Fundam. Appl. Limnol. **Vol. 179/2,** 103–113
Stuttgart, May 2011

Article

Ecological influences affecting the distribution of larval chironomid communities in the lakes on Yunnan Plateau, SW China

Enlou Zhang[1,*], **Peter Langdon**[2], **Hongqu Tang**[3], **Richard Jones**[4], **Xiangdong Yang**[1] and **Ji Shen**[1]

With 5 figures 1 table and 1 appendix

Abstract: Surface sediment samples were collected from 35 lakes on the Yunnan Plateau as part of an investigation into the relationship between surface sediment subfossil chironomid distribution and lake environmental variables. This region of China is unique as it contains large temperature gradients, from the subtropics to the foothills of the Himalaya, but also contains lakes that have been heavily impacted by anthropogenic activities. The chironomid communities were dominated by 8 taxa, which together accounted for 77.7 % of the fauna. The statistical analyses indicated that mean July air temperature and water depth were the most significant variables affecting the distribution of chironomids across these sites. After removing 3 major outliers from axis 1 in the ordination data set, temperature lost its significance but water depth and reductions in bottom dissolved oxygen (DO) were still found to be significant. In addition the diversity of the dataset was found to be low compared with other chironomid training sets throughout the world, suggesting that this region in China has different characteristics governing the abundance and distribution of chironomids compared with other parts of the world, hence the need for regional training sets within China. This is the first subfossil chironomid data set from this region and the understanding of key environmental influences on contemporary faunas will aid interpretations of palaeolimnological data sets to reconstruct past trends and magnitude of environmental change over a range of timescales.

Key words: Yunnan Plateau, Chironomids, temperature, diversity, environmental variables.

Introduction

The Yunnan Plateau in southwestern China has one of the densest distributions of lakes in China (Wang & Dou 1998), the majority of which are located in the watersheds of four main rivers, the Jinsha, Lancang, Yuanjiang, and Nanpan Rivers (Fig. 1). The lakes are distributed at elevations from 1200 to 3800 m a.s.l. across the plateau and vary in depth from 1–155 m. Lake type varies greatly and includes tectonic, volcanic, glacial and karst lakes. As 95 % of the Yunnan Plateau is mountainous, population and agricultural centres tend to be clustered around the valley lakes that are closely tied to the regional economy. The Yunnan lakes are therefore extremely important for water resources and development (Jin et al. 1990), but

Authors' addresses:

[1] State Key Laboratory of Lake Science and Environment, Nanjing Institute of Geography & Limnology, Chinese Academy of Sciences, Nanjing 210008, China.

[2] Geography and Environment, University of Southampton, Southampton, SO17 1BJ, U.K.

[3] Research center of Hydrobiology, JiNan University, Guangzhou 510632, China.

[4] School of Geography, University of Exeter, Exeter, EX4 4QJ, U.K.

[*] Corresponding author; elzhang@niglas.ac.cn

www.schweizerbart.de
DOI: 10.1127/1863-9135/2011/0179-0103
1863-9135/11/0179-0103 $ 2.75

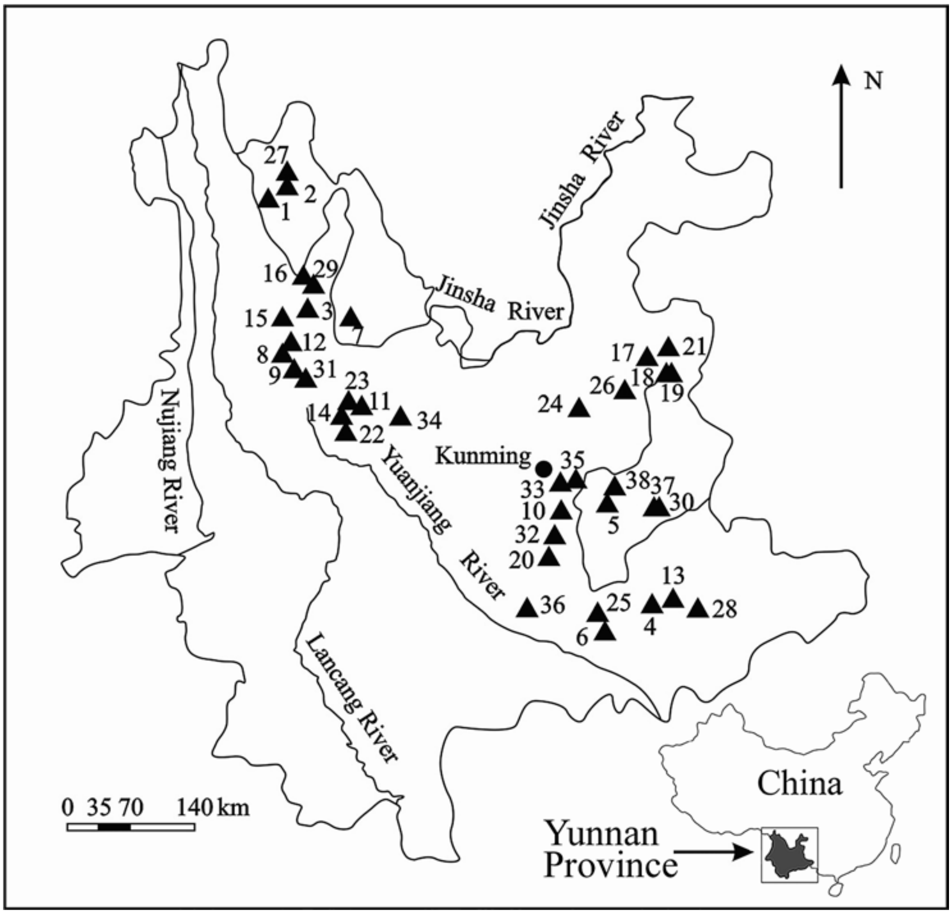

Fig. 1. Distribution of sampled lakes in the Yunnan Plateau. The high altitude lakes occur in the northwest of the region, with lower altitude and warmer lakes situated in the south.

are also subject to natural change. While inter-annual variations in precipitation can often cause water level fluctuations of 1–2 m (Jin et al. 1990) many of these lakes have changed significantly as a consequence of recent economic development. These changes have taken many different forms, and lake catchments in Yunnan Province have been subjected to deforestation, intensive agricultural cultivation, soil erosion, urbanization, and industrialization, and are among the most disturbed ecosystems in the world. It is likely that the current trajectory of how these lakes now function is in a completely new direction compared with historic and prehistoric trends (cf. Dearing et al. 2008). Several large lakes, such as Xinyunhu and Qiluhu, have experienced serious eutrophication, with algal blooms common in the summer. Although previous studies on physical and chemical characteristics have been undertaken on many of these lakes (Wang & Dou 1998), little is known about the aquatic fauna.

