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Key Points:

- Winter climate played a vital role for the spring phytoplankton community and biomass in Lake Taihu
- "Climate memory" effects of climate change were observed in subtropical shallow lakes
- Winter ecology should be considered when predicting the effects of climate change on lakes

Supporting Information:

- Supporting Information S1

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Winter Climate Shapes Spring Phytoplankton Development in Non-Ice-Covered Lakes: Subtropical Lake Taihu as an Example

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Abstract Winter warming plays a vital role in spring phytoplankton community succession in temperate lakes due to variation of ice cover duration in winter. How winter conditions affect spring phytoplankton in subtropical lakes without winter ice cover is, however, largely unknown. In this study, covering 26 years, we elucidated the effects of both climate conditions and nutrient levels in winter on the phytoplankton community (expressed as Morpho-Functional Groups) in spring in Lake Taihu, a large shallow subtropical lake in China. During this period, wind speed declined significantly in both winter and spring from 1992 to 2017 and the sunshine hours increased slightly from 2000 to 2017. The biomass of eight dominant phytoplankton groups showed increasing trends from 1992 to 2017, while it declined for one group, which mainly included filamentous green algae such as *Ulothrix* sp. Nonmetric multidimensional scaling (NMDS) results indicated that wind speed and sunshine duration in winter and spring were the most important factors affecting the spring phytoplankton community in Lake Taihu. Also, partial least squares path modeling (PLS-PM) suggested that the spring phytoplankton community was strongly affected by winter conditions. Our study indicated that the "climate memory" effects on phytoplankton, resulting from winter and acting on the following spring, not only occur in north temperate winter ice-covered shallow lakes but also in subtropical lakes without ice-covered in winter.

1. Introduction

Climate warming has been reported globally (IPCC, 2013), and climatic change effects in winter were long believed to be less important than those in the other seasons due to the cease of biological processes (Dokulil & Herzig, 2009). However, an increasing number of studies have confirmed that winter conditions play a vital role in the seasonality of plankton communities in European lakes with variable ice cover (Dokulil & Herzig, 2009; George, 2010). Phytoplankton, which develop in spring, might reach their population maxima earlier after mild winters and obtain a higher maximum biomass (Adrian et al., 1999). Hence, the influence of winter climate change on ecosystem responses to warming may have important implications for our understanding of ecosystem functioning in a changing climate (Hampton et al., 2017; Sanders-DeMott & Templer, 2017).

The main abiotic drivers of biological responses in winter are temperature and the extent and timing of snow/ice cover, which are all affected by the ongoing climate change. In temperate lakes, ice cover is the most important factor in winter (Dokulil et al., 2014). Physiological activities like photosynthesis can still take place under the ice cover, and the biomass of phytoplankton in the water column can sometimes be even higher in winter than in summer (Maeda & Ichimura, 1973). Effects of ice on the physical properties of freshwater lakes include convergence of temperatures toward 4°C in the bottom layer, altered mixing dynamics, loss of gas exchange between water and the atmosphere, and decline in light availability under the surface (Kirillin et al., 2012). A decline in ice duration has occurred during the past century in the

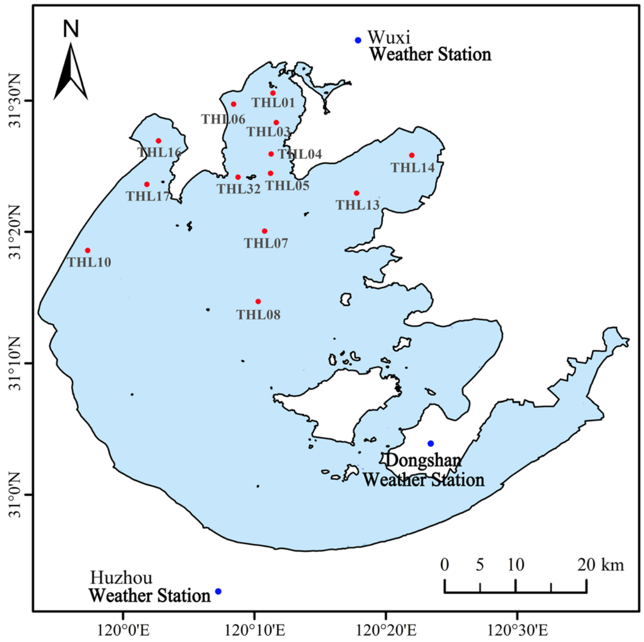

Figure 1. Weather stations (Wuxi, Dongshan, and Huzhou) and in situ sampling sites in our study. Weight factors for the sampling sites were calculated based on the relative polygon size to the total area of Lake Taihu (Deng et al., 2019). Monthly sampling sites indicated by red dots were included in the present study.

northern hemisphere due to global warming (Benson et al., 2012; Magnuson et al., 2000), and it has been found that winters with shorter ice duration may result in reduced total nitrification and lower peak nitrate concentrations in spring (Powers et al., 2017; Weyhenmeyer, 2009). Ice conditions, for instance, duration and thickness, have also been observed to affect the phytoplankton community in the subsequent ice-free seasons (Gerten & Adrian, 2000; Weyhenmeyer et al., 1999). For instance, the composition and biomass of spring phytoplankton in Lake Erken, Sweden, are influenced by overwintering species that are influenced by ice cover (Yang et al., 2016).

