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Research Paper

The key factors on the composition of phytoplankton functional groups in different watersheds in the Huanghe River basin*

Jing DONG[#], Feihu WANG[#], Shuwen ZHANG, Huatao YUAN, Xiaofei GAO,
Jingxiao ZHANG, Xuejun LI[**]

College of Fisheries, Henan Normal University, Xinxiang 453007, China

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Abstract To understand the distribution of phytoplankton functional groups (PFGs) and key factors on their compositions in different watersheds of the Huanghe (Yellow) River basin, 25 river sites and 25 lake-reservoirs sites were selected. The contents of nephelometric turbidity (NTU), total nitrogen (TN), and total phosphorus (TP) were significantly higher in rivers than that in lakes or reservoirs, whereas the pH and COD_{Mn} (chemical oxygen demand or potassium permanganate index) were lower. Results show that, 27 PFGs, namely, assemblages A, B, C, D, E, F, G, H, J, K, LM, Lo, M, MP, N, P, S1, S2, T, TC, W1, W2, X1, X2, X3, XPh, and Y, were identified. Additionally, ANOSIM correlation analysis demonstrated significant differences in PFG composition between the riverine and lake-reservoir sections in the Huanghe River basin. In the riverine watersheds, the group MP was dominant, while assemblages B and J were prevalent in lakes and reservoirs. The Mantel correlation tests and RDA analysis showed that environmental variables, such as NTU, water temperature (WT), conductivity (Cond), and TP, were key driving factors of shaping the dominant PFGs of the study area. Using the Venn diagram based on variation partitioning analysis, PFGs were mainly influenced by WT and TP in lake-reservoir sites, while in the river sites were affected mainly by geo-climatic variables. This study helps understanding the PFGs in river ecosystems, and unraveling the key driving factors in different watersheds, which shall be important for the protection and management of entire Huanghe River basin.

Keyword: Huanghe River; phytoplankton functional group; driving factor; riverine watershed; lake-reservoir region

1 INTRODUCTION

Phytoplankton, as primary producers, play a fundamental role in the biogeochemical cycling of energy in aquatic ecosystems and exhibit rapid responses to even subtle environmental changes (Eiler et al., 2013). The temporal and spatial distribution patterns of phytoplankton have significant effects on ecological processes, functions, and stability. Furthermore, phytoplankton are often used as crucial indicators for assessing environmental variables and water quality in aquatic ecosystems (Carvalho et al., 2013). Traditionally, studies have primarily focused on changes in phytoplankton biomass and chlorophyll *a* level to evaluate nutrient levels and reflect ecosystem functioning (Costa et al., 2009; Wang et al., 2011; Elliott, 2012). However, in comparison with biomass, the structure of the phytoplankton

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[**] Corresponding author: xjli@htu.cn

[#] Jing DONG and Feihu WANG contributed equally to this work and should be regarded as co-first authors.

community may provide more clues into water quality assessment (Hering et al., 2006; Yang et al., 2016).

Taxonomic classification is one of the conventional methods for identifying phytoplankton involving typically the categorization of them into different taxa based on Linnaean phylogenetic affiliations. Freshwater phytoplankton, classified in the traditional manner, usually consists of seven taxa: Cyanophyta, Chlorophyta, Bacillariophyta, Chrysophyta, Cryptophyta, Euglenophyta, and Pyrrophyta (Lúcia et al., 1998). Previous studies have made progresses in predicting the occurrence or dominance of certain species in specific habitats based on the interrelationships between these taxa and environmental variables. For instance, increased total phosphorus content is often accompanied by a surge in cyanobacteria. However, some studies have also reported that the abundance of blue-green algae may not be significantly related to total phosphorus content (Watson et al., 1997). In certain water bodies with high phosphorus content, the dominant species may belong to other taxa rather than blue-green algae (Jensen et al., 1994). Thus, relying solely on external environmental conditions to judge the composition of traditional taxonomic groups is incomplete. Furthermore, in the traditional Linnaean homologous classification system, various morphological characteristics, such as cell volume, maximum linear diameter, surface area to volume ratio, presence of gums, flagella, pseudo vacuoles, heteromorphic cells, and silicon skeleton structures, are considered within each group (Kruk et al., 2010). Studies have demonstrated a strong correlation between morphology and biological functional properties, such as growth rate, resource absorption, and photoinhibition properties, of which all depend on the cell diameter, volume, and surface area-to-volume ratio of organisms (Reynolds et al., 2002). Algal morphology also affects the filter-feeding efficiency of filter-feeding zooplankton (Burns, 1968; Yang and Li, 2007; Zhu et al., 2021). Therefore, various species within the same taxonomic group may adapt to different habitats due to differences in morphological characteristics. Additionally, species that occur within the same habitat may belong to different taxonomic groups.

Due to the limitations of traditional taxonomic classification in predicting environmental habitat characteristics, Reynolds et al. (2002) introduced the concept of phytoplankton functional groups (PFGs). PFGs consist of algae with similar adaptive characteristics, including surface area/volume ratio, motility, nutrient utilization efficiency, and sensitivity to predation. The concept of PFGs carries two key implications: the first, species with good adaptability within a functional group are more tolerant to deficiencies in certain factors than species with weaker adaptability; and the second, habitats that are significantly limited by light, phosphorus, carbon, nitrogen, or other factors are more likely to be inhabited by species suitable for those conditions. As a result, algae belonging to the same functional group tend to occur in similar habitats or under similar environmental conditions. Therefore, based on habitat characteristics, predicting the potential composition of phytoplankton communities and identifying the dominant species are possible. Additionally, habitat characteristics can be described based on the presence of specific functional groups. Consequently, PFGs have proven to be more valuable and useful than phylogenetic representation in predicting species occurrence and describing environmental conditions (Huszar et al., 2000; Kruk et al., 2002; Salmaso and Padisák, 2007).

The concept of PFGs was initially proposed based on data from some European temperate lakes (Reynolds et al., 2002; Padisák et al., 2009). Since then, this approach has been widely applied to assess the relationship between environmental factors and phytoplankton succession in lakes (da Costa et al., 2016; Cao et al., 2018; Dong et al., 2019), reservoirs (de Souza et al., 2016; Cui et al., 2021; Liao et al., 2021), and ponds (Chang et al., 2021). In recent decades, the concept of PFGs has also been applied in rivers for the quantitative assessment of productivity, function diversity, relationship between phytoplankton composition and water quality, and the habitats in river systems (Stanković et al., 2012; Rangel et al., 2016; Bolgovics et al., 2017; Nagy-László et al., 2020; Abonyi et al., 2021; Ding et al., 2022). Rivers, as vital freshwater resources, play an indispensable role in human social development and the provision of freshwater ecosystem services. However, rivers and associated freshwater ecosystems are currently facing increasing natural disturbances and anthropogenic stressors. Understanding the key ecological processes that govern riverine biota in aquatic ecosystems under multiple pressures is of crucial importance in evaluating their ecological functions. Unlike lake-reservoir systems, hydrological conditions and geo-climatic variables in free-flowing rivers may play a vital role in shaping the composition and structure of phytoplankton, rather than nutrients alone (Zhu et al., 2013; Ding et al., 2022). However, knowledge regarding the responses of PFGs to multiple stressors from a catchment perspective is still lacking. It is hypothesized that the phytoplankton composition in riverine and lake-reservoir watersheds in a catchment may respond differently to the diversified environmental variables, which could be very helpful for watersheds management of the whole basin.

The Huanghe (Yellow) River, a vital water resource for northwestern China, is the second largest in China and the fifth longest river in the world. Due to its unique characteristics of water flow and sediment (Miao et al., 2011; Li et al., 2021), as well as its low pollution carrying capacity and sensitivity to environmental changes, the river faces severe resource-based water shortages. The Huanghe River basin is made of the main stream, tributaries, lakes, and reservoirs. To the best of our knowledge, little is known about the rich aquatic organism resources within the basin, and the habitat illustration based on organisms is scarce. The Huanghe River basin can be divided into two distinct sections: the free-flowing rivers and lake/reservoir, which have different environmental variables. The free-flowing river section is known for its heavy sediment load that extends across the continent (Ding et al., 2021), whereas the lake-reservoir parts are more influenced by human activities. Therefore, distinct variables played a role in shaping the composition of PFGs in different parts of Huanghe River basin. Understanding the factors of PFG composition in the flowing river and lake-reservoir sections within the Huanghe River basin from the catchment perspective would contribute to study of PFGs in river ecosystem and hold great significance for protection and management of river ecosystems.

2 MATERIAL AND METHOD

2.1 Study area

The Huanghe River is known for its high sediment load, ranging from 0.25 to 11.68 kg/m^3 (Yu et al., 2013; Wang et al., 2016; Ding et al., 2021). It originates from the Yueguzongli Basin in the Qinghai-Tibet Plateau and flows from west to east, eventually reaching the Bohai Sea. The river spans a total length of 5 464 km and has a drainage basin of 752 400 km^2 (Wang et al., 2006, 2007a, 2008, 2017).

