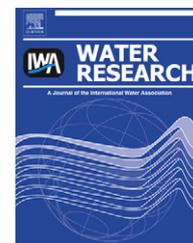


Available online at www.sciencedirect.com

SciVerse ScienceDirect

journal homepage: www.elsevier.com/locate/watres

Contributions of meteorology to the phenology of cyanobacterial blooms: Implications for future climate change

Min Zhang, Hongtao Duan, Xiaoli Shi, Yang Yu, Fanxiang Kong*

State Key Laboratory of Lake Science and Environment, Nanjing Institute of Geography and Limnology, Chinese Academy of Sciences, 73 East Beijing Road, Nanjing 210008, PR China

ARTICLE INFO

Article history:

Received 9 August 2011

Received in revised form

26 October 2011

Accepted 4 November 2011

Available online 17 November 2011

Keywords:

Climate change

Cyanobacterial blooms

Taihu

Satellite image

Temperature

ABSTRACT

Cyanobacterial blooms are often a result of eutrophication. Recently, however, their expansion has also been found to be associated with changes in climate. To elucidate the effects of climatic variables on the expansion of cyanobacterial blooms in Taihu, China, we analyzed the relationships between climatic variables and bloom events which were retrieved by satellite images. We then assessed the contribution of each climate variable to the phenology of blooms using multiple regression models. Our study demonstrates that retrieving ecological information from satellite images is meritorious for large-scale and long-term ecological research in freshwater ecosystems. Our results show that the phenological changes of blooms at an inter-annual scale are strongly linked to climate in Taihu during the past 23 yr. Cyanobacterial blooms occur earlier and last longer with the increase of temperature, sunshine hours, and global radiation and the decrease of wind speed. Furthermore, the duration increases when the daily averages of maximum, mean, and minimum temperature each exceed 20.3 °C, 16.7 °C, and 13.7 °C, respectively. Among these factors, sunshine hours and wind speed are the primary contributors to the onset of the blooms, explaining 84.6% of their variability over the past 23 yr. These factors are also good predictors of the variability in the duration of annual blooms and determined 58.9% of the variability in this parameter. Our results indicate that when nutrients are in sufficiently high quantities to sustain the formation of cyanobacterial blooms, climatic variables become crucial in predicting cyanobacterial bloom events. Climate changes should be considered when we evaluate how much the amount of nutrients should be reduced in Taihu for lake management.

© 2011 Elsevier Ltd. All rights reserved.

1. Introduction

Cyanobacterial blooms have become ubiquitous in many freshwater ecosystems affected by human activities, especially since the 1940s (Fogg, 1969; Huisman et al., 2005; Paerl and Fulton, 2006). Previous research has identified a host of causative factors spanning many ecological levels: bottom-up factors, such as nutrients; physiological capability of

cyanobacteria, including buoyancy regulation and low light requirements (Fogg, 1969; Zevenboom, 1982); the lack of or decrease in top-down predators on the community level (Porter, 1973); long water residence time (Paerl, 1996); and the altered structure and function of a whole water ecosystem (Elser, 1999). Recently, another factor, global warming, was found to promote the incidence of cyanobacterial blooms (Mooij et al., 2005; Jeppesen et al., 2007).

* Corresponding author. Tel.: +86 25 86882183; fax: +86 25 87714759.

E-mail address: fxkong@niglas.ac.cn (F. Kong).

0043-1354/\$ – see front matter © 2011 Elsevier Ltd. All rights reserved.

doi:10.1016/j.watres.2011.11.013

Anthropogenic climate change leads to warm weather, which in turn may promote the occurrence of cyanobacterial blooms directly and indirectly (Paerl and Huisman, 2009). High temperature (often above 25 °C) can directly promote the growth of cyanobacteria relative to other phytoplankton groups, such as diatoms and green algae (Reynolds, 2006; Jöhnk et al., 2008; Paerl and Huisman, 2009). Indirectly, warm weather induces many changes that may affect ecosystem processes and characteristics. First, warm weather, by heating the surface water, creates a stable water column that is advantageous for cyanobacterial growth in stratified water (Charpin et al., 1998; Dokulil and Teubner, 2000). Second, warm weather can result in either less or more precipitation, either of which can be beneficial to the development of blooms. For example, high winter rainfall may increase nutrient supply to surface waters and promote summer blooms, and increased summer drought will decrease flushing and promote the persistence of blooms (Paerl and Huisman, 2008). Third, despite some uncertainties, models have predicted that global warming will weaken the equator-to-pole temperature gradient and thus lessen mean summer wind speeds (Wentz et al., 2007). Slow wind promotes water stability and facilitates the gathering of cyanobacteria at the water surface to form blooms (Cao et al., 2006). Finally, global warming and associated changes in local climate alter light availability to phytoplankton. For example, increased cloud cover with increasing aerosol absorptivity decreased the surface solar radiation for the period of approximately 1960–1990. In the following years, however, solar radiation increased at most of the locations for which good records exist due to the interplay of direct and indirect aerosol effects (Wild et al., 2005; Perlwitz and Miller, 2010). However, all these factors would considerably affect the photosynthetic physiology of phytoplankton (Charpin et al., 1998). Compared with other phytoplankton groups, most planktonic cyanobacterium are known for adaptation to low light conditions (Richardson et al., 1983; Reynolds, 1984) and for their ability to gain more light by migrating up to the water surface by buoyancy (Sherman and Webster, 1994), where they can more effectively resist photoinhibition than other algae (Zhang et al., 2008). Therefore, global warming would have the potential to change the timing and scale of cyanobacterial bloom events.

Changes of biological events in aquatic ecosystems have been particularly apparent according to long-term ecological records and could serve as sensitive indicators of climate change (Winder and Schindler, 2004; Adrian et al., 2006; Blenckner et al., 2007; Smol, 2010). Climate-induced changes in the phenology of diatom blooms have been reported in Müggelsee, Germany (Huber et al., 2008). The shift in the timing of spring blooms is attributed to an advance in the timing of diatom dominance, mediated by an increase in growth rate driven by temperature (Meis et al., 2009). Quantitative analyses in Müggelsee suggest that climate warming enhances the probability of cyanobacterial dominance, and their incidence will certainly increase in aquatic systems in future warming climates (Wagner and Adrian, 2009). However, this lack of long-term ecological datasets in many lakes presents difficulties in proving the hypothesis that cyanobacterial blooms benefit from increased temperatures or other

climate factors under climate changes (Wagner and Adrian, 2009). Traditional methods of taking ship-borne water samples and analyzing them in a laboratory and/or performing on-site measurements are also incapable of such a spatial scale and frequency (Wang and Shi, 2008). Recently, remote sensing has become a powerful tool in understanding the long-term dynamics of algal blooms (Wang and Shi, 2008; Duan et al., 2009). From satellite-derived data, Duan et al. (2009) found that the onset time of cyanobacterial blooms has occurred earlier in the last decade, and their annual duration has extended in Taihu, China. Qin et al. (2010) noted that the advancement of cyanobacterial bloom events might be attributable to warming weather in the context of high nutrient levels. However, we still need long-term observation data and statistical analysis results to confirm this point and to obtain detailed insight into the contribution of the meteorological factors associated with climate change to the phenology of cyanobacterial blooms.