Compared with temperate lakes, only limited attention has been paid to winter ecology or winter warming effects on lakes without ice cover, such as lakes located in the subtropics. However, it has been well documented that climate change plays a vital role in phytoplankton community succession in subtropical shallow lakes (Srifa et al., 2016). By way of example, in Lake Taihu, a well-studied large subtropical shallow lake in China (Zhang et al., 2016), an increase in temperature during the past three decades induced by climate warming has extended the dominance of cyanobacteria (Deng et al., 2016). Decreasing wind speed has further intensified the blooms, partly due to vertical stratification of chlorophyll *a* (Chl*a*) at low wind speed (Wu et al., 2015) and partly due to nutrient release from sediments (Deng et al., 2018). However, so far, most studies have focused on the growing seasons, spring or summer. Generally, it is thought that phytoplankton will either sink to the sediment surface (Reynolds, 1973) or survive in winter in the form of specialized resting cells/spores/akinetes (Ellegaard & Ribeiro, 2018; Livingstone & Jaworski, 1980) or exhibit low activity in winter when the temperature is low (Ma et al., 2016). Scarce information is available about the interacting effects of climate change across seasons in subtropical lakes, and this knowledge gap might limit our ability to understand how winter condition variations will affect the ecology and phytoplankton communities in the following seasons in these lakes.

Lake Taihu is an important drinking water source for the Yangtze River Delta urban agglomeration and is the third largest freshwater lake in China. Phytoplankton blooms used to start in summer or late spring, but recently, they usually appear in early spring (Shi et al., 2019). The serious drinking water crisis in 2007 was caused by an early massive bloom event. Our previous study indicated that climate change (e.g., decrease in wind speed and increase in sunshine duration) played a vital role for phytoplankton in this lake in winter and spring (Deng et al., 2019). However, it is largely unknown whether the spring phytoplankton community composition and biomass are affected by winter conditions. In this study, we examined the direct and indirect effects of winter conditions on the succession of spring phytoplankton groups from 1992 to 2017 in Lake Taihu, and our results provide new insight into the relationship between winter conditions and phytoplankton in the following spring in subtropical shallow lakes. In addition, understanding the impact of winter conditions on spring phytoplankton is of great importance for improving ecosystem models predicting changes in phytoplankton blooms by taking into account cross-over seasonal effects, and our research will contribute to prevent water crises caused by massive blooms in eutrophic lakes.

2. Materials and Methods

2.1. Study Site

Lake Taihu is a shallow, eutrophic, subtropical lake in China. The lake has a mean depth of 1.9 m and a maximum depth of 2.6 m, according to an elevation of 3.0 m a.s.l. (Qin, 2008). Since the 1980s, rapid economic development in the Lake Taihu basin has resulted in increasing levels of pollutants that are directly discharged into tributaries and the lake itself. As a result, rapid water quality deterioration, accelerating eutrophication, and nuisance phytoplankton blooms (*Microcystis* spp.) have become regular phenomena in the northern and central part of the lake (Qin et al., 2007), while macrophytes still dominanted in the east (Zhao et al., 2013). Nowadays, Lake Taihu simultaneously has both turbid phytoplankton-dominated and clear macrophyte-dominated regions (Zhang et al., 2018).

Climate variations from 1992 to 2017 around the lake were documented by daily meteorological data from three weather stations (Dongshan, Wuxi, and Huzhou; Figure 1). The meteorological data, including daily records of wind speed (m/s), air temperature (°C), sunshine duration (hours per day), and rainfall (mm per day), were obtained from the China Meteorological Data Sharing Service System (http://data.cma.cn/). Both daily wind speed and air temperature were averaged from four observations (sampled at 02:00, 08:00, 14:00, and 20:00), while daily sunshine duration and rainfall were summed for the whole day. A monthly meteorological data set was calculated based on the daily records. Monthly wind speed and air temperature were calculated as mean values of daily values, and monthly sunshine duration and rainfall were calculated as sum of daily values.

Monthly monitoring of the northern part of Lake Taihu has generally been conducted in the middle of each month since 1992. Details about Secchi depth (SD), nutrient concentrations (total nitrogen (TN), ammonia (NH_4^+-N), total phosphorus (TP), and orthophosphate (PO_4^{3-}-P)) as well as Chl*a* measurements can be found in our previous studies (Deng et al., 2018, 2019).

Morpho-Functional Groups (MFGs) (Salmaso et al., 2015; Salmaso & Padisák, 2007) were used to classify phytoplankton taxa. Phytoplankton biomass were calculated from biovolumes, assuming that 1 mm^3 of volume is equivalent to 1 mg of fresh mass. The detailed methods and procedures for phytoplankton sampling and biovolume calculation can be found in Deng et al. (2019).

Weighted values of both nutrient concentrations and the phytoplankton biomass were used to address spatial heterogeneity in Lake Taihu according to Zhu et al. (2014). The detailed weights for each sampling site can be found in Deng et al. (2019). Continuous data since 1992 were available for the sampling sites indicated by red dots in Figure 1. Accordingly, 13 sampling sites with consistent monthly data located in the northern part of the lake were included in our study.

