

# Controlling factors of spring–summer phytoplankton succession in Lake Taihu (Meiliang Bay, China)

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**Abstract** The spring–summer successions of phytoplankton and crustacean zooplankton were examined weekly in Meiliang Bay of the subtropical Lake Taihu in 2004 and 2005. During the study period, the ecosystem of Meiliang Bay was characterized by (i) clearly declined nitrogen compounds (nitrate, TN, and ammonium) and slowly increased phosphorus compounds (TP and SRP), (ii) increased total phytoplankton density and rapid replacement of chlorophyta (mainly *Ulothrix*) by cyanobacteria (mainly *Microcystis*), and (iii) rapid replacement of large-sized crustaceans (*Daphnia* and *Moina*) by small-sized ones (*Bosmina*, *Limnoithona*, and *Ceriodaphnia*). Results from the CCA and correlation analysis indicate that the spring–summer phytoplankton succession was primarily controlled by abiotic factors. Cyanobacteria were mainly promoted by increased temperature and decreased concentrations of nitrogen compounds. The pure contribution of

crustacean was low for the variation of phytoplankton suggesting a weak top-down control by crustacean zooplankton in the subtropical Lake Taihu.

**Keywords** *Microcystis* · Crustacean zooplankton · Phytoplankton · Canonical correspondence analysis (CCA) · Lake Taihu

## Introduction

Cyanobacterial blooms have become a worldwide environmental problem (Carmichael, 2001), and the mechanisms and processes involved in the initiation of cyanobacterial blooms are of great concern. There are several hypotheses (e.g. temperature, light, nutrients, grazing pressure, and microbial interactions) to explain the outburst of cyanobacteria in summer (Smith, 1983; Sommer et al., 1986; Carpenter et al., 1987; Scheffer et al., 1997).

In general, temperature was thought to be the most important factor influencing the phytoplankton succession (Abrantes et al., 2006). High temperature tolerance may allow *Microcystis* better survival in warm, shallow, eutrophic environments. Scheffer et al. (1997) suggested that cyanobacteria may be superior light and CO<sub>2</sub> competitors under turbid, CO<sub>2</sub>-depleted conditions. Reynolds et al. (1987) indicated the photo-system and buoyancy regulation of *Microcystis* can allow them to photo-adapt to the extreme light conditions in summer in the subtropical

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lake. Many studies reported that TN/TP ratio plays an important role in cyanobacterial dominance. Smith (1983) reported that bloom-forming cyanobacteria tended to dominate in lakes where the TN/TP ratio was less than 29. However, through an enclosure experiment in Lake Donghu, Xie et al. (2003) indicated that low TN/TP ratio is not a cause but rather a result of *Microcystis* blooms, which cyanobacteria may indirectly enhance the release of P from sediments. In addition, cyanobacterial blooms are sometimes formed rapidly (within days) and can often not be explained by growth of the extant planktonic population alone. Ståhl-Delbanco et al. (2003) suggested that the recruitment of *Microcystis* from sediment to water may be important for initiating and sustaining of blooms. Many cyanobacterial species can produce microcystins, which may act as allelopathic compounds to have negative effects on both micro-invertebrates and photoautotrophic organisms (Leflaive & Ten-Hage, 2007).

