

# Earlier and warmer springs increase cyanobacterial (*Microcystis* spp.) blooms in subtropical Lake Taihu, China

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## SUMMARY

1. We examined the effects of regional warming and water quality on phytoplankton community succession, focussing on the bloom-forming cyanobacterial genus *Microcystis* in subtropical Lake Taihu, China. Daily air temperatures from 1991 to 2010 indicated that onset of the *Microcystis* growing season has advanced by approximately 20 days over the last two decades, and accumulated air temperature (from 1 March to 31 May) has increased significantly.

2. Since 2005, *Microcystis* blooms have begun in May more frequently than in June. An increase in degree days for growth indicated that the early warming trend in spring would have benefitted *Microcystis* populations that overwintered on the sediment surface, by allowing them to grow, gain buoyancy and float into water column earlier in the year.

3. Results of canonical correspondence analysis showed that both water quality (i.e. nutrient loading) and water temperature have affected phytoplankton community succession in spring over the past two decades. When nutrient concentrations are adequate to support *Microcystis* blooms, rising temperature promotes their earlier onset and proliferation, a phenomenon previously documented for temperate regions, and now demonstrated for this subtropical lake.

*Keywords:* accumulated temperature, canonical correspondence analysis, climate change, cyanobacterial blooms, Meiliang Bay

## Introduction

Eutrophication, a typical symptom of which is harmful cyanobacterial blooms, is becoming more widespread and threatens municipal and industrial water sources as well as the recreational and conservation value of some of the world's largest and most biodiverse waterbodies (Paerl, Hall & Calandrino, 2011), including Lake Victoria in Africa, Lake Erie in U.S.A.-Canada, Lake Okeechobee in Florida, U.S.A., Lake Kasumigaura in Japan (Havens *et al.*, 2001), the Baltic Sea in northern Europe (Conley *et al.*, 2009) and Lake Taihu in China (Qin *et al.*, 2010). Among the causes of cyanobacterial blooms, anthropogenic nutrient pollution has received the most attention. Numerous studies have demonstrated that cyanobacterial blooms are stimulated by hypernutrifica-

tion, especially of nitrogen (N) and/or phosphorus (P) (Smith, 1986; Trimbee & Prepas, 1987; Watson, Mccauley & Downing, 1997; Smith & Schindler, 2009). Recent studies have also shown that an increase in water temperature, due to a changing global climate could play an important role in the proliferation of cyanobacteria (Peperzak, 2003; Paerl & Huisman, 2008, 2009; Paul, 2008; O'Neil *et al.*, 2012). Global climate change, especially warming, is a complicated and increasingly problematic factor that must be considered when formulating N and P reduction strategies aimed at controlling cyanobacterial blooms (Paerl & Paul, 2012).

Previous studies indicate that warming can selectively promote cyanobacterial blooms, specifically those of the colonial genus *Microcystis* (de Senerpont Domis, Mooij & Huisman, 2007; Jöhnk *et al.*, 2008; Jeppesen *et al.*, 2009,

2011; Paerl & Huisman, 2009; Elliott, 2012). Other studies have shown that the population growth rates of freshwater eukaryotic phytoplankton generally stabilise or decrease when temperature approaches and exceeds 20 °C. In contrast, growth rates of bloom-forming cyanobacteria increase when temperatures exceed 20 °C (Paerl *et al.*, 2011); therefore, either short- or long-term increases in water temperature above 20 °C should confer a competitive advantage on cyanobacteria (Peperzak, 2003; Paerl & Huisman, 2009; Paerl *et al.*, 2011; O'Neil *et al.*, 2012) over eukaryotes, such as diatoms, chlorophytes, cryptophytes and dinoflagellates (Paerl *et al.*, 2011).

In addition to increasing temperature, climate change can also enhance nutrient loading to lakes through increases in rainfall, especially in winter (Jeppesen *et al.*, 2011). This nutrient loading can potentially intensify eutrophication of lakes, as shown for Northern Europe (Jeppesen *et al.*, 2009, 2011).

Climate warming will also intensify vertical stratification (Paerl & Huisman, 2009). These conditions favour bloom-forming cyanobacteria that, unlike eukaryotes, can adjust their buoyancy and thus regulate their vertical position by forming gas vesicles (Reynolds & Walsby, 1975; Huisman *et al.*, 2004). For instance, warming reduced mixing and led to the dominance of *Planktothrix rubescens* in Lake Zurich (Winder, 2012).

