



Re-evaluating coring sites in paleolimnological studies of a large, deep lake based on chironomid assemblage representativeness

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ABSTRACT

In paleolimnology, ecological trajectories of biological communities are typically reconstructed using a sediment core from the deepest part of a lake. However, the representativeness of chironomid assemblages from the profundal zone and its influence on ecological response to environmental change in large, deep lakes remain poorly understood. To address this knowledge gap, we conducted a study on subfossil chironomids in Fuxian Lake, including thirty-five surface sediment samples and two sediment cores from different water depths. Our findings reveal a distinct bathymetric distribution pattern of subfossil chironomid assemblages attributed to limited homogenization in the large, deep lake. The profundal assemblages exhibited the lowest richness representativeness, while nearshore assemblages showed the least similarity to the entire-lake assemblage. Consequently, the response pattern of chironomid assemblage to the environmental change varied with depth. Two notable shifts in the mid-depth core, occurring in 1979 CE and 2005 CE, were primarily attributed to eutrophication processes. However, the chironomid assemblage from the deepest zone exhibited only one significant change in 2005 CE, likely indicating exacerbated hypoxia in the profundal zone. Our combined analysis of surface samples and sediment cores underscores that the profundal zone, where bottom water is characterized by low temperature and anoxia, is unsuitable as a coring site in large, deep lakes due to its extremely simplified species composition. Instead, mid-depth zones should be prioritized as candidate coring sites in large, deep lakes, given their relatively high richness representativeness, head capsule concentration, and stable sedimentary conditions. Specifically, we recommended retrieving sedimentary cores around the water depth of 50 m when conducting subfossil chironomid analysis in Fuxian Lake.

1. Introduction

Lakes are essential ecosystems providing valuable resources to both the biosphere and human society. However, they are increasingly susceptible to disturbances caused by climate change and human activities (Michelutti et al., 2005; Quinlan et al., 2008). As a result, global lake ecosystems have experienced significant deterioration over the past decades, leading to biodiversity loss and functional degradation (Woolway et al., 2020). To address these challenges effectively, it is crucial to develop a comprehensive understanding of the long-term ecological dynamics of lake ecosystems in response to multiple

stressors (Dubois et al., 2018; Roberts et al., 2008). Lacustrine sediments act as natural archives that preserve valuable information about past environmental change (Shen et al., 2020; Williamson et al., 2009). Analyzing the biological and abiotic signals stored within those sediments makes it possible to reconstruct climatic and environmental changes over long timescales (Frey, 1988). This interdisciplinary approach, known as paleolimnology, provides valuable scientific support for ecosystem management and enables projections of future changes, complementing short-time monitoring data (Saulnier-Talbot, 2016; Smol, 1992). Paleolimnological reconstructions commonly employ a multiproxy analysis, which involves examining various

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independent signals, such as elemental composition, geochemical proxies, and biological remains, to obtain reliable and comprehensive inferences (Birks and Birks, 2006; Korosi et al., 2017).

Chironomids are cosmopolitan dipteran insects with great abundance in zoobenthos community (Ashe et al., 1987), often contributing up to 90% of the secondary production in freshwater ecosystems (Herren et al., 2017; Nazarova et al., 2004). The chironomid community is highly sensitive to various environmental variables such as air temperature, water temperature, pH, hydrological conditions, dissolved oxygen, salinity, and pollution (Heiri et al., 2011; Engels et al., 2020; Mayfield et al., 2021; Nazarova et al., 2017). Notably, the chitinous head capsules of chironomid larvae are well-preserved in lake sediments and can be identifiable at satisfactory taxonomical resolutions, making them a suitable proxy for paleolimnological reconstructions of climate and environment changes (Eggermont and Heiri, 2012; Fortin et al., 2015; Porinchu and Macdonald, 2003; Verbruggen et al., 2010). Numerous inference models have been established to quantitatively reconstruct specific environmental variables based on the ecological traits of modern chironomid biota (Woodward and Shulmeister, 2006), with a particular focus on summer air temperature (Upiter et al., 2014; Zhang et al., 2017), water depth (Korhola et al., 2000) and salinity (Henrichs et al., 2001).

In paleolimnological reconstructions, it has been common practice to rely on a single sediment core from the deepest zone of a lake, assuming it represents the entire lake community (Holmes et al., 2009; Kattell et al., 2007; Smol, 2008). This assumption is based on the understanding that littoral and sublittoral taxa can be transported to the profundal zone through sediment redeposition, while the reverse is less likely (Schmah, 1993). However, living chironomid larvae often exhibit a bathymetric distribution pattern, with higher diversity observed in shallow zones where taxa are constrained by depth-related factors such as dissolved oxygen, water temperature, and food availability (Heggen et al., 2012). Consequently, the representativeness of chironomid assemblages in the deepest zone has been subject to some controversy (Van Hardenbroek et al., 2011). Studies have suggested that subfossil chironomid assemblages exhibit relatively low spatial variation due to the homogenization effect during burial process (Brodersen and Lindgaard, 1999; Tarrats et al., 2018). However, some other studies propose that subfossil chironomid assemblages preserve a distinct bathymetric imprint of the extant community (Eggermont et al., 2007; Frossard et al., 2014; Raposeiro et al., 2018). These conflicting observations can be attributed to variations in basin topography, hydrographic features, and environmental factors that influence the distribution of living chironomid larvae or the transport of their head capsules (Hilton, 1985; Blais and Kalf, 1995). It is generally observed that the chironomid assemblages in small or shallow lakes exhibit more consistent spatial distribution compared to large and deep lakes (Eggermont et al., 2007; Langdon et al., 2010; Walker et al., 1984). Importantly, spatial variation in species composition of subfossil chironomid assemblages may lead to inconsistent paleolimnological inferences based on sediment cores from different water depths within a lake (Heinis and Davids, 1993; Perga et al., 2015; Stewart et al., 2013). For example, a paleolimnological study conducted on a subalpine lake highlighted that chironomid assemblages from the profundal zone (65 m) primarily respond to eutrophication, while assemblages from shallower zones (30 and 56 m) are mainly influenced by the top-down effects of introduced fish communities on the pelagic food web (Frossard et al., 2014).

Fuxian Lake, located in the Yunnan-Guizhou Plateau, is a large deep lake. While the overall water quality of Fuxian Lake is still in good status, monitoring data indicate progressive pollution resulting from human activities (Dai et al., 2017; Chen et al., 2018). Previous paleolimnological studies have demonstrated the ecological impacts of lake eutrophication and exotic fish invasions on diatom and cladoceran communities (Li et al., 2011; Liu et al., 2009). However, the ecological response of zoobenthos, including chironomids, to environmental changes in Fuxian Lake remains unknown. In this study, we aimed to: (1)

investigate the representative of subfossil chironomid assemblages along depth transects in terms of richness and overall assemblage composition; (2) compare the response patterns of subfossil assemblages from the profundal and mid-depth zones to environmental changes in Fuxian Lake over the past 150 years; and (3) discuss the implications of our findings for selecting coring sites in chironomid subfossil studies conducted in large, deep lakes. By understanding the spatial distribution of chironomid assemblages and their response to environmental changes in Fuxian Lake, we can gain valuable insights into the ecological history and inform the management and conservation strategies of the lake.

2. Study region

Fuxian Lake (24.35°–24.63°N, 102.82°–102.97°E) is a large oligotrophic lake covering an area of 216.6 km², with a maximum depth of 158.9 m and an average depth of 95.2 m (Fig. 1a, Dai et al., 2017). More than twenty short rivers feed the lake, while Haikou River is the only outflow river located on the mid-eastern shore (Fig. 1b). Water exchange in Fuxian Lake is slow, resulting in a mean residence time of approximately 167 years (Li et al., 2020). The lake is characterized as an alpine monomictic lake, with thermocline zones appearing at depths of 3–31 m during summer and 21–28 m during autumn (Miao et al., 2022). The catchment area of Fuxian Lake is relatively small, covering about 675 km² (Fig. 1b), and is influenced by the Indian Summer Monsoon. Historical monitoring data indicate a significant increase in air temperature in 1998 (Fig. 2a), while precipitation has fluctuated over the past six decades without a discernible monotonic trend (Fig. 2b).