On the other hand, grazing pressure is also thought to be an important factor to regulate the phytoplankton structure. Inedible algal species growth can be promoted by the high herbivore grazing pressure for the edible algae in the early summer (Sommer et al., 1986; Lampert et al., 1986). In eutrophic water, planktivorous fish can depress nanophytoplankton predators, such as small cladocerans and rotifers, and thus allow nanophytoplankton to increase (Carpenter et al., 1987; Miura, 1990). Zhang et al. (2006) indicated that small-sized algae were principally regulated by bottom-up forces (nutrients), while the large-sized phytoplankton was regulated both by top-down forces and competition with small-sized algae. However, Ortega-Mayagoitia et al. (2003) indicated that the presence of planktivorous fish and the different composition of zooplankton have minor importance in phytoplankton composition under hypereutrophic condition. Large cladocerans often cannot grow and reproduce fast enough to prevent bloom formation, and they always disappear when the bloom becomes dense (Chow-Fraser, 1986; Gliwicz, 1990). In a canonical correspondence analysis, de Figueiredo et al. (2006) indicated the occurrence of cyanobacterial blooms was an important explanatory variable for the phytoplankton assemblage due to the competitive advantage and/or allelopathy of the bloom-forming cyanobacteria toward microalgae. The mechanisms by which environmental factors affect the phytoplankton succession

are complex (Reynolds, 1999). Phytoplankton succession varies in freshwater according to their limnological features and trophic state (Jensen et al., 1994). Although general hypotheses and patterns of plankton succession are well described in temperate lakes (Sommer et al., 1986), there are still few studies assessing the plankton succession in shallow subtropical lakes.

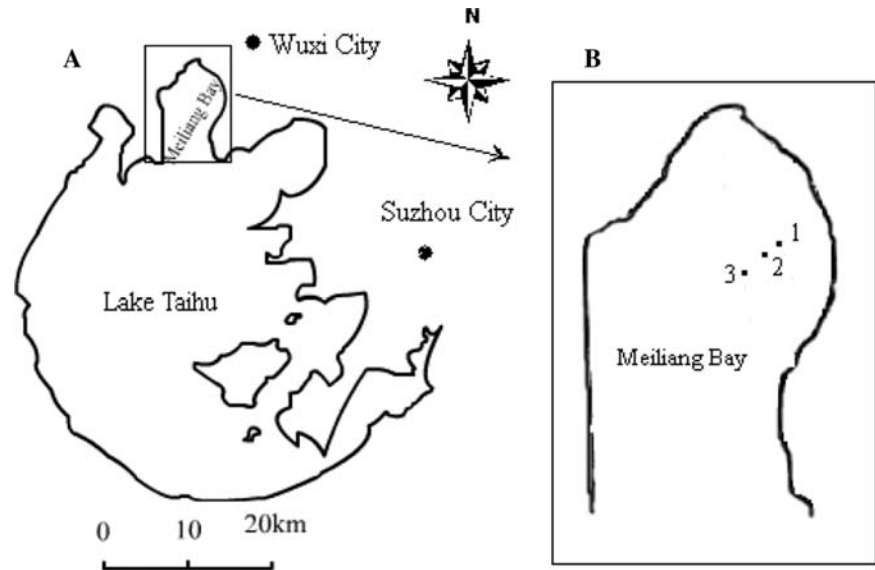
In the present study, we examined the phytoplankton succession during the spring-summer periods in 2004 and 2005 in Meiliang Bay of Lake Taihu. The aim of the present study was to identify the relationships between planktonic succession and their control factors and to increase our understanding of plankton succession patterns in this lake.

## Methods

Lake Taihu (E 30°56′–31°33′, N 119°54′–120°36′), the third largest freshwater lake in China, is located in the south of the Yangtze River Delta. The total area of the lake is 2,338 km<sup>2</sup>, with an average depth of 2 m and a total capacity of 47.6 × 10<sup>8</sup> m<sup>3</sup>. The region of Lake Taihu is situated in the temperate zone and subtropical zone, with a humid and semi-humid monsoon climate. The annual average temperature is 13–16°C, 2–4°C in January and 26–29°C in July. The greatest precipitation occurs during the spring-summer period. The annual average precipitation is about 1,000–1,400 mm (Qin et al., 2004). Meiliang Bay is located in the Northern part of Lake Taihu with a surface area of 100 km<sup>2</sup> and a depth of 1.8–2.3 m, which acts not only as the main water source for Wuxi City but also as an important tourist attraction. In recent years, the occurrence of cyanobacterial blooms has brought severe problems to this region. Heavy *Microcystis* blooms are recorded every year during the warmer seasons (from May to October). Meiliang Bay is in a hypereutrophic status.

