

Large-scale field evidence on the enhancement of small-sized cladocerans by *Microcystis* blooms in Lake Taihu, China

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To assess the effect of *Microcystis* blooms on the crustacean zooplankton community, we conducted a large-scale monthly survey from 2008 to 2010 in Lake Taihu, China. During the sampling period, *Microcystis* was the dominant genus in the phytoplankton community (>79% of total biomass), while the crustacean zooplankton community was dominated by small-sized cladocerans (primarily *Bosmina coregoni* and *Ceriodaphnia cornuta*) and copepods. During the study, plankton exhibited significant spatial heterogeneity. The northern and western regions suffered from harmful *Microcystis* blooms and had higher cladoceran production. In the eastern region where *Microcystis* blooms seldom occurred, copepods accounted for a relatively larger proportion. Both stepwise multiple linear regression and redundancy analysis demonstrated that *Microcystis* was the most important factor controlling the spatial dynamics of zooplankton. Linear regression analysis revealed that both cladocera and copepoda were positively correlated with *Microcystis* and the response of cladocerans ($R^2 = 0.73$, $P < 0.001$) to *Microcystis* was stronger than that of copepods ($R^2 = 0.44$, $P < 0.001$). Our study suggested that cyanobacterial blooms may change competitive relations of small-sized cladocerans and copepoda, favoring small cladocerans (except larger genera).

KEYWORDS: crustacean zooplankton; small cladocerans; copepods; *Microcystis* bloom; Lake Taihu

INTRODUCTION

As cyanobacterial blooms are a significant threat to many eutrophic systems around the world (Verschuren *et al.*, 2002; Paerl and Fulton, 2006; Paerl and Huisman, 2008), the relationship between cyanobacteria and zooplankton has become an important topic (De Bernardi

and Giussani, 1990; Gliwicz, 1990; Wilson *et al.*, 2006). During cyanobacterial blooms, the zooplankton community is generally dominated by copepods, rotifers and small-sized cladocerans (Allen, 1977; Hanazato, 1991; Deng *et al.*, 2008). Cyanobacteria are commonly believed to strongly inhibit large cladocerans and thus

improve the competitive ability of small-bodied cladocerans and copepods (Lampert, 1987; Fulton and Paerl, 1988). However, a few recent studies have suggested that *Daphnia* evolved an increased ability to cope with bloom-forming cyanobacteria in their diets, allowing them to co-exist with cyanobacteria (Hairston *et al.*, 1999, 2001; Sarnelle and Wilson, 2005). In addition, most of the studies on zooplankton–cyanobacteria interactions are based on laboratory experiments or small-scale field studies with *Daphnia* as a model. Hence, effects of cyanobacteria on zooplankton communities are complex in natural systems with a long history of cyanobacterial blooms. To better study the relationship between cyanobacteria and zooplankton, verification from large-scale field surveys is needed.

Lake Taihu has experienced harmful *Microcystis* blooms in the past three decades (Chen *et al.*, 2003; Guo, 2007; Qin *et al.*, 2007; Xu *et al.*, 2010). In contrast to small bodies of water, the large Lake Taihu consists of regions with different trophic status ranging from mesotrophic to hypertrophic. Thick blooms regularly cover its northern region but seldom occur in the eastern region (Duan *et al.*, 2009; Xu *et al.*, 2010). Evident spatial differences of *Microcystis* blooms within the same lake offer an ideal model system to evaluate the effects of cyanobacteria on crustacean zooplankton communities in natural systems. On the other hand, all previous whole-lake surveys on crustacean zooplankton were conducted before the mid-1980s. Several studies on crustacean zooplankton were performed in the lake after the mid-1980s when blooms of *Microcystis* were present, but these were limited to the northern region (Ke *et al.*, 2008; Yang *et al.*, 2009). From previous studies, we found that both abundance and proportion of cladocerans (primarily small variety) have increased dramatically in the past decades. As Richman and Dodson (Richman and Dodson, 1983) attempted to explain a temporal shift from *Daphnia* to copepods in Green Bay, it may be important to find explanations for the patterns in Lake Taihu. Because limited research had focused on the lake as a whole, whether or not the shift in the crustacean zooplankton community was linked to *Microcystis* blooms remains uncertain.

In the present study, we conducted a large-scale systematic survey across the whole of Lake Taihu to investigate whether *Microcystis* blooms played an important role in shaping crustacean zooplankton community structure. The presence of planktivorous fish (Brooks and Dodson, 1965) and high water temperature (Gillooly and Dodson, 2000) during cyanobacterial blooms are also considered as common factors that force dominant zooplankton to shift toward smaller species in natural eutrophic systems. To reduce the

interference of fish and water temperature, this paper provides the results for the same water body along a cyanobacteria gradient. We assumed that an increase in *Microcystis* density would force the crustacean zooplankton community toward dominance by small cladocerans. This study is expected to help in obtaining more details on the interaction between cyanobacteria and zooplankton under complex natural conditions.

