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Climate exerts a greater modulating effect on the phytoplankton community after 2007 in eutrophic Lake Taihu, China: Evidence from 25 years of recordings

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ABSTRACT

Long-term phytoplankton community changes indicate the trophic status under nutrient regulation conditions in eutrophic lakes, although the modulatory role of climate change scenarios in their indicative function has been underestimated. Hence, we analyzed the relative contributions of nutrient and climate factors to interannual and seasonal variations in the phytoplankton biomass and composition from 1992 to 2017 in Meiliang Bay, Lake Taihu, China. Discrete phytoplankton communities from five periods were classified according to their interannual features. Variations in the phytoplankton community composition were observed during the five periods, and these variations included a shift from exclusive cyanobacterial dominance before 2008 to diatom-cyanobacterial codominance in 2008–2010 and from cyanobacterial dominance in 2011–2014 to cyanobacterial-diatom codominance in 2015–2017. The phytoplankton biomass pattern typically peaked in summer, although peaks also occurred in winter 2008–2010 and autumn 2011–2014. Additionally, the phytoplankton biomass increased by threefold from 2015 to 2017, which might have been related to rising air temperatures and greater light availability. The variance in the phytoplankton community was significantly explained by nutrient (ammonium, nitrate and phosphate) and climatic (air temperature and wind speed) factors. However, the explaining effect of the factors varied among the five periods: nutrients strongly impacted the community composition from 1992 to 2007, whereas climatic variables became more important modulators after 2007. These results reveal that climatic factors play importance roles in shaping the phytoplankton community and cyanobacterial blooms and suggest that differences in the roles between specific climatic conditions should be considered. Future declines in cyanobacterial blooms require further dual nitrogen and phosphorus reduction and longer recovery times under current climate change scenarios in this and possibly other shallow eutrophic lakes.

1. Introduction

Nutrients and climate are well-recognized environmental drivers of changes in freshwater ecosystems (Ko et al., 2017; Monchamp et al., 2018). The phytoplankton in freshwater lakes represent an indicator of the limnological status, biodiversity, trophic condition and environmental changes (Cupertino et al., 2019; Mateo et al., 2015; Wang et al., 2016). The phytoplankton community dynamics in lakes have long been monitored in geographically diverse lakes over varying monitoring timespans (8–48 years) and have exhibited different aquatic ecosystem responses to nutrient availability and climatic fluctuations. In deep lakes, phytoplankton might show remarkable stability under external pressures (Zohary, 2004) or a relationship with gradual changes in nutrient levels that remains unrelated to climatic conditions (Jochimsen et al., 2013); these organisms might even be influenced by multiple stressors, such as eutrophication and climate warming (Pomati et al., 2016). For oligotrophic lakes, climate warming affects the phytoplankton structure and dynamics largely through its effects on nutrient availability in shallow Lake Tahoe (Winder and Hunter, 2008), whereas stratification is the driver underlying phytoplankton succession in deep Lake Erken (Yang et al., 2016a). In general, long-term phytoplankton community changes are caused by interactive or sequential effects of nutrient and climatic factors (Salmaso, 2010b; Thackeray et al., 2008; Kelly et al., 2017; Srifa et al., 2016b).

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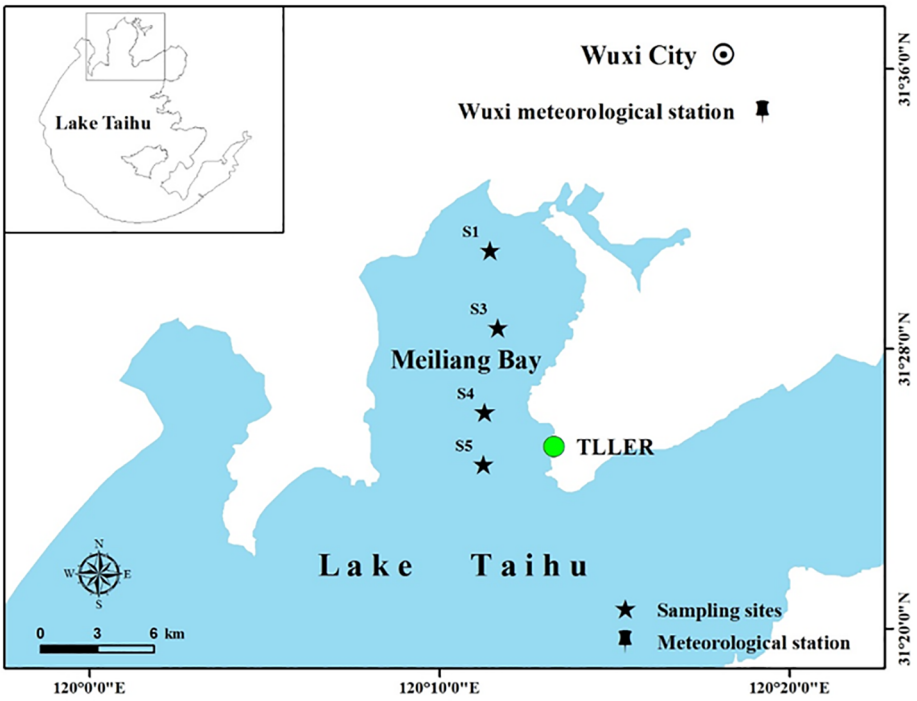

Fig. 1. Locations of sampling stations in Meiliang Bay, Lake Taihu, China.

Nevertheless, for eutrophic or hypertrophic shallow lakes that experience algal blooms, the drivers underlying phytoplankton community succession are often poorly documented or understood (Chen et al., 2003; Scheffer and van Nes, 2007; Whitmore et al., 2018). Although global warming and oligotrophication in European freshwater bodies have gained attention recently (Abonyi et al., 2018; Verbeek et al., 2018), eutrophication and blooms remain major and growing environmental concerns for lakes in developing countries (Jeppesen et al., 2007b; Qin, 2008). Lake recovery from blooms is a major challenge for environmental managers, and the long-term monitoring of phytoplankton communities may reveal lake ecosystem responses to global changes and the effects of catchment nutrient reductions and ecological restoration measures (Hanson et al., 2016; Jeppesen et al., 2007b).

