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Hydrological isolation accelerates algal blooms in floodplain lakes: Biomarker evidence from Dongting Lake, China and its satellite lake

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ABSTRACT

Hydrological disconnection from main channels (either via natural siltation or due to construction of hydrological infrastructures) is modifying biogeochemical cycling in river-floodplain systems. Knowledge on how this process influences phytoplankton composition and harmful algal blooms (HABs) in floodplain lakes is quite scant due to the lack of long-term water quality monitoring and the concurrent influence of multiple drivers of change. Here, chlorophyll and carotenoid pigment biomarkers from dated sediment cores were analyzed from Dongting Lake (China's second largest freshwater lake) and one of its satellite lakes (Donghu) in the Yangtze floodplain, to evaluate the long-term influence of hydrological isolation on algal community composition and HABs. The results showed that pigment concentrations and the ratio of canthaxanthin/diatoxanthin (which reflects the relative abundance of cyanobacteria to diatoms) increased after the 1910s in Donghu Lake, when it was separated from Dongting Lake due to siltation. In contrast, significant increases in pigments started from the 1980s in Dongting Lake. Variance partitioning analysis revealed that the combined influence of hydrology, temperature and anthropogenic pollutants explained the largest proportion of variance (33.4%) in the pigment assemblages in Donghu Lake, followed by the joint effects of anthropogeny pollutants and hydrology (23.6%) and the sole effects of anthropogenic pollutants (14.9%) and hydrology (11.2%). In Dongting Lake, anthropogenic pollutants explained 24.5% of the variance in pigment assemblages solely, followed by the additive effects of anthropogenic pollutants and temperature (17.8%). These long-term analyses therefore demonstrate that, in combination with anthropogenic pollutants and warming, hydrological isolation from the main channel may stimulate algal production and the prevalence of cyanobacteria, whereas free hydrological connection with the Yangtze main channel seems to alleviate such HABs in these Yangtze floodplain lakes.

1. Introduction

Shallow freshwater lakes around the globe are suffering from severe ecosystem deterioration such as harmful algal blooms (HABs) and diminished resilience, especially in the densely-populated floodplain areas (H. Wang et al., 2019; Hou et al., 2022; Han et al., 2024). For lentic waterbodies, algal production and community composition are mainly regulated by nutrients and climate change (Paerl and Huisman, 2008; Taranu et al., 2015; Hellweger et al., 2022). In river-floodplain systems, the periodical flooding sustains water, sediment and nutrient exchange between floodplain lake basins and the main channel (Junk et al., 2005; Palmer and Ruhi, 2019; Li et al., 2021). Therefore, natural hydrological connection with the main channel works as an important confounding factor controlling the key limnological conditions including hydrological settings (e.g., water residence times and water flushing rates), nutrient concentrations, light availability and hence algal production and community composition in floodplain lakes (Squires and Lesack, 2002; McGowan et al., 2011; Li et al., 2019; 2020). Previous studies suggest that the influence of flooding on algal production in floodplain lakes depends on the relative nutrient loading of the main channel and

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the floodplain lakes themselves. In floodplain lakes connected to a main channel with relatively higher nutrient levels, algal production responds to flood frequency in a unimodal way where lakes with intermediate flood frequency have the highest production due to the trade-off between light and nutrients, regulated by riverine sediment and nutrient influxes, respectively (Squires and Lesack, 2002). In floodplain lakes with a relatively nutrient-poor main channel, algal production declines with increasing flood frequency, as the suspended particles and water influxes from the main channel may deteriorate light conditions and dilute nutrients and algal biomass in floodplain lakes (Sokal et al., 2010; Li et al., 2023).

Although flooding maintains the dynamics and fertility of floodplains, it is one of the most damaging and life-threatening natural hazards (Johnson et al., 2020). Consequently, hydrological infrastructures such as dams and reservoirs are extensively built for flood control, as well as other benefits such as hydropower and navigation, especially in developing countries in tropical and sub-tropical areas (Moran et al., 2018). These hydrological infrastructures have profoundly modified the

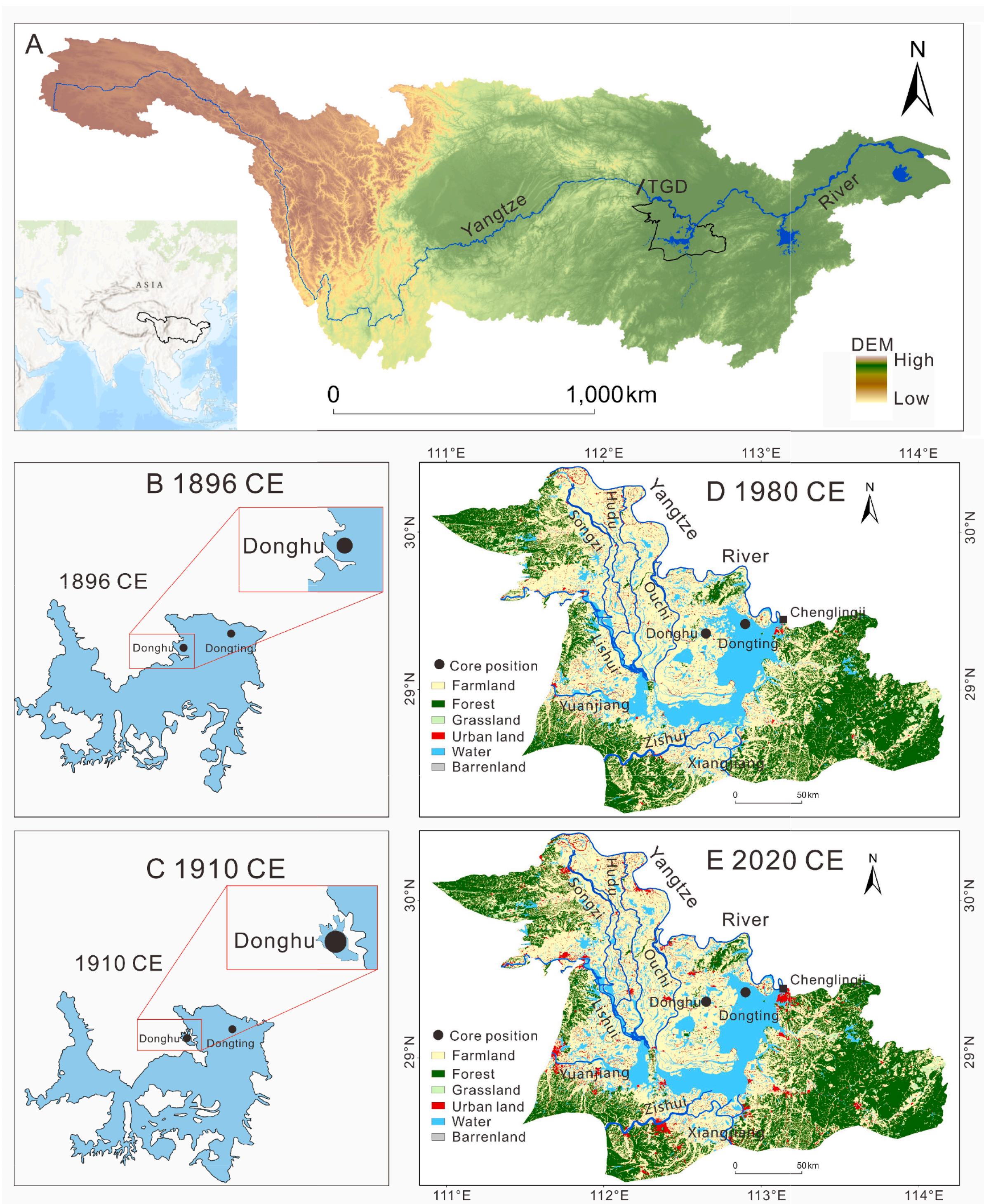

Fig. 1. Location of the study area in mainland China (A) with insets showing the changes in the water surface area of Dongting Lake and later isolation of Donghu Lake (B and C) and the land use and cover change in the Dongting Lake catchment (D and E). Maps B and C are sourced from Yu et al. (2020).

natural hydrological settings of the river continuum and the natural hydrological connection between the main channel and the lateral floodplain (J. Wang et al., 2019; R. Wang et al., 2019), as well as the biogeochemical cycling of nutrients (e.g., nitrogen, phosphorus and silica) in floodplain lakes and coastal areas (Maavara et al., 2020; Zeng et al., 2022). In combination with nutrients and climate change, the constructions of these hydrological infrastructures hold the potential to modulate eutrophication in floodplain lakes (Zeng et al., 2023; Salgado et al., 2024). The influences of hydrological infrastructures on algal production and community composition in floodplain lakes are sometimes controversial. On one hand, the prolonged water retention times after local dam construction promote the retention of algae, as well as nutrients, which fuel algal production (Chen et al., 2016). Therefore, hydrological infrastructure can facilitate algal production, in particular cyanobacteria which have a competitive advantage over diatoms in waterbodies with high water retention times (Richardson et al., 2018). One the other hand, local dam construction can stabilize water level fluctuations and improve water clarity by blocking riverine suspended particle influxes (McGowan et al., 2025; Zeng et al., 2024), which may stimulate the growth of submerged macrophytes that suppresses algae production (Scheffer et al., 1993). Therefore, hydrological infrastructures play a vital role, working either synergistically or antagonistically with nutrients and climate, in modulating eutrophication in floodplain lakes.

Under the scenario of global proliferation of dam construction and ongoing eutrophication, it is invaluable and necessary to gain a comprehensive understanding of the influence of hydrological disconnection from the main channel on water body eutrophication for the protection and restoration of these precious floodplain lakes. The influence of these hydrological infrastructures on algal community composition in floodplain lakes are difficult to define due to two main reasons (Zeng et al., 2024). Firstly, most of the hydrological infrastructures were built before the start of instrumental monitoring records, especially in developing countries (Battarbee et al., 2012). Therefore, the limnological consequences of hydrological alteration are inadequately captured by available monitoring datasets. Secondly, it is hard to disentangle the influences of hydrological alteration from other drivers such as anthropogenic nutrient inputs and climate change, both of which change concurrently with hydrological modification (Zeng et al., 2023). Alternatively, paleolimnological studies of lakes within the same catchment but contrasting hydrological connection (with the main channel) offer the best opportunity to generate records of sufficient length and quality to investigate the influence of hydrological alteration on floodplain lake ecosystems, while disentangling the impacts of other stressors.