METHOD

Study area

Lake Taihu (119°54′–120°36′N, 30°56′–31°33′E) is a subtropical, shallow, highly eutrophic freshwater lake located in the south of the Yangtze River Delta. It is the third largest freshwater lake in China with a surface area of 2338 km² and a mean depth of 1.89 m. Lake Taihu plays an important role in fisheries, water supply, recreation and flood control. Over the past decades, the fisheries within the lake have been highly stressed, with large increases in total fish abundance but a sharp decrease in the number of fish species (Chen and Zhu, 2008a; He *et al.*, 2009).

Sampling and analysis

Sampling was carried out at 30 sites for 23 months from February to December 2008 and from June 2009 to May 2010. Samples from Stations 1–14 were collected monthly throughout the entire study period, and others (15–30) were sampled seasonally in 2008 and monthly for the remaining seasons (Fig. 1). Niu *et al.* (Niu *et al.*, 2011) collected samples monthly from July 2008 to June 2009 at two sites in one of the northern bays (Gonghu Bay). Water samples from each site were collected from the top (i.e. 0.5 m below the water surface) and bottom (i.e. 0.5 m above the bottom of the lake) of the water column using a 5-L Schindler sampler, and they were then mixed together to produce an integrated sample that was used in subsequent analyses.

Values of pH, water temperature, dissolved oxygen, Secchi depth (SD) and conductivity were obtained *in situ* (Tao *et al.*, 2012) and total bacterial abundance was estimated according to Niu *et al.* (Niu *et al.*, 2011). Hydrochemical parameters—including total nitrogen (TN), ammonia nitrogen (NH₄-N), nitrate nitrogen (NO₃-N), nitrite nitrogen (NO₂-N), total phosphorus (TP) and phosphate phosphorus (PO₄-P)—were measured for each sample in the laboratory according to the methods described in detail by Huang (Huang, 1999).

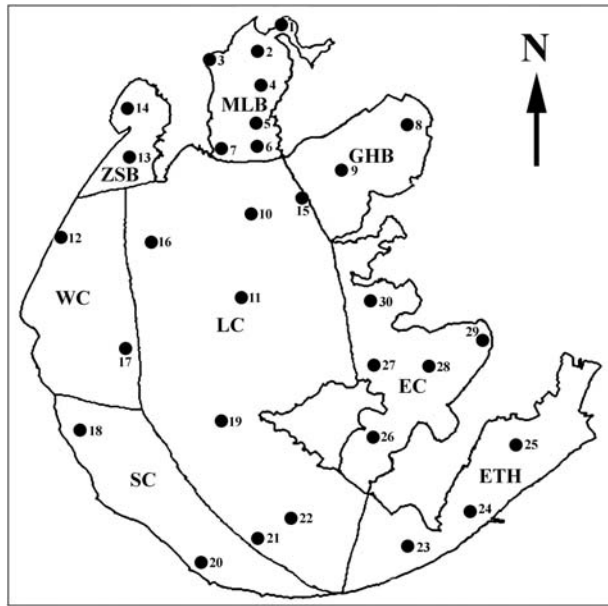


Fig. 1. Sampling sites in Lake Taihu. The lake divisions modified from Kelderman *et al.* (Kelderman *et al.*, 2005) MLB, Meiliang Bay; GHB, Gonghu Bay; ZSB, Zhushang Bay; WC, west coast, SC, south coast; EC, east coast; LC, lake center; ETH, eastern Taihu.

A 1-L phytoplankton sample was preserved in acetic Lugol's solution and concentrated to ~ 50 mL after sedimentation for 48 h. After complete mixing, counts were performed under $\times 400$ magnification using an Olympus microscope. We employed an ultrasonic crusher (JY88-II, Scientiz, Ningbo, China) to separate colonial *Microcystis* cells and counted the single cells. Phytoplankton were identified according to Hu and Wei (Hu and Wei, 2006).

For crustacean zooplankton, quantitative samples were collected by sieving 10-L water samples through a $64\text{-}\mu\text{m}$ plankton net; qualitative samples for species identification were obtained by towing a $112\text{-}\mu\text{m}$ plankton net through the water column. Both quantitative and qualitative samples were fixed in 5% formalin solution. A whole quantitative sample was used to count densities at $\times 40$ magnification (Olympus microscope). When densities were too high, subsamples were taken and at least 100 individuals in each subsample were counted. Crustacean zooplankton were identified according to Sheng (Sheng, 1979) and Chiang and Du (Chiang and Du, 1979). The biomass was calculated using standard length–mass relationships described by Huang (Huang, 1999). If possible, the body length for each species was considered as the average of 30 individuals in each sample.

Statistical analysis

To assess whether specific environmental variables influenced the spatial distribution of zooplankton

communities, we used regression analysis and redundancy analysis (RDA). The spatial variations in all values were calculated as an average of all months. All analysed data were $\log(x + 1)$ transformed prior to analysis to meet normality and homogeneity of variance assumptions. Regressions were performed using SPSS version 16.0 for Windows software (SPSS, Inc., Chicago, IL, USA).

