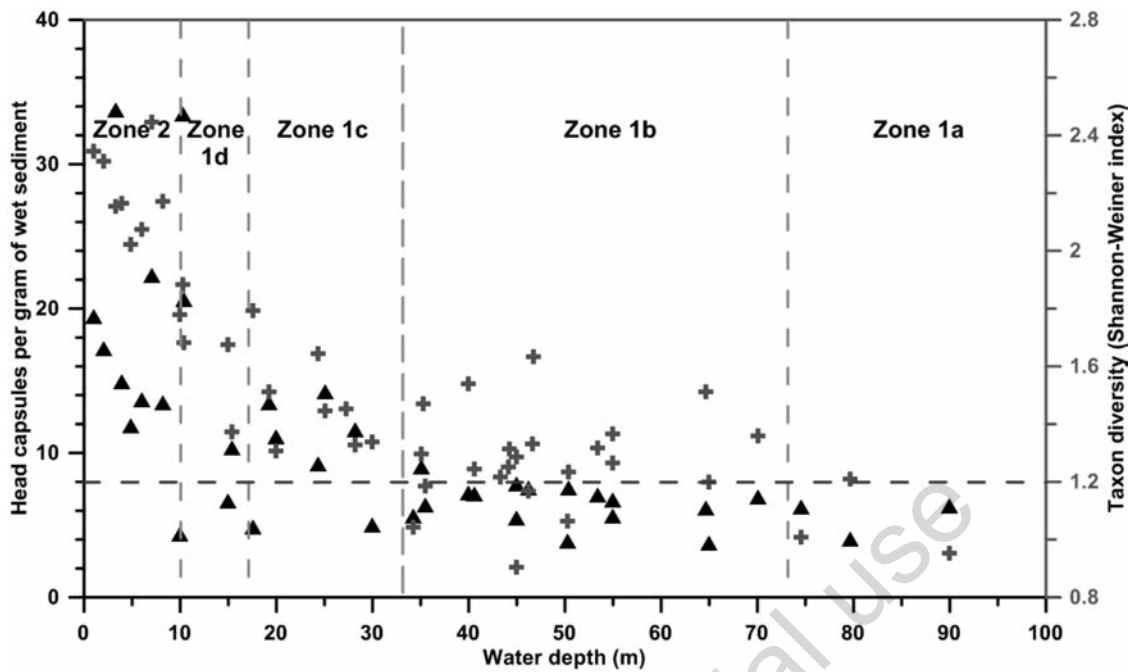


Fig. 4. Scatter plots of concentrations of chironomid presented by head capsules per gram of wet sediment (triangles) and Shannon-Wiener index (crosses) along with water depth. The vertical bars on the graphs are based on a depth-constrained cluster analysis. Zones are classified according to different water depths as follows: zone 2 is <10 m; zone 1d ranges from 10 to 17 m; zone 1c from 17 to 33 m; zone 1b from 33 to 73 m; and zone 1a is >73 m.