Fuxian Lake plays a vital role in providing ecological services for regional economic and social development, including aquaculture, agricultural irrigation, recreation, and drinking water. However, human activities have adversely impacted the lake ecosystem (Pan et al., 2008; Zhang et al., 2015). The area surrounding this lake has experienced rapid urbanization (Fig. 1c) and economic development (Fig. 2e). Although Fuxian Lake is currently in an oligotrophic state, its nutrient levels and primary productivity have significantly increased in the past two decades, as evidenced by the rapid rise in chlorophyll *a* and phytoplankton density (Fig. 2c and d). Moreover, the introduction of exotic commercial fish, specifically *Neosalanx taihuensis*, in the 1980s has posed a significant threat to endemic species. *N. taihuensis*, a small fish in the icefish family, invaded Fuxian Lake from the connected Xingyun Lake through the Gehe River. Due to its small size and high reproduction capacity, *N. taihuensis* outcompeted the native fish species, leading to a three-fold increase in annual fish production in Fuxian Lake (Fig. 2f). The invasion of alien fish has also altered the structure and function of local organism communities, including fish (Wang et al., 2013), diatom (Li et al., 2011) and cladoceran (Liu et al., 2009).

3. Materials and methods

3.1. Sample collection

In July 2022, a total of thirty-five surface sediment samples (0–1 cm) were collected using a Kajak gravity corer along two transects of Fuxian Lake: the North-South transect ($n = 19$, FZ1-FZ19) and West-East transect ($n = 16$, FH1-FH16). Twelve sampling locations were set in the nearshore zones (0, 5, 10 m), twelve in the mid-depth zones (20, 40, 60 m), and eleven in the profundal zones (80, 90, 100, 120, 140, 150 m). Additionally, two sediment cores with clear water-sediment interfaces were collected at the deepest zone (FN05, 150 m) and mid-depth zone (FN12, 40 m). Immediately after collection, the sediment cores were sectioned into 1 cm intervals and placed in sealed plastic bags for subsequent laboratory analysis. The water quality parameters, including bottom water temperature, pH, dissolved oxygen (DO), conductivity, and chlorophyll *a*, were measured using a Multi-Parameter Water Quality Sonde (YSI EXO2, Yellow Springs, U.S.A.) equipped with multiple probes. Besides, bottom water was collected at each site using a 5L

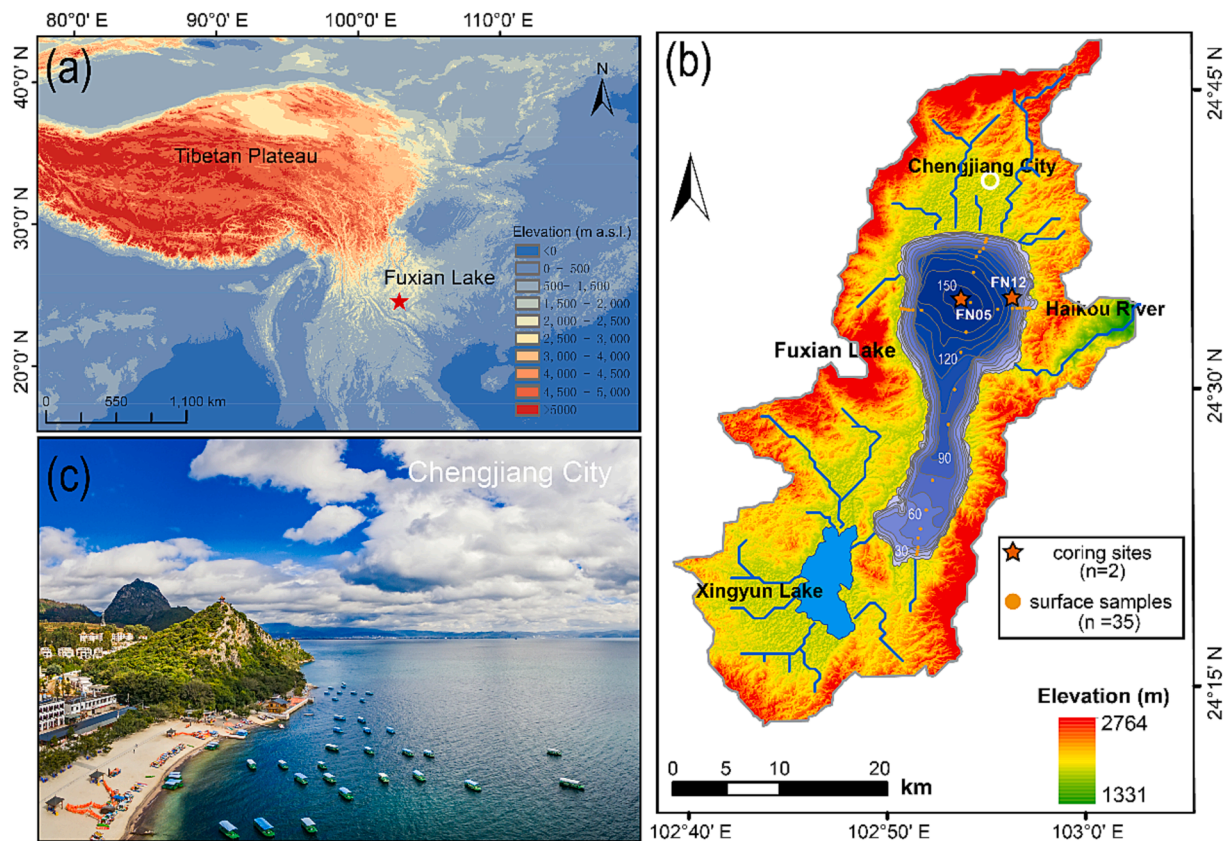


Fig. 1. Lake location and sampling sites. (a) Geographical location of Fuxian Lake Basin; (b) Geomorphology of Fuxian Lake catchment and distribution of sampling sites. Base map source: www.hydrosheds.org. (Lehner and Grill, 2013); (c) Villages near the western shore of Fuxian Lake.

plexiglass water sampler to determine nutrient indicators. The depth profiles of the determined water quality parameters can be found in Fig. S1.

3.2. Sediment core dating

The chronological sequence was established at 1 cm intervals based on the sediment core FN05 using the radiometric isotope ^{137}Cs and ^{210}Pb . The activities of ^{210}Pb , ^{137}Cs , and ^{226}Ra in the weighted freeze-dry sediment samples were measured using an ORTEC HPGc GWL series well-type, low coaxial background intrinsic germanium detector. The excess ^{210}Pb ($^{210}\text{Pb}_{\text{ex}}$) activity was calculated by subtracting the activity of ^{226}Ra (Appleby, 2002), and the piecewise constant rate of supply (CRS) model was applied to calculate ^{210}Pb data with the calibration of ^{137}Cs time maker. The dating result revealed that the 27-cm sediment core spanned approximately 147 years, with the bottom depth dating back to around 1875 CE. The age for another sediment core (FN12) was determined through core matching based on lithology and median grain size. More details regarding the chronology can be found in the supporting file (Fig. S2).

3.3. Nutrient indicators

The concentrations of total nitrogen (TN) and total phosphorous (TP) in bottom water samples were measured using a UV-visible spectrophotometer (UV2700, Shimadzu, Kyoto, Japan), while total organic carbon was analyzed using a total organic carbon (TOC) analyzer (TOC-L CPH, Shimadzu, Kyoto, Japan). Sedimentary nutrients (TOC, TN, TP) were obtained from published data with a time coverage of 135 years (1883–2018 CE) (Fig. S3; Ma et al., 2021).

3.4. Chironomid analysis

Chironomid analysis followed standard techniques proposed by Brooks et al. (2007). In brief, freeze-dried sediment was deflocculated with 10% KOH for 15 min in a water bath at 75 °C. After being sieved through a 90- μm sieve, chironomid head capsules were manually picked from sub-samples using tweezers under a stereomicroscope at 25 \times magnification. The head capsules were then mounted on microscope slides with Euparal for taxonomic identification. All samples contained >50 head capsules (Quinlan and Smol, 2001). Mounted specimens were identified under a microscope at 100–400 \times magnification, using reference chironomid identification tools (Brooks et al., 2007; Rieradevall and Brooks, 2001).