These previous studies have focussed mainly on temperate regions, where the steepest seasonal temperature increases occur during late winter and early spring (Van Oldenborgh & van Ulden, 2003; Thompson & Clark, 2008). Relatively few reports address the effect of climate change on eutrophic lakes in subtropical regions (e.g. Kosten *et al.*, 2011). In addition, warming is thought to have a much lower impact on the timing of the onset of phytoplankton growth in the subtropics compared to temperate regions (Peeters *et al.*, 2007); however, previous studies in Lake Taihu, the third largest freshwater lake in China, have indicated that climate change might affect cyanobacteria blooms (Qin *et al.*, 2010; Paerl & Paul, 2012; Zhang *et al.*, 2012). In addition, increasing greenhouse gases emissions result in significant warming in winter (Zhang, Qin & Chen, 2004), which might profoundly affect the development, persistence and severity of cyanobacterial bloom in the following summer (Qin *et al.*, 2010; Paerl & Paul, 2012; Zhang *et al.*, 2012). This is because the warming trend will also increase the probability that cyanobacterial bloom species will be exposed to high concentrations of nutrients in spring (Qin *et al.*, 2010).

The phenology of blooms events has been linked to climatic conditions in Lake Taihu over the last two

decades (Duan *et al.*, 2009; Zhang *et al.*, 2012). The onset dates for blooms and their duration have been extracted from remote sensing imagery. However, only one-third of daylight periods could be observed, due to clouds, which could introduce bias in interpretations of the temporal dynamics of algal blooms. For instance, only 394 remote sensing images were used in Duan *et al.* (2009) study, which covered the period 1987–2007, and only 24 images were useable in 2008 and 2009 (Zhang *et al.*, 2012). This points to the need for long-term monitoring data, especially of community composition, to support the conclusion that cyanobacterial blooms benefit from the warming trend in Lake Taihu.

Our main objective was to identify and interpret the effects of climate fluctuations on the development of *Microcystis* in spring in this subtropical lake. We first examined the changes in seasonality due to climatic warming. Secondly, we estimated the effects of a warming trend and changes in water quality on phytoplankton community structure and on the intensity of cyanobacterial blooms in Lake Taihu.

## Methods

### Study site

Lake Taihu ('Taihu' in Mandarin means large waterbody; surface area, 2428 km<sup>2</sup>) is a shallow (mean depth, 1.9 m; max depth, 2.6 m; altitude, 3.0 m asl), eutrophic, subtropical lake situated in the Changjiang (Yangtze) Delta (Fig. 1), the most industrialised and densely populated region in China. It is a well-mixed lake (Bachmann, Hoyer & Canfield, 2000), and the entire lakebed is subject to wave disturbance. Analysis of six-layer water temperature data at a station with 2.5 m depth indicates that the vertical temperature gradient is generally less than 1 °C (Zhao *et al.*, 2011).

Since the 1980s, rapid economic development in the Lake Taihu basin has resulted in increasing concentrations of pollutants discharged to tributaries and the lake. As a result, there has been rapid deterioration of water quality and accelerating eutrophication, while nuisance blooms (*Microcystis* spp.) now occur regularly (Qin *et al.*, 2007). Cyanobacterial blooms first occurred in summer during the 1960s, but they disappeared at the onset of autumn. More intense and persistent (May–October) blooms have occurred every year in Meiliang Bay since the 1990s, becoming even more frequent since 2003. Since 2006, both the duration and intensity (i.e. cyanobacterial biomass) of blooms have increased further (Shang *et al.*, 2010).