2.2 Sampling site

Water samples were collected in June–July, 2021, at 50 sampling sites to examine the physicochemical and biological variations between the lake-reservoir and rivers within the Huanghe River basin. The details of the sampling sites are provided in Table 1 and visualized in Fig.1 (ArcGIS, Version 10.2). In the present study, the Zhaling Lake, Eling Lake, and Dongping Lake are natural lakes formed at the source and downstream of the Huanghe River. The Huanghe River originates from the Kariqu and Yueguzonglie Qu (River) at the northern foot of the Bayan Kara Mountains and passes through the Xingxiu Hai (Lake) and the Maqu River, first flowing into Zhaling Lake, then into Eling Lake, and finally flowing out from the north. The source of Dongping Lake comes from the largest tributary of the Huanghe River (the Dawen River) and flows into the Huanghe River again through the Qinghe and Chenshankou gates at the north of Dongping Lake. The Wuliangsuhai Lake, also known as a large-scale multifunctional lake, is the largest lake wetland in the Huanghe River basin, which ultimately discharges southward into the Huanghe River. The Xiaolangdi Reservoir, spanning the Huanghe River, is located on the downstream of the Huanghe River.

2.3 Data collection

The water temperature (WT), pH, conductivity (Cond), and dissolved oxygen (DO) were recorded in situ with a YSI (Xylem Inc., USA). In addition, the collected surface water samples were immediately taken to the laboratory for nutrient analysis and phytoplankton identification. Total phosphorus (TP), total nitrogen (TN), ammonia (NH_4^+-N), chemical oxygen demand (COD_{Mn}), and nephelometric turbidity (NTU) were determined according to the Water and Wastewater Monitoring and Analysis Methods (Ministry of Environmental Protection of the People's Republic of China) (4th edition, 2002).

2-L phytoplankton samples were collected and immediately preserved with Lugol's solution in the field. These samples were then transferred to the laboratory for concentration (usually concentrated to 30 mL) and enumeration. Taxonomic identification of phytoplankton was carried out with an optical microscopy following the methods described by Hu and Wei (2006), while the classification of PFGs was based on the criteria outlined by Reynolds et al.

Table 1 Fifty sampling sites in the Huanghe River Basin

Number	Sites name	Abbreviation	Water type	Longitude (°)	Latitude (°)
1	Tangnai Hai	TNH	Rivers	100.143 3	35.510 3
2	Zhama Long	ZML		101.435 4	36.659 9
3	Ma Qu	MQ		102.080 2	33.960 7
4	Tang Ke	TK		102.461 5	33.410 9
5	Dahe Jia	DHJ		102.758 5	35.841 6
6	Bianqiang Cun	BQC		102.843 5	36.333 5
7	Ruoer Gai	REG		102.933 3	33.600 1
8	Hong Qi	HQ		103.463 3	35.888 3
9	Xincheng Qiao	XCQ		103.483 0	36.167 8
10	Wufo Si	WFS		104.295 3	37.170 1
11	Hua Lin	HL		104.855 4	34.754 9
i12	Yesheng Road Bridge	YSRB		106.216 1	38.137 3
13	Putao Yuan	PTY		106.708 2	34.372 5
14	Mahuang Gou	MHG		106.773 9	39.371 4
15	Deng Kou	DK		110.175 5	40.551 9
16	Tongguandiao Bridge	TGDB		110.237 6	34.610 3
17	Toudao Guai	TDG		111.074 3	40.263 5
18	South of Wangzhuang Bridge	SWZB		111.682 6	36.669 2
19	Huayuan Kou	HYK		113.680 1	34.919 0
20	Ai Shan	AS		116.338 0	36.297 5
21	Lijin Hydrological Station	LJHS		118.307 4	37.514 5
22	Ken Li	KL		118.531 1	37.603 9
23	Bingu Road Bridge on Diaokou River	BGR		118.721 8	37.886 6
24	Pontoon Bridge across Jian Lin	JLPB		118.758 7	37.737 4
25	T-junction	TJ		119.156 0	37.760 0
26	Zhaling Lake 1	ZLL1	Lakes and reservoirs	97.222 9	35.005 7
27	Zhaling Lake 2	ZLL2		97.340 0	35.025 1
28	Zhaling Lake 3	ZLL3		97.338 3	34.835 0
29	Zhaling Lake 4	ZLL4		97.283 5	34.816 9
30	Eling Lake 1	ELL1		97.449 2	34.821 9
31	Eling Lake 2	ELL2		97.586 7	34.934 0
32	Eling Lake 3	ELL3		97.687 9	35.047 5
33	Eling Lake 4	ELL4		97.774 1	35.092 9
34	Inlet of Longyang Gorge Reservoir	ILYGR		100.251 6	35.679 8
35	Center of Longyang Gorge Reservoir	CLYGR		100.784 4	36.136 4
36	Outlet of Longyang Gorge Reservoir	OLYGR		100.921 2	36.122 7
37	Wumaoji	WMJ		108.706 7	40.783 9
38	Hai Hao	HH		108.730 5	40.826 5
39	Center of Wuliangsuhai Lake	CWLSHL		108.794 2	40.867 5
40	Hongge Bo	HGB		108.822 1	40.997 3
41	Dabei Kou	DBK		108.836 1	40.912 1
42	Xida Tan	XDT		108.861 6	40.979 6
43	East of Bandong	EBD		108.870 3	40.923 5
44	Xiyang Chang	XYC		108.911 7	40.950 8
45	Dongda Tan	DDT		108.913 6	41.010 5
46	Nan Cun	NC		111.830 1	35.061 7
47	Nan Shan	NS		112.028 0	35.051 7
48	Daheng Ling	DHL		112.254 0	34.947 8
49	North of Dongping Lake	NDPL		116.197 6	35.978 6
50	South of Dongping Lake	SDPL		116.223 1	35.946 2

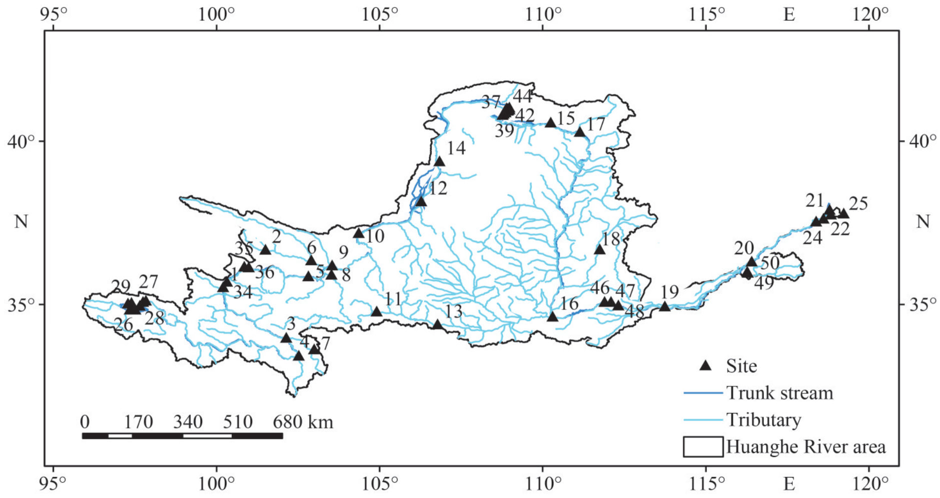

Fig.1 Sampling sites in the whole Huanghe River basin

(2002) and Padisák et al. (2009). For enumeration, the algal density was counted using the Utermöhl method (Utermöhl, 1931; Lund et al., 1958; Paxinos and Mitchell, 2000) in a 0.1-mL phytoplankton counting chamber. The counting error associated with this method was approximately ±10% (Venrick, 1978). Additionally, the algal biomass was measured by calculating the geometric volumes of each alga, following the methods reported by Hillebrand et al. (1999) and Sun and Liu (2003). In this analysis, functional assemblages that contributed to more than 5% of the total phytoplankton biomass were defined as dominant functional groups (Cao et al., 2018).

2.4 Graphing and statistical analysis

The abundance matrix of PFGs was subjected to a Hellinger transformation for the relevant analysis, following the methods described by Legendre and Gallagher (2001) and Legendre and Legendre (2012). To investigate the distribution of dominant PFGs across the entire Huanghe River basin, distance weighting methods and grid analysis were employed. Additionally, an analysis of similarity (ANOSIM) was conducted using PRIMER 7.0 to determine statistically significant variations in the spatial distribution of the PFGs between the riverine and lakes-reservoir systems in the Huanghe River basin (Clarke and Gorley, 2015).