Chironomid larvae constitute one of the most abundant benthic invertebrates in freshwater ecosystems (Cranston 1995). Chironomids have proved to be useful indicators of a wide variety of environmental impacts on freshwaters, including the effects of eutrophication, acidification, toxic metals and chemicals, and physical disturbances (Lindegaard 1995). The importance of the different environmental variables are scale dependent in both time and space (Walker & Mathewes 1989). Previous research has demonstrated that temperature is usually the most important environmental variable in explaining the broad-scale geographic distribution and abundance of midge taxa from all major regions on the planet (e.g. Brooks 2006, Barley et al. 2006, Walker & Cwynar 2006, Dieffenbacher-Krall et al. 2007, Langdon et al. 2008, Porinchu et al. 2009). At the local scale, where relative variations in temperature are minimal, chironomid distribution appears to be driven principally by in-lake variables such as lake depth, pH, dissolved oxygen, trophic status and substrate-type (Pinder 1995). Chironomid larvae possess heavily chitinised head capsules that are usually well preserved and identifiable in lake sediments (Brooks 2003). Therefore, in addition to being important for understanding contemporary lake functioning, chironomid fossil remains also allow us to examine past community structures. Chironomid subfossils thus represent an important lake management tool for reconstructing recent changes in lake structure and function (Langdon et al. 2006, 2010, Whitehouse et al. 2008).

This study examines a number of different lake types in Yunnan, across a large spatial area, incorporating a range of altitudes and associated temperature gradients (range = 10–22.6 °C mean July air temperature) from the foothills of the Himalaya to subtropical climates in southeast Yunnan. The majority of lakes are situated in areas that have been heavily disturbed by human activity, hence our study will allow us to test whether temperature is still the main environmental variable that influences chironomid distribution even in regions where anthropogenic lake disturbance is large. In addition, we will assess the role of other key environmental parameters, such as nutrient and dissolved oxygen levels on chironomid distribution within the Yunnan Plateau. It is hoped the results will provide useful information for palaeolimnological studies and water management.

Methods

Sampling and sample processing

An initial total of 38 lakes, located on the Yunnan Plateau were sampled from June to July in 2005 (Fig. 1 and Appendix 1), although 3 had few chironomid head capsule remains and so were not used further (see Results section). This investigation includes almost all the lakes in the region with a surface area > 1 km^2, except for Dianchi, which could not be sampled due to dangerous waves when sampling (Zhang et al. 2007). These lakes had all been previously analyzed for variation of chromophoric dissolved organic matter and attenuation depth of ultraviolet radiation (Zhang et al. 2007). The physical and chemical characteristics of the lakes are described in detail by Zhang et al. (2007) and the range of main environmental variables measured at the sampling sites is listed in Table 1.

Surface sediment samples (0–1 cm) were taken towards the centre of each lake at the maximum water depth (see Appendix 1) using a Kajak gravity corer with a 60-mm-diameter coring tube and were analysed for chironomids following standard methods (Brooks et al. 2007). The sediment was deflocculated in 10 % KOH in a water bath at 75 °C for 15 minutes. The samples were then sieved at 212 µm and 90 µm and the residue was examined under a stereo-zoom microscope at × 25. A minimum of 50 identifiable whole head capsules in each sample was normally required for later analysis (Larocque et al. 2001) although some samples contained slightly fewer (c. 40), any samples with lower numbers of head capsules than this were discounted (see results section). 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 & Roussel (1983), Rieradevall & Brooks (2001), and Brooks et al. (2007). Taxonomy follows Brooks et al. (2007) with the species *Propsilocerus akamusi*-type, which occurs in two lakes, being described previously in Zhang et al. (2010).

Statistical analysis

The chironomid diversity was measured by Shannon-Wiener index H' (Equation 1) (Shannon & Wiener 1949) and Pielou evenness index J' (Equation 2) (Pielou 1975) as follows:

$$H' = -\sum(n_i/N)\ln(n_i/N) \quad (1)$$
$$J' = H'/\ln S \quad (2)$$

where S is the total number of taxa in community, n_i is the number of taxon i, N represents the total number of all taxa.

Another measure of chironomid diversity was calculated using the Hill's N2 statistic (Hill 1973). It is the reciprocal of Simpson's index and an estimate of the effective number of occurrences of taxa. Numerical methods were used to determine the relative influence of the measured environmental parameters on the distribution of chironomids in the surface sediments. Species with a maximum abundance < 1 % or an occurrence in only one lake were removed (13 taxa) and environmental proxy data were $\log_{10}(x+1)$ or $\log_{10}(1000x+1)$ transformed (except pH) prior to ordination analysis. A detrended correspondence analysis (DCA; Hill & Gauch 1980) with detrending by segments and nonlinear rescaling was used to explore the chironomid distribution patterns, as well as to identify the gradient length within the chironomid data (ter Braak 1987). A linear (RDA, Redundancy Analysis) or an unimodal (CCA, Canoni-

Table 1. Range of the main environmental variables measured at the sampling sites from the Yunnan Plateau lakes.

Environmental variable	Range measured	Mean value
Water depth of sampling sites (m)	1–110	9.5
TN (mg L^{-1})	0.21–4.59	1.22
Total phosphorus (µg L^{-1})	1.7–1248	78.5
Altitude (m)	1291–3809	2020
pH	6.95–9.31	7.92
Bottom dissolved oxygen (mg L^{-1})	0.88–8.16	3.73
Secchi depth (cm)	20–615	132
July air T (°C)	10–22.6	19.2
Sediment Loss-on-ignition (%)	6.81–63.30	16.49