3.5. Statistical analysis

To offset the influence of sampling effort on observed richness in each sample, rarefaction analysis was conducted to compare richness among sites under equal head capsule counts ($n = 53$). Hill's N2 index (Hill, 1973) was calculated to estimate the alpha diversity of the chironomid assemblages. The representativeness of individual sample was evaluated in both aspects of richness coverage and assemblage structure. The degree to which chironomid assemblage in the individual surface sample represents whole-lake richness, a simple representative index, was calculated as the proportion of the total taxa of all samples observed in a single sample, as suggested by Heiri (2004). The Bray-Curtis distance was used to reflect the similarity of chironomid assemblages in individual surface sample to the entire-lake assemblage, which was obtained by the average of all surface samples. An UpSet analysis was completed to illustrate the distribution of unique and shared species along water depth gradient using the R package 'UpSetR' (Conway et al., 2017). Principal component analysis (PCA) was conducted to depict the

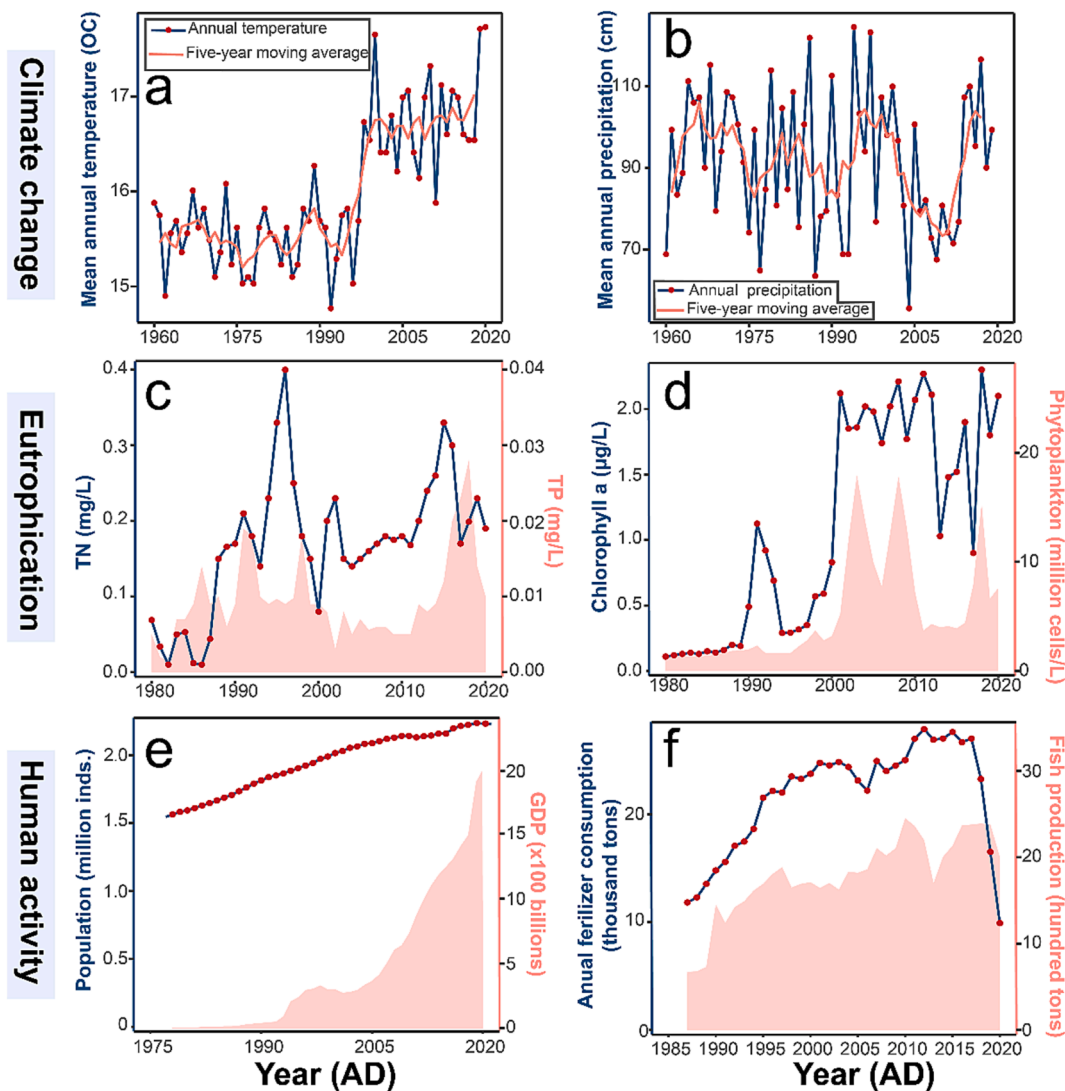


Fig. 2. Historical records of climate change, eutrophication status, and human activity in the Fuxian Lake catchment. Note that the starting times of available records are inconsistent, as shown by the x-axis labels. (a, b) Mean annual temperature and mean annual precipitation in Chengjiang county from 1959 to 2020; (c, d) Mean annual values of total nitrogen (TN, blue lines), total phosphorus (TP, pink polygon), chlorophyll *a* (blue lines), and phytoplankton density (pink polygon) of surface water in Fuxian Lake from 1980 to 2020; (e) Population size (blue lines) and gross domestic product (GDP, pink polygon) of Yuxi City from 1978 to 2020; (f) Total annual fertilizer consumption (blue lines) in Chengjiang county and fish production (pink polygon) in Fuxian Lake from 1987 to 2020. The climate and water quality data were shared by the Fuxian Lake Station of Plateau Deep Lake Research. The economic data was cited from the Bureau of Statistics of Yunnan Province. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

spatial variation of chironomid assemblages within Fuxian Lake, and the site scores on the first axis (PCA1) were retrieved as a proxy for the structure change of chironomid assemblages along the water depth gradient. Mantel tests were conducted to estimate the correlations between physicochemical properties and biotic features of subfossil chironomid assemblage, including head capsule concentration, alpha diversity and spatial structure (Mantel, 1967). Mantel's values were retrieved and illustrated in decreasing arrangement to visually show the degree of correlation between biological and environmental variables. The significance of Mantel test was calculated with 9999 permutations using the R package 'vegan'. The head capsule counts were transformed using the Hellinger method before PCA and Mantel test analysis (Legendre and Fortin, 2010).

The stratigraphy of chironomid assemblages in the sediment core was mapped using the R package 'rioja'. Stratigraphical constrained cluster analysis (CONISS) was conducted to zone chironomid assemblage. The statistical significance of zone boundaries was tested using the broken stick mode (Bennett, 1996). Pearson correlation and linear

regression analysis were conducted to explore the relationship between nutrient indicators and chironomid concentration. All statistical analyses and illustrations were completed in the R environment (R Core Team, 2016).