Next, certain variables (COD_{Mn} and NH_4^+-N) were removed from the environmental variable matrix due to their lower degree of explanation for ecological data variability, and the software Canoco 5 was utilized to analyze the relationship between the dominant functional groups and environmental variables across the entire basin. To improve homoscedasticity and normality, a $\lg(x+1)$ transformation was applied to nearly all environmental variables, except pH, following the approach described by Mo et al. (2018). Before conducting the analysis, a detrended correspondence analysis (DCA) of the dominant functional groups was performed to determine whether a linear or unimodal ordination method should be employed (Lepš and Šmilauer, 2003). If the maximum gradient value is <3, then the linear model, redundancy analysis (RDA), was utilized. If the maximum gradient value is >3, then the unimodal model canonical correspondence analysis (CCA) was employed.

A Mantel correlation test was conducted to analyze the driving factors influencing the dominant functional groups in the entire Huanghe River basin. Additionally, expansion factor coefficients of all environmental variables (with selected variables <20) were calculated, and significant environmental factors were determined using forward selection. The final model was tested using ANOVA (model, by="terms"), and the important predictors were reported in the results section. To comprehensively understand the main environmental factors contributing to the differences in PFG composition among different watersheds (riverine and lake-reservoir basin), the relative contributions of environmental variables (physical and chemical) and geographic variables to phytoplankton communities were conducted through variance partitioning analysis (VPA). The aforementioned analyses were performed using various packages in R v4.0.3, including "vegan", "fmsb", "dplyr", "ggplot2", and "ggcor" packages in R v4.0.3.

3 RESULT

3.1 Environmental variable

The nine environmental variables: NTU, pH, COD_{Mn}, TN, TP, Cond, DO, NH_4^+-N, and WT are demonstrated in Table 2. *T*-test analysis was performed on the nine factors. Significant differences were observed in NTU, pH, COD_{Mn}, TP, and TN between riverine water bodies and lake-reservoir (*t*-test, $P<0.05$), of which NTU and pH showed particularly significant differences (*t*-test, $P<0.01$). Figure 2 illustrates that NTU, TN, and TP data in riverine water bodies are significantly higher than those of the lake-reservoir. Conversely, the pH and COD_{Mn} data were much lower in riverine water bodies compared with the lake-reservoir. No significant differences were found in DO, Cond, WT, and NH_4^+-N data between the riverine water bodies and lake-reservoirs as indicated by *T*-test scores.

Table 2 Environmental variables of the riverine and lake-reservoir water bodies in the Huanghe River

Environmental variable	River	Lake-reservoir
NTU	512.27±442.72	34.73±90.41
pH	8.01±0.39	8.68±0.46
COD_{Mn} (mg/L)	2.82±1.60	3.82±1.60
TN (mg/L)	3.00±1.51	1.58±0.73
TP (mg/L)	0.07±0.04	0.04±0.02
Cond (ms/m)	153.49±269.02	280.26±298.90
DO (mg/L)	7.80±1.22	8.28±3.19
NH_4^+-N (mg/L)	0.18±0.13	0.20±0.13
WT (°C)	18.46±3.73	19.48±4.03

3.2 Phytoplankton taxa

During the sampling and analysis of the 50 sites within the Huanghe River basin, a total of 81 genera and 218 species belonging to seven phyla (e.g., Bacillariophyta, Cyanophyta, Chlorophyta, Cryptophyta, Pyrrophyta, Euglenophyta, and Chrysophyta) were observed, with diatoms being the dominant group. Across the entire Huanghe River basin, phytoplankton abundance ranged from 0.006×10^6 cells/L to 40.07×10^6 cells/L, with an average of $3.463\ 8\times10^6$ cells/L. The algal biomass ranged from 2.83 μg/L to 22.779 8 mg/L, with an average of 1.615 mg/L. The comparative differences in phytoplankton abundance and biomass between the riverine water bodies and lake-reservoirs are shown in Fig.3, indicating that the algal biomass was particularly high at two sampling sites (e.g., WMJ and XDT) in the lake-reservoir section.

3.3 Phytoplankton functional group (PFG)

According to Reynolds et al. (2002) and Padisák et al. (2009), the algae identified in the Huanghe

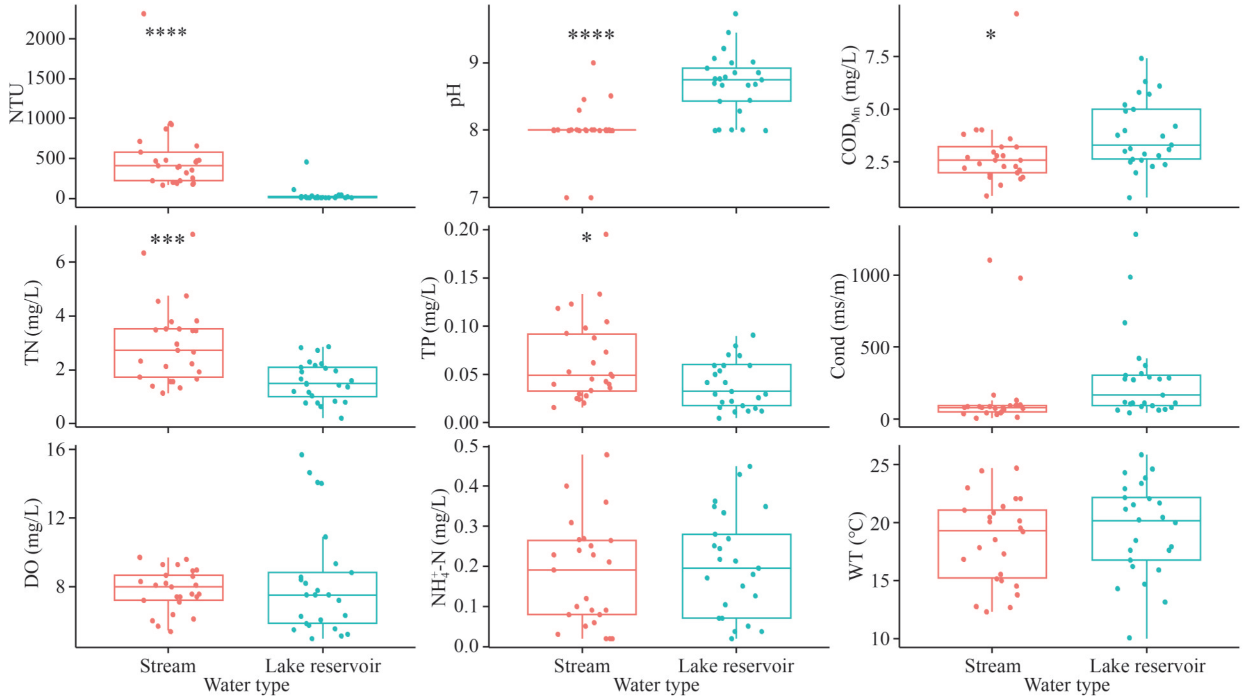

Fig.2 *T*-test analysis between the riverine water bodies and lake-reservoir in the Huanghe River basin

"*" means having significant differences; "**", "***", "****" means having especially significant differences.

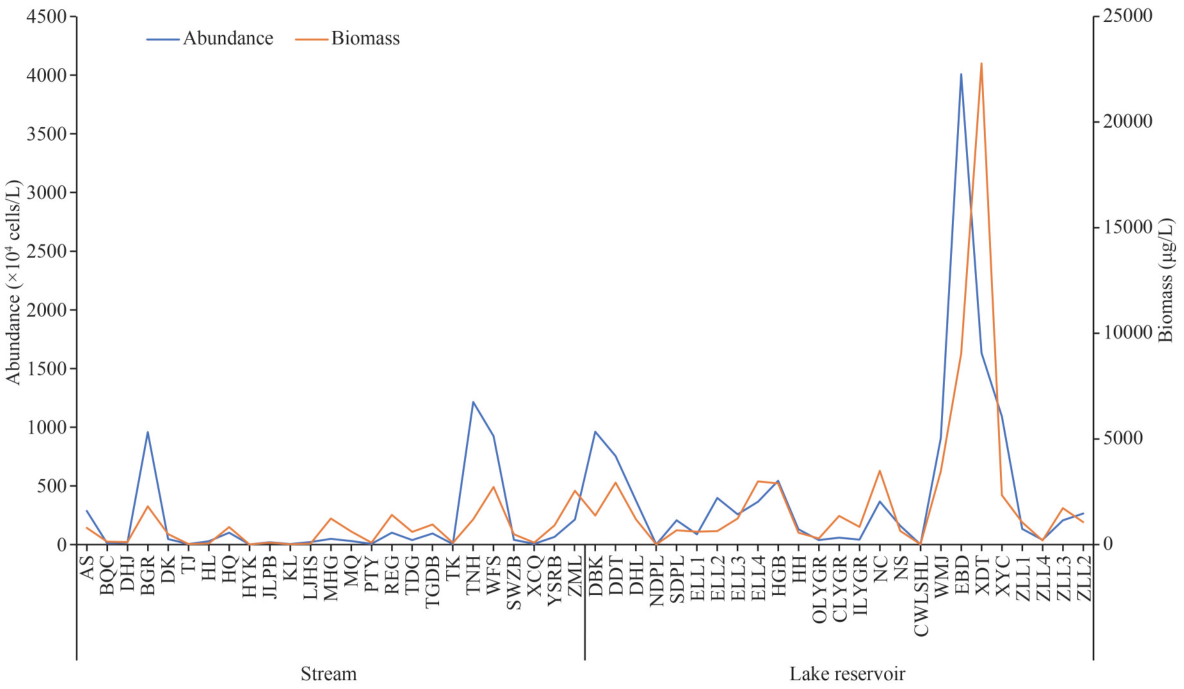

Fig.3 Comparative differences of abundance and biomass between the riverine water bodies and lake-reservoir in the whole Huanghe River basin