Shallow freshwater lakes tend to be located in low-lying fertile regions and to receive higher nutrient loading than deep lake ecosystems (Meerhoff and Jeppesen, 2009). The tropic state is not the only factor determining algal growth in shallow lakes (Dembowska et al., 2018). Lakes Okeechobee (USA) and Taihu (China) show significant relationships between the phytoplankton community structure and nutrients, although these relationships are inconsistent with the expectations (McCarthy et al., 2009). Thus, nutrients alone are not the only modulators of cyanobacterial dominance in large eutrophic shallow lakes. Climate change affects algal growth both directly and indirectly. Climatic modulators, such as higher temperatures and declining wind speeds, may potentially lead to cyanobacterial dominance and bloom outbursts in shallow eutrophic lakes (Deng et al., 2018; Rigosi et al., 2014; Wagner and Adrian, 2009). In temperate shallow Lake Balaton, the phytoplankton responses to nutrients are slight and sometimes counterintuitive, even though they fluctuate with the climate (Padisák and Reynolds, 1998). In subtropical shallow lakes, phytoplankton changes appear to be sensitive to external impacts, such as increased temperatures, water level changes, and nutrient increases (Havens et al., 2016; Jeppesen et al., 2007a; Ozkan et al., 2013; Srifa et al., 2016a). Nutrients and climate often synergistically affect algal growth in these lakes (Kosten et al., 2012; Rigosi et al., 2014). However, the quantified relative effects of climate change-eutrophication interactions on the long-term phytoplankton biomass and community in shallow eutrophic lakes remain uncertain (Carvalho and Kirika, 2003; Dembowska et al., 2018; Jeppesen et al., 2007a). Because the responses to climate change and eutrophication act simultaneously (Scheffer et al., 2001), shallow lake rehabilitation efforts may not succeed. Quantifying the influence of different stressors on phytoplankton can provide a better understanding of the effects of prior nutrient control and allow adjustments to future strategies for more efficient bloom mitigation and ecological restoration (Søndergaard et al., 2010; Jeppesen et al., 2007b; Hanson et al., 2016).

Lake Taihu has been the focus of eutrophication and algal bloom investigations in China. The increased proliferation of cyanobacterial blooms has gained widespread attention since 1997 (Qin et al., 2018; Yang et al., 2008). Strenuous management endeavors in the Lake Taihu basin were implemented during two periods [i.e., 1998 (zero-point action) and 2007 (after the Wuxi crisis)] to substantially reduce the nutrient inputs and improve the ecological conditions (Zhu et al., 2018; Peng et al., 2018; Xu et al., 2015). However, the Taihu Lake rehabilitation efforts might not succeed. Remote sensing analyses have shown an increase in the spatial coverage of bloom areas in Lake Taihu (Duan et al., 2009; Shi et al., 2017). To date, several reports have focused on certain drivers of changes in the total phytoplankton biomass, chlorophyll-a concentration or *Microcystis* blooms over various periods (Liu et al., 2011; Guo et al., 2017; Zhang et al., 2018a); however, few studies have focused on the factors that influenced algal communities at the genus level from 1991 to 1999 (Chen et al., 2003). Long-term changes in phytoplankton biomass and composition may reveal a comprehensive ecosystem response to global change and incessant nutrient reduction practices (Jeppesen et al., 2005). Here, we aimed to 1) examine the variations in the phytoplankton community during 1992–2017 and further group this entire period into various discrete periods based on the community composition, 2) analyze the relative influences of nutrients and climatic factors on variations in the phytoplankton community composition, and 3) discuss the seasonal phytoplankton biomass patterns during the above periods and the modulating roles of nutrients and climate.

2. Materials and methods

2.1. Description of the study area

Lake Taihu (30°56′–31°34′N, 119°54′–120°35′E; Fig. 1) is located in the lower reaches of the Yangtze River, China. This lake, which is the third largest freshwater lake in China, has a surface area of 2338 km^2, a mean depth of 1.95 m and a water residence time of approximately 220–309 days (Qin, 2008; Li et al., 2013). Meiliang Bay is located in northern Lake Taihu near the suburbs of Wuxi City and has an area of 132 km^2. The western parts of the lake basin are hilly, and the eastern parts are lowland plains. The hydrological system of the 36,500-km^2 drainage basin is complex, with interconnected rivers and dotted depression lakes of different sizes. The basin is influenced by the East Asian monsoon and exhibits a typical subtropical climate with four distinct seasons: spring (March–May), summer (June–August), autumn (September–November) and winter (December–February). The annual precipitation varies between 900 and 1900 mm and presents two dominant rainfall periods (April–June and August–September) (Zhang et al., 2018b).

The lake serves as a drinking water supply for more than 30 million people. As one of the most developed regions in China, the high population density, urbanization, and basin-wide economic development of this region pose a vital threat to lake water quality and ecosystem services. The massive nutrient (N and P) loads from the basin combined with hot summers (~28.7 °C in July) have led to accelerated eutrophication. The trophic state of Lake Taihu varies spatially, with hypertrophic conditions in the north, eutrophic conditions in the main area and mesotrophic conditions in the east (Qin, 2008; Zhang et al., 2018b). Algal blooms have occurred more frequently since 2000 and are frequently observed in northern Lake Taihu, particularly in Meiliang Bay (Xu et al., 2010).

2.2. Data collection

The Taihu Laboratory for Lake Ecosystem Research (TLLER) began routine limnological monitoring of Taihu in 1992. Meiliang Bay (Fig. 1) was one of the most heavily polluted and hypertrophic regions of Taihu and was the site at which the earliest bloom was reported, and more frequent bloom outbursts have been observed after this report (Chen et al., 2003; Qin, 2008). Water quality parameters and phytoplankton samples were collected as part of TLLER's long-term Lake Taihu monitoring program (Fig. 1). Sampling was performed monthly from January to December during 1992–2003 and 2005–2017. Four sampling stations covering Meiliang Bay (S1, S3, S4, and S5) were selected.

