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Seasonal dynamics of crustacean zooplankton community structure in Erhai Lake, a plateau lake, with reference to phytoplankton and environmental factors*

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Abstract The seasonal dynamics of a crustacean zooplankton community in Erhai Lake was investigated from May 2010 to April 2011. In total, 11 species were recorded, including six (6 genera) cladoceran and five (5 genera) copepod species. The crustacean zooplankton densities ranged from 24.3 to 155.4 ind./L. In winter and spring, the large-bodied cladoceran *Daphnia galeata* dominated the crustacean plankton community. In summer and autumn, when the colonial or filamentous algae dominated the phytoplankton communities, the small-bodied species (e.g. *Bosmina fatalis*, *Ceriodaphnia quadrangular*, and *Mesocyclops leuckarti*) replaced the large-bodied ones. One-way ANOVA and redundancy analysis revealed that community structure was dependent upon total nitrogen, total phosphorus, water temperature, transparency, and the biomass of small algae. The variation in both phytoplankton structure and environmental variables were important factors in the seasonal succession of crustacean zooplankton structure in Erhai Lake.

Keyword: Erhai Lake; crustacean zooplankton; community structure; seasonal dynamics

1 INTRODUCTION

Crustacean zooplankton play an important role in the structure and function of lake ecosystems, since they link primary producers to higher consumers (Lampert, 1997). Nutrients, phytoplankton, and fish are crucial regulators of zooplankton community structure (Sterner et al., 1993; Vanni et al., 1997; Deng et al., 2008). Usually, large colonial *Microcystis* and filamentous *Anabaena* are unsuitable food for crustacean zooplankton due to their morphology (Gliwicz, 1990; Chen and Xie, 2003). In some eutrophic lakes, the crustacean zooplankton community structure changes from large cladocerans to smaller ones, copepods, and rotifers during cyanobacterial blooms (Infante and Riehl, 1984; Fulton and Paerl, 1987; Deng et al., 2008). Fish also regulate crustacean zooplankton abundance through top-down effects (Vanni et al., 1997).

In August of 1957, the dominant crustacean zooplankton species in Erhai Lake included Cyclopoida, Calanoids, *Bosmina*, *Daphnia*, *Diaphanosoma*, and *Chydorus*. Copepod density was low, while that of the cladocera was high, with an average of 120 ind./L reaching 200 ind./L in the middle of Erhai Lake (Li et al., 1963). In 1980, cladocera and copepoda densities were 80 and 155 ind./L, respectively (Wu and Wang, 1999). *Neosalanx tangkahkeii taihuensis* was introduced to Erhai Lake in 1984 and produced a yield of 650 t in 1996 (Du, 1997). The introduction of *N. tangkahkeii taihuensis* greatly reduced zooplankton density in the Lake. In 1992 and 1997, the cladoceran and copepod densities and wet weights declined because of predation by *N. tangkahkeii taihuensis* (Wu and Wang, 1999).

Erhai Lake was an oligotrophic-mesotrophic lake

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in 1985, becoming mesotrophic by 1988 (Du, 1992). Total phosphorus (TP) concentration was 0.011 mg/L and 0.005 mg/L in 1982 and 1983, respectively (Jin, 1995). During 1992 to 2001, total nitrogen (TN) and phosphorus (TP) increased year by year, and water quality had changed from mesotrophic to eutrophic (Han et al., 2005). According to Yang (2006), the average TP concentration in the lake was 0.031 mg/L with a spatial distribution being higher in the southern and northern zones and lower in the middle. The average TN concentration in the lake was 0.574 mg/L with a similar spatial distribution characteristic to TP. Eutrophication and predation pressure by *Neosalanx* may have changed the structure of crustacean zooplankton and phytoplankton since 1984 in Erhai Lake.

This paper aims to investigate (1) the spatial and temporal variation of the Erhai Lake crustacean zooplankton community; (2) assess the influence of phytoplankton and environmental factors on the seasonal dynamics of crustacean zooplankton; and (3) provide an important reference for the monitoring and management of the fisheries and water quality of Erhai Lake. Since Erhai Lake has evolved towards a more eutrophic status, we also attempted to evaluate how this evolution has affected the zooplankton community.

