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Water quality and habitat drive phytoplankton taxonomic and functional group patterns in the Yangtze River

Wenqi Gao^{1,2}, Fangyuan Xiong¹, Ying Lu¹, Wei Xin¹, Haihua Wang³, Gangpeng Feng^{3,5}, Chiping Kong⁴, Lei Fang⁴, Xiaoping Gao⁴ and Yushun Chen^{1,2*} 

Abstract

Background Although phytoplankton are important primary producers in food webs, they are relatively less studied in large rivers compared to other types of systems. To fill this research gap, we studied phytoplankton taxonomic and functional composition and their relationships with water quality, habitat, climate, and land use across 30 river sections in the middle and lower reaches of the Yangtze River during 2017–2018.

Results Major observed phytoplankton groups were cyanobacteria, bacillariophyta, and chlorophyta. Phytoplankton total abundance, total biomass, and species richness significantly decreased in the dry season compared to the wet season, with the species and functional composition differing significantly between seasons. Phytoplankton species differences between seasons were mainly contributed by *Oscillatoria* sp., *Pseudanabaena* sp., and *Melosira granulata*. The differences in phytoplankton functional groups between seasons were mainly contributed by P (including *Closterium* sp., *Melosira* sp.), Lo (including *Merismopedia* sp., *Peridinium* sp., *Ceratium* sp., and *Gymnodinium* sp.), and J (including *Pediastrum* sp., *Tetraedron* sp., *Crucigenia* sp., *Scenedesmus* sp., and *Coelastrum* sp.). The variance partitioning showed that water quality (NO₃-N, total suspended solids, turbidity) and habitat (water flow, river bank and river channel conditions) were critical factors in shaping phytoplankton patterns, followed by climate and land use.

Conclusions Results indicated that there was significant seasonal variation of phytoplankton in the Yangtze River, with water quality and habitat primarily driving phytoplankton patterns. Our study contributes to the understanding of natural and anthropogenic factors that drive seasonal successional processes of phytoplankton in the Yangtze River. These findings have important implications for environmental management as well as towards the ecological restoration of large rivers.

Keywords Yangtze River, Phytoplankton, Functional group, Water quality, Physical habitat

*Correspondence:

Yushun Chen
yushunchen@ihb.ac.cn

Full list of author information is available at the end of the article



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Introduction

The world's great human civilizations have flourished along large rivers (Best 2019; Fang and Jawitz 2019). Rivers are one of the most dynamic ecosystems known, offering a variety of ecological services to life on earth and being crucial to human well-being across the planet (Chen et al. 2016; Xiong et al. 2021). Multiple anthropogenic disturbances have significant impacts on riverine ecosystems (Birk 2019; Qu et al. 2022; Xiong et al. 2022), which is partly why these ecosystems have among the highest rates of biodiversity declines of all ecosystems on earth (Dudgeon et al. 2006; Arneeth et al. 2020). For example, modification of rivers or floodplains affected river connectivity, which has in turn led to large declines in biodiversity (Stoffers et al. 2022; Xiong et al. 2023). In addition, urbanization leads to habitat fragmentation and increases the amount of impervious surfaces, which in turn, alters stormwater runoff patterns and ultimately hydrologic systems (Jacobson 2011). Climate change and human activities in concert modify rivers' hydrological and physicochemical properties (Chen et al. 2017; Gilvear et al. 2002; Xiong et al. 2022), which affects aquatic biota both directly and indirectly (Berger et al. 2017; Xiong et al. 2021). Overall, large river ecosystems face enormous challenges in terms of the sustainable development of water resources and biodiversity conservation (Vörösmarty et al. 2010; Chen et al. 2020; Liu et al. 2023). However, research on riverine ecosystems is relatively limited compared to other aquatic ecosystems such as streams and lakes (Qu et al. 2022; Xiong et al. 2023).

Phytoplankton are primary producers of aquatic ecosystems which perform a vital role in energy flow, material cycling, and material transfer (Song et al. 2020; Zhao et al. 2020). In addition, phytoplankton are sufficiently sensitive so that they serve as important biological indicators reflecting the health of aquatic ecosystems. For example, their densities, biomasses, and species compositions respond rapidly to biological, physical, and chemical changes in their environments (Guo et al. 2019; Shoener et al. 2019; Graco-Roza et al. 2021). With the intensifying impacts of human activities on the environment and the increasing requirements of ecosystem management, ecologists have focused on exploring the effects of water quality, hydrology, climate change, and land use on phytoplankton community—their structure in particular (Monchamp et al. 2018; Zhang et al. 2018a; Fu et al. 2022; Qu et al. 2022). Previous studies have shown that water quality parameters (e.g., nutrients and water temperature, etc.) are the main drivers of phytoplankton community successional processes (Bowes et al. 2012; Song et al. 2022), though these parameters could be modified by watershed land use and climate change (Wu et al. 2023a). Physical characteristics (e.g., river morphology) and light

conditions can also affect spatiotemporal distribution of phytoplankton in large rivers (Thorp and Delong 1994; Ding et al. 2022a). High-speed water flows and short residence times influence phytoplankton growth and reproduction (Reynolds 2000). Light is the primary energy source for photosynthesis in phytoplankton, and characteristics such as the ability to achieve net photosynthesis under poor light conditions and high growth rates are necessary for their survival and growth (Reynolds 1994). In addition, habitat and water quality degradation caused by land use changes can broadly affect phytoplankton community composition and resource use efficiency (Kakouei et al. 2021; Peng et al. 2021; Yang et al. 2022).

In addition to the taxonomic aspect, functional approaches have been used to interpret and predict the responses of phytoplankton to environmental changes (Kruk et al. 2002; Reynolds et al. 2002; Padišák et al. 2009). The grouping of phytoplankton with similar or identical physiology, morphology, and survival strategies into a functional group (Reynolds et al. 2002; Padišák et al. 2009) serves as the basic unit of phytoplankton responses to environmental changes, which can reflect their specific habitat requirements (Reynolds et al. 2002). The phytoplankton functional groups approach can supplement and possibly unravel phytoplankton dynamics in ecosystems (Kruk et al. 2002; Padišák et al. 2006; Izaguirre et al. 2012; Sun and Wang 2021). Studies on phytoplankton communities from a functional perspective can add more information to the mechanism of phytoplankton responses to environmental changes (Haque et al. 2021), which have been applied in many aquatic ecosystems (Padišák et al. 2006; Zhang et al. 2007; Abonyi et al. 2012; Kim et al. 2020; Sun and Wang 2021). However, there is relatively less research on phytoplankton functional groups in large rivers (Wang et al. 2021; Ding et al. 2022b).