Depth-integrated samples of water were collected at three depths (surface − 20 cm, middle and bottom + 20 cm) at all stations. The samples were placed in acid-cleaned plastic containers, maintained cool and sheltered, and transported to the laboratory. The levels of total nitrogen (TN), total phosphorus (TP), chemical oxygen demand (COD_{Mn}), ammonium (NH_4-N), nitrate (NO_3-N) and phosphate (PO_4-P) were determined in the laboratory using standard methods for eutrophication surveys (Jin and Tu, 1990). Biological parameters, such as the phytoplankton biomass and species composition, were routinely analyzed. The phytoplankton samples were fixed with Lugol's iodine solution (1%, V/V) and settled in a counting chamber for 48 h (APHA, 1992). The phytoplankton species in the samples were identified according to the methods described by Hu and Wei (2007) and Hu (2011). The cell numbers were counted directly in a 0.1-mL counting chamber using an Olympus BX53 microscope at 400× magnification. The *Microcystis* cell numbers were counted from colonies and single cells. Each taxon was calculated based on the measured morphometric characteristics (diameter, length, and width). The conversion to biomass was performed by assuming that a volume of 1 mm^3 was equivalent to 1 mg of fresh-weight biomass. The phytoplankton were identified at the genus level, and the dominant species were recorded.

The daily average air temperature, wind speed, and rainfall data were collected from 1992 to 2017 at the Wuxi meteorological station (31.58°N, 120.32°E) near Meiliang Bay, Lake Taihu (Fig. 1). All climatic data were downloaded from the China meteorological data sharing service system (http://data.cma.cn/).

2.3. Statistical analysis

The dominant genera were determined using the dominance index (Y_i), which was calculated as $Y_i = (n_i/N) \times f_i$, where n_i is the total biomass of each phytoplankton genus, N is the total phytoplankton biomass, and f_i is the occurrence frequency of each phytoplankton genus (Li et al., 2014). Genera at $Y_i \geq 0.02$ were selected as the dominant genera. The nonmetric multidimensional scaling (NMDS) analysis method was used to analyze the variations in the community composition over the last 25 years. Seasonal biomass data of the dominant genera were used for the NMDS analysis. Based on Bray-Curtis distances, three-dimensional solutions were produced to meet the criterion of a final stress < 0.2 (Clarke, 1993). The phytoplankton community was categorized into discrete groups based on the annual average scores. The NMDS analysis was performed using the function metaMDS in the R package 'vegan' (Oksanen et al., 2017). The Shannon-Weaver diversity index was also applied as a measure of phytoplankton diversity (Danilov and Ekelund, 2000). The differences in the Shannon-Weaver diversity of the discrete phytoplankton groups were compared by ANOVA. Pairwise comparisons were examined using Tukey's honestly significant difference (HSD) test. In all statistical tests, statistical significance was considered at $P < 0.05$. ANOVA was performed using the R statistical package, version 3.1 (R Core Team, 2017).

In the principal component analysis (PCA), the conductivity, turbidity, suspended solids (SS), pH, TN, TP, nitrate, ammonium, TN to TP (mass ratio), COD_{Mn}, wind speed, air temperature, water level, accumulated rainfall, Secchi depth-to-water level ratio, and air temperature-to-wind speed ratio were reduced to the first two principal components (PC1 and PC2) as explanatory variables representing environmental factors. These two extracted components accounted for 50.3% of the total variance. The PCA was conducted using R statistical software (http://www.R-project.org).

The influence of environmental variables on phytoplankton community variation was analyzed through multivariate analyses. Redundant environmental variables with a variance inflation factor (VIF) > 10 were removed before the analysis. A detrended correspondence analysis (DCA) was performed to determine whether linear or unimodal ordination methods should be applied. Prior to the multivariate analysis, the biotic data were subjected to Hellinger transformation for linear ordination methods (Legendre and Gallagher, 2001). The ability of environmental variables to explain the variance in the phytoplankton community was evaluated through redundancy analysis (RDA). Significant explanatory variables ($P < 0.05$) were selected using the conservative forward selection method (Blanchet et al., 2008). Finally, variation portioning analysis (VPA) was performed to further distinguish the relative importance of nutrients and climate for the community compositions (Oksanen et al., 2017). The ordiR2 step function in the R package vegan was employed for these procedures (R Core Team, 2017).

The temporal series of phytoplankton biomass and environmental factors were smoothed through local weighted regression (Salmaso, 2010b). The relationships between the total phytoplankton biomass and environmental factors were analyzed by multiple ordinary least squares (OLS) regression (Wang et al., 2011). Redundant environmental variables with a VIF > 10 were removed before the analysis. The best models were identified using the Akaike information criteria (Kosten et al., 2012). The procedure was performed using a step function in R 3.4.3 (R Core Team, 2017).