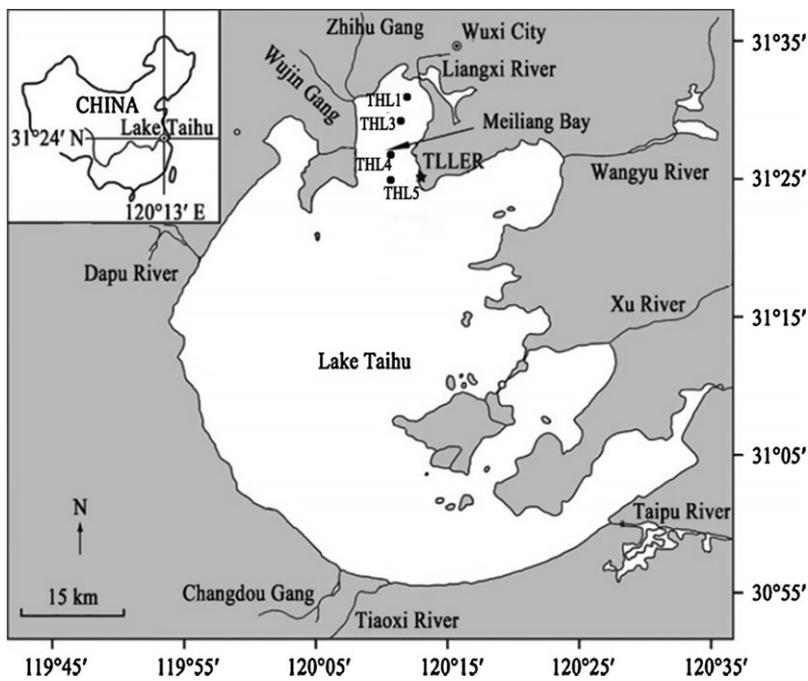


Fig. 1 Location of Lake Taihu in China and sampling sites (redrawn from Xu *et al.*, 2010). Phytoplankton biovolume together with environmental variables were monitored at THL1, THL3, THL4 and THL5 sites monthly, generally in the middle of each month.

Meiliang Bay, in the north of the lake, is one of the most eutrophic parts of Lake Taihu, and blooms there are more intense than in any other region (Xu *et al.*, 2010). Over the past 20 years, Meiliang Bay nutrient concentrations (data from this study) have remained high in May (total phosphorus,  $0.13 \pm 0.06 \text{ mg L}^{-1}$ ; total nitrogen,  $4.29 \pm 1.35 \text{ mg L}^{-1}$ ; total dissolved phosphorus,  $0.01 \pm 0.01 \text{ mg L}^{-1}$ ; total dissolved nitrogen,  $2.58 \pm 0.65 \text{ mg L}^{-1}$ ).

#### *Air temperature, water temperature and phytoplankton community dynamics*

Daily air temperatures, from 1 January 1991 to 31 December 2010 in Taihu basin, were obtained from China Meteorological Data Sharing Service System (<http://cdc.cma.gov.cn/>, site No. 58362;  $31^{\circ}24' \text{N}$ ,  $121^{\circ}27' \text{E}$ ). We selected a 5-day moving average of  $9^{\circ} \text{C}$  as the proposed threshold temperature for the onset of the *Microcystis* growing season in Lake Taihu because, based on previous observations (Cao *et al.*, 2008), that is the temperature at which overwintering *Microcystis* on the sediment surface begin to grow, gain buoyancy and then float into the water column. Accumulated air temperature for each year was compiled by adding together successive mean daily air temperatures during the spring (1 March to 31 May).

Four sampling stations (THL1, THL3, THL4 and THL5; Fig. 1) were selected to cover the entire Meiliang Bay. Sampling has generally been conducted during the

middle of each month from 1992 to 2010. Water temperature was measured with a mercury thermometer at 0.5 m below the water surface at all sampling sites. Accumulated water temperature was determined for each year by summing up monthly water temperature from March to May.

Integrated water samples were collected using a 2-m-long and 10-cm-diameter plastic tube at each sampling site. Physicochemical variables in May, such as Secchi depth (SD), conductivity (Cond), pH, chemical oxygen demand (COD), suspended solids (SS) and nutrient concentrations [including total nitrogen (TN), total phosphorus (TP), total dissolved phosphorus (TDP) and total dissolved nitrogen (TDN)] were analysed following Chinese standard methods (Jin & Tu, 1990).

For each sampling site, 1 L of the mixed water sample was collected for identifying and counting phytoplankton. Phytoplankton samples were fixed with Lugol's iodine solution and sedimented for 48 h prior to counting. Phytoplankton species were identified according to Hu, Li & Wei (1980) and Hu & Wei (2006). Phytoplankton cells numbers were counted, and at least 400 cells of total phytoplankton species were counted in each sample. Algal biovolumes were calculated from cell numbers and cell size measurements. Conversion to biomass assumes that  $1 \text{ mm}^3$  of volume is equivalent to  $1 \text{ mg}$  fresh mass. Phytoplankton biovolume data were not available during 2003 and 2004, and hence, our study included 68 samples (four sites  $\times$  19 years – four sites  $\times$  two excluded years) covering 1992 to 2010.

### Data analysis

Trends in temperature were evaluated using the non-parametric Mann–Kendall test (Helsel & Hirsch, 1992), because changes over time did not appear to be linear. Correlation analysis (Pearson correlation,  $r$ ) was performed between all environmental variables and *Microcystis* biovolume and its percentage of the total phytoplankton biovolume. Smoothing trends of the annual biovolume of *Microcystis* spp. and its percentage of the total phytoplankton biovolume were calculated for each five-year increment by applying a smoother (local polynomial regression fitting) with a span equal to 0.8 (Salmaso & Cerasino, 2012). *Microcystis* biovolume was square root transformed before Pearson correlation and smoothing analysis. Chemical determinants (TP, SD, TDP and TDN) were also square root transformed, and other variables  $\log_{10}(x)$  transformed.