A combination of multiple driving factors can directly or indirectly alter the phytoplankton community structure (Escalas et al. 2019; Peng et al. 2021; Qu et al. 2022). Consideration of only single environmental factors on phytoplankton community structure cannot effectively detect the complex relationships between phytoplankton and environmental factors, which calls for the joint effects from multiple factors (Peng et al. 2021). Understanding the major environmental factors that regulate riverine phytoplankton communities under multiple stressors is of critical importance, which serves as an essential prerequisite for effective biological assessments as well as riverine aquatic ecosystems management (Song et al. 2020). However, uncertainty exists in production and distribution of phytoplankton in rivers (Qu et al. 2018), and the extent to which land use change affects riverine phytoplankton remains largely unknown (Qu

et al. 2022; Yang et al. 2022). In addition, the joint and individual effects of multiple stressors on riverine phytoplankton species and functional groups remain understudied and poorly understood (Qu et al. 2018, 2019).

As the largest river in China, the Yangtze River and its basin supports one-third of the country's population and contributes about 40% of the gross domestic product (GDP) (Chen et al. 2017). In the past several decades, the Yangtze River has experienced disturbances from climate change and multiple human stressors such as dams, habitat modification, land use change, shipping, sand dredging, and overfishing, which resulted in the destruction of the river's original natural environment and depletion of aquatic biological resources (Chen et al. 2017, 2020). Climate change and multiple human stressors were found to affect water quality and fish communities in the Yangtze River (Xiong et al. 2021, 2022, 2023), but the response of phytoplankton to these stressors has never been quantified. Previous studies have investigated the biogeographic distribution of phytoplanktonic and benthic diatoms (Wang et al. 2019), the effect of a single environmental metric (e.g., water quality) on phytoplankton community structure (Liu et al. 2019), and using phytoplankton functional groups to evaluate water quality in the Yangtze River (Wu et al. 2023b). Spatially, local river segments and estuaries have received the majority of attentions (Li et al. 2012; Zhu et al. 2013a; Jiang et al. 2014, 2015; Liu et al. 2017; Tan et al. 2017), while the middle and lower reaches of the Yangtze River as a whole, where the most intensive human activity located, are much less studied.

Thus, the objectives of the current study were (1) to analyze community composition and succession of phytoplankton using both taxonomic (i.e., structural) and functional groups and (2) to quantify the effects of multiple driving factors (i.e., climate, habitat, land use, and water quality) on phytoplankton patterns in the middle and lower reaches of the Yangtze River. Assessments were conducted during both wet and dry seasons in 2017–2018. Based on previous studies, we hypothesized that phytoplankton taxa and functional groups would exhibit distinct seasonal patterns, and that water quality will play a critical role in influencing both the taxonomic (structural) and functional composition of phytoplankton communities in the Yangtze River (Xiong et al. 2022, 2023), with certain species are highly abundant in sites with more nutrients and lower turbidity.

Materials and methods

Study area and sampling sites

The Yangtze River is the third-longest in the world and the longest in Asia, which flows through 11 provincial administrative districts in central China, has a total length of around 6300 km (Chen et al. 2017). The Yangtze

River basin contains a dense network of rivers and well-developed aquatic systems, including more than 3000 tributaries and 4000 lakes; the basin area accounts for about one-fifth of the total land area of China (Chen et al. 2016). The middle and lower reaches of the Yangtze River are deep and wide enough to allow passage of large commercial ships year round, making it a renowned "golden waterway." However, along with rapid economic development in this portion of the basin, various human activities have inevitably affected the environmental and ecological conditions, especially urbanization, agriculture, industry, mining, shipping, overfishing, and habitat modifications (Chen et al. 2017, 2020; Xiong et al. 2021, 2022). The middle and lower reaches of the Yangtze River have a subtropical monsoon climate with four distinct seasons, and maximum temperatures reaching 40 °C in summer and minimum temperatures of about -4 °C in winter. During the wet (July–August) and dry (October–December) seasons of 2017–2018, a total of 30 and 25 river segments were investigated in the middle and lower reaches of the Yangtze River, respectively (Fig. 1, Additional file 1: Table S1). In each of these river segments, a total of three sampling sites per segment were used to collect biological and water quality samples (Xiong et al. 2021, 2022).

Phytoplankton and water quality analysis

At each sampling site, 1-L water samples were taken as quantitative phytoplankton samples. Each sample had 15 mL of Lugol's solution added and was returned to the laboratory to settle for more than 48 h. Samples were concentrated to 30–50 mL and counted in a 0.1 mL plankton counting chamber (20×20 mm) under an optical microscope (BX43, Olympus Corporation, Tokyo) at 400× magnification (Zhang et al. 2018b; Gao et al. 2023). Phytoplankton were identified at the lowest taxonomic level possible (Hu and Wei 2006), with biomass calculated based on cell volume and density (Huang et al. 2021; Gao et al. 2023). The MacNaughton dominance index (Y) was used to determine phytoplankton dominant species, and species with $Y \geq 0.02$ were considered as the dominant species (Han et al. 2020; Hu et al. 2022). The classification of phytoplankton functional groups was based on the criteria proposed by Reynolds et al. (2002) and Padišák et al. (2009). The phytoplankton functional group biomass was the sum of biomass of all phytoplankton species within each functional group. An important or dominant functional group was determined when its relative biomass was 10% or more at a given river segment (Zhu et al. 2013b). The dominant functional group represented the ecological condition and aquatic environment of the region.