In this study, we tested the hypothesis that climatic variables play an important role in mediating bloom events within the context of high nutrient levels using long-term data derived from satellite images. To elucidate the relationship between climate changes and cyanobacterial onset timing as well as annual duration in Taihu, we first characterized climate changes in terms of temperature, precipitation, wind speed, global radiation, and sunshine hours from local weather stations for 1987–2009 along with the onset time and duration of annual blooms in the same period. Next, we analyzed the relationship between the climatic variables and bloom events using linear correlation analysis and the contribution of climatic variables to the changes in bloom events by multiple regression.

2. Materials and methods

2.1. Study site

Taihu is in southeast Jiangsu Province, China (latitude 30°55′40″–31°32′58″N; longitude 119°52′32″–120°36′10″E, Fig. 1). The lake has a surface area of 2338 km², a maximum and average depth of 2.6 and 1.9 m, respectively, and a mean water residence time of approximately 309 days (Qin et al., 2004). Taihu receives inflows from nearby riverine networks, including over 200 streams, canals and rivers (Chen et al., 2003). Blooms of *Microcystis* have been dominant in the past few decades (Qin et al., 2007).

2.2. Data acquisition, processing, and analyses

Events (i.e., the onset time and annual duration) of cyanobacterial blooms were obtained from the satellite images from 1987 to 2009, except 1988 and 1999. A total of 418 remote sensing images over Taihu from 1987 to 2009 were obtained, including 178 scenes of Landsat TM/ETM covering nearly all cloud-free periods since 1987 and 240 scenes of MODIS images from 2002 to 2009. The MODIS images were downloaded from the NASA EOS Data Gateway (EDG), and the Landsat data were provided by the China Remote-Sensing Satellite Ground Station. The bloom information was retrieved with the

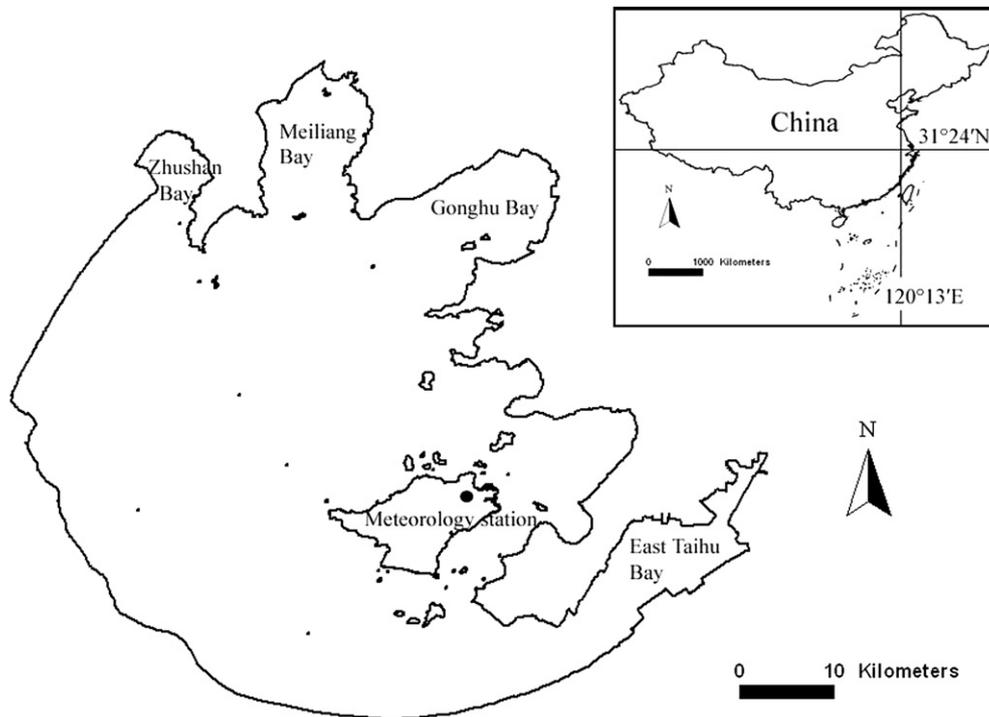


Fig. 1 – Location of Taihu in China. The weather station from which the climate data were collected is shown as a dot.

detectable reflectance signals from cyanobacterial cells in water primarily as described (Duan et al., 2009). Detectable reflectance signals were observed at a wavelength of 900 nm (TM and MODIS) from the algal blooms floating on the water surface and at wavelengths of 550 nm (TM) and 650 nm (TM and MODIS) from water with an abundance of algae (no scum). The distinguishable reflectance signal (different from the signal of clear water) can be used to delineate the areas of algal blooms by a threshold. To avoid underestimating the bloom information due to the long revisiting period (16 days) of Landsat and the unavoidable cloudy conditions, MODIS data with daily revisiting intervals were used to improve frequency and spatial accuracy, which was feasible to reconstruct the long-term information of cyanobacterial blooms (Duan et al., 2009). Although the threshold value based on visible images may have some uncertainties in determining the information of the blooms, it provides the possibility of mapping blooms over longer time scales and larger spatial scales without in situ data.

In this study, we focused on two bloom aspects: the onset time and the annual duration of blooms. We analyzed the relationship between the onset time and the climate changes during the period from recruitment initiation (when cyanobacteria start to migrate from sediments after growth therein) to the onset of the blooms. The onset time was defined as the date when cyanobacterial blooms were first recorded by remote sensing. Changes in climatic variables, including maximum temperature, mean temperature, minimum temperature, wind speed, precipitation, sunshine hours, and global radiation, were each calculated as the difference between their daily average in the given year and the standard

value (the mean of the daily average of each variable from 1971 to 1980) during the period between the initiation of cyanobacterial recruitment and the bloom's onset; these variables are represented as ΔT_{\max} , ΔT_{mean} , ΔT_{\min} , ΔW , ΔP , ΔS and ΔG , respectively. *Microcystis aeruginosa* grow and transfer from the sediment surface to the water column when the water temperature reaches 9 °C in early spring (Latour et al., 2004; Cao et al., 2008). Meanwhile, water temperature responds rapidly to changes in the air temperature in shallow lakes (Carpenter et al., 1992), so we approximately considered the air temperature as the water temperature. We also found that if the temperature exceeded 9 °C for 10 consecutive days, it would hardly decrease to <9 °C in the following days of the year. Therefore, we defined the recruitment initiation time as the day when the air temperature exceeded 9 °C followed by 10 consecutive days, each with temperature no lower than 9 °C. We also analyzed the relationships between annual bloom duration and annual climatic variables. The annual bloom duration was defined as the number of months per year during which the algal blooms were detected.