Dongting Lake (28°18′–30°12′ N, 110°24′–113°6′ E) which is located in the middle Yangtze reaches is currently the second largest freshwater lake in China (Fig. 1). It is known as the “kidney”, which filters out the sediment load of the Yangtze River. The natural sediment siltation of Dongting Lake, in combination with land reclamation, has led to the shrinkage of the water surface area of Dongting Lake from > 5200 km^2 before 1900 CE to ~2500 km^2 after 2020 CE (Yu et al., 2020). This has resulted in the formation of more than 70 satellite lakes in the Dongting Lake catchment which have lost their hydrological connection with the Yangtze River (Fig. 1D and1E) (Wang et al., 2024), providing ideal materials for disentangling the influence of hydrological isolation on floodplain lake ecosystems from climate and nutrients. By comparing chlorophyll and carotenoid pigments in ^{137}Cs and ^{210}Pb dated sediment cores from Dongting Lake and one of its satellite lakes (Donghu Lake), this study aims to investigate how hydrological disconnection from the Yangtze main channel may influence algal community composition in the Yangtze floodplain lakes. Considering the large influxes of anthropogenic nutrients from the catchment, we hypothesize that hydrological isolation from the main channel may impede the flushing of the relatively nutrient-poor water from the Yangtze River and increase nutrient residence time, resulting in accelerating algal blooms in Donghu Lake. The results will provide guidelines for alleviating eutrophication in floodplain lakes and for evaluating the ecological consequences of newly planned dams.

2. Materials and methods

2.1. Study area

The Yangtze River (~ 6300 km) is the third longest river in the world. The middle and lower reaches of the Yangtze Basin are characterized by a floodplain landscape where flooding and meandering of the main channel formed ~ 600 shallow lakes with a water surface area >1 km^2 (NIGLAS, 2019). These Yangtze floodplain lakes uphold high biodiversity and > 15 of them have been designated as Ramsar Wetlands of International Importance (Ramsar Convention Bureau, 2025). As one of the most developed and densely-populated areas in China (more than 400 million people live in the Yangtze Basin), it generates ca. 40% of the nation’s economy (Dong et al., 2016) but due to intensive human activities, ~85% the Yangtze floodplain lakes are suffering from eutrophication (NIGLAS, 2019). Meanwhile, more than 50,000 dams were built in the Yangtze Basin, including the Three Gorges Dam (TGD) (Yang et al., 2011), which has resulted in changes in nutrient composition and declines in algal primary production in the East China Sea (Gong et al., 2006; Zeng et al., 2023).

The Dongting Lake Wetland (middle Yangtze floodplain, China) is one of the world’s 200 priority ecological protection areas. The three sub-lakes (East Dongting, West Dongting and South Dongting) of Dongting Lake have all been designated as Ramsar Wetlands of International Importance (Ramsar Convention Bureau, 2025). After the construction of the TGD, water and suspended sediment discharge substantially decreased (Yu et al., 2018), leading to the further shrinkage of the water surface area, and the edges of the lake became terrestrialised and covered with vegetation (Xie et al., 2015). Dongting Lake has a mean water surface area of ~ 2500 km^2 and mean water depth of ~ 6.4 m. The Dongting Lake catchment has experienced intensive social-economic development. Agricultural activities such as land reclamation have a long history in the catchment (Yu et al., 2020). After the release of the “reform and opening up” policy, industrial and urban activities profoundly intensified in the catchment, with urban areas increasing from 2.2% in 1980 CE to 4.1% in 2020 CE (Fig. 1D and 1E). Hydrologically, Dongting Lake is freely connected with the Yangtze River. Water discharge of the Yangtze flows into Dongting Lake via the “three outlets” (Songzi River, Hudu River and Ouchi River) in the west and flows back to the Yangtze River at Chenglingji at the northeast of the lake (Fig. 1A). During this process, large amounts of water and sediments from the Yangtze River are retained in Dongting Lake. It is estimated that > 30% of the annual water volume and ~ 80% of the annual sediment load (ca. 1.07 × 10^8 tons) of Dongting Lake were from the Yangtze River before the TGD operation in 2003 CE (Chen et al., 2016). Donghu Lake (29°18′ –29°25′ N; 112°31′–112°41′ E) used to be a part of Dongting Lake before the 1910s, and became separated from Dongting Lake after the 1910s due to land reclamation and natural siltation (Fig. 1B and 1C) (Yu et al., 2020). The water surface area and mean water depth of Donghu Lake is ~ 50 km^2 and ~ 2.3 m, respectively.

2.2. Sediment coring and dating

The Donghu Lake sediment core was collected in the central part of the lake basin (which normally represents the area of most uniform sedimentation) in 2022 CE. In larger Dongting Lake, the sediment core was taken from the east part of the lake in 2017 CE (Fig. 1), where the sedimentation conditions are relatively stable and hence more likely to build a reliable chronology (Xiang et al., 2002). Moreover, the east part of Dongting Lake is closer to Donghu Lake in terms of distance, making the two sediment records more comparable (Fig. 1). The water-sediment interface of the sediment cores was well preserved. The sediment cores were sectioned at 1-cm intervals in the field. Subsamples for the chronology and sedimentary elemental analysis were stored at 4 °C. Subsamples for pigment analysis were stored in the dark at −20 °C. ^{210}Pb and ^{137}Cs in the two sediment cores were presented in Wang et al. (2024) and Zeng et al. (2022).

2.3. Sedimentary pigment analysis

Sedimentary chlorophyll and carotenoid pigments in freeze-dried samples were firstly extracted using a mixture (5 ml) of acetone, methanol and deionized water (80: 15: 5, v/v) and dried under N_2. Then, the extracted pigments were dissolved using an injection solvent which is a mixture of acetone, ion-pairing reagent and methanol (70: 25: 5, v/v) and injected into a high performance liquid chromatography unit (HPLC) comprised of an Agilent 1200 series quaternary pump, autosampler, ODS Hypersil column (250 × 4.6 mm; 5 mm particle size) and photo-diode array (PDA) detector for separation, quantification and identification. Concentrations of the pigments were calibrated using commercial standards from DHI (Denmark) and expressed as nanomole pigment per gram organic carbon (nmol/g TOC). In this study, thirteen pigments indicating siliceous algae (diatoxanthin), cryptophytes (alloxanthin), cyanobacteria (canthaxanthin), N_2-fixing cyanobacteria (aphanizophyll), chlorophytes-cyanobacteria (lutein-zeaxanthin), chlorophytes (Chl *b*, pheophytin *b* and pheophytin *b*'), and total algae (Chl *a*, phaeophorbide *a*, pheophytin *a*, pyropheophytin *a*, and *β*-carotene) were quantified and are reported. Original data of sedimentary pigments in the Dongting Lake sediment core is from Zeng et al. (2023).

2.4. Geochemical analysis

After being digested using a mixture of HF, HCl, HNO_3 and $HClO_4$ (3: 0.5: 6: 0.5, v/v), major metal elements (i.e., Al and K) and total phosphorus (TP) were analyzed using inductively coupled plasma-atomic emission spectrometry (ICP-AES); and trace elements (i.e., Zn and Pb) were analyzed using inductively coupled plasma-mass spectrometry (ICP-MS). Zn and Pb mainly originate from mining activities and are used to reflect industrial activities in the catchment (Chen et al., 2016). Weathering of the Upper Yangtze Basin, which constitutes of Jurassic sandstone and the carbonates, releases large quantities of K into the Yangtze River (Chen et al., 2022). After eliminating the potential influence of grain size and organic matter by dividing K by Al, a typical inert and conservative lithogenic element in the earth surface, previous studies shows that the K/Al ratios in Dongting Lake is significantly related with the sediment load in middle Yangtze River (Chen et al., 2022; Wang et al., 2024). Therefore, the K/Al ratios was used to reflect the hydrological connectivity with the Yangtze main channel in this study. After the removal of carbonates using 5% HCl, total organic carbon (TOC) and total nitrogen (TN) in the sediment cores were analyzed using an element analyzer. Al, K, and TP in the sediment core from Donghu Lake are from Wang et al. (2024). TP and TN in the sediment core from Dongting Lake are from Zeng et al. (2023). TOC in the Dongting Lake sediment core is from Zeng et al. (2022).

2.5. Statistical analysis

Principal component analysis (PCA) was used to simplify and summarize the trend of the pigment dataset as the gradient length of the first axis of the detrended correspondence analysis was < 2 standard deviations (SD), indicating a linear analysis was most appropriate (Zeng et al., 2023). To compare the pigment records of the two lakes on a common scale, a single PCA was performed using a dataset combining the $\log(x + 1)$-transformed pigment data from the two lakes. To assess periods of major change in algal production in the two lakes, generalized additive models (GAMs) were fitted to time series of pigment PCA axis 1 using the gamm() function with the "mgcv" (version 1.8.31) package and the first derivatives were calculated using the "gratia" package. In order to investigate the potential drivers of algal production and community change (indicated by sedimentary pigments) in the two lakes, redundancy analysis (RDA) was carried out. According to previous studies from the middle Yangtze floodplain lakes (Chen et al., 2016; Zhang et al., 2019; Zeng et al., 2023), explanatory variables in RDA include proxies indicating hydrological connectivity with the Yangtze main channel (i.e., K/Al ratio) (Chen et al., 2022), anthropogenic pollutants from the catchment (i.e., Zn, Pb, TP and TN) (Wang et al., 2024), and climate variables (i.e., annual temperature anomalies and the drought-flooding index) (Supporting Information Figure S1). Both the pigment dataset and the explanatory variables were $\log(x + 1)$-transformed before RDA. For the RDA, explanatory variables with a variation inflation factors (VIF) > 10 were excluded due to high collinearity, and only the significant variables were presented. Significant variables were then assigned into the three groups (i.e., hydrological connectivity, anthropogenic pollutants and climate), and the variance partitioning analysis (VPA) was performed to evaluate the relative importance of hydrological connectivity, anthropogenic pollutants and climate change on algal production and community composition change in the two lakes (Hall et al., 1999). PCA and RDA were performed using Canoco 5.0 (Šmilauer and Lepš, 2014). The VPA was carried out in R (R Core Team, 2023) using the "vegan 2.5–4″ package (Oksanen et al., 2019).

3. Results

3.1. Chronologies of sediment cores

In Donghu Lake, the ^{137}Cs was firstly detected at 35 cm and gradually increased to a peak value of ~ 16.2 Bq/kg at 25 cm, followed by a decreasing trend to the top of the sediment core (Fig. 2A). In Dongting Lake, the peak value of ^{137}Cs (~ 22.1 Bq/kg) was reported at 39 cm (Fig. 2B). Therefore, this peak value of ^{137}Cs at 25 cm in the Donghu Lake sediment core and at 39 cm in the Dongting Lake sediment core was identified as 1963 CE, corresponding to the year with maximum nuclear weapon tests (Chen et al., 2019). In both Donghu Lake and Dongting Lake, excess ^{210}Pb ($^{210}Pb_{ex}$) showed a general exponential decreasing trend from the top to the bottom of the sediment cores (Fig. 2A and 2B). The chronologies of the sediment cores were established using ^{210}Pb and ^{137}Cs with the constant rate of supply (CRS) model.