Canonical correspondence analysis (CCA) was conducted to examine effects of accumulated spring water temperature, water temperature in May and physicochemical variables (SD, Cond, DO, SS, TN, TP, TDP and TDN) on phytoplankton community composition in May over the past 20 years. To run the analysis, species that contributed more than 1% of total phytoplankton biovolume and occurred in more than 34 of the 68 total samples were included. Hence, eight genera, including *Microcystis*, *Cryptomonas*, *Fragilaria*, *Cyclotella*, *Aulacoseira*, *Planctonema*, *Pediastrum* and *Scenedesmus* were selected and contributed more than 93% of total phytoplankton biovolume in May. All species biovolumes were square root transformed before analysis. Environmental variables were transformed as for correlation analysis. A forward manual selection CCA and Monte Carlo permutation tests identified a subset of environmental variables that explained significant proportions ( $P < 0.05$ ) of the variations in the species data. Hence, TDN, pH and COD were excluded from the final analysis, and TP, SS, Cond, AWT, WT, SD, TN and TDP were included.

Degree days for growth (growing degree days; GDD) are the number of degrees ( $^{\circ}\text{C}$ ), over a given period in days, above a certain threshold temperature (McMaster & Wilhelm, 1997), below which the process of interest does not progress. We calculated GDD in our study, using daily maximum and minimum air temperature, to estimate whether the warming trend would benefit the population growth of *Microcystis*, following eqn 1.

$$\text{GDD} = \left[ \frac{T_{\text{MAX}} + T_{\text{MIN}}}{2} \right] - T_{\text{BASE}}, \quad (1)$$

where  $T_{\text{MAX}}$  is the daily maximum temperature, and  $T_{\text{MIN}}$  is the daily minimum temperature. If  $T_{\text{MAX}} < T_{\text{BASE}}$ , then  $T_{\text{MAX}} = T_{\text{BASE}}$ , and if  $T_{\text{MIN}} < T_{\text{BASE}}$ , then  $T_{\text{MIN}} = T_{\text{BASE}}$ .

Growing degree days (GDDs) are accumulated by adding each day's GDD contribution as the season (here 92 days from March to May) progressed. A higher GDD value during this period means the water temperature was more suitable (i.e.  $>9^{\circ}\text{C}$ ) for *Microcystis* growth during spring, allowing them to leave the sediment; that is, *Microcystis* will benefit from higher GDD.

The Mann–Kendall test was performed with the R statistical software (R Core Team, 2013) using the Kendall package for R; smoothing splines were fitted to every five-year *Microcystis* biovolume using the loess procedure in R. Correlation analyses were conducted using PASW 18.0 (Chicago, IL, U.S.A), graphs drawn with OriginPro 8.0, CCA conducted using CANOCO version 4.5 for Windows (New York, NY, U.S.A).

## Results

### Changes in spring seasonality and *Microcystis* spp. biovolume

Daily air temperature indicated that the onset of the *Microcystis* growing season has occurred earlier over the last two decades ( $P < 0.05$ ). Both accumulated air temperatures and growing degree days (GDDs) increased significantly in the Lake Taihu basin from 1991 to 2010 ( $\tau_{\text{AAT}} = 0.5$ ,  $\tau_{\text{GDDs}} = 0.51$ ,  $P < 0.01$ , results of Mann–Kendall test hereinafter) (Fig. 2).

*Microcystis* biovolume was unimodal in each year of the study (Fig. 3). Biovolume was low in winter and early spring, increased in late spring to reach a maximum in late summer and early autumn. *Microcystis* has recently begun to bloom in May, a month earlier than in the 1990s. The highest *Microcystis* biovolume value in May occurred at THL1 in 2007 ( $7.6 \text{ mg L}^{-1}$ ), when the warmest spring in the last two decades was recorded. According to the smooth splines, *Microcystis* biovolume, and its percentage of the total phytoplankton biovolume in May, has been greater in recent winters and springs (2006–2010) than formerly (1995–2005; Fig. 3).