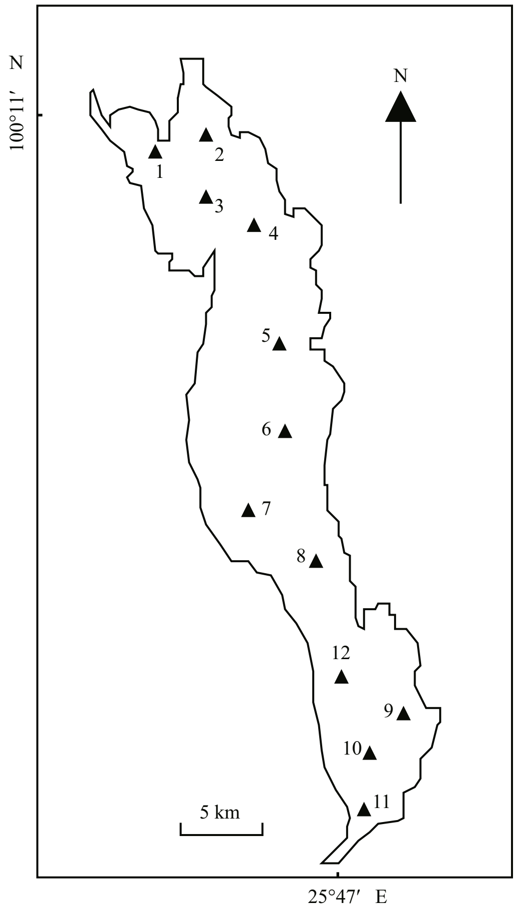

Fig.1 Geographical location of Erhai Lake and sampling stations

2 MATERIAL AND METHOD

2.1 Sampling sites

Erhai Lake (100°06′–100°18′E, 25°36′–25°58′N) is the second largest freshwater lake in Yunnan Province, situated in the heartland of Dali Bai Autonomous Prefecture, which is across Eryuan county and Dali city. The area of Erhai Lake is 249.0 km^2, with an average depth of 10.17 m. The climate in the area is subtropical plateau monsoon, and vertical distribution of water temperature is mainly equal and thermotropic (Wang and Dou, 1998). According to the lake morphology, it is divided into the northern, middle, and southern regions (Li et al., 1999). The circulation in the northern region exhibits vertical distribution, while it is anticlockwise in the middle region and cyclonic in the southern region. However, the circulation in the bottom layer is contrary to that in the surface layer (Du, 1992). Moreover, the northern area is mainly cultivated land and the southern area is near the city of Dali. The trophic levels of both the northern and southern regions are higher than that of the middle region (Yin et al., 2011).

Prior to the 1970s, Erhai Lake had good water quality and was the main potable, irrigation, and industrial water source for the areas surrounding the lake. Since the 1990s, the aquatic vegetation has decreased substantially, and water quality has seriously degraded. Cyanobacterial blooms occurred in 1996 and the autumn of 2003 (Lü et al., 2010).

The seasonal dynamics of the Erhai Lake crustacean zooplankton community were investigated from May 2010 to April 2011. The samples were collected from 12 sampling stations each month (Fig.1). Stations 1–4 are situated in the northern region of the lake, stations 5–8 and 9–12 were in the middle and southern regions, respectively.

2.2 Analysis of physico-chemical parameters

Water samples were collected from the surface to the bottom in a 5-L modified Patalas' bottle sampler at 2 or 4 m intervals at each sampling station, a mixed sample was also obtained for phytoplankton and physico-chemical analyses. pH, water temperature, and transparency were measured with a PHB-4 pH meter (Shanghai, Jinpeng), WMY-01 digital thermometer (Shanghai Medical Instrument Factory), and a Secchi disk, respectively. The mixed lake water was filtered through Whatman GF/C filters (Whatman International Ltd., Maidstone England) prior to nitrate (NO_3^--N), ammonium (NH_4^+-N), and orthophosphate (PO_4^{3-}-P) measurements. Nitrate (NO_3^--N) was analyzed by the automated cadmium reduction method, and ammonium (NH_4^+-N) by the Nessler method (Huang, 1999). Orthophosphate (PO_4^{3-}-P) was determined by colorimetry after the water sample had reacted with ammonium molybdate and stannous chloride. TP was analyzed according to the method of Ebina et al. (1983). TN was measured by the UV spectrophotometric method (Huang, 1999) after the digestion with $K_2S_2O_8$+NaOH. Chemical Oxygen Demand (COD) was analyzed by the potassium dichromate ($K_2Cr_2O_7$) method after digestion.