River basin were classified into 27 functional groups, namely, assemblages A, B, C, D, E, F, G, H1, J, K, LM, Lo, M, MP, N, P, S1, S2, T, TC, W1, W2, X1, X2, X3, XPh, and Y (Table 3). The occurrence frequency of functional groups MP, B, and Y were more than 80%, which was considered the common assemblages distributed in the Huanghe River basin; the groups D, Lo, J, F, S1, X1, LM, P, K, M, X3, C, T, and X2 of which was in between 30% and 80%. Additional to these groups, other groups were rarely detected, the occurrence frequency was lower than 30% (Fig.4).

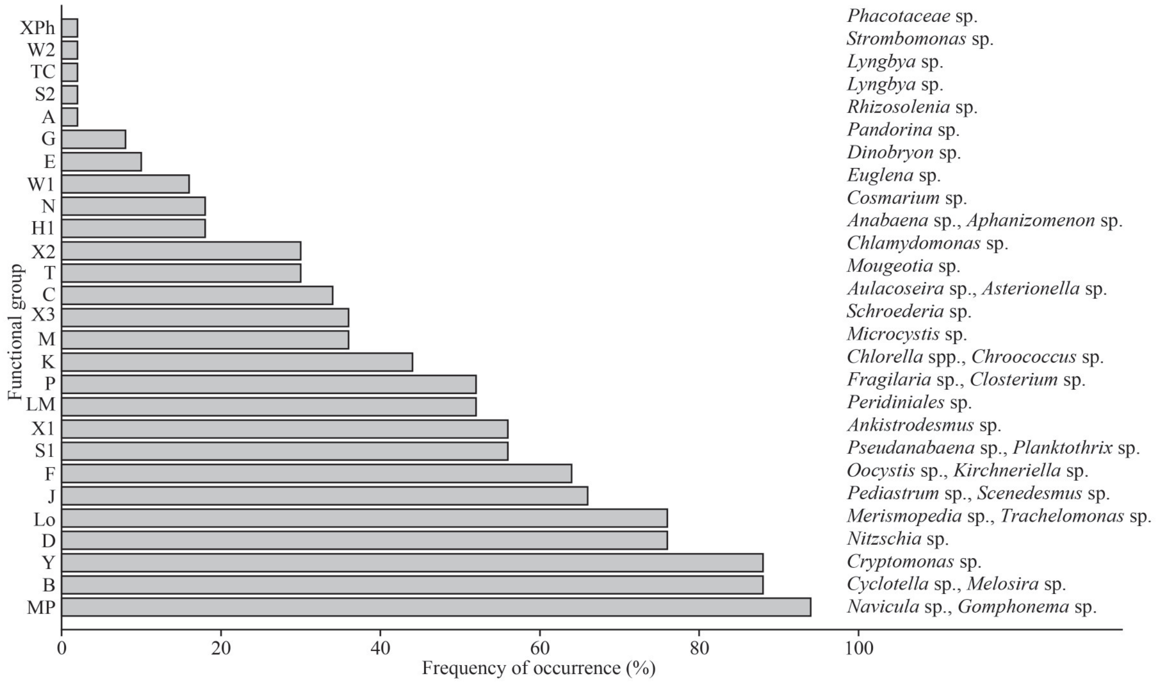

Fig.4 The occurrence frequency and representative species of the functional groups within the Huanghe River basin

Table 3 Functional groups and its habitat characteristics in the whole Huanghe River basin (Reynolds et al., 2002; Padisák et al., 2009)

Functional group	Taxa	Habitat characteristic	Sensitivity	Tolerance
A	*Rhizosolenia* sp.	Clear, deep, base poor lakes	pH rise	Nutrient deficiency
B	*Melosira varians*, *Stephanodiscus* sp., *Cyclotella* sp.	Vertically mixed, mesotrophic small- and medium-sized lakes	The onset of stratification; Si depletion; pH rise	Light deficiency
C	*Aulacoseira pusilla*, *Aulacoseira* sp., *Aulacoseira granulate*, *Aulacoseira granulata* var. *angustissima*, *Asterionella formosa*, *Asterionella* sp.	Mixed, eutrophic, small to medium-sized lakes	The onset of stratification; Si exhaustion	Light deficiency, carbon deficiency
D	*Nitzschia stagnorum*, *Nitzschia palea*, *Synedra acus*, *Nitzschia* sp., *Synedra* sp., *Nitizschia sigma*, *Nitzschia gracilis*, *Nitzschia denticule*, *Nitzschia linearis*, *Nitzschia subacicularis*, *Synedra* sp., *Nitzschia acicularis*, *Nitzschia intermedia*, *Synedra ulna*	Shallow, enriched turbid regions including rivers	Nutrient depletion	Flushing
E	*Dinobryon cylindricum*, *Dinobryon divergens*	Usually small, poor lakes or heterotrophic ponds	CO_2 deficiency	Low nutrients (resort to mixotrophy)
F	*Dictyosphaerium ehrenbergianum*, *Kirchneriella contorta*, *Kirchneriella obesa*, *Kirchneriella* sp., *Micractinium pusillum*, *Nephrocytium agardhianum*, *Oocystis borgei*, *Oocystis elliptica*, *Oocystis lacustris*, *Oocystis* sp., *Selenastrum* sp.	Clear, deeply mixed meso-eutrophic lakes	CO_2 deficiency	Low nutrients, high turbidity
G	*Eudorina* sp., *Pandorina* sp.	Nutrient-rich conditions in stagnating water columns; small eutrophic lakes; reservoirs and stable phases in larger river-fed basins	Nutrient deficiency	High light
H1	*Anabaena azotica*, *Anabaena circinalis*, *Anabena flos-aquae*, *Aphanizomenon* sp.	Stratified or shallow eutrophic lakes with low nitrogen content	Mixing, poor light, low phosphorus	Low nitrogens, Low carbon
J	*Scenedesmus acuminatus*, *Scenedesmus perforates*, *Actinastrum* sp., *Chlorococcum* sp., *Coelastrum astroideum*, *Coelastrum indicum*, *Coelastrum microporum*, *Coelastrum reticulatum*, *Coelastrum* sp., *Crucigenia apiculate*, *Crucigenia quadrata*, *Crucigenia rectangularis*, *Crucigenia tetrapedia*, *Golenkinia radiata*, *Lagerheimiella* sp., *Lagerheimiella wratislaviensis*, *Pediastrum boryanum*, *Pediastrum duplex* var. *gracillimum Pediastrum duplex* var. *reticulatum*, *Pediastrum integrum*, *Pediastrum tetras*, *Scenedesmus arcuatus*, *Scenedesmus bicanda*, *Scenedesmus bijuga*, *Scenedesmus cavinatus*, *Scenedesmus dimorphus*, *Scenedesmus javaensis*, *Scenedesmus oblipuus*, *Scenedesmus quadricauda*, *Scenedesmus* sp., *Scenedesmus spinosus*, *Tetraedron caudatum*, *Tetraedron minimum*, *Tetraedron trigonum*, *Tetraedron trigonum* var. *capitellatum*, *Tetrastrum staurogeniaeforme*, *Willea apiculata*	Highly enriched, shallow, mixed water regions including many low-gradient rivers	Settling into low light	High nutrients
K	*Chlorella* sp., *Chroococcus* sp., *Dactylococcopsis* sp.	Shallow, nutrient-rich water columns	Deep mixing	High nutrients
LM	*Ceratium* sp., *Peridiniales* sp., *Peridinium gutwinskii*, *Peridinium pusillum*, *Peridinium volzii*	Eutrophic to hypertrophic, small to medium-sized lakes	Mixing, poor stratification light	Very low carbon
Lo	*Amphora* sp., *Coelosphaerium* sp., *Diatoma tenue*, *Diatoma mesodon*, *Diatoma monilifonmis*, *Diatoma* sp., *Diatoma vulgare*, *Merismopedia glauca*, *Merismopedia minima*, *Merismopedia* sp., *Merismopedia tenuissima*, *Pinnularia* sp., *Synechocystis* sp.	Oligotrophic or eutrophic, mediate to large, deep or shallow lakes	Prolonged or deep mixing	Segregated nutrients
M	*Microcystis* sp.	Eutrophic to hypereutrophic, stable, small to medium lakes	Flushing, low total light	High insolation

