



Do changes in water depth and water level influence the diatom diversity of Yunlong Lake, in Yunnan Province, Southwest China?

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Abstract Exploring whether diatom diversity in a lake sediment core is representative of that of the entire lake is important for determining the response of lake diatom diversity to global climatic warming. In this study, Yunlong Lake, an alpine lake located in Yunnan Province, Southwest China, was investigated to explore this question over both space and time. Spatially, we investigated diatom diversity patterns in 62 surface sediment samples from different locations and depth zones of Yunlong lake and found essentially

constant diatom diversity across the entire lake basin. Temporally, we studied a well-dated sediment core from the lake center to explore whether long-term water-level changes influenced diatom diversity over the last ~ 100 years. Changes in the annual average sediment accumulation rates indicate that the water level of Yunlong Lake increased substantially after the construction of a dam. However, there is no obvious relationship between diatom diversity and water-level changes, which suggests at this site long-term water-level changes did not influence diatom diversity. Comparative analysis of the results for Yunlong Lake with those for other lakes indicates that for relatively strongly mixed lakes with a simple morphology and

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uniform shoreline microhabitat, such as Yunlong Lake, differences in water depth and changes in water level may not influence diatom diversity. In such cases, the diatom diversity from a sediment core is likely to be representative of that of the entire lake during specific time intervals. Therefore, such lakes may be optimal for studies of changes in past diatom diversity using sediment cores.

Keywords Yunlong lake · Water depth · Water-level changes · Twentieth century · Diatom diversity

Introduction

The maintenance of biodiversity is important in promoting the stability of ecosystem functioning (Worm et al. 2006). In recent years, a trend of global climatic warming has become increasingly obvious and it is substantially impacting the biodiversity of different ecosystems (Pounds et al. 1999; Parmesan and Yohe 2003). However, a large number of studies have found that the response of biodiversity to climatic warming is different for both species and ecosystems (Root et al. 2003; Thomas et al. 2004). For example, climatic warming has caused extensive bleaching and a sharp decline in the biodiversity of coral reefs in marine ecosystems, which has led to a steep decline in the biodiversity of fish that inhabit coral reefs (Jones et al. 2004). In contrast, in the cool northern uplands of England, climatic warming is considered to be the main cause of a major increase in butterfly biodiversity (Menéndez et al. 2006). At present, the response of biodiversity in different ecosystems to climatic warming has become a major scientific issue (Lake et al. 2000; Wagner and Adrian 2011), which is of great significance for predicting the responses of different ecosystems to warming and hence for the determination of appropriate management strategies against the background of future warming.

Lakes support a large amount of global freshwater biodiversity (Hayford et al. 2015), acting as an essential component of global ecosystems. Moreover, the diversity of the aquatic biota is an important

indicator of a healthy lake ecosystem (Xu et al. 2001). Diatoms are important primary producers in lake ecosystems. They occupy the base of the trophic pyramid in lakes, and changes in diatom composition can cascade through the lake food web (Winder and Schindler 2004; Adrian et al. 2006), thus directly affecting lake productivity (Mann 1999; Chen et al. 2011, 2015) and exerting an important influence on the structural and functional stability of lake ecosystems. In addition, diatom species are often diverse and their siliceous valves are generally well preserved in lacustrine sediments (Smol and Cumming 2000; Chen et al. 2008; Wang et al. 2008, 2012a, b). These characteristics make diatoms very useful for reconstructing changes in aquatic biodiversity on various timescales (Gregory-Eaves and Beisner 2011).

Numerous recent studies have confirmed that diatom assemblages in many lakes from different regions of the world have changed substantially in response to global climatic warming (Smol et al. 2005; Rühland et al. 2005, 2015; Yan et al. 2018). For example, warming has increased the intensity of lake stratification, resulting in the dominance of a series of small cyclotelloid taxa and elongate fragilarioid taxa which have an advantage in the competition for nutrients and light under conditions of strong lake stratification (Litchman et al. 2006; Winder et al. 2009). Thus, they have gradually replaced the heavy planktonic species, such as the *Aulacoseira* spp., that previously dominated diatom assemblages (Rühland et al. 2015). However, it remains unclear whether these changes in diatom assemblages also lead to changes in diatom diversity and therefore it is difficult to reach a consensus opinion. Thus more studies are needed to resolve the issue (Gregory-Eaves and Beisner 2011).

With regard to understanding of responses of lake diatom assemblages and diatom diversity to global climatic warming, most current studies are mainly based on diatom analysis of sediment cores (Karabanov et al. 2004; Smol et al. 2005; Hayashi et al. 2011; Yan et al. 2018). However, whether the results from a single sediment core are representative of the diatom diversity of an entire lake at a specific time interval is a fundamental question. This issue must be addressed before exploring the response of diatom diversity to global climatic warming, for two reasons. First, changes in diatom diversity in a sediment core may be misleading and do not reflect changes in diatom diversity throughout the lake. As is well known,

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different microhabitats exist in different depth zones of a lake (Stone and Fritz 2004). For example, the shallower water zones, where there is sufficient light penetration, consist of rocky, sandy, and clayey substrates and are also colonized by various types of aquatic vegetation that provide habitats for benthic and epiphytic diatom species (Hoagland and Peterson 1990; Kingsbury et al. 2012). However, since lakes are often not entirely translucent, benthic diatoms can only grow within this shallow-water photic zone, while planktonic diatoms can remain suspended in the upper photic layer of the entire lake by free-floating (depending on the mixing mechanism), thus causing them to be distributed within all depth zones. Accordingly, it is generally supposed that diatom diversity in the sediments of the shallower-water zones, with diverse microhabitats and diatom species, is likely to be much higher than that in the deep profundal zone dominated by planktonic diatoms (Hayashi 2011). In this case, changes in diatom diversity of a single sediment core are not representative of the entire lake. Second, changes in the diatom diversity of a sediment core may be caused by changes in water level rather than by climatic warming. In this case, if changes in water level occur, the diverse littoral microhabitats and the corresponding benthic diatom zones will change accordingly, which may lead to changing diatom diversity within a sediment core (Hayashi 2011). However, this may only reflect the migration between different microhabitats caused by changing water level, rather than a change in the diatom diversity of the entire lake. Thus, the response signals of diatom diversity to global climatic warming may be obscured.

Therefore, in order to determine whether diatom diversity in a lake sediment core is representative of the entire lake, two questions need to be addressed. First, it should be determined whether diatom diversity in contemporaneous lake sediments differs with water depth and location. In this case, the results of studies of different types of lakes are inconsistent. For example, studies of several boreal lakes show that diatom diversity in the sediments from different depth zones of lakes are generally different: diatom diversity in the shallow water zones with diverse microhabitats is much higher than that in the deep-water zones (Stevenson and Stoermer 1981; Moos et al. 2005; Cantonati et al. 2009; Laird et al. 2010, 2011). In contrast, in a study of the major diatom diversity patterns of a subtropical mountain lake, Yunlong Lake, in Southwest China, Zou et al.

(2015) found an almost unchanging pattern of surface diatom diversity with changing water depth. They concluded that the diatom diversity of the surface sediments of Yunlong Lake was representative of the diatom diversity of the entire lake, and they attributed this to the relatively simple lake morphology and uniform shoreline microhabitats. If their conclusions are correct, it implies that diatom diversity in a single sediment core may be representative of the diatom diversity of the entire lake. However, case studies of several northern temperate to boreal lakes with a relatively simple shoreline environment, such as Lake Michigan and Lake Tovel (Stevenson and Stoermer 1981; Cantonati et al. 2009), showed that diatom diversity in the sediments from different depth zones was significantly different. These findings imply that the relatively simple lake morphology and uniform shoreline microhabitat of Yunlong Lake may not be the only reason for the similarity in diatom diversity at different water depths, and other reasons need to be considered. Moreover, the conclusions of Zou et al. (2015) are of concern for two reasons: (1) the number of surface samples was relatively small (25 in total) and there were obvious sampling gaps along the water depth gradient; and (2) the diatom counts of 300 valves may not have been sufficient for diatom diversity analysis, which may cause rare taxa to be omitted. Therefore, more studies are needed to substantiate this changing pattern of sedimentary diatom diversity.

Secondly, it is necessary to clarify whether long-term changes in water level influence sedimentary diatom diversity. To date, there is still no consensus regarding this issue because of the lack of relevant studies. Although water-level changes can greatly influence the composition of lake diatom assemblages, such as the ratio of planktonic to benthic diatom species (Brugam et al. 1998; Stone and Fritz 2004; Heinsalu et al. 2008; Laird and Cumming 2008; Wolin and Stone 2010; Leira et al. 2015), it remains unclear whether they affect diatom diversity.