2.3 Measurements of phytoplankton and chlorophyll *a*

A one-liter phytoplankton sample was preserved with Lugol's iodine solution at each sampling station. The supernatant was suctioned after 48 h sedimentation, and the remainder was gathered. *Microcystis* colonies were split up into cells by sonication at a frequency of 6 times/min and an exposure time of three minutes. Phytoplankton cell volume was obtained by measuring the average cell dimensions for each species. Phytoplankton bio-volume (wet weight) was evaluated according to Shei et al. (1993). Phytoplankton species identification was performed according to Hu et al. (1980).

For chlorophyll *a* (Chl-*a*) measurements, the 500 mL mixed samples were filtered through a Whatman GF/C glass fiber filter (1.2 μm). The filters were then extracted using 90% acetone in the dark (4°C). Following a 24 h extraction, the samples were centrifuged for 10–15 min (4 000 r/min), and the supernatant solutions were eluted. The Chl-*a* concentrations were spectrophotometrically determined.

2.4 Estimations of crustacean zooplankton

When collecting qualitative samples of crustacean zooplankton, a #13 plankton net (mesh size 112 μm and an open diameter of 20 cm) was thrown into water and ∞-curves were made repeatedly to collect the samples. When collecting quantitative samples, crustacean zooplankton samples were collected in a 5-L modified Patalas' bottle sampler at depths of 0.5, 4, and 8 m, except at sampling stations 6 (0.5, 4, 8, and 18 m) and 11 (0.5, 2, and 4 m). Subsequently, 15–20 L of mixed lake water was filtered through a 64-μm mesh plankton net. The samples were fixed in 5% formaldehyde solution. The phytoplankton samples were also used for the enumeration of copepod nauplii. The biomass of crustacean zooplankton (wet weight) was evaluated according to the method of Zhang and Huang (1991). The identification of crustacean zooplankton was according to Jiang and Du (1979) and Sheng (1979).

2.5 Shannon-Weiner diversity index (*H'*)

$$H' = -\sum_{i=1}^{s} p_i \log_2{}^{p_i} ,$$

where *s* represents species number, P_i represents the proportion of *i* species densities among total crustacean zooplankton densities in the sample. *H'* was used to evaluate water quality (>4.5: cleanliness; 3–4.5: slight pollution; 2–3: moderate pollution; 1–2: heavy pollution; <1: severe pollution) (Zheng et al., 2007).

2.6 Data analysis

To evaluate the relationship between crustacean zooplankton and environmental variables from 12 sampling stations in Erhai Lake (*n*=144), Canonical Correspondence Analysis (CCA) was performed by CANOCO for Windows 4.5. To verify if CCA was appropriate, a Detrended Correspondence Analysis (DCA) was run first to determine if the gradient length of the axis 1 exceeded 3.0 SD to ensure a unimodal rather than a linear distribution. Automatic forward stepwise regression was used to select the environmental variables. Those variables not significantly related ($P \geq 0.05$) were deleted during the data processing. Monte Carlo permutation was used to select the variables explaining crustacean zooplankton. Total species abundance and all of the environmental variables were ln(*x*+1) transformed prior to the analysis.

The effects of the environmental variables on crustacean zooplankton were analyzed by one-way ANOVA, with SPSS 17.0 (Cai et al., 2012). We used two-way ANOVA to test the influence of spatial vs. temporal variability on the density of *Daphnia* and crustacean zooplankton. Log-transformed data [ln(*x*+1)] were standardized.