To be continued

Table 3 Continued

Functional group	Taxa	Habitat characteristic	Sensitivity	Tolerance
MP	*Gomphonema parvulum* var. *subellipticum*, *Achnanthes* sp., *Baciliaria paradoxa*, *Ceratoneis arcus*, *Ceratoneis* sp., *Cocconeis hustditi*, *Cocconeis* sp., *Cocconeis tenuistrata*, *Cymbella affinis*, *Cymbella cistula*, *Cymbella gracillis*, *Cymbella perpusilla*, *Cymbella tumida*, *Cymbella.cymbiformis*, *Eolimna* sp., *Eunotia aequalis*, *Eunotia lunaris*, *Gomphonema angustatum*, *Gomphonema angustatum* var. *producta* *Gomphonema constrictum*, *Gomphonema gracile*, *Gomphonema intermedia*, *Gomphonema meridionalum* *Gomphonema olivaceum*, *Gomphonema pala*, *Gomphonema parvulum*, *Gomphonema* sp., *Hantzschia* sp., *Licmophora* sp., *Navicula amphiceropsis*, *Navicula cincta*, *Navicula exigua*, *Navicula gracile*, *Navicula halophila*, *Navicula lanceolata*, *Navicula leistikowii*, *Navicula nivalis*, *Navicula oblonga*, *Navicula protracta*, *Navicula radiosa*, *Navicula schonfeldii*, *Navicula simplex*, *Navicula* sp., *Navicula symmetrica*, *Navicula viridula*, *Nitzschia closterium* f. *minutissima*, *Stauroneis* sp., *Surirella minuta*, *Surirella ovata*, *Surirella* sp., *Ulothrix* sp.	Frequently stirred up, inorganically turbid shallow lakes		Frequently, stirred up
N	*Cosmarium* sp., *Cosmarium circulare*, *Cosmarium depressum*, *Cosmarium* sp., *Cosmarium subtumidum*, *Euastrum ansatum*, *Platrotaenium trabecula*, *Spondylosium planum*, *Spondylosium* sp., *Tetmemcrus* sp.	Continuous or semi-continuous mixed layer of 2–3 m in thickness	Stratification, pH rise	Nutrient deficiency
P	*Clostcrlum cynthia*, *Closterium acerosum*, *Closterium gracile*, *Closterium* sp., *Fragilaria acus*, *Fragilaria brevistriata*, *Fragilaria capucina*, *Fragilaria intermedia*, *Fragilaria* sp.	Similar to that of codon N but at higher trophic states	Stratification, Si depletion	Mild light and carbon deficiency
S1	*Limnothrix* sp., *Oedocladium* sp., *Planktolyngbya* sp., *Planktothricoides* sp., *Planktothrix* sp., *Psephonema aenigmaticus*, *Pseudanabaena* sp.	Turbid mixed environments; This codon includes only shade-adapted cyanoprokaryotes	Flushing	Highly light deficient conditions
S2	*Spirulina* sp.	Warm, shallow, and often highly alkaline waters	Flushing	Light deficient conditions
T	*Mougeotia parvula*, *Mougeotia* sp., *Quadrigula* sp.	Persistently mixed layers, in which light is increasingly the limiting constraint and thus optically deep, mixed environments including clear epilimnia of deep lakes in summer	Nutrient deficiency	Light deficiency
TC	*Planktolyngbya subtilis*	Eutrophic standing waters, or slow-flowing rivers with emergent macrophytes	Flushing	
W1	*Euglena gasterosteus*, *Euglena pisciformis*, *Euglena* sp., *Phacus* sp.	Rich in organic matter	Grazing	High BOD
W2	*Strombomonas* sp., *Trachelomonas* spp.	Meso- to eutrophic ponds or shallow lakes		
X1	*Ankistrodesmus acicularis*, *Ankistrodesmus angustus*, *Ankistrodesmus convolutes*, *Ankistrodesmus* sp., *Ankistrodesmus spiralis*	Eutrophic and hypertrophic shallow regions	Nutrient deficiency, filter feeding	Stratification
X2	*Chamydomonas* sp., *Pteromonas angulosa*	Meso- to eutrophic shallow regions	Mixing, filter feeding	Stratification
X3	*Characium* sp., *Cymatopleura* sp., *Diploneis ovalis*, *Diploneis purlla*, *Gyrosigma acuminatum*, *Schroederia robusta*, *Schroederia* sp., *Schroederia spiralis*	Shallow, well mixed oligotrophic environments	Mixing, grazing	Low base status
XPh	*Phacotaceae* sp.	Small, even temporary, calcium rich, well illuminated, alkaline lakes	Acid oligotrophication	
Y	*Chroomonas acuta*, *Cryptomonas erosa*, *Cryptomonas ovata*, *Cryptomonas rostrata*	Almost all lentic ecosystems when grazing pressure is low	Phagotrophs	Low light

Meanwhile, the composition of PFGs showed significant differences between the riverine and lake-reservoir sections in the Huanghe River basin. In riverine water bodies, 23 functional groups, including the assemblages B, C, D, E, F, G, H1, J, K, LM, Lo, M, MP, N, P, S1, T, W1, W2, X1, X2, X3, and Y, were identified, whereas 26 functional assemblages, namely, A, B, C, D, E, F, G, H1, J, K, LM, Lo, M, MP, N, P, S1, S2, T, TC, W1, X1, X2, X3, XPh, and Y, were classified in the lake-reservoir section in the Huanghe River basin. Resorting to ANOSIM correlation analysis, significant differences of the algal abundance and biomass of the functional groups also existed between the riverine and lake-reservoir sectionsin the Huanghe River basin (R>0, P<0.01), as illustrated in Fig.5.

3.4 Dominant PFG

The dominant PFGs, identified as those contributing more than 5% of the total biomass (Xiao et al., 2011), included assemblages B, C, D, J, LM, Lo, and MP within the whole Huanghe River basin. The distribution of these dominant groups across the basin is depicted in Fig.6. Assemblage B was found in the riverine and lake-reservoir sections. Group C was rarely observed in the source and upper-middle stream of the Huanghe River basin, primarily distributed in the sampling sites of Deng Kou and Toudao Guai after the outlet of Wuliangsuhai Lake. Groups D and MP were found to be predominant in the riverine section of the upper-middle stream, with limited occurrence in the lake-reservoir section of the Huanghe River basin. Group J occupied mainly the lake-reservoir in the upper-middle stream of the basin. Group LM was distributed in the middle tributary mainly, with limited presence in the lakes and reservoirs in the basin. Group Lo was found primarily within Wuliangsuhai Lake with rare occurrences in the riverine section.

In accordance with our expectation, significant differences were observed in the dominant functional groups between the riverine and lake-reservoir sections of the entire basin. Six groups, namely, assemblages B, C, D, LM, Lo, and MP, were dominant in the river section, whereas five groups, including B, D, J, LM, and MP, were in the lake-reservoir sections. Moreover, based on the biomass analysis of the dominant functional groups, assemblage MP was predominant in the riverine section, whereas the groups B and J were predominant in the lake-reservoir sections (Fig.7).

3.5 Mantel correlation test and RDA analysis

The Mantel correlation tests revealed that the environmental variables WT and NTU significantly influenced the dominant functional assemblages of the entire Huanghe River basin (NTU, P<0.01; WT, P<0.05) (Fig.8a). Furthermore, based on the previous DCA of the dominant functional groups (B, C, D, MP, LM, Lo, J), a linear model RDA was employed to explore the relationships between dominant functional groups and environmental variables, as the maximum gradient value was 2.2. The first two axes accounted for 82.06% of the