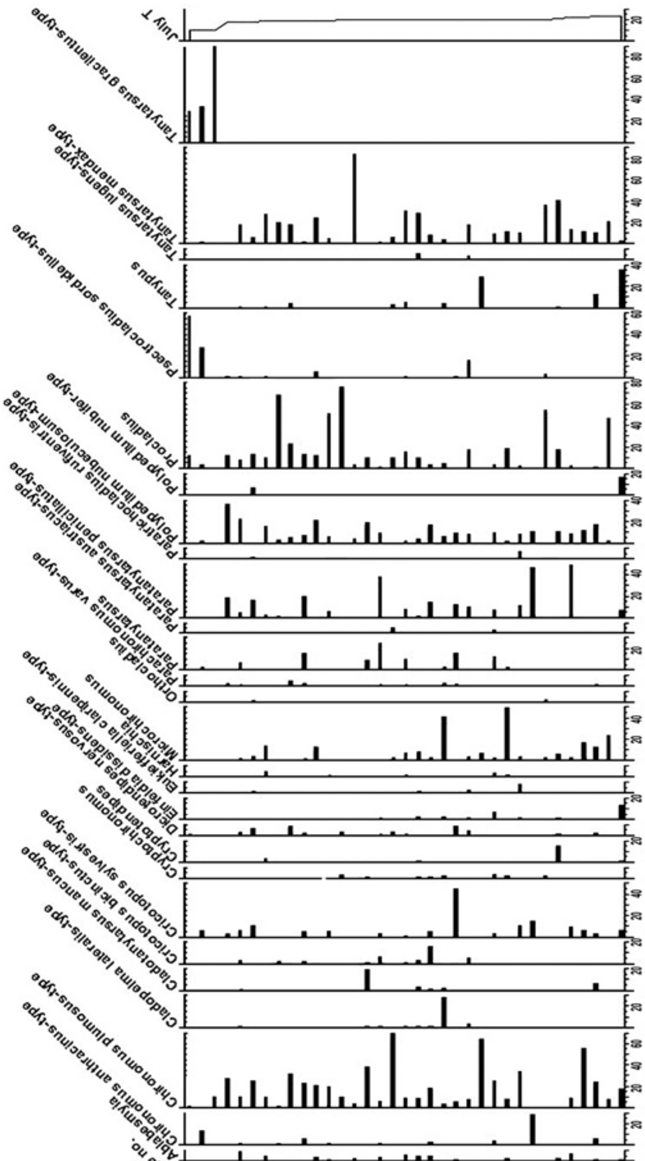

Fig. 2. Distribution of selected chironomid taxa (which occur in > 1 lake and > 1 % abundance) along the July T gradient. The numbers (codes) of each lake are shown in Appendix 1. The × axes relate to the % abundance of each taxon.

cal correspondence analysis) with forward selection and Monte Carlo permutation tests (n = 999 unrestricted permutations) was then selected to identify the most important variables influencing chironomid distribution (ter Braak & Šmilauer 2002). Consequently, only significant variables ($p < 0.05$) were used in the final RDA/CCA ordination. All the ordination analyses were based on square root transformed percentage data with down-weighting of rare taxa, and the program CANOCO version 4.5 was applied (ter Braak & Šmilauer 2002).

Results

Chironomid distribution

Out of the 38 lakes initially sampled in this study, three yielded very few (< 10) chironomid head capsules (Chaheihai Lake, Haishaoshuiku Lake and Tinghu Lake) and these were removed from the study. From the remaining 35 lakes, 53 chironomid taxa were identified with a total of 3301 head capsules picked and mounted (Fig. 2). Pielou evenness index varied only slightly from 0.39 (Haixihai Lake) to 0.92 (Lijiawa Lake), indicating an even distribution of chironomids in 35 lakes. Shannon-Wiener index, however, displayed a conspicuous lack of chironomid diversity among these lakes from 0.33 (Bitahai Lake) to 2.47 (Yuanhu Lake), with an average diversity across the 35 lakes of 1.64 (Fig. 3). Many of the lakes had very low species richness, with some only containing 3–5 taxa. Of the 53 taxa only 40 had a minimum abundance > 1 % and an occurrence in more than one lake. Eight

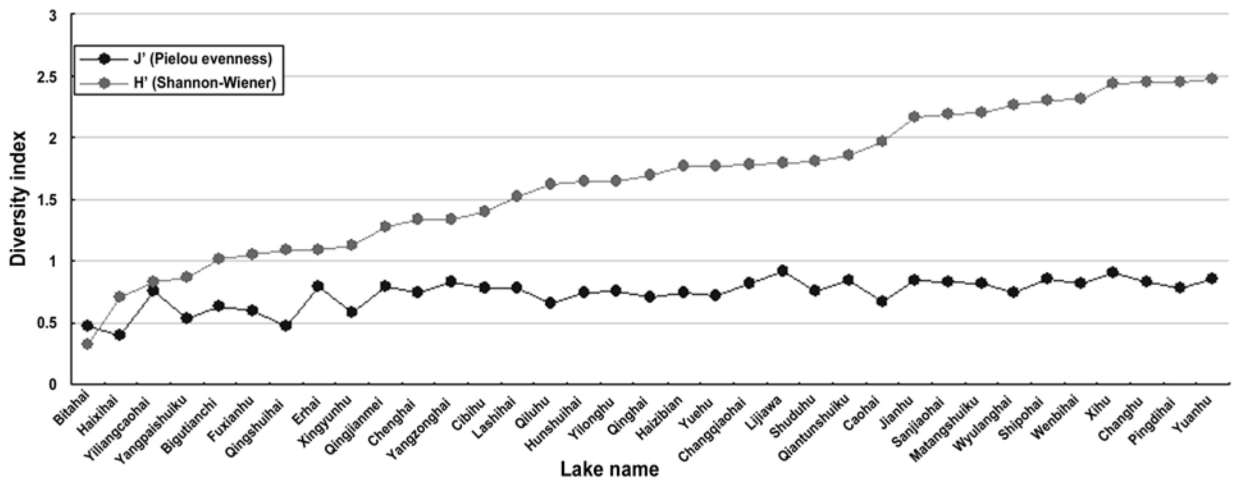

Fig. 3. The diversity of chironomid dataset of the studied lakes in Yunnan Province arranged from the least to most diverse.

taxa together made up 77.7 % of the fauna: *Tanytarsus mendax*-type, *Procladius*, *Chironomus plumosus*-type, *Polypedilum nubeculosum*-type, *Paratanytarsus penicillatus*-type, *Cricotopus sylvestris*-type, *Psectrocladius sordidellus*-type, and *Microchironomus*. These taxa tend to dominate in most of the Chinese lakes previously analysed for subfossil chironomids (e.g. Zhang et al. 2006, 2010, Jones et al., unpublished data). Of these, *Chironomus plumosus*-type was the most common taxon, occurring in 31 out of the 35 lakes. It also had the highest Hill's N2 number (N2 = 17.2552). Other common taxa, in addition to the 8 most common taxa listed above, that were found in more than 10 lakes and had a high Hill's number included: *Ablabesmyia, Dicrotendipes nervosus*-type, *Cryptochironomus, Paratanytarsus, Tanypus,* and *Chironomus anthracinus*-type (Fig. 2).