Table 1 Range and mean values (±standard deviation) of physico-chemical variables and Chl-*a* and their effects on the density of crustacean zooplankton in Erhai Lake

Variables	Range	Mean value±SD	*F*	*P*
TN (mg/L)	0.26–0.93	0.63±0.24	3.550	0.040
NH_4^+-N (mg/L)	0.06–0.45	0.18±0.11	1.640	0.090
NO_3^--N (mg/L)	0.04–0.19	0.11±0.05	2.588	0.001
TP (mg/L)	0.016–0.042	0.03±0.01	2.832	<0.001
PO_4^{3-}-P (mg/L)	0.003–0.007	0.01±0.001	4.281	<0.001
pH	8.58–9.09	8.86±0.16	2.225	0.004
Transparency (m)	1.30–4.42	2.58±1.10	4.671	<0.001
Water temperature (°C)	11.4–23.8	18.0±4.33	7.891	<0.001
Wind speed (m/s)	0.77–4.48	2.69±1.18	0.890	0.687
Water height (m)	5.35–19.8	11.3±3.63	0.892	0.687
Chl-*a* (μg/L)	4.11–24.3	10.4±6.52	2.539	<0.001

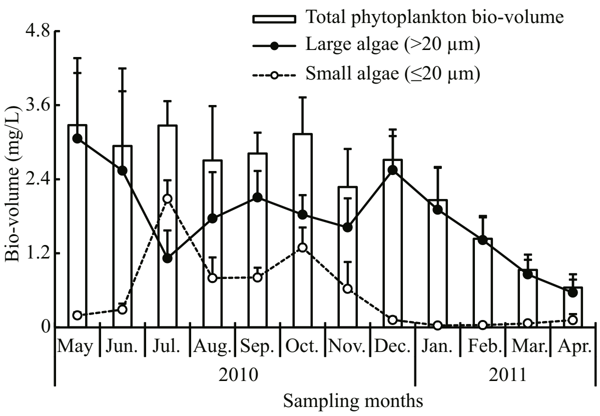

Fig.2 Seasonal variations in phytoplankton bio-volume in Erhai Lake from May 2010 to April 2011

3 RESULT

3.1 Physico-chemical variables and chl-*a*

The range and average values of physico-chemical variables and chl-*a* concentrations in Erhai Lake are displayed in Table 1. Water temperature had obvious seasonal variations, rising from spring, reaching the maximum (~23.8°C) in summer (August), falling in autumn and reaching the minimum (~11.4°C) in winter (January). The average water temperature was approximately 18.0±4.3°C. pH had an average of 8.86±0.16 with a maximum value of 9.09 in November. The transparency was higher in winter and spring with a maximum value of 4.42 m in April. TN was relatively high from May to September and lower in other months. The average TN and TP were 0.63 and 0.028 mg/L, respectively. TN concentrations in the northern and southern regions of Erhai Lake were higher than in the middle region. The average chl-*a* concentration was 10.4±6.5 μg/L, with a maximum value of 24.3 μg/L in September and minimum value of 4.11 μg/L in March.

One-way ANOVA indicated that environmental factors such as TN (P=0.040), NO_3^--N (P=0.001), TP (P<0.001), PO_4^{3-}-P (P<0.001), pH (P=0.004), transparency (P<0.001), water temperature (P<0.001), and Chl-*a* (P<0.001) all had significant influences on the density of crustacean zooplankton (Table 1).

3.2 Seasonal variations in phytoplankton bio-volume

In late spring, *Melosira granulata* and *Psephonema aenigmatiuin* were the dominant species. In summer, with the increase in water temperature, the small-sized diatom *Cyclotella meneghiniana* and the colony-forming *Microcystis* (*M. aeruginosa*, *M. wesenbergii*, and *M. viridis*) were dominant. In autumn, the diatoms *M. granulata* and *C. meneghiniana*, and *Microcystis* (*M. viridis*) were dominant. In winter, the dominant species changed into *M. granulata* and *Fragilaria capucina*. During August–November, the bio-volume of filamentous green algae (*Ulothrix* sp.) was highest and ranged from 0.25–1.78 mg/L. The bio-volume of phytoplankton ranged from 0.68–3.25 mg/L, and its annual mean value was 2.31 mg/L. The maximum (3.25 mg/L) occurred in May 2010, and the minimum (0.68 mg/L) in April 2011. In most months, the bio-volume of large-size algae (>20 μm) was higher than that of small-size algae (≤20 μm) (Fig.2).