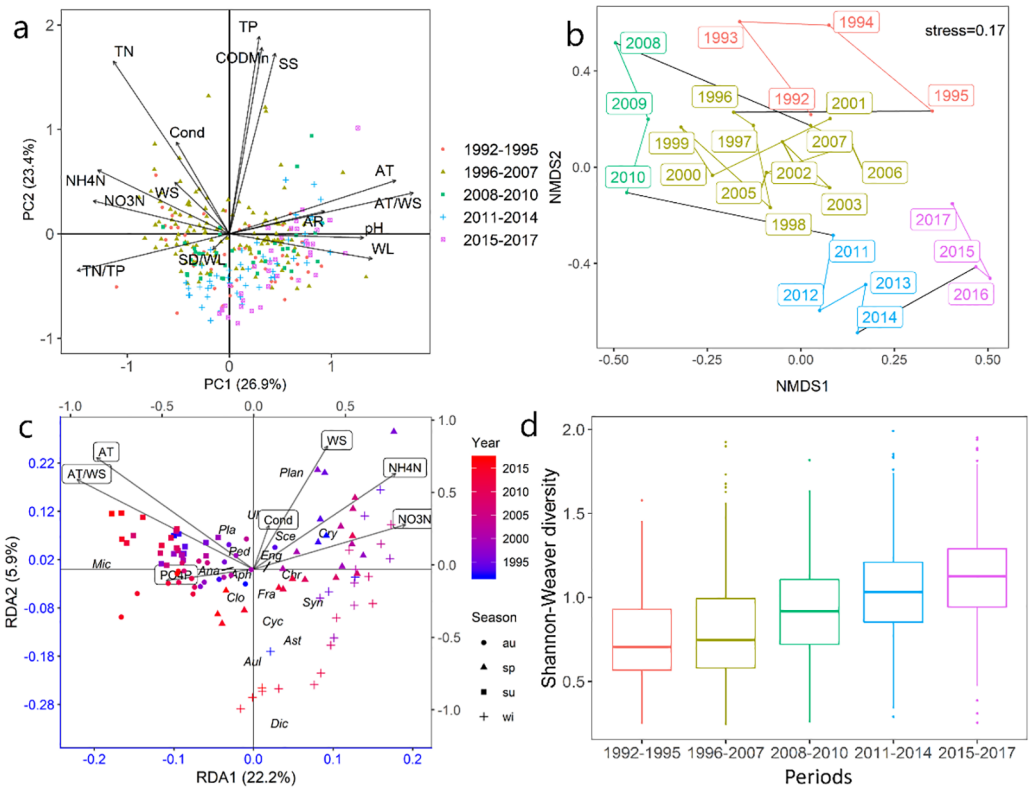

Fig. 2. (a) Principal component analysis (PCA) of nutrients and climatic variables. (b) Nonmetric multidimensional scaling (NMDS) analysis of the annual phytoplankton community composition over 25 years. The dark line indicates the route of succession with the year. Five periods were identified: 1992–1995, 1996–2007, 2008–2010, 2011–2014, and 2015–2017. (c) Redundancy analysis (RDA) ordination of dominant algae and environmental variables from 1992 to 2017 in Meiliang Bay, Lake Taihu. The dark line represents environmental variables, the circles represent autumn, the triangles represent spring, the squares represent summer, and the crosses represent winter. The species variables are shown with the first three letters of the Latin name of each genus. (d) Shannon-Weaver diversity index of the phytoplankton community during the five periods. Analysis of variance (ANOVA) showed significant differences among the five periods ($P < 0.05$), and pairwise comparisons showed that only the 1992–1995 and 1996–2007 periods were nonsignificant. Nutrient variables: Cond (conductivity); pH; SS (suspended solids); TN (total nitrogen); NH_4-N (ammonium); NO_3-N (nitrate); TP (total phosphorus); PO_4-P (phosphate); COD_{Mn} (chemical oxygen demand); and TN/TP (ratio of total nitrogen to total phosphorus). Climatic variables: AT (air temperature); WS (wind speed); AT/WS (ratio of air temperature to wind speed); AR (accumulated rainfall); and WL (water level). Abbreviations of phytoplankton genera: *Microcystis* (Mic); *Anabaena* (Ana); *Planktothrix* (Pla); *Aphanizomenon* (Aph); *Fragilaria* (Fra); *Cyclotella* (Cyc); *Asterionella* (Ast); *Synedra* (Syn); *Aulacoseira* (Aul); *Euglena* (Eng); *Pediastrum* (Ped); *Planctonema* (Plan); *Scenedesmus* (Sce); *Chroomonas* (Chr); *Cryptomonas* (Cry); *Dictyosphaerium* (Dic); *Closterium* (Clo); and *Ulothrix* (Ulo).

3. Results

3.1. Environmental variables influencing phytoplankton

The highest seasonal variance in physicochemical variables was observed in the early periods (1992–1995 and 1996–2007; Fig. 2a). The nitrogen concentrations, including nitrite, ammonium and TN, showed decreasing trends toward the recent periods, such as 2015–2017 (Fig. 2a), whereas TP remained high (> 0.1 mg/L) throughout the entire period with few variations (Figs. 2a and 3). The TN:TP ratios were higher (20–35) before 2007 but declined to less than 20 after 2015 (Fig. 3). The air temperature increased continuously from 1992 to 2007 (+1.8 °C) and has remained at a high level since 2007. The water level and TN were positively correlated before 2007 and negatively correlated after 2007. The wind speed declined continuously after 2000 (−0.9 m/s), and the correlation between wind speed and TN showed an opposite pattern, with a negative trend before 2007 and a positive trend afterwards (Fig. 3).

These nutrient and climate changes are consistent with the phytoplankton community variations (Fig. 2b). The NMDS revealed five

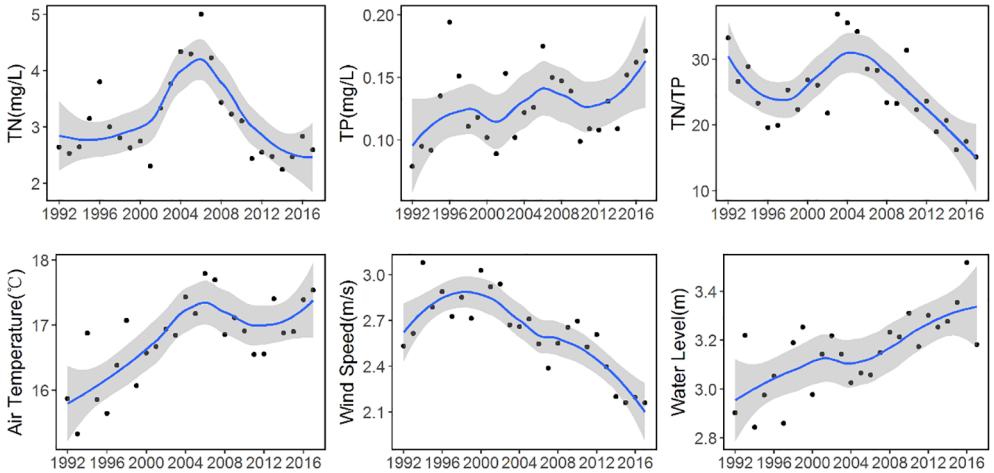

Fig. 3. Long-term nutrient and climate variable trends in Meiliang Bay, Lake Taihu, from 1992 to 2017. Data are smoothed using the local weighted regression (LOWESS) procedure.

clustering groups for the community composition: 1992–1995, 1996–2007, 2008–2010, 2011–2014 and 2015–2017. The compositions of these groups clearly shifted from 2008–2010 to 2015–2017 (Fig. 2b). The Shannon-Weaver diversity index was low during the first two periods ($P > 0.05$) but continually increased after 2007 ($P < 0.05$) (Fig. 2d). The RDA showed that the main environmental variables underlying community succession included both nutrient and climatic factors, such as ammonium, nitrate, phosphate, air temperature, wind speed and the air temperature-to-wind speed ratio ($P < 0.05$) (Fig. 2c), which explained 28.1% of the total variance in the phytoplankton community composition. Interestingly, in contrast to the other environmental variables, phosphate was poorly correlated with the phytoplankton community during the long monitoring period (1992–2017) (Fig. 2c) and only explained 1% of the variance independently ($P < 0.05$).