Constrained ordination

The final calibration data set consisted of 22 measured water quality parameters and 40 chironomid taxa from 35 lakes. These data were analysed in conjunction with the key environmental variables to assess the main patterns of chironomid distribution. Detrended correspondence analysis produced an axis 1 score with gradient length 2.832 (> 2.0) SD units thus indicating that unimodal methods (CCA, Canonical correspondence analysis) were appropriate for the constrained ordinations (ter Braak & Prentice 1988). The first axis in a DCA ordination (35 sites and 40 taxa) accounted for 18.4 % of the variance in the chironomid data (Fig. 4). After deletion of redundant variables, automatic forward selection in CCA indicated that mean July air temperature, water depth, SD, TP and bottom dissolved oxygen acted as the significant variables ($p < 0.05$) and captured 59.4 % of variance of taxon data in total. The single variance explained by each variable ranged from 8.0 % (bottom dissolved oxygen) to 19.8 % (July air temperature). There were 3 major outliers along axis 1, lakes 1, 2 and 27 from the CCA data set. These represented the coldest lakes at relatively high altitudes, and had fauna that were not common to any of the other lakes in the data set. *Psectrocladius sordidellus*-type and *Tanytarsus gracilentus*-type acted as the predominant taxa in these 3 cold lakes. *Tanytarsus gracilentus*-type was absent in all other lakes from the training set (Fig. 2) indicating it is a cold stenotherm in this region. The mean July air temperatures of these sites were just over 10 °C, whereas the next highest temperature of another lake in the data set was 17.9 °C. It is clear, therefore, that these three lakes were driving the temperature response of the data set, and hence to understand the impact of temperature on these fauna more sites need to be sampled in the temperature range 10–17 °C. In order to assess the significance of other environmental drivers on the data set, considering the absence of lakes sampled between 10–17 °C, the 3 cold lakes were removed from the training set and multivariate analyses repeated. The results showed that temperature was no longer a significant variable, and the variance captured by significant variables was reduced to 43.9 % while the independent explained variance by each variable ranged from 5.2 % (water depth) to 10.6 % (TP) (Fig. 5).

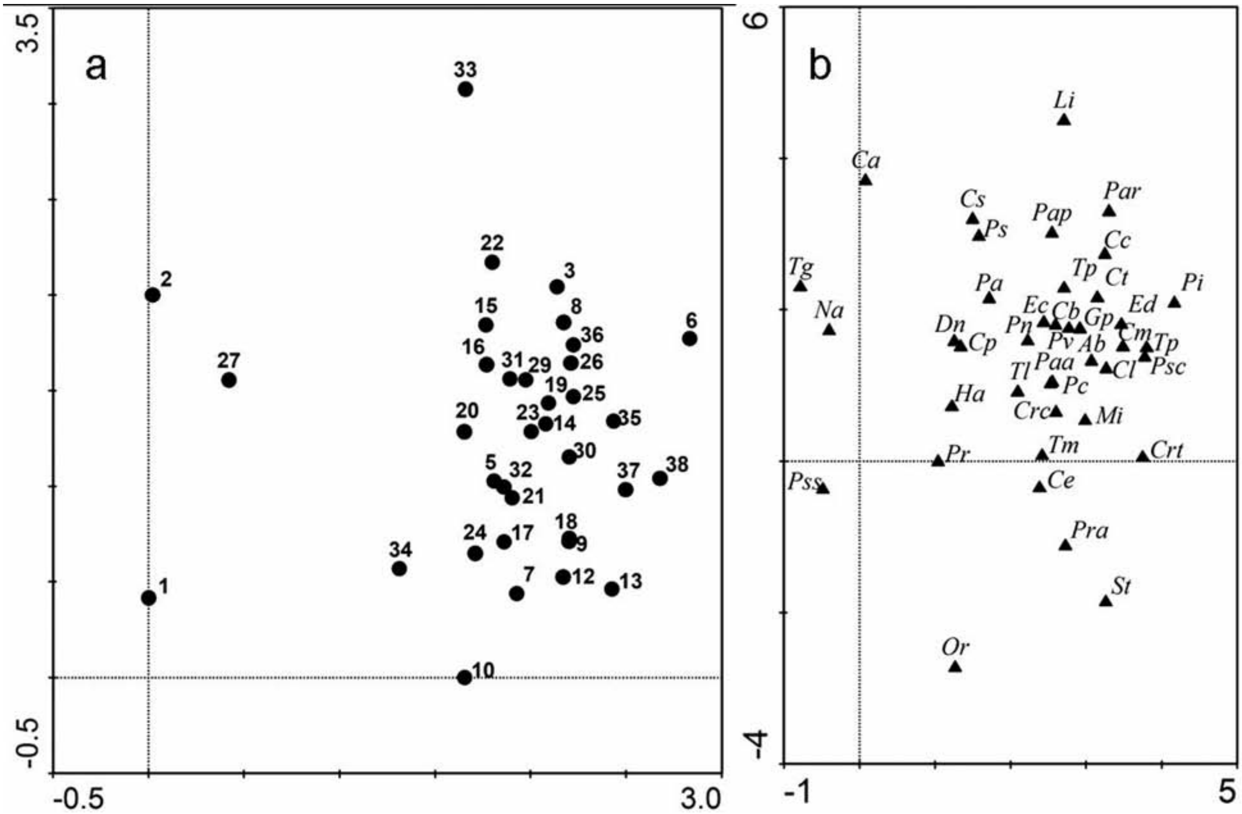

Fig. 4. Results of a DCA ordination using 35 sites **(a)** and 40 chironomid taxa **(b)**. The taxa codes are: Ab, *Ablabesmyia*; Ca, *Chironomus anthracinus*-type; Cb, *Cricotopus bicinctus*-type; Cc, *Corynoneura carriana*-type; Ce, *Corynoneura edwardsi*-type; Cl, *Cladopelma lateralis*-type; Cm, *Cladotanytarsus mancus*-type; Cp, *Chironomus plumosus*-type; Crc, *Cryptochironomus*; Crt, *Cryptotendipes*; Cs, *Cricotopus sylvestris*-type; Ct, *Cricotopus trifasciatus*-type; Dn, *Dicrotendipes nervosus*-type; Ec, *Eukiefferiella claripennis*-type; Ed, *Einfeldia dissidens*-type; Gp, *Glyptotendipes pallens*-type; Ha, *Harnischia*; Li, *Limnophyes*; Mi, *Microchironomus*; Na, *Natarsia*; Or, *Orthocladius*; Pa, *Paratanytarsus*; Paa, *Paratanytarsus austriacus*-type; Pap, *Paratanytarsus penicillatus*-type; Par, *Paratrichocladius rufiventris*-type; Pc, *Polypedilum convictum*-type; Pi, *Polypedilum nubifer*-type; Pn, *Polypedilum nubeculosum*-type; Pr, *Procladius*; Pra, *Propsilocerus akamusi*-type; Ps, *Polypedilum sordens*-type; Psc, *Psectrocladius calcaratus*-type; Pss, *Psectrocladius sordidellus*-type; Pv, *Parachironomus varus*-type; St, *Stempellinella*; Tg, *Tanytarsus gracilentus*-type; Tl, *Tanytarsus lugens*-type; Tm, *Tanytarsus mendax*-type; Tp, *Tanypus*; Tp1, *Tanytarsus pallidicornis*-type.