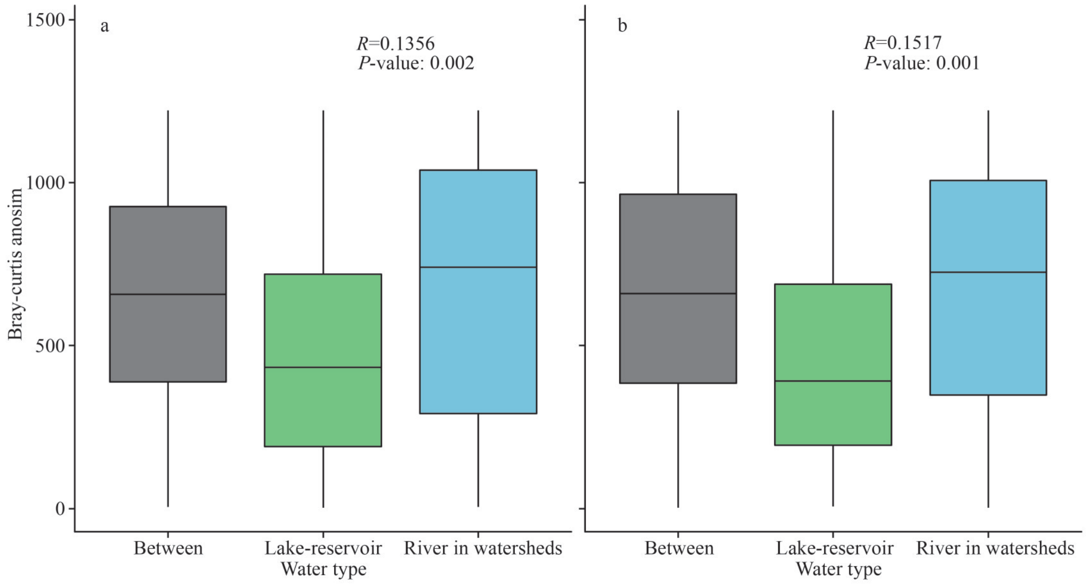

Fig.5 ANOSIM correlation analysis of phytoplankton functional groups in abundance (a) and in biomass (b) between riverine water bodies and lake-reservoir in the Huanghe River basin

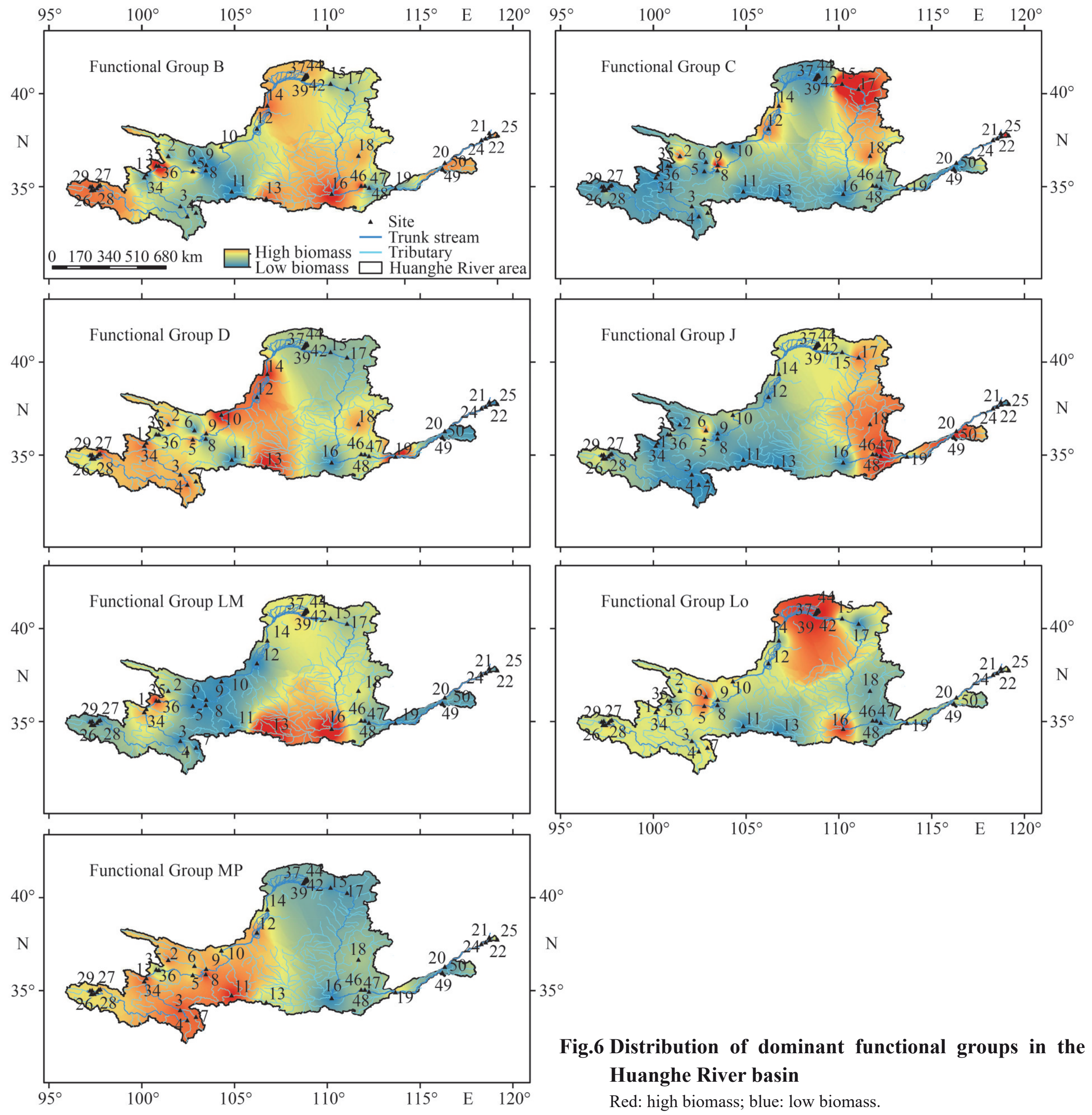

Fig.6 Distribution of dominant functional groups in the Huanghe River basin

Red: high biomass; blue: low biomass.

relation between dominant PFGs and environmental variables, with the first axis explaining 56.34% and the second axis explaining 25.72% of the variation (Fig.8b). The Monte Carlo permutation tests indicated that the functional groups MP, C, and D were positively correlated with NTU, whereas B, LM, Lo, and J were negatively correlated. Assemblage C was positively correlated with TN, whereas Lo was negatively correlated. Groups J and LM were positively correlated with WT, DO, and Cond, while MP was negatively correlated. Additionally, Lo and B were positively correlated with pH, COD_{Mn}, NH_4^+-N, and TP. The environmental variables NTU (P=0.002), WT (P=0.002), and COD_{Mn} (P=0.04) were identified as the main driving factors influencing the PFGs in the entire Huanghe River basin (Fig.8b).

The RDA analysis of the PFGs and environmental variables within the lake–reservoir section of the Huanghe River basin explained 56.17% for the first axis and 25.29% for the second axis. These two axes provided a good explanation for the impacts of environmental variables on the dominant functional groups. Monte Carlo permutation tests revealed that the functional groups MP and D were positively correlated with NTU.

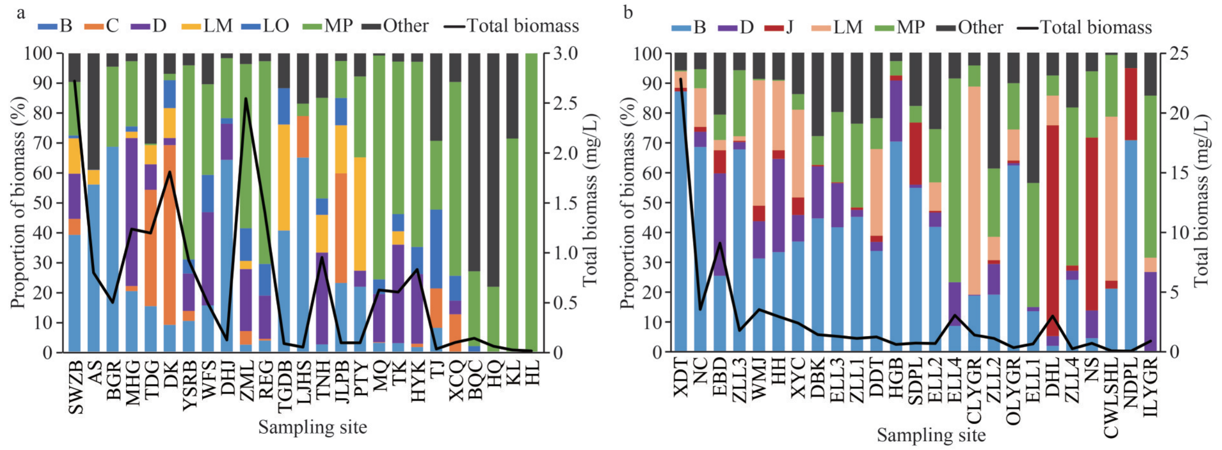

Fig.7 The biomass and proportion of dominant functional groups in the riverine water bodies (a) and the lake-reservoir (b) in the Huanghe River basin