4. Results

4.1. Subfossil chironomid assemblage across the water depth transects

In this study, 2756 chironomid head capsules from the thirty-five surface sediment samples were identified into 32 morphospecies (Table S1). The three subfamilies Chironominae, Orthocladiinae and Tanytopodinae account for 56.25%, 34.38% and 49.37% of the total richness, and 48.84%, 3.61% and 47.57% of the total abundance, respectively. The most dominant species were profundal *Procladius* and *Tanytarsus mendax* type, contributing to 47.06 and 30.91% of total abundance (Table S1, Fig. 3). The species composition of chironomid assemblages exhibited a distinct bathymetric pattern. The abundance of

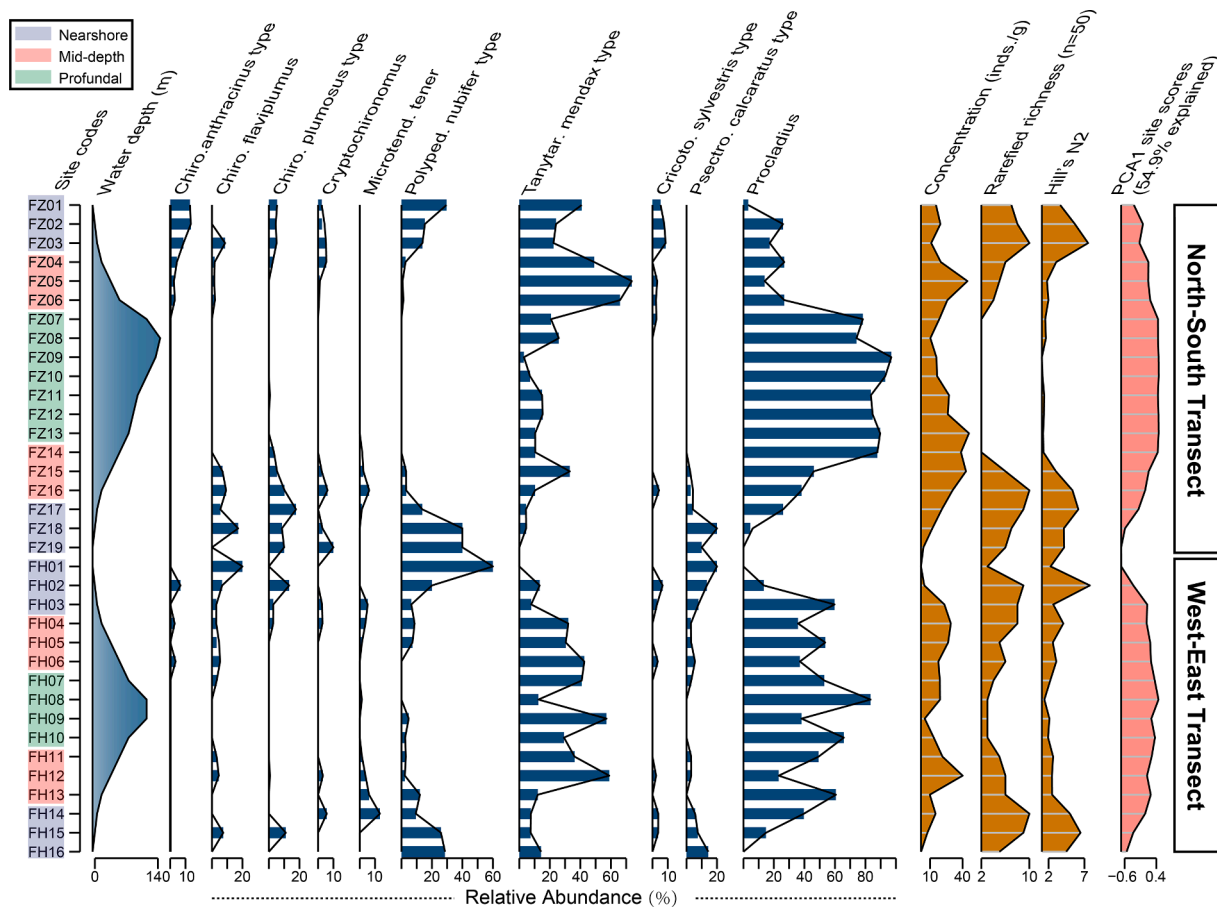


Fig. 3. Spatial variation in species composition, head capsule concentration, diversity index, and PCA 1 scores of chironomid assemblage along the two transects. Only taxa with a relative abundance >1% were presented. Abbreviation: *Chiro.*, *Chironomus*; *Microtend.*, *Microtendipes*; *Polyped.*, *Polypedilum*; *Tanytar.*, *Tanytarsus*; *Cricoto.*, *Cricotopus*; *Psectro.*, *Psectrocladius*.

littoral species, such as *Polypedilum nubifer* type, *Psectrocladius calcaratus* type, *Cricotopus sylvestris* type and *Chironomus*, rapidly decreased along water depth gradient with sporadic occurrence in mid-depth and profundal zones. *T. mendax* type was most abundant in mid-depth zones, accounting for $37.9 \pm 20.3\%$ of total abundance (Fig. 3, Fig. S4). The dominance of taxa *Procladius* increased with water depth, with a relative abundance of $76.4 \pm 17\%$ in profundal samples. The concentration of head capsules showed a general unimodal distribution pattern, with the highest value in the mid-depth zone, followed by the nearshore and profundal zones (Table 1, Fig. 3, Fig. S5a – c). As indicated by the rarefied richness and Hill's N2 index, the alpha diversity of subfossil chironomid assemblages exhibited a decreasing trend along the water depth gradient (Table 1, Fig. 3, Fig. S5d – f). The representativeness index of richness showed that nearshore and mid-depth samples comprised 0.28 ± 0.09 and 0.21 ± 0.07 of whole-lake richness but rapidly decreased to 0.09 ± 0.03 in profundal samples (Table 1, Fig. 4). For assemblage composition, the Bray-Curtis distance revealed that the mid-depth zone had the highest similarity with the entire chironomid assemblage, followed by profundal and nearshore zones (Table 1, Fig. 4). The ordination analysis showed that assemblage structure varied

along the water depth gradients, mainly characterized by the increased abundance of *Procladius* and the decrease of some littoral taxa. In addition, the whole-lake assemblage was located near the center of the mid-depth samples and represented by the average of all sites (Fig. 5).

Pearson correlation analysis suggested that all physicochemical parameters of bottom water significantly correlated with water depth except for nutrients (i.e., TOC, TN and TP). The DO, water temperature, and chlorophyll *a* were highest and relatively stable in nearshore zones while rapidly declining from mid-depth to profundal zones, with the minimum values of 1.81 mg/L, 13.7 °C and 0.39 µg/L. The Mantel test indicated that the spatial variation in the head capsule concentration (HCs), rarefied richness, and assemblage structure of the chironomid assemblage was significantly correlated with water depth and depth-related variables (Fig. S6).

UpSetR analysis further depicted the species occurrence patterns of subfossil chironomid along the water depth gradients (Fig. 6). Two species were only observed in the nearshore samples, six in mid-depth samples, and one in profundal samples. Twenty-one species were shared between nearshore and mid-depth zones, however, only eleven species were shared between profundal and shallow zones.

Table 1
Features of chironomid assemblage from surface samples in Fuxian Lake.

Zones	Nb. of sites (n)	Concentration (ind./g)	Rarefied richness	Hill's 2 Number	Representativeness Index	Bray Index
Nearshore	12	$11.44^a \pm 7.25^b$	7.58 ± 2.02	4.98 ± 1.69	0.28 ± 0.09	0.57 ± 0.17
Mid-depth	12	28.99 ± 10.44	5.75 ± 1.88	2.81 ± 1.02	0.21 ± 0.07	0.76 ± 0.08
Profundal	11	19.81 ± 10.26	2.45 ± 0.66	1.54 ± 1.02	0.09 ± 0.03	0.61 ± 0.08

Notes: a, average value; b, standard deviation.