3.2. Sedimentary pigments

The pigment assemblages showed a general increasing trend in the Donghu Lake sediments over the last 200 years (Fig. 3A). In Donghu Lake, concentrations of pigments indicating siliceous algae (diatoxanthin), cryptophytes (alloxanthin), cyanobacteria (canthaxanthin), N_2-fixing cyanobacteria (aphanizophyll), chlorophytes (lutein-zeaxanthin, Chl *b*, pheophytin *b* and pheophytin *b*') and all algae (Chl *a*, phaeophorbide *a*, pheophytin *a*, pyropheophytin *a* and *β*-carotene) were low and stable before the 1910s. Between 1910s and the 1980s, concentrations of most of the pigments started to increase with the exception of *β*-carotene which slightly decreased. During this period, biomarkers of N_2-fixing cyanobacteria (aphanizophyll), which were barely detected before the 1910s, appeared. After the 1980s, concentrations of all the pigments substantially increased and reached the maximum in the 2010s.

Similar to Donghu Lake, pigment assemblages in Dongting Lake sediments also showed an overall increasing trend over the last 200 years (Fig. 3B). The concentrations of all pigments were low in Dongting Lake before the 1980s. After the 1980s, concentrations of all pigments substantially increased, especially after the construction of the TGD in 2003 CE. Aphanizophyll (indicators of N_2-fixing cyanobacteria) were initially undetectable and profoundly increased after ~ 2005 in Dongting Lake.

The first and second PCA axis explained 80.47% and 9.79% respectively of the variance in the sedimentary pigments (Fig. 4). Correlation

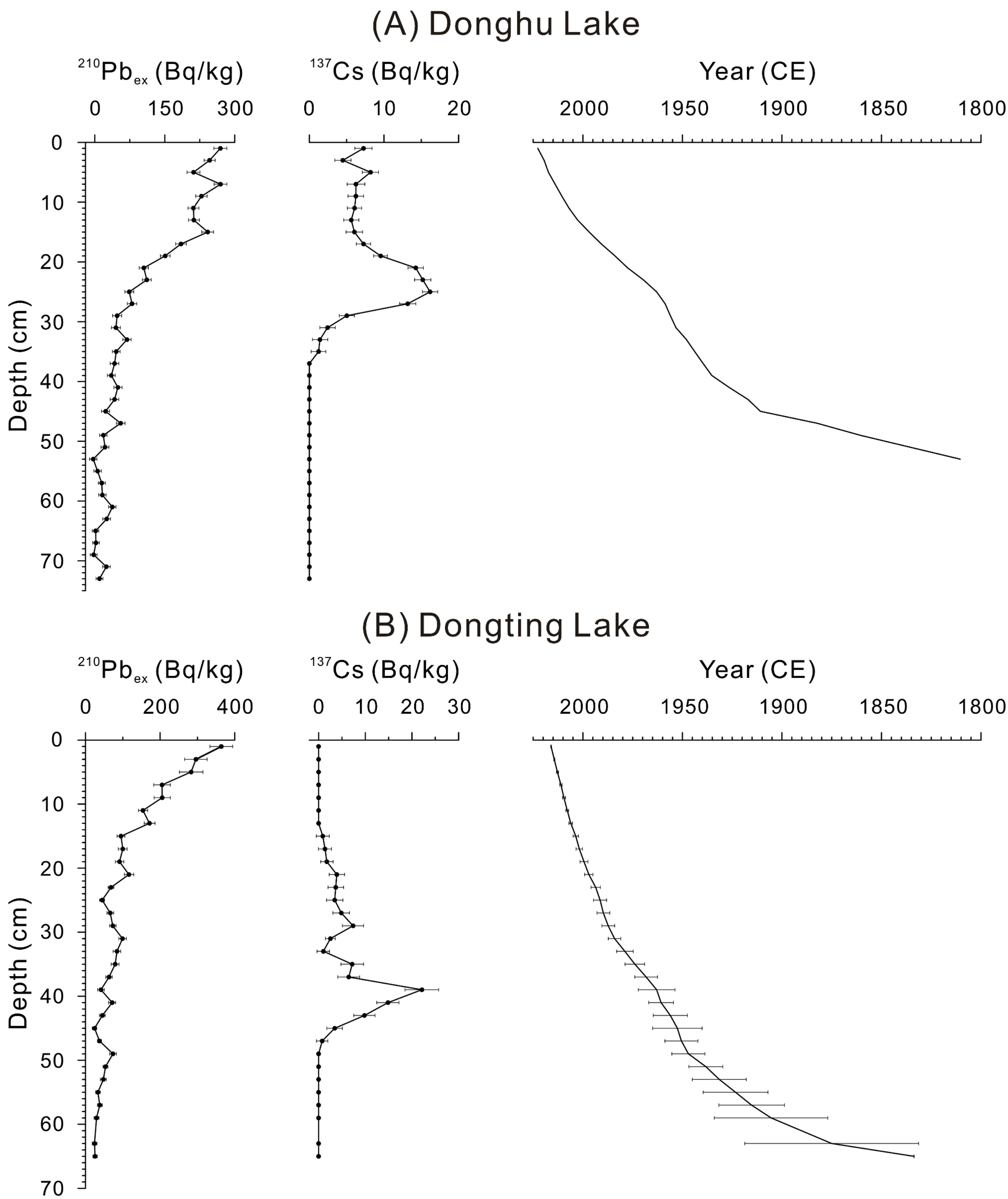

Fig. 2. Profiles of excess ^{210}Pb ($^{210}Pb_{ex}$), ^{137}Cs and the chronology of the sediment cores from Donghu Lake (A) and Dongting Lake (B).

analysis showed that the first PCA axis was significantly ($p < 0.001$) and positively ($r > 0.80$) correlated with all the pigments, and the second PCA axis was significantly ($p < 0.001$) and negatively ($r = -0.5$) correlated with indicators of N_2-fixing cyanobacteria (aphanizophyll). The trajectories of changes in both lakes mainly reflects increased abundance of all pigments. Sample scores on the first PCA axis were generally smaller in Dongting Lake than in Donghu Lake, suggesting that algal production (including N_2-fixing cyanobacteria) was higher in Donghu Lake.

3.2. Comparison between sedimentary proxies

In Donghu Lake, K/Al ratios stabilized at a relatively high value of ~ 0.275 before the 1910s, followed by a gradual decrease to ~ 0.24 in the 1980s and then remained stable thereafter (Fig. 5A). The concentration of Zn was relatively stable before the 1910s and strongly fluctuated

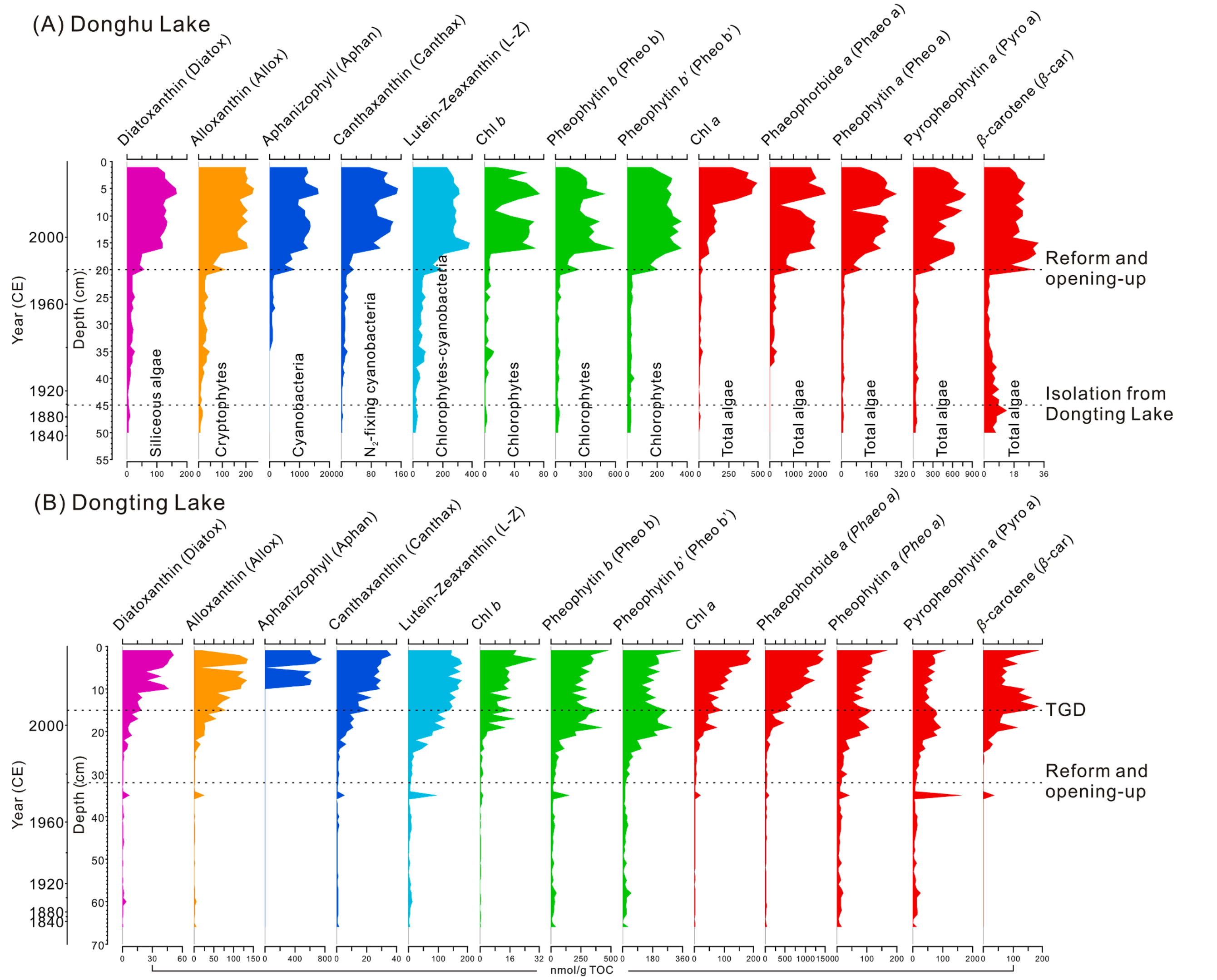

Fig. 3. Changes in chlorophyll and carotenoid pigment concentrations in the sediment cores from Donghu Lake (A) and Dongting Lake (B). Letters in the brackets after the names of the pigments are the abbreviations. The zones of pigments were identified according to key events that may potentially influence primary production in the lakes. In Donghu Lake, the zones were divided based on the isolation from Dongting Lake in the 1910s and the release of the reform and opening-up policy in the late 1970s. In Dongting Lake, the three zones were divided based on the release of the reform and opening-up policy in the late 1970s and the operation of the Three Gorges Dam in 2003 CE.

thereafter (Fig. 5B). Variations in Pb, TP and TN showed similar trends in Donghu Lake over the last 200 years (Fig. 5C, 5D and 5E). Concentrations of these four elements were low before the 1910s, followed by a gradual increase between the 1910s and the 1980s before substantially increasing after the 1980s. TOC and C/D ratios (canthaxanthin/diatoxanthin ratio) were low before the 1910s, followed by a gradual increase between the 1910s and the 1980s before substantially increasing after the 1980s (Fig. 5F and 5G). The results of GAMs showed that sample scores on the first pigment PCA axis stabilized at relatively low values before the 1910s, and significantly ($p < 0.05$) increased between the 1910s and ~ 2002 CE in Donghu Lake (Fig. 5H).