Annual mean concentrations of total nitrogen and total phosphorus were derived from the statistical yearbooks of Jiangsu Province, which were analyzed and calculated by the Environmental Protection Agency of Jiangsu Province according to samples from different lake zones once a month (APHA, 1985). The data of nutrient loadings (1998–2007), primarily originated from Jiangsu, were obtained from Ma et al. (2010). The climate data, including temperature, sunshine hours, wind speed, precipitation, and global radiation, were obtained from meteorology station #58358 of the China Meteorological Administration (Fig. 1).

The relationships between the potential explanatory variables and the events variables of cyanobacterial blooms were analyzed using multiple ordinary least squares (OLS) regression. Before the analysis, all data were standardized at a mean of 0 and a standard deviation of 1. Analysis of Variance (ANOVA) was used to test the colinearity of variables. We tested the variance inflation factor (VIF), which is a good indicator of whether one predictor has a strong linear relationship with other predictors. Where the VIF was <10 , we concluded that the predictor variables were not strongly related (Myers, 1990). The best models were identified using Akaike's information criterion (AICc) (Fotheringham et al., 2002). The AICc values of the models with all possible combinations of predictors were compared as a model set. The OLS was performed using the software SAM 4.0. Residual analysis was then used to check the influential points and outliers and the verification of the applicability of the regression models.

3. Results

3.1. Changes in climates and nutrients

The annual maximum, mean, and minimum temperatures all showed warming trends, with an asymmetric increase in maximum and minimum temperature, each rising by 1.40°C , 1.41°C , and 1.42°C , respectively, from 1987 to 2009 ($P < 0.01$, Table 1). The annual precipitation had no significant trend ($P > 0.05$). The daily mean wind speed decreased dramatically, by 0.47 m/s , in the same period ($P < 0.05$, Table 1). The sunshine hours over the past 23 yr showed two patterns of change: from 1987 to 1999, it declined at a rate of 49.76 h per year until 2000 ($P < 0.01$, Table 1), but increased since 2000 by 50.08 h per year ($P < 0.01$, Table 1). The global radiation increased by 144.25 W/m^2 after a steady rise from 1987 to 2009 ($P < 0.01$, Table 1).

The changes in climatic variables showed that the temperatures for most of each year studied were higher than the standard values. The ΔT_{max} , ΔT_{mean} and ΔT_{min} temperatures, all showed significant increases by 4.14°C , 3.26°C , and 2.66°C , respectively, over the 23 yr, except for 1997 ($P < 0.01$, Fig. 2a–c). There was little change in ΔP , which was only significant at $\alpha = 0.1$ ($P = 0.09$, Fig. 2d). Compared with the standard values, ΔW showed an overall decrease of 0.64 m/s over the 23 yr ($P < 0.01$, Fig. 2e). Changes in ΔS and in annual sunshine hours in the same period both followed a similar pattern: a decrease occurred from 1987 to 1999 ($P < 0.01$), followed by an increase since 2000 ($P = 0.02$, Fig. 2f). ΔG showed a significant increase of 70.30 W/m^2 from 1987 to 2009 ($P < 0.01$, Fig. 2g).

Total nitrogen ($1.64\text{--}3.53\text{ mg/L}$), total phosphorus ($0.05\text{--}0.14\text{ mg/L}$), and the TN:TP ratio during the past two decades fluctuated with economic development and lake management (Supporting Information Fig. S1), and there were no clear trends from the correlation analyses. From 1988 to 1996, however, there was a significant increase in TP concentration ($R_{\text{Adj}}^2 = 0.77$, $P = 0.001$, Table 1) and a significant decrease in the ratio of TN:TP from 1988 to 1996 ($R_{\text{Adj}}^2 = 0.80$, $P = 0.004$, Table 1). TN and TP loading did not increase significantly since the late 1980's (Table 2), nor did they show any trends in the most recent ten years (Supporting Information Fig. S2).

3.2. Changes in the observed events of cyanobacterial blooms, 1987–2009

Over the 23 yr, the onset time showed two different trends (Fig. 3a): from 1987 to 1997, the bloom onset was delayed by 5 d per year ($P < 0.01$); and from 1998 to 2009, the bloom onset advanced by approximately 10 d per year ($P = 0.01$). In addition, the recruitment initiation time of cyanobacteria advanced significantly with increases in mean annual temperature, by 0.9 d each year ($P < 0.05$). The time from recruitment initiation to bloom onset became increasingly shorter, especially in the recent 5 yr (2005–2009), when none were beyond 45 d . In 2006, in particular, blooms were found within nine days since recruitment initiation. The annual duration of cyanobacterial blooms only lasted for one month before 1998, but extended to more than two months since 1998, and ended up lasting over eight months from 2005 to 2009 (Fig. 3b).

3.3. Relationship between climate changes and cyanobacterial bloom events

The onset time of cyanobacterial blooms was highly correlated with ΔT_{max} , ΔT_{mean} , ΔT_{min} , ΔW , and ΔS (Fig. 4a–c, e and f, $P < 0.01$), and slightly correlated with ΔG (Fig. 4g, $P = 0.04$). No significant correlation was found between the onset time and ΔP (Fig. 4d, $P > 0.05$). Blooms duration had no remarkable linear relationship with the annual averages of climatic variables. However, the duration increased when the daily averages of maximum, mean, and minimum temperatures each exceeded 20.3°C , 16.7°C , and 13.7°C , respectively, and the annual sunshine hours exceeded 1650 h . The duration also increased as precipitation and wind speed

Table 1 – Linear regression parameters of climate and nutrient variables against years.

	Years	Intercept	Slope	n	P	R_{Adj}^2
T_{max}	1987–2009	−1066.71	0.64	23	0.000	0.46
T_{mean}	1987–2009	−1116.95	0.64	23	0.000	0.48
T_{min}	1987–2009	−1160.69	0.65	23	0.000	0.46
Precipitation	1987–2009	122,933.37	−55.63	23	0.405	0.01
Wind speed	1987–2009	458.15	−0.21	23	0.000	0.54
Sun hours	1987–2009	−3036.44	2.44	23	0.705	0.04
	1987–1999	84,429.93	−41.47	13	0.001	0.59
	2000–2009	−98,506.88	50.08	10	0.008	0.52
Global radiation	1987–2009	−11,891.87	6.56	23	0.005	0.29
TN	1988–2008	−38.17	0.02	19	0.386	0.01
TP	1988–2008	−2.05	0.01	20	0.242	0.02
	1988–1996	−21.659	0.01	9	0.001	0.77
TN/TP	1988–2008	497.07	−0.23	19	0.593	0.04
	1988–1996	11,428.73	−5.72	7	0.004	0.80
TN loading	1998–2007	−1.82	927.88	10	0.310	0.13
TP loading	1998–2007	−22,126.71	11.88	10	0.712	0.02