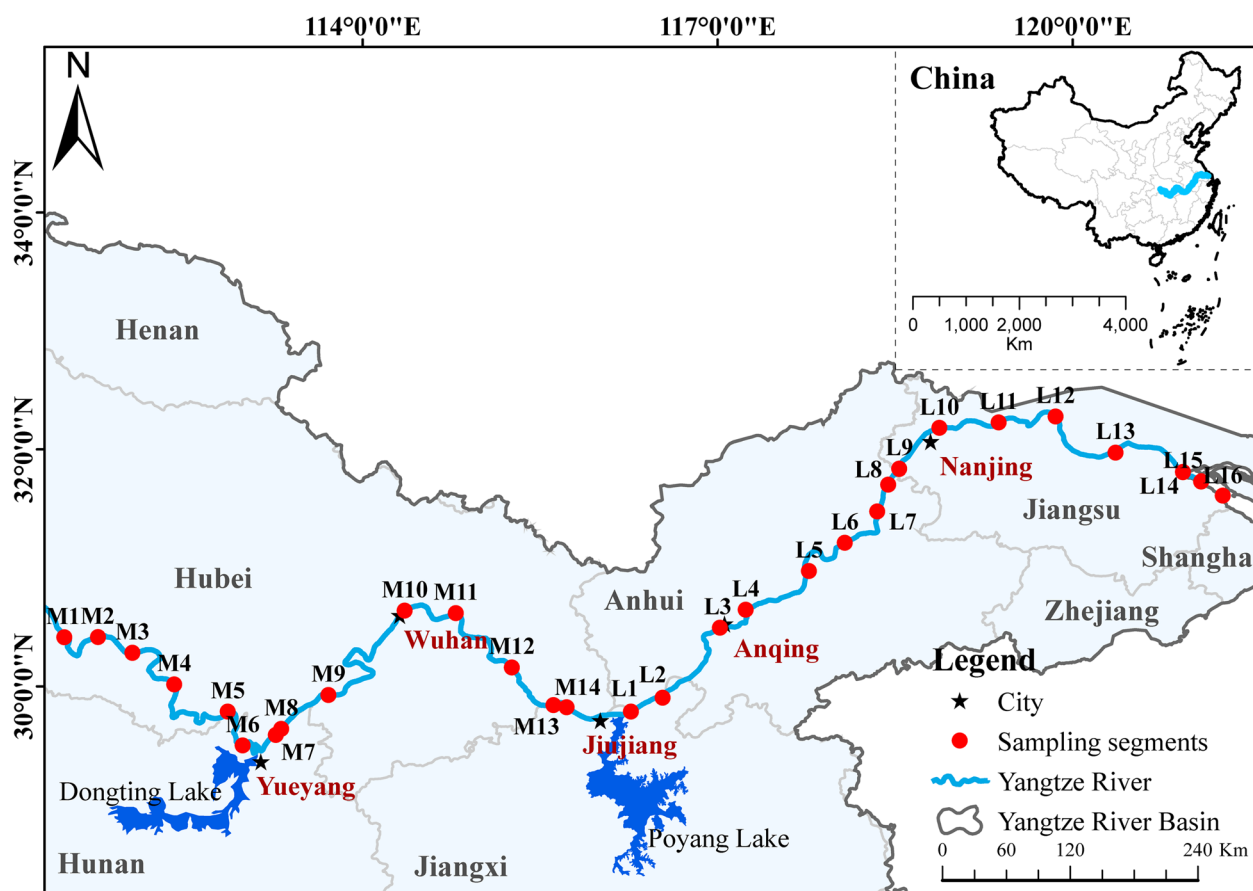


Fig. 1 Location of studied river segments in the middle and lower reaches of the Yangtze River, China during 2017–2018

A total of 14 water quality parameters were analyzed. In the field, we used a portable multi-parameter water quality meter (YSI ProPlus, Yellow Springs, Ohio USA) to measure dissolved oxygen (DO, mg/L), conductivity (CON, $\mu\text{S}/\text{cm}$), water temperature (WT, $^{\circ}\text{C}$), and pH. We used a portable turbidimeter (HACH 2100Q; Loveland, Colorado USA) to measure turbidity (TUR, NTU). We then collected 2-L water samples at 0.5 m below the water surface with a 5-L plexiglass sampler at each of the sampling sites, which were immediately transported back to the laboratory with ice for subsequent analysis. In the laboratory, we used standard methods (APHA 2005) to measure total nitrogen (TN, mg/L), total phosphorus (TP, mg/L), orthophosphate ($\text{PO}_4\text{-P}$, mg/L), nitrate ($\text{NO}_3\text{-N}$, mg/L), nitrite ($\text{NO}_2\text{-N}$, mg/L), total ammonia (TAN, mg/L), chemical oxygen demand (COD, mg/L), total suspended solids (TSS, mg/L), and chlorophyll a (Chl-a, $\mu\text{g}/\text{L}$), with details of the analysis methods referenced to previous related studies (Qu et al. 2020; Xiong et al. 2022).

Climate, habitat, and land use data collection

We collected average monthly average air temperature and precipitation for climate data. These data were obtained from the yearbooks of the provinces where the river sections were sampled and the National Environmental Information Center (<https://www.ncei.noaa.gov/>) (Xiong et al. 2022).

The habitat dataset compiled included hydrologic data (i.e., monthly mean flow and water level) and habitat assessment data (i.e., river bank, river channel, and river bed conditions). Hydrological data were collected from eight national hydrographic stations (i.e., Yichang, Zhicheng, Shashi, Jianli, Luoshan, Hankou, Jiujiang, and Datong) on the Yangtze River main-stem, with data from the nearest hydrographic station used for each sampling site (Xiong et al. 2022).

The river habitat assessment focused on three categories: river bank, river channel, and river bed, with habitat assessment methods and results obtained from a previous study (Lu 2020). The river bank category contained

five indicators, including riparian zone width, riparian land use, riparian vegetation condition, river bank modifications, and river bank human activities (Lu 2020). The river channel category included three indicators, namely hydrology and water quality condition, river channel modifications, and river channel habitat complexity (e.g., conditions of islands, sandbars, and secondary channels) (Lu 2020). The river bed category contained two indicators, including river bed substrates, and river bed stability (Lu 2020). Each of these 10 habitat indicators was scored on a 0–20 scale, which corresponded to four evaluation levels ranging from high to low, i.e., excellent (16–20), good (11–15), moderate (6–10), and poor (0–5). The overall habitat score in each site was the sum of the scores from the 10 indicators, which ranged from 0 to 200 (Lu 2020). The total habitat score was also classified into four evaluation levels ranging from high to low, i.e., excellent (150–200), good (120–150), moderate (90–120), and poor (0–90) (Lu 2020).

The riparian land use (e.g., cropland, forest, wetland, and urban) was analyzed using free 10 m resolution images of global land cover from 2017 (FROM-GLC10-2017 V0.1.3) (Gong et al. 2019; Xiong et al. 2021). In the current study, we used the buffer utility in ArcMap 10.7 software (ESRI, USA) to create 5-km×5-km buffer zones on both banks of the river segments (Xiong et al. 2021).

Data analysis

One-way analysis of variance (ANOVA) was used to test seasonal differences in phytoplankton total abundance, total biomass, species richness, and species diversity (i.e., Shannon–Wiener index [H'], based on species abundances). All data were $\lg(x+1)$ transformed to satisfy normal distribution assumptions (Qu et al. 2020), with all analyses done using IBM SPSS Ver. 24 software. Non-metric multidimensional scaling (NMDS) based on a Bray–Curtis similarity distance measure were used to assess seasonal variations in phytoplankton species abundance and functional group abundance. The analysis of similarity (ANOSIM) was further used to evaluate seasonal differences in communities as depicted by phytoplankton species abundance and functional group abundance. Larger absolute values of R (ANOSIM Global R) indicated greater relative differences, whereas smaller p values indicated more significant differences. Analysis and visualization of NMDS and ANOSIM were done using the ‘vegan’ and ‘ggplot2’ packages in R. The similarity percentage (SIMPER) was used to identify the major taxa responsible for the seasonal differences in the communities depicted by both phytoplankton species abundance and functional group biomass (Yang et al. 2022) in R.