First, we performed stepwise multiple regression analysis with forward selection to identify the most important environmental variables explaining cladoceran% (percentage of cladoceran relative to the total zooplankton biomass), an index of cladoceran dominance. Environmental variables included the phytoplankton biomass, small algae ($\leq 20\ \mu\text{m}$, except *Microcystis*) biomass, *Microcystis* biomass and 13 other abiotic parameters shown in Table I. Variables were selected in the multiple regression only if $P < 0.05$. Secondly, to assess the effects of environmental variables on the zooplankton community as a whole, RDA within CANOCO 4.5 (ter Braak and Smilauer, 2002) was used as the lengths of the DCA axis were short. Dependent variables considered were the biomass of cladocera, *Bosmina coregoni*, *Ceriodaphnia cornuta*, copepoda, *Sinocalanus dorrii* and *Limnithona sinensis*. After a forward selection, the final RDA ordination only included significant independent variables ($P < 0.05$). Lastly, to gain further understanding of the linkage between zooplankton and the most important environmental variables, we employed linear regression analysis.

Table I: The mean and ranges of the abiotic parameters in different areas of Lake Taihu from January 2008 to December and June 2009 to May 2010

| | NB, mean (range) | ETH, mean (range) | SC, mean (range) | WC, mean (range) | LC, mean (range) | EC, mean (range) |
|---------------------------|--------------------|--------------------|--------------------|---------------------|--------------------|--------------------|
| DO (mg/L) | 9.1 (2.1–17.5) | 9.4 (4.4–14.4) | 9.3 (3.2–14.8) | 7.9 (3.7–12.4) | 9.4 (5.0–15.2) | 9.7 (5.1–15.3) |
| pH | 8.1 (7.0–9.6) | 7.9 (7.1–9.2) | 8.0 (7.8–9.0) | 8.0 (7.5–9.1) | 8.1 (7.5–8.9) | 8.1 (7.6–9.5) |
| PO ₄ -P (μM/L) | 1.1 (0.2–5.8) | 0.5 (0.0–1.0) | 0.7 (0.1–1.3) | 1.7 (0.2–3.7) | 0.7 (0.0–3.1) | 0.5 (0.0–1.7) |
| NO ₂ -N (μM/L) | 4.3 (0.5–28.6) | 0.7 (0.0–2.9) | 1.5 (0.0–5.0) | 7.9 (0.0–25.0) | 1.1 (0.0–6.4) | 0.9 (0.0–3.6) |
| NO ₃ -N (μM/L) | 57.9 (0.5–342.1) | 27.1 (0.3–127.1) | 54.3 (0.7–269.3) | 68.6 (4.3–209.3) | 58.6 (0.2–313.6) | 39.3 (0.0–195.0) |
| NH ₄ -N (μM/L) | 65.7 (0.6–439.3) | 23.6 (0.7–236.4) | 23.6 (4.3–60.7) | 112.1 (7.9–267.9) | 34.3 (2.1–485.0) | 20.0 (0.0–130.7) |
| COD (mg/L) | 5.8 (2.7–13.0) | 4.9 (2.3–10.8) | 4.9 (2.1–15.8) | 7.4 (3.0–20.4) | 4.8 (1.6–15.9) | 4.6 (2.2–16.2) |
| TP (μM/L) | 4.6 (0.4–18.2) | 1.9 (0.1–10.4) | 2.8 (0.7–7.7) | 6.9 (1.6–18.3) | 2.4 (0.1–14.9) | 1.8 (0.4–13.7) |
| TN (μM/L) | 247.1 (50.7–812.9) | 122.9 (33.6–401.4) | 201.4 (65.7–407.1) | 342.9 (190.0–615.7) | 177.1 (55.7–458.6) | 128.6 (24.3–396.4) |
| T (°C) | 18.4 (5.0–33.2) | 18.1 (5.6–32.0) | 17.0 (5.0–31.0) | 18.2 (5.1–31.5) | 17.6 (4.8–35.9) | 18.8 (5.5–35.5) |
| SD (cm) | 41 (5–160) | 64 (8–250) | 27 (5–75) | 32 (5–120) | 30 (8–140) | 55 (5–200) |
| Cond (μS/cm) | 525 (51–1100) | 408 (45–565) | 362 (31–550) | 523 (68–829) | 457 (36–765) | 448 (45–632) |
| TN/TP | 33 (7–145) | 57 (13–407) | 44 (15–140) | 28 (9–55) | 43 (12–178) | 47 (4–164) |

NB, northern bays (MLB, GHB and ZSB); Cond, conductivity; DO, dissolved oxygen; SD, Secchi depth, see Figure 1 for the other abbreviations.

RESULTS

Abiotic parameters

The mean and ranges of abiotic parameters during the study period are presented in Table I. Compared with other parameters, TP, TN and SD exhibited higher spatial variability. Higher concentrations of average TN and TP were observed in Zhushan Bay and Meiliang Bay, and on the western coast, whereas lower values were found in the eastern Taihu and the eastern coast. However, average SD showed an opposite pattern of TP and TN in the horizontal distribution. No significant spatial variation was observed in the water temperature, but clear temporal variation was found in the monthly mean temperature, with the highest observed values (>20°C) in the growing season (Table I, Fig. 2A). Data on total bacterial abundance were published by Niu *et al.* (Niu *et al.*, 2011).