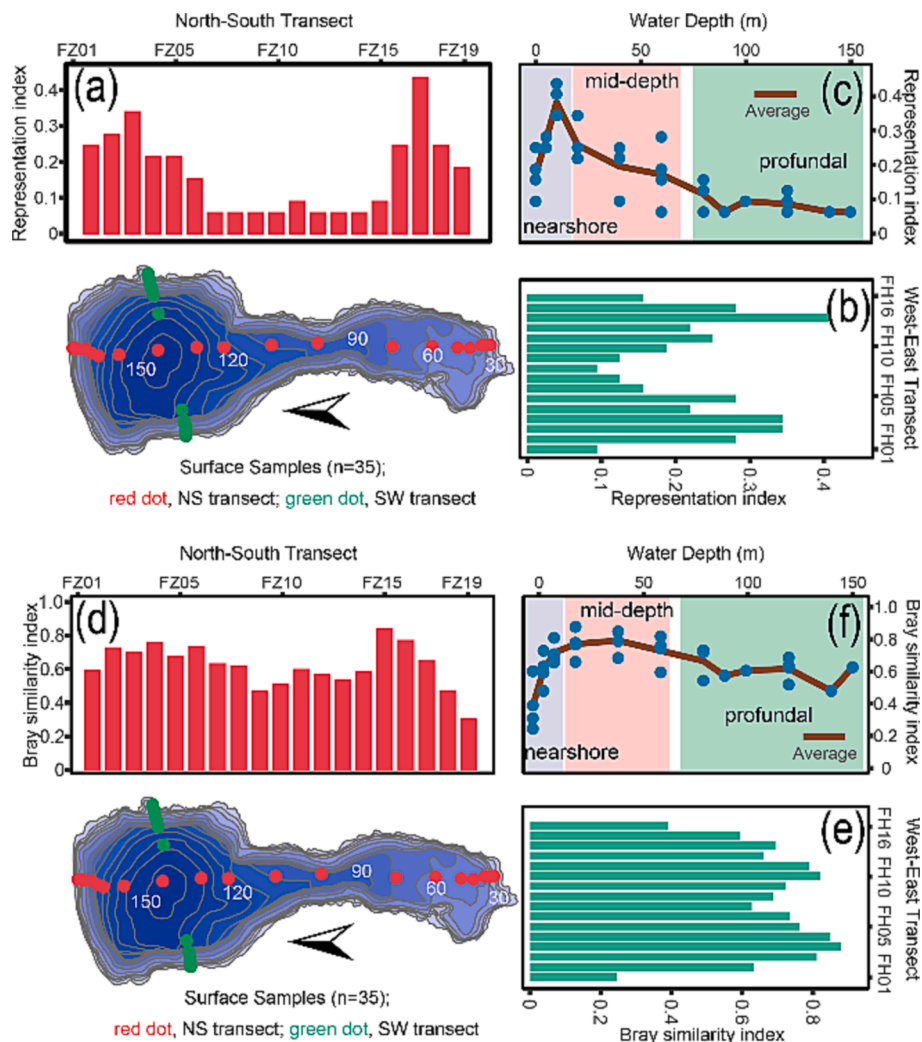


Fig. 4. The spatial variation in the representativeness of chironomid assemblages from surface samples. The bar plots reveal that littoral and mid-depth samples outperform profundal samples in representing whole-lake richness (a-b) and species composition (d-e). The scatter plots show the relationship between water depth and richness representativeness index (c) and Bray similarity index (e).

4.2. Comparison of chironomid stratigraphy between the two sediment cores

In this study, chironomid assemblages were analyzed from two sediment cores obtained at different water depths (40, 150 m) to examine the impact of coring sites on paleolimnological inference. Consistent with the findings from surface samples, the sediment core FN12 from the mid-depth zone exhibited a much higher species richness than the profundal zone core FN05, with 15 species in FN12 and eight species in FN05. The dominant species in core FN12 was *T. mendax* type (Fig. 7), accounting for $50.9 \pm 14.8\%$ of total abundance, followed by *Procladius* ($21.1 \pm 8.8\%$) and *Cryptochironomus* ($6.6 \pm 6.8\%$). In contrast, core FN05 was dominated by profundal species *Procladius* ($95.8 \pm 4.7\%$), while *T. mendax* type ($3.9 \pm 4.5\%$) and other species ($<1\%$) exhibited extremely low abundance with sporadic occurrence throughout the sediment core (Fig. 8). The head capsule concentration remained relatively stable and low before 2005 CE, but showed a rapid increase after that in both sediment cores (Fig. 7, Fig. 8).

The chironomid zones were determined using CONISS cluster analysis in combination with the broken stick model. Three significant zones were identified in 1979 CE and 2005 CE in core FN12, while core FN05 exhibited two zones at the age of 2005 CE. The PCA 1 site scores, a commonly used proxy for community structure, also supported the identified zones with abrupt changes occurring at the same timing points

(Fig. 7, Fig. 8). The temporal changes in chironomid assemblage differed between the two cores due to significant variations in species composition. Specifically, the transition from zone a (1877–1979 CE) to zone b (1979–2005 CE) in core FN12 was characterized by a marked increase in *T. mendax* type and a decrease in *Cryptochironomus*, *P. nubifer* type, *Psectrocladius*, *Cryptotendipes* and *Chironomus flaviplumus* type (Fig. 7). The onset of zone c (2005–2022 CE) was accompanied by an increase of *Procladius*, *C. flaviplumus* type, and *C. sylvestris*, while *T. mendax* type, *Cryptochironomus*, *P. nubifer* type and *Psectrocladius* exhibited a decline (Fig. 7). In core FN05, the notable shift in chironomid assemblage was primarily driven by the surge of *T. mendax* type since 2005 CE. It is noteworthy that the head capsule concentration of *T. mendax* type and *Procladius* showed a positive correlation with sedimentary TOC content ($p < 0.05$). However, *Procladius* deviated from this linear relationship with TOC content in the upper three samples of core FN05 (Fig. 9).

5. Discussion

5.1. Poor representativeness of the chironomid assemblages in profundal zone

Paleolimnological reconstructions often rely on subfossil assemblages retrieved from a single sediment core in the deepest zone of a lake, assuming it represents the entire-lake assemblage (Heiri, 2004;

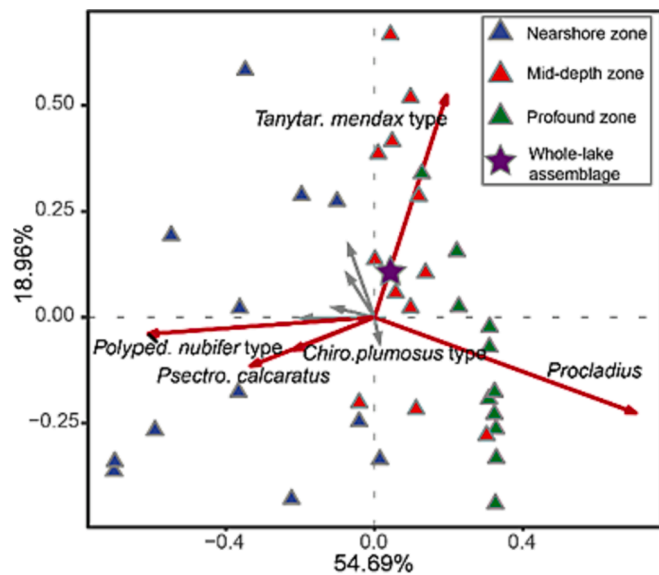


Fig. 5. Ordination analysis of chironomid assemblages from surface samples. Individual taxa with abundance >1% were represented with solid vectors and the five most important taxa are labeled in red. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

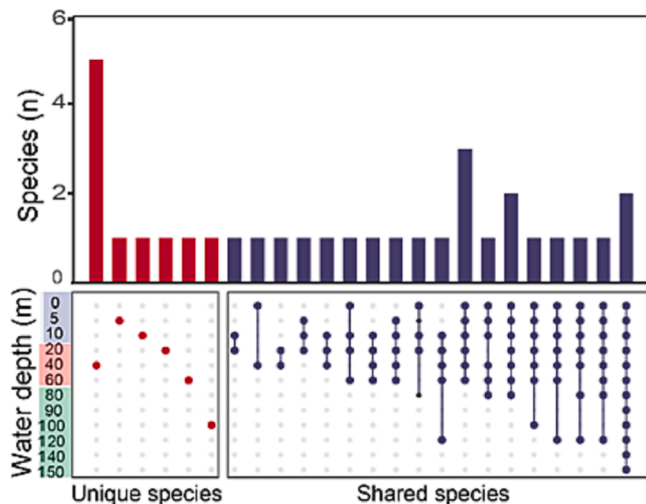


Fig. 6. The number of unique and shared species of surface sediment samples along water depth gradients.