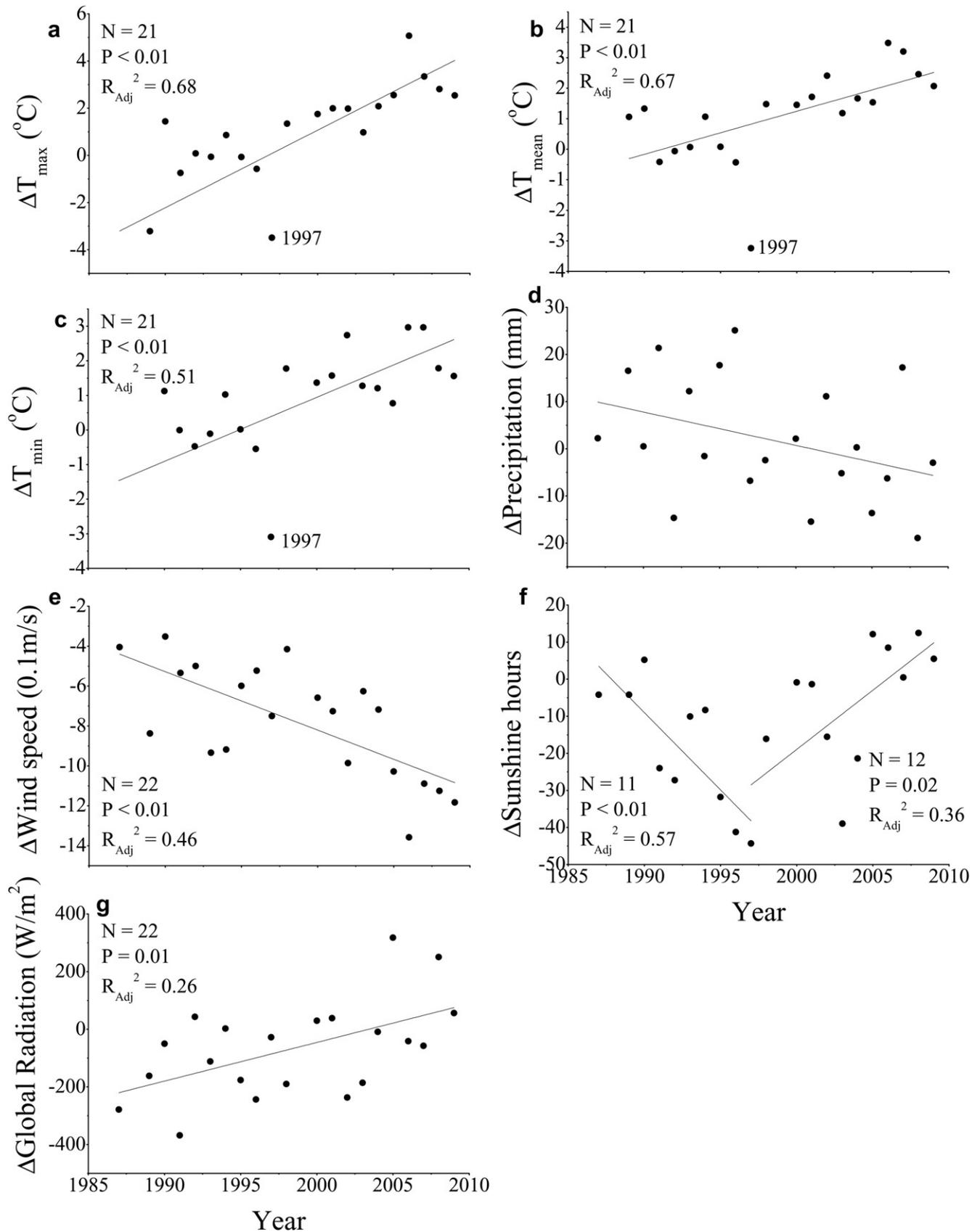


Fig. 2 – Trends in daily average anomalies of maximum (a), mean (b), and minimum (c) temperatures, precipitation (d), wind speed (e), sunshine hours (f), and global radiation (g) with respect to the 1971–1980 mean values during the period from cyanobacterial recruitment initiation to bloom formation in Taihu. The line shows the linear regression against year.

Table 2 – Loading of total nitrogen and total phosphorus in Taihu from late 1980's to early 2000's.

	TN loading ($\times 10^3$ t/a)	TP loading ($\times 10^3$ t/a)	Source
Late 1980's	20.24	1.55	(Sun and Huang, 1993)
Early 1990's	31.00	1.75	(SEPA, 2000)
Late 1990's	25.34	1.33	(Huang, 2004)
Early 2000's	28.66	1.03	(Xu and Qin, 2005)

decreased and as global radiation increased (Supporting Information Fig. S3).

The two predictors we selected, ΔW and ΔS , in the predictive model for the onset time by multiple regression analysis, could explain 84.6% of the variability in the onset time (Table 3). The predicted values of the onset time using the

model agreed well with the observed values (Fig. 5a). The multiple regression for bloom duration showed that wind speed and sunshine hours were the main contributors, accounting for 58.9% of the variation in duration (Table 3). Other variables, including TN and TP concentration, loading and TN:TP ratio, annual maximum, mean, and minimum temperatures, annual precipitation, and global radiation, were not significantly relevant ($P > 0.05$). Furthermore, wind speed had a negative impact on bloom duration, while sunshine hours had a positive impact. In other words, the bloom duration would increase when wind speed decreased and sunshine hours were prolonged (Fig. 5b). The results of the residual analysis were then used for the verification of the applicability of the two regression models. The existence of influential points and outlier observations were checked, but not found, in the models.