Mantel tests are correlation test methods for determining the correlation between two sets of distance measure matrices. We used mantel tests to determine relationships between phytoplankton indices (i.e., total abundance, total biomass, species richness, and species diversity) and environmental variables (i.e., climate, habitat, land use, and water quality) (Rusanov et al. 2022). Phytoplankton and environmental variables were used with the Bray–Curtis distance and Euclidean distance, respectively. The environmental data were standardized to eliminate dimensional differences, using the ‘vegan’ package in R for the analysis. To quantify joint and separate effects of climate, habitat, land use, and water quality on phytoplankton taxonomic and functional group, a variance partitioning analysis (VPA) was performed using the ‘varpart’ function in the ‘vegan’ package. Taxonomic and functional groups with <10% frequency of occurrence were removed before analysis. Environmental variables were used as the explanatory variables, and phytoplankton species abundance and functional group abundance were used as the response variables. Hellinger transformations were applied to the response variables to reduce the impacts of rare species and double-zero problems (Qu et al. 2023), and $\log_{10}(x+1)$ transformations were applied to the explanatory variables. The forward selection was performed using the “ordiR2step” function in the ‘vegan’ package to screen explanatory variables based on 999 permutation tests, and each response variable (taxonomic and functional groups) was screened separately (Rusanov et al. 2022). The overall variance was divided into components based on adjusted R values: i.e., climate, habitat, land use, water quality, and residuals. ANOVA was used to test the significance of each category of these environmental variables. The significance level for all statistical analyses was set at 0.05.

Results

Characteristics of phytoplankton taxonomic structure

A total of 150 taxa from 8 phyla of phytoplankton were identified from the middle and lower reaches of the Yangtze River. Chlorophyta had the greatest species richness (67 species), followed by bacillariophyta (49 species), cyanophyta (21 species), dinophyta (6 species), and euglenophyta (4 species), with cryptophyta, chrysophyta, and xanthophyta having the lowest species richness (1 species each). Overall, there were 140 and 84 phytoplankton taxa identified during the wet and dry seasons, respectively; mean values for each season were 18 and 16 species, respectively (Fig. 2c). Phytoplankton total abundance in the wet and dry seasons were 1.53×10^4 – 1.04×10^6 cells/L and 1.62×10^4 – 1.05×10^6 cells/L, respectively; mean values for each season were 3.43×10^5 cells/L and 1.81×10^5 cell/L, respectively (Fig. 2a). Similarly, Phytoplankton

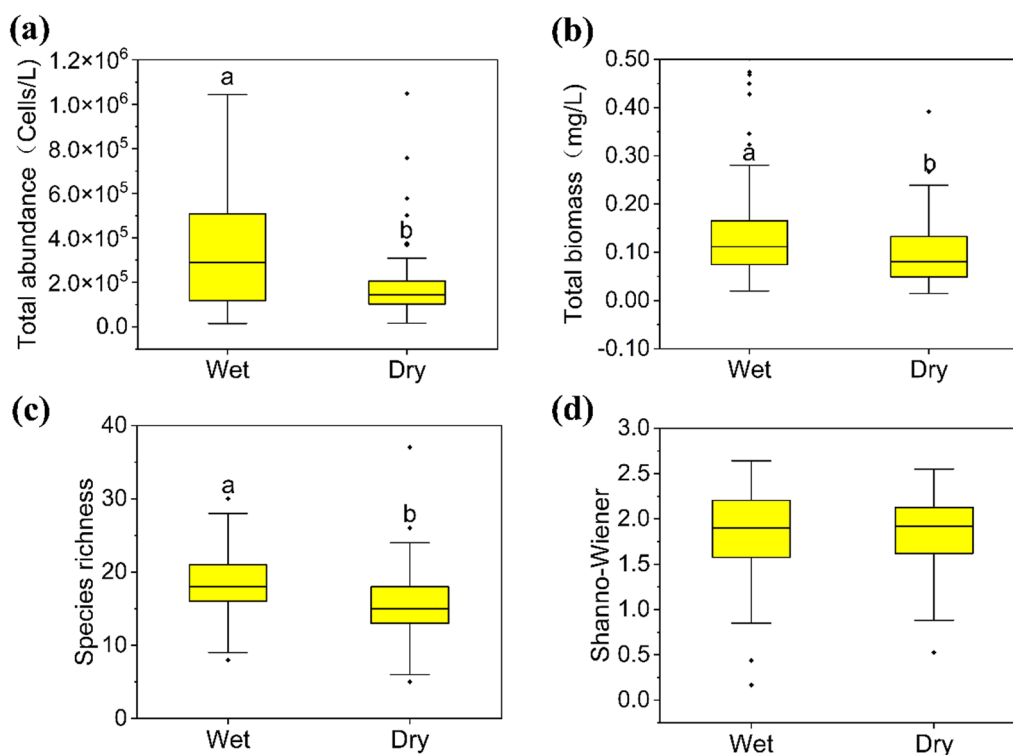


Fig. 2 Seasonal patterns of phytoplankton **a** abundance, **b** biomass, **c** species richness and **d** Shannon–Wiener diversity index in the middle and lower reaches of the Yangtze River during 2017–2018. Box plots with different lowercase letters indicate statistical differences between seasons, i.e., $P < 0.05$

total biomass during the wet and dry seasons were 0.02–1.01 mg/L and 0.01–0.39 mg/L, respectively, with mean values of 0.16 mg/L and 0.10 mg/L, respectively (Fig. 2b). Phytoplankton diversity (H') ranged from 0.17 to 2.64 and 0.53 to 2.55 during the wet and dry seasons, respectively (Fig. 2d). ANOVA indicated that phytoplankton total abundances, total biomasses, and species richness were significantly greater ($P < 0.01$) during the wet season compared to the dry season (Fig. 2). Phytoplankton diversity was similar between seasons.

Cyanophyta, bacillariophyta, and chlorophyta were the dominant phyla in terms of phytoplankton abundance, with average relative abundances of 55%, 28%, and 16%, respectively. The relative abundance of cyanophyta decreased in the dry season compared to the wet season, while the relative abundance of bacillariophyta and chlorophyta exhibited opposite trends. Biomass of bacillariophyta was the greatest throughout the year (58%), followed by chlorophyta (22%), dinophyta (13%) and cyanophyta (4%). Biomass of bacillariophyta increased in the dry season compared to the wet season. In terms of abundance, four and seven phytoplankton species were dominant in the wet and dry seasons, respectively, with *Pseudanabaena* sp., *Oscillatoria* sp., *Cyclotella* sp., and *Melosira granulata* being dominant in both seasons.

In addition, *Scenedesmus* sp., *Synedra* sp., and *Melosira granulata* var. *angustissima* also were the dominant phytoplankton species in the dry season. NMDS and ANOSIM indicated significant differences in phytoplankton community composition between the wet and dry seasons (Global $R = 0.20$, $P < 0.01$) (Fig. 3a), with cyanobacteria, bacillariophyta, and chlorophyta contributing to 99% of the seasonal variation at the phylum level (Fig. 3b). *Oscillatoria* sp., *Pseudanabaena* sp., and *Melosira granulata* contributed to 15%, 12%, and 8% of the seasonal variation at the species level, respectively (Fig. 3c, Additional file 1: Table S2).