Hofmann, 1988). However, this assumption is primarily based on studies conducted in small and shallow lakes (Table S2), where the transport and redeposition process more thoroughly homogenization the head capsules of chironomid larvae (Eggermont et al., 2007). In this study, we assessed the validity of this assumption in a large and deep oligotrophic lake by evaluating the representativeness of the chironomid assemblage in the deepest zone, both at the individual taxa and community levels (i.e., richness and species composition). The representativeness index of richness revealed that the subfossil chironomid assemblage in profundal samples contained an extremely low proportion of the total richness (Table 1, Fig. 3). Our findings align with previous studies conducted in large, deep lakes, such as Lugu Lake (Zhang et al., 2013) and Bosten Lake (Zhang et al., 2012). As numerous studies have shown, most chironomid larvae prefer to inhabit nearshore zones due to the availability of diverse microhabitats and favorable environmental conditions compared to deep zones (Kurek and Cwynar, 2009; Zhao

et al., 2019). The Mantel test indicated that the richness of subfossil chironomid assemblage was closely related to some physicochemical properties of bottom water (Fig. S6). Specifically, pH, conductivity, water temperature, and dissolved oxygen were identified as essential factors controlling the distribution of chironomids (Mousavi, 2002; Zhang et al., 2011; Verbruggen et al., 2011). In a large stratified lake like Fuxian Lake, the low temperature and anoxic conditions in the deep zones strictly limit the colonization of many chironomid taxa, except for those profundal species that can tolerate extreme environments. In addition, other unrecorded habitat characteristics, such as aquatic vegetation coverage and substrate type, also influence the occurrence of certain species. For instance, submerged plants are primarily distributed along the margin of Fuxian Lake (0.5–14 m, Zhang et al., 2023), which may explain the low abundance of some vegetation-related species in mid-depth and profundal zones (e.g., *P. nubifer* type and *C. sylvestris* type, Fig. 3).

Despite dissolved oxygen levels rapidly declining below 10 m, the mid-depth zone exhibited comparable richness to the nearshore zone (Table 1, Fig. S5). The UpSetR analysis showed that 21 (65.6%) taxa were shared between the nearshore and mid-depth zones, indicating the presence of many littoral species in mid-depth zones (Fig. 6). The steep slope of the lake basin and wave-induced sediment resuspension facilitate the horizontal transport of head capsules process from the nearshore to offshore zones (Howard et al., 2010; Verschuren and Eggermont, 2006). However, in large, deep lakes, where the lake basin is relatively flat and wave disturbance on sediment is weaker in deep zones, the homogenization effect on subfossils during the burial process is reduced (Eggermont et al., 2007; Larsen and MacDonald, 1993; Huang et al., 2016). Consequently, only eleven species were shared between mid-depth and profundal zones (Fig. 6).

As expected, the chironomid assemblage in profundal zones showed the lowest resemblance to the entire-lake assemblage due to its extremely simple species composition. The PCA analysis indicated that the species composition of chironomid assemblages varied with water depth (Fig. 5), characterized by an increased dominance of profundal species *Procladius* (Fig. 3). The subfossil chironomid assemblages in mid-depth samples exhibited the highest similarity with entire-lake assemblage, rather than nearshore samples (Fig. 4). The result is reasonable as mid-depth zones include nearshore species and maintain the dominance of *T. mentax* type and *Procladius*, as observed in the profundal samples. Consistent with our study, the excellent representativeness of subfossil chironomid in mid-depth zones has also been reported in other deep lakes (Raposeiro et al., 2018; Biskaborn et al., 2019).

5.2. Depth-specific responses of the chironomid assemblage to environmental change in Fuxian Lake

In deep stratified lakes, chironomid assemblages may exhibit bathymetry-specific responses to the environmental forcings within the lake (Frossard et al., 2014). This study compared the ecological response patterns of chironomid assemblages from mid-depth (40 m) and profundal zones (150 m) to environmental change in Fuxian Lake. The results showed that the mid-depth sediment core could provide more comprehensive and robust paleo-ecological information than the deepest zone due to the better representativeness of local chironomid assemblage. The CONISS analysis indicated that the subfossil chironomid assemblage from the core FN12 experienced two distinct shifts at the timing points of 1979 and 2005 CE, while the core FN05 only recorded the latter shift. Previous studies demonstrated that the assemblage structure of diatoms (Li et al., 2011) and cladocerans (Liu et al., 2009) underwent significant changes due to the accelerated eutrophication process and colonization of *N. taihuensis* since the 1980s. The change of chironomid assemblage in 1979 CE could be attributed to the same driving factors. In oligotrophic lakes, nutrient enrichment increases organic matter accumulation in lake sediment (Alcocer et al., 2021). The nutrient indicators showed that more organic

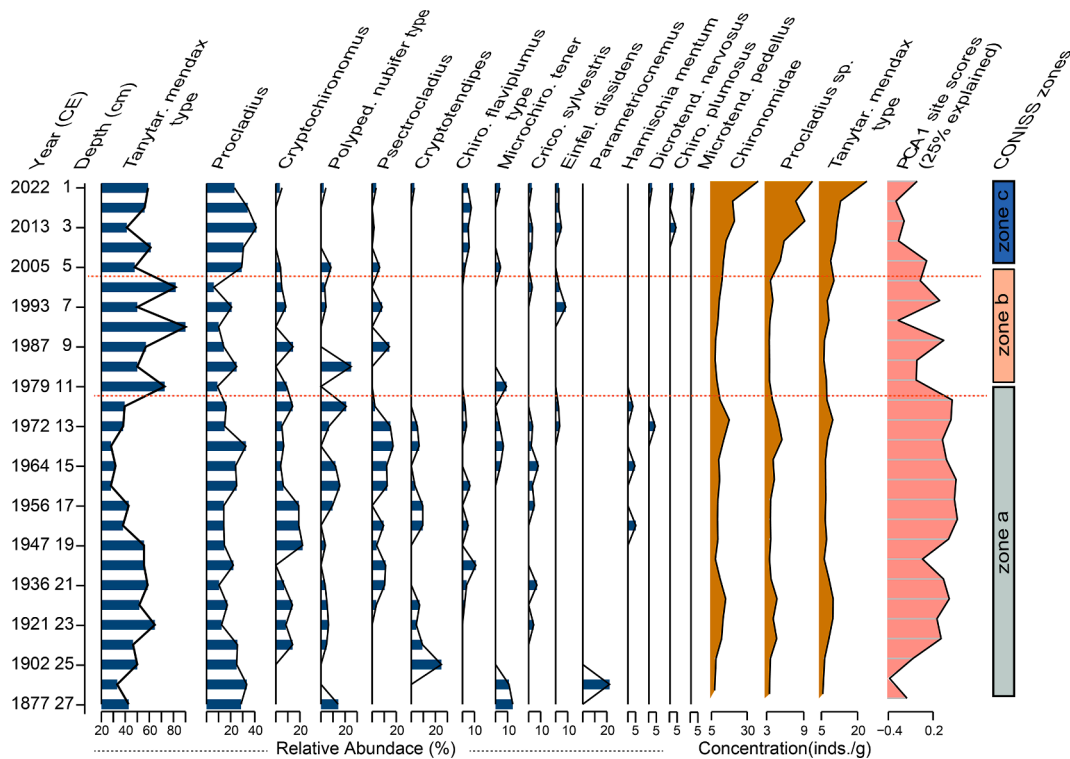


Fig. 7. Stratigraphic plot of chironomid assemblages in core FN12 (40 m). The brown area plots indicate that the head capsule concentration of chironomids and the two dominant taxa rapidly increased since 2005 CE. PCA1 site scores show that the chironomid assemblage experienced two distinct changes in 1979 CE and 2005 CE. Abbreviation: *Tanytar.*, *Tanytarsus*; *Polyped.*, *Polypedilum*; *Chiro.*, *Chironomus*.

matter was preserved in sediment since the 1980s, mainly originating from autochthonous sources (He et al., 2020). The synchronic increase of *T. mendax* type, a typical small collector-filterers that feeds on suspended organic matter from 1979 to 2005, could be attributed to the nourishing effect of more available food (Vodopich and Cowell, 1984). The positive correlation between the concentration of *T. mendax* type and sedimentary TOC content also supports the influence of the nutrient process on the chironomid assemblage. Indeed, the whole chironomid community likely benefited from the increased TOC in Fuxian Lake, as a comparison between two historical investigations showed that the biomass and density of chironomids in 2005 increased 1.7 times compared to that in 1980 (Xiong et al., 2008). Although *N. taihuensis* is zooplanktivorous without direct predation on zoobenthos, it could indirectly influence chironomid assemblage through the top-down effects on the pelagic food web (Selene et al., 2020).

