

Field and experimental studies on the combined impacts of cyanobacterial blooms and small algae on crustacean zooplankton in a large, eutrophic, subtropical, Chinese lake

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Abstract Field and experimental studies were conducted to evaluate the combined impacts of cyanobacterial blooms and small algae on seasonal and long-term changes in the abundance and community structure of crustacean zooplankton in a large, eutrophic, Chinese lake, Lake Chaohu. Seasonal changes of the crustacean zooplankton from 22 sampling stations were investigated during September 2002 and August 2003, and 23 species belonging to 20 genera were recorded. *Daphnia* spp. dominated in spring but disappeared in mid-summer, while *Bosmina coregoni* and *Ceriodaphnia cornuta* dominated in summer and autumn. Both maximum cladoceran density (310 ind. l^{-1}) and biomass (5.2 mg l^{-1}) appeared in autumn. *Limnoithona sinensis*, *Sinocalanus dorrii* and *Schmackeria inopinus* were the main species of copepods. *Microcystis* spp. were the dominant phytoplankton species and formed dense blooms in the warm seasons. In the laboratory, inhibitory effects of small colonial *Microcystis* on growth and reproduction of *Daphnia carinata* were more remarkable than those of large ones, and population size of *D. carinata* was negatively correlated with density of fresh large colonial *Microcystis* within a density range of 0–100 mg l^{-1} ($r = -0.82$, $P < 0.05$). Both field and experimental results suggested that seasonal and long-term changes in the community structure of crustacean zooplankton in the lake were shaped by cyanobacterial blooms and biomass of the

small algae, respectively, i.e., colonial and filamentous cyanobacteria contributed to the summer replacement of dominant crustacean zooplankton from large *Daphnia* spp. to small *B. coregoni* and *C. cornuta*, while increased small algae might be responsible for the increased abundance of crustacean zooplankton during the past decades.

Keywords Crustacean zooplankton ·
Cyanobacterial blooms · Small algae · Lake Chaohu

Introduction

The effects of colonial or filamentous cyanobacteria on crustacean zooplankton have been intensively studied in both the laboratory (Fulton and Paerl 1987a, b; Rohrlack et al. 1999; Chen and Xie 2003) and the field (Hanazato 1991; Work and Havens 2003). It is well known that large colonial or filamentous cyanobacteria, such as *Microcystis* and *Anabaena*, are not suitable food for crustacean zooplankton because of their morphology (Gliwicz 1990; Rohrlack et al. 1999; Chen and Xie 2003; Ghadouani et al. 2003) or production of natural toxins (e.g., microcystins) (Rohrlack et al. 2001, 2005). In many eutrophic lakes, crustacean zooplankton suffers from cyanobacterial blooms with replacement of dominant species from large cladocerans to smaller cladocerans, rotifers and copepods (Infante and Riehl 1984; Fulton and Paerl 1987b). However, some small colonial *Microcystis* can be grazed by crustacean zooplankton (Fulton and Paerl 1987a; Jarvis et al. 1987; Chen and Xie 2003). It is also suggested that community structure of crustacean zooplankton under cyanobacterial blooms may be shaped by the numbers of both cyanobacteria and other small algae (Gliwicz 1990; Chen and Xie 2003). Up to now, relevant field studies have mostly been

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limited to temperate and tropical lakes (Infante and Riehl 1984; Hanazato 1991; Scheffer 1998), and are relatively lacking in subtropical lakes.

Lake Chaohu ($117^{\circ}17'–117^{\circ}52'$ E, $31^{\circ}25'–31^{\circ}43'$ N) is a shallow (mean depth 3 m), eutrophic, subtropical lake. It is one of the five largest freshwater lakes in China, with a total surface area of 780 km². Vertical stratification is absent in the lake ($<1^{\circ}\text{C}$ at 1 m intervals) (Deng et al. 2006). It is extensively used as a source for drinking and irrigation, and as a fishery. Eutrophication of the lake water has progressed during the past decades. Cyanobacterial blooms appeared firstly from the beginning of the 1950s, but they were still absent in the pelagic and southern zones of the lake in 1961 (Jin 1995), and in the 1980s, cyanobacterial blooms occurred from May to November each year and throughout the lake (Liu and Meng 1989; Tu et al. 1990). Owing to heavy algal blooms and worsening water quality, the local government has stopped operations of waterworks near Hefei City since 1999 (Zhao et al. 2002). Previous work had indicated that *Microcystis* spp. collected from Lake Chaohu produced microcystins (Carmichael et al. 1988). So far, most studies have been on phytoplankton and water chemistry (Tu et al. 1990; Jin 1995; Xu et al. 2003), but little is known about the changes of other components (i.e., crustacean zooplankton) during the process of eutrophication in the lake.

Crustaceans are an important component of freshwater zooplankton and important food resources for many fishes. However, there has been very limited information on crustacean zooplankton in Lake Chaohu. Investigations in 1981 indicated the presence of 19 species of crustacean zooplankton, with an annual mean density of 29.0 ind. l⁻¹ (Ye; unpublished data). Annual fish yield of the lake was high (8,644 tons) in 2002 (Fishery Administration Committee of Lake Chaohu; unpublished data). Zooplanktivorous fish such as *Coilia ectenes* (comprising 70% of the total fish yield) and *Neosalanx tangkahkeii taihuensis* (about 5%) have been dominant since the 1970s (Wang 1987).

The purpose of this work was to describe seasonal changes of abundance and the species composition of crustacean zooplankton in Lake Chaohu, with an emphasis on the effects of cyanobacterial blooms and small algae on seasonal and long-term changes of crustacean zooplankton.