3.3 Annual variations in crustacean zooplankton density in Erhai Lake

In total, 11 crustacean zooplankton species were recorded, among which six (6 genera) were cladocerans and five (5 genera) were copepods (Table 2). Of the annual average crustacean zooplankton density, *Bosmina coregoni* comprised 33.7%, *Daphnia galeata* (16.6%), *Ceriodaphnia quadrangula* (11.9%), *Chydorus sphaericus* (7.6%), *Phyllodiaptomus tunguidus* (5.4%), and *Mesocyclops leuckarti* (21.8%).

The crustacean zooplankton density ranged from 24.3 to 155.4 ind./L, with a mean annual value of 66.8 ind./L. Crustacean zooplankton density was comparatively high in warm seasons (summer and

Table 2 Seasonal variation in crustacean zooplankton density (±standard deviation) and Shannon-Weiner index (*H′*) in Erhai Lake from May 2010 to April 2011

Species name	2010								2011			
	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.
Bosmina coregoni	6.8±6.4	47.2±17.5	107.2±57.5	14.2±9.6	35.2±23.8	36.7±11.8	5.0±2.5	8.6±2.9	1.2±1.0	0.4±0.3	2.4±1.1	5.2±3.5
Ceriodaphnia quadrangula	46.4±47.3	19.3±21.4	-	2.0±2.3	15.4±11.1	7.3±5.6	3.9±2.3	1.0±0.76	0.1±0.2	0.02±0.1	0.04±0.1	0.1±0.1
Chydorus sphaericus	1.0±0.7	2.7±2.5	9.4±8.7	21.8±17.6	14.3±10.4	2.9±1.1	4.5±2.8	1.7±0.7	0.5±0.4	0.9±0.7	0.7±0.75	0.4±0.6
Alona quadrangularis	0.2±0.3	0.02±0.1	0.2±0.3	0.2±0.3	0.1±0.3	0.1±0.12	-	0.02±0.1	-	0.04±0.1	0.01±0.02	0.1±0.3
Daphnia galeata	7.4±10.5	-	-	-	-	1.4±1.3	17.7±22.3	16.5±4.6	27.6±10.0	16.9±6.7	27.9±9.0	17.7±10.6
Diaphanosoma brachyurum	-	-	8.2±4.8	2.7±3.3	10.1±4.6	1.8±1.1	0.6±0.7	-	-	-	-	-
Thermocyclops hyalinus	3.0±4.3	1.1±1.3	23.1±9.3	8.3±4.2	0.02±0.05	-	0.2±0.3	-	-	-	-	-
Eucylops serrulatus	0.1±0.3	0.1±0.2	-	-	-	-	-	-	-	-	-	-
Cyclops vicinus vicinus	-	-	-	-	-	-	-	-	-	0.04±0.1	0.01±0.02	0.03±0.1
Mesocyclops leuckarti	14.1±6.8	5.2±2.3	2.8±2.2	25.9±10.6	24.8±10.1	26.2±6.9	16.2±5.0	4.6±1.7	4.6±2.0	5.0±2.4	3.5±2.4	5.8±3.4
Phyllodiaptomus tunguidus	0.9±0.6	0.8±0.6	4.5±2.3	5.8±3.8	9.9±5.2	6.0±3.6	6.2±3.6	3.4±1.5	3.6±2.2	1.2±0.7	0.5±0.4	0.3±0.3
Nauplius	8.6±4.5	3.0±2.1	9.9±3.9	20.9±5.0	29.4±8.2	19.9±6.7	22.0±7.4	16.0±6.1	14.1±5.2	4.5±2.9	12.0±3.1	7.5±0.8
Number of species	9	8	7	8	8	8	8	7	6	8	8	8
Total crustacean zooplankton density (ind./L)	79.8±60.2	76.3±28.3	155.4±68.0	80.9±42.1	110±37.7	82.4±18.3	54.2±30.9	35.7±7.7	37.7±12.3	24.3±9.2	35.1±11.2	29.6±15.1
Shannon-Weiner index (*H′*)	1.724±0.25	1.188±0.41	1.429±0.27	2.168±0.34	2.289±0.20	1.954±0.26	2.283±0.19	2.019±0.16	1.253±0.15	1.273±0.22	1.014±0.28	1.525±0.24

-: no species recorded.