In Dongting Lake, K/Al ratios fluctuated around 0.295 before 2003 CE, followed by a sharp decrease to 0.275 in the 2020s (Fig. 5a). The concentrations of Zn and Pb fluctuated before 2003 CE and then profoundly increased after 2003 CE (Fig. 5b and 5c). TN and TP fluctuated around 0.1% and 0.52 mg/g before the 1980s in Dongting Lake, respectively (Fig. 5d and 5e). Between the 1980s and 2003 CE, TN content slightly decreased from ~1.5% to ~ 0.5%, whereas TP content increased from 0.5 mg/g to 0.6 mg/g. After 2003 CE, both TN and TP profoundly increased, reaching ~0.35% and 0.75 mg/g after the 2010s, respectively. TOC content was low before 2003 CE and increased thereafter (Fig. 5f). The C/D ratios highly fluctuated before the 1980s and slightly decreased thereafter (Fig. 5g). The GAMs showed that sample scores on the first pigment PCA axis remained at relatively low values before the 1980s, and significantly increased thereafter (Fig. 5h).

3.3. Relationship between sedimentary pigments and potential drivers

The first RDA axes explained 81.6% and 70.3% of the total variance in the sedimentary pigments in Donghu Lake and Dongting Lake, respectively (Fig. 6). In Donghu Lake, all pigments were positively correlated with temperature and sedimentary TN, TP and temperature, and negatively correlated with K/Al ratios (Fig. 6A). In Dongting Lake, all pigments were positively correlated with Zn and temperature, but negatively correlated with K/Al ratios (Fig. 6B).

VPA showed that the joint effects (33.4%) of hydrological connectivity, anthropogenic pollutants and temperature explained the largest amounts of variances in sedimentary pigments in Donghu Lake, followed by the combined effects of hydrological connectivity and anthropogenic pollutants (23.6%) (Fig. 7A). While the sole effect of hydrological

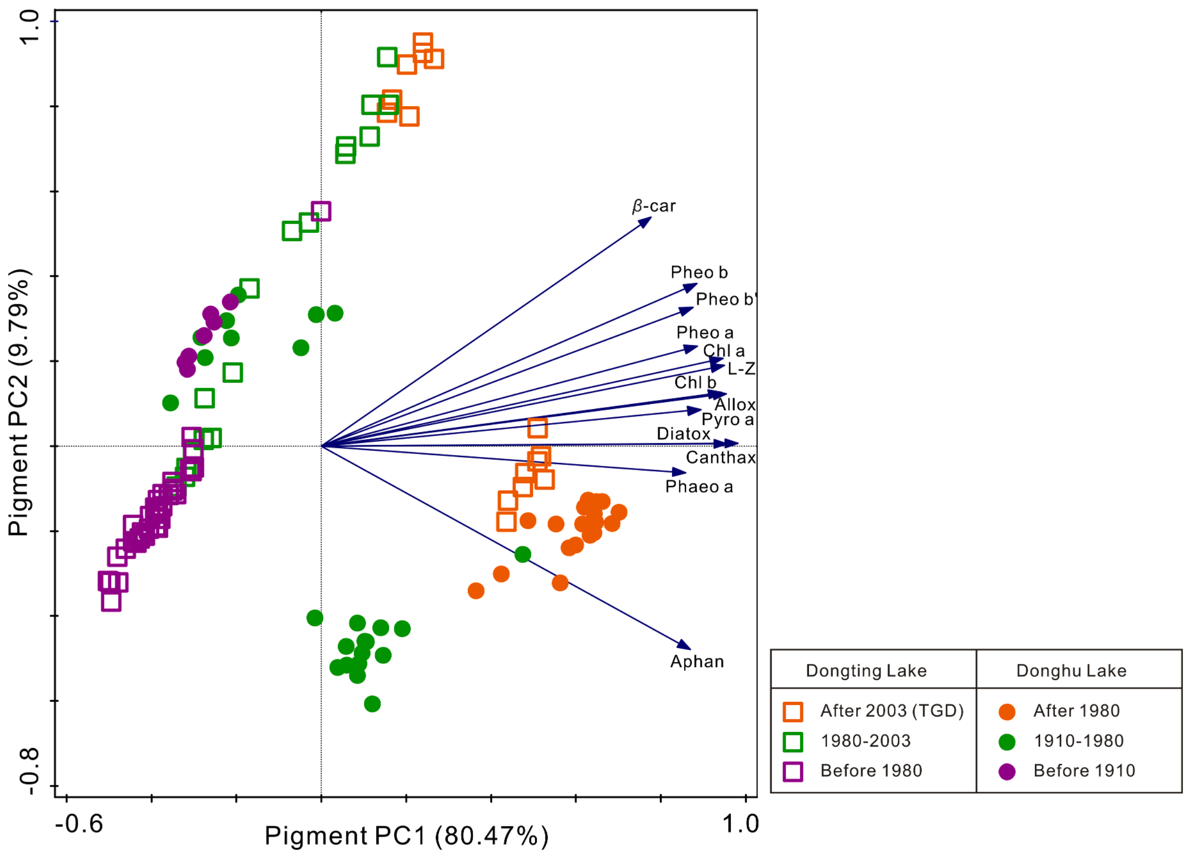

Fig. 4. Biplot of PCA of sedimentary pigments from Donghu Lake and Dongting Lake. The abbreviations of pigments are presented in Fig. 3.

connectivity (11.2%), anthropogenic pollutants (14.9%) and temperature (0.8%) on sedimentary pigments were relatively smaller, they were significant ($p < 0.05$) (Fig. 7A) in Donghu Lake. In Dongting Lake, anthropogenic pollutants alone explained the largest amounts of variances in sedimentary pigments (24.5%, $p < 0.001$), followed by the additive effects of anthropogenic pollutants and temperature (17.8%) and the joint effects of anthropogenic pollutants, temperature and hydrological connectivity (14.4%) (Fig. 7B). In contrast, the sole effects of hydrological connectivity (6.4%) and temperature (3.4%) on sedimentary pigments were smaller ($p < 0.01$).

Regression analysis shows that the C/D ratios are significantly and negatively related with K/Al ratios (adj-R^2= 0.63; $p < 0.001$), and positively related to sedimentary TN (adj-R^2= 0.61; $p < 0.001$) and TP (adj-R^2= 0.29; $p < 0.001$) in Donghu Lake (Fig. 8A). In Dongting Lake, the C/D ratios are only significantly and negatively related with sedimentary TN (adj-R^2= 0.12; $p < 0.01$) (Fig. 8B). In contrast, the relationships between C/D ratios and K/Al ratios ($p = 0.07$) and sedimentary TP ($p = 0.06$) are not significant.

4. Discussion

4.1. Changes in algal production

Chlorophyll and carotenoid pigments in lake sediments have been widely used to reflect algal community composition in paleolimnology and paleoecology, provided that the influences of degradation are thoughtfully evaluated (Leavitt and Hodgson, 2002; Stevenson et al., 2016; Moorhouse et al., 2018). In this study, we argue that changes in sedimentary pigments mainly reflect the changes in algal community composition rather than resulting from degradation. Firstly, the increases in sedimentary pigments were concurrent with the increases in sedimentary TP and TOC in both Donghu Lake and Dongting Lake (Supporting Information Figure S2). In Dongting Lake, the increase in sedimentary pigments after the 1990s was also consistent with the increase in Chl *a* and phytoplankton biomass in the water column, as reflected by water monitoring data (Huang et al., 2013). Indeed, regression analysis shows that both Chl *a* in the sediments (adj-R^2 = 0.60; $p < 0.001$) and sedimentary pigment PC1 (adj-R^2 = 0.50; $p < 0.001$) were significantly positively correlated with the phytoplankton biomass in the water column in Dongting Lake (Supporting Information Figure S4). Secondly, the Chl *a*/pheophytin *a* ratio increased after the 1910s in Donghu Lake (Supporting Information Figure S2A), probably indicating improved pigment preservation which is associated with algal production increases (Dixit et al., 2000; McGowan et al., 2012). Thirdly, the concentrations of sedimentary pigments would be expected to exponentially decline with depth if the changes in sedimentary pigments were solely driven by degradation. Instead, pigment concentrations remained stable after ~2010 CE and concentrations of diatoxanthin and canthaxanthin even slightly decreased after 2015 CE in Donghu Lake. For the large Dongting Lake, location of sampling site may cause bias in explaining the sedimentary pigments due to potential spatial heterogeneities (Lin et al., 2021). Some key paleolimnological records of the sediment core used in this study including canthaxanthin, TOC and $\delta^{13}C$ were similar to previously published records by Chen et al. (2016) and records of an unpublished sediment core in Dongting Lake (Supporting Information S3). This suggests that sediment records gathered from the sampling point in this study are broadly representative of the history of Dongting Lake. Therefore, the overall increasing trends in the chlorophyll and carotenoid pigments appear to reflect the increases in algal production in both Donghu Lake and Dongting Lake over the last 200 years, as witnessed in other freshwater lake basins (Dixit et al., 2000; Stevenson et al., 2016; Moorhouse et al., 2018), as well as other Yangtze floodplain lakes (Lin et al., 2023; Zeng et al., 2023). The relatively greater magnitude of increase in sedimentary pigments in Donghu Lake