3.2. Phytoplankton community variation during the five periods

The communities exhibited relatively high similarities during the first two periods (1992–1995 and 1996–2007) (Fig. 2b), and during these time periods, cyanobacteria contributed most of the total biomass. Diatoms and cryptophytes were also abundant during 1992–1995, whereas filamentous chlorophytes (*Planctonema* sp. and *Ulothrix* sp.) were codominant with the diatoms and cryptophytes from 1996 to 2007 (Fig. 4). In contrast to the abundance of cyanobacteria during these two periods, they were less abundant during 2008–2010. The abundance of large diatoms (e.g., *Aulacoseira, Synedra* and *Asterionella*) and small, fast-growing cryptophytes increased, and the total diatom and cryptophyte biomass was higher than that of the cyanobacteria (Fig. 5). During 2011–2014, cyanobacteria became dominant again, and their biomass nearly doubled compared with those at the previous three periods (Fig. 5). The eukaryotic algae exhibited further increases in large diatoms (*Aulacoseira* spp. and *Asterionella* sp.) and small-colonial green algae (*Dictyosphaerium* sp.) and decreases in cryptophytes (*Cryptomonas* spp. and *Chroomonas* spp.). During the late period (2015–2017), the total biomass increased drastically, with cyanobacteria (mainly *Microcystis* spp.) and diatoms (mainly *Aulacoseira* spp.) dominating. The remaining algal groups became less important due to an obvious increase in the cyanobacterial biomass throughout the four seasons and larger diatoms in winter and spring (Figs. 4 and 5).

VPA was performed to further distinguish the relative contributions of nutrients and climate to the community composition (Fig. 6). Throughout the 25-year period, the trends in climatic variables and nutrient contributions were similar to those of the phytoplankton community composition of Lake Taihu. However, substantial changes were observed in the relative roles played by nutrient and climatic variables in influencing phytoplankton community succession across the five periods. For example, during 1992–1995 and 1996–2007, the contribution of nutrients was greater than that of climate. However, climatic factors better explained the variation in the community composition than nutrients during the three periods after 2007 (Fig. 6).

3.3. Seasonal patterns of the phytoplankton biomass

The analysis of the seasonal patterns of the total phytoplankton biomass revealed unimodal patterns during 1992–1995, 1996–2007 and 2015–2017, with peaks in the summer. However, other patterns, such as winter peaks in 2008–2010 and autumn peaks in 2011–2014, were also observed. During the last period (2015–2017), the seasonal biomass peak returned to a unimodal pattern similar to that found in the first two periods and was three-fold higher than that during 1992–2007. However, during 2008–2010, the peak shifted to winter

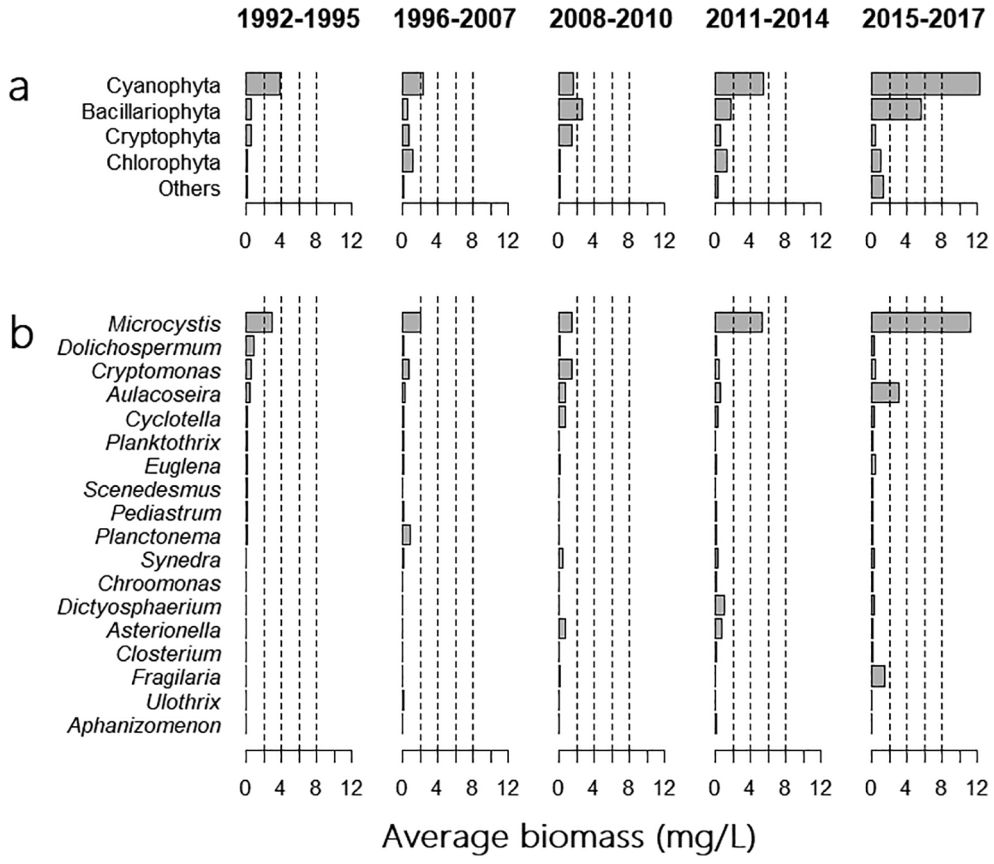

Fig. 4. Averaged biomasses of the different phytoplankton classes and dominant genera during the five periods identified by the NMDS analysis. a: class level and b: genus level.