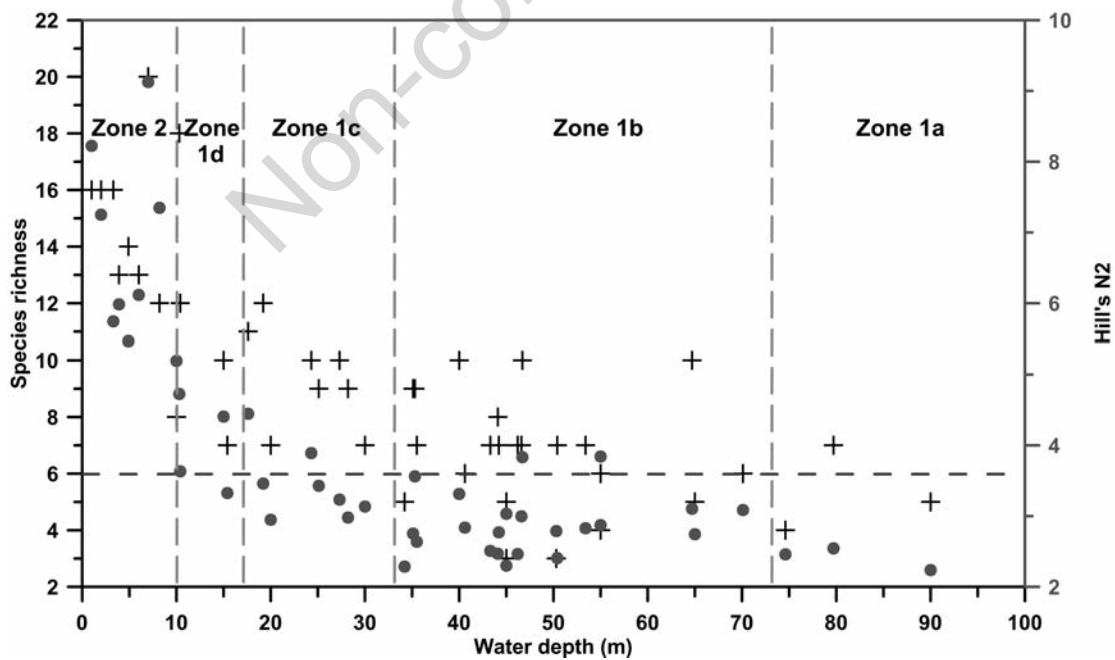


Fig. 5. Scatter plot showing species richness (crosses) and Hill's N2 (grey circles) in different zones along with water depth. The vertical bars on the graphs are based on a depth-constrained cluster analysis: zone 2 is <10 m; zone 1d ranges from 10 to 17 m; zone 1c from 17 to 33 m; zone 1b from 33 to 73 m; and zone 1a is >73 m.

depth (cf. Eggermont *et al.*, 2007; Holmes *et al.*, 2009; Schmäh, 1993). In Lugu lake, higher concentration nearshore may be also primarily due to the fact that large amounts of submerged macrophytes were distributed within the shallow parts of the lake at less than 11 m of depth (Wang and Dou, 1998), which in turn support large invertebrate communities. The taxa associated with macrophytes, such as *P. penicillatus*-type, *Ablabesmyia*, *Cricotopus sylvestris*-type, *Paramerina*, *Dicrotendipes nervosus*-type (Brodersen *et al.*, 2001; Langdon *et al.*, 2010; Gathorne-Hardy *et al.*, 2007), were restricted to the near-shore locations at a depth less than 11 m. This also confirms the relationship between macrophytes and the chironomid fauna in Lugu lake. Furthermore, Fig. 6 indicates that the samples at the edge of the lake had coarser sediment grain size and higher TP concentration in water column. The high nutrient loading from human activities, including tourism and agriculture in the catchment, mainly influences the shallow offshore area, favouring the

development of plankton, and thus supports the high concentration of chironomid fauna. Lower chironomid concentration in deeper locations may be due to the fact that Lugu lake is a deep seasonally stratified lake, and lower temperature and seasonally anoxic hypolimnion lead to low chironomid production (Schmäh, 1993). Monitoring during 2010 shows that Lugu lake behaves as a typical warm monomictic lake. In summer and autumn the lake water is stratified, while during early spring and winter the lake is unstratified (Wang *et al.*, unpublished data). Various studies show that the extent to which chironomid remains are moved offshore is not consistent, regardless of depth and morphometry (Schmäh, 1993; Heiri, 2004; Eggermont *et al.*, 2007). In Lugu lake, several chironomid taxa, such as *P. penicillatus*-type, *C. anthracinus*-type, *Ablabesmyia*, *C. sylvestris*-type, *Paramerina*, *Cricotopus/Orthocladus*, *D. nervosus*-type, *Tanytarsus pallidicornis*-type, were restricted to shallow sites, indicating that the transportation of littoral head capsules into the