Materials and methods

Study site

Quantitative samples were taken monthly from 22 sampling stations in Lake Chaohu during September 2002 and August 2003 (Fig. 1), except nine sampling stations (namely 2, 3, 4, 8, 13, 14, 15, 17, 22) in 4 months

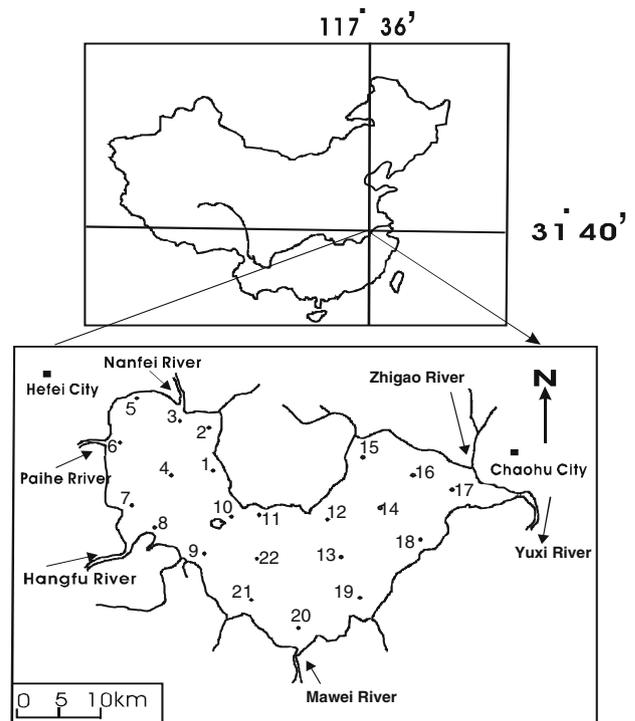


Fig. 1 Map of Lake Chaohu and location of sampling stations (cited from Deng et al. 2007)

(September and November in 2002, and January and March in 2003). Stations 1–8 were situated in the more eutrophic western region of the lake, close to Hefei City, while stations 9–22 were in the less eutrophic eastern region of the lake, near Chaohu City.

Physical and chemical analyses

Water samples for enumeration of phytoplankton and physico-chemical analyses were a mixture of sub-samples taken from the surface to the bottom with a 2.5 l modified Patalas' bottle sampler at 1 m intervals on each occasion. Water temperature, pH and conductivity were measured with a WMY-01 digital thermometer (Medicinal Instruments, Shanghai, China), PHB-4 pH meter (Leici Instruments, Shanghai, China) and DDB-303A conductivity meter (Leici Instruments), respectively, using the mixed water samples in the field. Secchi depth was measured with a Secchi disk.

Lake water for determining orthophosphate ($\text{PO}_4^{3-}\text{-P}$), nitrate ($\text{NO}_3^-\text{-N}$), and ammonium ($\text{NH}_4^+\text{-N}$) concentrations was filtered through Whatman GF/C filters prior to the measurements. Orthophosphate was analyzed by colorimetry after reaction with ammonium molybdate and stannous chloride. Nitrate was measured by the automated Korolev/

cadmium reduction method (Huang 1999). Ammonium ($\text{NH}_4^+\text{-N}$) was determined by the Nessler method (Huang 1999). Total phosphorus (TP) was measured by colorimetry after digestion of unfiltered water samples with $\text{K}_2\text{S}_2\text{O}_8 + \text{NaOH}$ to orthophosphate (Ebina et al. 1983). Total nitrogen (TN) was analyzed by the UV spectrophotometric method (Huang 1999) after the unfiltered water samples had been digested with $\text{K}_2\text{S}_2\text{O}_8 + \text{NaOH}$.

Determination of phytoplankton

The phytoplankton samples were fixed with Lugol's iodine solution and deposited for 48 h prior to being counted under a microscope. Cyanobacterial colonies were split up into cells by sonication. Phytoplankton cell volume was evaluated by determination of the average cell dimensions for each species. Estimations of phytoplankton biomass (wet weight) were according to the method of Shei et al. (1993). Phytoplankton species were identified according to the method of Hu et al. (1980).

Estimations of zooplankton densities

Zooplankton samples were taken with a 5 l modified Patalas' bottle sampler. Each sample was a mixture of several sub-samples collected from the surface to the bottom at 0.5 m or 1 m intervals. One liter of the mixed lake water preserved with Lugol's iodine and formaldehyde on each occasion was transferred into a glass column. After 48 h sedimentation, the supernatant was carefully removed, and the residue was used for the enumeration of copepod nauplii. Cladocerans and copepods, with the exclusion of nauplii, were collected from the remaining 15–20 l of the mixed lake water with a 64 μm mesh plankton net. Zooplankton biomass (wet weight) was estimated according to the method of Zhang and Huang (1991). The crustaceans were identified according to the methods of Jiang and Du (1979) and Sheng (1979).

Microcystins

One liter of the mixed water samples on each occasion was filtered through a glass-fiber filter (Whatman GF/C) and adjusted to pH 7. Each filter was homogenized; 25 ml of 90% methanol was added and the mixture shaken for 3 h three times. After centrifugation, the supernatant was applied to an ODS cartridge (0.5 g) (Dalian Institute of Chemical Physics, The Chinese Academy of Science). The cartridge was eluted with 90% methanol, the eluate was evaporated to dryness, and the residue was dissolved in methanol and then injected into a high-performance liquid chromatography (HPLC) system for determination (Zhen et al. 2004).

Principal component and classification analysis

Multivariate analyses were based on the density of each crustacean zooplankton species obtained from 22 sampling stations ($n = 212$). Log-transformed data [$\ln(x + 1)$] were standardized for principal component and classification analysis (PCCA) with STATISTICA 6.0.