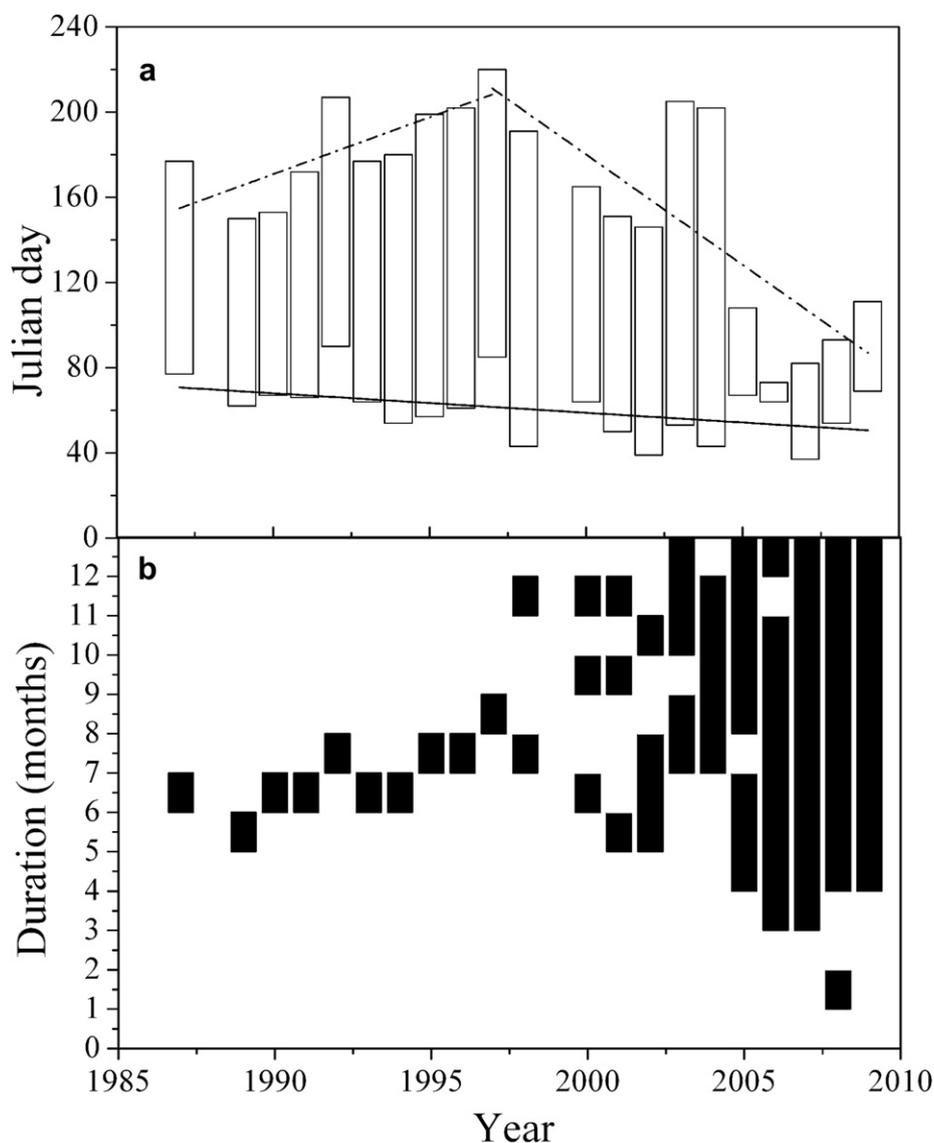


Fig. 3 – The intervals between cyanobacterial recruitment initiation (bottom point of each bar) and bloom onset (top point of each bar) (a) and the duration of cyanobacterial blooms (b) in Taihu from 1987 to 2009. The dash dot lines are the regression lines of bloom onset (1987–1996, $R_{adj}^2 = 0.501$, $P = 0.013$; 1997–2009, $R_{adj}^2 = 0.560$, $P = 0.003$), and the solid line is the regression line of recruitment initiation ($R_{adj}^2 = 0.154$, $P = 0.044$).

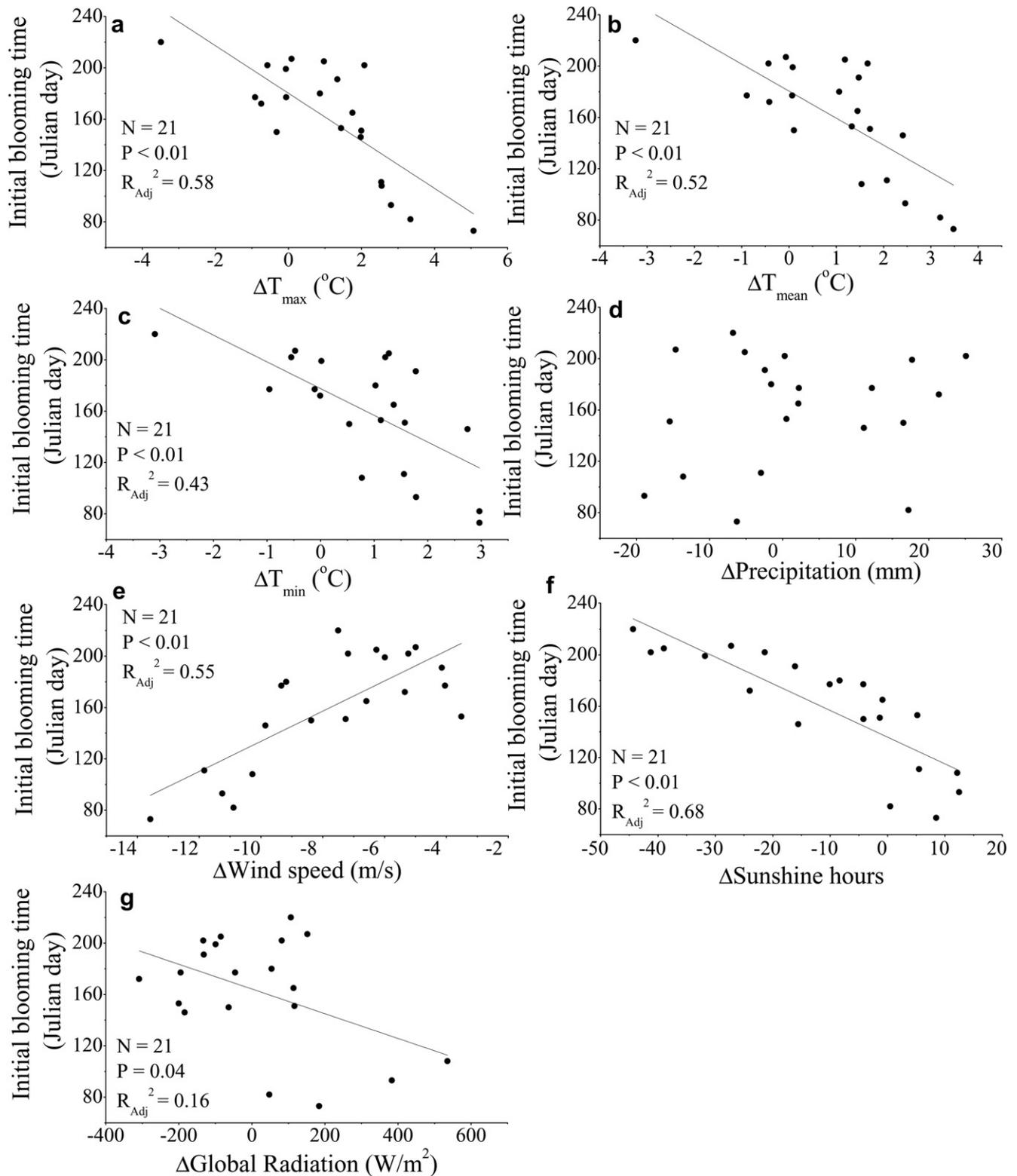


Fig. 4 – Correlation between mean daily anomalies of climatic variables (maximum (a), mean (b) and minimum (c) temperatures, precipitation (d), wind speed (e), sunshine hours (f), and global radiation (g)) and onset time of cyanobacterial blooms.