Phytoplankton community

Seasonal variations in the composition of the phytoplankton biomass as an average of all stations are shown in Figure 3A. Average total phytoplankton biomass showed remarkable differences between the 2 years, forming 22.42 mg/L in 2008 and 4.10 mg/L from 2009 to 2010. Most variations in the phytoplankton community were primarily caused by cyanobacteria (>81% of the total biomass) and Bacillariophyceae. Bacillariophyta (primarily *Cyclotella* spp.) only dominated in winter and early spring. A biomass peak of cyanobacteria was recorded in May–December 2008 and June–November 2009. *Microcystis* was the dominant genus in the Cyanophyta (>97%); temporal variation of *Microcystis* is displayed in Figure 2A. *Microcystis* exhibited

significant spatial distribution during the study period, and the average *Microcystis* biomass in the Zhushan Bay and Meiliang Bay was nearly 30 times greater than that in the eastern Taihu and on the eastern coast (Fig. 2C).

Crustacean zooplankton community

During the 2-year study, the crustacean zooplankton community of the whole lake was characterized by high abundance and low diversity. Similar to the phytoplankton, zooplankton were more abundant in 2008 (1.97 mg/L) than in 2009–2010 (0.92 mg/L). Crustacean zooplankton showed a similar temporal pattern of high abundance from late spring to autumn with *Microcystis* (Fig. 3C). Cladocerans dominated the crustacean zooplankton community in most seasons (i.e. from March to November 2008, from June to October 2009, and in May 2010). We identified a total of 30 taxa in the study lake: cladocerans and copepods were represented by 19 and 11 taxa, respectively. The most abundant cladoceran species were *B. coregoni* and *C. cornuta*, together comprising 81% of the total biomass. Copepods were dominated by *S. dorrii* (1.25 mm), *L. sinensis* (0.48 mm) and nauplii, which contributed 84% of the total biomass. Several other species such as *Diaphanosoma brachyurum*, *Mesocyclops leuckarti* and *Miona* spp. (*Moina micrura* and *Moina macrocopa*) were common as well. *Simocalanus dorrii* is a relatively large species in the crustacean zooplankton community. The Crustacean zooplankton community in the northern and western regions of the lake was characterized by more cladocerans, and it was substantially different from the eastern region where copepods accounted for a relatively large portion (Fig. 3D). The biomass of cladocerans was ~30

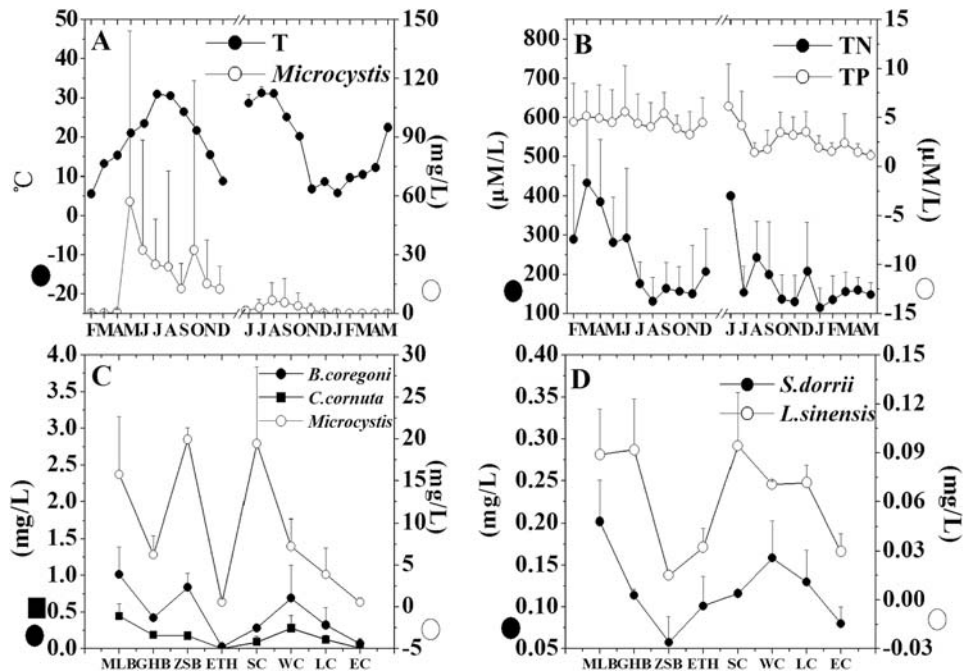


Fig. 2. Temporal and spatial variation of abiotic parameters and dominant species of plankton from January 2008 to December and June 2009 to May 2010 (A) *Microcystis* biomass and water temperature (T), (B) total phosphorus (TP) and total nitrogen (TN), (C) biomass of *B. coregoni*, *C. cornuta* and *Microcystis*, (D) biomass of *S. dorrii* and *L. sinensis*.