Characteristics of phytoplankton functional groups

Phytoplankton in the middle and lower reaches of the Yangtze River were classified into 26 functional groups, including A, B, C, D, E, F, G, H1, J, Lo, M, MP, N, N_A, P, S1, S2, S_N, T, T_B, W1, W2, X1, X2, X3, and Y (Additional file 1: Table S3). In the wet season, there were 26 functional groups, 12 of which (i.e., A, B, D, F, H1, J, Lo, MP, P, T_B, W2, and X3) were dominant. Functional groups P, J, and Lo had the greatest mean relative biomasses at 38%, 17%, and 13%, respectively (Fig. 4a). In the dry season, there were 23 functional groups, 10 of which (i.e., B, D, J, Lo, MP, P, T_B, W1, X3, and Y) were dominant. The

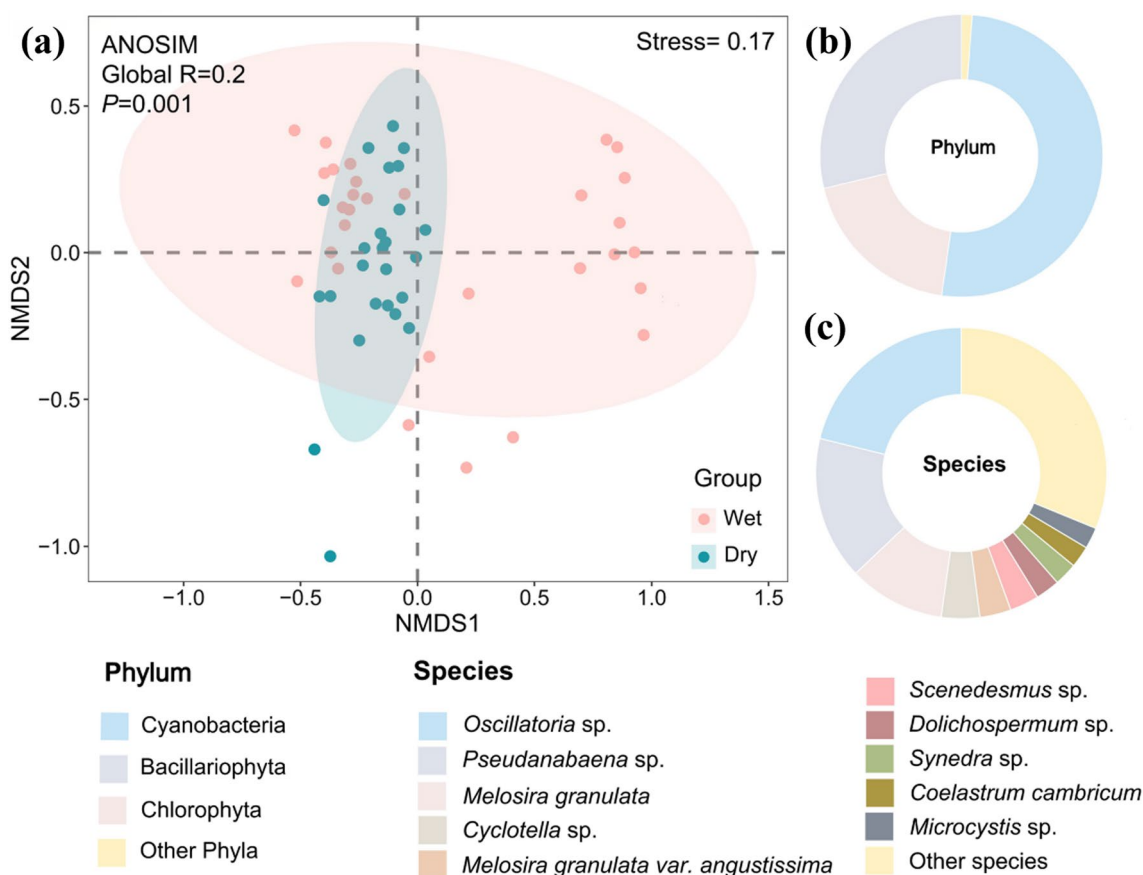


Fig. 3 Community composition of phytoplankton species from the middle and lower reaches of the Yangtze River during 2017–2018. **a** Results of non-metric multidimensional scaling (NMDS) and similarity analysis (ANOSIM) based on phytoplankton species abundance, indicates the seasonal distribution patterns. The **b** phylum and **c** species levels of contributions to phytoplankton community variations, respectively

mean relative biomass of functional groups P, J, and Lo decreased to 35%, 13%, and 10%, respectively (Fig. 4b). NMDS and ANOSIM indicated a significant difference ($P < 0.01$) in the composition of phytoplankton functional groups between the wet and dry seasons (Fig. 5a), with functional groups P, Lo, and J contributing the most seasonal variation at with 17%, 9%, and 9%, respectively (Fig. 5b, Additional file 1: Table S4).

Driving factors of phytoplankton community

Mantel tests detected significant effects of environmental factors on phytoplankton total abundances, total biomasses, and species richness ($P < 0.05$). Water quality had significant effects on phytoplankton abundances, biomasses, species richness, and diversity ($P < 0.05$). Climate had significant effects on phytoplankton abundances and species richness ($P < 0.01$) whereas habitat significantly affected only abundances ($P < 0.05$) (Additional file 1: Table S5).

The variance partitioning indicated that climate, habitat, land use, and water quality all made contributions

to shaping the structure of phytoplankton communities, both taxonomically and functionally (Fig. 6). The total variance explained by environmental factors for phytoplankton taxonomic and functional groups was 24% and 20%, respectively. Water quality (mainly $\text{NO}_3\text{-N}$, TAN, TSS, and TUR) and habitat (mainly water flow, water level, and river channel and bank conditions) explained most of the variation in phytoplankton species abundances (water quality total 17%, independently 10%; habitat total 10%, independently 5%) and functional groups biomasses (water quality total 12%, independently 5%; habitat total 11%, independently 4%) (Fig. 6, Additional file 1: Table S6). Climate (mainly air temperature and precipitation) explained some of the variation in phytoplankton species abundances (total 9%, independently 2%) and functional groups biomasses (total 8%, independently 2%) (Fig. 6, Additional file 1: Table S6). Land use (mainly wetland and forest) explained the least variance in phytoplankton communities whether expressed taxonomically and functionally (Fig. 6, Additional file 1: Table S6).

