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Spatial autocorrelation of phytoplankton biomass is weak in the rivers of Lake Taihu Basin, China

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Abstract – We investigated the characteristic of phytoplankton community structure across the entire Lake Taihu Basin (LTB), one of the most developed areas in China. A morphologically based functional group (MBFG) proposed by Kruk *et al.* (2010), especially potential toxic cyanobacteria (group III and VII), was also illustrated. Samples were collected at 96 sites along main rivers throughout the four seasons from September 2014 to January 2016. Significant differences in the phytoplankton community structure were observed at spatial (particularly between Huangpu/Tiaoxi and the other 4 river systems) and seasonal scales. On a spatial basis, high variability was observed in the mean phytoplankton biomass, with a relatively high value of 3.13 mg L^{-1} in Yanjiang system and a relatively low value in Huangpu (1.23 mg L^{-1}) and Tiaoxi (1.44 mg L^{-1}) systems. The mean biomass of potential toxic cyanobacteria accounted for 18.28% of the mean total biomass spatially, which was more abundant in Nanhe and Yanjiang systems. Spatial autocorrelation was weak for the total biomass and its four main components (bacillariophyta, chlorophyta, euglenophyta, and cyanobacteria) at whole basin scale regardless of season. Regarding the river system, significant autocorrelation was scarcely observed in all the river systems except Huangpu, especially in the inflows. The characteristic in terms of hydrological and environmental conditions may determine the community structure of the 6 river systems. Our study highlighted the importance of monitoring based on a large spatial scale, and more attention should be paid to potential toxic cyanobacteria for water quality management purposes.

Keywords: Phytoplankton / Lake Taihu Basin / river / spatial autocorrelation

Résumé – **L'autocorrélation spatiale de la biomasse phytoplanctonique est faible dans les rivières du bassin du lac Taihu, en Chine.** Nous avons étudié les caractéristiques de la structure de la communauté phytoplanctonique dans l'ensemble du bassin du lac Taihu (LTB), l'une des régions les plus développées de Chine. Un groupe fonctionnel morphologique (MBFG) proposé par Kruk *et al.* (2010), en particulier les cyanobactéries toxiques potentielles (groupes III et VII), a également été décrit. Des échantillons ont été prélevés en 96 sites le long des principales rivières au cours des quatre saisons de septembre 2014 à janvier 2016. Des différences significatives dans la structure de la communauté phytoplanctonique ont été observées à l'échelle spatiale (en particulier entre Huangpu/Tiaoxi et les 4 autres systèmes fluviaux) et saisonnière. A l'échelle spatiale, une grande variabilité a été observée dans la biomasse moyenne du phytoplancton, avec une valeur relativement élevée de 3,13 mg L^{-1} dans le système Yanjiang et une valeur relativement faible dans les systèmes Huangpu (1,23 mg L^{-1}) et Tiaoxi (1,44 mg L^{-1}). La biomasse moyenne des cyanobactéries potentiellement toxiques représentait 18,28 % de la biomasse totale moyenne spatialisée, qui était plus abondante dans les systèmes Nanhe et Yanjiang. L'autocorrélation spatiale était faible pour la biomasse totale et ses quatre principales composantes (bacillariophytes, chlorophytes, euglénophytes et cyanobactéries) à l'échelle du bassin, quelque soit la saison. En ce qui concerne le système fluvial, une

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autocorrélation significative n'a guère été observée dans tous les systèmes fluviaux à l'exception de Huangpu, en particulier dans les apports d'eau. Les caractéristiques en termes de conditions hydrologiques et environnementales peuvent déterminer la structure des communautés des 6 systèmes fluviaux. Notre étude a souligné l'importance d'une surveillance à grande échelle spatiale, et il faudrait accorder plus d'attention aux cyanobactéries potentiellement toxiques aux fins de gestion de la qualité de l'eau.

Mots-clés: Phytoplancton / bassin du lac Taihu / rivière / autocorrélation spatiale

1 Introduction

Rivers play an essential role in providing water resources for several purposes, such as industry and agriculture, among other human uses. However, rivers are easily polluted by human activities, and concerns about the water quality of rivers have increased worldwide (Behmel *et al.*, 2016; Olmanson *et al.*, 2013; Singh *et al.*, 2005). Phytoplankton is the fundamental component in aquatic food chains and is sensitive to environmental changes, as shown by changes in community structure (Reynolds, 1984). Although commonly observed in lentic ecosystems, phytoplankton blooms, especially toxic blooms, occur frequently in rivers under increasing anthropogenic pressure (Acharyya *et al.*, 2012; Hutchins *et al.*, 2010; Lapointe *et al.*, 2015; Otten *et al.*, 2015). Consequently, more attention should be paid to the phytoplankton community structure and distribution in rivers, as well as its influencing factors (Paerl and Huisman, 2009).

In general, the main taxonomic groups of phytoplankton can be used to clarify important ecological differences at certain scales and are adopted to illustrate phytoplankton distribution and variation (Allende *et al.*, 2019; Kruk *et al.*, 2011). Additionally, functional groups are proposed from the view of classifying phytoplankton species with common traits and similar features in response to environmental changes (Mihaljevic *et al.*, 2015; Reynolds *et al.*, 2002; Salmaso and Padisák, 2007). In particular, the classification proposed by Reynolds *et al.* (2002), which played a critical role in the development of phytoplankton functional groups, combined individual functional traits and a range of environmental conditions. However, there are many misuses of this classification, which requires not only rich base information but also expert judgment (Padisák *et al.*, 2009). To simplify the classification, Kruk *et al.* (2010) suggested another functional group based on morphological traits, *i.e.*, a morphologically based functional group (MBFG). In a subsequent study, Kruk *et al.* (2011) noted that morphological groups can be used to predict phytoplankton community composition. In particular, group III and VII, requires further attention because of potential threats from notorious cyanobacteria blooms, especially those that produce toxins.