2.2. Data Analysis

Long-term trends of meteorological factors and nutrient concentrations were synergistically analyzed by the nonparametric Mann-Kendall trend test (MK) from package *Kendall* (Helsel & Hirsch, 1992) and additive models (AMs) from package *mgcv* (Harding et al., 2016) in R (R Core Team, 2018). Correlations between winter and spring conditions were evaluated by Spearman correlation (ρ); the significant levels were adjusted by Benjamini and Hochberg correction, which was carried out using package *ltm* (Dimitris, 2006). Dominant groups were determined by a dominance index (Y_i), and $Y_i \geq 0.02$ were selected as dominant groups (Deng et al., 2019; Li et al., 2014).

Relationships between MFGs and the environmental factors were analyzed by nonmetric multidimensional scaling (NMDS) based on Bray and Curtis' dissimilarity matrices (Legendre & Legendre, 1998). We used the *metaMDS* procedure in R package *vegan*, and environmental factors were fitted to the configuration by vector fitting (*envfit*) with 1,000 permutations (Oksanen et al., 2017). All the environmental variables were included in the analysis, and those found to be statistically significant ($p < 0.05$) are presented. More details about NMDS are available from our previous study (Deng et al., 2019).

Partial least squares path modeling (PLS-PM) was used to evaluate the relationships between both winter and spring meteorological factors, nutrient levels and the spring phytoplankton biomass and community, using Chl*a* and NMDS axis 1 as proxies, respectively (Sanchez, 2013), since the first axis was identified as explaining the most significant proportions of the variance in the species data. All the environmental factors were assigned to four latent variables: climatic variables in both winter and spring (e.g., wind speed, air temperature, sunshine hours, and rainfall), nutrient concentrations in both spring and winter (e.g., TN, TP, NH_4^+-N, and PO_4^{3-}-P). PLS-PM were run in the R package *plspm* (V0.4.7) following the procedure described by Deng et al. (2018) and Wang et al. (2016). In our study, winter was defined as the period from December to February and spring from March to May.

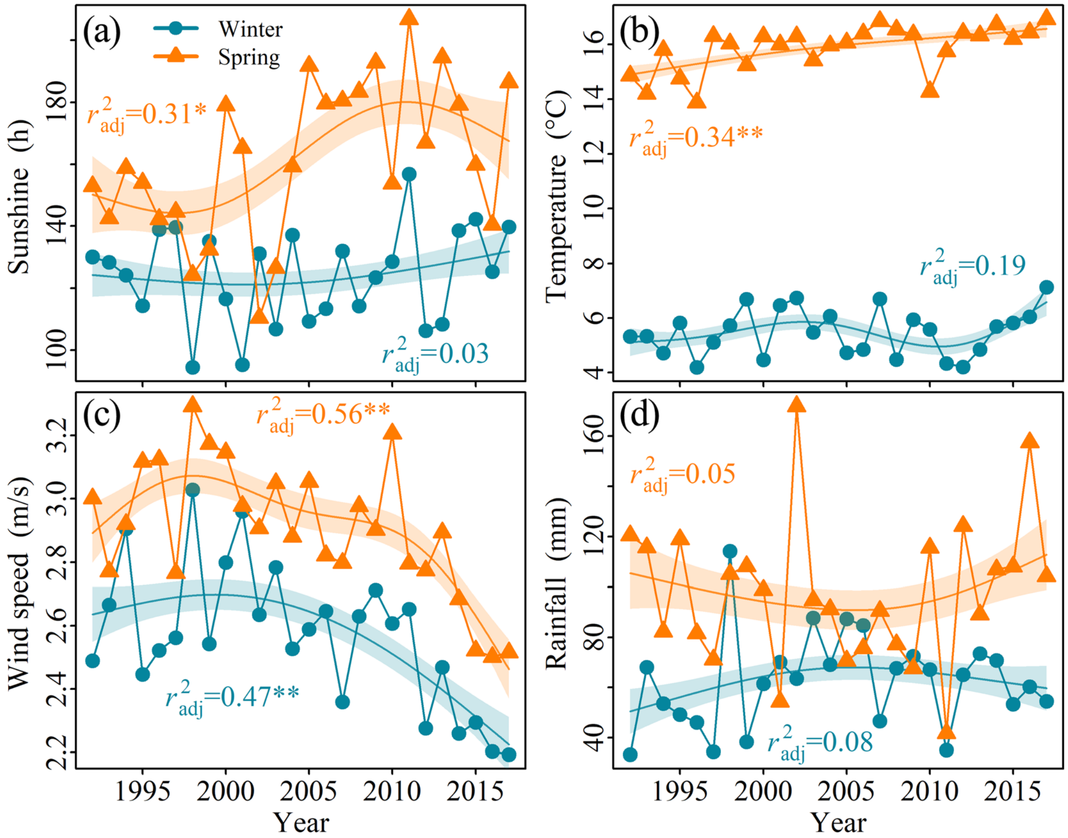

Figure 2. Long-term trends of meteorological factors (sunshine duration, air temperature, wind speed and rainfall) in both winter (blue circles) and spring (yellow triangles) in Lake Taihu. The solid lines represent the long-term trends estimated by additive models (AMs), and the shaded area is the standard error of the estimate. r^2_{adj}: Adjusted R square of AMs; $^{**}p < 0.01$; $^{*}p < 0.05$.