In the present study, we tested and expanded the results of Zou et al. (2015) by analyzing 62 surface samples from different depth zones of Yunlong Lake. In addition, we reanalyzed the diatom diversity using a rarefied calculation to a base sum of 600 valves and assessed the chances of the occurrence of rare species. We used a variety of statistical methods to analyze the differences in diatom diversity in different depth zones, including diatom β -diversity. In order to

identify the role of mixing in influencing the changes in diatom diversity, we obtained a two-year, two-hour interval, record of water temperature monitoring data for Yunlong Lake. In addition, we used a 60-year meteorological monitoring dataset from the nearby Dali Station to analyze the relationship between diatom diversity and climate changes.

The principal questions to be addressed in our study are as follows: (1) Does surface diatom diversity differ in different locations and in different depth zones of a lake? (2) Is diatom diversity affected by long-term water-level changes? By exploring these two questions, we aimed to assess the representativeness of diatom diversity in lake sediments, and to lay a foundation for future studies of the effect of climatic warming on lake diatom diversity.

Study site

Yunlong Lake (25°52′12.89″N, 99°16′49.75″E), also called Shuchang Sea, is located in the Tianchi National Nature Reserve in Yunnan Province, Southwest China (Fig. 1). The climate of the region, influenced mainly by the subtropical monsoon, is cool and moist with typical dry and wet seasons. The altitude of the lake is 2551 m.a.s.l. and the drainage area is ~ 11.25 km². The average water depth is ~ 8.5 m (measured by water volume) and the maximum depth is ~ 14.1 m. It is a typical tectonic lake formed mainly by faulting. The substrate of the lake is mainly silty, apart from a

steep gravel bank in the northwestern part. Different macrophyte species are distributed in the gently sloping littoral zone of the northeastern, southern and southwestern areas (Fig. 1); they include floating *Nuphar pumila* (Timm) DC. and submerged *Myriophyllum spicatum* Linnaeus. A two-year water temperature monitoring program at four different water depths (1, 5, 7 and 12.8 m) from August 2013 to August 2015 revealed that complete mixing occurs in the winter half-year (October to late February) (ESM 1). The lake is thermally stratified in the summer half-year (March to October) and the depth of the thermocline is greater than 7 m.

Yunlong Lake was originally a natural mountain lake. Because it is located in a remote mountainous area, the human population of the catchment is low. No large-scale deforestation or farming activities are documented and therefore the impact of human activities on the lake is generally minor. Moreover, the lake is still oligo-mesotrophic and has not yet been subject to eutrophication. The modern physical and chemical parameters of the lake are summarized in Zou et al. (2018). The lake has no natural inflows but a natural outflow in the east existed prior to the 1950s (Fig. 1), which flowed into a branch of the Lantsang River. However, in order to alleviate the local scarcity of water resources, from the 1950s onwards the lake was gradually transformed into a reservoir. A dam with a total height of ~ 12.74 m was constructed between 1953 and 1985 on the eastern outflow in order

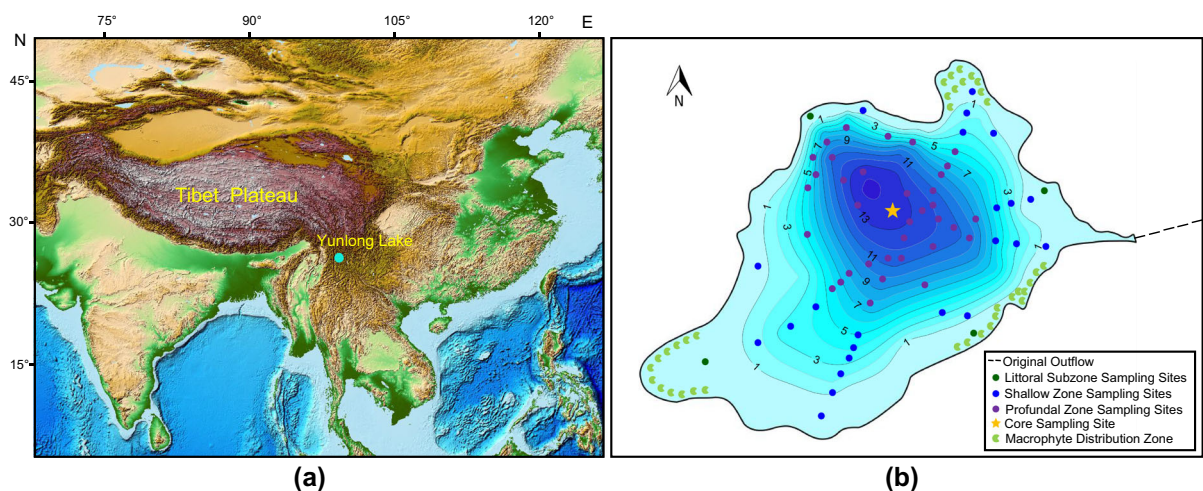


Fig. 1 **a** Location of Yunlong Lake in China; **b** Bathymetry map of Yunlong Lake with the locations of the 62 surface sediment samples and sediment core YL2013-A. The distribution of macrophytes and the location of the original outflow are also shown

to store water, which was mainly used as a local domestic water source and for field irrigation. Thus, it was transformed into a small reservoir with a total water capacity of $7.9 \times 10^6 \text{ m}^3$. In October 2003, in response to increasing demand for water resources, an outside water input project was initiated and was completed in July 2009. Subsequently, it was enlarged to form a medium-sized reservoir with a total water capacity of $1.09 \times 10^7 \text{ m}^3$.

Materials and methods

Sampling design

In July 2013, we obtained 25 surface sediment samples from Yunlong Lake along north–south and east–west transects using a UWITEC gravity corer (Zou et al. 2015). In August 2015, we increased the sampling density by collecting an additional 37 surface samples using the same method. The topmost 0.5 cm of each sediment core was carefully extruded and used for diatom diversity analysis. For each surface sediment sample collected, the corresponding water depth was measured using an echo sounder and the site location was recorded using GPS. A total of 62 surface sediment samples were obtained during these two periods of field work, covering almost the entire depth range of the lake (Fig. 1). In addition, we retrieved a sediment core (YL2013-A), with a total length of 1.27 m, from the deepest area of the lake ($\sim 13.3 \text{ m}$, Fig. 1) using the UWITEC gravity corer. The upper 15 cm of the core was extruded into 0.5-cm intervals and the remainder of the core into 1-cm intervals.

Laboratory methods and chronology

The chronology of the uppermost 39 cm (including 55 freeze-dried samples) of core YL2013-A was determined using the ^{210}Pb CRS (Constant Rate of Supply) model together with the location of peaks in the distribution of ^{137}Cs (Appleby and Oldfield 1978). The specific radioactivity of ^{137}Cs , ^{214}Pb and $^{210}\text{Pb}_{\text{ex}}$ was measured by gamma spectrometry using a low-background well-type germanium detector (EGPC 100P-15R) at the Institute of Geology and Geophysics, Chinese Academy of Sciences, Beijing.

A total of 62 surface sediment samples and 27 samples of the upper part of the sediment core (interval

sampling) from Yunlong Lake were used for diatom assemblage and diversity analysis, which included the following steps. First, the samples were freeze-dried using an FDU-1200 freezing vacuum dryer and the weights of the dried samples were recorded so that the dry bulk density of the samples could be calculated. Next, the samples were oxidized and cleaned using the method of Battarbee et al. (2001). This involved heating $\sim 0.05 \text{ g}$ of dry sediment with HCl and subsequently with H_2O_2 to remove carbonates and organic material, respectively. The diatom concentration (valves per gram) of each sample was estimated by adding divinyl benzene microspheres to the cleaned suspensions (Battarbee and Kneen 1982). Diatom slides were prepared by mounting with Naphrax (Refractive Index = 1.7) on a hot ($\sim 180^\circ\text{C}$) stove. Diatoms were identified under oil immersion with a phase-contrast light microscope at $\times 1000$ magnification and were identified to species level mainly using taxonomic references of Krammer and Lange-Bertalot (1986–1991). For each sedimentary interval, the diatom data were expressed as percentage relative abundance of the total number of valves counted. The diatom concentrations of the surface sediment samples were logarithmically transformed.