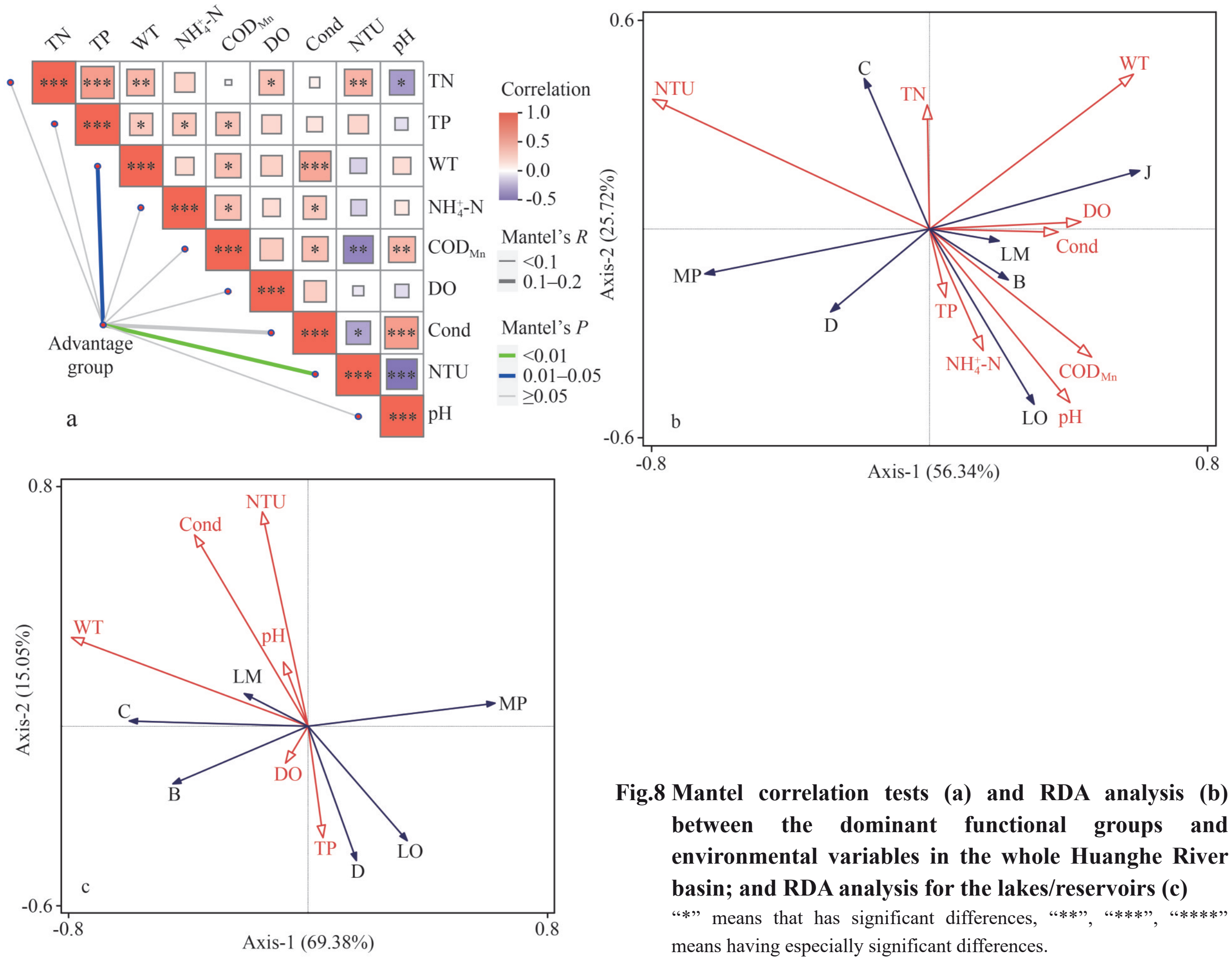

Fig.8 Mantel correlation tests (a) and RDA analysis (b) between the dominant functional groups and environmental variables in the whole Huanghe River basin; and RDA analysis for the lakes/reservoirs (c)

"*" means that has significant differences, "**", "***", "****" means having especially significant differences.

Assemblages B and L$_M$ were positively correlated with TP, pH, and Cond. Furthermore, Group J was positively correlated with WT, COD$_{Mn}$, TN, and DO. The environmental variables NTU (*P*=0.002), WT (*P*=0.018), Cond (*P*=0.014), and TP (*P*=0.032) were identified as the main driving factors influencing the PFGs within the lake-reservoir in the Huanghe River basin (Fig.8c).

3.6 Relative contribution of environmental and geo-climatic variables in shaping the PFGs

To better explore the main driving factors of the phytoplankton functional group, we divided the exploratory driving factors into three categories for analysis: physical (NTU, WT, Cond), chemical (TP, TN, DO, NH_4^+-N, pH, COD_{Mn}), and geographical variables. The results of variance partitioning analysis (VPA) illustrated the significant influences of environmental and geographical variables on the diversified structure of the PFGs. However, the contribution of these variables varied across different watersheds within the Huanghe River basin. As shown in Fig.9a, the combined effects of environmental and geographical variables accounted for 22.7% of the explanatory variables for the variability of PFGs structure in the whole Huanghe River basin. Notably, the geographical variables were the most contributor driving the PFGs structure and NTU was the most important environmental variables.

Based on the analysis results of the lake and reservoir sections (Fig.9b), the combined effects of environmental and geographical variables explained 35.2% of the explanatory variables. The PFGs structures were interactively influenced by the environmental and the geographical variables. The WT, together with TP exhibiting the highest contribution among the environmental factors considered. In the case of riverine watersheds (Fig.9c), the joint influences of environmental and geographical variables accounted for 55.2% of the explanatory variables. Interestingly, the related geographical variables contributed over 90% to the explanation of the PFG structure, suggesting that changes in the riverine section of the Huanghe River basin were influenced primarily by geographical factors rather than environmental variables.

4 DISCUSSION

Due to global changes and the high demands of economic development, the Huanghe River basin is facing significant threats from ecological problems, such as river blockages, water quality deterioration, pollutant emissions, overfishing, and biological invasions. These factors have led to a decline in the biological diversity of the Huanghe River. As we hypothesized, the physio-chemical variables and driving factors in shaping phytoplankton structure of the riverine and lake-reservoir watersheds in the Huanghe River basin were distinct. The analysis of the phytoplankton community structure can provide essential data for water quality evaluation, biological monitoring, and management of the entire Huanghe River basin.

4.1 Variance in the physio-chemical variables between riverine and lake/reservoir water bodies

The Huanghe River, the fifth longest river in the world, is characterized by heavy sediment loads

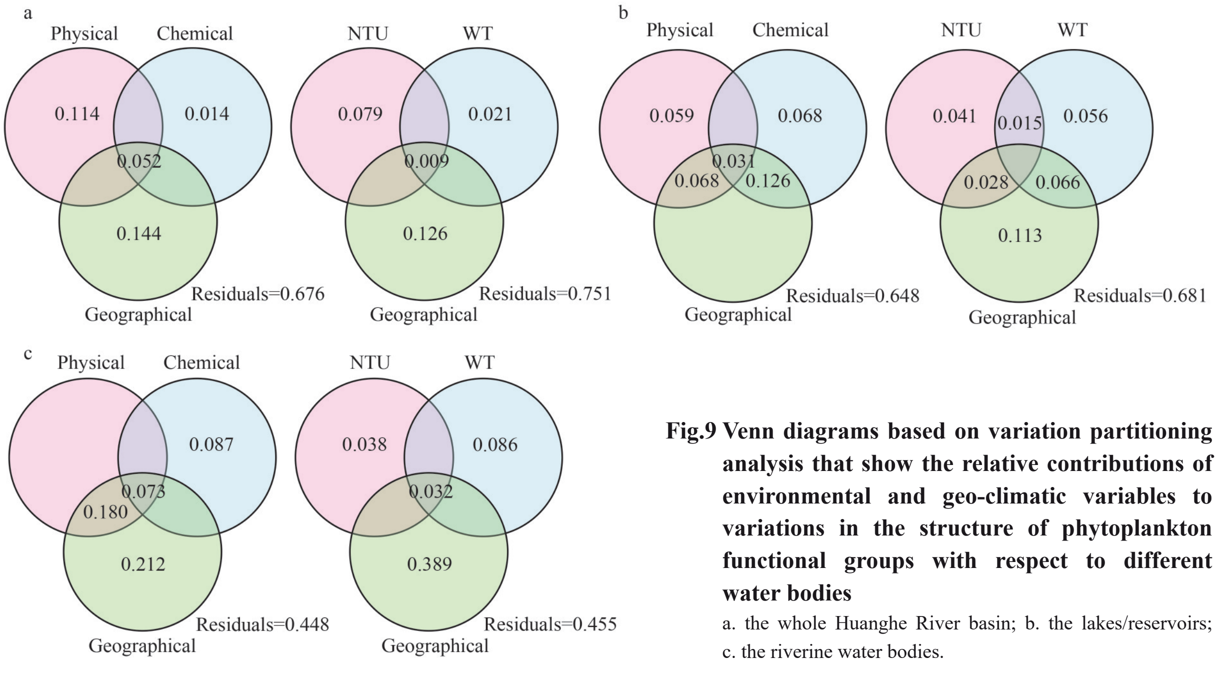

Fig.9 Venn diagrams based on variation partitioning analysis that show the relative contributions of environmental and geo-climatic variables to variations in the structure of phytoplankton functional groups with respect to different water bodies

a. the whole Huanghe River basin; b. the lakes/reservoirs; c. the riverine water bodies.