Laboratory experiments

Daphnia carinata used in laboratory experiments were collected from Lake Chaohu. The green alga *Scenedesmus obliquus*, obtained from the Algae Culture Collection of the Institute of Hydrobiology, the Chinese Academy of Science, was used as food for the daphnid. *S. obliquus* was cultured in Shuisheng VI medium (Li et al. 1959), with aeration at $25 \pm 1^\circ\text{C}$ and with a 12 h light:12 h dark (12 L:12 D) photoperiod. Colonial *Microcystis* spp. (90–95% *M. aeruginosa*) were collected from Lake Chaohu during outbreaks of cyanobacterial blooms in June and July. The fresh colonial *Microcystis* spp. were divided into two different-sized fractions ($< 112 \mu\text{m}$ and $> 112 \mu\text{m}$) with a plankton net, and five biomass levels were set (0 mg l^{-1} , 5 mg l^{-1} , 10 mg l^{-1} , 50 mg l^{-1} and 100 mg l^{-1}). To supply sufficient amount of available food, *S. obliquus* (2.0×10^5 cells ml^{-1} or 40 $\text{mg wet weight l}^{-1}$) was added to each treatment. Each treatment consisted of ten *D. carinata* neonates (< 12 h old). The experiments for each treatment were conducted in triplicate using a 400 ml flask filled with 250 ml of filtered (0.45 μm) lake water. The flasks were placed on a shaker, and the experiment was carried out at $25 \pm 1^\circ\text{C}$ under a 12 L:12 D photoperiod. The culture medium was refreshed every day. The experiment lasted for 8 days. The body length of *D. carinata* was measured with an ocular micrometer, and the number of offspring was recorded every 2 days.

Results

Physical and chemical variables

Physical and chemical parameters during the study period are shown in Table 1. The maximum water temperature (approximately 31°C) appeared in July and August, and the minimum (3.3°C) was in January. The highest pH (10.4) appeared during the outburst of cyanobacterial blooms in the western zones of the lake (station 3). The variation in mean water depth was small before June in 2003, but it increased to a maximum of 5.46 m in July, after heavy rainfall. The Secchi depth was usually low, with a mean value of 0.49 m. Conductivity was relatively stable, with a peak value of 472 $\mu\text{S cm}^{-1}$ in July (station 12).

Table 1 Physical and chemical parameters during the study period in Lake Chaohu

Parameters	Stations 1–8		Stations 9–22	
	Range	Mean	Range	Mean
Temperature (°C)	3.3–29.7	16.3	3.6–30.9	17.7
pH	6.92–9.44	7.81	7.41–8.66	8.11
Conductivity ($\mu\text{S cm}^{-1}$)	185.8–400.4	267.7	152.0–345.5	240.3
Secchi depth (m)	0.21–0.49	0.34	0.38–0.85	0.59
Water height (m)	1.66–4.94	2.63	2.70–5.76	3.36
TP (mg l^{-1})	0.112–0.215	0.155	0.052–0.119	0.085
$\text{PO}_4^{3-}\text{-P}$ (mg l^{-1})	0.005–0.045	0.028	0.001–0.016	0.009
TN (mg l^{-1})	1.90–6.09	4.66	0.92–3.23	2.26
$\text{NO}_3^-\text{-N}$ (mg l^{-1})	0.63–2.96	1.91	0.25–2.32	1.15
$\text{NH}_4^+\text{-N}$ (mg l^{-1})	0.13–1.14	0.72	0.05–0.82	0.32

The lake water had relatively high nutrient concentrations except for orthophosphate ($\text{PO}_4^{3-}\text{-P}$), and variations in concentration of these nutrients were quite large (Table 1). Higher TN and $\text{NO}_3^-\text{-N}$ concentrations occurred in winter. The maximum TP concentration (0.215 mg l^{-1}) appeared in the western region during the outburst of cyanobacterial blooms. The average TN and TP concentrations were 4.66 mg l^{-1} and 0.16 mg l^{-1} in the western region, and 2.26 mg l^{-1} and 0.09 mg l^{-1} in the eastern region, respectively, indicating that Lake Chaohu was in a eutrophic–hypereutrophic state.

Phytoplankton

The dominant phytoplankters were cyanobacteria (*Microcystis aeruginosa* Kütz., *M. flos-aquae* Kirch, *Anabaena spiroides* Kleb. and *A. flos-aquae* Breb.), diatoms (*Cyclotella* sp. and *Aulacoseira granulata* Ralfs), green algae (*Pediastrum* sp., *Scenedemus* sp. and *Chlamydomonas* sp.) and cryptophytes (*Chroomonas acuta* Uterm. and *Cryptomonas* sp.).

The seasonal changes in biomass of total algae, small ($\leq 20 \mu\text{m}$) algae and large ($> 20 \mu\text{m}$) algae are shown in Fig. 2. Total algal biomass had two peaks; one peak of 15.7 mg l^{-1} in March, when the centric diatoms were predominant, and another peak of 19.7 mg l^{-1} in June, when the colonial *Microcystis* spp. and the filamentous *Anabaena* spp. dominated. Small algae ($\leq 20 \mu\text{m}$) consisted mostly of Bacillariophyta, Chlorophyta and Cryptophyta. The peak of the small algal biomass (12.1 mg l^{-1}) appeared in March. Afterwards, it decreased sharply and reached the minimum (1.8 mg l^{-1}) in June, during dense cyanobacterial blooms. Large algae ($> 20 \mu\text{m}$) were mainly composed of Cyanophyta, large colonial Chlorophyta and *Ceratium hirundinella* Schr. Large algal biomass was low in April, but it increased

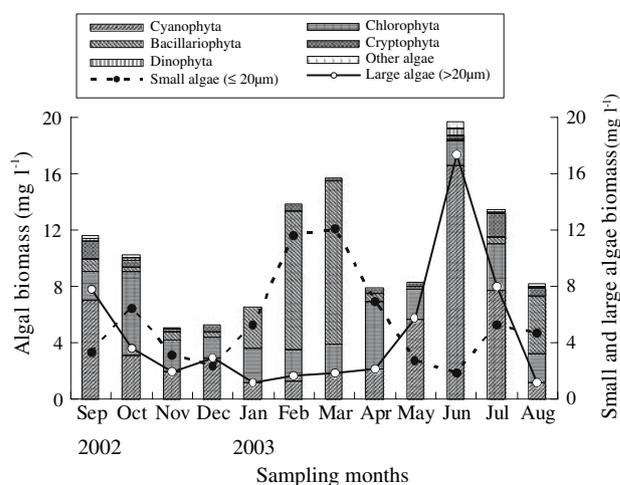


Fig. 2 Seasonal changes in biomass of total, small ($\leq 20 \mu\text{m}$) and large ($> 20 \mu\text{m}$) algae during the study period in Lake Chaohu

rapidly with increasing water temperature, reaching a maximum of 17.5 mg l^{-1} in June.