As one of the most developed regions in China, Lake Taihu Basin (LTB) plays an important role in economic development and experiences severe pollution from human activities. Notably, as the third largest freshwater lake in China, Lake Taihu has been subjected to environmental problems for decades, especially eutrophication and cyanobacterial blooms (Chen *et al.*, 2003; Paerl *et al.*, 2011; Xu *et al.*, 2010). In addition, inflows with external loading, affect the water quality of the lake to a certain extent (Wu *et al.*, 2018). Therefore, numerous studies illustrated the water chemical parameters (*e.g.*, nutrients, heavy metals, etc.) in the rivers of the LTB (Bian *et al.*, 2016; Huang *et al.*, 2017; Mu *et al.*, 2015). By contrast, phytoplankton in these rivers have received less attention compared with Lake Taihu which suffers serious algal blooms (Deng *et al.*, 2011; Du *et al.*, 2014; Wu *et al.*, 2016). Furthermore, the variations in rivers were highly heterogeneous, which should be illustrated at appropriate spatial and temporal scales (Qadir *et al.*, 2008; Singh *et al.*, 2005). There are many factors that control phytoplankton dynamics and structure in rivers, such as water discharge, underwater light conditions and temperature (Reynolds and Descy, 1996; Shen *et al.*, 2011; Townsend and Douglas, 2017). Particularly, the relationship between phytoplankton and environmental parameters in lotic ecosystems may vary depending on the spatial scale (Wu *et al.*, 2014a). In addition, spatial autocorrelation is an essential factor that influences the variability of the biotic community structure. In general, it makes sense that similar distribution patterns exist among observations collected in close proximity due to similar environmental parameters (Legendre and Troussellier, 1988; Liu *et al.*, 2018). Xiao *et al.* (2013) observed significant spatial autocorrelation in wet and dry seasons in the southern LTB. However, two questions remain: Will this significance still exist at a larger spatial scale, *i.e.*, the whole of the LTB? and will the autocorrelation have changed during the past years? Therefore, a seasonal-scale study that covers the whole basin is needed to determine the phytoplankton distribution pattern in this basin.

In this study, the phytoplankton community structure and its spatial and seasonal distributions were examined in the rivers of the LTB. Our study was based on a seasonal investigation across 96 sites covering the whole LTB. Our primary objectives were (1) to illustrate the spatial and seasonal distributions of phytoplankton community structure and (2) to explore the potential factors including spatial autocorrelation that influenced this community structure. Our study will provide a basis for understanding phytoplankton community structure that is crucial for monitoring ecological changes in this basin.

2 Materials and methods

2.1 Study area

Lake Taihu Basin (30°7′19″–32°14′56″ N, 119°3′1″–121°54′ 26″ E) is in the downstream of the Yangtze River (Fig. S1), and its watershed area is 36,895 km^2, The basin covers Jiangsu and Zhejiang Provinces, as well as Shanghai municipality, which are highly developed and severe polluted. There are numerous rivers (>200) distributed across the basin, covering 7% of the total basin, with a total distributary length and density of approximately 120,000 km and 3.25 km km^{-2}, respectively.

2.2 Sample collection and laboratory analysis

We carefully selected 96 sampling sites to cover the main rivers, representing the whole of LTB (Fig. S1). According to Wu *et al.* (2018), sampling sites were divided into 6 river systems, *i.e.*, the Taoge (TG), Nanhe (NH), Tiaoxi (TX), Yanjiang (YJ), Huangpu (HP), and Hangzhou Bay and the Yangtze Estuary (HY) river systems.There are 11, 7, 15, 21, 28, and 14 samplings sites covered in TG, NH, TX, YJ, HP, and HY systems, respectively. Regarding seasonal variation, our sampling were conducted in September 2014, March 2015, July 2015, and January 2016, representing autumn, spring, summer, and winter, respectively.

The surface water samples were collected. A Hydrolab Datasonde 5 sensor (USA) was used to measure 5 environmental parameters *in situ*, including pH, surface water temperature (T), turbidity (tur), conductivity (cond) and dissolved oxygen (DO). The water transparency (SD) was determined using a Secchi disk. Other parameters, *i.e.*, total nitrogen (TN), ammonium (NH_4–N), nitrate (NO_3–N), nitrite (NO_2–N), total phosphorus (TP), permanganate index (COD_{Mn}), concentrations were also analyzed., With regard to the relevant analytical methods and primary procedures, more details are available in Wu *et al.* (2018).

Phytoplankton samples were fixed with Lugol's iodine solution (1% v/v) and allowed to settle for 48 h prior to counting using a microscope (Leica DM2500, Germany). Population for each sample was enumerated in random fields with a 0.1-mL fixed sample that was concentrated from 1 L to 30 mL. A minimum of 300 values were enumerated for each phytoplankton sample. Phytoplankton identification was performed according to Hu and Wei (2006). Mean cell volume was calculated using appropriate geometric configurations (Hillebrand *et al.*, 1999). Volume values were converted to biomass assuming that 1 mm^3 of volume was equivalent to 1 mg of fresh-weight biomass (Holmes *et al.*, 1969).

2.3 Data analysis

The classification of morphologically based functional group was according to Kruk *et al.* (2010), which divided phytoplankton species into seven groups (I, II, III, IV, V, VI, and VII). Particularly, group III only includes cyanobacteria, and group VII is constituted by chlorophyta and cyanobacteria. Furthermore, group III and VII both have the potential to form toxic blooms. In addition, cyanobacteria blooms were severe in LTB (Chen *et al.*, 2003; Paerl *et al.*, 2011). Therefore, we illustrated the variation of these two groups together, *i.e.*, potential toxic cyanobacteria, in our study.