Multiple biodiversity indices were calculated to evaluate diatom α -diversity. They include Taxa-S, Pielou index, Shannon index, Simpson index and Berger-Parker index (Lande 1996; Stevenson et al. 2008). Taxa-S, namely the total number of taxa in each sample, was used to evaluate diatom richness. Prior to calculating species richness, diatom counts were first rarefacted (Birks and Line 1992) to a base sum of 600 valves (the number of diatom valves counted ranged from 601 to 673). The potential errors of Taxa-S were calculated at the 95% confidence level. The Pielou index was selected to provide an index of species evenness and to avoid the loss of community structure information when only evaluating species richness (James and Rathburn 1981). The Shannon index and Simpson index are composite diversity indices, which not only indicate species richness but also reveal the evenness of species distribution; thus they are generally used to indicate the heterogeneity of the biocenosis (Simpson 1949; Lande 1996). The Berger-Parker index was calculated to provide a measure of species dominance.

To quantify the statistical significance of the differences in surface diatom α -diversity among

different depth zones, a one-way analysis of variance (ANOVA) using SPSS 22.0 was conducted on the surface diatom diversity pattern using the rarefied Taxa-S as the representative biodiversity index. The procedure used included the following: first, the normality and homogeneity of the Taxa-S dataset were analyzed using a Kolmogorov–Smirnov test and Levene's test, respectively; second, the significance of differences in diatom diversity between different depth zones was analyzed using one-way ANOVA at the 95% confidence level; and third, multiple comparisons were made using the post-hoc test of the Bonferroni correction.

Diatom β -diversity, or the compositional turnover of diatom assemblages between samples along different depth zones, was evaluated using Detrended Canonical Correspondence Analysis (DCCA) constrained to water depth as the predictor variable. It was estimated in Standard Deviation (SD) units, following the referenced method of Smol et al. (2005) and Birks (2007).

In order to explore the relationship between changes in the diatom diversity of Yunlong Lake and climate change, we collected annual average meteorological monitoring data for the past 60 years from the nearby Dali Station (~ 150 km away). The selected meteorological parameters included the annual average air temperature, the annual precipitation, and the annual average wind speed.

Stratigraphic diagrams were drawn using C2 version 1.5.1. Major diatom stratigraphic zones were defined using constrained incremental sum of squares (CONISS) cluster analysis (with Euclidean distance used for the dissimilarity matrix, Grimm 1987) implemented with TILIA version 2.02. The biodiversity indices were calculated using Past version 1.89, and all of the species counted were included in the analysis. The DCCA was conducted using CANOCO 5.0.

Results

Surface diatom assemblages and diatom diversity

Analysis of the 62 surface sediment samples resulted in the identification of 28 diatom genera and 131 species (ESM 3). The diatom assemblage composition of the surface samples varied with water depth

(Fig. 2). The results of the CONISS analysis and the measured water depth of the 62 surface samples were used to identify three different depth zones, including one subzone: the near-shore littoral subzone, the shallow-water zone and the deep profundal zone. The 62 surface samples were mainly distributed within the shallow-water zone and the deep profundal zone, which accounted for 93.6% of all surface samples. Of the 62 surface samples, 35 samples were located in the profundal zone, with measured depths ranging from 5.5 m to 14.1 m; and 23 surface samples were from the shallow water zone, with measured depths ranging from 0.3 to 5 m. Only 4 samples were located in the near-shore littoral subzone in four different directions of the lake, with a measured water depth of 0.1 m (Fig. 1).

The distribution of diatom assemblages along a depth gradient clearly delineated two main groups based on specific physiological habits: planktonic species and benthic species (including several epiphytic species). There was a distinct ecotonal boundary between the distributions of planktonic and benthic diatom assemblages at the water depth of ~ 5 m which CONISS identified as the difference between the shallow and the profundal zones (Fig. 2). In addition, the near-shore littoral subzone and the shallow water zone also had a threshold at ~ 0.1 m (Fig. 2). The two shallower zones were mainly dominated by benthic diatom species, with some epiphytic species dominant in the littoral subzone, while the relative abundance of the planktonic species increased substantially in the profundal zone (Fig. 2).

The diatom concentrations of different depth zones ranged from 0.95×10^7 valves g^{-1} to 1.06×10^9 valves g^{-1} , increasing insignificantly with water depth (Fig. 2). All five α -diversity indices revealed a similar pattern of relatively constant diatom diversity with increasing water depth. The total number of diatom taxa in the 62 surface samples ranged from 40 to 76 (Fig. 3), and the average number of diatom taxa was 59, with a confidence level of 95%. Potential errors in estimating the numbers of diatom taxa were revealed by rarefaction analysis, ranging from 0.11 to 1.19 (Fig. 4). When the valve counts reached 600, the diatom taxa in all surface samples increased only very slightly. Thus, in this case, it was valid to use a rarefied Taxa-S to indicate diatom richness for a count of 600 valves. The diatom evenness indicated by the Pielou

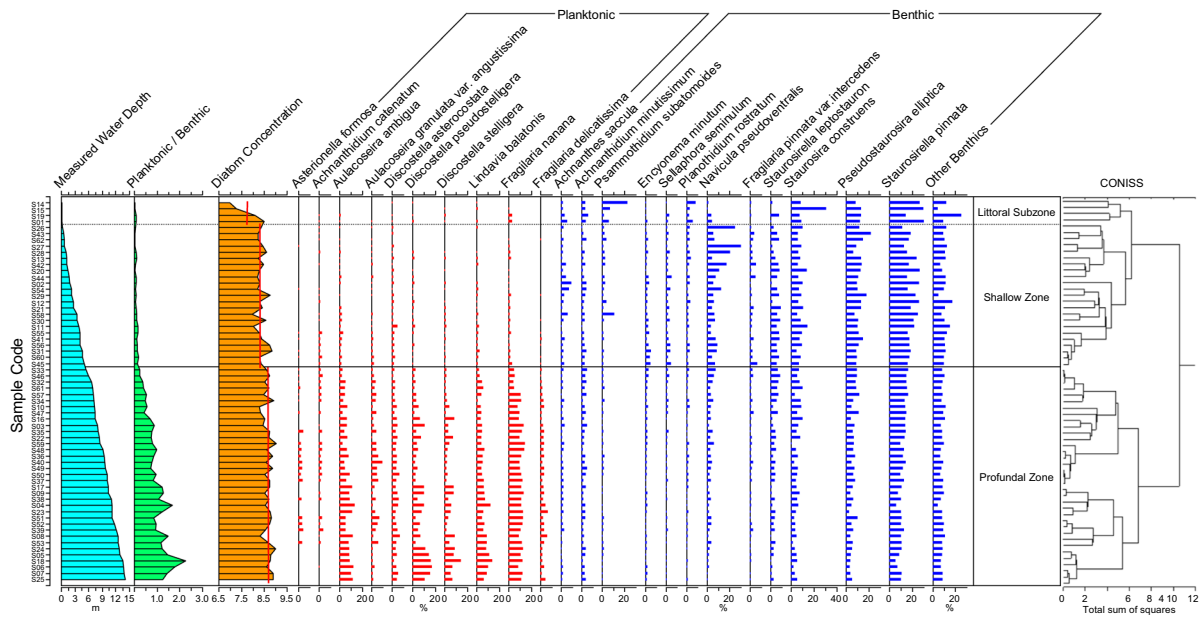


Fig. 2 Changes in diatom assemblages versus water depth for the 62 surface samples from Yunlong Lake. Only planktonic species and benthic species with a total relative abundance > 1% are shown. The samples are arranged in order of increasing water depth, and the diatom concentration data are

logarithmically transformed; the red line shows the average value. The zones are defined using CONISS implemented in TILIA version 2.02 and the measured water depth of the surface samples