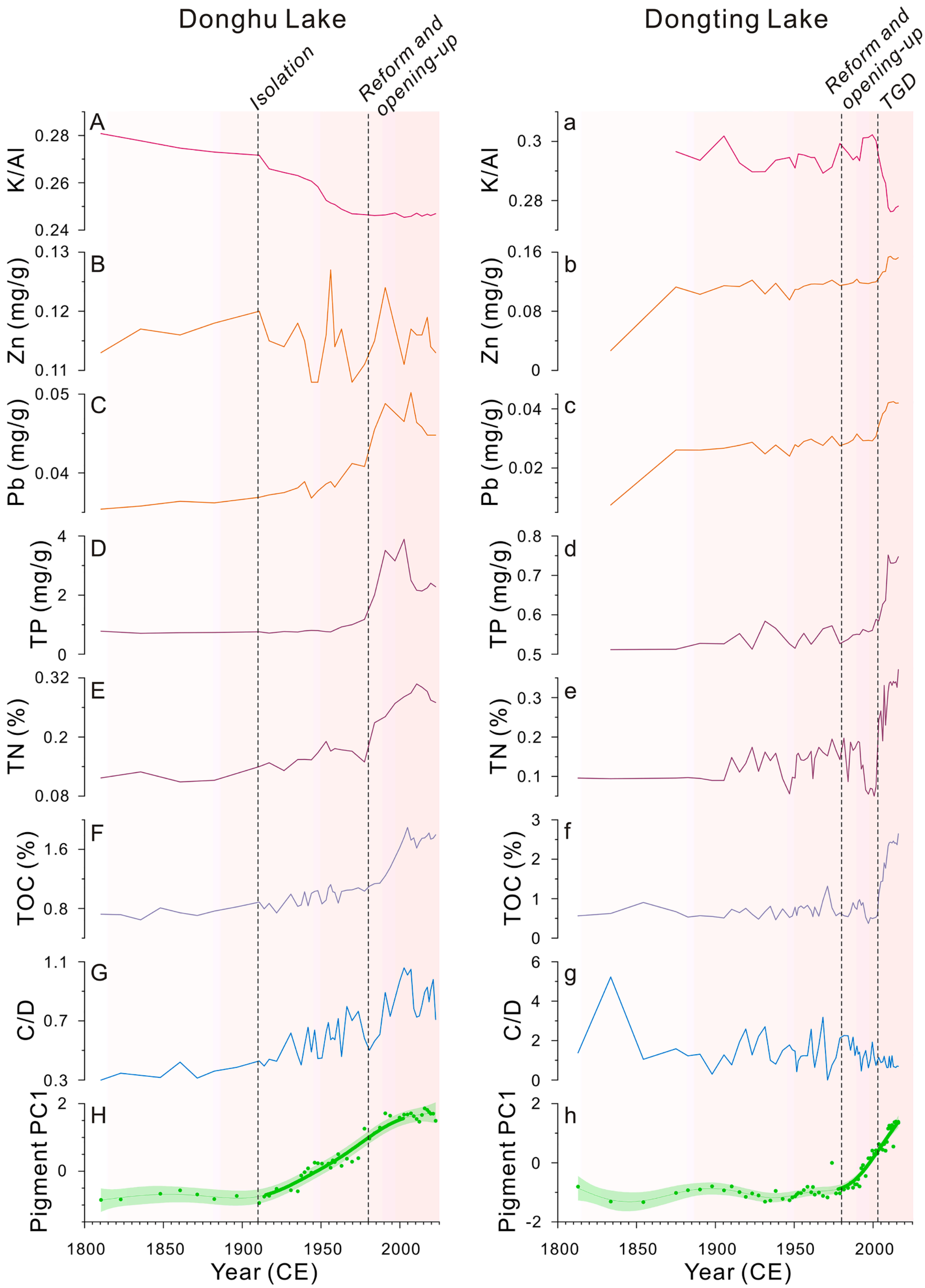

Fig. 5. Comparison of changes in K/Al ratios (A, a), Zn (B, b), Pb (C, c), TP (D, d), TN (E, e), TOC (F, f), C/D ratios (G, g) and observed and GAM fitted sample scores on the first pigment PCA axis (H, g) in the sedimentary records of Donghu Lake (left) and Dongting Lake (right). The shaded bands in the pigment PC1 plot are the 95% pointwise confidence interval on the fitted values. The bold fitted lines in the pigment PC1 plot indicate the period when the first derivates of pigment PCA axis are significantly different from 0.

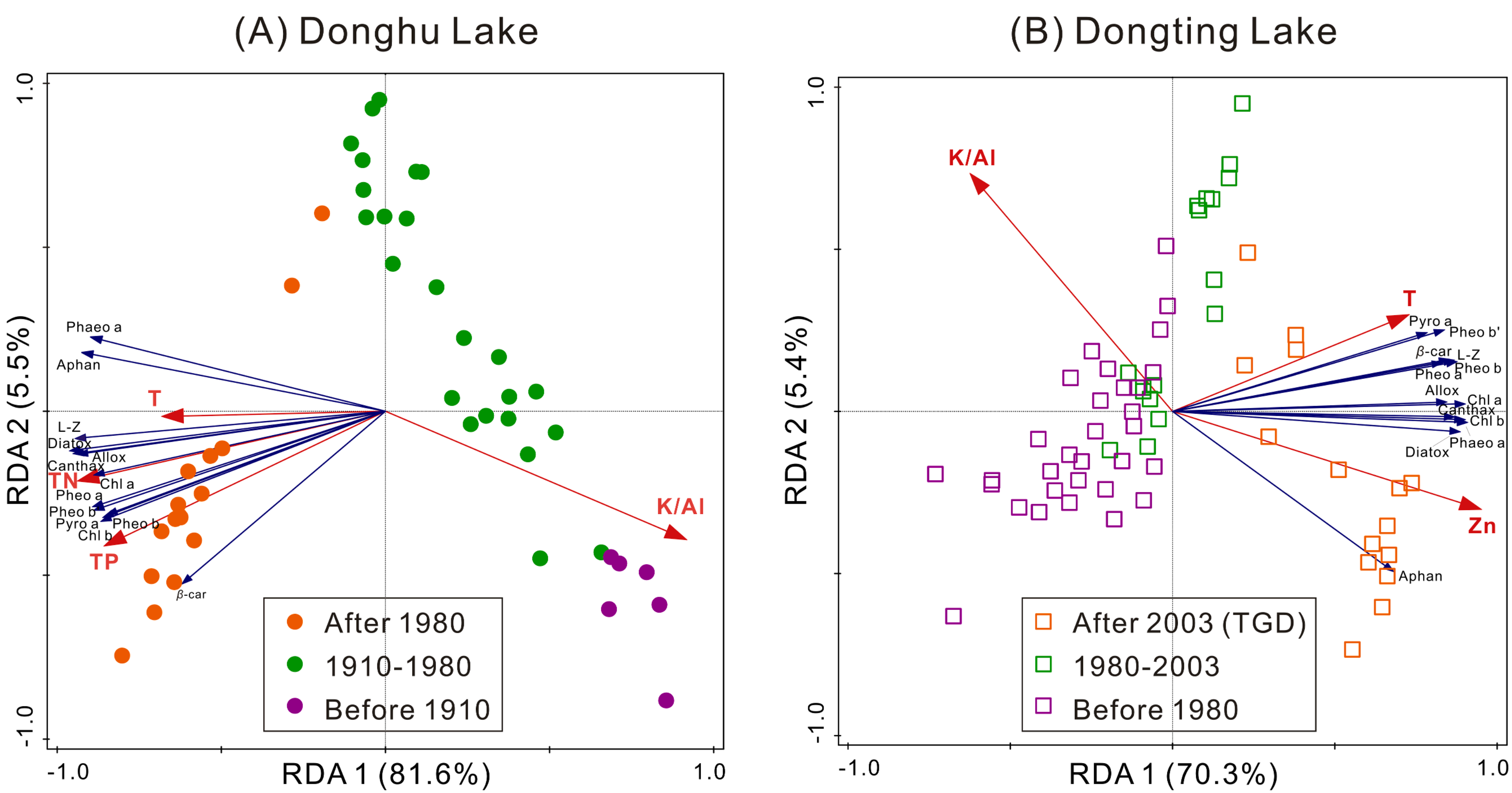

Fig. 6. Redundancy analysis to explore the relationships between sedimentary pigments (red arrows) and significantly correlated ($p < 0.05$) explanatory variables (blue arrows) in Donghu Lake (A) and Dongting Lake (B). T is the abbreviations of temperature. The abbreviations of pigments are presented in Fig. 3.

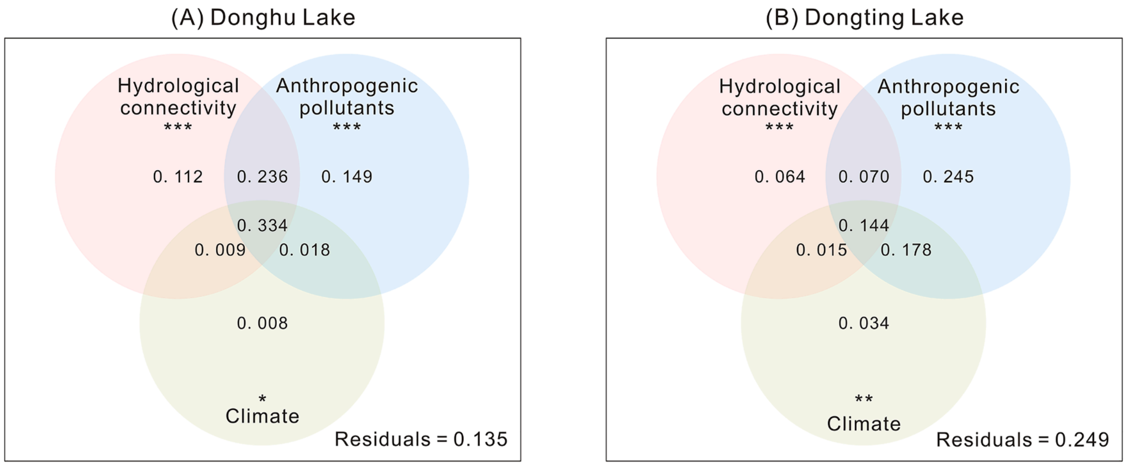

Fig. 7. Variance partitioning analysis showing the proportions of variance in algal community compositions explained by hydrological connectivity, anthropogenic nutrients and temperature in Donghu Lake (A) and Dongting Lake (B). *, **, and *** indicate significance levels at <0.05, <0.01 and < 0.001, respectively.

suggests a more sizeable algal community shift (Fig. 3). Moreover, increases in the ratios of C/D in Donghu Lake after the 1910s implied the prevalence of cyanobacteria over diatoms (Fig. 5G). This indicated the gradual increase of cyanobacteria dominance in the algal community, which has been widely reported in north temperate and subarctic lakes (Taranu et al., 2015).