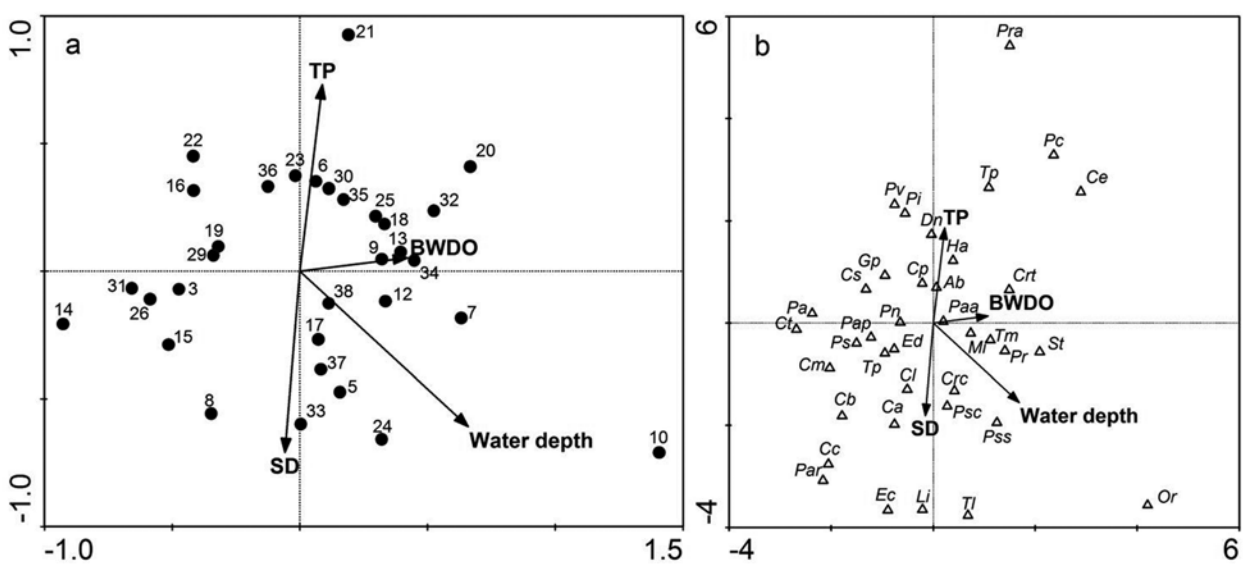

Fig. 5. A CCA ordination, showing sample **(a)**, chironomid taxa **(b)** scores and significant environment variables for the 32 lake dataset, once the 3 outliers had been removed. The codes are the same as in Fig 4.

Discussion

At least five environmental variables show a significant relationship with chironomid distribution, notably temperature, water depth, transparency, TP and bottom water dissolved oxygen (BWDO). The chironomid community relationship with summer air temperature loses its significance once three 'outlying' lakes have been removed; these lakes were at the lower end of the temperature gradient and exerted a considerable influence in the dataset. To fully understand the role of temperature on chironomid communities in Yunnan lakes should be sampled to include sites with mean July temperatures between 10–17 °C, and colder lakes could also be added to the data set. Nonetheless, from the initial statistical analyses undertaken on the 35 lake dataset, and the fact that some taxa, such as *Tanytarsus gracilentus*-type and *Psectrocladius sordidellus*-type are cold stenotherms in this region, indicates the clear potential of developing a temperature based inference model in SW China.

Once the outliers had been removed from the data, it was clear that the predominant driver of chironomid distribution within the lakes was the influence of water depth, transparency, TP and bottom dissolved oxygen. Water depth has a strong influence on the distribution of chironomid larvae with many taxa showing depth preferences (e.g. Brundin 1949, Schmäh 1993, Heiri 2004). It is common to find water depth as a significant environmental variable in other chironomid training sets (e.g. Larocque et al. 2001, Barley et al. 2006) and models have been developed for the reconstruction of lake water depth using chironomids (Korhola et al. 2000, Kurek & Cwynar 2009, Luoto 2009). Typically, in modern studies and in studies of subfossil assemblages multivariate analyses align chironomid taxa along gradients where lake depth and temperature are negatively correlated to nutrients or lake trophic state (Brodersen & Quinlan 2006). Deep lakes will usually display an oligotrophic nature compared with shallow lakes over the same nutrient level (Jeppesen et al. 1997) as water depth is closely related to food availability and oxygen conditions, which in turn determine the chironomid communities in the profundal zone of regularly stratified lakes (Lindegaard 1995). In the Yunnan dataset lake depth and bottom water oxygen are positively related when analysed by CCA (Fig. 5), indicating that water depth is also a major control on anoxia in this region. Other key factors that can control anoxia are lake productivity, lake morphometry and stratification, temperature and length of ice cover, although the latter is unlikely to be influential in Yunnan. In addition to depth, the most likely factor controlling anoxia in Yunnan, given the large recent anthropogenic impact on many of these sites, is lake productivity. The impact of extensive deforestation, intensive agriculture, soil erosion, urbanization, and industrialization in the catchments of many Yunnan Plateau lakes has led to a marked increase in the input of sediment and nutrients into these lakes. The result in many cases has been a higher amount of decaying organic material accumulated at the lake bottom causing oxygen depletion and anoxia in the hypolimnion. While the dataset presented here suggests that the chironomid fauna within these Yunnan lakes are strongly influenced by contemporary hypolimnetic anoxia, it is orthogonal to nutrients (TP) in the CCA analyses, suggesting that these relationships may be independent in this dataset. Reasons behind this may be that, for example, many of the sites may be naturally anoxic, through natural morphometric and/or temperature controls. It could be that recent anthropogenic activities have exacerbated the degree of anoxia, but without palaeolimnological data this is impossible to discern and there are no data as yet to confirm whether this relationship has been stable over time. Other models have been developed to reconstruct changes in hypolimnetic oxygen conditions (Quinlan et al. 1998, Little & Smol 2001, Quinlan & Smol 2001), although using these models for reconstructing past oxygen conditions can be problematic due to the integration of littoral and profundal taxa within profundal core sediments, potentially biasing the reconstruction (Brodersen et al. 2004).