3. Results

3.1. Winter/Spring Meteorological Variables

Climatic conditions in winter differ fundamentally from those in spring. Mean sunshine duration in winter (December, January, February) was 124.3 ± 15.4 hr and showed an unchanged pattern from 1992 to 2017 (Figure 2a; MK = 0.10, $p > 0.05$), with a slight increase from 2000 to 2017, though. Sunshine duration in spring (from March to May) increased from approximately 160 hr before 1995 to about 180 hr after 2005 (Figure 2a; MK = 0.35, $p < 0.05$).

Mean winter temperature was 5.48 ± 0.85°C; no marked tendency emerged for winter temperatures from 1992 to 2017 (Figure 2b; MK = 0.12, $p > 0.05$). The highest temperature in winter occurred in 2017. Mean spring temperature was 15.9 ± 0.84°C during 1992–2017, exhibiting a significant increase (MK = 0.49, $p < 0.001$).

Wind speeds in both winter and spring around Lake Taihu increased slightly from 1992 to 1997, followed by a significant decrease from 1997 to 2017 (Figure 2c; MK > 0.5, $p < 0.01$). Wind speed was higher in spring than in winter.

The rainfall in winter was low from 1992 to 1997 (47.5 ± 12.9 mm) and then decreased significantly from 1998 to 2017, especially from 2003 to 2017 (Figure 2d; MK = −0.43, $p < 0.05$). The spring rainfall decreased from 120 to approximately 70 mm from 1992 to 2009, followed by a slight increase until 2017.

3.2. Winter/Spring Nutrient Levels

Both winter and spring TN concentrations increased rapidly from 1999 to 2007 ($p < 0.01$) and subsequently decreased significantly until 2017 ($p < 0.01$) (Figure 3a). Spring TN concentrations were higher than in

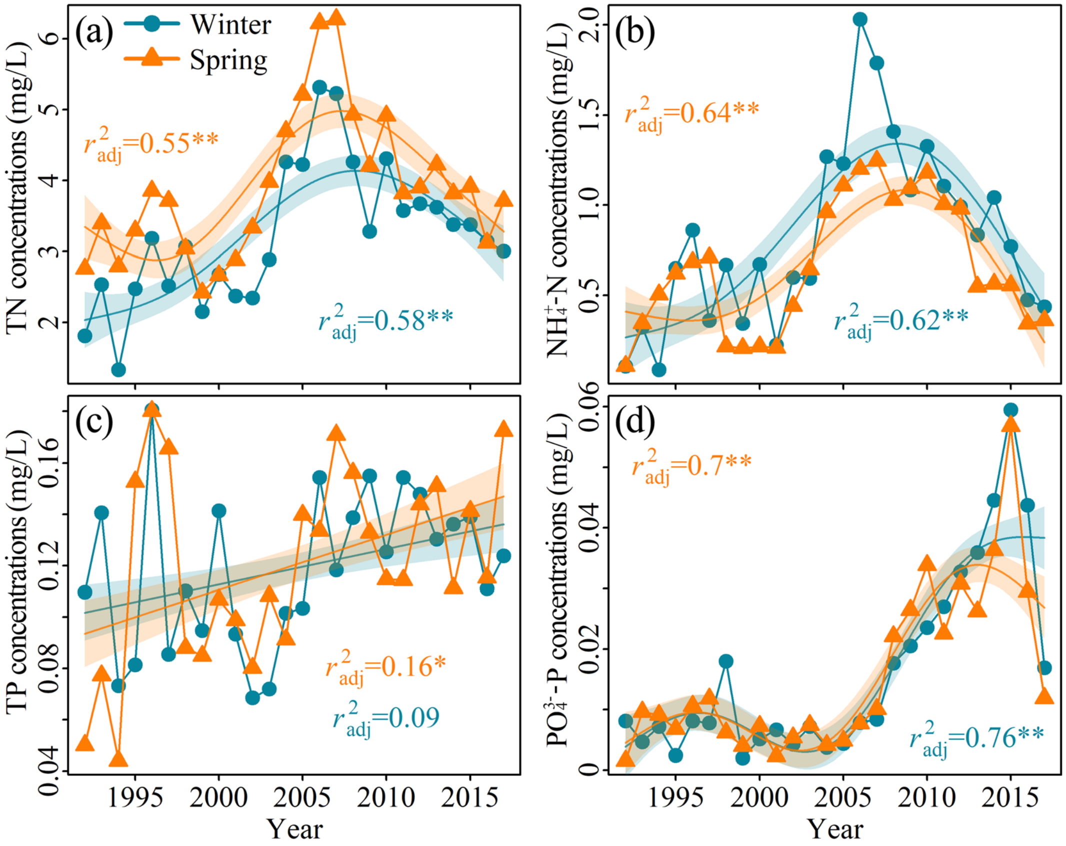

Figure 3. Long-term trends of nutrient (total nitrogen, ammonia nitrogen, total phosphorus, and orthophosphate) in winter (blue circles) and spring (yellow triangles) in Lake Taihu. The solid lines represent the long-term trends estimated by additive models (AMs), and the shaded area is the standard error of the estimate. r^2_{adj}: adjusted *R* squared of AMs; $^{**}p < 0.01$; $^{*}p < 0.05$.

winter (*t* test, $p < 0.01$). Winter and spring NH_4^+-N concentrations showed a pattern similar to that of TN concentrations from 1992 to 2017 (Figure 3b). There was no significant difference between spring and winter NH_4^+-N concentrations.