Interestingly, the abundance of *T. mendax* type in the core FN05 remained stable and low during the same period. *Procladius* showed an overwhelming dominance in the deepest zone before 2005 CE. Since *Procladius* is a top predator in the chironomid community that primarily feeds on microcrustaceans and other chironomids (Baker and McLachlan, 1979; Sephton, 1987; Zhang et al., 2011), their predation on *T. mendax* may offset the nourishing effect of increased nutrients. The assumption is reasonable as the concentration of *Procladius* showed an increasing trend during the period (Fig. 8). In 2005 CE, chironomid assemblage from both cores experienced distinct changes in species composition and head capsule concentration, synchronic with the abrupt increase in allochthonous nutrients. The increased abundance of eutrophic taxa *C. flaviplumus* and *C. plumosus* in the mid-depth zone suggested that eutrophication was still the main driving factor of chironomid assemblage change. It is worth noting that the relative abundance of *Procladius* exhibited a contrasting trend in the mid-depth and profound zones.

The concentration of *Procladius* exhibited a positive correlation with TOC content in both sediment cores; however, it switched to a negative

relationship since 2013 CE in the sediment core FN05 (Fig. 9d). The adverse relationship between sedimentary content and *Procladius* has also been reported in the previous study on a deep lake (Frossard et al., 2014). The availability of oxygen is often the critical factor determining the distribution of chironomids in the profundal zone of deep stratified lakes (Raposeiro et al., 2018). *Procladius* is a key profundal indicator frequently found in the hypolimnetic zone of deep lakes (Francis, 2001). Its mobility enables its widespread distribution within a lake (Chique and Potito, 2019, Fig. S4). The increased TOC accumulation in sediment can promote bacterial respiration, which further exacerbates hypoxic conditions in profundal zones and likely triggers the migration of *Procladius* to shallow zones (Jones et al., 2008; Zhang et al., 2013).

5.3. The implication for choosing coring site in large, deep lakes

For paleolimnological studies, it is crucial that the retrieved biological assemblages comprehensively reflect the entire-lake assemblages, which are often based on a single core from the profundal region of lakes (Rumes et al., 2005). Previous studies have well proved the rationality of this approach in small, shallow lakes, while the controversy is still present when it comes to large, deep lakes (Table S2). In this study, we evaluated the representativeness of chironomid assemblage along the water depth transects using 35 surface samples and compared the response patterns to environmental change with two sediment cores from different depth zones. Our findings suggest that profundal zones are not ideal coring sites for paleolimnological studies on chironomids in Fuxian Lake due to their lowest richness, head capsule concentration and similarity to entire-lake assemblage (Table 1, Fig. 3). As mentioned earlier, the harsh environmental conditions and weak transport processes in profundal zones likely contribute to the low representative of chironomid assemblage. The simplicity of assemblage composition also limits the statistical significance of conducting sophisticated numeric methods (e.g., redundancy analysis, RDA; variance partitioning analysis, VPA) for assessing the ecological effects of different driving factors,

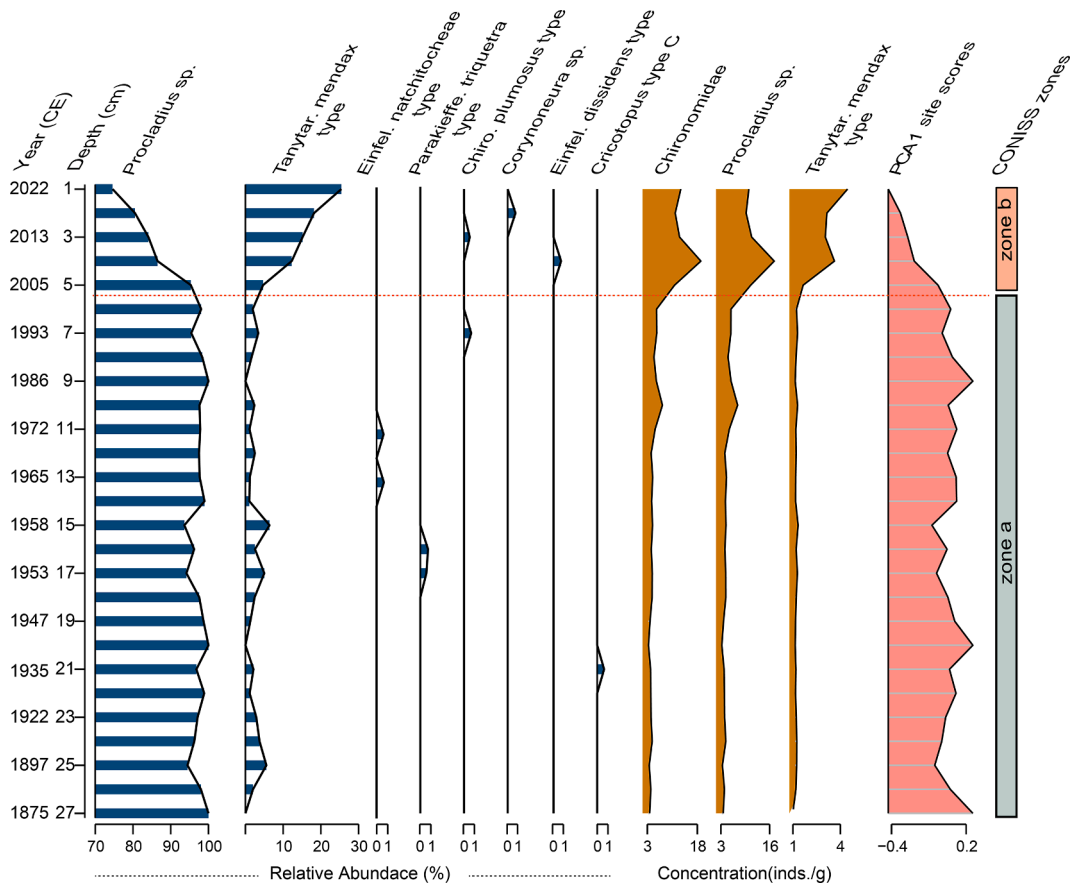


Fig. 8. Stratigraphic plot of chironomid assemblages in core FN05 (150 m). The brown area plots indicate that the head capsule concentration of chironomids and the two dominant taxa rapidly increased since 2005 CE. PCA1 site scores show that the chironomid assemblage experienced one distinct change in 2008 CE. Abbreviation: *Tanytar.*, *Tanytarsus*; *Einfe.*, *Einfeldia*; *Parakieffe*, *Parakiefferiella*; *Chiro.*, *Chironomus*.

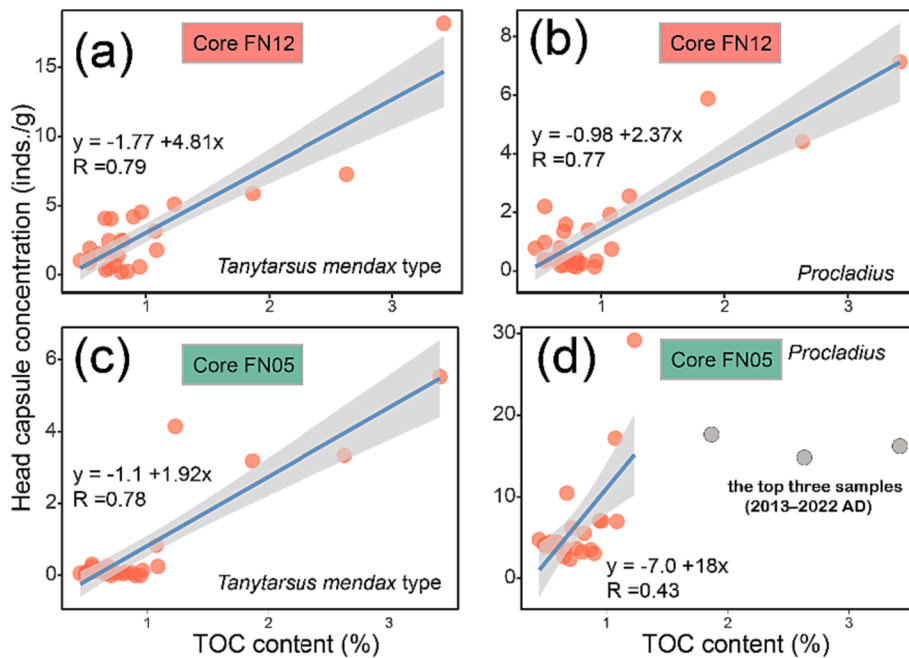


Fig. 9. Scatter plots depicting the relationship between TOC content and the concentration of *T. mendax* type (a,c) and *Procladius* (b,d) in the sediment core. Note that the concentration of *Procladius* in the upper three samples displayed a distinct variation pattern and was excluded from the linear regression analysis (d).