4.2. Influence of anthropogenic nutrient inputs and climate warming

The timing (since 1980 CE) of significant changes in pigment communities in Dongting Lake was consistent with the release of the "Reform and opening-up" policy in China (Fig. 4h), implying that human activities in the catchment led to the shifts in algal communities in Dongting Lake (Zeng et al., 2023). This is also in agreement with VPA which showed that anthropogenic pollution alone explained the largest amounts (24.5%) of the variance in the pigment assemblages in Dongting Lake (Fig. 6B). In Donghu Lake, anthropogenic nutrients also had the largest sole effects on the variance of sedimentary pigments (Fig. 6A). Pollutants from agricultural and industrial activities in the catchment are the main source of external nutrient inputs, including nitrogen and phosphorus, leading to algal blooms in lake ecosystems worldwide (Hou et al., 2022). As one of the most developed areas in China, the Yangtze floodplain has experienced intensive social economic development since the 1980s (Dearing et al., 2012), leading to increases in nutrient influx to the floodplain lakes (Liu et al., 2018). In the Donghu-Dongting Lake catchment LUCC showed that the urban area nearly doubled from 2.2% to ~ 4.1% between the 1980s and the 2020s (Fig. 1), reflecting the intensification of urbanization and industrial development, which was recorded by the profound increases in sedimentary Pb after the 1980s in both lakes (Chen et al., 2016). Meanwhile, agricultural activities also intensely developed in the catchment during this period. For example, the fertilizer usage increased ~ 1.75-fold from the 1980s to the 2020s in the Dongting Lake catchment (Chen et al., 2016). These resulted in the increases in anthropogenic pollutants including nutrients into the lakes, as reflected by water monitoring records which showed increased TN and TP in the water column after the 1990s in Dongting Lake (Huang et al., 2013). As a consequence, algal production increased in Dongting Lake and Donghu Lake during this period (Huang et al., 2013). Therefore, our results support the idea that anthropogenic nutrient inputs play an important role in driving the shifts in algal assemblage in both Dongting Lake and Donghu Lake as reported in many other Yangtze floodplain lakes (Lin et al., 2023; Zeng et al., 2023).

While the changes in algal communities are consistent with responses to increasing anthropogenic nutrients, it is possible that warming also caused the variation in algal communities in the lakes as revealed by RDA (Fig. 6). The results of VPA indicated that the joint effects of temperature and anthropogenic pollutants explained a large part of the variance in sedimentary pigments in Dongting Lake since the 1800s (Fig. 7B). This suggests that warming acted in synergy with nutrients in influencing the algal community in Dongting Lake over the last 200 years, which has been extensively reported in other Yangtze floodplain lakes (Cao et al., 2014; Lin et al., 2021; Ran et al., 2023), as well as many temperate and subarctic lakes in the northern hemisphere (Taranu et al., 2015). By enhancing the release of sedimentary nutrients and algal growth rates, warming can exacerbate the blooms of phytoplankton, especially cyanobacteria (Lin et al., 2023). It is worth-noting that results of this study were different from previous studies on Dongting Lake which suggested that temperature was insignificantly related with sedimentary pigments (Chen et al., 2016; Zeng et al., 2023). This might be attributed to the differences in the time scales of the studies. Our study covers records of the last 200 years, whereas previous studies mainly focus on records of the last 70 years. This is in agreement with findings from Taibai Lake showing that temperature changed from a significant variable to an insignificant variable in explaining sedimentary chironomid assemblages as the focuses of the study changed from centurial-scales to decadal-scales, implying that the influence of warming on the lake ecosystem declined as anthropogenic activities in the catchment intensified after the 1950s (Cao et al., 2014).

4.3. Influence of hydrological isolation from the Yangtze River

Although algal production also profoundly increased after the 1980s and anthropogenic pollutants had the largest sole influence on sedimentary pigments in Donghu Lake, the GAMs showed that significant ($p < 0.05$) increases in algal production started from the 1910s when it was separated from Dongting Lake (Fig. 4H). Moreover, VPA indicated that hydrological connectivity also explained substantial quantities of variance in sedimentary pigments in Donghu Lake, either solely (11.2%), in combination with anthropogenic pollutants (23.6%) or working jointly with both warming and anthropogenic nutrients (33.4%) (Fig. 7A). This provides strong evidence that hydrological isolation, in addition to anthropogenic nutrient loading and warming, caused the most substantial increases in algal production and sedimentation in Donghu Lake. After separating from Dongting Lake due to land reclamation and natural siltation after the 1910s (Yu et al., 2020), Donghu Lake turned into a hydrologically isolated lake which was disconnected from the Yangtze main channel. This can be reflected by the decrease in K/Al ratios after the 1910s (Fig. 4A), which indicates declining riverine sediment influxes from the Yangtze River (Chen et al., 2022; Wang et al.,

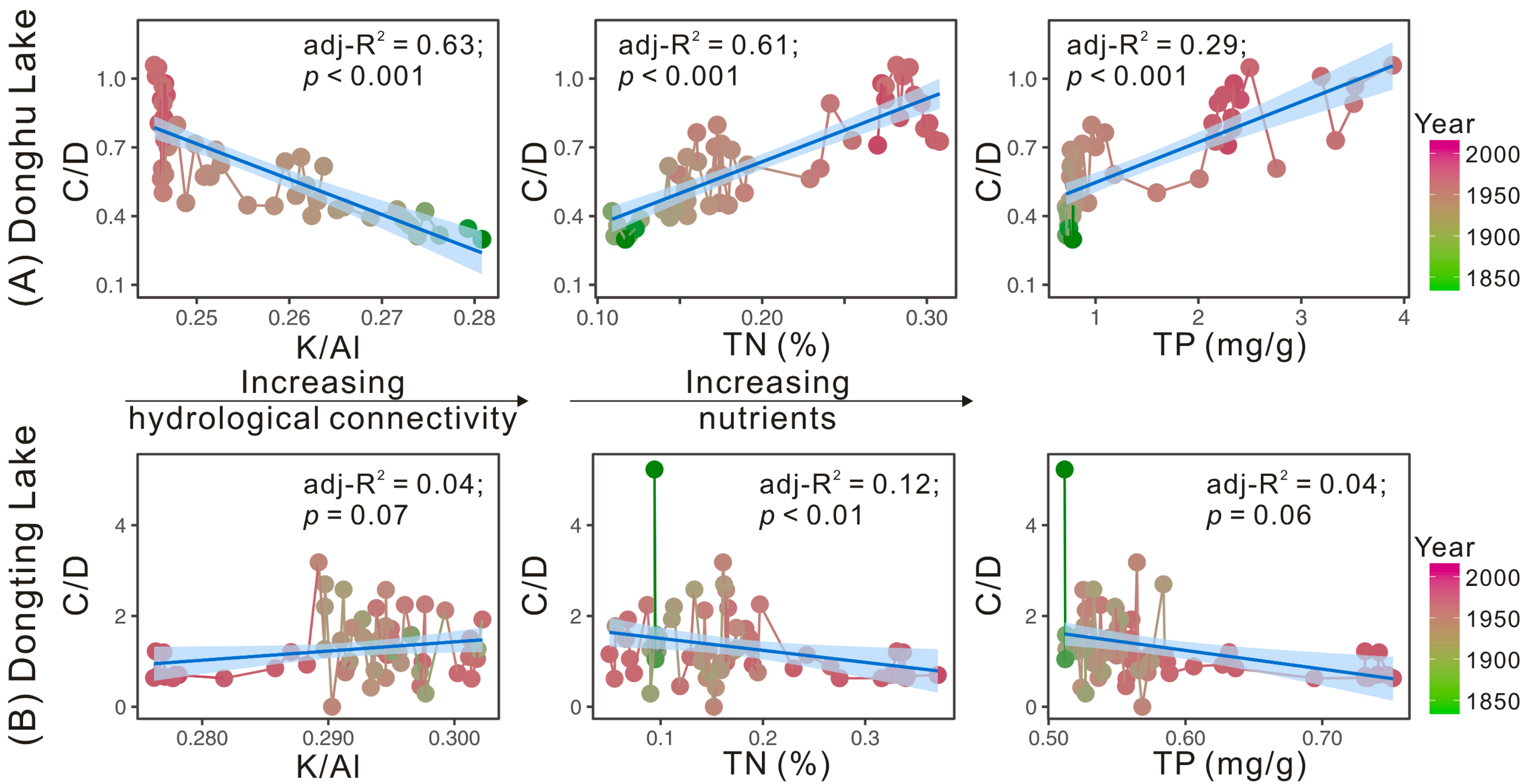

Fig. 8. Scatter plot showing the relationships between C/D ratios (the canthaxanthin/diatoxanthin ratios) and K/Al ratios and sedimentary TN and TP contents. The blue line is the linear fitted line. The shaded band surrounding the fitted line indicates the approximately 95% confidence intervals.

2024). Hydrological isolation from the main channel can stabilize hydrological conditions by prolonging water retention times, reducing water exchange, water velocity and water level fluctuation in floodplain lakes (Li et al., 2013; McGowan et al., 2011). This prolonged water retention time and decreased water exchange ratios in floodplain lakes may stimulate the retention of pollutants including nutrients and hence amplify internal nutrient cycling which fuel primary production and the sedimentation of algae (McGowan et al., 2011; Zeng et al., 2024). Consistent with this explanation, sedimentary Pb, TN and TP increased in Donghu Lake after the 1910s (Fig. 4C, 4D and 4E).

The changes in sedimentary proxies in Dongting Lake after 2003 CE also support the idea that decreased hydrological connection with the Yangtze main channel, in combination with the anthropogenic nutrient inputs, caused the shifts in algal communities in the Yangtze floodplain lakes. This explanation is supported by the VPA which showed that the second largest proportion of variance in pigment assemblages were explained by the combined effects of hydrology and human activities (Fig. 6B). After the construction of the TGD in 2003 CE, the water retention times increased from ~18 days to ~29 days and the water exchange ratio decreased by ~ 35% in Dongting Lake, while the lake retains free hydrological connection with the Yangtze River (Chen et al., 2016; Wang et al., 2024). As a result, the supply of riverine suspended particles decreased, as indicated by the sharp decreases in the K/Al ratios after 2003 CE in Dongting Lake (Fig. 4A) (Chen et al., 2022). On the other hand, the content of sedimentary Zn, Pb, TN and TP profoundly increased during this period, suggesting the retention of pollutants and nutrients (Chen et al., 2016), which probably resulted in the further increase in algal production in Dongting Lake after 2003 CE.