An analysis of similarity (ANOSIM) was used to detect alterations in phytoplankton species composition and biomass (Clarke, 1993), based on Bray–Curtis similarity coefficient. Furthermore, when a significant difference in species composition and biomass existed for two or more groups, the similarity percentage (SIMPER) was used to determine taxa that could be responsible for the difference. Kruskal-Wallis nonparametric test was used to examine that whether significance difference existed for phytoplankton biomass on both temporal and spatial levels. These analyses were performed using PAST software (Paleontological Statistics v2.15). Spatial autocorrelation analysis was performed using ArcMap 10.1.

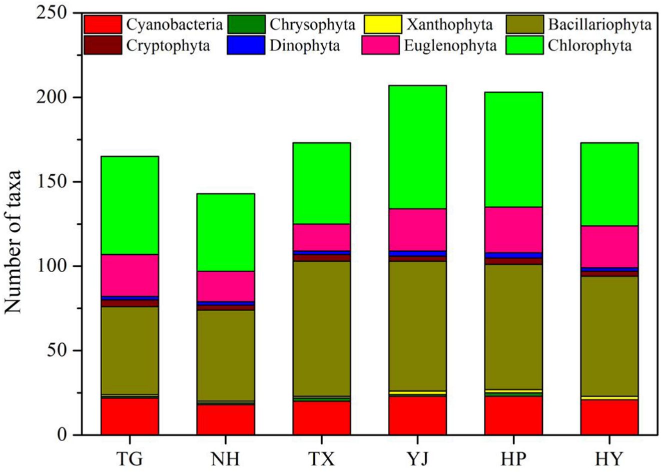

Fig. 1. The number of species belonging to the different phytoplankton groups in the 6 river systems of the LTB.

To explore the main components and key environmental parameters that influence phytoplankton biomass in LTB, stepwise multiple linear regressions were used, including biomass of each group and environmental parameters, such as T, pH, cond, tur, DO, TN, NH_4–N, NO_2–N, NO_3–N, TP, COD_{Mn}. All data were log $(x+1)$ transformed prior to analysis. This analysis was conducted using the SPSS statistical package for Windows (version 17.0). An extremely large phytoplankton biomass (421.86 mg L^{-1}) was observed in one of sampling sites in winter, followed by 36.32 mg L^{-1}, which probably affected the spatial and seasonal patterns. Therefore this outlier was not considered in our analyses.

3 Results

3.1 Phytoplankton community structure

In total, 311 species belonging to eight phytoplankton classes were identified during the four seasonal samplings events, including cyanobacteria, chrysophyta, xanthophyta, bacillariophyta, cryptophyta, dinophyta, euglenophyta, and chlorophyta. Most taxa (191) were infrequently observed, with an occurrence rate of less than 10% across all 96 sampling sites; 18.75% were commonly observed at >50% of the sites. *Synedra acus*, *Cyclotella* sp., and *Chlorella* sp. were observed at all sampling sites in the LTB. Bacillariophyta (128) were the most important group, representing 40% of the total number of species, followed by chlorophyta (98), euglenophyta (42), and cyanobacteria (30) based on the whole basin. The highest species number was observed in YJ (207), followed by HP (203), and the lowest value was observed in NH, with a value of 143 (Fig. 1). The species numbers of other groups (*i.e.*, chrysophyta, xanthophyta, cryptophyta, and dinophyta) were

Table 1. Percentage of phytoplankton taxa that accounted for at least 1% of the average biomass based on four samplings events and contribution to differences in the community structure at spatial river system) and seasonal scales in the rivers of Lake Taihu Basin.

	Species	Percentage	Contribution (%)	
			Spatial	Seasonal
Cyanobacteria	*Spirulina princeps*	5.01	2.67	2.70
	Anabaena circinalis	3.39	1.85	1.89
	Planktothrix sp.	3.25	1.96	1.98
	Microcystis aeruginosa	2.15	1.22	1.20
	M. flos-aquae	1.73	1.07	1.02
Bacillariophyta	*Coscinodiscus* sp.	6.32	4.45	4.77
	Surirella sp.	3.93	5.03	4.81
	Aulacoseira sulcata	3.67	4.43	4.49
	A. varians	3.63	5.00	4.90
	A. granulata	3.07	3.65	3.76
	Cyclotella sp.	2.47	1.91	1.93
	Pinnularia sp.	2.00	2.83	2.89
	Synedra acus	1.86	1.91	1.85
	Navicula sp.	1.30	1.84	1.78
	Actinocyclus ehrenbergii	1.08	1.26	1.25
Cryptophyta	*Cryptomonas erosa*	2.23	2.51	2.56
Dinophyta	*Gymnodinium aeruginosum*	3.20	2.95	3.15
	Peridinium sp.	1.51	2.35	2.36
	Phacus sp.	3.35	3.60	3.56
Euglenophyta	*Euglena oxyuris*	2.97	3.23	3.23
	E. polymorpha	1.40	1.88	1.84
	E. sp.	1.76	1.76	1.69
	Phacus longicauda	2.44	1.97	1.95
Chlorophyta	*Eudorina elegans*	4.23	3.86	3.43
	Pediastrum duplex	2.58	2.03	2.07
	P. simplex	1.21	0.88	0.85
	Pandorina morum	1.73	1.25	1.23
	Oocystis sp.	1.16	0.73	0.77
	Coelastrum microporum	1.05	0.79	0.79
Total		75.70	70.86	71.19

relatively low, and no chrysophyta species occurred in HY. Seasonally, the species numbers of cyanobacteria were the highest in summer regardless of the river system, while the highest values of bacillariophyta were all observed in winter. Phytoplankton biomass in the rivers of the LTB were dominated by cyanobacteria, bacillariophyta, euglenophyta, and chlorophyta, and the biomass of these four groups were highly correlated with total biomass ($R^2 = 0.99$, $P < 0.0001$, $n = 383$).