thus reducing the information conveyed by subfossil chironomid assemblages (Quinlan et al., 2001). Moreover, the unrepresentative assemblages from profundal sediment core may decrease the sensitivity of chironomid assemblages to environmental change. In contrast, the diatom and zooplankton assemblages in Fuxian Lake have shown significant changes in biomass and species composition since the 1980s in response to accelerated eutrophication and exotic fish invasion (Li et al., 2011; Liu et al., 2009; Fig. 2; Fig. 10). However, no such signals of environmental change were detected in the core from the profundal zone, despite the synchronic shift observed in the subfossil chironomid assemblage from the mid-depth zones. Reliable paleolimnological inferences can be made based on the ecological traits of observed species, especially indicator taxa (Larocque et al., 2001). However, the sparse diversity in profundal zones makes it risky to draw any conclusions without the support of robust statistical analysis and abundant autecological information (Biskaborn et al., 2019; Chique and Potito, 2019). Instead, the diverse chironomid assemblage from the mid-depth zones provides a more comprehensive and robust source of paleolimnological information.

Consistent with previous studies on large lakes (Brodersen and Lindegaard, 1999; Raposeiro et al., 2018), our study found that samples from mid-depth zones have higher species richness, head capsule concentration, and similarity with the entire-lake assemblage than profundal zones (Fig. 4, Fig. S5). Additionally, mid-depth zones generally exhibit more stable sedimentary conditions and head capsule concentration than nearshore zones (Larsen and MacDonald, 1993; Bloesch, 1995). Investigating the spatial distribution of chironomid assemblages can aid in selecting an appropriate sampling site. However, if such information is unavailable, we recommend mid-depth zones as coring sites when chironomid capsules are used as biological indicators in paleolimnological studies of large, deep lakes.

6. Conclusion

This study investigated subfossil chironomid along two transects in Fuxian Lake to assess the methodological rationality of using a single sediment core to represent the entire-lake assemblage. Analysis of 35 surface samples revealed that chironomid assemblage from each sample site accounted for only a tiny proportion of the total richness in Fuxian Lake. Richness decreased along the water depth gradients, with the profundal zones showing the poorest representativeness. Instead, chironomids from mid-depth zones exhibited the highest similarity to the entire-lake assemblage in aspect of species composition, followed by the profundal zone and nearshore zone. The poor representativeness of chironomid assemblages in the profundal sample was likely attributed to the harsh living environment and weak transport process in deep zones. Further, we compared the response patterns of chironomid assemblage from different depth zones to environmental change in Fuxian Lake over the past 150 years. Our result indicated that chironomid assemblages showed depth-specific responses to local environmental change. In response to eutrophication, the chironomid assemblages from the mid-depth zones experienced two distinct shifts in 1979 CE and 2005 CE. However, the core from the profundal zone only detected one change in 2005 CE, likely reflecting the exacerbated hypoxic conditions in the deep zone. These different response patterns likely resulted from the significant discrepancy in species composition of chironomid assemblages and corresponding interspecies interactions between the two coring sites. Based on evidence from surface sediment and sediment cores, the optimal coring sites for conducting subfossil chironomid analysis are around the water depth of 50 m in Fuxian Lake. Considering its good representativeness, high capsule concentration, and relatively stable sediment conditions, the mid-depth zones should be prioritized as the coring sites in paleolimnological studies to obtain more comprehensive and robust inferences rather than commonly supposed

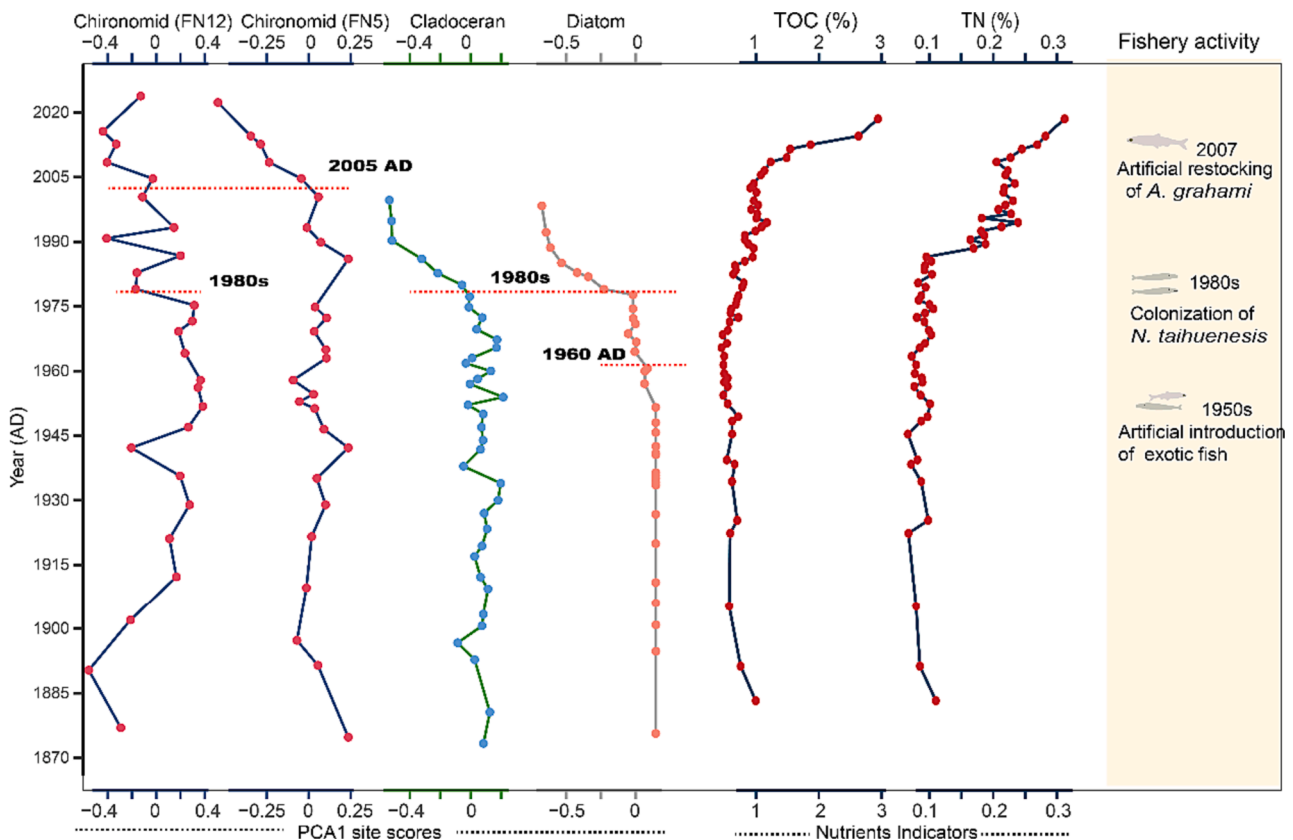


Fig. 10. A comparison of the temporal changes in biological assemblages, eutrophication process, and fishery activities. The diatom and cladoceran data were obtained from Li et al. (2011) and Liu et al. (2009), respectively.

profundal zones.

CRedit authorship contribution statement

Wenlei Luo: Methodology, Conceptualization. **Wu Han:** Methodology, Software, Writing – review & editing. **Zhenyu Ni:** Data curation, Supervision, Software. **Qi Lin:** Methodology, Writing – review & editing. **Weiwei Sun:** Methodology, Writing – review & editing. **Yan Wang:** Writing – review & editing, Investigation. **Yang You:** Methodology, Writing – review & editing. **Enlou Zhang:** Writing – review & editing, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2023.110848>.

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