During the cyanobacterial blooms from May to November, monthly mean concentration of microcystins (MC-LR + MC-RR) in cyanobacterial cells varied between $0.7 \mu\text{g l}^{-1}$ and $3.3 \mu\text{g l}^{-1}$, with a maximum of $17 \mu\text{g l}^{-1}$ in June at station 13. Dissolved concentrations of the microcystins (MC-LR + MC-RR) were less than $20\text{--}30 \times 10^{-3} \mu\text{g l}^{-1}$.

Field observations of crustacean zooplankton

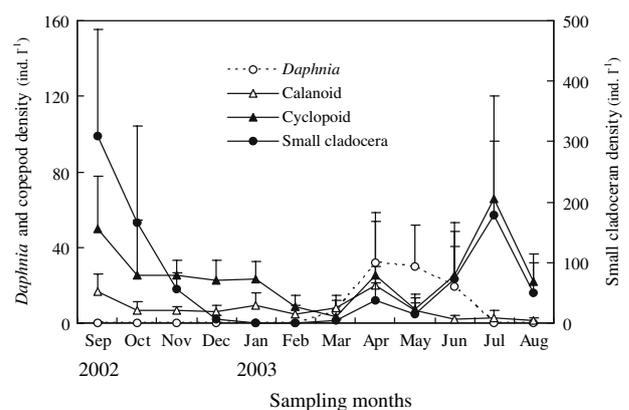
A total of 23 species was recorded (Table 2): 12 species (ten genera) of Cladocera and 11 species (ten genera) of Copepoda. Spatially, the numbers of species in the crustacean zooplankton remained relatively stable at each sampling station, with the range between 17 and 23. Seasonally, the number of species reached the maximum (21)

Table 2 Seasonal occurrence of species density (ind. l⁻¹) and total density (ind. l⁻¹) and biomass (mg l⁻¹) of crustacean zooplankton during 2002–2003

Species name	Months											
	September	October	November	December	January	February	March	April	May	June	July	August
<i>Ceriodaphnia cornuta</i>	86.3	53.7	9.9	0.9					0.3	8.1	91.6	19.8
<i>Bosmina coregoni</i>	163.0	85.2	36.1	5.0	0.2	0.1	2.9	37.8	11.0	60.8	72.2	20.0
<i>Moina micrura</i>	26.0	3.7	1.4					0.01	3.3	0.7	2.6	2.1
<i>Chydorus ovalis</i>	23.7	21.2	8.4	0.2	0.02	0.04	0.2	0.2	0.05	0.2	5.7	5.5
<i>Diaphanosoma brachyurum</i>	10.6	2.2	0.6						0.6	3.3	6.2	3.1
<i>Daphnia pulex</i>							2.1	6.5	0.1			
<i>D. hyalina</i>				0.02	0.02	0.1	0.8	23.9	4.2	0.9		
<i>D. carinata</i>								1.4	25.4	18.5		
<i>Leptodora kindti</i>	0.2	0.05					0.02		0.2	0.02		
<i>Bosminopsis deitersi</i>								0.01	0.2			
<i>Simocephalus vetulus</i>									0.02			
<i>Alona rectangular</i>				0.02	0.06	0.01			0.03		0.03	0.2
<i>Limnoithona sinensis</i>	13.1	12.9	16.5	20.5	22.1	7.8	0.8	0.7	0.5	1.7	12.5	7.9
<i>Sinocalanus dorrii</i>	10.9	3.2	4.0	4.8	8.7	5.5	6.0	19.4	5.3	1.4	1.6	0.7
<i>Schmackeria forbesi</i>	5.0	2.4	2.0	0.7				0.3	0.8	0.3	0.8	
<i>S. inopinus</i>	0.5	1.3	0.4	0.2	0.2	0.2		0.1	0.2	0.1	0.2	0.6
<i>Mesocyclops leuckarti</i>	0.9	3.3	1.8	0.02			2.6	1.4	0.8	0.1	6.2	13.4
<i>Cyclops vicinus vicinus</i>				0.04	0.09	0.3	0.9	0.6				
<i>Thermocyclops taihokuensis</i>	2.5	0.02	0.1					0.07	2.5	1.4	9.4	0.3
<i>Tropocyclops prasinus</i>	7.5	1.0	1.6	1.4				0.8	1.7	22.1	37.3	
<i>Eucyclops serrulatus</i>								0.01	1.1	0.1		
<i>Microcyclops</i> sp.	25.9	8.2	5.0	0.9	0.9		1.0	21.4	1.4	0.2		
<i>Halicyclops sinensis</i>				0.01							0.02	0.1
Number of species	14	14	13	14	9	8	10	17	21	18	14	11
Total crustacean density	376.1	198.4	87.8	34.7	32.3	14.1	17.3	114.6	59.7	119.9	246.5	73.6
Total crustacean biomass	6.7	3.1	1.6	0.5	0.5	0.3	0.8	2.7	1.8	2.6	3.2	1.2