4. Discussion

The formation of cyanobacterial blooms is a result of complex and synergistic environmental factors rather than a single

dominant variable (Dokulil and Teubner, 2000). First, nutrients are considered the foundation for bloom formation (Huisman et al., 2005; Paerl and Fulton, 2006), which could influence long-term cyanobacterial relative biomass dynamics (Chen

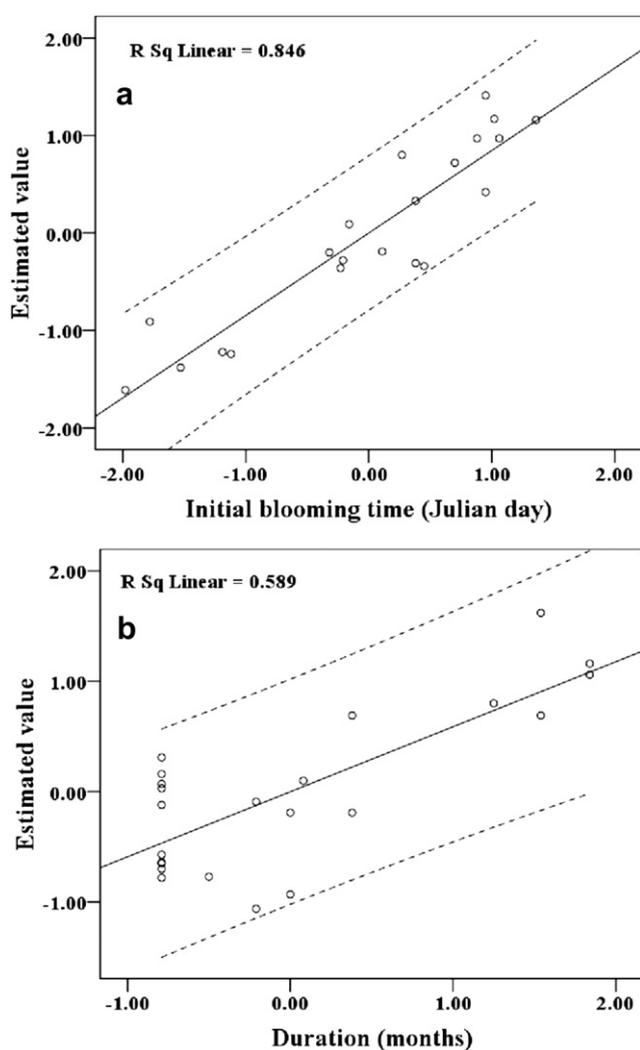


Fig. 5 – Scatterplots of the multiple linear regression analysis on onset time (a) and duration (b) of cyanobacterial blooms. The solid line represents regression, and the dotted line indicates the 95% confidence interval. All of the variables were standardized (mean = 0; SD = 1).

Table 3 – Relationships between initial blooming time, duration time of cyanobacteria blooms and potential explanatory variables modelled using multiple ordinary least squares (OLS) regression from 1987 to 2009. The best models were identified using Akaike’s information criterion (AICc). All of the variables were standardized (mean = 0; SD = 1).

Model	R ²	R ² _{adj}	AICc	n	β	P
Initial blooming time model						
Constant	0.846	0.839	29.173	23	<0.001	
ΔSunshine hours					-0.609	<0.001
ΔWind speed					0.446	<0.001
Blooms duration model						
Constant	0.589	0.568	51.884	23	<0.001	
Wind speed					-0.598	<0.001
Sunshine hours					0.419	0.006

et al., 2003). Moreover, there is a general consensus that the magnitude and duration of the blooms increase with increasing nutrient loads (Rydin et al., 2002) and are controlled by limiting nutrients, which are exhausted by the growth of blooming algae (Xu et al., 2010; Paerl et al., 2011). In our case, however, the correlation analyses showed that TN and TP, along with their loadings, had no significant relationship with the onset time or duration of annual blooms. In fact, from 2005 to 2009, cyanobacterial blooms lasted more than eight months per year and became invisible until early winter, which indicates that a bloom’s duration is not shortened by the seasonal limitation of nutrients showed by Xu et al. (2010). Furthermore, multiple linear regression indicates that the TN and TP concentrations and loadings, and even the TN:TP ratios, could not predict the two cyanobacterial bloom events. Even, though the nutrient concentrations and loadings in Taihu increased dramatically from the 1960s to 1980s, their increasing trends have slowed down since the 1990s. In the last ten years, the nutrient loads and concentrations have already been maintaining high levels (TP: 0.09 ± 0.02 mg/L; TN: 2.63 ± 0.55 mg/L), and have even exceeded cyanobacterial growth requirements in some lake regions (Qin et al., 2010). Furthermore, blooming algae also obtain nutrients to keep the persistence of blooms from the degradation of blooms (Sfriso et al., 1987) and the internal release of nutrient loads (Jöhnk et al., 2008). Thus, although nutrient enrichment is a prerequisite to bloom formation, the contribution of nutrients to the changes in the phenology of cyanobacterial blooms might be weak in Taihu over the 23 yr because the nutrients had reached high levels with low inter-annual variation.

When nutrients are high enough to sustain algal blooms, the magnitude, spatial extent and duration of blooms are mainly modulated by physical factors (Qin et al., 2010). In our case, in the context of the high nutrient level, climatic variables were crucial modulating factors of cyanobacterial bloom events in Taihu over the 23 yr. The onset time of cyanobacterial blooms has a negative correlation with the changes in daily maximum, mean, and minimum temperature, sunshine hours, and global radiation, and it has a positive correlation with the changes in wind speed and precipitation. Moreover, the daily averages of minimum temperature, wind speed and sunshine hours are primary contributors to the advance of the onset time and the extension of the duration of cyanobacterial blooms. Among these climate factors, increased temperature promotes the growth of cyanobacteria and allow them to develop earlier (Wiedner et al., 2007). It has been predicted that global warming will increase the frequency of cyanobacterial blooms through the direct effects of high water temperatures (Jöhnk et al., 2008; Paerl and Huisman, 2008). However, in situ observational evidence is still required to confirm that cyanobacteria profit directly from increased water temperature (Adrian et al., 2006). In the present study, temperature displays a negative correlation with the onset time of cyanobacterial blooms, implying that low temperatures early in the year could delay cyanobacterial blooms.

The formation of cyanobacterial blooms is also favoured by warm and calm weather, and disfavoured by windy and precipitating conditions (Kanoshina et al., 2003). Reduced wind speeds and precipitation are thus favourable for buoyant

Microcystis to accumulate on the water surface (Jöhnk et al., 2008). A low wind speed of approximately 3–4 m/s (George and Edwards, 1976; Cao et al., 2006) is favourable for *Microcystis* to accumulate at the water surface, mainly at the surface to 0.3 m depth (Zhang et al., 2008). In Taihu, the falling wind speed increases the stability of the water column, thereby reducing vertical turbulent mixing, which may shift the competitive balance in favour of the buoyant cyanobacteria, promoting the formation of cyanobacterial blooms.

Additionally, increasing global solar radiation may be more favourable for cyanobacteria because they have the major advantage of accessing light by accumulating on the water surface and casting shade upon other competitors (Walsby et al., 1997; Klausmeier and Litchman, 2001; Huisman et al., 2004). Furthermore, even at the water surface, cyanobacteria are a good competitor compared with other phytoplankton because they can resist photoinhibition from increasing global solar radiation more effectively than other algae by nonphotochemical quenching, when solar radiation intensity exceeds the light saturation point of phytoplankton (Zhang et al., 2008). The negative correlation between the sunshine hours and the onset time also indicates that increasing light duration favours the development of cyanobacterial dominance. Therefore, light conditions are one of the crucial determinants of the onset time and duration of cyanobacterial blooms.