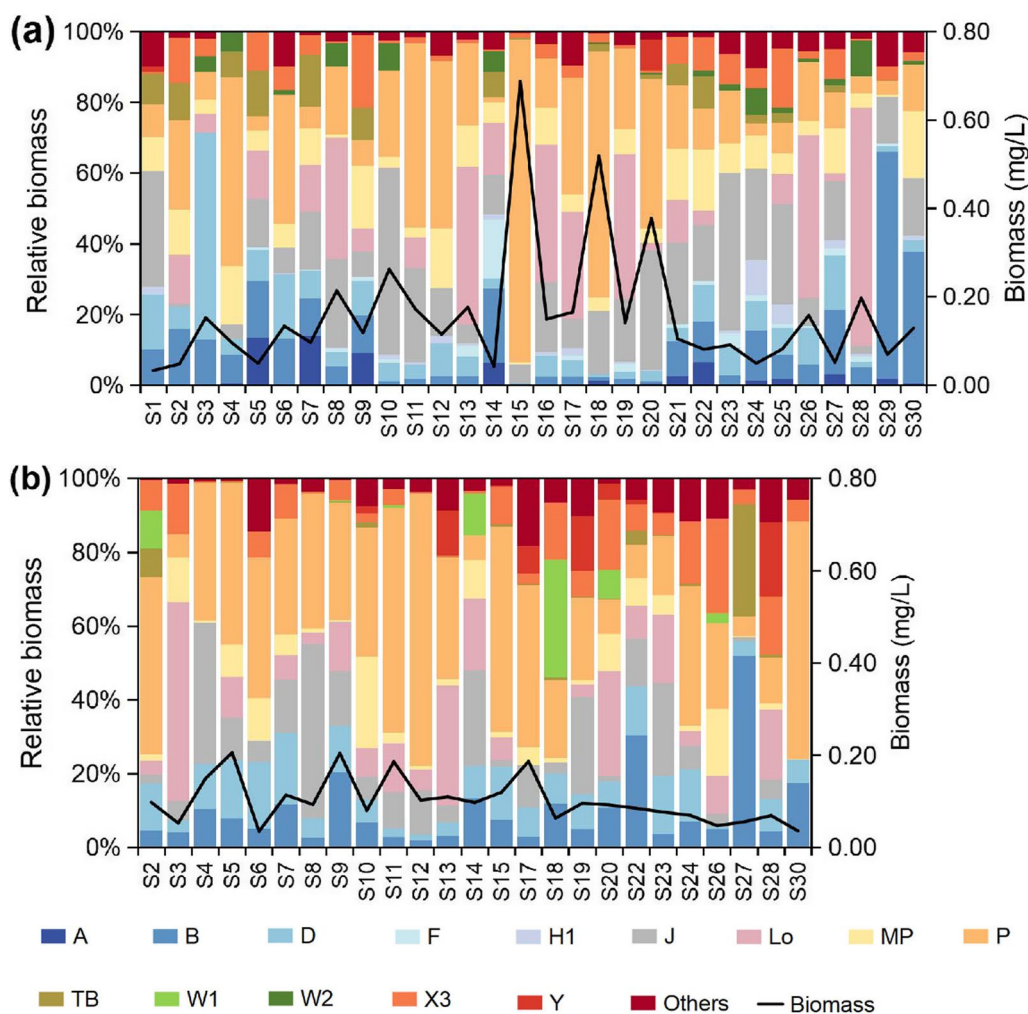


Fig. 4 Spatial and temporal distribution patterns of important functional groups in the (a) wet and (b) dry seasons in the middle and lower reaches of the Yangtze River during 2017–2018

Discussion

Phytoplankton community structure

We identified a total of 150 taxa of phytoplankton in the middle and lower reaches of the Yangtze River, more than the 117 species found by Wu et al. (2023b) and the 59 species found by Liu et al. (2019). This could be related to larger sampling efforts (e.g., spatial ranges, number of sites, multiple seasons, and multiple years) in the current study. Cyanobacteria, bacillariophyta, and chlorophyta were the main contributors to phytoplankton abundance, which was consistent with previous findings (Liu et al. 2019). High nitrogen and low phosphorus concentrations are beneficial to preventing cyanobacterial blooms (Wang et al. 2020). When the ratio of TN/TP is greater than 22, it is phosphorus-limited and not conducive to cyanobacterial growth and reproduction (Ding et al. 2022a). In the current study, the wet and dry season average TN/TP ratios were 18.6 and 21.7 in the Yangtze River,

respectively, which would be consistent with a dominance of cyanobacteria. We found that bacillariophyta were dominant in terms of biomass, which occur frequently in other rivers (Ding et al. 2022a; Rusanov et al. 2022). We detected greater phytoplankton abundances, biomasses, and species richness during the wet season. Sufficient light and greater temperatures during the wet season (i.e., summer) appeared to have facilitated the growth and reproduction of phytoplankton (Tian et al. 2021). The relative abundances of cyanobacteria and chlorophyta also were greater during the wet season than the dry season, while diatoms exhibited the opposite pattern. Water temperature affects growth of phytoplankton by controlling the enzymatic reactions of photosynthesis and the intensity of respiration, which consequently affects variations in community structure (Blinn 1993). Cyanobacteria and chlorophyta prefer warmer conditions, while diatoms can be dominant at a wide range of water temperatures.

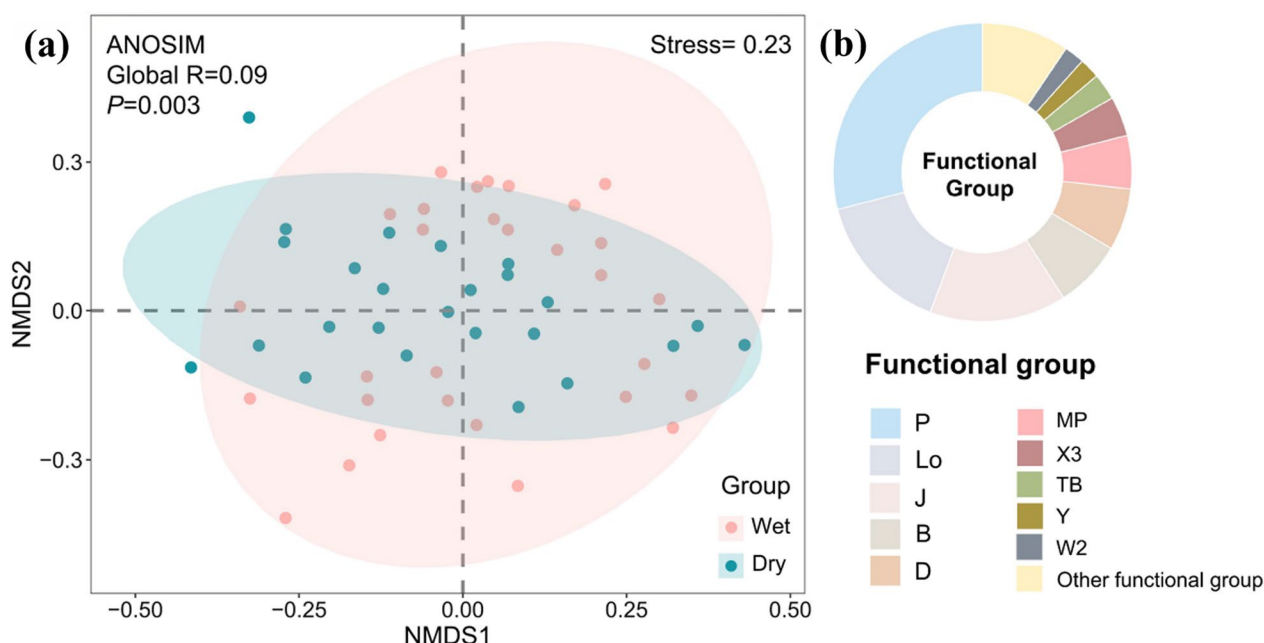


Fig. 5 Community composition of phytoplankton functional groups from the middle and lower reaches of the Yangtze River during 2017–2018. **a** Results of non-metric multidimensional scaling (NMDS) and similarity analysis (ANOSIM) based on the abundance of phytoplankton functional groups, indicates the seasonal distribution patterns. **b** Functional group contributions to phytoplankton community variations

In addition, the runoff from abundant rainfall during the wet season increases nutrient inputs to the river (Xiong et al. 2022), which could have favored the growth and reproduction of filamentous cyanobacteria (Duong et al. 2019). The dominant species *Pseudanabaena* sp. and *Oscillatoria* sp. are filamentous cyanobacteria with high metabolic capacities and good mobility, which would certainly be a favorable trait for survival and reproduction in the Yangtze River, where flows and water level fluctuations can be excessive (Wang et al. 2020).