*Microcystis* biovolume in May, and its percentage of total phytoplankton biovolume, showed significant positive correlations with accumulated water temperature and other water quality variables (Table 1). Higher correlation coefficients were found with water temperature data when 2002 was excluded. Water temperature

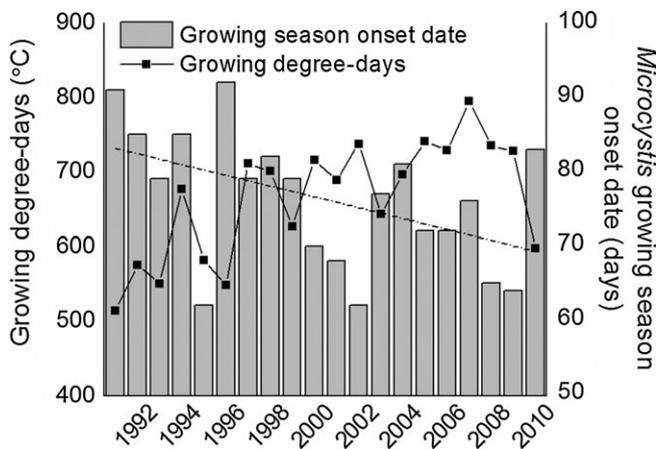


Fig. 2 Onset of the *Microcystis* growing season and growing degree days in spring season (from March to May). The negatively sloping line shows the earlier onset date for *Microcystis* growth ( $y = -0.73x + 1535$ ,  $r^2 = 0.23$ ,  $P < 0.05$ ).

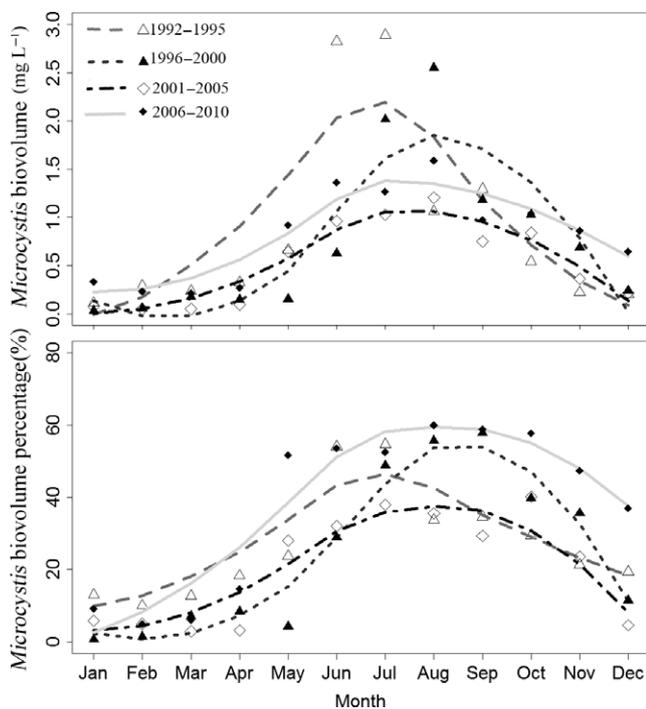


Fig. 3 *Microcystis* biovolume (square root transformed) and its percentage contribution to total phytoplankton biovolume in each month from 1992–2010. The mean value for every 5 years was calculated. Monthly phytoplankton biovolume data showed that earlier *Microcystis* blooms were more frequent after 2005. Smoothing splines were fitted to *Microcystis* biovolume by the loess procedure in R for every five-year interval. Dashed line represents 1992–1995, dotted line represents 1996–2000, dotted-dashed line represents 2001–2005, and solid line represents 2006–2010.

in March 2002 was much higher than in other years (mean water temperature  $16 \pm 0.5$  °C compared with a mean  $\pm$  SE of  $11.6 \pm 1.4$  °C in March of other years),

while water temperature in May was low in 2002 ( $19.8 \pm 0.1$  °C compared to  $21.8 \pm 2.2$  °C in other years).

#### Changes in the phytoplankton and the relationship between spring water temperature and *Microcystis* biovolume in May

Cyanophyta and Chlorophyta have been the two dominant phyla over the past 20 years, followed by Cryptophyta and Bacillariophyta (diatoms). These four phyla accounted for 97% (from 53 to 100% among the 68 samples) of total phytoplankton biovolumes (Fig. 4). Data are shown as mean values for every 5 years.