5. Conclusion

In the studied case, we used satellite images as a data source to obtain historical cyanobacterial bloom information in Taihu, and we analyzed their correlation with climatic variables. Our study demonstrates that retrieving ecological information from satellite images is meritorious for large scale and long-term ecological research in freshwater ecosystems, despite uncertainties due to technological limitations and the complexity of aquatic systems.

Our findings highlight the importance of meteorological factors associated with climate change on the phenology of cyanobacterial blooms in Taihu during the past 23 yr. Within the context of sufficiently high nutrient loadings and concentrations for the formation of cyanobacterial blooms, climatic variables play an important role in mediating bloom events. Increased temperature directly affects cyanobacterial bloom events by advancing its onset time and extending its duration. Furthermore, wind speed and sunshine hours are also important contributors for advancing the onset time and prolonging the duration of cyanobacterial blooms in Taihu from 1987 to 2009. Therefore, our study offers evidence that although nutrients must be substantially reduced, climate changes should be considered when evaluating how much the amount of nutrients should be reduced in Taihu for future lake management.

Acknowledgements

We thank Dr. Ronghua Ma for retrieving cyanobacterial bloom information from the satellite images, Dr. Huansheng Cao at

Fordham University for reviewing the manuscript, and the anonymous reviewers for their crucial comments. The work was supported by the project of Jiangsu Province National Science Foundation (BK2011877), the National Basic Research Program of China '973' (No. 2008CB418005), and the project of the Front Fields Program (CXNIGLAS200810).

Appendix. Supplementary material

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.watres.2011.11.013.

REFERENCES

- Adrian, R., Wilhelm, S., Gerten, D., 2006. Life-history traits of lake plankton species may govern their phenological response to climate warming. *Global Change Biology* 12 (4), 652–661.
- APHA, 1985. *Standard Methods for the Examination of Water and Wastewater*, sixteenth ed. American Public Health Association, Washington, D. C.
- Blenckner, T., Adrian, R., Livingstone, D.M., Jennings, E., Weyhenmeyer, G.A., George, D., Jankowski, T., Jrvinen, M., Aonghusa, C.N., Noges, T., 2007. Large-scale climatic signatures in lakes across Europe: a meta-analysis. *Global Change Biology* 13 (7), 1314–1326.
- Cao, H.S., Kong, F.X., Luo, L.C., Shi, X.L., Yang, Z., Zhang, X.F., Tao, Y., 2006. Effects of wind and wind-induced waves on vertical phytoplankton distribution and surface blooms of *Microcystis aeruginosa* in Lake Taihu. *Journal of Freshwater Ecology* 21 (2), 231–238.
- Cao, H.S., Tao, Y., Kong, F.X., Yang, Z., 2008. Relationship between temperature and cyanobacterial recruitment from sediments in laboratory and field studies. *Journal of Freshwater Ecology* 23 (3), 405–412.
- Carpenter, S.R., Fisher, S.G., Grimm, N.B., Kitchell, J.F., 1992. Global change and freshwater ecosystems. *Annual Review of Ecology and Systematics* 23, 119–139.
- Charpin, M.F., Maurin, N., Amblard, C., Devaux, J., 1998. Seasonal variations of phytoplankton photosynthate partitioning in two lakes of different trophic level. *Journal of Plankton Research* 20 (5), 901–921.
- Chen, Y.W., Qin, B.Q., Teubner, K., Dokulil, M.T., 2003. Long-term dynamics of phytoplankton assemblages: *Microcystis*-domination in Lake Taihu, a large shallow lake in China. *Journal of Plankton Research* 25 (4), 445–453.
- Dokulil, M.T., Teubner, K., 2000. Cyanobacterial dominance in lakes. *Hydrobiologia* 438 (1), 1–12.
- Duan, H.T., Ma, R.H., Xu, X.F., Kong, F.X., Zhang, S.D., Kong, W.J., Hao, J.Y., Shang, L.L., 2009. Two-decade reconstruction of algal blooms in China's Lake Taihu. *Environmental Science & Technology* 43 (10), 3522–3528.
- Elser, J.J., 1999. The pathway to noxious cyanobacteria blooms in lakes: the food web as the final turn. *Freshwater Biology* 42 (3), 537–543.
- Fogg, G.E., 1969. The physiology of an algal nuisance. *Proceedings of the Royal Society of London Series B – Biological Sciences* 173, 175–189.
- Fotheringham, A.S., Brunson, C., Charlton, M., 2002. *Geographically Weighted Regression: The Analysis of Spatially Varying Relationships*. John Wiley & Sons Inc, Chichester, UK.