Based on the species composition and biomass of phytoplankton, the community structure in HP was significantly different from that in the other river systems (all P values < 0.01), and a significant difference in phytoplankton community structure was also observed between HY and TG/NH/TX, with P values of 0.021, 0.0025 and 0.0001, respectively. In addition, there was a significant difference between TX and TG/YJ, with P values of 0.016 and 0.0001, respectively. At the seasonal scale, a significant difference was detected among the four seasons based on the whole basin and all six river systems, with all P values of 0.0001. Bacillariophyta was the most important taxa that affected the phytoplankton community structure and contributed 32.32% and 32.43% to the total deviation at the spatial and seasonal levels, respectively (Tab. 1), based on the species that accounted for at least 1% of the average biomass. Euglenophyta was the second most important taxa, accounting for 12.45% and 12.27% of the differences at the spatial and seasonal scales, respectively. Chlorophyta and cyanobacteria also played an essential role in the observed differences.

3.2 Spatial and seasonal difference in biomass

On a spatial basis, high variability was observed in the mean phytoplankton biomass and in each taxonomic class across the whole basin. The mean biomass ranged from 0.20 mg L^{-1} to 11.58 mg L^{-1} among the 96 sampling sites (Fig. 2A). The average total biomass in HP and TX was 1.23 mg L^{-1} and 1.44 mg L^{-1}, respectively, while the values were significantly higher in the other river systems (Fig. 3A). The mean biomass was the highest in YJ, with a value of 3.13 mg L^{-1}, followed by HY (3.05 mg L^{-1}). In NH, the mean

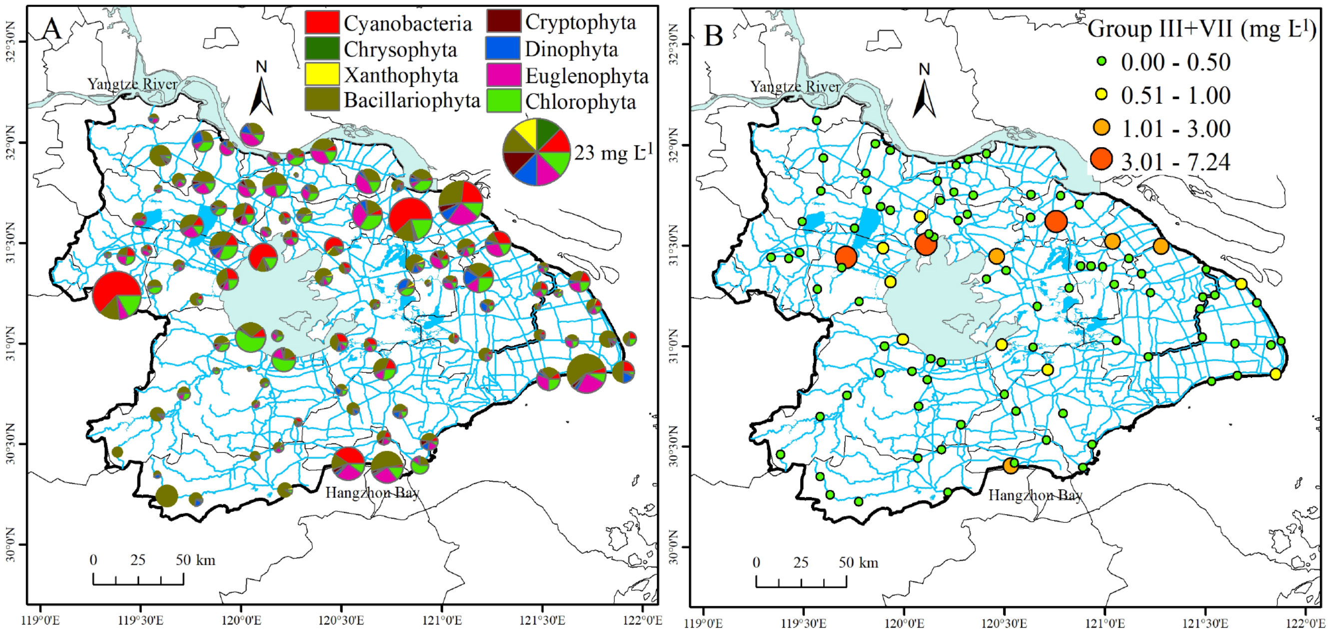

Fig. 2. Spatial distribution of phytoplankton biomass in each taxonomic group (A) and potential toxic cyanobacteria (MBFG III and VII) (B) based on seasonal averages in the rivers of the LTB.

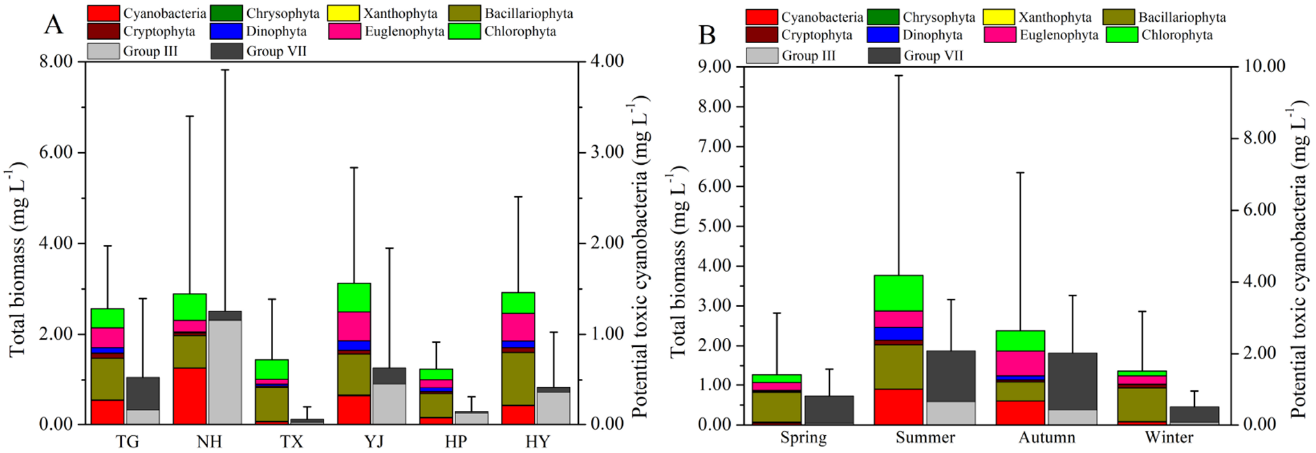

Fig. 3. Spatial (A) and seasonal (B) distribution of phytoplankton biomass in the rivers of the LTB; standard deviation was based on total biomass and potential toxic cyanobacteria biomass, respectively.