The mean winter TP concentrations was 0.12 mg/L, and TP was higher from 2005 to 2017 than from 1992 to 2004, the concentrations being 0.10 and 0.13 mg/L, respectively (Figure 3c; *t* test, $p < 0.01$). The mean spring TP concentrations was 0.12 mg/L. There were no marked trends in long-term TP, which was higher from 2005 to 2017 than from 1992 to 2004 (*t* test, $p < 0.05$). Both winter and spring PO_4^{3-}-P concentrations were low and stable from 1992 to 2004 and then increased significantly from 2005 to 2015 (Figure 3d; MK > 0.5, $p < 0.01$).

During the last two decades, nutrient availability in spring in Lake Taihu related positively to winter nutrient levels as indicated in Table 1. For instance, PO_4^{3-}-P concentrations in spring were highly related to TP and PO_4^{3-}-P concentrations in winter ($\rho = 0.55$ and 0.84, respectively, $p < 0.05$), and also NH_4^+-N concentrations in spring were highly related to TN and NH_4^+-N concentrations in winter ($\rho = 0.79$ and 0.83, respectively, $p < 0.01$).

3.3. Spring Phytoplankton

The mean winter Chl*a* concentration was 10.5 μg/L and increased significantly from 1992 to 2017 (MK =0.35, $p < 0.05$) (Figure 4). The mean Chl*a* concentration in spring was 16.8 μg/L. Spring Chl*a* concentrations were low before 1995 (mean value = 6.6 μg/L) and increased significantly from 1998 to 2017 (MK = 0.48, $p < 0.01$). Due to heavy blooms in May, the spring Chl*a* concentration in 2017

Table 1

Correlations Between Spring and Winter Conditions as Indicated by Spearman Correlation Coefficients (ρ)

	SpMeanT	SpWind	SpRain	SpSun	SpTP	SpTN	SpPO4	SpNH4	SpSD	WiMeanT	WiWind	WiRain	WiSun	WiTP	WiTN	WiPO4	WiNH4	WiSD	WiChla
SpWind	−0.58*																		
SpRain	−0.09	−0.05																	
SpSun	0.48	−0.3	−0.57*																
SpTP	0.42	−0.26	−0.27	0.43															
SpTN	0.3	−0.19	−0.37	0.49	0.55*														
SpPO4	0.4	−0.54*	0.04	0.34	0.48	0.38													
SpNH4	0.22	−0.11	−0.42	0.47	0.54*	0.89***	0.39												
SpSD	−0.03	−0.06	0.22	−0.14	−0.51	−0.19	0.11	−0.1											
WiMeanT	0.2	−0.17	0.3	−0.23	−0.13	−0.13	−0.19	−0.26	−0.11										
WiWind	−0.37	0.52	−0.42	−0.14	−0.53	−0.18	−0.42	−0.08	0.22	−0.21									
WiRain	0.19	0.14	−0.17	0.14	−0.14	0.37	−0.01	0.17	0.2	0.01	0.36								
WiSun	−0.03	−0.42	0.05	0.01	0.14	−0.03	0.26	0.04	−0.13	0.19	−0.43	−0.68**							
WiTP	0.18	−0.21	−0.21	0.49	0.35	0.34	0.55*	0.32	0.1	−0.45	−0.11	0.05	0.12						
WiTN	0.39	−0.19	−0.27	0.55*	0.51	0.88***	0.47	0.79***	−0.08	−0.2	−0.24	0.36	−0.04	0.54*					
WiPO4	0.45	−0.45	0.01	0.34	0.35	0.28	0.84***	0.2	0.28	−0.16	−0.37	0.05	0.11	0.54*	0.45				
WiNH4	0.32	−0.01	−0.3	0.52	0.46	0.84***	0.35	0.83***	−0.07	−0.2	−0.13	0.3	−0.01	0.51	0.93***	0.3			
WiSD	0.51	−0.06	0.44	−0.05	−0.01	−0.09	0	−0.28	−0.17	0.34	−0.32	0.13	−0.19	−0.21	0.02	0.09	0.01		
WiChla	0.32	−0.39	−0.18	0.27	0.45	0.29	0.53*	0.25	0.01	−0.13	−0.42	−0.07	0.42	0.4	0.31	0.58*	0.24	−0.18	
SpChla	0.56*	−0.48	−0.24	0.3	0.68**	0.32	0.39	0.22	−0.37	0.05	−0.57*	−0.18	0.39	0.3	0.34	0.38	0.24	0.1	0.63*

Note: The first two letters indicate the season, Sp = spring, Wi = Winter.
*$p < 0.05$.
**$p < 0.01$.
***$p < 0.001$.