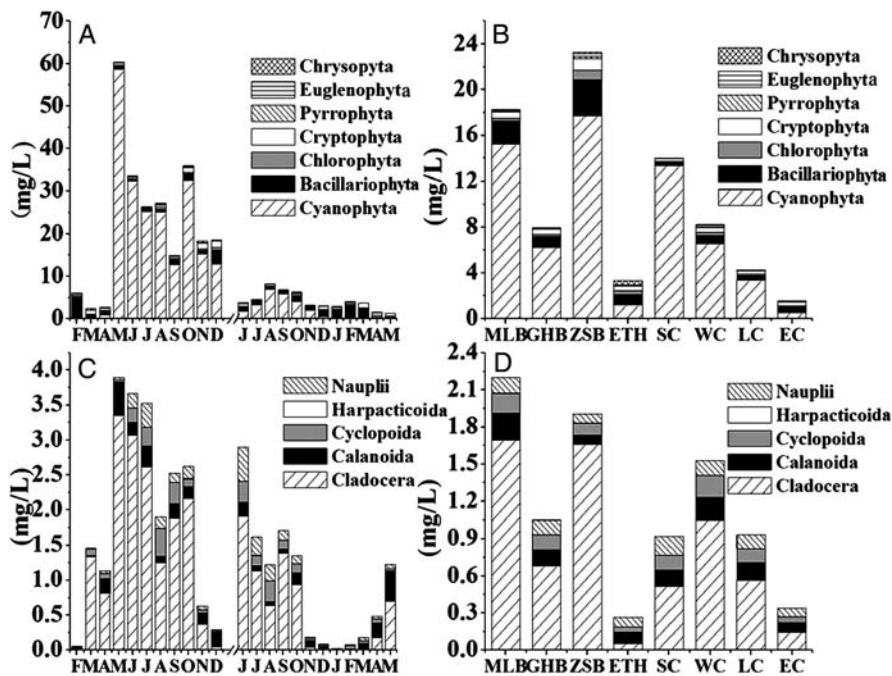


Fig. 3. Seasonal variations in (A) biomass of phytoplankton, (B) biomass of crustacean zooplankton; spatial variation in (C) biomass of phytoplankton, (D) biomass of crustacean zooplankton from February 2008 to December and June 2009 to May 2010.

times higher in Zhushan Bay and Meiliang Bay than in the eastern Taihu.

Statistical analysis

Multiple regression analysis showed that cladoceran% was correlated with three environmental variables (Table II). *Microcystis* accounted for most of the variation in cladoceran% followed by conductivity and SD. After a forward selection, the final RDA ordination only included five significant ($P < 0.05$) independent variables (*Microcystis*, conductivity, PH, COD and SD) which explained 85.9% of variance in the zooplankton community data (Fig. 4). *Microcystis* was the most important factor affecting the crustacean zooplankton distribution. A clear positive relationship was observed between the *Microcystis* biomass and the cladoceran biomass ($r^2 = 0.73$, $P < 0.001$, Fig. 5A). Separating the cladocerans into species likewise revealed highly positive responses for all dominant species (*B. coregoni*; $r^2 = 0.69$, $P < 0.001$, *C. cornuta*; $r^2 = 0.52$, $P < 0.001$) (Fig. 5C and D). However, the relationship between the copepod biomass and *Microcystis* was relatively weak (Fig. 5B, E and F).

Table II: Stepwise multiple regression model details for cladoceran% and environmental variables

| Variables entered | r_{adj}^2 | P-value |
|-------------------|-------------|---------|
| Microcystis | 0.63 | <0.001 |
| Conductivity | 0.78 | <0.001 |
| SD | 0.82 | <.0001 |

Note: Residual df = 26.

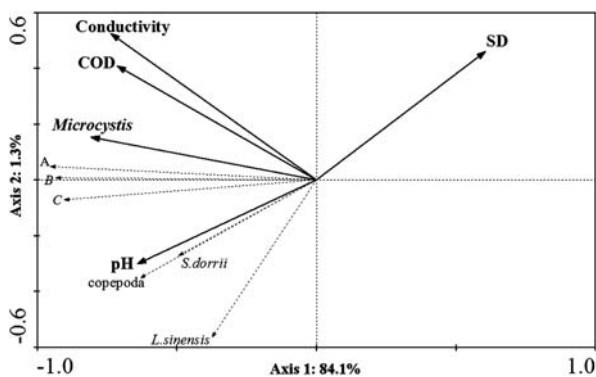


Fig. 4. Redundancy analysis (RDA) biplot based on zooplankton data and environmental variables of Lake Taihu from January 2008 to December and June 2009 to May 2010 A, cladocera; B, *B. coregoni*; C, *C. cornuta*.