We set three sampling stations in the restoration region of Meiliang Bay (Fig. 1). Sampling was carried out weekly between May and July in 2004 and 2005. Integrated water column samples (0.5, 1.0, 1.5 m) from each sampling site were collected with a 5-l modified Patalas' bottle sampler. Surface temperature of the water was measured with a thermometer. pH and conductivity were, respectively, measured by pHB-4pH meter and DDB-303A meter (Leici instrument

**Fig. 1** Sketch map of Lake Taihu and the sampling stations at Meiliang Bay



Co., Shanghai, China). Water transparency was measured with a 20-cm diameter black and white Secchi disk. Soluble reactive phosphorus (SRP) was analyzed by the ammonium molybdate-ascorbic acid method. Total phosphorus (TP) was measured by the same method after persulfate digestion in disposable polycarbonate bottles in an autoclave at 120°C for 45 min. Total nitrogen (TN) was digested with alkaline potassium persulfate and absorbance measured at 220 nm and 275 nm. Nitrate was analyzed using the automated korolev/cadmium reduction method. Ammonium was determined by the Nessler method and nitrite by the a-naphthylamine method (APHA, 1992). For chlorophyll *a* measurements, additional 350-ml sub-samples of the integrated water were filtered through a Whatman GF/C glass fiber filter (0.45  $\mu\text{m}$ ). The filtered water was retained for analysis of the filterable nutrients. The filters were then grounded using 90% acetone in the dark (4°C). The chlorophyll *a* concentrations were determined spectrophotometrically after 24 h extraction in acetone.

For phytoplankton, a 1-l sample was preserved with 1% Lugol's iodine solution immediately after sampling and concentrated to 50 ml after sedimentation for 48 h (APHA, 1992). After complete mixing, 0.1-ml of concentrated sample was counted directly in a 0.1 ml counting chamber under microscope at 400 $\times$  magnification. The algae were counted on a cell-by-cell basis. Colonial *Microcystis* cells were separated using an ultrasonic crusher, JY88-II (Scientiz, Ningbo, China). Taxonomic identification was made according to Hu

et al. (1979). Phytoplankton cells were sized to derive volumes from appropriate geometric shapes. Biomass (wet weight) was calculated assuming a wet weight density of 1 g cm<sup>-3</sup>. Zooplankton was sampled with a 69- $\mu\text{m}$  net and fixed in 5% formalin. Densities were determined by counting all individuals in the sample using microscope at 40 $\times$  magnification. When densities were too high, sub-samples were taken and at least 100 individuals in each sub-sample were counted. Copepods and cladocerans were identified according to Sheng (1979) and Chiang & Du (1979). If possible, up to 30 individuals were measured for body length. Length–weight relationships were used to estimate biomass according to Huang (1984).

Pearson's Correlation Analysis was used to determine the relationships between the physico-chemical parameter and phytoplankton abundance. A series of CCA (canonical correspondence analysis) was performed using CANOCO 4.5 (ter Braak, 1995) to elucidate the relationships between the phytoplankton, zooplankton and environmental variables along the study period. To satisfy the assumption of normality and homogeneity of variance in data, all data were logarithmically transformed before the analyses. The significance of environmental variables to explain the variance of phytoplankton in CCA was tested using Monte Carlo simulations with 499 unrestricted permutations. Variables were considered to be significant when  $P < 0.05$ . Variation partitioning was performed according to the method developed by Borcard et al. (1992).