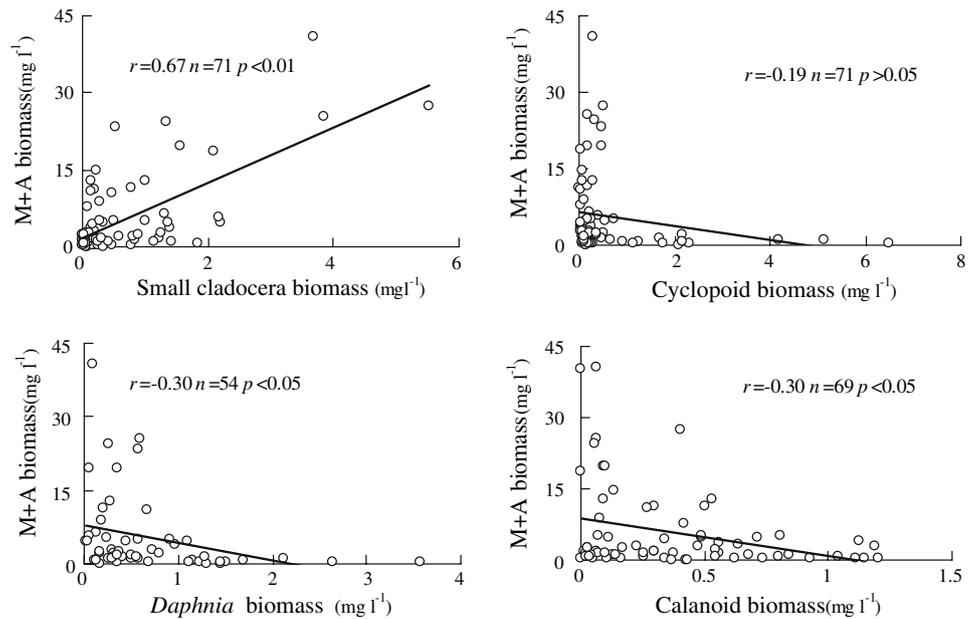
in spring and the minimum (8) in winter. In terms of annual mean density, the dominant crustacean zooplankters were the cladocerans *Bosmina coregoni* (35.9%), *Ceriodaphnia cornuta* (19.7%), *Daphnia* spp. (6.1%), *Chydorus ovalis* (4.8%) and *Moina micrura* (2.9%), and the copepods *Limnoithona sinensis* (8.5%), *Tropocyclops prasinus* (5.3%), *Sinocalanus dorrii* (5.3%) and *Mesocyclops leuckarti* (2.0%).

Small-bodied cladocerans co-existed with cyanobacterial blooms and dominated in summer and autumn, while large-bodied species (such as *Daphnia* spp.) were dominant in spring, accounting for 16.5–49.7% of the total crustacean zooplankton densities (Fig. 3). However, *Daphnia* spp. declined or disappeared in summer (June–July) during the outbursts of cyanobacterial blooms. During the cyanobacterial blooms, biomass of colonial *Microcystis* spp. and filamentous *Anabaena* spp. correlated positively with small cladoceran biomass ($r = 0.67$, $n = 71$, $P < 0.01$) but negatively with the biomass of *Daphnia* spp.

**Fig. 3** Seasonal changes of crustacean zooplankton in Lake Chaohu from September 2002 to August 2003

($r = -0.30$, $n = 54$, $P < 0.05$) and calanoids ($r = -0.30$, $n = 69$, $P < 0.05$) (Fig. 4). In addition, there was no correlation between biomass of colonial *Microcystis* spp. and

Fig. 4 Relationships between biomass of crustacean zooplankton and colonial *Microcystis* (*M*) plus filamental *Anabaena* (*A*) during the cyanobacterial bloom. Lines represent regression line



filamentous *Anabaena* spp. and the biomass of cyclopoids ($r = -0.19$, $n = 71$, $P > 0.05$). Higher density of cyclopoids appeared in summer and autumn, while calanoids were rare in summer (see Fig. 3).

The annual mean density and biomass of total crustacean zooplankton were 115 ind. l^{-1} and 2.07 mg l^{-1} , respectively. Both the maximum density (376 ind. l^{-1}) and biomass (6.7 mg l^{-1}) appeared in September, when the small-bodied cladocerans dominated, and the minimum (14 ind. l^{-1} and 0.3 mg l^{-1}) was in February (Table 2). The annual mean density of copepod nauplii was 55 ind. l^{-1} , with the highest density (207 ind. l^{-1}) in October and the lowest one (4 ind. l^{-1}) in January.

The predatory crustaceans were *M. leuckarti*, *Cyclops vicinus vicinus* and *Leptodora kindti*. The density peak of *M. leuckarti* (13 ind. l^{-1}) appeared in August. *C. vicinus vicinus* were often observed in winter and spring, while *L. kindti* ($<1 \text{ ind. l}^{-1}$) were present at higher temperatures.

Principal component and classification analysis

PCCA identified patterns of variation in the crustacean zooplankton assemblage of Lake Chaohu relative to environmental variables (Fig. 5). The relative positions of the crustacean species on the first two components reflected a temporal progression of species associations throughout the study. Quadrant I included three *Daphnia* species and *S. dorrii*, which were dominant species in spring, and such crustacean species were associated with high TN concentration and abundant small algae (e.g., *C. acuta* and *Scenedesmus* sp.). Predatory *C. vicinus vicinus* had a higher abundance because of sufficient food resources (e.g., *Daphnia* spp.). Quadrant II included several small

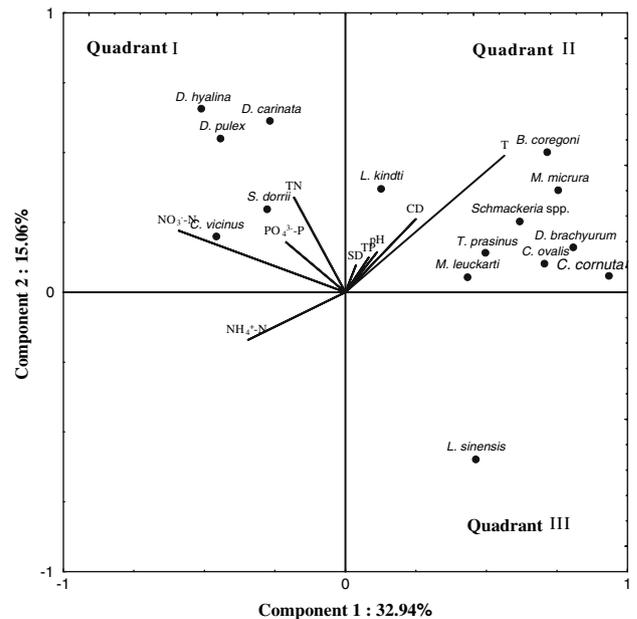


Fig. 5 Principal component and classification analysis plot of the main crustacean zooplankton species against environmental variables, i.e., conductivity (*CD*), Secchi depth (*SD*), temperature (*T*), total nitrogen (*TN*), and total phosphorus (*TP*)

cladocerans (such as *B. coregoni*, *M. micrura*, *Diaphanosoma brachyurum*, *C. ovalis* and *C. cornuta*) and three copepods (*Schmackeria forbsi*, *S. inopinus* and *T. prasinus*), which were dominant species in summer and autumn, and such crustacean species were related to high water temperature, *TP*, *pH*, conductivity and dominant large algae (e.g., *Microcystis* spp., *Anabaena* spp. and *C. hirsundinella*). Quadrant III (*L. sinensis*) held dominant

species in winter, related to low TN concentration and abundant diatom species.