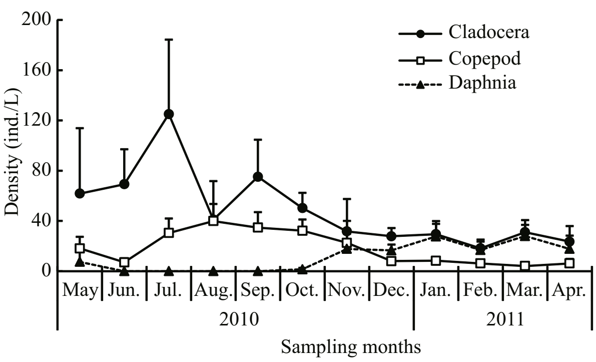

Fig.3 Annual variation in cladoceran, copepod, and *Daphnia* densities in Erhai Lake from May 2010 to April 2011

autumn) with the maximum (155.4 ind./L) occurring in July 2010, and was low in winter with the minimum (24.3 ind./L) occurring in February 2011 (Table 2). Cladocera and the copepoda occurred at their maximum densities in July and August of 2010, respectively (Fig.3).

Two-way ANOVA revealed that the influence of temporal variability (df=11, *F*=27.18, *P*<0.001) and the interaction of temporal and spatial variability (df=22, *F*=4.39, *P*<0.001) on crustacean zooplankton density were significant. Spatial variability did not significantly affect crustacean zooplankton density (df=2, *F*=2.88, *P*=0.06). Post-hoc tests (Tukey HSD) revealed a significant difference between the southern and northern regions (*P*=0.048) of the lake, but not between other regions of the lake (*P*>0.05).

Shannon-Wiener index ranged from 1.014 to 2.289, so Erhai Lake was in a moderate to heavy state of pollution.

The density of *D*. *galeata* was high in winter and

Table 3 Results of redundancy analysis (RAD) between crustacean zooplankton and environmental variables in Erhai Lake

Axes	1	2	3	4	Total inertia
Eigenvalues	0.480	0.107	0.026	0.013	1.000
Species-environment correlations	0.961	0.715	0.663	0.451	
Cumulative percentage variance:					
of species data	48.0	58.7	61.4	62.7	
of species-environment relation	75.5	92.3	96.5	98.6	
Test of Monte Carlo permutation on variable: *F*=123.872, *P*=0.002					

Total inertia: total variance in species abundance data.

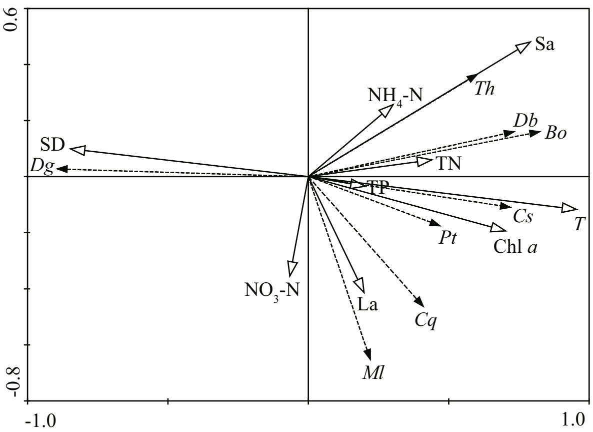

Fig.4 Redundancy analysis between crustacean zooplankton and environmental factors in Erhai Lake

Bo: *Bosmina*; *Cq*: *C. quadrangular*; *Cs*: *C. sphaericus*; *Dg*: *D. galeata*; *Db*: *D. brachyurum*; *Ml*: *M. leuckarti*; *Pt*: *P. tunguidus*; *Th*: *T. hyalinus*; La: large algae bio-volume; NH_4-N: ammonium; NO_3-N: nitrate; SD: transparency; Sa: small algae bio-volume; *T*: water temperature; TN: total nitrogen; TP: total phosphorus.

spring, with the maximums (27.6 and 27.9 ind./L) in January and March 2011, respectively (Fig.3). *B. coregoni* density was high in summer and its maximum (107.2 ind./L) occurred in July 2010, but the density was low in winter and spring. *C. quadrangula* had a high density in spring with the maximum (46.4 ind./L) in May 2010. Both *P. tunguidus* and *M. leuckarti* had high densities in summer and autumn, and their maximum densities (9.9 and 26.2 ind./L) occurred in September and October 2010. *T. hyalinus* density was highest in July 2010 (Table 2).