The length of the first gradient in the detrended correspondence analysis was 2.7 (not shown), and CCA was appropriate (Table 2). The first two CCA axes ordinations accounted for 39.4% of total taxonomic variance. The primary CCA axis ( $x$ -axis,  $\lambda_1 = 0.27$ ) of the biplot was related to represent water temperature and explained 24.4% of the total taxonomic variance. Secondary CCA axes ( $y$ -axis,  $\lambda_2 = 0.17$ ) represented water quality, including nutrient concentrations and conductivity, and explained 15% of the total taxonomic variance. *Planctonema* spp. and *Aulacoseira* spp. seemed more closely related to total phosphorus, while *Microcystis* spp. biovolume showed a positive relationship to water temperature, especially to accumulated temperature in spring season (Fig. 5).

## Discussion

#### Changes in the spring season in Lake Taihu over the last two decades

Our data indicate that the onset of the *Microcystis* growing season in Lake Taihu has advanced by nearly 20 days (Fig. 2), in accordance with observations made on other temperate lakes (Thompson & Clark, 2008). For instance, spring peaks in phytoplankton occurred 20 days earlier in Lake Washington from 1977 to 2002, 30 days earlier in Lake Erken, Sweden, and 30 days earlier in Lake Müggelsee, Germany (Wiedner *et al.*, 2007 and references therein).

The regional shift to an earlier growing season (Fig. 2) and warmer springs seems to be associated with the recently reported global warming trend. In our study, increasing GDDs indicate that warming may have led to relative increases in cyanobacterial dominance, especially by the bloom-forming genus *Microcystis*. This dominance was revealed by Pearson correlation analysis

**Table 1** Pearson correlations between *Microcystis* biovolume and its percentage contribution to total phytoplankton biovolume in May and available environmental variables in May. For brevity, only the statistical significant environmental factors are listed

	AWT	AWT02	WT	Cond	COD	SD	TP
<i>Microcystis</i> biovolume in May	0.28*	0.34**	0.13	0.35**	0.34**	-0.37**	0.31**
<i>Microcystis</i> biovolume percentage in May	0.31**	0.37**	0.28*	0.34**	0.03	-0.23	-0.03
Samples number	68	64	68	68	68	68	68

\* $P < 0.05$ .

\*\* $P < 0.01$ .

AWT, accumulated water temperature in spring; AWT02, accumulated water temperature in spring excluded 2002; WT, water temperature in May; Cond, conductivity in May; COD, chemical oxygen demand in May; SD, Secchi depth in May; TP, total phosphorus in May. *Microcystis* biovolume and its percentage to total phytoplankton biovolume, AWT, AWT02, WT and Cond and COD were square root transformed before analysis, and others were  $\log(x)$  transformed.

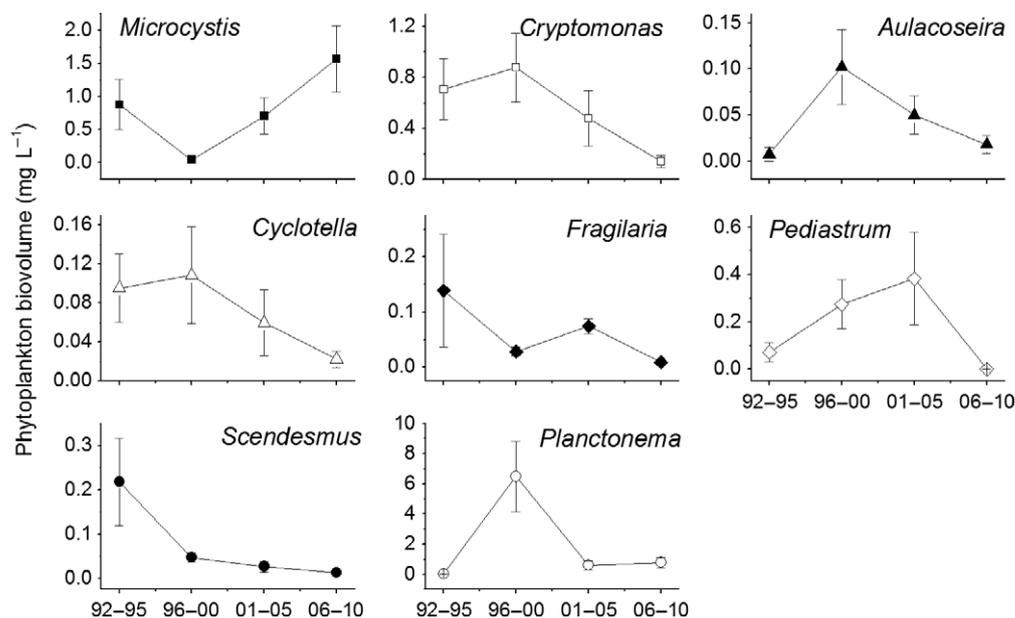
(Table 1), which showed that *Microcystis* biovolume and its percentage of total phytoplankton biovolume in May was significantly related to accumulated water temperature. In addition, the exclusion of the 2002 data might also indicate that either water temperatures in early spring, or in May, were crucial for late blooms.