Phytoplankton functional group MP (including *Oscillatoria* sp., *Navicula* sp., *Surirella* sp., *Cymbella* sp., etc.) are able to adapt to turbid environments with frequent disturbances (Padisák et al. 2009). Functional groups B (*Cyclotella* sp.) and D (including *Synedra* sp. and *Nitzschia* sp.) that are mainly composed of diatoms, have larger sizes, and higher surface areas, which facilitates efficient light harvesting and is advantageous for growth and reproduction in highly turbid conditions (Padisák et al. 2009). The Yangtze River is the largest river in China with high flow velocities and high sand content. It seems plausible that these conditions coupled with the turbid water environment would facilitate MP, and B and D at becoming the dominant functional groups. Functional groups P, J, and Lo generally explained the most seasonal community variation and all had lower relative biomass in the dry season than those in the wet season. Functional group J (including *Pediastrum* sp., *Tetraedron*

sp., *Crucigenia* sp., *Scenedesmus* sp., and *Coelastrum* sp.) was mainly composed of chlorophyta whereas functional group P (including *Closterium* sp., *Melosira* sp.) consisted mainly of chlorophyta and diatoms. These functional groups are adapted to frequently stirred waters with high nutrient levels (Padisák et al. 2009). The functional group Lo (including *Merismopedia* sp., *Peridinium* sp., *Ceratium* sp., and *Gymnodinium* sp.) is one of the most common taxa in large rivers. They are adapted to a wide variety of habitats, including both deep and shallow water, and occur across a wide range of nutrient concentrations (Padisák et al. 2009; Xiao et al. 2011). *Peridinium* sp., the key species of functional group Lo, prefers to reproduce at high temperatures (20–27 °C) (Grigorszky et al. 2006), while the high-temperature environment in the Yangtze River during the wet season also appears suitable for functional groups P and J (Liu et al. 2019). Urban and cropland are the main land uses in the middle and lower reaches of the Yangtze River (Xiong et al. 2021). Abundant rainfall during the wet season transfers pollutants from land into the river through surface runoff processes, which would be consistent with nutrient concentration increases in the river (Tong et al. 2017). Previous studies in the Yangtze River indicated that COD, turbidity, TP, and TN concentrations also were significantly greater during wet than dry seasons (Xiong et al. 2022), which also would be favorable for functional groups P, J, and Lo (Padisák et al. 2009; Long et al. 2020).

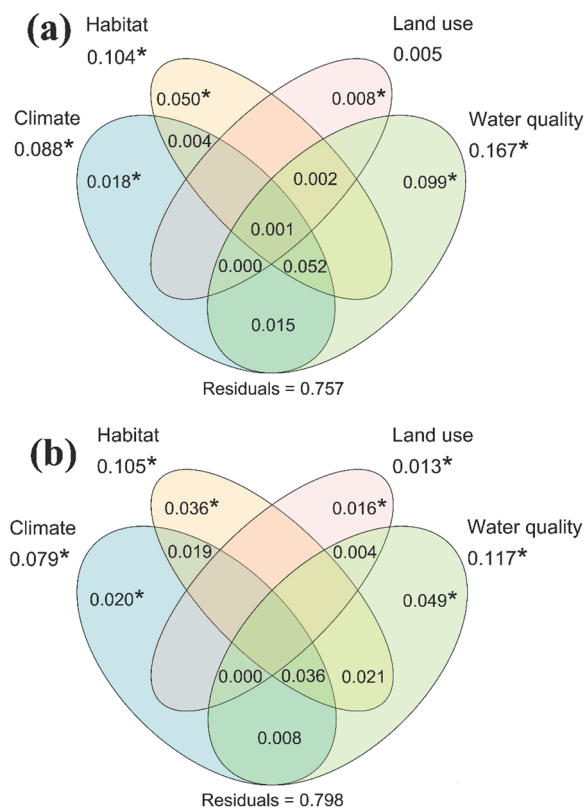


Fig. 6 Results of variation partitioning of the driving factors affecting variations in phytoplankton (a) taxonomic and (b) functional group patterns in the middle and lower reaches of the Yangtze River during 2017–2018. Values out of the circles represent the total contribution of climate, habitat, land use, and water quality, while values in the circles represent independent or joint contributions. All scores are based on adjusted R^2 values; negative fractional values are not shown, and residuals are shown below the Venn diagrams, with * indicating $P < 0.05$

Driving factors of phytoplankton communities

Phytoplankton community structure in aquatic ecosystems is determined by the dynamic interplay of growth and losses. To a large extent, growth is regulated by resource availability, i.e., nutrients, light, temperature, etc., while losses are influenced by scouring, grazing, cell death, and subsidence (Interlandi and Kilham 2001; Reynolds 2006; Cao et al. 2018; Sommer et al. 2018). Environmental variables can disrupt the ecological balance of more pristine waters, thus, leading to a new community equilibrium through successional processes. Multiple factors can affect phytoplankton communities, including water quality, climate, hydrology, and land use among others. However, the influences that drive phytoplankton succession often vary among study areas (Xu et al. 2010; Zhou et al. 2016; Wu et al. 2019; Huang et al. 2021; Qu et al. 2022; Rusanov et al. 2022). Water quality and physical habitat influence riverine aquatic life significantly

(Pilière et al. 2014; Green et al. 2022), and local factors such as water quality and hydrology have direct impacts on riverine phytoplankton (Tian et al. 2021). Our results demonstrate that water quality, habitat, climate, and land use all played important roles in shaping phytoplankton taxonomic and functional groups, with water quality and habitat being the main driving factors.