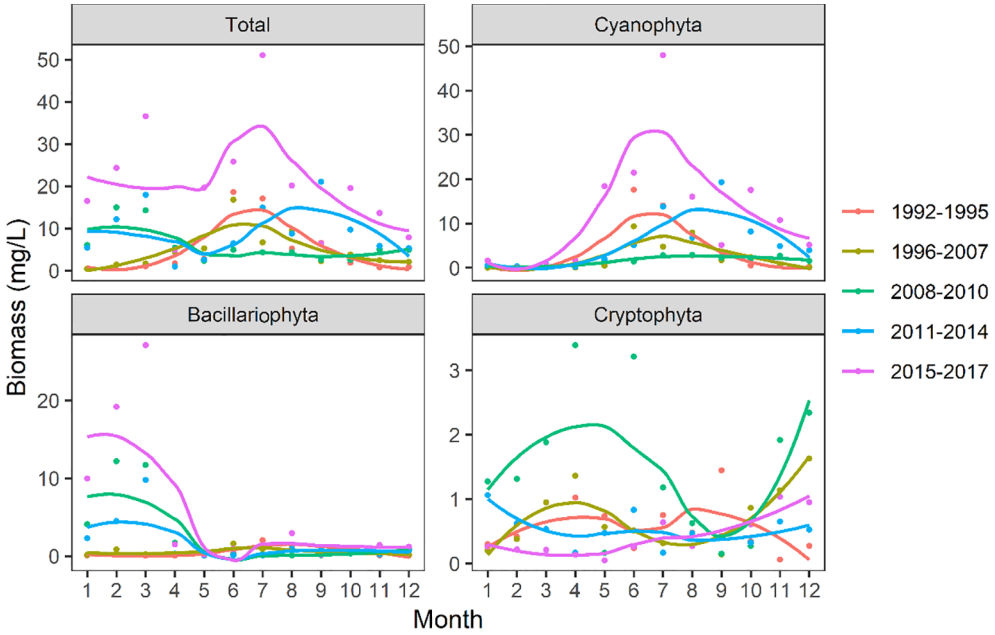

Fig. 5. Seasonal patterns of the phytoplankton, Cyanophyta, Bacillariophyta, and Cryptophyta biomasses during the five periods (1992–1995, 1996–2007, 2008–2010, 2011–2014, and 2015–2017). The data were smoothed using the local weighted regression (LOWESS) procedure.

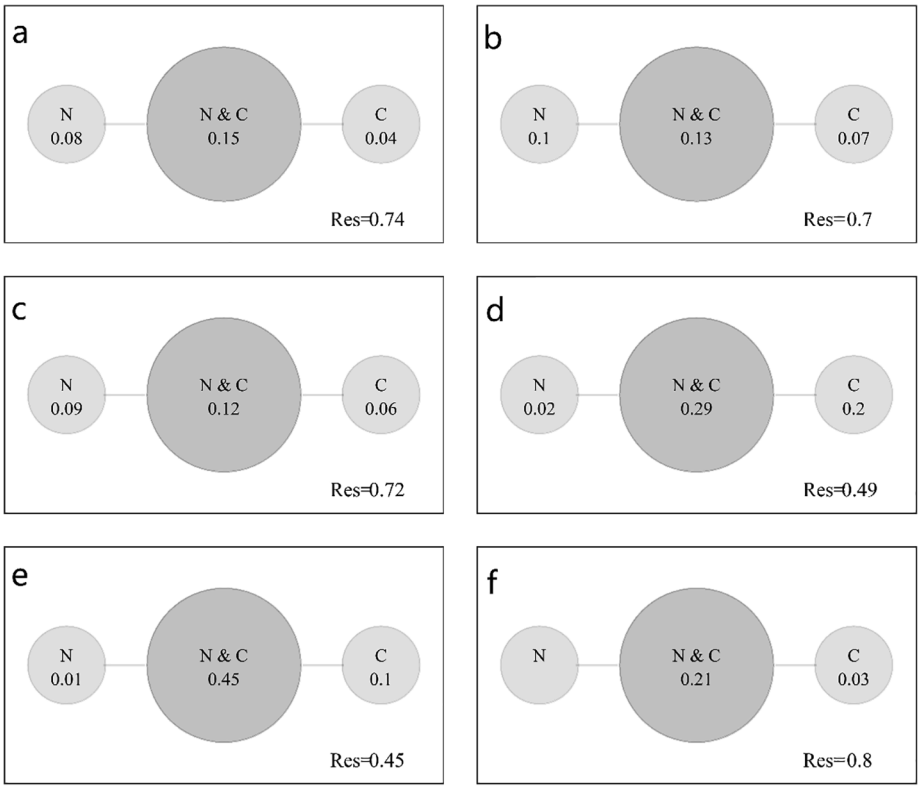

Fig. 6. Variation portioning analysis (VPA) of the effects of the significant nutrient (N) and climatic (C) variables on the variance in the phytoplankton community during the different periods. a: 1992–2017, b: 1992–1995, c: 1996–2007, d: 2008–2010, e: 2011–2014, and f: 2015–2017.

due to the relatively high biomasses of both bacillariophytes and cryptophytes. Furthermore, the total biomass peak shifted to autumn during 2011–2014, which indicated that the cyanobacterial biomass was higher in autumn than in summer.

The relationships between the total biomass and the explanatory variables were examined by multiple OLS after selecting the best model (Table 1). The seasonal biomass variation during 1992–1995 was best explained by air temperature ($r^2 = 0.324$, $P < 0.05$). During 1996–2007, the rainfall, water level and air temperature jointly affected the seasonal biomass variation ($r^2 = 0.242$, $P < 0.001$). During 2008–2010, the air temperature and conductivity were the strongest factors associated with seasonal biomass variation ($r^2 = 0.180$, $P < 0.001$). However, the seasonal biomass variation during 2011–2014 was better explained by the TP and air temperature ($r^2 = 0.250$, $P < 0.001$), whereas the seasonal biomass variations during 2015–2017 were associated with the TN, air temperature and

Table 1
Relationships between the seasonal phytoplankton biomass in different periods and potential explanatory variables modelled using multiple ordinary least squares (OLS) regression. All of the variables were standardized (mean = 0; SD = 1) and are displayed with increasing *P*-values.

	Adjusted r^2	Explanatory variables and β-weights				
1992–1995	0.324***	AT***				
		0.325				
1996–2007	0.242***	AR***	WL***	AT**	Cond*	SD*
		0.263	−0.265	0.198	−0.120	0.08
2008–2010	0.180**	AT**	Cond*			
		−0.21	0.22			
2011–2014	0.250**	TP**	AT*	WL*		
		0.59	−0.40	0.308		
2015–2017	0.637***	TN**	SD**	WL**	Cond*	AT*
		4.232	3.29	−0.764	−1.04	0.848

TN (total nitrogen); TP (total phosphorus); Cond (conductivity); SD (Secchi depth); AT (air temperature); WS (wind speed); and WL (water level).
*Standardized partial regression coefficients, ***$P < 0.001$; **$P < 0.01$; and *$P < 0.05$.

light availability ($r^2 = 0.637$, $P < 0.001$).