#### *Microcystis* blooms in Lake Taihu

Both water quality (i.e. eutrophication) and warming have affected phytoplankton succession in spring over last two decades in Lake Taihu (Fig. 5). When TP reached high values in 1996 and 1997, *Microcystis* became less dominant and chlorophytes more dominant (Fig. 4), a finding supported by other studies such as

that of Jensen *et al.* (1994), which indicated that chlorophyte dominance in hypertrophic shallow Danish lakes was attributable to continuous input of nutrients and inorganic carbon (e.g.  $\text{CO}_2$ ) both from the sediment and external sources.

There is general agreement that hypereutrophication is the key factor promoting lake eutrophication and supporting algal blooms. In addition, our results suggest that when nutrients were sufficient, *Microcystis* biovolume was more closely related to accumulated water surface temperature than nutrient concentrations. Approximately  $0.80 \text{ mg L}^{-1}$  total dissolved inorganic nitrogen is needed to sustain a cyanobacterial bloom (Xu *et al.*, 2010). Moreover, through luxury consumption, cyanobacteria can accumulate and store sufficient cellu-



**Fig. 4** Trends in the biovolume of dominant genera in May based on mean values for every five-year interval.

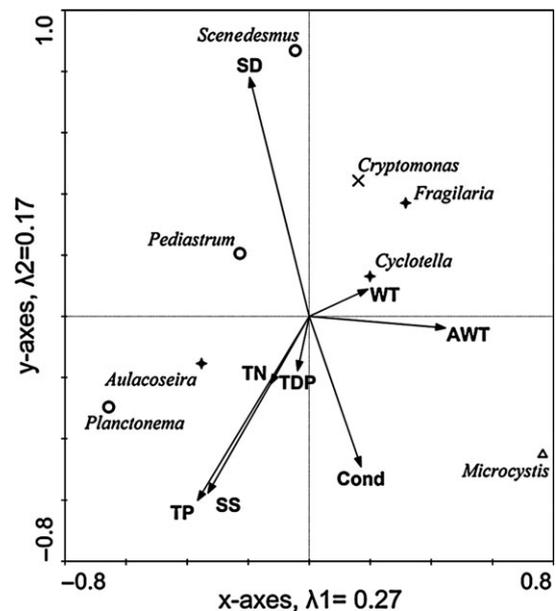
**Table 2** Summary statistics for the first four axes of CCA results and correlations between environmental variable and first two axes. A forward manual selection CCA and Monte Carlo permutation tests identified a subset of environmental variables that explained significant proportions ( $P < 0.05$ ) of the variations in the species data. TP, SS, Cond, AWT, WT, SD, TN and TDP were entered in the final analysis

	Axes		Total inertia
	1	2	
Eigenvalues	0.269	0.167	1.106
Species–environment correlations	0.76	0.782	
Cumulative percentage variance of species data	24.4	39.4	
Sum of all canonical eigenvalues			0.502
AWT	0.45**	-0.04	
WT	0.19	0.09	
TN	-0.13	-0.22	
TP	-0.37	-0.6**	
SD	-0.20	0.78**	
SS	-0.33	-0.58**	
Cond	0.17	-0.49**	
TDP	-0.04	-0.18	

\*\* $P < 0.01$ .

lar P for several rounds of cell division. Under these conditions, their growth potential may not necessarily reflect ambient phosphate concentration (Goldman, Caron & Dennett, 1987); therefore, the current nutrient concentrations in Lake Taihu in May are likely to be sufficient to sustain bloom formation. Nutrient sufficiency probably explains why the onset of blooms was most closely related to accumulated air temperature and GDD in spring. This hypothesis is also supported by previous work, which showed that when nutrients were sufficiently high to sustain blooms, the magnitude, spatial extent and duration of blooms were mainly modulated by physical factors, including temperature and wind-driven currents (Qin *et al.*, 2010). Additional evidence can be found in temperate lakes (Wagner & Adrian, 2009; Huber *et al.*, 2012). The dominant genera *Aphanizomenon*, *Anabaena* and *Microcystis* achieved the highest biomass where nutrients concentrations exceeded certain threshold values.