DISCUSSION

In the present study, we investigated whether *Microcystis* blooms played an important role in structuring the crustacean zooplankton community in Lake Taihu. The spatial distribution of the plankton community revealed that coincident with the occurrence of massive *Microcystis* blooms, cladocerans dominated the crustacean zooplankton community in the northern and western regions. Copepods accounted for a relatively large portion in the eastern region where blooms were rare. Stepwise multiple regression analysis and RDA verified the importance of *Microcystis* in structuring crustacean zooplankton spatial distribution. Linear regression analysis demonstrated that cladocera showed a more significantly positive response to *Microcystis* compared with copepods. These whole-lake field results supported our hypothesis that *Microcystis* blooms forced the crustacean zooplankton community toward dominance by small cladocerans (except larger genera).

Microcystis has a dominant influence on crustacean zooplankton

The Lake Taihu suffered from harmful *Microcystis* blooms during our study period. The spatial distribution of *Microcystis* (Fig. 2C) was similar to patterns observed in previous studies that revealed greater susceptibility to *Microcystis* blooms in the northern and western regions in recent years (Duan *et al.*, 2009; Xu *et al.*, 2010). Similar to *Microcystis*, both cladocerans and copepods were more abundant in the northern and western regions than the eastern region of the Lake. The spatial distribution of crustacean zooplankton displayed high variability in composition as well (Fig. 3D). The cladoceran biomass was considerably higher than copepods in the northern and western regions of the lake. Nauplii and cyclopoid copepods were relatively more abundant in the eastern region. Similarly, copepods (primarily cyclopoid copepods and nauplii) dominated the crustacean zooplankton group in the lake before the mid-1980s when the lake rarely suffered blooms (Table III). A previous study also suggested that maximum cladoceran production (primarily small species) coincided with the maximum *Microcystis* production in Lake Kasumigaura (Nanazato and Yasuno, 1985).

Both stepwise multiple regression analysis and RDA revealed that *Microcystis*, conductivity and the SD influenced the crustacean zooplankton spatial distribution and *Microcystis* was the most important factor. A previous study also demonstrated that conductivity is one of important factors controlling the distribution of zooplankton (Kessler *et al.*, 2008). A low SD is well known

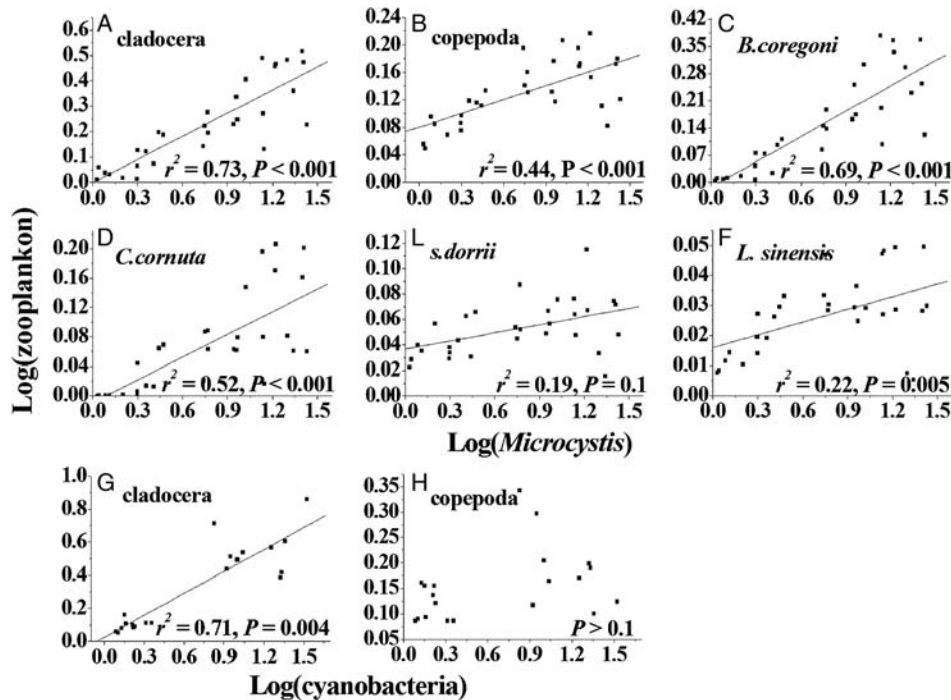


Fig. 5. Results of regression analysis between (A) cladocera and *Microcystis*, (B) copepoda and *Microcystis*, (C) *B. coregoni* and *Microcystis*, (D) *C. cornuta* and *Microcystis*, (E) *S. dorrii* and *Microcystis*, (F) *L. sinensis* and *Microcystis*, (G) cladocera and cyanobacteria, (H) copepoda and cyanobacteria