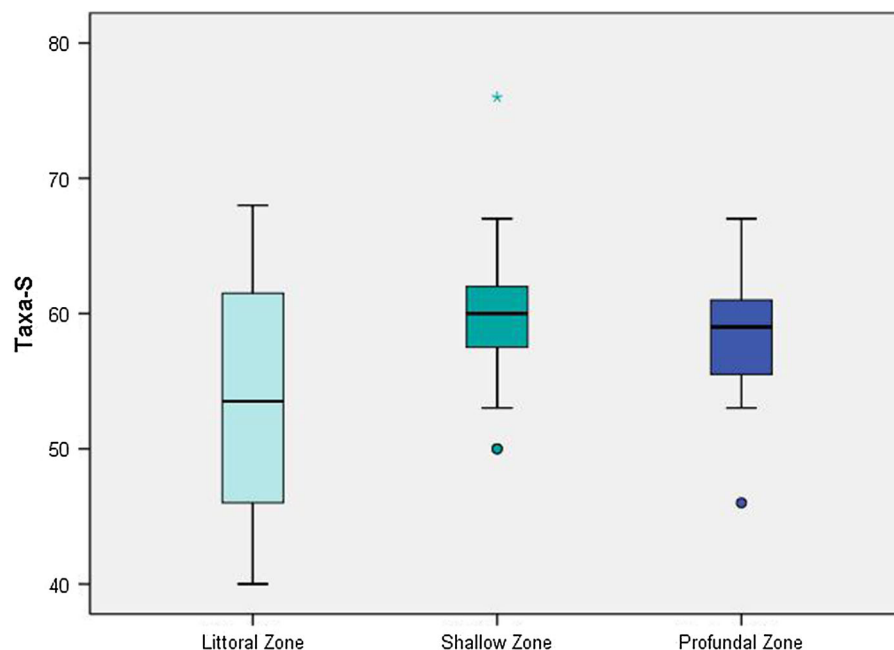


Fig. 3 Statistical distribution of the Taxa-S dataset in three depth zones of Yunlong Lake. The stars and circles represent data points that are highly positively or negatively deviated from the entire dataset and thus were omitted from the statistical analysis

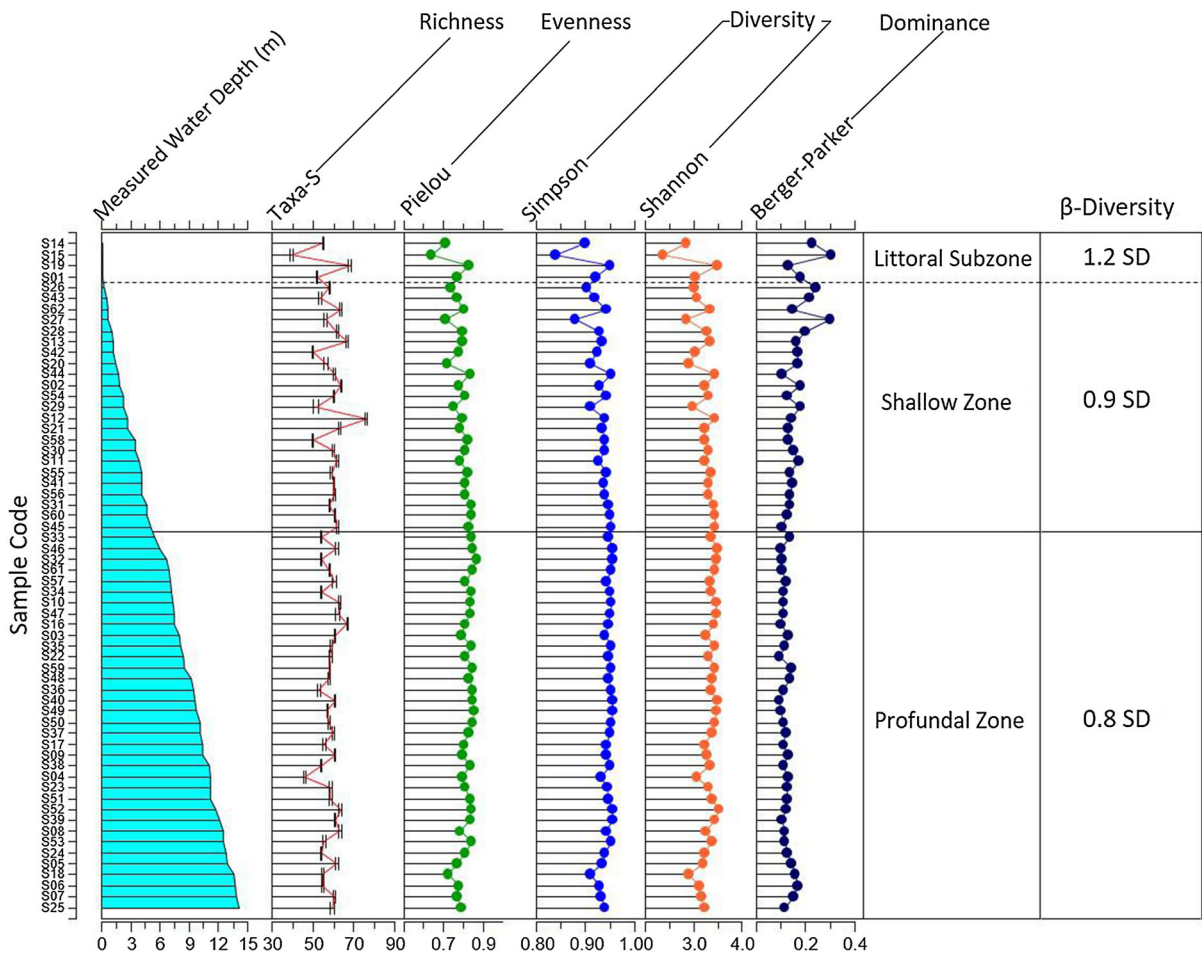


Fig. 4 Relationship between surface diatom diversity and water depth at Yunlong Lake as indicated by multiple α -diversity indices and DCCA. The 62 surface sediment samples are plotted according to increasing water depth. The vertical bars in the plot

of Taxa-S represent the errors of the species using rarefaction analysis implemented in Past version 1.89. Diatom β -diversity is evaluated by DCCA and implemented in CANOCO 5.0

index ranged from 0.64 to 0.87. Two composite diversity indices were calculated: the Simpson index ranged from 0.84 to 0.96, and the Shannon index ranged from 2.36 to 3.51. The species dominance index, the Berger-Parker index, ranged from 0.1 to 0.31 (Fig. 4).

The test results of the normality ($p = 0.20$, $\alpha = 0.05$) and homogeneity ($p = 0.05$, $\alpha = 0.05$) of the Taxa-S dataset facilitated the next step of ANOVA. The results of one-way ANOVA (Table 1, $F = 2.38$, $p = 0.10 > 0.05$) indicated that there were no significant differences in Taxa-S among the three depth zones, providing statistical confirmation that diatom richness was relatively constant at different water depths. This was also demonstrated by pairwise

comparisons among the three depth zones (Table 2, $p > 0.05$ for all three pairwise groups, $\alpha = 0.05$). Although there were no statistically significant differences in diatom richness among the three depth zones based on the results of ANOVA (Tables 1, 2), the amplitude of variation of diatom richness in each depth zone varied substantially (Fig. 3). Both the pairwise ANOVA results (Table 2) and the statistical distribution of the Taxa-S dataset (Fig. 3) indicated that the amplitude of variation of diatom richness within the shallow zone and profundal zone was less than in the littoral subzone.

As was the case for the results of the DCCA, the β -diversity of the diatom community in the littoral subzone was 1.2 SD, while for the shallow and

Table 1 Results of one-way ANOVA results for the Taxa-S dataset for Yunlong Lake, focusing on three different depth zones

Dataset	Sum of squares	df	Mean square	F	p
Between groups	133.02	2	66.51	2.376	0.102
Within groups	1651.319	59	27.988		
Total	1784.339	61			

Table 2 Comparisons of the Taxa-S dataset among three depth zones of Yunlong Lake using the post-hoc test of Bonferroni correction

Group comparison	Mean difference	Standard error	p
1 2	− 6.16304	2.86601	0.107
1 3	− 4.76429	2.79227	0.28
2 3	1.39876	1.42006	0.986

Groups 1–3 represent the Taxa-S dataset for the littoral subzone, the shallow zone and the profundal zone, respectively

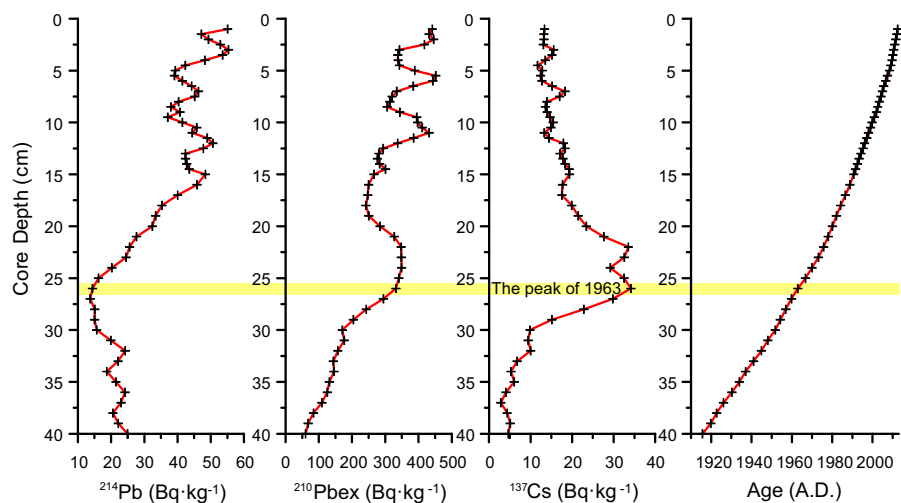
profundal zones, the values were 0.9 SD and 0.8 SD, respectively, with essentially no difference (Fig. 4).