Laboratory experiment

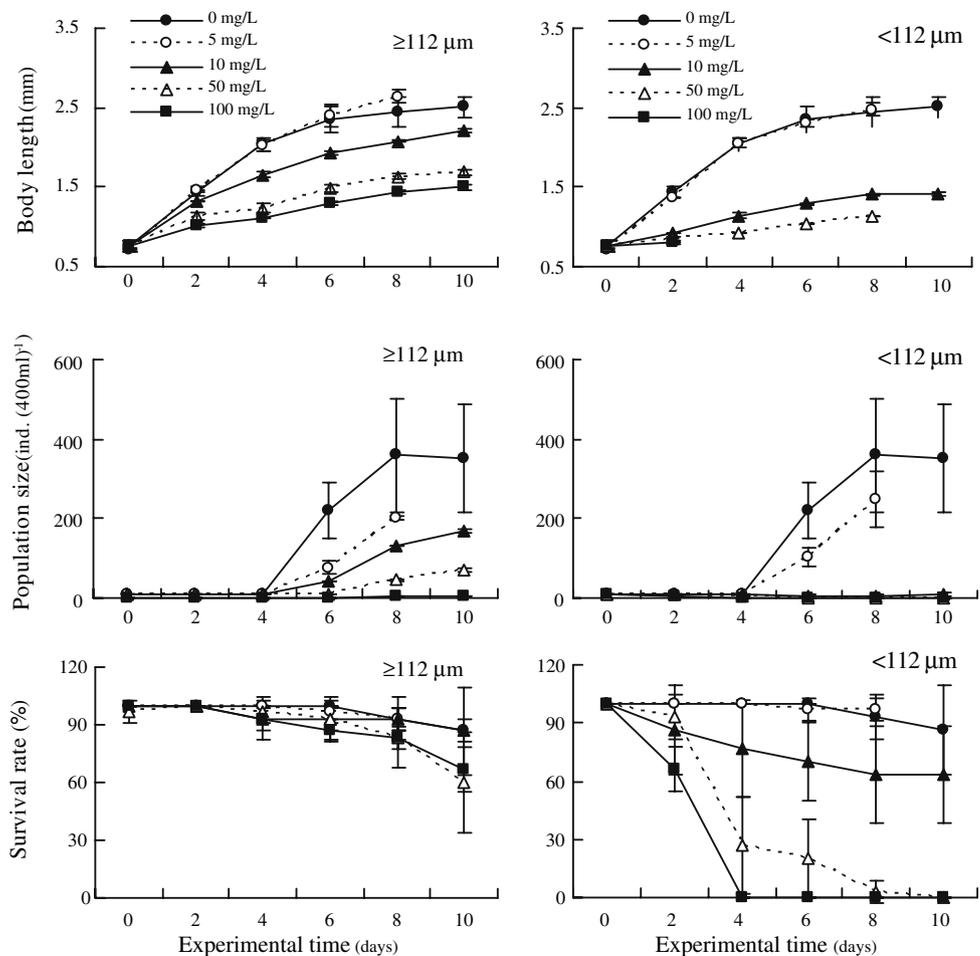
In spite of the sufficient number of *S. obliquus*, the population size of *D. carinata* dropped rapidly with increasing *Microcystis* biomass, while the growth and survival rate of *D. carinata* in the control group were similar to those of the 5 mg l⁻¹ *Microcystis* biomass (Fig. 6). Moreover, with the increase of *Microcystis* biomass, growth, survival and population density of *D. carinata* were more intensely inhibited by small colonial *Microcystis* spp. (< 112 μm) than by large colonial *Microcystis* spp. (> 112 μm) (Fig. 6). The population size of *D. carinata* was negatively correlated with biomass of large colonial *Microcystis* spp. within a range of 0–100 mg l⁻¹ ($r = -0.82$, $n = 5$, $P < 0.05$). There was a negative relationship between the population size of *D. carinata* and biomass of small colonial *Microcystis* spp., although it was not statistically significant ($r = -0.66$, $n = 5$, $P > 0.05$). During the

experiment, microcystin content in small colonial *Microcystis* was 4.49 μg mg⁻¹ dry weight (DW).

Discussion

In Lake Chaohu, seasonal succession of crustacean zooplankton was consistent with the Plankton Ecology Group (PEG) model (Sommer et al. 1986). Large herbivorous species were predominant (e.g., *Daphnia hyalina*, *D. pulex*, and *D. carinata*) in spring, while small herbivores (e.g., *C. cornuta*, *B. coregoni*, *M. micrura*, *C. ovalis*, *D. brachyurum*, *M. leuckarti*, and *T. prasinus*) dominated in summer and autumn, and then some copepods (e.g., *S. dorrii*, *L. sinensis*) reached higher density in winter (Table 2 and Fig. 3). PCCA indicated that water temperature was associated with several summer-predominant taxa (*C. cornuta*, *B. coregoni*, *M. micrura*, *C. ovalis*, *D. brachyurum*, *M. leuckarti*, *T. prasinus* and *D. carinata*), suggesting that water temperature was one of the most important factors affecting seasonal occurrence of crustacean zooplankton

Fig. 6 Effects of large (≥ 112 μm) and small (< 112 μm) colonial *Microcystis* spp. on body length, population size and survival rate of *Daphnia carinata* reared under sufficient supply of *Scenedesmus obliquus* (2.0 × 10⁵ cells ml⁻¹)



(Fig. 5). Since seasonal variations in temperature and nutrients are accompanied by successional shift of phytoplankton community in Lake Chaohu (Deng et al. 2007), seasonal patterns of zooplankton abundance might be shaped by changes in phytoplankton community.