Water quality parameters such as nitrogenous nutrients, turbidity, TSS, and WT were important in affecting the variations in phytoplankton taxonomic and functional groups. This finding was consistent with previous studies (Michalak 2016; Tian et al. 2021) where nutrient levels were extremely critical for phytoplankton growth and community succession (Baines and Pace 1991; Xu et al. 2010; Liu et al. 2019). Although nitrogenous nutrients are often the main factors driving phytoplankton functional groups (Ding et al. 2022b), most phytoplankton prioritize the utilization of $\text{NH}_4\text{-N}$ (Dortch 1990), with combinations of high nitrogen and low phosphorus beneficial at preventing cyanobacterial blooms (Wang et al. 2020). The Yangtze River is a typical river with poor nutrients (Liu et al. 2019), and nitrogen is critical for phytoplankton growth when it is in an oligotrophic condition (Jiang and Nakano 2022). In contrast, low nitrogen has less effect on nitrogen-fixing cyanobacteria (Boyer et al. 2006), thus, it is likely that *Oscillatoria* sp. had been dominant for a long period of time before the study. The underwater light condition is a major factor affecting phytoplankton growth, which had been detected in lake studies in the Yangtze River basin (Wu et al. 2013, 2019). Yang et al. (2019) also reported that mixing regime, water temperature, and light availability were the driving factors controlling phytoplankton community dynamics in an estuarine reservoir of the Yangtze River. Since discharge, turbidity, and suspended solids are the main environmental factors affecting river phytoplankton, they are able to perform their functions by regulating water quantity and underwater light (Salmaso and Braioni 2008; Jia et al. 2020; Tian et al. 2021; Ding et al. 2022b). As a large river with high water volume and high sand content, the species selectivity in turbid habitats of the Yangtze River may favor diatoms, especially those with high surface/volume ratios and low light acclimation (Reynolds 1994). In addition to water quality, flow, and channel habitat conditions, river bank conditions such as riparian buffers can be critical in that they protect the river from negative impacts from surrounding land uses (Mundahl and Mundahl 2022). Adequate areas and intact vegetated buffers can effectively intercept surface runoff into streams. Vegetation can filter and absorb pollutants to reduce nutrient levels in surface runoff and groundwater (Osborne and Kovacic 1993; Yates et al. 2007; Mundahl and Mundahl 2022) by reducing nutrients in the river, thus,

increasing water transparency and driving phytoplankton succession.

Climate also plays an important role in driving variations in phytoplankton taxonomic and functional groups. Precipitation and air temperature contributed significantly to phytoplankton community changes, which have been reported in other studies (Blois et al. 2013). Climate is one of the major factors contributing to differences across rivers worldwide. Thus, it is plausible that phytoplankton variation in large rivers may be largely driven by interregional differences in climate (Rusanov et al. 2022). Ding et al. (2022b) found significant effects of precipitation and air temperature on phytoplankton diversity in spring and autumn in the Yellow River, China. Greater air temperatures also can lead to significant increases in river phytoplankton, especially cyanobacteria (Haakonsson et al. 2017; Bao et al. 2022). Conversely, precipitation effects on phytoplankton community structure are related to altered nutrients and other abiotic factors in aquatic ecosystems (Zhou et al. 2016; Peng et al. 2021).

Land use contributed less to the variations in phytoplankton taxonomic and functional groups than other factors in the current study. The effects of land use on phytoplankton are mainly through the increase or decrease of nutrients and water transparency to regulate the phytoplankton community, with the effects differing across different between land uses (Peng et al. 2021). Moreover, land use is a comprehensive indicator that combines multiple factors (Qu et al. 2022), and is associated with nutrients (Xiong et al. 2022), hydrology (Guse et al. 2015), physical habitat (Mundahl and Mundahl 2022), and other pollutants (Kelso and Baker 2022). However, land use in the Yangtze River seems to affect other aquatic biota such as fish more directly than other organisms (Xiong et al. 2021, 2023). This may jointly result from the water quality and habitat characteristics in large rivers (e.g., high flows, turbid water, rapid changes in habitat conditions) and the succession of phytoplankton in these systems (Reynolds 2006; Padisák et al. 2006). The different responses of aquatic biota to land use and other human stressors warrants further comprehensive studies in large river ecosystems.

Limitations and recommendations

Limitations exist in the current study. First, we focused on seasonal variations of phytoplankton during the 2 year period of wet and dry seasons. However, results from this relatively low-frequency, short-timespan monitoring may not fully represent the overall pattern of phytoplankton community dynamics in the Yangtze River. In the future, studies involving more seasons and larger spatial scales would be recommended. Second, the Yangtze River, as China's largest river, is subject to a complex and

diverse array of anthropogenic disturbances (Chen et al. 2016; Chen et al. 2017, 2020), including dams, navigation, sand mining, overfishing, urbanization, and riparian development among others—all of which have been demonstrating as having significant effects on river ecosystems (Zhang et al. 2019; Xiong et al. 2021, 2022, 2023; Gao et al. 2023). In this study, we focused on the effects of land use, water quality, habitat, and climate on phytoplankton communities. However, there are still a multitude of other unmeasured or unquantified factors that drive variations of phytoplankton communities (Sommer et al. 2012). Phytoplankton is an intermediate link in the energy flow of aquatic ecosystems, which should not only take into account the effects of numerous abiotic factors (Lv et al. 2014), but also consider the effects of biotic factors, such as predation by zooplankton and planktivorous fishes (Zhang et al. 2018b; Yin et al. 2022; Guo et al. 2023). Interspecific interactions such as these were not considered in this study, though they also may play important roles in shaping phytoplankton community patterns (Yang et al. 2018). In summary, longer-term, more intensive, and studies across larger spatial scales are needed in the future to fully understand phytoplankton patterns and their driving mechanisms in large river systems such as the Yangtze River.

Conclusions

The main conclusions of this study include:

- (1) A total of 150 phytoplankton taxa belonging to 26 functional groups were identified in the middle and lower reaches of the Yangtze River. The phytoplankton were mainly composed of cyanobacteria, bacillariophyta, and chlorophyta, and the abundance, biomass, and species richness of phytoplankton were significantly greater during the wet season compared to the dry season.
- (2) Phytoplankton taxonomic and functional group compositions differed significantly between seasons. The taxonomic variation in phytoplankton communities between wet and dry seasons were driven mainly by the abundances of *Oscillatoria* sp., *Pseudanabaena* sp., and *Melosira granulata*. The variation in the functional composition of phytoplankton communities between seasons was mainly contributed by P, Lo, and J.
- (3) Water quality (NO₃-N, total suspended solids, turbidity) and habitat (water flow, riverbank and river channel conditions) were the primary driving factors for phytoplankton community variation, followed by climate (air temperature and precipitation) and land use.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s13717-024-00489-6>.

Additional file 1. Supplementary tables.

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Author contributions

YC designed the study. WG, FX, and YL collected the data. WG analyzed the data. WG, FX, YL, WX, HW, GF, CK, LF, XG, and YC wrote the manuscript. All authors contributed to revising, commenting, and finalizing the manuscript.

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Availability of data and materials

All data will be available in the data center of Institute of Hydrobiology, Chinese Academy of Sciences (www.ihb.ac.cn).

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interest.

Author details

¹State Key Laboratory of Freshwater Ecology and Biotechnology, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan 430072, Hubei, China. ²University of Chinese Academy of Sciences, Beijing 100049, China. ³Jiangxi Institute for Fisheries Sciences, Poyang Lake Fisheries Research Centre of Jiangxi Province, Nanchang 330039, Jiangxi, China. ⁴Jiujiang Institute of Agricultural Sciences, Jiujiang 332005, Jiangxi, China. ⁵East China Sea Fisheries Research Institute, Chinese Academy of Fishery Sciences, Shanghai 200090, China.

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