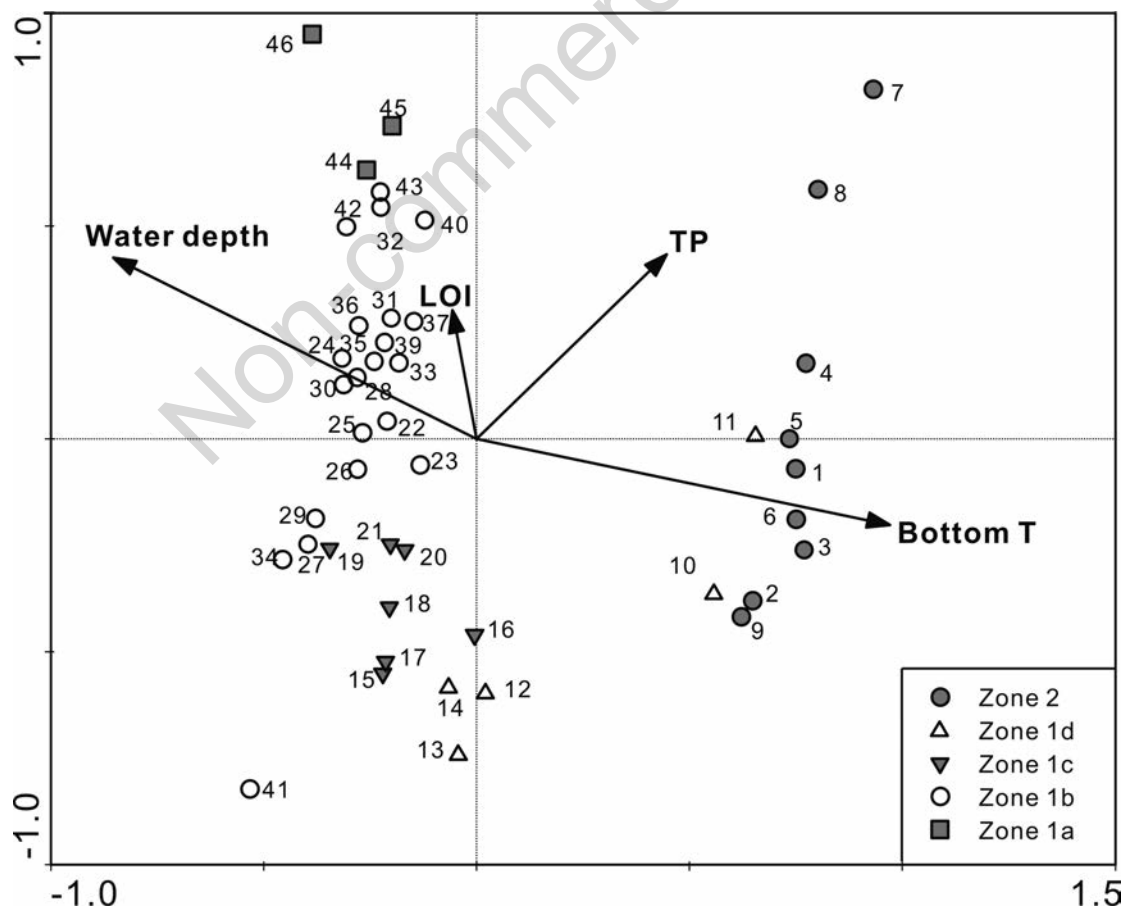


Fig. 6. Scatter biplot of the chironomid assemblage and the environmental variables [bottom water temperature (Bottom T), water depth, loss-on-ignition (LOI), and water total phosphorus (TP)] for the samples from Lugu lake.

deeper parts of the lake is minimal. This may be due to the fact that the wind-driven current can only influence the near-shore locations of such a large lake with a depth <30 m (Wang and Dou, 1998).

Redundancy analyses revealed that the predominant drivers of chironomid distribution within the Lugu lake were the influence of bottom water temperature, water depth, LOI and water TP (Fig. 6). As a large deep stratified dimictic lake, the thermocline of Lugu lake extends between 10 and 17.5m in July and the temperature of the epilimnion is about 10°C higher than that of the hypolimnion. The position of the thermocline of Lugu lake has a significant influence on the distribution of macrophytes and the substrate, thus influencing the composition of the chironomid communities. Water depth negatively correlates with water temperature (Figs. 2a and 6) and has a strong influence on the distribution of chironomid larvae with many taxa showing depth preferences. Similar patterns are also reported in other studies (Brundin, 1949; Schmäh, 1993; Heiri, 2004). Water depth is commonly significant in driving the distribution and abundance of chironomids (Larocque *et al.*, 2001; Barley *et al.*, 2006) and models have been developed to reconstruct lake water depth using chironomids (Korhola *et al.*, 2000; Luoto, 2009). Water depth is closely related to temperature, food availability and oxygen conditions, which in turn determine the composition of chironomid communities in the profundal zone of regularly stratified lakes (Lindegaard, 1995). Typically the chironomid assemblages become uniform below ca. 15 m (Kurek and Cwynar, 2009). Loss-on-ignition is another important environmental driver of the chironomid distribution and abundance within Lugu lake. Loss-on-ignition has also been found to be important in other chironomid training sets (Nyman *et al.*, 2005; Langdon *et al.*, 2008). Loss-on-ignition can influence the composition of chironomid communities through a range of mechanisms, including relationships with substrate, lake productivity and larval feeding strategies. Fig. 2c shows that the sites with higher LOI were mainly distributed in deep central areas with fine grain sizes.

Lakes on the Yunnan plateau have changed considerably in recent decades as a consequence of a rapid eco-

nom development. In addition, the chironomid data set from lakes in this region indicates that depth and DO are key environmental factors influencing contemporary faunas (Zhang *et al.*, 2011). Lugu lake is located in a rural alpine area, and is still oligotrophic. Bottom DO is higher than in other deep eutrophic lakes on the Yunnan plateau (Zhang *et al.*, 2011). In recent years, however, Lugu lake has become a nature reserve, thus it has been facing pressure from the huge number of visitors, but also from improved agricultural techniques (Wu *et al.*, 2008). Pollution caused by human activities is currently limited to the lake edge, as indicated by the distribution of the water TP concentration within the lake (Fig. 2b) and its effect on the chironomid assemblage in these sites.