Changes in water level over the last ~ 100 years indicated by sedimentary and dam-construction records

The chronology of core YL2013-A (Fig. 5) indicated that the upper 39 cm spanned the last ~ 100 years, from ~ 1919 to 2013, with an age error ranging from 0.1 to 5.4 years. There was a prominent spike in ^{137}Cs concentration at 26 cm depth, corresponding to the peak of 1963, which was consistent with the radiometric age based on the decay of ^{210}Pb (Fig. 5). The

lithology of the sediment core during the studied interval was essentially constant, consisting of brown clay-rich lacustrine sediments.

From the chronology, changes in the annual average sediment accumulation rate (AASAR) and the annual average sediment flux (AASF) could be calculated. The AASAR and AASF exhibited a gradually increasing trend since the interval of dam construction, especially after ~ 1975, which reflected the continuous accumulation of lake sediments after the dam was constructed (ESM 2). In addition, we estimated the approximate water level of four different phases based on the water capacity of the reservoir recorded by the dam construction project and

Fig. 5 Profiles of the activities of ^{214}Pb , ^{210}Pb , ^{137}Cs and the resulting age-depth model for sediment core YL2013-A defined by the CRS model

the measured water level in 2013 (Table 3). Thus, we were able to compare the trend to a record of changes in water level of Yunlong Lake during the last ~ 60 years (ESM 2). The results showed that since the beginning of dam construction in 1953, the water level of Yunlong Lake had gradually increased due to the dam construction and the reservoir extension project: the water level rose from 7 m in 1953 to 7.79 m when the dam construction was completed in 1985. When the reservoir extension project was completed in 2009, the reservoir water level increased to 11.45 m, and the final water level measured during field work in 2013 was 13.3 m. The estimated water level based on the reservoir water capacity was largely consistent with the changes in the AASAR and AASF (ESM 2).

Synchronous and in-phase changes in sediment accumulation rate and water level were supported by the changes of other independent sedimentation indices, such as the dry density and water content of the down-core sediments, the sedimentary diatom concentration, and the diatom flux (ESM 2). The history of long-term water-level changes at Yunlong Lake, indicated by these sedimentation indices, could be divided into four phases (ESM 2) which were described below:

Phase I (~ 1919 to ~ 1975), the phase of natural fluctuations. The water content of the sediments was relatively high, while the dry density of the sediments, AASAR, AASF, the sedimentary diatom concentration and diatom flux, were generally low. All of these parameters fluctuated within a narrow range which indicated a generally stable water level influenced by natural climatic fluctuations.

Phase II (~ 1975 to ~ 1995), the phase of lake impoundment. The dry density of the sediments,

AASAR, AASF, sedimentary diatom concentration and diatom flux began to increase at the same time, while the water content of the sediments decreased. This indicated a steadily rising water level due to the gradual implementation of the dam construction project and the impoundment of the lake.

Phase III (~ 1995 to ~ 2009), the phase of reservoir utilization. Compared with the second phase, the dry density of the sediments, AASAR, AASF, sedimentary diatom concentration, and diatom flux increased synchronously, indicating the further impoundment of the reservoir. However, these sedimentation indices were also characterized by frequent short-term fluctuations which indicated corresponding short-term fluctuation in water level, probably due to the increasing frequency of reservoir water discharge.

Phase IV (~ 2009 to 2013), the phase of reservoir extension. The dry density of the sediments decreased gradually, while the sedimentary water content, AASAR, AASF, sedimentary diatom concentration and diatom flux increased substantially again, especially the AASAR, which increased from 0.7 to 1.2 cm year⁻¹. These changes may indicate that an abrupt rise in water level occurred after 2009, probably as a response to the completed reservoir extension project.

Changes in diatom assemblages and diversity in core YL2013-A over the last ~ 100 years

Analyses of the 27 sediment core samples resulted in the identification of 24 diatom genera and 110 species (ESM 3). The diatom assemblages changed greatly over the last ~ 100 years, and they could be divided into four zones according to the results of the CONISS analysis (Fig. 6), which were described below.

Table 3 Changes in water capacity of the reservoir, estimated water level, AASAR (annual average sediment accumulation rate) and AASF (annual average sediment accumulation flux)

Time (A.D.)	Water capacity of the reservoir (m ³)	Measured water level (m)	AASAR (cm year ⁻¹)	AASF (g cm ² year ⁻¹)
1953	7.26×10^6	7	0.274	0.02
1985	7.9×10^6	7.79	0.434	0.049
2009	1.09×10^7	11.45	1.18	0.078
2013	—	13.3	1.19	0.033

The data are based on dam-construction records and the chronology of core YL2013-A

of Yunlong Lake before and after dam construction and the reservoir extension project

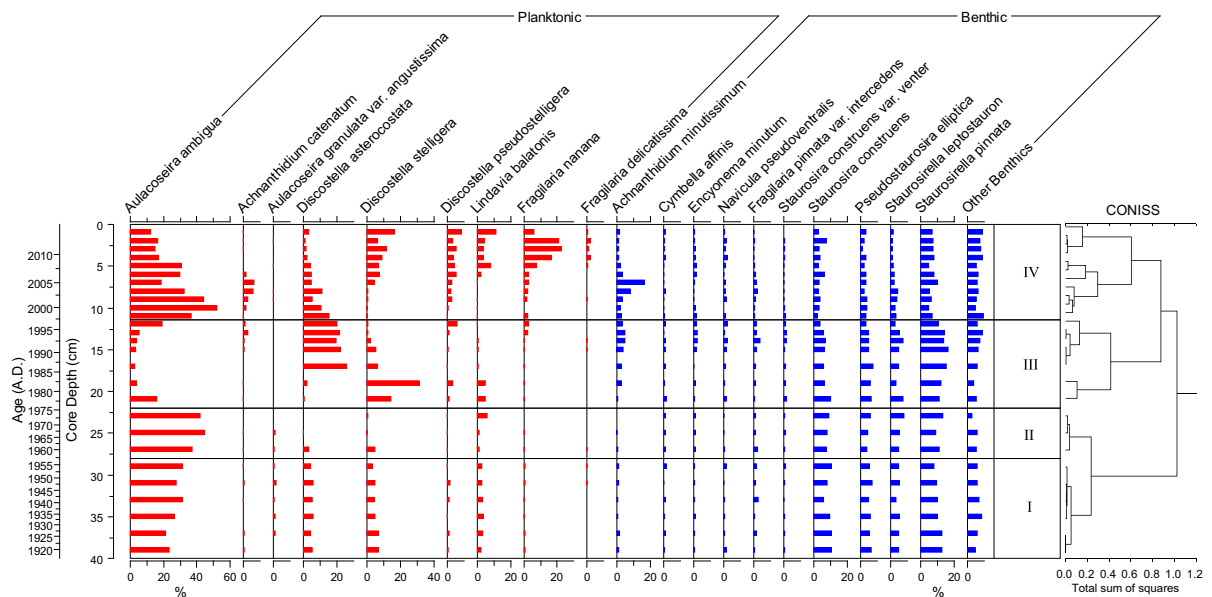


Fig. 6 Changes in diatom assemblages in core YL2013-A during the last 100 years. Only the main diatom species (relative abundance > 1%) are shown, and the rare benthic species are

combined together as other benthics. The zones are defined using CONISS implemented in TILIA version 2.02

Zone I (39–28 cm, ~ 1919 to ~ 1957). The dominant planktonic species was *Aulacoseira ambigua* (Grunow) Simonsen, with a relative abundance of 27.3%. Other relatively abundant species included *Discostella asterocostata* (Lin, Xie & Cai) Houk & Klee and *Discostella stelligera* (Cleve & Grunow) Houk & Klee, both with a relative abundance of 5.6%. The abundance of benthic species was relatively high, dominated by benthic fragilarioid taxa, including *Staurosirella pinnata* (Ehrenberg) D.M. Williams & Round, *Staurosirella leptostauron* (Ehrenberg) D.M. Williams & Round, *Pseudostaurosira elliptica* (Schumann) Edlund et al., *Staurosira construens* (Ehrenberg) E. Morales, *Staurosira construens* var. *venter* (Ehrenberg) Hamilton and *Fragilaria pinnata* var. *intercedens* (Grunow) Hustedt, with a total average relative abundance of 35.9%.