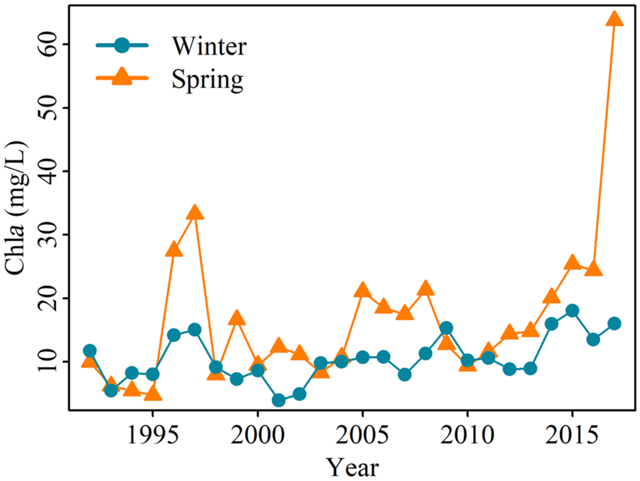

Figure 4. Long-term trends of Chl*a* in winter (blue circles) and spring (yellow triangles) in Lake Taihu.

was the highest recorded in our study. According to Spearman correlation, Chl*a* concentrations in spring were highly related to winter Chl*a* concentrations (Table 1; $\rho = 0.63$, $p < 0.05$).

Nine dominant phytoplankton groups were identified from 1992 to 2017 in Lake Taihu ($Y_i \geq 0.02$; Figure 5). Of these nine groups, two were cyanobacteria (5b, 5e), mainly including *Microcystis* spp. and Nostocales; four were diatoms (6a1, 6b1, 6b2, 7a), mainly including large colonial centrices, large colonial/unicellular pennates, and small centrics; two were green algae (10a and 11a), mainly including *Ulothrix* spp. and naked colonies of Chlorococcales; and, finally, there was one group of cryptophytes (2d). The biomass of eight groups showed increasing trends (Figure 5), and the biomass of group 10a was high before 2010.

3.4. Effects of Environmental Factors on Spring Phytoplankton

Spring Chl*a* concentrations were highly related to spring TP concentrations, followed by winter Chl*a* concentrations, spring mean temperature, winter wind speed, and phytoplankton community composition (as indicated by the NMDS axis 1) (Table 1; $\rho > 0.5$, $p < 0.05$). According to Spearman correlation, the biomasses of the dominant groups in spring were also highly related to their biomasses in winter (Table 2). The spring phytoplankton community was highly related to the winter phytoplankton community ($\rho = -0.80$, $p < 0.001$), followed by spring and winter PO_4^{3-}-P concentrations, winter wind speed, spring sunshine duration, spring Chl*a* concentrations, and spring wind speed ($\rho > 0.5$, $p < 0.05$).

The ordination analysis revealed that the spring phytoplankton community was highly related to the phytoplankton community in winter, winter wind speed, and spring TP, followed by winter PO_4^{3-}-P, spring wind speed and spring sunshine duration, the last significant variable being spring mean temperature (Figure 6).

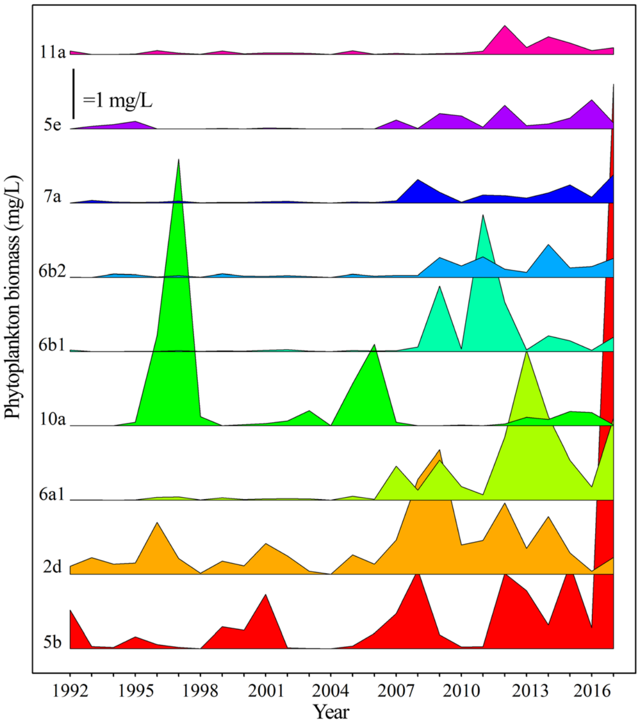

Figure 5. Long-term trends of dominant phytoplankton groups in spring in Lake Taihu.

The dominant phytoplankton groups were generally related negatively to both winter and spring wind speed and positively to spring sunshine duration.