Some of the Yunnan lakes are among the most disturbed ecosystems in the world. Several large lakes, such as Xinyunhu (181 $\mu g\ L^{-1}$ TP) and Dianchi (138 $\mu g\ L^{-1}$ TP) have serious eutrophication problems and major algal blooms in summer (Guo et al. 2009). A strong relationship between chironomid distribution and TP was found in this dataset, which is common when such large environmental gradients are sampled (Brooks et al. 2001, Langdon et al. 2006, Brodersen & Quinlan 2006). According to the OECD trophic classification system (Ryding & Rast 1989), the majority of sites (23) were classed as oligotrophic or mesotrophic (TP $< 35\ \mu g\ L^{-1}$), whereas 8 sites were classed as eutrophic (TP: 35–100 $\mu g\ L^{-1}$), and 4 sites as hypereutrophic ($> 100\ \mu g\ L^{-1}$). TP in Qiantunshuiku is an outlier from the dataset (see Appendix 1) and this high value maybe be due to the temporary sewage input from a chemical fertiliser factory nearby the lake. The chironomid fauna of lakes with high TP concentration were dominated by similar taxa, such as *Chironomus plumosus*-type and *Tanypus*. These species are commonly used as an indicator of eutrophic/anoxic conditions (Zhang et al. 2006, Brooks et al. 2007) and can be dominant in lakes on the heavily impacted middle-lower reaches of the Yangtze River (Zhang et al. 2010). In the CCA analysis, TP showed an extremely negative correlation with transparency. It is likely that the increased input of sediment and nutrient matters resulting from the extensive anthropogenic activities reduced the SD in lakes while increasing heavily the nutrient levels.

One final point of interest is the range of diversity (Shannon-Wiener index) within this dataset, and specifically the high number of lakes that show low diversity. No lake has a diversity > 2.5 and the average diversity for the dataset is 1.64. There are no clear relationships between diversity and environmental factors, other than relatively normal distributions, in other words the lakes with the lowest diversity are not the coolest, or have the lowest/highest nutrient loading. When compared with other regions in the world, the chironomid diversity of these lakes appears anomalously low. For example, two chironomid surface sample calibration datasets from UK shallow lakes, covering a nutrient range ~5 – > 1000 μg L^{-1} TP have average diversity values (Shannon-Wiener index) 2.6 and 2.3 for a 57 lake and 39 lake training set respectively (original data in Langdon et al. 2006, 2010). Furthermore, lakes from Iceland, which are cooler and more oligotrophic, and situated on an island in the middle of the North Atlantic ocean, have a mean diversity of 2.06 (original data in Langdon et al. 2008), still markedly greater than the Yunnan dataset. Indeed chironomid colonization of Icelandic lakes, being a relatively remote island, is likely to be harder than in Yunnan, and hence there must be other reasons as to why the Yunnan lakes have such relatively low diversity. This may be linked to the human impacts noted above, and it may be that diversity was greater in the past, although evidence from one lake, ShuDu, suggests that chironomid diversity at this site has always been relatively low (Jones et al., unpublished data). Further comparisons with other regions in China are needed to evaluate whether this finding is regional to Yunnan, or a wider issue within other parts of China and indeed SE Asia.

Conclusions

Few chironomid data sets currently exist from China, yet this country possesses some of the most heavily impacted lakes in the world. No chironomid datasets have previously been developed from the Yunnan region and the taxonomic make up of assemblages in this region is quite different to other regions. Furthermore the lakes in this region have less taxa and lower diversity than other previously studied locations on a global context. The reasons for this are currently unclear, but one hypothesis is that they could be linked to the high human impact in the region. Detailed palaeolimnological studies will be needed to test this theory. Despite the heavy human footprint on these lakes, analyses indicate that when the temperature gradient is of sufficient length clear potential exists for developing a temperature inference model for the region. Over shorter temperature gradients, the chironomids are most influenced by lake depth and bottom water dissolved oxygen. Further development of these models, by increasing the size of the dataset and length of key environmental gradients, as well as testing the models against recent changes, will illustrate the potential of chironomids for reconstructing past environmental change in this region.

Acknowledgments

We are grateful to Dr. Chunhai Li, Dr. Xuhui Dong for their help on fieldwork, to Prof. Yunlin Zhang for providing the physicochemical parameters of sampled lakes. This study was supported by the National Basic Research Program of China (Grant No. 2010CB833404), NIGLAS (2011KXJ002) and the National Natural Science Foundation of China (Grant No. 40772204,41072267).

References

Barley, E. M., Walker, I. R., Kurek, J., Cwynar, L. C., Mathewes, R. W., Gajewski, K. & Finney, B. P., 2006: A northwest North American training set: distribution of freshwater midges in relation to air temperature and lake depth. – J. Paleolimnol. **36**: 295–314.

Brodersen, K. P., Pedersen, O., Lindegaard, C. & Hamburger, K., 2004: Chironomids (Diptera) and oxy-regulatory capacity: An experimental approach to paleolimnological interpretation. – Limnol. Oceanogr. **49**: 1549–1559.

Brodersen, K. P. & Quinlan, R., 2006: Midges as palaeoindicators of lake productivity, eutrophication and hypolimnetic oxygen. – Quat. Sci. Rev. **25**: 1995–2012.

Brooks, S. J., 2003: Chironomid analysis to interpret and quantify Holocene climate change. – In: Mackay, A., Battarbee, R. W., Birks, H. J. B. & Oldfield, F. (eds): Global change in the Holocene. – Arnold, London, pp. 328–341.

Brooks, S. J., 2006: Fossil midges (Diptera: Chironomidae) as palaeoclimatic indicators for the Eurasian region. – Quat. Sci. Rev. **25**:1894–1910.

Brooks, S. J., Bennion, H. & Birks, H. J. B., 2001: Tracing lake trophic history with a chironomid-total phoshorus inference model. – Freshwat. Biol. **46**: 513–533.

Brooks, S. J., Langdon, P. G. & Heiri, O., 2007: The identification and use of Palaearctic Chironomidae larvae in palaeoecology. QRA Technical Guide No. 10. – Quaternary Research Association, London, 276 pp.

Brundin, L., 1949: Chironomiden und andere Bodentiere der südschwedischen Urgebirgseen. Ein Beitrag zur Kenntnis der bodenfaunistischen Charakterzüge schwedischer oligotropher Seen. – Report of the Institute of Freshwater Research, Drottningholm **30**: 1–914.