The effects of global warming on phytoplankton succession, especially increased dominance by nuisance genera such as *Microcystis*, may be cumulative in Lake Taihu. No such phenomenon has been reported for eukaryotic algae, largely because algae are not believed to have distinct stages of development in their life history that might serve as 'receptors' of cumulative temperature effects (Cao *et al.*, 2008); however, rising



**Fig. 5** Ordination biplot from CCA results of phytoplankton with respect to physical and chemical variables. Both species and environment variables were transformed before analysis (see Methods for details). A forward manual selection CCA and Monte Carlo permutation tests identified a subset of environmental variables that explained significant proportions ( $P < 0.05$ ) of the variations in the species data. Secchi depth (SD), conductivity (Cond), suspended solids (SS), total nitrogen (TN), total phosphorus (TP), total dissolved phosphorus (TDP), accumulated water temperature in spring (AWT) and water temperature in May (WT) were entered in the final analysis.

water temperature can increase cyanobacterial growth rates directly (O'Neil *et al.*, 2012). *Microcystis* grows faster when water temperature exceeds 10 °C, and its growth rate increases rapidly when temperature exceeds 16 °C (Jöhnk *et al.*, 2008). Our results indicate that, in Lake Taihu, mean water temperature in March was 11 °C and mean water temperature in April was 17 °C. Hence, even modest of warming during such short but critical periods would benefit *Microcystis* growth rates, and as a result, more small bloom inocula, 'seeds', would accumulate in warmer water columns than cooler ones. Water temperature during May usually rises above 20 °C in Lake Taihu, making it suitable for *Microcystis* bloom development and proliferation. During this period, *Microcystis* is capable of rapid cell division and increases in biovolume, and blooms could occur earlier and more intensively. Further, winter temperature could influence spring phytoplankton development (Adrian *et al.*, 1999; Martens, 2001; Van Beusekom, Loebl & Martens, 2009). Several factors may contribute to this effect of winter temperature. Some of these are zooplankton grazing or benthic filtration which are

sensitive to water temperature (Van Beusekom *et al.*, 2009). In addition, nutrients concentrations and other physicochemical variables in spring may be influenced by temperature in the preceding winter (Martens, 2001).

In polar lakes, climate warming will affect phytoplankton by lengthening of the growing season (earlier ice out date) (Ruhland, Paterson & Smol, 2008) and periods of nutrient loading (Levine & Whalen, 2001) under warmer conditions. In temperate lakes, a seasonal pattern with two plankton biomass peaks – in spring and summer – can shift to one with a single but longer and larger biomass peak as nutrient loading increases. Climate change will exacerbate these trends by increasing nutrient loading (de Senerpont Domis *et al.*, 2012). As an ice-free lake that is located in the subtropical zone, Lake Taihu's cyanobacterial blooms have been affected by climate warming through increasing accumulated water temperature in spring. In contrast to lakes in the temperate and subtropical zones, tropical shallow lakes have been less frequently analysed quantitatively (Verburg, Hecky & Kling, 2003). Effects of climate change alone on shallow lakes might be slight in this area. Hence, Lake Taihu appears to be situated at the southern boundary of a region where climate warming strongly affects shallow lakes.

#### Implications for lake management

In 2007, the Intergovernmental Panel on Climate Change concluded that climate warming is now 'unequivocal', based on observations of increases in global mean air and ocean temperatures, widespread melting snow and ice and a rising global average sea level (IPCC, 2007). Less attention has been paid to the effects of changes in seasonality on cyanobacterial blooms in the subtropic. A median warming of 3.3 °C is projected in East Asia by the end of the 21st century (Solomon *et al.*, 2007), a scenario that will cause rivers, lakes and reservoirs to experience increased temperatures, more intense and persistent thermal stratification, modified hydrology and altered nutrient loading. These environmental drivers will have substantial effects on the growth rate and species composition of freshwater phytoplankton, potentially favouring cyanobacteria over other phytoplankton (Paerl & Huisman, 2008, 2009).

In addition to benefitting cyanobacteria, temperature increases may also lower the nutrient thresholds at which blooms can be initiated and sustained; that is, with higher temperature, cyanobacterial blooms can be initiated and proceed at lower nutrient input rates and concentrations than if temperatures are relatively lower

(Paerl & Paul, 2012). From a nutrient management perspective, this means that nutrient inputs will probably need to be reduced even more aggressively than those projected for today's climate.

In conclusion, in subtropical Lake Taihu, global warming has significantly altered seasonal temperature patterns, with longer periods of high temperature and an earlier and prolonged *Microcystis* growing season. Our study suggests that as previously observed at temperate latitudes, phytoplankton communities inhabiting lower latitude lakes are also susceptible to warming and changes in seasonality.

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