According to PLS-PM (Figure 7), the spring phytoplankton community was mainly mediated by the winter phytoplankton community, which was affected by both the winter climate (wind speed and sunshine duration) and winter nutrients (PO_4^{3-}-P, TP, and TN). Spring Chl*a* was mainly determined by winter Chl*a*, which was affected by the winter climate (e.g., wind speed and sunshine duration; Figure S1) and further determined by the spring climate (wind speed, sunshine duration, and mean temperature; Figure S1).

4. Discussion

Our study indicated that the composition and biomass of spring phytoplankton were significantly affected by winter conditions in Lake Taihu. Although these results are, to some extent, similar to those observed in many temperate lakes (Gerten & Adrian, 2000; Özkundakci et al., 2016; Straile et al., 2010), the key driving factors are different. In the former studies mentioned, phytoplankton growth in spring in temperate lakes was initiated by elimination of the light limitation associated with lake ice and/or snow cover in winter and was then driven by the increased stability of the water column. Both factors led to phytoplankton growth, which ultimately influenced the spring bloom in temperate lakes (Alvarez et al., 2009). In addition to ice cover and thermal stratification, the study in Long

Table 2
Biomass of the Nine Dominant Phytoplankton Groups in Spring Related to Their Biomass in Winter as Evaluated by Spearman Correlation Coefficients (ρ) in Lake Taihu

Group names	Spearman correlation coefficient	Group names	Spearman correlation coefficient
5b	0.75**	6b2	0.69**
2d	0.47*	7a	0.87**
6a1	0.79**	5e	0.76**
10a	0.83**	11a	0.78**
6b1	0.79**		

Note.
*$p < 0.05$.
**$p < 0.01$.

Island Sound indicted that the winter-spring phytoplankton bloom negatively related to winter temperature due to high zooplankton grazing under warm winters (George et al., 2015). However, our results indicated that winter wind speed and solar radiation were the most dominant climatic factors affecting the spring phytoplankton community in subtropical Lake Taihu (Table 1, Figure 7, Figure S1).

First, during the past 20 years, wind speed has declined significantly in winter and spring in the Lake Taihu area (Figure 2). This decrease may have several effects on large shallow lakes. Low wind speed will reduce sediment resuspension, which could reduce the concentrations of suspended solids and thus increase the light availability in the water column as indicated in a study by Zhang et al. (2006) and reported for Lake Pyhäjärvi, a large shallow lake in Finland, by Deng et al. (2016). In addition, decreased wind speed may enhance the dissolved nutrient release from sediments under low dissolved oxygen conditions caused by a more stable water column (Deng et al., 2018; Tang et al., 2015).

Second, light conditions are important for phytoplankton succession in both winter and early spring in large shallow well-mixed and highly turbid lakes (Berger et al., 2010; Sommer et al., 2012; Torremorell et al., 2009). Research into the effects of light and temperature on the growth of phytoplankton in winter also showed that light is a key factor limiting the growth of phytoplankton (Eloranta, 1982; Fritsen & Priscu, 1999). The contribution of sunshine hours to the phytoplankton community was confirmed by NMDS (Figure 6). Six of the nine dominant phytoplankton groups were positively related to sunshine hours, namely, large unicellular pennates (6b2), small centrics (7a), large colonial pennates (6b1), Nostocales (5e), large Chroococcales (5b), and cryptophytes (2d). Our study reported increasing trends for diatoms in spring from 1992 to 2017 (Figure 5). Owing to their relatively heavy cell walls, the growth of diatoms could be limited by light because of sinking. Hence, increasing water clarity and sunshine duration could provide a sufficiently long period of time for diatoms to proliferate.

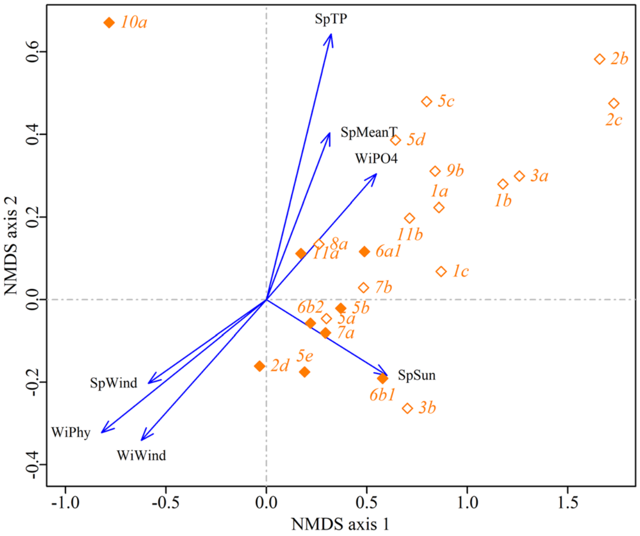

Figure 6. Ordinations of samples based on spring Morpho-Functional Group (MFG) biomass from 1992 to 2017 in Lake Taihu (no data are available for 2004). The dominant groups ($Y_i \geq 0.02$) are shown with filled symbols. All the environmental factors were included in the analysis, but only significant vectors ($p < 0.05$) are shown in the figure. SpTP: spring TP; SpMeanT: spring mean temperature; SpSun: spring sunshine duration; SpWind: spring wind speed; WiWind: winter wind speed; WiPO4: winter PO_4^{3-}-P; WiPhy: winter phytoplankton community as indicated by the winter NMDS axis 1.