Table III: Changes in summer crustacean zooplankton community of Lake Taihu over the past 50 years

| Years | Eastern Taihu | | | Western Taihu | | | Sources |
|-------|---------------|----------|---------------------------|---------------|----------|---------------------------|--|
| | Cladocera | Copepoda | <i>Microcystis</i> blooms | Cladocera | Copepoda | <i>Microcystis</i> blooms | |
| 1959 | 8.1 | 61.9 | Rare | — | — | Rare | (Bao and Chen, 1983; Qin <i>et al.</i> , 2007) |
| 1960 | 0.0 | 69.0 | Rare | 40.0 | 99.5 | Rare | (NIGLAS, 1965; Qin <i>et al.</i> , 2007) |
| 1981 | 30.6 | 303.1 | Rare | 77.4 | 308.1 | Rare | (Bao and Chen, 1983; Qin <i>et al.</i> , 2007) |
| 2004 | — | — | Rare | 231.4 | 189.3 | Serious | (Yang <i>et al.</i> , 2009; Duan <i>et al.</i> , 2009) |
| 2008 | 23.7 | 94.7 | Rare | 322.2 | 199.5 | Serious | This paper |
| 2009 | 15.4 | 116.2 | Rare | 232.3 | 215.8 | Serious | This paper |

to provide a refuge wherein crustacean zooplankton can avoid predators (Zaret and Suffern, 1976). Differences in the escape ability of cladocera and copepods (Drenner *et al.*, 1978; Estlander *et al.*, 2009; Kiørboe, 2011) provide a good explanation for the findings. The SD is directly related to algal blooms. When the blooms of *Microcystis* spread, dense surface blooms could dramatically decrease the availability of light underwater (Scheffer *et al.*, 1997; Jacoby *et al.*, 2000). Lake Taihu is a shallow lake, indicating that vertical migration as a means of avoiding predation of crustacean zooplankton is restricted (Castro *et al.*, 2007; Jensen *et al.*, 2010). Thus, cyanobacterial bloom refuge became more important for crustacean zooplankton in the lake where macrophytes appeared to be insufficient in providing a refuge (Schriver *et al.*, 1995). Overall, our results

reinforce the role of *Microcystis* as one of the main drivers of the structure and abundance of the crustacean zooplankton community.

Cladocera were more dependent on *Microcystis* than copepods

Cladocerans exhibited a clear positive correlation to *Microcystis* ($r^2 = 0.73, P < 0.001$, Fig. 5A), whereas copepods showed a weaker positive trend ($r^2 = 0.44, P < 0.001$, Fig. 5B). This agrees with the observations of Deng *et al.* (Deng *et al.*, 2008) that the density of cladocerans showed an 11-fold increase in the early years of the twenty-first century compared with the 1980s, but only a doubling in copepods over the same period in the shallow Lake Chaohu that also experienced harmful

cyanobacterial blooms. Using the data published by Xie and Xie (Xie and Xie, 2002) from the 1970s to the 1990s on Lake Donghu, where heavy cyanobacterial blooms had appeared since the mid-1970s and continued until the mid-1980s (Liu, 1990), we found that the relationship between zooplankton and cyanobacteria was similar with that of Lake Taihu. Cladocerans increased with an increasing cyanobacterial biomass ($r^2 = 0.71$, $P < 0.05$, Fig. 5G), and the copepod biomass varied independently of the cyanobacteria in the lake ($P > 0.1$, Fig. 5H). Similarly to long-term changes of plankton in the eutrophic Lake Dianchi (Li *et al.*, 1963; Wang, 1985; Peng, 1995; Liu *et al.*, 2006; Sun and Yang, 2010), we found that coincident with the appearance of cyanobacterial blooms, small cladocerans increased dramatically and became dominant.

Cladocerans were dominated by small-sized *B. coregoni* and *C. cornuta*. Available evidence indicates that these two species are often associated with cyanobacterial blooms (Allen, 1977). Deng *et al.* (Deng *et al.*, 2008) even found that small-bodied cladocerans, dominated by *B. coregoni* and *C. cornuta*, increased with cyanobacteria in Lake Chaohu. Small cladocerans and copepods are unable to consume large colonies of *Microcystis* and consequently are less affected by them (Fulton and Paerl, 1987; Guo and Xie, 2006). Hence, *Microcystis*–crustacean zooplankton relationships may be indirect in Lake Taihu, whose crustacean community was dominated by small species, especially in the cyanobacterial bloom period. It is well established that cyanobacteria blooms often severely restrict large cladocerans and then improve the competitive ability of small-bodied cladocerans and copepods (Lampert, 1987; Fulton and Paerl, 1988). If that is the case, copepods would have the same benefits as small-bodied cladocerans. Possibly due to the presence of planktivorous fish? large cladocerans have maintained a low proportion in the past 50 years in Lake Taihu regardless of *Microcystis* blooms (Du *et al.*, 1964; Bao and Chen, 1983; Qin *et al.*, 2007; Yang *et al.*, 2009). In addition, high water temperature during the *Microcystis* bloom period may have also limited large cladocerans from occurring (Gillooly and Dodson, 2000). Thus, the argument is far from conclusive since results from other lakes may not apply to Lake Taihu. A key question is why small-bodied cladocerans were more dependent on *Microcystis* compared with copepods.