With increasing nutrient influxes from human activities and warming, isolation from Dongting Lake seems to have also resulted in enhanced prevalence of cyanobacteria in Donghu Lake, as reported in many temperate lakes in the Northern Hemisphere (Taranu et al., 2015). Firstly, the C/D ratio gradually increased after the 1910s in Donghu Lake (Fig. 4G), indicating more pronounced increases in cyanobacteria than siliceous algae. Secondly, regression analysis shows that the C/D ratios are negatively related to K/Al ratios (adj-$R^2 = 0.63$; $p < 0.001$) but positively related to sedimentary TN (adj-$R^2 = 0.61$; $p < 0.001$) and TP (adj-$R^2 = 0.29$; $p < 0.001$) (Fig. 7A) in Donghu Lake. Stabilized and lentic hydrological conditions after disconnection from the Yangtze River (e.g., decreased flow velocity and water level fluctuations) were more favorable for cyanobacteria rather than diatoms, the latter of which have a physiological advantage in high-flushing and turbulent water bodies (Richardson et al., 2018; Lin et al., 2021). Such lentic conditions will also promote the retention of nutrients in such floodplain lakes as these. Therefore, our results showed that hydrological isolation of floodplain lakes from the main channel not only promoted overall algal productivity, but also resulted in the dominance of cyanobacteria.

5. Conclusions

Our study provides clear evidence that hydrology connectivity is an important factor in regulating algal community composition in Yangtze floodplain lakes. Comparison of chlorophyll and carotenoid pigments in Dongting Lake and one of its satellite lakes (Donghu Lake) showed that algal production and the relative abundance of cyanobacteria to siliceous algae, increased after the 1910s in Donghu Lake when it was hydrologically separated from Dongting Lake and the Yangtze main channel. Our results indicate that hydrological isolation from the main channel accelerates algal and cyanobacteria blooms in Yangtze floodplain lakes, under a scenario of rapid urbanization and industrialization. With the ongoing construction and planning of new dams, as well as land reclamation, more floodplain lakes will lose their natural hydrological connectivity with the main channel, especially in developing regions. For example, there are more than 70 satellite lakes which have lost their hydrological connectivity with the Yangtze main channel due to natural siltation and the construction of the TGD in the Dongting Lake wetland (Wang et al., 2024). This will likely escalate the continuous HABs in floodplain lakes. For the purpose of combating harmful algal blooms in these floodplain lakes, it is vital to regain the free hydrological connection with the main channel.

CRediT authorship contribution statement

Linghan Zeng: Writing – review & editing, Writing – original draft, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation. **Virginia N. Panizzo:** Writing – review & editing, Formal analysis, Data curation. **Zekun Wang:** Writing – review & editing, Visualization, Data curation. **Xianyu Huang:** Writing – review & editing, Funding acquisition, Formal analysis. **Xu Chen:** Writing – review & editing, Funding acquisition, Data curation, Conceptualization. **Suzanne McGowan:** Writing – review & editing, Supervision, Data curation, Conceptualization.

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.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.watres.2025.123430.

Data availability

Data will be made available on request.

References

Battarbee, R.W., Bennion, H., 2012. Using palaeolimnological and limnological data to reconstruct the recent history of European lake ecosystems: introduction. Freshw. Biol. 57, 1979–1985. https://doi.org/10.1111/j.1365-2427.2012.02857.x.

Cao, Y., Zhang, E., Langdon, P.G., Liu, E., Shen, J., 2014. Chironomid-inferred environmental change over the past 1400 years in the shallow, eutrophic Taibai Lake (south-east China): separating impacts of climate and human activity. Holocene 24, 581–590. https://doi.org/10.1177/0959683614522308.

Chen, X., McGowan, S., Xu, L., Zeng, L., Yang, X., 2016. Effects of hydrological regulation and anthropogenic pollutants on Dongting Lake in the Yangtze floodplain: the impacts of hydrological regulation and anthropogenic pollutants on a floodplain lake. Ecohydrology. 9, 315–325. https://doi.org/10.1002/eco.1637.

Chen, X., McGowan, S., Ji, J., Zeng, L., Cao, Y., Huang, C., Qiao, Q., Liang, J., Nie, L., 2022. Paleolimnological records for tracking dam-induced changes in the composition and supply of sediment to middle Yangtze floodplain lakes. Catena (Amst) 219, 106643. https://doi.org/10.1016/j.catena.2022.106643.

Chen, X., Qiao, Q., McGowan, S., Zeng, L., Stevenson, M.A., Xu, L., Huang, C., Liang, J., Cao, Y., 2019. Determination of geochronology and sedimentation rates of shallow lakes in the middle Yangtze reaches using ^{210}Pb, ^{137}Cs and spheroidal carbonaceous particles. CATENA 174, 546–556. https://doi.org/10.1016/j.catena.2018.11.041.

Dearing, J.A., Yang, X., Dong, X., Zhang, E., Chen, X., Langdon, P.G., Zhang, K., Zhang, W., Dawson, T.P., 2012. Extending the timescale and range of ecosystem services through paleoenvironmental analyses, exemplified in the lower Yangtze basin. Proc. Natl. Acad. Sci. U.S.A. 109, E1111–E1120. https://doi.org/10.1073/pnas.1118263109.

Dixit, A.S., Hall, R.I., Leavitt, P.R., Quinlan, R., Smol, J.P., 2000. Effects of sequential depositional basins on lake response to urban and agricultural pollution: a palaeoecological analysis of the Qu'Appelle Valley, Saskatchewan, Canada. Freshw. Biol. 43, 319–337. https://doi.org/10.1046/j.1365-2427.2000.00516.x.

Dong, X., Yang, X., Chen, X., Liu, Q., Yao, M., Wang, R., Xu, M., 2016. Using sedimentary diatoms to identify reference conditions and historical variability in shallow lake ecosystems in the Yangtze floodplain. Mar. Freshw. Res. 67, 803. https://doi.org/10.1071/MF14262.

Gong, G., Chang, J., Chiang, K., Hsiung, T., Hung, C., Duan, S., Codispoti, L.A., 2006. Reduction of primary production and changing of nutrient ratio in the East China Sea: effect of the Three Gorges Dam? Geophys. Res. Lett. 33, L07610. https://doi.org/10.1029/2006GL025800.

Hall, R.I., Leavitt, P.R., Quinlan, R., Dixit, A.S., Smol, J.P., 1999. Effects of agriculture, urbanization, and climate on water quality in the northern Great Plains. Limnol. Oceanography 44, 739–756. https://doi.org/10.4319/lo.1999.44.3_part_2.0739.

Han, Y., Lin, Q., Huang, S., Du, C., Shen, J., Zhang, K., 2024. Human Impacts Dominate Global Loss of Lake Ecosystem Resilience. Geophys. Res. Lett. 51, e2024GL109298. https://doi.org/10.1029/2024GL109298.

Hellweger, F.L., Martin, R.M., Eigemann, F., Smith, D.J., Dick, G.J., Wilhelm, S.W., 2022. Models predict planned phosphorus load reduction will make Lake Erie more toxic. Science 376, 1001–1005. https://doi.org/10.1126/science.abm6791.

Hou, X., Feng, L., Dai, Y., Hu, C., Gibson, L., Tang, J., Lee, Z., Wang, Y., Cai, X., Liu, J., Zheng, Y., Zheng, C., 2022. Global mapping reveals increase in lacustrine algal blooms over the past decade. Nat. Geosci. 15, 130–134. https://doi.org/10.1038/s41561-021-00887-x.

Huang, D., Wan, Q., Li, L., Wang, T., Lu, S., Ou, F., Tian, Q., 2013. Changes of water quality and eutrophic state in recent 20 years of Dongting Lake. Res. Environ. Sci. 26, 27–33.

Johnson, K.A., Wing, O.E.J., Bates, P.D., Fargione, J., Kroeger, T., Larson, W.D., Sampson, C.C., Smith, A.M., 2020. A benefit–cost analysis of floodplain land acquisition for US flood damage reduction. Nat. Sustain. 3, 56–62. https://doi.org/10.1038/s41893-019-0437-5.

Junk, W.J., 2005. Flood pulsing and the linkages between terrestrial, aquatic, and wetland systems. Verhandlungen – Internationale Vereinigung für Theoretische und Angewandte Limnologie 29, 11–38. https://doi.org/10.1080/03680770.2005.11901972.

Leavitt, P.R., Hodgson, D.A. (2002) Sedimentary Pigments. In: Smol, J.P., Birks, H.J.B., Last, W.M., Bradley, R.S., Alverson, K. (eds) Tracking Environmental Change Using Lake Sediments. Developments in Paleoenvironmental Research, vol 3. Springer, Dordrecht. 10.1007/0-306-47668-1_15.

Li, J., Zhou, Y., Ou, C., Cheng, W., Yang, Y., Zhao, Z., 2013. Evolution of water exchange ability between Dongting Lake and Yangtze River and its response to the operation of the Three Gorges Reservoir. Acta Geographica Sinica 68, 108–117. https://doi.org/10.11821/xb201301012.

Li, Y., Tan, Z., Zhang, Q., Liu, X., Chen, J., Yao, J., 2021. Refining the concept of hydrological connectivity for large floodplain systems: framework and implications for eco-environmental assessments. Water. Res. 195, 117005. https://doi.org/10.1016/j.watres.2021.117005.

Li, Y., Zhang, Q., Liu, X., Tan, Z., Yao, J., 2019. The role of a seasonal lake groups in the complex Poyang Lake-floodplain system (China): insights into hydrological behaviors. J. Hydrol. 578, 124055. https://doi.org/10.1016/j.jhydrol.2019.124055.

Li, Y., Zhang, Q., Tan, Z., Yao, J., 2020. On the hydrodynamic behavior of floodplain vegetation in a flood-pulse-influenced river-lake system (Poyang Lake, China). J. Hydrol. 585, 124852. https://doi.org/10.1016/j.jhydrol.2020.124852.

Li, Z., Gao, Y., Wang, S., Jia, J., Ha, X., Lu, Y., 2023. Floodplain lake response to climate-nutrient-hydrological pressure revealed through phytoplankton community succession over the past century. J. Hydrol. 623, 129838. https://doi.org/10.1016/j.jhydrol.2023.129838.

Lin, Q., Zhang, K., McGowan, S., Capo, E., Shen, J., 2021. Synergistic impacts of nutrient enrichment and climate change on long-term water quality and ecological dynamics in contrasting shallow-lake zones. Limnol. Oceanogr. 66, 3271–3286. https://doi.org/10.1002/lno.11878.

Lin, Q., Zhang, K., McGowan, S., Huang, S., Xue, Q., Capo, E., Zhang, C., Zhao, C., Shen, J., 2023. Characterization of lacustrine harmful algal blooms using multiple biomarkers: historical processes, driving synergy, and ecological shifts. Water. Res. 235, 119916. https://doi.org/10.1016/j.watres.2023.119916.