Cyanobacterial blooms are often associated with declines in populations of large-bodied cladocerans and with increased importance of small cladocerans, copepods and rotifers (Fulton and Paerl 1987b). In Lake Chaohu, as *Microcystis* spp. and *Anabaena* spp. were predominant in the warm seasons, and large algal biomass increased quickly from April to June, while small algal biomass dropped rapidly from March to June (Fig. 2). With the outburst of cyanobacterial blooms, dominance of the large-bodied *Daphnia* spp. was replaced by small-bodied species such as *B. coregoni* and *C. cornuta*. Therefore, the increase in density/biomass of colonial or filamentous cyanobacteria and the decrease in small algal biomass exerted great influences on the seasonal variations of crustacean zooplankton in our study lake (Fig. 4). It was also reported that, in Lake Kinner, small grazers such as *Bosmina* and *Ceriodaphnia* were more successful in avoiding the inhibitory effect of filamentous algae than large *Daphnia* were (Hambright et al. 2001). However, Chen and Xie (2003) observed that when edible food was insufficient, population growth rate of the large-bodied *D. carinata* was less affected by the presence of fresh colonial *M. aeruginosa* (64–112 μm) than were the small-bodied cladocerans.

Gliwicz (1990) supposed that there was a critical filament concentration at which *Daphnia* growth rate was halted and reproduction was not possible. It has been widely reported that difference in concentration of cyanobacterial colonies or filaments has obvious effects on the growth and reproduction of the crustacean zooplankton (Infante and Riehl 1984; Dawidowicz et al. 1988; Ghadouani et al. 2003). Dawidowicz et al. (1988) found that when the concentration of filamentous cyanobacteria reached 8×10^7 filaments l^{-1} , growth of *Daphnia magna* halted and their population density decreased obviously. In Lake Valencia, when concentrations of *Lyngbya* and *Oscillatoria* were higher than 9×10^7 filaments m^{-2} , no cladocerans survived (Infante and Riehl 1984). An enclosure experiment also confirmed that large-bodied cladocerans were suppressed strongly by colonial and filamentous cyanobacteria (Ghadouani et al. 2003). Webster and Peters (1978) found that the filtering rate and reproduction of *D. pulex* were more evidently influenced by increasing densities of *Lyngbya* sp. than those of small-bodied cladocerans (such as *Ceriodaphnia* sp. and *Bosmina* sp.). In Lake Chaohu, mean densities of *Microcystis* colonies and *Anabaena* filaments ranged from 6×10^4 to 138×10^4 colonies/filaments l^{-1} at station 5 in June. Such

high densities of cyanobacteria might be a potential factor for the decline of large-bodied *Daphnia* spp. during the cyanobacterial blooms.

The effect of *Microcystis* on *Daphnia* populations also depends on colonial size, biomass and toxicity of *Microcystis*. Several laboratory experiments have confirmed that some large-bodied cladocerans could utilize small colonial *Microcystis*. Chen and Xie (2003) reported that *D. carinata* could use fresh colonial *M. aeruginosa* at a size range of 64–112 μm and at a biomass level of 10 mg l^{-1} . Thompson et al. (1982) observed that small ($< 64 \mu\text{m}$) *M. aeruginosa* colonies were ingested by *D. hyalina*, but large colonies seriously depressed their filtering rate. Jarvis et al. (1987) found that *D. pulex* fed significantly on *Microcystis* colonies of up to 60–100 μm , while colonies of 100–150 μm were not ingested by any zooplankton tested. This was also evident from field observations of *Daphnia* gut contents (Fulton and Paerl 1987a; Work and Havens 2003). In our experiment, the inhibitory effect of smaller *Microcystis* colonies ($< 112 \mu\text{m}$) on the growth, reproduction and survival of *D. carinata* was more than that of larger ones ($\geq 112 \mu\text{m}$) when *Microcystis* biomass was more than 5 mg l^{-1} . In spite of adequate food (2.0×10^5 cells ml^{-1} *S. obliquus*), reproduction of *D. carinata* halted when small colonial *Microcystis* biomass was more than 10 mg l^{-1} , and all daphnids died within 10 days when *Microcystis* biomass was more than 50 mg l^{-1} (Fig. 6). Both our experiment and previous investigation indicated that *D. carinata* could feed and ingest small colonial *Microcystis*, although they might be toxic to *D. carinata* because of microcystin and/or other toxic compounds (Chen and Xie 2004).

In Lake Chaohu, concentrations of microcystins (MC-LR and MC-RR) were high during cyanobacterial bloom from May to July, and they reached $2.8 \mu\text{g l}^{-1}$ in June. Simultaneously, *Daphnia* density declined quickly and disappeared in July. Moreover, some empty ectoblasts of *Microcystis* colonies and decomposed *Microcystis* fractions were observed by microscopy in phytoplankton samples during cyanobacterial blooms, especially in June and July. It implied that some colonial *Microcystis* had decomposed to smaller colonies or single cells at higher temperature (about 30°C). It is likely that *Daphnia* may feed on some smaller colonies or decomposed single cells in the absence of small algae in Lake Chaohu. When *Microcystis* cells are ingested by *Daphnia*, microcystins are rapidly transported from the digestive cavity into the blood, and, consequently, they harm the organisms and affect the beat rates of filter-feeding organs (Rohrlack et al. 2001, 2005). It is more toxic for *D. carinata* to feed on liberated *M. aeruginosa* than on single-celled *M. aeruginosa* (Chen and Xie 2004). Based on survival experiments with *Microcystis* cells and cell extracts, Jungmann (1992) suggested that the toxicity

of *Microcystis* to *Daphnia* is not due to microcystins but to other compounds. Protease inhibitors frequently occur in *Microcystis* and might interfere with the digestion process (Martin et al. 1993) or molting (Rohrlack et al. 2004) of *Daphnia*. A previous investigation had shown that *Microcystis* in Lake Chaohu was toxic to mice (Carmichael et al. 1988). Both our field and laboratory studies and previous investigations indicate that the mid-summer decline or disappearance of *Daphnia* in Lake Chaohu was likely caused by microcystins or other compounds produced by *Microcystis*.