biomass was 2.89 mg L^{-1}. Bacillariophyta dominated the biomass in all 6 river systems except NH, especially in TX, in which this group contributed 52.82% to the mean biomass. The average bacillariophyta biomass was the highest in HY (1.19 mg L^{-1}) and the lowest in HP (0.52 mg L^{-1}). Cyanobacteria played a vital role in the biomass composition in NH, with the highest mean value of 1.26 mg L^{-1} among the river systems. The biomass of cyanobacteria and chlorophyta in TX was significantly lower than that in the other river systems (all P values < 0.01). A significant difference was also observed in the biomass of cryptophyta and euglenophyta between TX and TG/YJ/HY, as well as in the biomass of dinophyta between TX and HY (all P values < 0.05). There was no significant difference in the distribution of chrysophyta and xanthophyta among river systems. According to MBFG classification, group VII was almost entirely constituted by cyanobacteria in our study, with *Botryococcus braunii* observed once, and its main species were *Microcystis* (such as *Microcystis flos-aquae*, *Microcystis firma*, *Microcystis aeruginosa*, and *Microcystis* sp.); the biomass of *Microcystis* were highly correlated with the biomass of group VII ($R^2 = 0.998$, $P < 0.0001$, $n = 383$). The mean biomass of potential toxic cyanobacteria (group III and VII) accounted for 99.70% and 18.28% of the mean cyanobacteria and total biomass, respectively, at spatial scale, and was typically (81 sites) lower than 0.50 mg L^{-1} (Fig. 2B). There were 7 sampling sites that exhibited a mean biomass of group III and VII in total greater than 1 mg L^{-1} (these sites were mostly located near the northern part of Lake Taihu), with a maximum biomass proportion of 67.29%. The highest mean biomass of potential toxic cyanobacteria was observed in one sampling site of NH (7.24 mg L^{-1}), and its biomass accounted for 62.55% of the mean total biomass. The other two sites in red in Figure 2B were in TG and YJ, with the biomass of group III and VII larger than 3 mg L^{-1} in total. The mean biomass proportion of potential toxic cyanobacteria was larger than 10% in 43 of all the 96 sampling sites. A relatively high mean biomass of potential toxic cyanobacteria was observed in NH and YJ, with values of 1.26 mg L^{-1} and 0.63 mg L^{-1}, contributing of 13.38% and 10.90% to the total mean biomass, respectively (Fig. 3A). The biomass of potential toxic cyanobacteria in TX and HP was relatively low, with a mean value of 0.06 mg L^{-1} and 0.14 mg L^{-1}, respectively.

Generally, the phytoplankton biomass exhibited extremely significant differences between summer and the other 3 seasons (all P values < 0.001) (Fig. 3B); the mean value was 3.77 mg L^{-1} in summer, followed by autumn (2.38 mg L^{-1}), while the mean biomass in winter and spring was relatively low. Cyanobacteria were more abundant in summer and autumn, with the percentages of 23.66% and 25.15%, respectively, based on seasonal averages. The mean biomass of chlorophyta was 0.90 mg L^{-1} in summer and was significantly higher than that in the other 3 seasons. The mean bacillariophyta biomass was significantly lower (0.49 mg L^{-1}) in autumn. The mean biomass of euglenophyta was 0.62 mg L^{-1} in autumn, followed by summer (0.41 mg L^{-1}), which were both significantly higher than that in spring (both P values < 0.001). The mean biomass of potential toxic cyanobacteria was also relatively high in summer and autumn, and contributed to 23.58% and 25.08%, respectively, of the mean total biomass (Fig. 3B).

3.3 Spatial autocorrelation and regression analysis

The mean Moran's I value for mean total biomass across the 96 sites was 0.12; with regard to the mean biomass of the four main group (*i.e.*, bacillariophyta, chlorophyta, euglenophyta, and cyanobacteria.) and potential toxic cyanobacteria, the values were also relatively low, with the exception of chlorophyta. Seasonally, there was a few extremely significant autocorrelation for the biomass of some main groups, *i.e.*, cyanobacteria (Fig. 4A) and euglenophyta (Fig. 4B) in spring, bacillariophyta in summer (Fig. 4C), euglenophyta (Fig. 4D) and chlorophyta (Fig. 4E) in autumn, as well as euglenophyta in winter (Fig. 4F).

Regarding the spatial difference, we also detected autocorrelation of phytoplankton biomass in all 6 river systems. Compared with the other river systems, the significant autocorrelation was relative frequently observed in HP, including cyanobacteria and bacillariophyta in spring, total biomass and chlorophyta in autumn, and total biomass, cyanobacteria, and euglenophyta in winter (Tab. 2). In addition, a few significant autocorrelations were detected in YJ and HY, especially in total biomass and euglenophyta. Seldom significant autocorrelation was found in inflows of Lake Taihu, especially in NH and TX.

Stepwise multiple linear regressions showed that COD_{Mn}, T, NH_4–N, tur, pH, and NO_3–N entered the model that explain total phytoplankton biomass, with P and R^2_{adj} values of <0.001 and 0.198, respectively (Tab. 3). Based on the data averaged by site, NH_4–N entered first, followed by tur, pH, and cond. Environmental parameters explained a relatively large part of the biomass variation regardless of season except in spring, with all ${R_{\mathrm{adj}}}^2$ values higher than 0.30. NH_4–N entered the models for summer, autumn, and winter.