## Results

### Physical and chemical variables

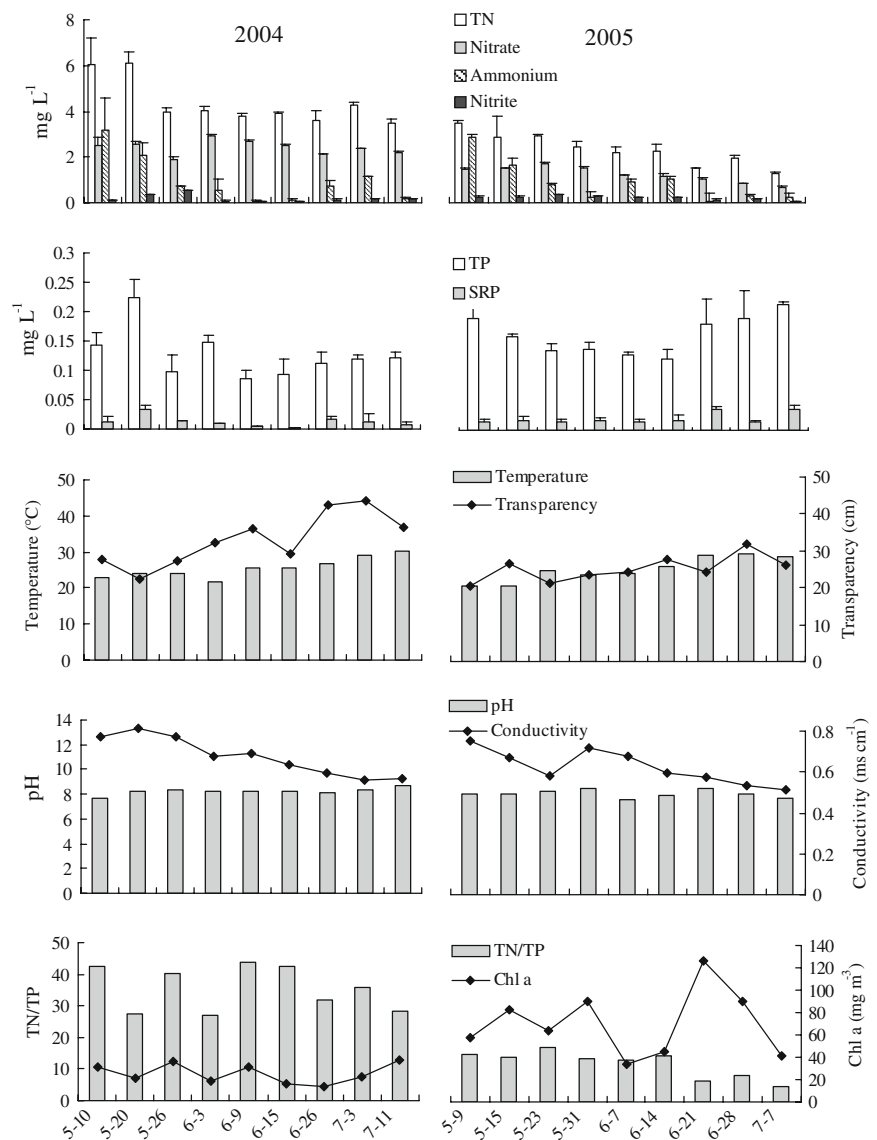
During the study period, the water temperature increased along the sampling period (from about 20°C in early May to 29°C in July, Fig. 2). Transparency and pH did not show significant variations with time. Conductivity of lake water decreased over the season during both years. Water transparency was very low during the study period with Secchi reading usually less than 40 cm. Nitrogen (ammonium, nitrite, nitrate, and TN) showed a decline trend during the

sampling periods. However, phosphorus (TP and SRP) slowly increased over time. TN/TP ratio did not show a clear trend in 2004, but in 2005, these values were strongly reduced over time (down to 5).