4. Discussion

Our results identified five periods of discrete phytoplankton communities according to their interannual features. These periods were mainly classified by variations in the phytoplankton community composition but were well supported by the nutrient, climate, phytoplankton diversity and biomass values. For example, the nutrient enrichment of TN intensified before 2007 and declined continuously afterwards, and thus, TN exhibited a hump-shaped pattern during the study period. Furthermore, the TN:TP ratio also decreased after 2007, mainly due to measures taken to reduce external nutrient loading and mitigation steps taken after the 2007 Wuxi crisis, such as catchment nutrient pollution control, mechanical bloom collection, water diversion from the Yangtze River, dredging and ecological restoration (Peng et al., 2018; Xu et al., 2015). The analysis of climatic variables in the Lake Taihu region revealed the occurrence of continuous warming, with an average annual temperature increase from 15.3 °C at 1992 to 17.5 °C at 2007, although the rate of increase slowed after 2007. The annual wind speed peaked in approximately 1996 but decreased thereafter, reaching the lowest values in 2015–2017 (Deng et al., 2018). The seasonal biomass patterns also contrasted during these periods. We found the occurrence of other patterns aside from the unimodal patterns with summer peaks in 1992–1995, 1996–2007 and 2015–2017, such as winter peaks in 2008–2010 and autumn peaks in 2011–2014.

In addition to the unprecedented long-term datasets for Lake Taihu, the five periods revealed here were also partly supported by previous reports of changes in the phytoplankton community composition and biomass. For example, the phytoplankton community in Lake Taihu changed to a predominantly cyanobacterial community from 1988 to 1995 (Chen et al., 2003), and the total biomass in autumn/winter was significantly higher in 2007–2015 than in 1993–2006 (Zhang et al., 2018a). Compared with those of previous studies, we noted longer terms of phytoplankton community variations and further extended our observations to the recent period of 2015–2017. During this period, the total biomass increased drastically and reached the highest level on record, which was largely due to the dominance of cyanobacteria in summer/autumn and diatoms in winter/spring.

During the entire 25-year period, the climatic factors and nutrient contributions were similar to the phytoplankton community composition variations in Lake Taihu. The importance of climatic variables and nutrients has also been reported in previous studies but has varied based on the trophic states of the studied lakes (Kosten et al., 2012; Rigosi et al., 2014). For example, in oligotrophic waters, such as the shallow lakes Erken and George and deeper Lake Zurich, physical factors rather than nutrients represented the underlying drivers of phytoplankton succession (Yang et al., 2016a). In eutrophic waters, such as deep Lake Garda and shallow Lake Muggelsee, nutrients and climate influenced the phytoplankton composition and biomass (Salmaso, 2010a; Wagner and Adrian, 2009). However, for the hypertrophic shallow Lake Taihu, our RDA model determined that nutrient and climatic factors, including nitrogen, phosphorus, air temperature and wind speed, were the underlying drivers of community variation. Interestingly, in contrast to the other environmental variables, phosphorus was poorly correlated with changes in the community composition and biomass throughout the long monitoring period. The relatively weak relationship might have been due to the high TP level and low magnitude of variation (Phillips et al., 2008). The TP concentration was always greater than 0.1 mg/L and had little variation in Meiliang Bay, even with reduced inputs (Fig. 2). This finding suggested that nitrogen left the lake more quickly (via denitrification) than phosphorus, most likely because phosphorus has no gaseous form to allow its escape (Paerl et al., 2016). As a large shallow lake, Lake Taihu has a large buffering capacity for phosphorus. Shallow lakes in warm regions are more sensitive to internal nutrient cycling, and monitoring of the wind field and resuspension *in situ* have shown that TP in the water column varies significantly with wind-wave disturbances, particularly in summer (Zhu et al., 2005, 2014, 2013). Because the water column has sufficient particulate and dissolved organic phosphorus, phytoplankton can produce sufficient APA enzymes to decompose particulate phosphorus to inorganic phosphorus when phytoplankton growth is needed (Gao et al., 2006). This phenomenon results in a phosphorus-sufficient environment for algal growth in shallow Lake Taihu. Therefore, compared with those of deep lakes, climatic factors and nitrogen availability become more important than phosphorus as controls of phytoplankton growth in shallow lakes (Ko et al., 2017; Salmaso, 2010b).

Across the five identified periods, substantial differences were observed in the relative influence of nutrients and climate on phytoplankton community succession. For example, during 1992–1995 and 1996–2007, nutrients were more important than climatic variables. However, climate explained more variations in the phytoplankton community composition than nutrients during the three periods after 2007. Because profound changes in the physical environment of Lake Taihu occurred over the last 25 years (Deng et al., 2018; Zhang et al., 2018b), the effect of climate change was more obvious for cyanobacterial blooms over the last 10 years (2008–2017). For example, the frequency of heavy algal blooms is positively correlated with extreme weather events in shallow lakes (Yang et al., 2016b). In addition, the chlorophyll-*a* concentration and algal bloom area were significantly negatively correlated with reduced wind speed because reduced wind might enhance water column stability and internal loading (Deng et al., 2018). Overall, cyanobacterial blooms are likely to become prolonged and more intense in eutrophic shallow lakes, in part because of climate change (Huisman et al., 2018; Wagner and Adrian, 2009; Winder and Sommer, 2012). The long-term trend of the nutrient load in Lake Taihu is unclear (Wang et al., 2019; Xu et al., 2015). Nonetheless, efficient

management endeavors by the government that promote changes in the TN and TP concentrations (Fig. 3) might partially explain the switch from nutrient-modulated changes during 1992–2007 to climatic-modulated changes after 2007.