(Mu et al., 2012). It stretches approximately 5 464 km, passing through ecologically fragile regions, from the Qinghai-Tibet Plateau, Inner Mongolia Plateau, Loess Plateau, to North China Plain, exhibiting complex geomorphological features (Zhang et al., 2020). Previous studies on river ecosystems often divided the main river into three parts: the upper reaches, middle reaches, and lower reaches, as performed by the Huanghe River Conservancy Commission of the Ministry of Water Resources of the People's Republic of China (Xu et al., 2002). Comparing these reaches can provide insights into environmental variables and species distribution along the entire river. However, the Huanghe River basin also includes numerous man-made reservoirs and important lakes, each with its own environmental variables and hydrological characteristics that can elicit different responses from phytoplankton. Few studies have focused on comparing the riverine section with the lakes and reservoirs of the Huanghe River basin. In this study, distinct differences were observed in the environmental variables between the riverine and lake-reservoir sections of the Huanghe River basin. This finding contrasts with the results of Ding et al. (2022), who found no significant differences in environmental properties among different water bodies. As shown in Fig.2, the riverine section exhibited significantly higher levels of NTU, TN, and TP than lakes and reservoirs. Sediments, a natural component of rivers, can absorb nutrients from the water and directly affect its physicochemical properties (Zhao et al., 2020). Additionally, the high NTU levels in the riverine section can reduce light availability and potentially decrease phytoplankton growth rates. Furthermore, pH and COD_{Mn} levels were much lower in the riverine section than in lakes and reservoirs. These different environmental conditions can, in turn, influence the abundance and density of phytoplankton in the two types of watersheds within the Huanghe River basin (Clarke and Wharton, 2001; Huang et al., 2019).

4.2 Variance in PFGs composition between riverine and lake-reservoir water bodies

In line with our expectations, the ANOSIM correlation analysis indicated significant differences in algal abundance and biomass of the PFGs between the riverine and lake-reservoir sections of the Huanghe River basin (Fig.5). These results support the rationale behind dividing the Huanghe River basin into these two distinct sections. A total of 27 functional groups within the entire Huanghe River basin, including assemblages A, B, C, D, E, F, G, H1, J, K, LM, Lo, M, MP, N, P, S1, S2, T, LC, W1, W2, X1, X2, X3, XPh, and Y, were identified. Among these groups, groups B, C, D, J, LM, Lo, and MP were dominant. In riverine water bodies, the MP group was predominant, whereas the B and J assemblages prevailed in lakes and reservoirs. Group B consisted of diatoms, such as *Aulacoseira* sp., *Stephanodiscus* sp., and *Cyclotella* sp. Descriptions by Reynolds et al. (2002) and Padisák et al. (2009) indicated that these species were tolerant of low light conditions and adapt to mesotrophic small- and medium-sized water bodies. Group D consisted of species, such as *Synedra* sp., *Nitzschia* sp., and *Fragilaria* sp. The MP group mainly consisted of Pennatae taxa, such as *Suirrella* sp., *Eunotia* sp., *Cymbella* sp., and *Gomphonema* sp. According to Reynolds et al. (2002) and Padisák et al. (2009), these species thrive in shallow turbid waters or frequently stirred-up, inorganically turbid regions. The Huanghe River, known for its high sediment load, has low transparency, which significantly inhibits algal growth (Wehr and Descy, 1998), thereby explaining the dominance of Group D in the riverine water bodies of the Huanghe River basin. The Lo group primarily consists of large dinoflagellates, such as *Peridinium* sp., and cyanobacteria, such as *Merismopedia* sp., which are more abundant during summer (Huszar et al., 2003; Petar et al., 2014; Huang et al., 2018). According to Reynolds et al. (2002) and Padisák et al. (2009), these species prefer deep and shallow oligo to eutrophic medium to large lakes. The group J mainly consists of green algae, such as *Pediastrum* sp., *Scenedesmus* sp., *Tetraedron* sp., *Crucigenia* sp., *Coelastrum* sp., and *Lagerheimiella* sp. Reynolds et al. (2002) and Padisák et al. (2009) described the assemblage J as commonly found in shallow, mixed, highly enriched systems. Our survey aligns with the habitat characteristics described by Reynolds et al. (2002) and Padisák et al. (2009): Group B was commonly found in riverine and lake-reservoir water bodies, Groups D and MP are mainly distributed in riverine water bodies and rarely found in lake/reservoir, and Group Lo primarily exists in Wuliangsuhai Lake, with limited presence in rivers within the entire Huanghe River basin (Fig.6). These results further support the effectiveness of utilizing PFGs in this heavily sediment-laden river (Ding et al., 2022) and demonstrate that the concept of PFGs effectively describes habitat characteristics and serves as good ecological indicators for entire Huanghe River basin.

4.3 Response of PFGs to environmental variables

The distribution of phytoplankton communities in river ecosystems is easily influenced by changes in hydrodynamics (Joensuu et al., 2013) and physicochemical conditions (Lancelot and Muylaert, 2011; Qu et al., 2018) in water bodies. Mantel correlation tests and RDA analysis revealed that the environmental variables WT and NTU were significant factors that shape the dominant functional assemblage structure in the entire Huanghe River basin. These findings align with those of Chapman et al. (2017) and Liang et al. (2013), who also indicated that NTU could affect the abundance and compositional structure of phytoplankton. Additionally, COD_{Mn} was identified as another key factor shaping the dominant phytoplankton structure in Huanghe River basin. Previous studies have highlighted that the concentration of dissolved organic carbon (DOC) is influenced by sediment load in aquatic ecosystems, which in turn affects planktonic food webs, particularly the mixotroph/autotroph ratio in phytoplankton, and subsequently impacts PFGs (Creed et al., 2015; Jacquemin et al., 2019).

Moreover, when considering only lakes and reservoirs in the Huanghe River basin, in addition to NTU, WT, and COD_{Mn}, the concentration of TP was also identified as a key driving factor influencing the dominant PFGs. This result aligns with numerous studies indicating that phosphorus is a limiting nutrient for phytoplankton in reservoirs and lakes (Becker et al., 2010; Cao et al., 2018). As a natural component of water, the sediment and hydrodynamic conditions in the lakes and reservoirs also indirectly affect the density, growth rate, and growth capacity of phytoplankton by changing the physical and chemical properties of water (Zhu et al., 2013; de Souza et al., 2016; Chapman et al., 2017; Qu et al., 2019). The water flow and water level, influencing the turbidity (Zhu et al., 2013), and the high phosphorus adsorption by sediment (Zhou et al., 2005) might also be key factors in shaping the phytoplankton structure of the lakes studied in the present study. Despite the absence of data analysis in the present study, the idea gains support from Niemistö et al. (2008) who suggested that the resuspension of sediments could change and reduce the ratio of TN:TP, which affected the growth of phytoplankton in shallow lakes, especially nitrogen-fixing cyanobacteria.

4.4 Determinant for the variation of PFGs between riverine and lake-reservoir water bodies

The Huanghe River, as a heavily sediment-laden river spanning across continents, is subject to significant influences from geo-climatic conditions and hydrological regimes, which can have profound effects on the structure of PFGs (Xu and Cheng, 2002; Chang et al., 2021). The present study revealed that environmental (50%) and geo-climatic (45%) variables contributed to the structure of PFGs in the entire Huanghe River basin, with NTU identified as the most important contributor. This finding aligns with the results of Ding et al. (2022), who also emphasized the distinct effect of heavy sediment load on PFGs compared with the nutrient availability in the Huanghe River. However, unlike the study by Ding et al. (2022), which suggested limited interpretation of environmental and geo-climatic variables in shaping PFGs in free-flowing river water bodies, our present study demonstrated that geo-climatic variables accounted for up to 90% of the explanatory power.

Meanwhile, the study also suggested that changes explained solely by environmental and physical variables are larger in the river section than in the lake reservoir section. Phytoplankton is greatly affected by the interaction between environmental and geographical variables in the lake reservoir basin, while the contribution of geographical variables in the river basin occupies the main position. Of course, there is still a large variability that could be explained by these variables and interactions.

5 CONCLUSION

The application of PFGs in studying the entire Huanghe River catchment proved to be effective and reasonable. The analysis identified NTU, WT, Cond, and TP as driving factors that significantly influenced the structure of PFGs in the catchment areas. This finding highlights the importance of sediment management, climate factors, and nutrient control in safeguarding the functioning of the river ecosystem. Furthermore, the study revealed that TP as a key factor influenced the structure of PFGs specifically in lakes and reservoirs in the catchment, indicating the negative impacts of human activities. Additionally, the riverine watersheds were more influenced by geo-climatic variables compared with other factors.

6 DATA AVAILABILITY STATEMENT

All data generated and/or analyzed during this study are available from the corresponding author on reasonable request.

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