### Spring–summer succession of phytoplankton community

During the study period, the algal population of lake water was very abundant with an average biomass of 5.51 mg l<sup>-1</sup> in 2004 and 11.31 mg l<sup>-1</sup> in 2005, respectively. A total of 38 phytoplankton genera were identified in the 2-year samples. They were

**Fig. 2** Variation of physico-chemical characteristics of Meiliang Bay from May to July of 2004 and 2005. Data are mean of the three sites. Error bars represent 1 S.D.



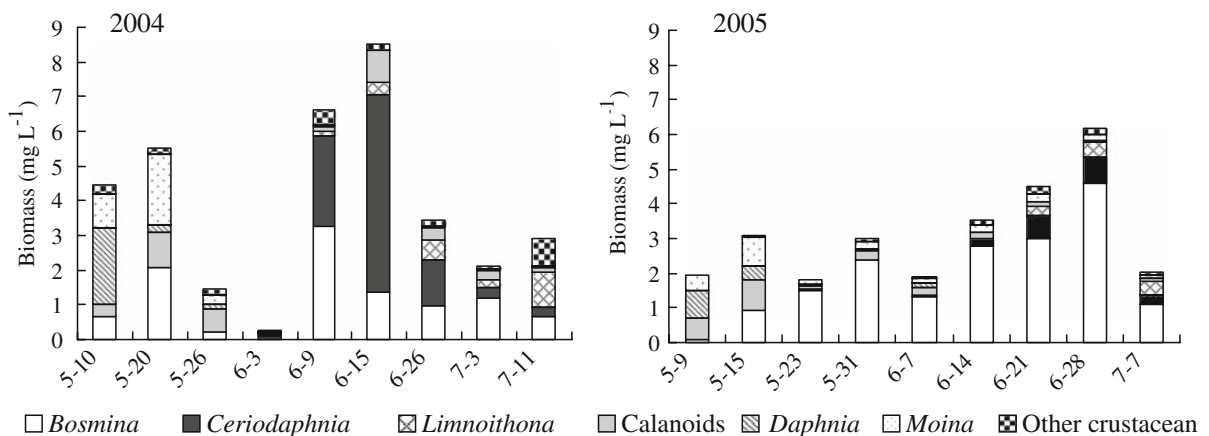
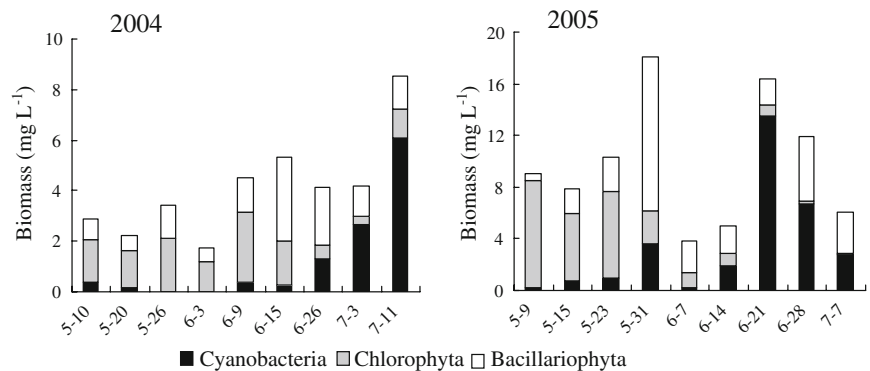
essentially limited to Cyanobacteria, Bacillariophyta, and Chlorophyta. The Cyanobacteria were mainly dominated by *Microcystis*, *Anabaena*, and *Spirulina*. The Chlorophyta community was mainly dominated by *Ulothrix*, *Oocystis*, and *Scenedesmus*. The dominant Bacillariophyta were mainly *Cyclotella* and *Melosira*. The phytoplankton communities drastically changed over time during the study period of both years (Fig. 3). The biomass composition (%) of most abundant phytoplankton genus is shown in Appendix 1. In general, at first, chlorophyta (mainly filamentous *Ulothrix tenerrima*) predominated in the water and constituted more than 50% of the total phytoplankton biomass. However, their abundance decreased over time and their dominance was replaced by cyanobacteria (mainly *Microcystis aeruginos*) in the end of June. Cyanobacteria became to dominate the phytoplankton community from July 3 in 2004 and from May 31 in 2005, respectively. Bacillariophyta biomass

always comprised a considerable proportion of total phytoplankton biomass in all of the time.