Obvious changes in the chironomid assemblages were apparent at 10 m of water depth. The concentration of head capsules, evenness and richness of species were higher in samples located at <10 m. The upper boundary of the thermocline is at about 11 m in July, which approximates to a major change in the chironomid assemblage at this depth. The position of the thermocline is recognised as an important boundary with respect to many lake processes (Wetzel, 2001), and may also structure within-lake chironomid distribution patterns. Furthermore, the thermocline also occurs at a depth where macrophytes can survive in Lugu lake, and the presence of macrophyte communities provides more microhabitats. This results in higher species richness and concentration of chironomids. In Lugu lake depth-related faunal shifts primarily reflect the dominant controls of temperature and macrophyte distribution on the chironomids.

There are clear relationships between diversity (species richness and Shannon-Wiener index) and environmental factors. The chironomid diversity decreases along the depth and bottom water temperature gradients. However, the chironomid diversity (Shannon-Wiener index) is relatively low, with an average diversity of 1.51, and none of the sites sampled exceeded 2.4. The anomalously low chironomid diversity is similar to that of the lakes on Yunnan plateau (Zhang *et al.*, 2011). Human impact, such as enhanced soil erosion of the catchment and increased nutrient level of the

Tab. 1. Results of partial redundancy analyses for the significant variables including/excluding the bottom water temperature.

	Variable	Significance (P value)	λ_1/λ_2	Explained percent of total variance (%)
Run 1	Bottom water temperature	0.002	0.77	10.8
	Water depth	0.014	0.24	3.3
	LOI	0.02	0.21	3.0
	TP	0.044	0.19	2.6
Run 2	Water depth	0.002	1.23	24.8
	LOI	0.028	0.17	3.5
	TP	0.036	0.17	3.4

LOI, loss-on-ignition; TP, total phosphorus.

lake in recent years, may be a possible reason for this phenomenon. The chironomid fauna of the samples from the deep area of Lugu lake is similar to that of the deep lakes in Yunnan, which usually have low species richness and are dominated by taxa such as *Procladius* and *Tantarsus* genus (Zhang *et al.*, 2011).

Taken together, water depth – which interacts with bottom temperature – is the most significant environmental variable forcing chironomid composition and distribution in a deep, plateau lake. Fossil chironomid gradient from near-shore to offshore can reflect the real living chironomid compositions near a specific habitat. In palaeolimnological studies, this means a deficient representativeness of single core for the whole lake basin. Substituting space for time, more attention should be paid to dominant factors potentially varying through time, either to avoid bias in palaeoenvironmental reconstructions or for modern lake management. For example, water depth is determined as the most important driver in faunal community, but nutrient loading resulting from anthropogenic interference might predominate if effective conservation protocols are not executed.

CONCLUSIONS

Ordination analyses reveal that the predominant drivers of chironomid distribution within the Lugu lake were the influence of bottom water temperature, water depth, LOI and water TP. The chironomid assemblage shows distinct depth-related faunal shifts, and an abrupt change in the chironomid distribution appears at 10 m of water depth. Several chironomid taxa were restricted to the shallow sites, which indicate that the transportation of littoral head capsules into deeper parts of the lake is minimal. The abrupt change in the chironomid assemblage is closely related to the macrophyte distribution and the position of the thermocline. There are only minor changes of chironomid assemblages below approximately 15 m of water depth. This may reflect the effects of temperature on the chironomid distribution, as the temperature falls rapidly between 0–15 m, but less steeply in hypolimnion during summer. In Lugu lake depth-related chironomid faunal shifts primarily reflect the dominant controls of temperature and macrophyte distribution. Spatial heterogeneity in the chironomid structure demonstrates a high representativeness of fossil remains for *pre*-buried chironomid assemblages, but a defective substitution of a single core for the whole lake basin in palaeolimnology. Although anthropogenic impacts are still limited to the edge of Lugu lake, more attention need to be paid and farseeing strategies need to be developed to keep a sustainable development of the lake. Given the developing tourism and the scarcity of conservation protocols, this study gives some hints and warnings for initiatives of modern ecological management. The heterogeneity in chironomid commu-

nities in such a stratified lake would also provide a reference case for sampling site selection in palaeolimnological studies. Additionally, the preference of specific species for water depth and their ecological limitations will aid the future interpretations of palaeolimnological data.

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