Liu, X., Beusen, A.H.W., Van Beek, L.P.H., Mogollón, J.M., Ran, X., Bouwman, A.F., 2018. Exploring spatiotemporal changes of the Yangtze River (Changjiang) nitrogen and phosphorus sources, retention and export to the East China Sea and Yellow Sea. Water. Res. 142, 246–255. https://doi.org/10.1016/j.watres.2018.06.006.

Maavara, T., Chen, Q., Van Meter, K., Brown, L.E., Zhang, J., Ni, J., Zarfl, C., 2020. River dam impacts on biogeochemical cycling. Nat. Rev. Earth Environ. 1, 103–116. https://doi.org/10.1038/s43017-019-0019-0.

McGowan, S., Barker, P., Haworth, E.Y., Leavitt, P.R., Maberly, S.C., Pates, J., 2012. Humans and climate as drivers of algal community change in Windermere since 1850. Freshw. Biol. 57, 260–277. https://doi.org/10.1111/j.1365-2427.2011.02689.x.

McGowan, S., Lacey, J.H., Engels, S., Boyle, J., Briddon, C., Leng, M.J., Moorhouse, H.L., Panizzo, V., Shafiq, M., 2025. Land use, hydroclimate and damming influence organic carbon sedimentation in a flood pulse wetland, Malaysia. J. Quaternary. Sci. 1–14. https://doi.org/10.1002/jqs.3672.

McGowan, S., Leavitt, P., Hall, R.I., Wolfe, B.B., Edwards, T.W., Karst-Riddoch, T., Vardy, S.R., 2011. Interdecadal declines in flood frequency increase primary production in lakes of a northern river delta. Glob. Chang. Biol. 17, 1212–1224. https://doi.org/10.1111/j.1365-2486.2010.02304.x.

Moorhouse, H.L., McGowan, S., Taranu, Z.E., Gregory-Eaves, I., Leavitt, P.R., Jones, M. D., Barker, P., Brayshaw, S.A., 2018. Regional versus local drivers of water quality in the Windermere catchment, Lake District, United Kingdom: the dominant influence of wastewater pollution over the past 200 years. Glob. Chang. Biol. 24, 4009–4022. https://doi.org/10.1111/gcb.14299.

Moran, E.F., Lopez, M.C., Moore, N., Müller, N., Hyndman, D.W., 2018. Sustainable hydropower in the 21st century. Proc. Natl. Acad. Sci. U.S.A. 115, 11891–11898. https://doi.org/10.1073/pnas.1809426115.

Nanjing Institute of Geography and Limnology, Chinese Academy of Sciences (NIGLAS), 2019. Survey Report of Chinese Lakes. Science Press, Beijing. Chinese.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., Caceres, M.D., Durand, S., Evangelista, H.B.A., FitzJohn, R., Friendly, M., Furneaux, B., Hannigan, G., Hill, M.O., Lahti, L., McGlinn, D., Ouellette, M.-H., Cunha, E.R., et al., 2019. Vegan: Community Ecology Package. R Package version 2.5-6. https://CRAN.R-project.org/package=vegan.

Paerl, H.W., Huisman, J., 2008. Blooms like it hot. Science 320, 57–58. https://doi.org/10.1126/science.1155398.

Palmer, M., Ruhi, A., 2019. Linkages between flow regime, biota, and ecosystem processes: implications for river restoration. Science 365, eaaw2087. https://doi.org/10.1126/science.aaw2087.

R Core Team, 2023. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Ramsar Convention Bureau, 2025. The List of Wetlands of International Importance. https://www.ramsar.org/sites/default/files/2023-08/sitelist.pdf.

Ran, F., Nie, X., Wang, S., Xiao, T., Yang, C., Liu, Y., Wang, L., Liu, Y., Chu, X., Li, Z., 2023. A significant loop of lake sedimentation state links catchment eco-surroundings and lake biogenic regime shifts. Limnol. Oceanogr. 68, 1775–1790. https://doi.org/10.1002/lno.12385.

Richardson, J., Miller, C., Maberly, S.C., Taylor, P., Globevnik, L., Hunter, P., Jeppesen, E., Mischke, U., Moe, S.J., Pasztaleniec, A., Søndergaard, M., Carvalho, L., 2018. Effects of multiple stressors on cyanobacteria abundance vary with lake type. Glob. Chang. Biol. 24, 5044–5055. https://doi.org/10.1111/gcb.14396.

Salgado, J., Jaramillo-Monroy, C., Link, A., Lopera-Congote, L., Velez, M.I., Gonzalez-Arango, C., Yang, H., Panizzo, V.N., McGowan, S., 2024. Riverine connectivity modulates elemental fluxes through a 200- year period of intensive anthropic change in the Magdalena River floodplains, Colombia. Water Res. 268, 122633. https://doi.org/10.1016/j.watres.2024.122633.

Scheffer, M., Hosper, S.H., Meijer, M-L., Moss, B., Jeppesen, E., 1993. Alternative equilibria in shallow lakes. Trends Ecol. Evol. 8, 275–279. https://doi.org/10.1016/0169-5347(93)90254-M.

Šmilauer, P., Lepš, J., 2014. Multivariate Analysis of Ecological Data Using CANOCO 5. Cambridge university press, Cambridge.

Sokal, M.A., Hall, R.I., Wolfe, B.B., 2010. The role of flooding on inter-annual and seasonal variability of lake water chemistry, phytoplankton diatom communities and macrophyte biomass in the Slave River Delta (Northwest Territories, Canada). Ecohydrology. 3, 41–54. https://doi.org/10.1002/eco.93.

Squires, M.M., Lesack, L.F.W., 2002. Water transparency and nutrients as controls on phytoplankton along a flood-frequency gradient among lakes of the Mackenzie Delta. Canadian J. Fisheries Aquat. Sci. 59, 1339–1349. https://doi.org/10.1139/f02-085.

Stevenson, M.A., McGowan, S., Anderson, N.J., Foy, R.H., Leavitt, P.R., McElarney, Y.R., Engstrom, D.R., Pla-Rabés, S., 2016. Impacts of forestry planting on primary production in upland lakes from north-west Ireland. Glob. Chang. Biol. 22, 1490–1504. https://doi.org/10.1111/gcb.13194.

Taranu, Z.E., Gregory-Eaves, I., Leavitt, P.R., Bunting, L., Buchaca, T., Catalan, J., Domaizon, I., Guilizzoni, P., Lami, A., McGowan, S., Moorhouse, H., Morabito, G., Pick, F.R., Stevenson, M.A., Thompson, P.L., Vinebrooke, R.D., 2015. Acceleration of cyanobacterial dominance in north temperate-subarctic lakes during the Anthropocene. Ecol. Lett. 18, 375–384. https://doi.org/10.1111/ele.12420.

Wang, H., Liu, X., Wang, H., 2019. The Yangtze river-floodplain ecosystem: multiple threats and holistic conservation. Acta Hydrobiologica Sinica 43, 157–182. https://doi.org/10.7541/2019.178.

Wang, J., Chen, G., Kang, W., Hu, K., Wang, L., 2019. Impoundment intensity determines temporal patterns of hydrological fluctuation, carbon cycling and algal succession in a dammed lake of Southwest China. Water. Res. 148, 162–175. https://doi.org/10.1016/j.watres.2018.10.032.

Wang, R., Dearing, J.A., Doncaster, C.P., Yang, X., Zhang, E., Langdon, P.G., Yang, H., Dong, X., Hu, Z., Xu, M., Zhao, Y., Shen, J., 2019. Network parameters quantify loss of assemblage structure in human-impacted lake ecosystems. Glob. Chang. Biol. 25, 3871–3882. https://doi.org/10.1111/gcb.14776.

Wang, Z., Zeng, L., Wang, H., Long, X., Peng, J., Chen, X., 2024. Different effects of natural siltation, damming and pollution on two adjacent lakes of Dongting Lake Wetland: evidence from paleolimnology. J. Hydrol. 638, 131499. https://doi.org/10.1016/j.jhydrol.2024.131499.

Xiang, L., Lu, X., Higgitt, D.L., Wang, S., 2002. Recent lake sedimentation in the middle and lower Yangtze basin inferred from ^{137}Cs and ^{210}Pb measurements. J. Asian Earth Sci. 21, 77–86. https://doi.org/10.1016/S1367-9120(02)00015-9.

Xie, Y., Tang, Y., Chen, X., Li, F., Deng, Z., 2015. The impact of Three Gorges Dam on the downstream eco-hydrological environment and vegetation distribution of East Dongting Lake. Ecohydrology. 8, 738–746. https://doi.org/10.1002/eco.1543.

Yu, S., Wang, L., Xia, W., Yu, D., Li, C., He, Q., 2020. Spatio-temporal evolution of riparian lakes in Dongting Lake area since the late Qing Dynasty. Acta Geographica Sinica 75, 2346–2361. https://doi.org/10.11821/dlxb202011006.

Yang, S.L., Milliman, J.D., Li, P., Xu, K., 2011. 50,000 dams later: erosion of the Yangtze River and its delta. Glob. Planet. Change 75, 14–20. https://doi.org/10.1016/j.gloplacha.2010.09.006.

Yu, Y., Mei, X., Dai, Z., Gao, J., Li, J., Wang, J., Lou, Y., 2018. Hydromorphological processes of Dongting Lake in China between 1951 and 2014. J. Hydrol. 562, 254–266. https://doi.org/10.1016/j.jhydrol.2018.05.015.

Zeng, L., Engels, S., Swann, G.E.A., Chen, X., Huang, X., Cao, Y., McGowan, S., 2024. Dual impacts of hydrology and damming on eutrophication: comparison of two

Ramsar wetlands in the middle Yangtze floodplain. J. Hydrol. 641, 131839. https://doi.org/10.1016/j.jhydrol.2024.131839.

Zeng, L., McGowan, S., Swann, G.E.A., Leng, M.J., Chen, X., 2022. Eutrophication has a greater influence on floodplain lake carbon cycling than dam installation across the middle Yangtze region. J. Hydrol. 614, 128510. https://doi.org/10.1016/j.jhydrol.2022.128510.

Zeng, L., Swann, G.E.A., Leng, M.J., Chen, X., Ji, J., Huang, X., McGown, S., 2023. Ecosystem deterioration in the middle Yangtze floodplain lakes over the last two centuries: evidence from sedimentary pigments. Quat. Sci. Rev. 302, 107954. https://doi.org/10.1016/j.quascirev.2023.107954.

Zhang, Q., Dong, X., Yang, X., Odgaard, B.V., Jeppesen, E., 2019. Hydrologic and anthropogenic influences on aquatic macrophyte development in a large, shallow lake in China. Freshwater Biol. 64, 799–812. https://doi.org/10.1111/fwb.13263.