Spring–summer succession of crustacean zooplankton community

Crustacean zooplankton community was characterized by low diversity and high abundance in Meiliang Bay during the study period. A total of 17 crustacean taxa were found and the crustacean community was mainly dominated by *Bosmina*, *Ceriodaphnia*, *Limnoithona*, *Daphnia*, and *Moina*. Abundance and composition of the crustacean also showed significant temporal variation (Fig. 4). In general, crustacean zooplankton shifted from large-sized species to small-sized ones. In the first sampling, the large-sized crustaceans (mainly *Daphnia* and *Moina*) dominated the crustacean community, comprising 69% and 64% of the total crustacean biomass in 2004

**Fig. 3** Spring–summer variation of the biomass of main phytoplankton groups from May to July of 2004 and 2005. Data are mean of the three sites



**Fig. 4** Spring–summer variation of the biomass of mainly crustacean zooplankton from May to July of 2004 and 2005

and 2005, respectively. However, their dominance was rapidly replaced by small-sized crustaceans (mainly *Bosmina*, *Ceriodaphnia*, and *Limnoithona*), and in the end of May, *Daphnia* almost disappeared. The total crustacean biomass (excluding *Nauplii*) reached a peak on 15th June 2004 (8.89 mg l<sup>-1</sup>) and on 28th June 2005 (6.25 mg l<sup>-1</sup>), respectively. *Bosmina* reached the highest biomass after the outbreak of *Microcystis* blooms (3.24 mg l<sup>-1</sup> on 9th June 2004 and 4.58 mg l<sup>-1</sup> on 28th June 2005, respectively).

### Correlations and CCA analysis

Total phytoplankton biomass was negatively correlated with nitrate, TN, SRP, and TN/TP, but positively with TP and pH (Table 1). Cyanobacteria were negatively related with ammonium, nitrate, conductivity, TN, and TN/TP, but positively with TP, temperature, and pH. Chlorophyta showed positive correlations with ammonium, conductivity, nitrite, and pH, but negative correlations with temperature and transparency. Bacillariophyta showed negative correlations with ammonium, nitrate, TN, and SRP, but a positive correlation with pH.

Forward selection indicated that nine of the eleven physico-chemical variables (except for TP and SRP) made independent and significant contributions to the variance in phytoplankton data ( $P < 0.05$ , Monte Carlo test). Results from CCA ordination of most abundant phytoplankton genus and environmental factors (physico-chemical variables and crustacean community) indicate that the abiotic factors significantly influenced the phytoplankton community, explaining 63% of the total variance (Table 2 and Fig. 5). The most discriminant variable was temperature, which explained 24% of the total variance followed by nitrate (14%), transparency (5%), ammonium (4%), and nitrite (3%). The crustacean species exerted less influence on the phytoplankton community, explaining 43% of the total variance (Table 2 and Fig. 6). The most discriminant crustaceans were *Limnoithona*, *Ceriodaphnia*, and *Bosmina*. From the results of variation partitioning analysis, the pure contribution of the physical and chemical variables was large (explained 31%), while the pure contribution of the crustacean was low (explained 11%). The total variation, explained by the abiotic and biotic factors and their interaction, was relatively high with a total of 74%.