According to unpublished data from the Fishery Administration Committee of Lake Chaohu, the annual fish yield was 8,644 tons in 2002, of which about 75% were two zooplanktivorous fishes (*C. ectenes* 70% and *N. tangkahkeii taihuensis* 5%). According to the surface area of 780 km² and an average water depth of 3 m, the fish yield was 110.8 kg ha⁻¹ or 3.7 g m⁻³ in 2002. Assuming that the exploitation rate by the fishermen was 50% (Shei et al. 1993), the fish biomass during the fishing period was estimated to be 7.4 g m⁻³. Taking the annual fish yield and the exploitation rate into account, fish biomass was > 3.7–7.4 g m⁻³. This was 1.8–3.5 times higher than the monthly mean crustacean zooplankton biomass (2.07 g m⁻³) in this study. The daily food consumption of *C. ectenes* has been estimated at 37.87 g wet weight/100 g body weight in spring and 137.7 g wet weight/100 g body weight in summer (Guo 2005). Gut content analysis of *C. ectenes* suggested that its food items were mainly composed of *Bosmina* and calanoids in summer and autumn, and *Daphnia* spp. in spring (Guo 2005). Therefore, grazing pressure by *C. ectenes* on the seasonal succession of the

crustacean zooplankton (especially *Daphnia*) should be rather strong in Lake Chaohu.

Physiologically limited temperatures for cladocerans have been widely observed in both the laboratory and the field. *Daphnia rosea* cannot survive at 30°C, in spite of abundant food supply, indicating an upper limit of 30°C (Xie et al. 2000). Other *Daphnia* species can grow and reproduce at higher temperature and available food levels, such as *D. hyalina* (30°C) and *D. carinata* (35°C) (Huang 1984), and *D. pulex* (35°C) (Cao et al. 1996). However, it has been observed that net reproductive rate or brood size of daphnids decreases with increasing water temperature (Cao et al. 1996; Huang 1984; Xie et al. 2000). In Lake Chaohu, three *Daphnia* species reached their maxima in April (*D. pulex*, *D. hyalina*) or May (*D. carinata*) and disappeared in June (*D. pulex*) or July (*D. carinata*, *D. hyalina*) when water temperature was below 30°C. Therefore, it seems that water temperature did not reach the physiological limit for the survival of the three *Daphnia* species in Lake Chaohu although the water temperature might have been high enough to cause a decrease in net reproductive rate (Table 1). Based on the above discussions, it is deduced that the quality and quantity of phytoplankton, predation of zooplanktivorous fish, and water temperature, co-controlled seasonal succession of crustacean zooplankton in Lake Chaohu.

Long-term changes in phytoplankton biomass and composition in Lake Chaohu are shown in Table 3. Compared with those in 1980–1981, colonial and filamentous cyanobacterial densities (mostly *Microcystis* and *Anabaena*) were higher in spring and summer in 2002–2003, and the density of small algae (including diatoms, green

Table 3 Long-term changes in abundance (cells or colonies l⁻¹) of four phytoplankton groups during 1980–2000 in Lake Chaohu (*M + A* colonial *Microcystis* and filamentous *Anabaena*, *Baci.* bacillariophyta, *Chlo.* Chlorophyta, *Eugl.* Euglenophyta, *Cryp.* cryptophyta. *Dashes* indicate no data)

Years	Season	M + A	Baci.	Chlo.	Eugl. + Cryp.	References
1980–1981	Spring	10.3	0.35	0.13	0.15	Ye (unpublished data)
	Summer	17.8	0.18	0.18	0.10	
	Autumn	24.76	0.11	0.15	0.15	
	Winter	10.99	0.23	0.11	0.11	
1984	Spring	–	1.47	1.82	0.37	Liu and Meng (1989)
	Summer	–	0.26	13.87	0.28	
	Autumn	–	1.74	39.58	32.27	
	Winter	–	72.51	6.26	3.09	
1987–1988	Spring	–	9.70	43.78	230.05	Tu et al. (1990)
	Summer	–	13.02	19.58	84.32	
	Autumn	–	28.01	35.95	137.88	
	Winter	–	101.12	51.83	66.93	
2002–2003	Spring	13.03	245.19	401.12	84.78	This paper
	Summer	27.90	80.90	272.66	55.29	
	Autumn	12.78	30.92	256.03	62.98	
	Winter	6.55	379.06	520.38	46.51	

Table 4 Average densities of cladocerans and copepods in the four seasons during 1980–1981 (Ye; unpublished data) and 2002–2003 in Lake Chaohu

Season	Cladocerans (ind. l ⁻¹)		Copepods (ind. l ⁻¹)	
	1980–1981	2002–2003	1980–1981	2002–2003
Spring	27.6	40.4	24.3	23.8
Summer	7.9	207.1	16.4	42.8
Autumn	3.7	177.4	10.5	43.5
Winter	0.4	2.3	16.1	23.8
Annual mean	11.4	106.8	17.5	33.5

algae and dinoflagellates) also increased obviously in 2002–2003. The density change in crustacean zooplankton was consistent with that of small algae. The density of cladocerans was 11-times higher in 2002–2003 than in 1980–1981, and an increase of two times was observed for copepods (Table 4). On the other hand, annual fish production in Lake Chaohu has also witnessed a steady increase since the 1970s (Wang 1987). It is likely that the long-term increase in abundance of crustacean zooplankton in Lake Chaohu has been associated with an increase in the availability of small algae, consequently also leading to increased fish production.

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