Changes in the importance of climate and nutrients explained the variations in the relative abundances of dominant algal groups and species. Cyanobacteria (mainly *Microcystis*) and large diatoms were the two major dominant groups in Lake Taihu**.** For cyanobacteria, increased nutrients positively affected *Microcystis* growth (Chen et al., 2003; Xu et al., 2010). In subtropical shallow lakes in Florida, cyanobacteria progressively displaced and outcompeted *Aulacoseira* and other eukaryotic planktonic taxa as eutrophication proceeded (Whitmore et al., 2018). Similar to other eutrophic lakes, targeted management strategies were implemented in Lake Taihu to reduce the cyanobacterial bloom risk after the 2007 water crisis (Tsai et al., 2014; Xu et al., 2017). Consequently, the nitrogen concentrations have declined significantly while the phosphorous concentrations have shown little variation. However, *Microcystis* spp. became subsequently less dominant in 2008–2010. Although reduced nitrogen input might not stop the incidence of *Microcystis* blooms, it could decrease the dominance of *Microcystis* in summer and autumn (Brookes and Carey, 2011). However, the less-dominant state of *Microcystis* might not have succeeded because *Microcystis* spp. became predominant again during the two most recent periods (2011–2017). High temperatures and low wind speed enhance both vertical stratification and nutrient availability, thus favoring buoyant *Microcystis* (Deng et al., 2018). Low TN:TP ratios during 2011–2017 also favor cyanobacterial dominance (Aubriot and Bonilla, 2018), and eutrophication and climate influence the diatom composition (Rühland et al., 2015; Winder et al., 2009). The dominance of large diatoms (*Aulacoseira* spp., *Asterionella* spp. and *Fragilaria* spp.) increased significantly after 2007 in Lake Taihu. The gradual increase in the diatom biomass under rising water levels likely indicated better adaptation to a heterogeneous and structured environment and more nutrient inputs due to higher freshwater discharge into the lake (Dai et al., 2018; Whitmore et al., 2018). In winter, a weakened sediment suspension due to decreased wind speed can improve light availability, thereby further favoring diatom growth (Deng et al., 2018).

We also found that changes in the influence of climate and nutrients explained the seasonal phytoplankton biomass pattern. Seasonal biomass cycles are linked to annual fluctuations in nutrients, temperature and light (Anneville et al., 2004; Jiang et al., 2014). The hump-shaped seasonal biomass patterns typically peaked in summer due to higher temperatures during 1992–1995, 1996–2007, and 2015–2017, and these phytoplankton biomass peaks are typical for subtropical eutrophic lakes in summer (Dokulil and Teubner, 2000). However, during 2015–2017, the biomass peak was three-fold higher than that in the first two periods, which might have been driven by nutrient enrichment, higher air temperature and improved light availability throughout the water column. The reduced nitrogen loading after 2007 did not instantly decrease the biomass because climate change enhances the nutrient availability in eutrophic shallow lakes (Jeppesen et al., 2005; Kosten et al., 2012; Verbeek et al., 2018). Increases in air temperature and light availability should lead to higher phytoplankton growth rates and biomass accumulation under conditions with adequate nutrient supplies (Paerl and Paul, 2012; Winder and Cloern, 2010). Furthermore, temperature was negatively correlated with biomass during 2008–2010 and 2011–2014. The biomass peak in winter during 2008–2010 was due to the relatively higher biomasses of both diatoms and cryptophytes compared with that of cyanobacteria. The biomass peak in autumn resulted from cyanobacterial dominance extending from summer to autumn during 2011–2014.

The phytoplankton dynamics over the last 25 years indicate that mitigating blooms in Lake Taihu will be more challenging than previously anticipated. In shallow lakes across the US, Europe, and elsewhere, the resilience of turbid states often limits recovery despite initial improvements, and the lake conditions frequently deteriorate again within 5–10 years (Hanson et al., 2016; Søndergaard et al., 2010). For shallow eutrophic Lake Taihu, reduced external nutrient loading has been insufficient to shift the lake ecosystem from a turbid to a clear-water state. Janssen et al. (2017) suggested that both phosphorus and nitrogen loads needed to be reduced by nearly 90% to prevent phytoplankton blooms throughout Lake Taihu. The 2015–2017 period reflected a resilient turbid state with a higher biomass. Shallow lake rehabilitation efforts might not succeed in the short term, and when improvements occur, management may need to be repeated to maintain favorable ecological conditions (Hanson et al., 2016). Recent studies have suggested that nutrient control might be more important for increasing the resilience of aquatic ecosystems to algal blooms (Brookes and Carey, 2011; Jochimsen et al., 2013). Returning aquatic systems to a low-nutrient state will ultimately make them less vulnerable to the predicted negative impacts of global climate change, particularly increased cyanobacterial blooms (Arnott et al., 2003; Asadian et al., 2018).

5. Conclusions

The phytoplankton community composition and biomass were analyzed in Meiliang Bay, Lake Taihu, during 1992–2017. Five discrete periods were identified with regard to variations in the community composition, and the communities shifted significantly from 2008–2010 to 2015–2017. During 2008–2010, the community shifted from a predominantly cyanobacterial community to diatom-cyanobacterial codominance. However, cyanobacteria became dominant again after 2011. An alternating dominance between cyanobacteria in summer/autumn and diatoms in winter/spring occurred during 2015–2017. The analysis of the seasonal patterns of the total phytoplankton biomass revealed unimodal patterns with summer peaks during 1992–1995, 1996–2007 and 2015–2017; however, other patterns, such as winter peaks in 2008–2010 and autumn peaks in 2011–2014, were observed. During the most recent period (2015–2017), the biomass was three-fold higher than that during the first two periods, which was most likely due to improved light availability and rising air temperatures. The nitrogen supply, air temperature and wind speed drove long-term phytoplankton community variation, whereas phosphorus exerted less control in the RDA. Throughout the entire period, the relative influence of climatic variables on the phytoplankton community composition was similar to the influence of nutrients but shifted before and after 2007. Specifically, nutrients were more important than climatic variables during 1992–2007, but after 2007, climatic variables were able to explain a greater amount of the variance than nutrients. The phytoplankton community variation during 2015–2017 indicated a resilient turbid state with a higher biomass because phosphorus remained high. To mitigate bloom outbursts and better remediate Meiliang Bay, the phosphorus legacy plays a key role, which emphasizes a reduction of external P inputs. Parallel reductions in N inputs will speed up recovery, although longer recovery times might be expected under the current climate change scenarios.

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