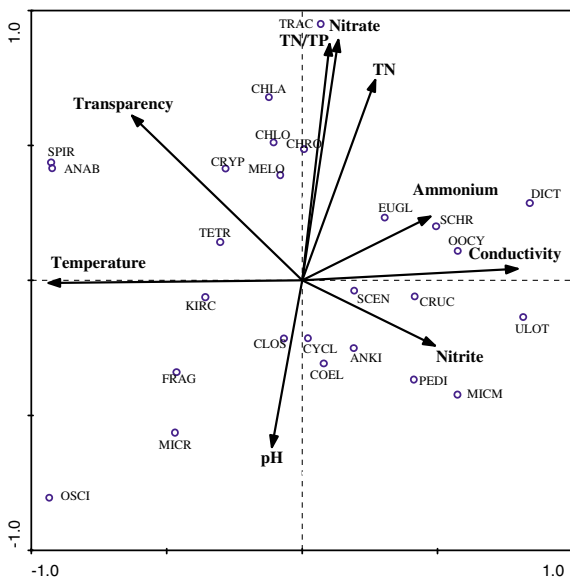
**Table 1** Correlation coefficients between phytoplankton biomass and environmental factors variables

	Ammonium	Nitrate	Nitrite	TN	SRP	TP	Temperature	Transparency	Conductivity	pH	TN/TP
Total phytoplankton	-	-0.434**	-	-0.419**	-0.377**	0.314*	-	-	-	0.764**	-0.389**
Cyanobacteria	-0.303*	-0.346*	-	-0.347*	-	0.350**	0.477**	-	-0.330*	0.544**	-0.344**
Chlorophyta	0.369**	-	0.339*	-	-	-	-0.624**	-0.468**	0.447**	0.275*	-
Bacillariophyta	-0.309*	-0.347*	-	-0.389**	-0.295*	-	-	-	-	0.454**	-
Cryptophyta	-	-	-	-	-	-0.317**	0.443**	0.550**	-0.333*	-	-
Euglenophyta	0.373**	0.318*	-	0.496**	-	-0.408**	-	-	0.399**	-0.314*	0.571**

Data were log transformed before analysis. (\* for  $P < 0.05$ , \*\*  $P < 0.01$ , - not significant,  $n = 54$ )

**Table 2** Summary of CCA analysis between most abundant phytoplankton species and different variables for the studied period

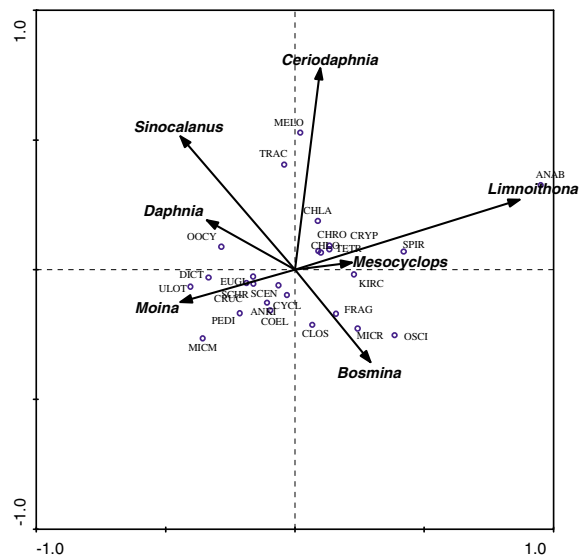
	Physico-chemical factors		Crustacean species	
	Axis 1	Axis 2	Axis 1	Axis 2
Eigenvalues	0.295	0.192	0.229	0.125
Species-environment correlations	0.949	0.938	0.851	0.834
Cumulative percentage variance				
of species data	26.6	44.0	20.7	32.0
of species–environment relation	42.2	69.8	48.7	75.2
Sum of all eigenvalues	1.106		1.106	
Sum of all canonical eigenvalues	0.697		0.471	
Variance explained by the CCA	63.02%		42.59%	



**Fig. 5** Spatial ordination resulting from CCA of most abundant phytoplankton species with respect to physical and chemical parameters. See Table 1 for phytoplankton genus name abbreviations

**Discussion**

In the present study, a clear succession in phytoplankton community was observed in both years: the phytoplankton was dominated by Chlorophyta in spring but rapidly replaced by Cyanobacteria in early summer. Chen et al. (2003) indicated that temperature played an important role in the phytoplankton composition in Lake Taihu. Our results showed that temperature is the most important discriminant variable for the changes of phytoplankton community during the spring-summer succession period.