4 Discussion

4.1 Phytoplankton community structure in the LTB

Our study provided a comprehensive understanding of the phytoplankton community structure and its spatial and temporal distribution in the LTB. According to our investigation, more species were observed at a large scale in the LTB across the four seasons, compared with previous studies that focused on only one (or two) seasons or partial coverage of the LTB, which was no more than 139 species observed (Du *et al.*, 2014; Wu *et al.*, 2016; Xiao *et al.*, 2013). Many species were infrequently observed probably due to the turbid characteristics of the rivers (the mean secchi depth and tur was 0.29 m and 109.55 NTU, respectively).

Bacillariophyta played an important role in the total variation of the phytoplankton community structure at both the spatial and seasonal levels. Bacillariophyta was abundant in terms of species, similar to chlorophyta, which is in accordance with previous studies in the LTB (Du *et al.*, 2014; Wu *et al.*, 2016). Bacillariophyta are commonly dominat in a well-mixed water column, such as rivers and lakes with short retention times (Stankovic *et al.*, 2012; Wu *et al.*, 2013). As one of the main groups, bacillariophyta contributed largely to the total biomass and dominated regardless of the season in our study area. Chlorophyta is another successful group in large rivers, and tends to be more abundant in summer (Wehr and Descy, 1998). According to our data, the average chlorophyta biomass was relatively high in summer, which was probably due to its high threshold of light requirements to sustain net productivity (Reynolds *et al.*, 1994).

Cyanobacteria contributed to the total biomass at a certain level in the LTB, and the concern surrounding this group should not be limited to lakes such as Lake Taihu and Lake Ge. According to our study, cyanobacteria accounted for more than 18% of the total biomass, and the values were relatively high in NH and TG (spatially) and in summer and autumn (seasonally). Potential toxic cyanobacteria accounted for nearly 20% of the total biomass on a spatial basis; the biomass was relatively high in NH, followed by YJ and TG. Notably, there was no significant difference in cyanobacteria biomass between the inflows and outflows of Lake Taihu, except for TX. In addition, the percentage of cyanobacteria was relatively low in TX, which may be due to the relatively low nutrient concentrations in TX. Our previous study noted that the concentrations of nitrogen (including TN, NH_4–N, and NO_3–N), as well as TP, were relatively low in TX (Wu *et al.*, 2011, 2018).

4.2 Factors determining the phytoplankton community structure

The characteristics of river systems in terms of hydrological and environmental conditions may determine the community structure among the 6 river systems. First, hydrology is an important factor that affects living organisms