- George, D.G., Edwards, R.W., 1976. The effect of wind on the distribution of chlorophyll *a* and crustacean plankton in a shallow eutrophic reservoir. *Journal of Applied Ecology* 13 (3), 667–690.
- Huang, W., 2004. The pollutant budget in Lake Taihu. In: Qin, B.Q., Hu, W.P., Chen, W.M. (Eds.), *Process and Mechanism of Environmental Changes of Lake Taihu*. Science Press, Beijing, pp. 21–28 (in Chinese).
- Huber, V., Adrian, R., Gerten, D., 2008. Phytoplankton response to climate warming modified by trophic state. *Limnology and Oceanography* 53 (1), 1–13.
- Huisman, J., Matthijs, H.C.P., Visser, P.M., 2005. *Harmful Cyanobacteria*. Springer, Dordrecht, Netherlands.
- Huisman, J., Sharples, J., Stroom, J.M., Visser, P.M., Kardinaal, W.E.A., Verspagen, J.M.H., Sommeijer, B., 2004. Changes in turbulent mixing shift competition for light between phytoplankton species. *Ecology* 85 (11), 2960–2970.
- Jöhnk, K.D., Huisman, J., Sharples, J., Sommeijer, B., Visser, P.M., Stroom, J.M., 2008. Summer heatwaves promote blooms of harmful cyanobacteria. *Global Change Biology* 14 (3), 495–512.
- Jepesen, E., Meerhoff, M., Jacobsen, B., Hansen, R., Søndergaard, M., Jensen, J., Lauridsen, T., Mazzeo, N., Branco, C., 2007. Restoration of shallow lakes by nutrient control and biomanipulation—the successful strategy varies with lake size and climate. *Hydrobiologia* 581 (1), 269–285.
- Kanoshina, I., Lips, U., Leppänen, J.M., 2003. The influence of weather conditions (temperature and wind) on cyanobacterial bloom development in the Gulf of Finland (Baltic Sea). *Harmful Algae* 2 (1), 29–41.
- Klausmeier, C.A., Litchman, E., 2001. Algal games: the vertical distribution of phytoplankton in poorly mixed water columns. *Limnology and Oceanography* 46 (8), 1998–2007.
- Latour, D., Sabido, O., Salençon, M.J., Giraudet, H., 2004. Dynamics and metabolic activity of the benthic cyanobacterium *Microcystis aeruginosa* in the Grangent reservoir (France). *Journal of Plankton Research* 26 (7), 719–726.
- Ma, Q., Liu, J., Gao, M., 2010. Amount of pollutants discharged into Lake Taihu from Jiangsu province, 1998–2007. *Journal of Lake Science* 22 (1), 29–34 (in Chinese).
- Meis, S., Thackeray, S.J., Jones, I.D., 2009. Effects of recent climate change on phytoplankton phenology in a temperate lake. *Freshwater Biology* 54 (8), 1888–1898.
- Mooij, W., Hülsmann, S., De Senerpont Domis, L., Nolet, B., Bodelier, P., Boers, P., Pires, L., Gons, H., Ibelings, B., Noordhuis, R., Portielje, R., Wolfstein, K., Lammens, E., 2005. The impact of climate change on lakes in the Netherlands: a review. *Aquatic Ecology* 39 (4), 381–400.
- Myers, R., 1990. *Classical and Modern Regression with Applications*. PWS and Kent Publishing Company, Boston.
- Paerl, H.W., 1996. A comparison of cyanobacterial bloom dynamics in freshwater, estuarine and marine environments. *Phycologia* 35, 25–35.
- Paerl, H.W., Fulton, R.S., 2006. In: Granéli, E., Turner, J.T. (Eds.), *Ecology of Harmful Algae*. Springer, Berlin Heidelberg, pp. 95–109.
- Paerl, H.W., Huisman, J., 2008. Climate: blooms like it hot. *Science* 320 (5872), 57–58.
- Paerl, H.W., Xu, H., McCarthy, M.J., Zhu, G., Qin, B., Li, Y., Gardner, W.S., 2011. Controlling harmful cyanobacterial blooms in a hyper-eutrophic lake (Lake Taihu, China): the need for a dual nutrient (N & P) management strategy. *Water Research* 45 (5), 1973–1983.
- Paerl, W.H., Huisman, J., 2009. Climate change: a catalyst for global expansion of harmful cyanobacterial blooms. *Environmental Microbiology Reports* 1 (1), 27–37.
- Perlwitz, J., Miller, R.L., 2010. Cloud cover increase with increasing aerosol absorptivity: a counterexample to the conventional semidirect aerosol effect. *Journal of Geophysical Research* 115 (D8), D08203.
- Porter, K.G., 1973. Selective grazing and differential digestion of algae by zooplankton. *Nature* 244, 179–180.
- Qin, B.Q., Zhu, G.W., Gao, G., Zhang, Y.L., Li, W., Paerl, H., Carmichael, W., 2010. A drinking water crisis in Lake Taihu, China: linkage to climatic variability and lake management. *Environmental Management* 45 (1), 105–112.
- Qin, B.Q., Hu, W.P., Chen, W.M., 2004. *Process and Mechanism of Environmental Changes of the Taihu Lake*. Science Press, Beijing.
- Qin, B.Q., Xu, P.M., Wu, Q.L., Luo, L.C., Zhang, Y.L., 2007. In: Qin, B., Liu, Z., Havens, K. (Eds.), *Eutrophication of Shallow Lakes with Special Reference to Lake Taihu, China*. Springer, Netherlands, pp. 3–14.
- Reynolds, C.S., 1984. *The Ecology of Freshwater Phytoplankton*. Cambridge Univ. Press, Cambridge, UK.
- Reynolds, C.S., 2006. *Ecology of Phytoplankton (Ecology, Biodiversity and Conservation)*. Cambridge Univ. Press, Cambridge, UK.
- Richardson, K., Beardall, J., Raven, J.A., 1983. Adaptation of unicellular algae to irradiance: an analysis of strategies. *New Phytologist* 93 (2), 157–191.
- Rydin, E., Hyenstrand, P., Gunnerhed, M., Blomqvist, P., 2002. Nutrient limitation of cyanobacterial blooms: an enclosure experiment from the coastal zone of the NW Baltic proper. *Marine Ecology-progress Series* 239, 31–36.
- Sfriso, A., Marcomini, A., Pavoni, B., 1987. Relationships between macroalgal biomass and nutrient concentrations in a hypertrophic area of the Venice Lagoon. *Marine Environmental Research* 22 (4), 297–312.
- Sherman, B.E., Webster, I.T., 1994. A model for the light-limited growth of buoyant phytoplankton in a shallow, turbid waterbody. *Australian Journal of Marine and Freshwater Research* 45 (5), 847–862.
- Smol, J.P., 2010. The power of the past: using sediments to track the effects of multiple stressors on lake ecosystems. *Freshwater Biology* 55, 43–59.
- State Environmental Protection Administration (SEPA), 2000. *Water Protection in the Three Rivers and Three Lakes of China*. Chinese Environmental Press, Beijing, pp. 151–175 (in Chinese).
- Sun, S.C., Huang, Y.P., 1993. *Lake Taihu*. China Ocean Press, Beijing, pp. 23–89 (in Chinese).
- Wagner, C., Adrian, R., 2009. Cyanobacteria dominance: quantifying the effects of climate change. *Limnology and Oceanography* 54, 2460–2468.
- Walsby, A.E., Hayes, P.K., Boje, R., Stal, L.J., 1997. The selective advantage of buoyancy provided by gas vesicles for planktonic cyanobacteria in the Baltic Sea. *New Phytologist* 136 (3), 407–417.
- Wang, M., Shi, W., 2008. Satellite-observed algae blooms in China's Lake Taihu. *Eos Transactions, American Geophysical Union* 89 (22), 201.
- Wentz, F.J., Ricciardulli, L., Hilburn, K., Mears, C., 2007. How much more rain will global warming bring? *Science* 317 (5835), 233–235.
- Wiedner, C., Rucker, J., Brüggemann, R., Nixdorf, B., 2007. Climate change affects timing and size of populations of an invasive cyanobacterium in temperate regions. *Oecologia* 152 (3), 473–484.
- Wild, M., Gilgen, H., Roesch, A., Ohmura, A., Long, C.N., Dutton, E.G., Forgan, B., Kallis, A., Russak, V., Tsvetkov, A.H., 2005. From dimming to brightening: decadal changes in solar radiation at earth's surface. *Science* 308 (5723), 847.
- Winder, M., Schindler, D.E., 2004. Climate change uncouples trophic interactions in an aquatic ecosystem. *Ecology* 85 (8), 2100–2106.

- Xu, H., Paerl, H.W., Qin, B., Zhu, G., Gao, G., 2010. Nitrogen and phosphorus inputs control phytoplankton growth in eutrophic Lake Taihu, China. *Limnology and Oceanography* 55 (1), 420–432.
- Xu, P.Z., Qin, B.Q., 2005. Water quantity and pollutant fluxes of the surrounding rivers of Lake Taihu during the hydrological year of 2001–2002. *Journal of Lake Science* 17 (3), 213–218 (in Chinese).
- Zevenboom, W., 1982. N²-fixing cyanobacteria: why they do not become dominant in shallow hypertrophic lakes. *Aquatic Ecology* 16 (2), 289–290.
- Zhang, M., Kong, F.X., Wu, X.D., Xing, P., 2008. Different photochemical responses of phytoplankters from the large shallow Taihu Lake of subtropical China in relation to light and mixing. *Hydrobiologia* 603 (1), 267–278.