Cranston, P. S., 1995: Introduction to the chironomidae. – In: Armitage, P., Cranston, P. S. & Pinder, C. V. (eds): The chironomidae: the biology and ecology of nonbiting midges. – Chapman and Hall, New York, pp. 1–7.

Dearing, J. A., Jones, R. T., Shen, J., Yang, X., Boyle, J. F., Foster, G. C., Crook, D. S. & Elvin, M. J. D., 2008: Using multiple archives to understand past and present climate-human-environment interactions: the lake Erhai catchment, Yunnan Province, China. – J. Paleolimnol. **40**: 3–31.

Dieffenbacher-Krall, A. C., Vandergoes, M. J. & Denton, G. H., 2007: An inference model for mean summer air temperatures in the Southern Alps, New Zealand using subfossil chironomids. – Quat. Sci. Rev. **26**: 2487–2504.

Guo, N. C., Zhang, M., Yu, Y., Qian, S. Q., Li, D. M. & Kong, F. X., 2009: Crustacean zooplankton communities in 13 lakes of Yunnan-Guizhou plateau: Relationship between crustacean zooplankton biomass or size structure and trophic indicators after invasion by exotic fish. Ann. Limnol. – Internat. J. Limnol. **45**: 279–288.

Heiri, O., 2004: Within-lake variability of subfossil chironomid assemblages in shallow Norwegian lakes. – J. Paleolimnol. **32**: 67–84.

Hill, M. O., 1973: Diversity and evenness: a unifying notation and its consequences. – Ecology **54**: 427–432.

Hill, M. O. & Gauch, H. G., 1980: Detrended correspondence analysis, an improved ordination technique. – Vegetation **42**: 47–58.

Jeppesen, E., Jensen, J. P., Søndergaard, M., Lauridsen, T., Pedersen, L. J. & Jensen, L., 1997: Top-down control in freshwater lakes: the role of nutrient state, submerged macrophytes and water depth. – Hydrobiologia **342/343**: 151–164.

Jin, X. C., Liu, H. L., Tu, Q. Y., Zhang, Z. S. & Zhu, X., 1990: Eutrophication of lakes in China. – Chinese Research Academy of Environmental Sciences, Beijing. (in Chinese)

Korhola, A., Olander, H. & Blom, T., 2000: Cladoceran and chironomid assemblages as quantitative indicators of water depth in subarctic Fennoscandian lakes. – J. Paleolimnol. **24**: 43–53.

Kurek, J. & Cwynar, L. C., 2009: The potential of site-specific and local chironomid-based inference models for reconstructing past lake levels. – J. Paleolimnol. **42**: 37–50.

Langdon, P. G., Holmes, N. & Caseldine, C. J., 2008: Environmental controls on modern chironomid faunas from NW Iceland and implications for reconstructing climate change. – J. Paleolimnol. **40**: 273–293.

Langdon, P. G., Ruiz, Z., Brodersen, K. P. & Foster, I. D. L., 2006: Assessing lake eutrophication using chironomids: understanding the nature of community response in different lake types. – Freshwat. Biol. **51**: 562–577.

Langdon, P. G., Ruiz, Z., Wynne, S., Sayer, C. D. & Davidson, T. A., 2010: Ecological influences on larval chironomid communities in shallow lakes: implications for palaeolimnological interpretations. – Freshwat. Biol. **55**: 531–545.

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

Lindegaard, C., 1995: Classification of water-bodies and pollution. – In: Armitage, P. D., Cranston, P. S. & Pinder, L. C. V. (eds): The Chironomidae: Biology and Ecology of Nonbiting Midges. – Chapman and Hall, London, pp. 384–404.

Little, J. L. & Smol, J. P., 2001: A chironomid-based model for inferring late-summer hypolimnetic oxygen in southeastern Ontario lakes. – J. Paleolimnol. **26**: 259–270.

Luoto, T. P., 2009: A Finnish chironomid- and chaoborid-based inference model for reconstructing past lake levels. – Quat. Sci. Rev. **28**: 1481–1489.

Oliver, D. R. & Roussel, M. E., 1983: The Insects and Arachnids of Canada. Part 11. The Genera of Larval Midges of Canada. Diptera: Chironomidae. – Agric. Can. Publ. **1746**: 263 pp.

Pielou, E. C., 1975: Ecological Diversity. – Wiley-Inters, New York.

Pinder, L. C. V., 1995: The habitats of chironomid larvae. – In: Armitage, P., Cranston, P. S. & Pinder, L. C. V. (eds): The chironomidae: the biology and ecology of non-biting midges. – Chapman and Hall, London, pp. 107–135.

Porinchu, D. F., Rolland, N. & Moser, K. A., 2009: Development of a chironomid-based air temperature inference model for the Central Canadian Arctic. – J. Paleolimnol. **41**: 349–368.

Quinlan, R. & Smol, J. P., 2001: Chironomid-based inference models for estimating end-of-summer hypolimnetic oxygen from south-central Ontario shield lakes. – Freshwat. Biol. **46**: 1529–1551.

Quinlan, R., Smol, J. P. & Hall, R. I. 1998: Quantitative inferences on past hypolimnetic anoxia in south-central Ontario lakes using fossil midges (Diptera: Chironomidae). – Can. J. Fish. Aquat. Sci. **55**: 587–596.

Rieradevall, M. & Brooks, S. J., 2001: An identification guide to subfossil Tanypodinae larvae (Insecta: Diptera: Chironomidae) based on cephalic setation. – J. Paleolimnol. **25**: 81–99.

Ryding, S. O. & Rast, W., 1989: The Control of Eutrophication of Lakes and Reservoirs. – The United Nations Educational Scientific and Cultural Organization, Paris, pp. 37–43.

Schmäh, A., 1993: Variation among fossil chironomid assemblages in surficial sediments of Bodensee-Untersee (SW Germany): implications for paleolimnological interpretation. – J. Paleolimnol. **9**: 99–108.

Shannon, C. E. & Wiener, W. J., 1949: The Mathematical Theory of Communication. – University of Illinois Press, Urbana, p. 117.

ter Braak, C. J. F., 1987: The analysis of vegetation–environment relationships by canonical correspondence analysis. – Vegetatio **69**: 69–77.

ter Braak, C. J. F. & Prentice, I. C., 1988: A theory of gradient analysis. – Advanc. Ecol. Res. **18**: 271–317.

ter Braak, C. J. F. & Šmilauer, P., 2002: CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination (Version 4.5). – Microcomputer Power, Ithaca, NY.

Walker, I. R. & Cwynar, L. C., 2006: Midges and palaeotemperature reconstruction – the North American experience. – Quat. Sci. Rev.**25**: 1911–1925.