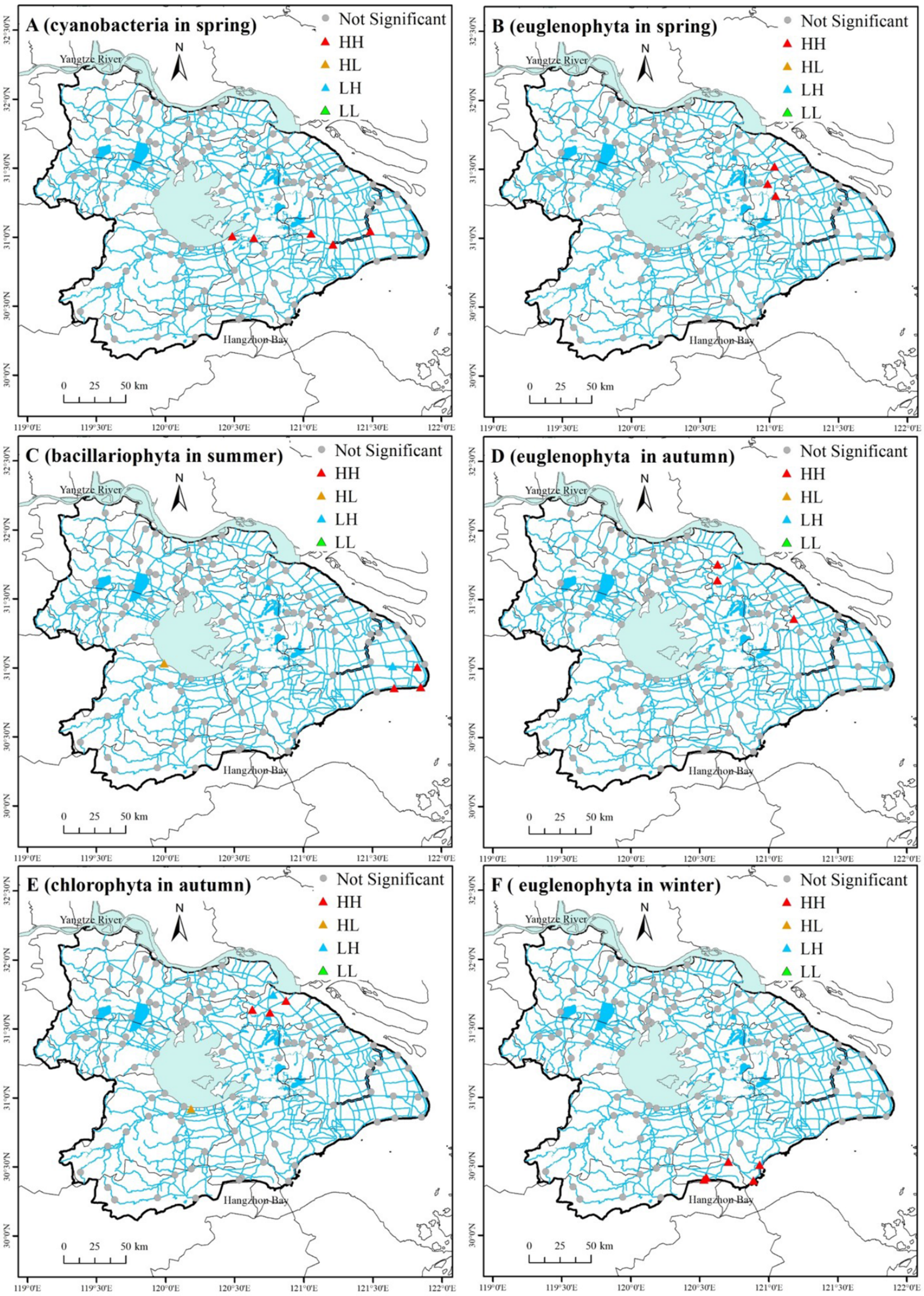

Fig. 4. Location of clusters and types of significant spatial autocorrelation of main constituents of phytoplankton biomass in the rivers of the LTB. A and B indicated cyanobacteria and euglenophyta in spring, respectively; C indicated bacillariophyta in summer; D and E indicated euglenophyta and chlorophyta in autumn, respectively; F indicated euglenophyta in winter.

in lotic environments (Devercelli and O'Farrell, 2013; Wetzel, 2001). Discharge, which is related to residence time and other variables, plays a critical role in determining phytoplankton growth (Wu *et al.*, 2014b). In particular, the phytoplankton community structure in HP/TX was extremely different from that in NH, TG, YJ, and HY; Notably, the significant difference also existed between HP and TX. As the mainstream of HP, the Huangpu River is the only river freely

Table 2. Moran's I and Z values of total phytoplankton biomass and its four main components in all river systems.

		Total biomass		Cyanobacteria		Bacillariophyta		Euglenophyta		Chlorophyta	
		I	Z	I	Z	I	Z	I	Z	I	Z
TG	Spring	0.26	1.06	−0.01	0.28	0.14	0.71	−0.38	−0.90	0.42	1.90
	Summer	0.22	1.00	0.09	0.57	0.25	1.01	−0.01	0.61	0.05	0.61
	Autumn	−0.07	0.16	−0.07	0.30	0.35	1.96*	−0.05	0.27	−0.03	0.43
	Winter	−0.15	−0.22	−0.07	0.42	−0.08	0.09	−0.36	−0.85	0.15	0.74
NH	Spring	0.33	1.11	−0.51	−0.87	0.35	1.11	−0.24	−0.19	0.20	0.74
	Summer	−0.26	−0.49	−0.17	−0.58	−0.25	−0.25	−0.31	−0.48	−0.70	−1.26
	Autumn	−0.14	0.09	−0.27	−0.24	0.55	1.45	−0.24	−0.24	−0.19	−0.14
	Winter	0.44	1.65	−0.92	−1.76	0.30	1.25	0.04	0.58	−0.15	0.04
TX	Spring	0.12	1.06	0.14	1.38	0.09	0.96	−0.04	0.22	−0.30	−1.85
	Summer	−0.13	−0.57	0.09	0.94	−0.26	−1.19	−0.33	−1.50	−0.04	0.34
	Autumn	−0.13	−0.31	−0.15	−0.86	0.03	0.96	−0.19	−1.09	−0.10	−0.30
	Winter	0.00	0.42	0.01	0.54	−0.10	−0.17	−0.17	−0.56	−0.03	0.38
YJ	Spring	0.15	2.08^{*}	0.02	0.68	0.09	1.31	0.16	2.22^{*}	−0.06	−0.08
	Summer	−0.01	0.31	−0.02	0.23	−0.11	−0.53	0.02	0.70	−0.17	−1.00
	Autumn	0.14	1.75	−0.02	0.46	0.18	1.83	−0.01	0.33	0.20	2.21^{*}
	Winter	−0.09	−0.38	0.58	6.09^{**}	−0.07	−0.15	−0.17	−1.25	−0.12	−0.80
HP	Spring	0.14	0.95	0.37	2.88^{**}	0.35	2.12^{*}	−0.03	0.08	−0.06	−0.14
	Summer	−0.08	−0.26	−0.04	−0.03	−0.02	0.08	−0.19	−0.91	−0.22	−1.07
	Autumn	0.33	2.06^{*}	−0.01	0.17	0.06	0.57	0.15	1.17	0.40	2.61^{*}
	Winter	0.38	2.61^{**}	0.41	3.01^{**}	0.10	0.86	0.51	3.09^{**}	0.01	0.29
HY	Spring	0.60	2.11^{*}	−0.08	−0.03	−0.22	−0.45	−0.03	0.08	0.24	1.29
	Summer	−0.19	−0.43	−0.12	−0.31	−0.32	−1.67	0.40	1.68	−0.08	−0.02
	Autumn	0.72	2.40^{*}	0.01	0.28	0.30	1.09	0.57	2.13^{*}	0.19	1.22
	Winter	−0.12	−0.21	−0.38	−0.97	−0.28	−0.08	0.39	1.84	−0.24	−0.46

$^{*}P < 0.05$.
$^{**}P < 0.01$.

Table 3. Linear models explaining the total biomass. The models result from a stepwise selection procedure using the independent factors: temperature, pH, conductivity, turbidity, dissolved oxygen, total nitrogen, ammonium, nitrite, nitrate, total phosphorus, permanganate index.