**Fig. 6** Spatial ordination resulting from CCA of most abundant phytoplankton species with respect to mainly crustacean species. See Table 1 for phytoplankton genus name abbreviations

Many previous studies suggested that cyanobacteria tend to dominate under low TN/TP ratio conditions. However, Reynolds’ objections to a deterministic role for N/P ratios cast many doubts on the theoretical understanding of causal links between the TN/TP ratio and the cyanobacteria dominance in some water bodies (Reynolds, 1999). In Lake Taihu, Dokulil & Teubner (2000) reported that *Microcystis* were usually the dominant contributors to summer plankton even though sometimes TN/TP ratios were much higher. Xie et al. (2003) indicated that the low TN/TP ratio is not a cause but a



result from cyanobacterial dominance, as *Microcystis* can pump up selectively P from the sediments and thus decrease the TN/TP ratio. Takamura et al. (1992) found that in Lake Kasumigaura, the changes of TN/TP ratio were mainly attributed to the fluctuation of nitrogen loading. In the present study, the results of CCA showed TN/TP only explained 2% of the total variance in phytoplankton data. Nitrogen compounds (nitrate, nitrite, and ammonium) explained more than 20% variance of phytoplankton abundance. Moreover, our results (Fig. 2) showed that the decline of TN/TP ratio was mainly attributed to the decrease of nitrate and ammonia during the year 2005. Except for temperature, it can be inferred that cyanobacteria were mainly preceded by the declined concentrations of nitrogen compounds.

In the present study, cyanobacteria exerted most significant influences on *Daphnia* and *Moina*, leading to their rapid disappearance in mid June. Meanwhile, the small crustacean (*Bosmina*, *Ceriodaphnia* and *Limnoithona*) reached a peak with the development of cyanobacterial blooms. Previous studies have found that cyanobacteria can cause rapid decrease of large crustaceans, because of low digestibility, filtration interference, and toxins production (Chow-Fraser, 1986; Carmichael, 2001; DeMott, 1999). In Meiliang Bay of Lake Taihu, Yang et al. (2006) reported that the intracellular microcystins concentration increased from  $0.22 \mu\text{g l}^{-1}$  to  $0.83 \mu\text{g l}^{-1}$  during our study period. Guo et al. (2006) reported that small-sized cladocerans may develop stronger tolerance against toxic *Microcystis* than large-sized ones. In general, phytoplankton diversity is thought to be one of the main factors determining the seasonal succession of crustacean zooplankton (Abrantes et al., 2006). On the other hand, abundant small crustaceans can cause a strong grazing pressure on nanoplankton and may help the development of large non-edible phytoplankton by eliminating competitors for limiting nutrients (McCarthy et al., 2007). According to studies on zooplankton composition and feeding rates of crustaceans, Chen & Nauwerck (1996) indicated that the zooplankton in Lake Taihu could never reach values high enough to control *Microcystis* production. In the present study, total crustacean abundance showed no apparent relation with phytoplankton abundance and chlorophyll *a*. From the results of CCA, the pure contribution of crustacean also was low for the

variation of phytoplankton. It suggested that top-down control by crustacean zooplankton may be weak in the subtropical Lake Taihu.

In conclusion, the phytoplankton communities were mainly determined by nitrogen and temperature during spring-summer season in Meiliang Bay, Lake Taihu. Predation by crustaceans was not important in the regulation of phytoplankton dynamics. The considerable unexplained variation (26%) suggests that some environmental factors (such as light, wind, fish predation, and so on) should be included in a future study.

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