It is generally accepted that temperature is an important factor affecting the growth of phytoplankton, especially in temperate lakes (Alvarez et al., 2009). However, winter temperature increase did not emerge as the most important factor for spring phytoplankton community succession in our results (Table 1, Figure 6, Figure S1), perhaps because of the relatively high winter temperatures around Lake Taihu (mean water temperature for 1992–2017 = approximately 5°C). The biological processes do, therefore, not cease in winter but only run at relatively lower rates than in spring and summer. By way of example, Visser et al. (2005) found that *Microcystis* (the dominant group 5b in our study) can persist throughout the year in tropical lakes, whereas they mainly grow in summer in temperate lakes. Remote sensing and field observations have shown that cyanobacterial blooms appeared year-round in Lake Taihu (Ma et al., 2016). This explains why other factors than temperature were of key importance for the phytoplankton growth during winter in Lake Taihu.

As indicated in our study, there were two pathways for winter climate effects on spring phytoplankton regarding both biomass and the community (Figure 7). The main pathway related to the winter phytoplankton community was direct effects of the winter climate on winter phytoplankton community and biomass, with a strong carry-over effect on spring phytoplankton community and biomass (Figure 7, Table 2). The other pathway was the winter climate effect on winter nutrient levels, with a carry-over effect fulling the spring

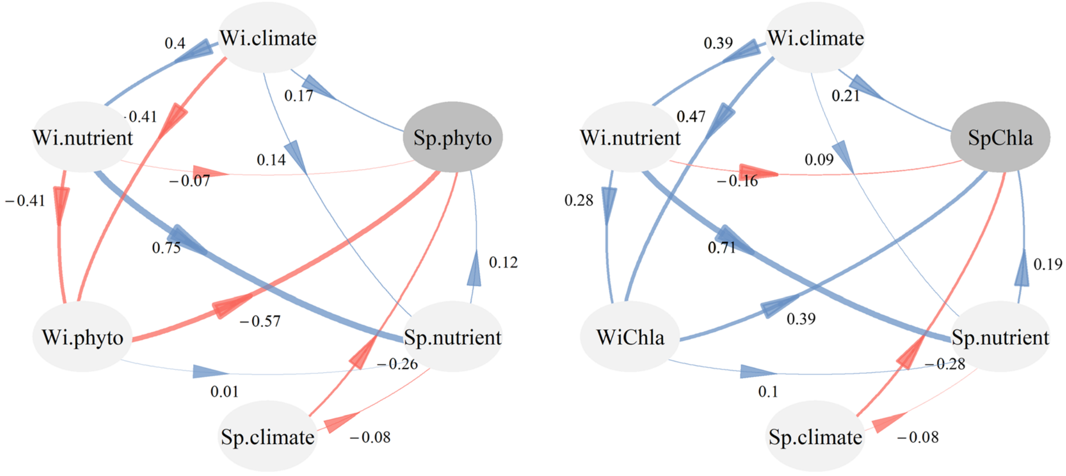

Figure 7. The effect paths of winter conditions on the spring phytoplankton community (as indicated by the spring NMDS axis 1) and Chl*a* as determined by partial least squares path modeling (PLS-PM).

phytoplankton community and biomass (Figure 7, Table 1). The former pathway played apparently a more vital role than the latter, which might reflect that since the nutrient levels were relatively high in Lake Taihu, the dominant phytoplankton groups were generally limited by physical factors rather than by nutrients.

It is well established that the winter climate has a “climate memory” effect on deep lakes as the hypolimnetic temperatures are determined by both winter conditions and the amount of heat reaching the deep-water layers before the onset of thermal stratification (Ambrosetti & Barbanti, 1999; Kernan et al., 2011). “Climate memory” effects have been found in temperate shallow lakes, mainly related to duration of the ice cover in winter (Yang et al., 2016), and our study indicates that “climate memory” effects also occur in subtropical shallow lakes. The “climate memory” effect of winter conditions in subtropical shallow lakes, as observed in our study, likely has a two-factor explanation as summarized in Figure 7 and discussed above.

In general, our study indicated a carry-over effect from winter to spring in Lake Taihu. It confirmed the existence of short-term “memory effects” of climate change on shallow lakes in subtropical regions, improving our understanding of the impact of climate change on ecosystems and the mechanisms behind.

5. Conclusions

With the long-term monthly monitoring data covering 26 years, the effects of winter climate conditions and nutrient levels on the spring phytoplankton community were evaluated for the subtropical large shallow Lake Taihu in China. The development of the spring phytoplankton was highly determined by winter conditions (e.g., wind speed and sunshine duration in winter). Nutrient levels in spring were found to be less important than winter climate conditions for the phytoplankton development. Both decreasing wind speed and increasing sunshine duration enhance light availability in the water column, which is an important driver of phytoplankton succession in winter and early spring in large shallow lakes. Our study indicated that “climate memory” effects on phytoplankton are valid not only in temperate lakes but also in subtropical, non-ice-covered shallow lakes.

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