Zone II (28–22 cm, ~ 1957 to ~ 1975). *A. ambigua* remained the dominant species with a peak relative abundance of 45.3%, while the relative abundances of *D. asterocostata* and *D. stelligera* decreased substantially. The percentages of benthic diatoms were almost unchanged in comparison with the previous zone, and the total average relative abundance of the dominant fragilarioid taxa was 35.4%.

Zone III (22–11.5 cm, ~ 1975 to ~ 1997). *D. stelligera* and *D. asterocostata* were the dominant planktonic species, with successive increases in their relative abundance, with maxima of 31.8% and 26.4%, respectively. In contrast, the relative abundance of *A. ambigua* decreased markedly (average relative abundance of only 8.1%) and *Aulacoseira granulata* var. *angustissima* (O. Müller) Simonsen, with low abundances in zones I and II virtually disappeared. Benthic diatoms showed no notable changes compared with the previous two zones and the total average relative abundance of the dominant fragilarioid taxa was 37.1%.

Zone IV (11.5–0.5 cm, ~ 1997 to 2013). The abundance of *A. ambigua* again increased greatly, with a maximum relative abundance of 52.4%; however, it gradually decreased after ~ 2005, with an average abundance of 20.7%. The abundance of *Achnanthyidium catenatum* (Bily & Marvan) Lange-Bertalot increased substantially in the early part of the zone, with an average relative abundance of 4%, but with only trace levels after ~ 2005. The relative abundance of other euplanktonic species, including cyclotelloid taxa such as *Discostella pseudostelligera* (Hustedt) Houk & Klee, *D. stelligera* and *Lindavia balatonis* (Pantocsek) Nakov, Guillory, Julius, Theriot

& Alverson, and the elongate fragilarioid taxa such as *Fragilaria nanana* Lange-Bertalot and *Fragilaria delicatissima* (W. Smith) Lange-Bertalot, increased substantially within this interval, especially after ~ 2005. In contrast, the relative abundance of *D. asterocostata* decreased gradually. In addition, the relative abundance of the dominant benthic fragilarioid taxa also decreased substantially compared with the previous three zones, with a total average relative abundance of 20.2%. However, the abundance of *Achnanthyidium minutissimum* Kützinger, present in only trace amounts in the previous zones, increased substantially in this zone, with a maximum abundance of 17.1%. However, it decreased greatly after ~ 2005.

The α -diversity of diatoms over the last ~ 100 years remained virtually constant, apart from two intervals with relatively low values: from ~ 1955 to ~ 1975 and from ~ 1995 to ~ 2005 (Fig. 7). During the first interval (~ 1955–1975), diatom richness, evenness and composite diversity decreased simultaneously, whereas during the second interval (~ 1995–2005), there was a marked decrease in diatom evenness and composite diversity with no significant changes in diatom richness.

In order to explore the main causes of the changes in diatom diversity of Yunlong Lake over the last ~ 100 years, we conducted Pearson correlation analysis of the relative abundance of the principal diatom taxa over the last ~ 100 years and the five α -diversity indices. The results showed that the relative abundance of *A. ambigua*, the most dominant diatom

species at Yunlong Lake over the last ~ 100 years, was highly positively correlated with diatom dominance (Berger-Parker index) ($r = 0.82$, $p < 0.05$), and highly negatively correlated with diatom evenness (Pielou index) and composite diversity (Shannon and Simpson index), with correlation coefficients of -0.77 , -0.79 and -0.81 ($p < 0.05$), respectively. The correlation coefficient between the abundance of *A. ambigua* and diatom richness (Taxa-S index) was relatively low ($r = -0.33$, $p = 0.08$), which may indicate that changes in the relative abundance of the most dominant species in the whole community significantly impacted changes in biodiversity, especially species evenness, while species richness was not only related to changes in the abundance of the dominant species, but also to other factors.

Climate change in the studied region over the past 60 years

The changes in the three main meteorological factors (annual average air temperature, annual precipitation, and annual average wind speed) in the lake region (Dali Station) over the last 60 years (Fig. 7) showed that the air temperature first decreased, during 1951–1995, and then began to increase after 1995. This indicated that the region has warmed since the 1990s, especially after 2000, with an average air temperature increase of ~ 0.5 °C. Over the past 60 years, the annual precipitations showed no significant trend ($R^2 = 0.0017$), but with obvious

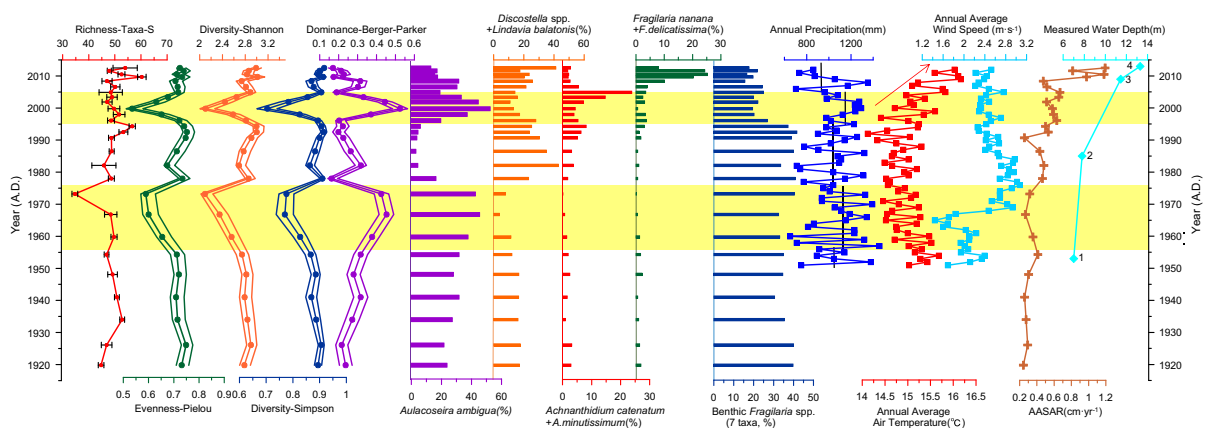


Fig. 7 Changes in diatom diversity, main diatom assemblage composition, and the estimated water level over the last 100 years at Yunlong Lake, with the annual average meteorological monitoring data of the last 60 years from Dali Station.

The two intervals with notably decreased diatom diversity are highlighted in yellow. AASAR is the annual average sediment accumulation rate. The numbers 1 to 4 correspond to the four periods listed in Table 3

fluctuations during different periods, increasing during the two intervals when diatom diversity notably decreased. The annual average wind speed over the last 60 years had an overall inverse correlation with changes in air temperature. Before 1965, the annual average wind speed was generally low and the average value was 1.98 m s^{-1} . After 1965 the wind speed increased substantially to 2.63 m s^{-1} , but after the warming of the region it began to decrease, with an average of 2.42 m s^{-1} .

Discussion

Relationship between surface diatom diversity and water depth

Several studies have shown that changes in the composition of diatom assemblages occur across a water depth gradient within a lake (Punning and Puusepp 2007; Cantonati et al. 2009; Laird et al. 2010), and this is also the case for Yunlong Lake. Unsurprisingly the littoral subzone and the shallow water zone are dominated by benthic species, while the profundal zone is dominated by planktonic species (Fig. 2). Our data indicate that the demarcation between shallow and profundal zones in Yunlong Lake occurs at the depth of $\sim 5 \text{ m}$, based on diatom compositional changes (Fig. 2).

It has been speculated that diatom diversity in the shallower benthic zones, with diverse microhabitats, is likely to be much higher than in the deep planktonic zone (Hayashi 2011). The results of several studies of the relationship between surface diatom diversity and water depth are in accordance with this inference (Moos et al. 2005; Cantonati et al. 2009; Laird et al. 2010, 2011); for example, at Worth Lake, the diatom diversity in the shallower benthic zone was much higher than in the deep profundal zone (Laird et al. 2010).