Microcystis blooms provided a food source for crustacean zooplankton

Relatively little is known why small cladocerans increase with cyanobacteria. However, a few studies suggest that

decomposed cyanobacteria and bacteria may be the main food for cladocerans in eutrophic systems (Nanazato and Yasuno, 1985; Hanazato, 1991). As demonstrated in many studies, cyanobacteria do provide good growth conditions for bacteria (Hoppe, 1981; Heinänen *et al.*, 1995) in Lake Taihu (Li *et al.*, 2010; Niu *et al.*, 2011). It is commonly accepted that protozoa can transfer the carbon and energy of bacteria to zooplankton (Pomeroy, 1974; Azam *et al.*, 1983). Cladocerans have been observed to consume bacteria directly (Sanders *et al.*, 1989). Although Brucet *et al.* found that *Calanipeda aquaedulcis* could feed on bacterioplankton (Brucet *et al.*, 2008), many studies suggested that copepods (Cyclopoida) could not (Sanders *et al.*, 1989; Thouvenot *et al.*, 1999). Different responses to bacteria agree with the food size spectra and feeding behavior of cladocerans and copepods (Geller and Muller, 1981; Sanders *et al.*, 1989).

A clear positive relation was observed between bacterial abundance and the total number of cladocerans ($r^2 = 0.34$, $P < 0.05$), but no evident relationship existed between bacteria and copepods ($P > 0.1$, Table IV) in one bay of the lake from 2008 to 2009 based on data from Niu *et al.* (Niu *et al.*, 2011). This result agrees with the research of Wylie and Currie (Wylie and Currie, 1991), who found that cladocerans were more dependent on the carbon resource of bacteria than copepods. Although certain abundance of small algae was always available, cladocera% was independent of those algae ($P > 0.05$). This finding is in line with the result that cladocerans more easily digested bacteria than algae (Gophen *et al.*, 1974). Our study indicated that bacteria were one of the most important food resources for cladocerans. The opinion that bacteria serve as a food source for cladocerans is commonly accepted with regard to eutrophic lakes (Gliwicz, 1969). Moreover, decomposed *Microcystis* can also be effectively utilized by cladocerans as a food source (Hanazato and Yasuno, 1987; Chen and Xie, 2003). We suggest that in Lake

*Table IV: Partial correlation coefficients (r_{adj}^2) between cladocera and copepoda abundance and bacteria abundance in one Bay of the lake from July 2008 to June 2009 (Niu *et al.*, 2011)*

| | r_{adj}^2 | P | Residual df |
|-----------|-------------|-------|-------------|
| Cladocera | 0.34 | 0.004 | 19 |
| Copepoda | 0.00 | 0.907 | 19 |

Notes: To remove the influence of time and water temperature (T), we used time and T as controlled factor. All values for correlation were log (x + 1) transformed prior to analyses to meet normality and homogeneity of variance assumptions.

Taihu cyanobacterial blooms tend to provide more of a food source for crustacean zooplankton, especially cladocerans.

Effects of fish on the crustacean zooplankton community

Another mechanism that may be responsible for the spatial distribution of crustacean zooplankton is predation (Romare *et al.*, 2003). Unfortunately, fish could not be included as an environmental factor in the analysis because detailed data were lacking. Both the fish biomass (production) and the percentage of planktivorous fish have significantly increased in Lake Taihu since the 1990s (Chen and Zhu, 2008a; He *et al.*, 2009, Mao *et al.*, 2011). The increase in planktivorous fish was mainly due to an increased production of *Coilia ectenes*, showing a 5.7-fold increase in 2008 compared with 1993 (Mao *et al.*, 2011). The percentage of *C. ectenes* of the total production also increased from <25% in 1993 to 63% in 2008. *Coilia ectenes* feeds on zooplankton, especially on small cladocerans (Chen and Zhu, 2008b). Thus, the predation pressure by fish on small cladocerans in Lake Taihu was probably higher in recent years than in the 1990s.

Coilia ectenes is an open-water fish, with relatively high abundance in the center of Lake Taihu (Mao *et al.*, 2011). In 1993, *C. ectenes* comprised 43% of the total fish production in center of the lake, 40% in the northern region and 18% in the eastern region. In 2008, the proportion increased to 80% in the lake center, 70% in the northern region and 44% in the eastern region. Although abundance of planktivores was higher in the center of the lake than in the eastern region, the proportion of small cladocerans was higher in the center of the lake than in the eastern region. On the other hand, the abundance of the planktivorous fish in the northern region was higher in recent years than in the 1990s, but small cladocerans have dramatically increased in recent years. Thus, it seems unlikely that the spatial distribution of crustacean zooplankton is mainly shaped by fish predation.

In conclusion, the spatial distribution of crustacean zooplankton was consistent with developments of *Microcystis* blooms. *Microcystis* blooms provide a source of more food and a low SD refuge for crustacean zooplankton against fish. Compared with copepods, small cladocerans benefitted more from *Microcystis* blooms. Thus, *Microcystis* blooms may enhance competitiveness of small cladocerans compared with copepods. Interactions between small crustacean zooplankton and cyanobacteria are so complex that further comprehensive comparative ecological studies are necessary to

understand the regulation of this important yet poorly understood system.

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