Walker, I. R. & Mathewes, R. W., 1989: Chironomidae (Diptera) remains in surficial lake sediments from the Canadian Cordillera: analysis of the fauna across an altitudinal gradient. – J. Paleolimnol. **2**: 61–80.

Wang, S. M. & Dou, H. S., 1998: Lakes in China. – Sciences Press, Beijing. (in Chinese)

Whitehouse, N., Langdon, P. G., Bustin, R. & Galsworthy, S., 2008: Sub-fossil insects and ecosystem dynamics in wetlands; implications for biodiversity and conservation. – Biodiv. Conserv. **17**: 2055–2078.

Wiederholm, T., 1983: Chironomidae of the Holarctic Region. Keys and diagnoses. Part I. Larvae. – Entomol. Scand. Suppl., 457 pp.

Zhang, E. L., Bedford, A., Richard, J., Shen, J., Wang, S. M. & Tang, H. Q., 2006: A subfossil chironomid-total phosphorus inference model from the middle and lower reaches of Yangtze River lakes. – Chin. Sci. Bull. **51** (17): 2125–2132.

Zhang, E., Liu, E., Jones, R. T., Langdon, P. G., Yang, X. & Shen, J., 2010: A 150-year record of recent changes in human activity and eutrophication of Lake Wushan from the middle reach of the Yangze River, China. – J. Limnol. **69**: 235–241.

Zhang, Y. L., Zhang, E. L., Liu, M. L., Wang, L. X. & Qin, B. Q., 2007: Variation of chromophoric dissolved organic matter and possible attenuation depth of ultraviolet radiation in Yunnan Plateau lakes. – Limnology **8**: 311–319.

Submitted: 1 January 2011; accepted: 27 May 2011.

Appendix 1. Main physicochemical parameters of sampled lakes on Yunnan Plateau (Zhang et al. 2007).

No	Lake name	Altitude (m a.s.l)	Water depth of sampling site (m)	SD (m)	July T (°C)	Conductivity ms cm^{-2}	TN (mg L^{-1})	TP (mg L^{-1})	pH	Chla (μg L^{-1})	Bottom Do (mg L^{-1})
1	Bigutianchi	3809	1.5	1.5	10.0	0.281	0.76	0.0055	8.17	1.64	2.79
2	Bitahai	3568	8.5	1.5	10.5	0.252	0.46	0.0188	8.74	1.89	2.72
3	Caohai	2208	2.3	1.2	19.5	0.234	0.30	0.0087	8.37	1.49	3.52
4	Chaheihai	1484	2	0.2	21.3	0.224	0.67	0.0190	8.66	7.08	5.76
5	Changhu	1870	12	2.66	19.8	0.229	0.35	0.0018	8.69	2.38	6.68
6	Changqiaohai	1291	2.1	0.5	22.9	0.219	1.98	0.0348	9.41	11.10	5.87
7	Chenghai	1550	18	1.6	22.7	0.225	0.61	0.0213	9.23	0.72	3.87
8	Cibihu	2033	17	6.14	20.0	0.226	0.26	0.0109	8.11	4.79	2.88
9	Erhai	1954	8.9	1.3	20.0	0.228	0.59	0.0453	8.6	6.65	3.50
10	Fuxianhu	1720	110	4.1	20.2	0.245	0.26	0.0039	8.69	4.36	8.16
11	Haishaoshuiku	1632	13.5	0.6	21.6	0.211	0.89	0.0322	8.92	10.84	2.39
12	Haixihai	2128	11	1.24	19.5	0.226	0.21	0.0268	8.54	0.77	2.68
13	Haizibian	1508	6	0.9	21.1	0.221	0.83	0.0162	8.65	3.27	6.57
14	Hunshuihai	2006	2.3	2.3	19.5	0.232	1.24	0.0102	8.33	5.91	2.33
15	Jianhu	2201	5.2	2.3	19.0	0.235	0.56	0.0107	8.91	0.01	2.32
16	Lashihai	2436	1.2	0.65	17.9	0.234	0.67	0.0438	8.81	2.20	3.36
17	Lijiawa	2025	10.5	3	19.0	0.237	0.30	0.0085	8.54	2.16	6.24
18	Matangshuiku	2113	4.2	0.6	18.2	0.242	1.76	0.0209	8.32	1.63	6.18
19	Pingdihai	2147	2	1.1	18.0	0.234	0.91	0.0127	8.66	3.24	5.45
20	Qiluhu	1801	5.8	0.5	19.1	0.248	3.35	0.0820	8.82	84.20	6.41
21	Qiantunshuiku	2032	2	0.4	18.7	0.238	2.50	1.2483	8.17	1.70	3.68
22	Qinghai	1980	1	1	19.7	0.226	1.85	0.0619	9.73	2.31	5.71
23	Qingjianmei	1954	2	0.3	22.0	0.227	2.63	0.0613	8.55	9.92	3.22
24	Qingshuihai	2182	21	2.5	18.4	0.238	0.43	0.0017	8.82	3.75	3.66
25	Sanjiaohai	1316	4.7	0.5	22.6	0.214	1.54	0.0456	9.10	6.41	3.50
26	Shipohai	1957	2.45	0.6	19.7	0.232	0.69	0.0199	9.46	1.50	0.99
27	Shuduhu	3611	8	1.1	10.2	0.165	0.49	0.0253	8.74	2.35	3.05
28	Tinghu	1516	3	0.2	20.8	0.2	3.86	0.3295	8.71	133.22	3.31
29	Wenbihai	2374	3	1.45	18.1	0.233	0.55	0.0235	9.06	2.32	3.79
30	Wyulanghai	1876	3.6	0.6	19.6	0.231	2.69	0.0851	8.34	9.42	3.15
31	Xihu	1979	2.5	0.76	20.0	0.224	1.00	0.0326	8.29	3.96	0.88
32	Xingyunhu	1732	10	0.3	19.6	0.238	3.10	0.2715	8.99	105.62	1.00
33	Yangzonghai	1775	20	2.4	20.1	0.23	0.49	0.0111	8.74	1.10	1.12
34	Yangpaishuiku	1930	8.9	0.4	19.4	0.22	0.92	0.0568	8.85	3.10	1.59
35	Yiliangcaohai	1853	4.8	0.6	19.8	0.228	1.38	0.1128	8.55	14.18	2.28
36	Yilonghu	1405	3	0.5	21.9	0.266	4.59	0.1499	7.31	14.18	1.60
37	Yuanhu	1902	12.5	2.2	19.6	0.227	0.45	0.0087	8.33	1.63	2.90
38	Yuehu	1893	3.4	0.6	19.7	0.232	0.33	0.0021	8.37	2.33	6.78