However, in the case of Yunlong Lake, there is no evidence of major variations in species biodiversity metrics (richness, evenness, diversity) with water depth, with the exception of a moderately lower level in a few samples from the near-shore littoral subzone (Fig. 4). The changes in Taxa-S together with the ANOVA results indicate that there are no significant changes in diatom richness in the different depth zones (Fig. 3, Table 1). Species evenness indicated by the

Pielou index also indicates that there is little difference in surface diatom evenness with changing water depth (Fig. 4). Composite diversity indices, including the Simpson index and Shannon index, also show almost no differences among the three depth zones (Fig. 4). In addition, the species dominance indicated by the Berger-Parker index also shows no notable differences in different water depths and locations (Fig. 4).

The results of DCCA (Fig. 4) indicate that surface diatom β -diversity is similar between the 23 sites of the shallow zone (0.9 SD) and the 35 sites of the profundal zone (0.8 SD). For the shallowest four sites ($\sim 0.1 \text{ m}$), the littoral subzone has the highest beta-diversity (1.2 SD), which may be the result of a greater number of microhabitats in this subzone. However, this finding should be viewed with caution given that this subzone is represented by only four samples. Overall, it can be concluded that there is no discernible difference in surface diatom β -diversity throughout the entire lake.

Diatom diversity in the near-shore littoral subzone is moderately lower but with significant fluctuations (Figs. 3, 4). This may reflect a relatively uniform environment but with substantially different diatom microhabitats. Various microhabitats are inhabited by different benthic diatom assemblages, thus causing greater differences in diatom diversity of the littoral subzone compared to the shallow water and profundal zones (Fig. 3). The diatom composition of surface sample S15, from the northwestern stony bank (Fig. 1), is mainly dominated by the benthic species *S. construens*, whose percentages reach 30%, which is the maximum relative abundance in all of the surface samples. However, the diatom diversity of this sample is the lowest for the entire lake, which may be the result of the relatively uniform substrate environment in this area where macrophytes are scarce. Another surface sample (S14) was obtained from near the eastern outflow from a water depth of $\sim 0.1 \text{ m}$ (Fig. 1). Its diatom assemblage is dominated by epipsammic diatom species (e.g. *Psammothidium subatomoides* (Hustedt) Bukhtiyarova & Round, Fig. 2), probably because of the higher influx of sand in this area. The species dominance in these samples may explain the lower diatom diversity of this subzone. In the other two surface samples from this subzone (S19 and S01), also from the water depth of $\sim 0.1 \text{ m}$ (Fig. 1), the higher diatom diversity probably results from the more evenly distributed

macrophytes and the greater diversity of microhabitats, which provide a favorable substrate for the growth of a wide variety benthic diatom species. However, considering the small number of samples (four) and the extremely shallow water depth (~ 0.1 m) in this subzone, this variation can be ignored when evaluating the diatom diversity changes of the entire lake.

Although the calculation of diatom diversity indices for the sediment samples can be affected by different sediment accumulation rates, as outlined by Smol (1981), the diatom diversity in the benthic-dominated shallow zone and the planktonic-dominated profundal zone of Yunlong Lake exhibits no significant variations (Figs. 3, 4), which suggests that the difference in sediment accumulation rates between these two depth zones does not influence their patterns of diatom diversity. The effect of differences in sediment accumulation rate in different depth zones on surface diatom diversity appears to be insignificant at Yunlong Lake, and consequently we did not evaluate the potential errors of this effect in this study.

In summary, there are almost no differences in surface diatom diversity with changing water depth throughout the entire lake, in terms of both α -diversity between species and β -diversity between habitats.

The mechanisms responsible for the relative depth invariance of the diatom diversity of Yunlong Lake may include the following. First, Yunlong Lake is relatively strongly mixed. Lakes generally have intervals in which the water column is mixed. Some lakes are mixed several times in a year (polymictic), while others are monomictic (Lotter and Bigler 2000; Tolotti et al. 2007) or dimictic (Mackay et al. 2003). Convection currents driven by the surface wind can cause the resuspension and redeposition of sediments in the shallow littoral zone. Thus, diatoms originally deposited in the littoral zone can be transported to the deep profundal zone (Wang et al. 2008, 2012a, b), and this mechanism may result in relatively constant diatom diversity in the sediments from different zones of a lake. In the case of Yunlong Lake, although the profundal zone is mainly dominated by planktonic diatom species, most of the benthic species that dominate in the shallow zones also occur in this zone with low or moderate abundance (Fig. 2), which may cause the relatively constant diatom diversity throughout the entire lake.

The relatively constant diatom diversity throughout all the depth zones of Yunlong Lake is probably associated with the relatively strong mixing conditions, which is demonstrated by water temperature monitoring records (ESM 1). A two-year record of water temperatures using automated temperature loggers (HOBO-C2) moored on a chain at the water depths of 1, 5, 7 and 12.8 m in Yunlong Lake reveals that there is an interval during which the water column is fully mixed, from late autumn to early spring (ESM 1, Zou et al. 2018). In addition, the water temperature monitoring records show that the upper at least ~ 7 -m water layer of Yunlong Lake, which occupies a considerable part of the lake area, is fully mixed throughout the year (ESM 1). The long mixing interval and the large mixing area have resulted in the strong mixing of the lake throughout the year.

In contrast, lakes such as Worth Lake (Laird et al. 2010), located in a relatively high-latitude region, are characterized by a relatively long interval of ice cover during which there is no lake mixing. At the same time, the break-up of the ice cover and the lake stratification also take up a specific time interval, resulting in the far weaker mixing of such lakes compared with Yunlong Lake, in terms of both the length of the mixing time and the mixing area. Consequently, relatively weak mixing of the water column may occur in these lakes, causing large differences in diatom diversity between different depth zones.

Second, the complex morphology and shoreline substrate environment of lakes such as Worth Lake may result in a high degree of diversity of diatom microhabitats, which can promote a higher diatom diversity in the shallower zones. In contrast, there were also no changes in surface diatom diversity with changing water depth in Gonghai Lake (Yan et al. 2018), a temperate alpine lake in the monsoon region of China, which is consistent with the diatom diversity pattern of Yunlong Lake. Although Gonghai Lake is also located at a temperate latitude and is ice-covered for part of the year, similar to the above referenced boreal lakes (Yan et al. 2018), its pattern of surface diatom diversity differs substantially. The large difference in the pattern of surface diatom diversity between these two lakes may be attributed to the differences in the complexity of lake morphology and shoreline microhabitats. Gonghai Lake is a relatively small, circular lake with a maximum water depth

of ~ 10 m, which may promote efficient water exchange between different areas, a simple pattern of water circulation, and relatively uniform shoreline microhabitats, similar to Yunlong Lake (Zou et al. 2015; Yan et al. 2018). These factors may thus have caused a relatively lower benthic diatom diversity in the littoral zone and an overall constant surface diatom diversity throughout the lake. The comparison between these lakes implies that the complexity of lake morphology and shoreline microhabitats is another important factor controlling the diatom diversity patterns in lake sediments.

The absence of any notable variations in surface diatom diversity at Yunlong Lake indicates that diatom diversity of the sediments at a single location is representative of the entire lake. By analogy, this conclusion can also be applied to those lakes which have relatively strong mixing conditions and simple lake morphology and shoreline microhabitats. However, as explained previously, the representativeness of diatom diversity in lake sediments needs to be verified from a temporal perspective, for which the diatom record from a sediment core is required.