Total biomass	Parameters included	*n*	*P*	R^2_{adj}
All data	COD_{Mn}, T, NH_4–N, tur, pH, NO_3	383	<0.001	0.198
Data averaged by site	NH_4–N, tur, pH, cond	96	<0.001	0.285
Spring	COD_{Mn}	96	0.006	0.066
Summer	Cond, NO_3–N, COD_{Mn}, NH_4–N, TP, pH	96	<0.001	0.393
Autumn	NH_4–N, DO, pH, tur, TN, cond	96	<0.001	0.477
Winter	DO, NH_4–N, pH, tur	95	<0.001	0.311

connected to the Yangtze River. By contrast, other systems are constituted by a number of other rivers, and flow regulation commonly exists. Some sites in HY were located in the estuary, connecting to Hangzhou Bay and the Yangtze Estuary, which may explain the significant difference in the community structure compared with other river systems. According to the unpublished winter data, the water flow rate was relatively high in HP and TX, with values of 0.17 m/s (Wu *et al.*, 2019) and 0.10 m/s, respectively, and the water retention time may explain the relatively low biomass in HP and TX (Reynolds, 2000). Furthermore, the community structure is also regulated by the variation in environmental factors (Reynolds *et al.*, 1994; Zebek and Szymanska, 2017). Based on the regression analysis, several environmental parameters, such as NH_4–N and tur, explained total phytoplankton biomass both spatially and seasonally except in spring to a certain extent. NH_4–N almost entered all models that explained total phytoplankton biomass except for the spring data. Tur, COD_{Mn}, and pH also commonly appeared in the linear regression models. All these parameters mentioned above played an important role in determining the water quality assessed by Wu *et al.* (2018) using water quality index method in this area, which pointed out that the water quality was generally determined by NH_4–N, tur, COD_{Mn}, NO_3–N and DO. Therefore it is likely that phytoplankton biomass and water quality were affected by similar environmental parameters. Our study showed that the phytoplankton community structure reflected water quality differences among river systems, especially between TX and other river systems. According to our previous assessment, the water quality index value in TX was significantly higher than that in the other 5 river systems, representing relative good water quality (Wu *et al.*, 2018). Particularly, as we mentioned above, the mean nutrient concentrations were relative low in TX (Wu *et al.*, 2018). Correspondingly, the phytoplankton community structure also differed significantly between TX and the other river systems. Temperature was another parameter that explained part of the phytoplankton biomass variability based on all sampling data. Seasonally, the significant difference in community structure may be due to temperature, discharge or other variables in temperate rivers (Lange and Rada, 1993; Reynolds *et al.*, 1994; Townsend and Douglas, 2017).

The spatial autocorrelation of phytoplankton was weak in the LTB, based on our survey at the whole basin level. According to the data averaged seasonally, only chlorophyta biomass exhibited a significant autocorrelation. Seasonally, significant autocorrelation was observed in 3 of 4 seasons for euglenophyta, but only in one season for bacillariophyta, chlorophyta, and cyanobacteria. By contrast, Xiao *et al.* (2013) demonstrated that significant spatial autocorrelation existed in phytoplankton abundance and diversity based on an investigation of the southern LTB in 2010. The difference in the investigation area may be an important factor influencing the relative controversial conclusion on autocorrelation. Furthermore, flow regulation probably changes hydrological connectivity among rivers and subsequently affects biogeographical diversity (Nilsson *et al.*, 2005). As mentioned above, HP is freely connected to the Yangtze River, and the significant autocorrelation was relative frequently observed in this river system. Notably, the spatial autocorrelation was scarcely detected in the inflows of Lake Taihu. Additionally, Huszar *et al.* (2015) suggested that environmental processes shaped the phytoplankton composition and functional groups in a large subtropical river basin, and space was not significant, considering non-directional and directional processes. Regarding the LTB, the water quality was significantly different among the six river systems, which may have resulted in the lack of strong autocorrelation for phytoplankton (Wu *et al.*, 2018).

4.3 Implication for local management

The phytoplankton community structure, including the composition and biomass, varied in the LTB depending on the spatial scale. A higher number of phytoplankton species was observed in our study based on the investigation of the whole LTB. Furthermore, there were significant differences in the phytoplankton community structure at spatial and seasonal scales. In addition, the spatial autocorrelation of total biomass and its main component was weak in LTB. Therefore, monitoring based on a large scale is crucial for understanding the phytoplankton community structure in the LTB. Phytoplankton biomass was mainly composed of cyanobacteria, bacillariophyta, euglenophyta, and chlorophyta, which also played an important role in the spatial and seasonal variations in the community structure. Cyanobacteria have received considerable attention worldwide due to their threat to freshwater ecosystems and human health, and cyanobacterial blooms are severe in the LTB, especially in Lake Taihu. According to our study, on a spatial basis, cyanobacteria accounted for a relatively high proportion of the total biomass. Specifically, potential toxic cyanobacteria built up 18.28% of total biomass spatially, which requires more attention in the LTB, especially in NH and YJ. Notably, with the exception of TX, there was no significant difference in cyanobacteria biomass between the inflows and outflows of Lake Taihu.

5 Conclusions

Our study provided a comprehensive understanding of the phytoplankton community structure in the rivers of LTB. The results showed that the total biomass was mainly constituted by four classes (*i.e.*, bacillariophyta, chlorophyta, euglenophyta, and cyanobacteria), which mainly resulted in differences in the phytoplankton community structure at spatial and seasonal scales. Total phytoplankton biomass was relatively high in YJ and HY and relatively low in HP and TX. Potential toxic cyanobacteria built up nearly 20% of total biomass, which was more abundant in NH and YJ. Spatial autocorrelation was weak for total biomass and its four main components at the whole basin level. Regarding the river system, significant autocorrelation was scarcely observed in all the river systems except Huangpu, especially in the inflows. The characteristics in terms of hydrological and environmental conditions may determine the community structure of the 6 river systems.

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Conflicts of interest. The authors declare no conflict of interest.

Supplementary Material

Figure S1 Location of the sampling sites in Lake Taihu Basin, China (TG: Tiaoge river system; NH: Nanhe river system; TX: Tiaoxi river system; YJ: Yanjiang river system; HP: Huangpu river system; HY: Hangzhou Bay and the Yangtze Estuary river system) (Wu *et al.*, 2018).

The Supplementary Material is available at https://www.kmae-journal.org/10.1051/kmae/2019027/olm.

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