Changes in water level and diatom diversity over the last ~ 100 years

Changes in lake sedimentation indices can be a reliable indicator of lake water-level changes, especially for reservoirs after human manipulation (Wang et al. 2006, 2007). This is largely because in a semi-closed reservoir system the accumulation of sediments and the water capacity of the reservoir are highly positively correlated. Dams can trap a large volume of water and sediment in the reservoir, leading to simultaneous increases in water level and sediment influx. For example, during the four-year interval (2003–2006) after the impoundment of the Three Gorges Dam in China, $\sim 60\%$ of the sediment entering the reservoir was trapped during the high water-level months (June to September) (Xu and Milliman 2009). At the same time, increasing water consumption can cause simultaneous decreases in water level and sedimentation. For example, in the case of the Yellow River in China, the sediment load has decreased by $\sim 90\%$ due to dam construction and increased water consumption over the last 25 years (Wang et al. 2006, 2007). Albeit on a much smaller scale, this may also be the case for Yunlong Lake. In

the last ~ 100 years, with the construction of the dam and the extension of the reservoir, the impoundment of sediments has occurred. This is reflected by multiple independent sedimentation indices, including the AASAR, AASF, dry density and water content of the sediments, diatom concentration and diatom flux (ESM 2). These parameters, especially AASAR, show an obvious stepwise increasing trend (Fig. 7, ESM 2), indicating a gradual rise of the lake water level. At the same time, the estimated water-level changes based on the water capacity of the reservoir (Table 3) are largely consistent with the changes in the AASAR (Fig. 7), which indicates that in the case of Yunlong Lake the changes in AASAR reliably reflect the history of water-level changes.

The water level of Yunlong Lake shows an obvious stepwise increasing trend over the last ~ 100 years, as indicated by multiple sedimentation indices and the reservoir's water capacity record. If diatom diversity is affected by this long-term change in the water level, diatom diversity in the sediment core should show a corresponding decreasing trend as presumed by Hayashi (2011). However, according to our results, changes in diatom diversity observed over the last ~ 100 years do not correspond to changes in water level (Fig. 7), which suggests that long-term water-level changes have not influenced diatom diversity in the lake sediment core.

The diatom diversity of Yunlong Lake over the last ~ 100 years remained stable apart from two intervals during which it was relatively low: from ~ 1955 to ~ 1975 and from ~ 1995 to ~ 2005 (Fig. 7). The changes in diatom diversity during these two intervals, especially the changes in diatom evenness, are largely caused by notable changes in the relative abundance of the dominant species *A. ambigua*, which is indicated by the increase in the Berger-Parker dominance index (Fig. 7) and verified by the results of Pearson correlation analysis. The dominance of the principal species in the population will substantially affect species evenness, which is an essential factor for assessing the biodiversity of the entire community (Hill 1973). Therefore, the substantial increases in the relative abundance of the dominant diatom species, *A. ambigua*, may be the main reason for the decrease in the diatom diversity of Yunlong Lake during these two intervals. We now explore the possible mechanisms responsible for these

two changes in diatom diversity, based mainly on the autoecology of *A. ambigua*.

(1) From ~ 1955 to ~ 1975, diatom richness, evenness and composite diversity decreased simultaneously, while diatom dominance increased notably (Fig. 7). The water level at this time, indicated by the AASAR and other sedimentation indices, did not increase significantly, indicating that no impoundment occurred in the lake and that it was still open at this time, although dam construction had begun in 1953. However, based on the meteorological records of the Dali Station, the annual precipitation increased substantially during this interval (Fig. 7), which may have resulted in a large volume of the outflowing water. The resulting large amount of water leakage from the lake may have led to a large increase in the intensity of turbulent mixing of the lake water compared to previously, which may have resulted in the predominance of the planktonic diatom species *A. ambigua*. Because of its relatively heavy silicious frustules, it has a high sinking rate and can only remain suspended in the photic zone when water column mixing is sufficiently strong (Pilskaln and Johnson 1991; Lindenschmidt and Chorus 1998; Rühland and Smol 2005; Poister et al. 2012). This relatively strong mixing likely favored the proliferation of this species during this interval, which led to an increase in species dominance, together with a decrease in species evenness and thus decreasing diatom diversity.

In addition, the meteorological monitoring data show that the annual average air temperature at this interval also gradually decreased, with the wind speed increasing rapidly after 1965 (Fig. 7). The relatively cold climatic conditions, with strong winds, may also have promoted lake mixing and favored the blooming of *A. ambigua* (Pilskaln and Johnson 1991; Lindenschmidt and Chorus 1998; Rühland and Smol 2005; Poister et al. 2012). However, although after ~ 1975 the climatic conditions were even colder and the wind speed was higher, the relative abundance of *A. ambigua* decreased greatly (Fig. 7), which may indicate that these two climatic factors were not the main cause of the dominance of the species and the resulting decreasing diatom diversity during this period.

Therefore, the greatly increased precipitation and water discharge from the lake may have enhanced turbulent mixing, resulting in the increasing abundance of *A. ambigua* and the notable decrease in diatom diversity during this interval.

(2) From ~ 1995 to ~ 2005, diatom dominance largely increased, while diatom evenness and composite diversity decreased substantially with no obvious change in diatom richness (Fig. 7). Dam construction was completed during this interval and the lake began to be utilized as a reservoir. The meteorological monitoring data show that the annual precipitation during this period was much higher than in the previous interval and the impoundment effect of the reservoir may have caused an overall high water level. However, almost all of the sedimentation indices, including the AASF, the sedimentary diatom concentration, diatom flux, dry density and water content, fluctuated frequently during this period, which indicates frequent water discharge from the reservoir. The increasing discharge frequency may have enhanced lake mixing compared with the previous impoundment period when lake mixing was driven solely by wind; this may have resulted in the renewed predominance of *A. ambigua* and a notable reduction in diatom evenness (Fig. 7).

However, the diatom richness at this interval does not show a clear decreasing trend as was the case during ~ 1955–1975 (Fig. 7), indicating that although species richness may also be influenced by changes in the relative abundance of the dominant species, there were likely to have been other influencing factors. The main reason for the absence of a decrease in diatom richness during this period may be regional climatic warming, which is evident in the meteorological monitoring records. After 2000, the annual average air temperature began to rise (Fig. 7). The regional warming may have resulted in the blooming of several thermophilic diatom species, such as *A. catenatum* (Zou et al. 2018). In addition, the warmer climatic conditions may have promoted the growth of aquatic plants in the lake littoral zone, thus providing more habitat space for epiphytic diatom species, such as *A. minutissimum* (Douglas et al. 1994; Beauger et al. 2015). Thus, the relative abundance of these two species increased notably after the pronounced regional warming trend (Fig. 7), which may have contributed to the absence of a decrease in diatom richness during this period.

After 2005 there was a slight increase in diatom richness (Fig. 7), and in addition a series of small planktonic species became abundant, such as the small-celled, pancake-shaped cyclotelloid taxa (including *D. stelligera*, *D. pseudostelligera* and *L.*

balatonis) and the elongate fragilarioid taxa (including *F. nanana* and *F. delicatissima*) (Figs. 6, 7), suggesting a high correlation between them. The notable increase in the relative abundance of these small planktonic species was likely the result of the further warming of the region and the extension of the reservoir, both of which could have caused the increase in lake thermal stratification, which would have promoted the blooming of these taxa. The relatively high surface area to volume ratio of these taxa provides a competitive advantage in obtaining nutrients and accessing light under conditions of lake stratification (Litchman et al. 2006; Winder et al. 2009; Rühland et al. 2015). The notable abundance of these taxa may be the reason why diatom richness increased during the period of regional warming; however, reservoir extension and regional warming occurred roughly simultaneously and both factors may have promoted the increased stratification of the water column. Thus, the origin of the response of diatom diversity to climate change is unclear as a result of the impact of human activities (i.e. the reservoir extension project).

In summary, the increasing intensity of lake mixing may be the main reason for the two notable decreases in diatom diversity at Yunlong Lake, from ~ 1955 to ~ 1975 and from ~ 1995 to ~ 2005. However, the reason for the changes in lake mixing conditions were different: during the first period (~ 1955–1975), it was probably caused largely by increased precipitation, while during the second period (~ 1995–2005), the increase in the frequency of water discharge from the reservoir may have been the main reason. However, it can at least be confirmed that the change in diatom diversity during these two periods was unrelated to the increasing water level. This indicates that long-term water-level changes did not influence the record of diatom diversity in the sediment core, which is representative of the whole of Yunlong Lake.

Conclusions

- (1) For lakes with relatively strong mixing mechanism and a simple morphology and shoreline microhabitats, like Yunlong Lake, diatom diversity in the sediments is relatively constant between different locations and water depths and is probably not influenced by changes in water level. It is likely that in such lakes diatom diversity in the sediments is representative of that of the entire lake at specific time intervals, and thus such lakes may be optimal for studying long-term changes in diatom diversity based on the diatom analysis of sediment cores.
- (2) Our results suggest that when exploring the response of lake diatom diversity to climatic warming, lakes that are relatively unaffected by human activities should be selected. This is because the impact of human activities (e.g. dam construction, reservoir extension) may perturb the response of lake diatom diversity to climatic warming.

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