Two-way ANOVA revealed that the influence of temporal (df=11, *F*=172.75, *P*<0.001), spatial variability (df=2, *F*=15.19, *P*<0.001), and their interaction (df=22, *F*=4.84, *P*<0.001) on *Daphnia* density were significant. Post hoc tests (Tukey HSD) revealed significant differences between the southern and northern (*P*<0.001) and middle regions (*P*=0.005) of the lake, there was no significant difference between the northern and middle regions (*P*=0.058) of the lake.

3.4 Redundancy analysis between crustacean zooplankton and environmental factors

The assumption that the data were linear rather than unimodal was verified by the gradient length of the first DCA (2.605 SD units). The first four DCA axes contributed 69.7% of crustacean zooplankton variation. Forward stepwise regression selected 9 of the 12 environmental variables which significantly explained biological variations using RDA. The results revealed that 96.5% of the variance in species abundance was accounted for by the first three ordination axes (Table 3). The first ordination axis showed a gradient mostly correlated with water temperature, total nitrogen, total phosphorous, Chl-*a*, small algae, and transparency. The second ordination axis indicated that large algae, ammonium, and nitrate nitrogen had the second largest effects on species composition (Fig.4). *Bosmina*, *D. brachyurum*, and *C. sphaericus* were positively associated with water temperature, total phosphorus, and total nitrogen. There was a significant relationship between chl-*a* and *P. tunguidus*. *C. quadrangula*, and *M. leuckarti* were correlated with large algae bio-volume and nitrate nitrogen. *T. hyalinus* was associated with small algae bio-volume and ammonium nitrogen. *D. galeata* was positively associated with transparency but negatively associated with water temperature, Chl-*a*, and small algae bio-volume (Fig.4).

4 DISCUSSION

In freshwater ecosystems, algae can change the nutrient content in their body through nutritional supply, becoming limiting factors for zooplankton growth (Olsen et al., 1986; Brett et al., 2000; Elser et al., 2007). Some experimental investigations have shown that nitrogen or phosphorus deficiency can reduce the quality of *Daphnia* (Weers and Gulati, 1997) and *Bosmina* (Schulz and Sterner, 1999) food, affecting their growth and reproduction.

According to the Shannon-Wiener index and total nitrogen and phosphorus concentrations, the trophic level in Erhai Lake was mesotrophic. Both TN and TP concentrations in Erhai Lake were higher in the southern and northern regions and lower in the middle region (Yang, 2006). During the present study, the influence of spatial variability and the interaction of temporal vs. spatial variability on *Daphnia* were all significant ($P<0.001$). Moreover, significant differences between the southern and northern regions ($P<0.001$) and middle region of the lake were also observed. Our RDA analysis and one-way ANOVA revealed that the dominant (*Bosmina*, *D. brachyurum*, *C. sphaericus*, *C. quadrangular*, and *M. leuckarti*) crustacean zooplankton species were positively associated with environmental factors (water temperature, phosphorus, or nitrogen concentration), while it was negatively associated with *D. galeata*. Therefore, it is likely that environmental factors (mainly water temperature and nutrient concentrations) affected the seasonal succession of crustacean zooplankton structure in Erhai Lake. McCarthy et al. (2006) also observed that crustacean zooplankton biomass was not correlated with phosphorus or nitrogen availability, but they were sensitive to phosphorus or nitrogen limitation.

The biomass and individual colony or filamentous cyanobacteria size affects the growth and reproduction of large-bodied cladocerans (e.g. *Daphnia*) (Thompson et al., 1982; Fulton and Paerl, 1987; Chen and Xie, 2003; Chen et al., 2007; Deng et al., 2008, 2010). Thompson et al. (1982) found that *Daphnia hyalina* fed on small colony *Microcystis* (≤64 μm), while its feeding rate was greatly inhibited by large colony *Microcystis*. Other studies have suggested that *Daphnia pulex* fed substantially on colony *Microcystis* of 60–100 μm but not on colony *Microcystis* of 100–150 μm (Jarvis et al., 1987). When colony *Microcystis* was smaller than 112 μm with a biomass of above 50 mg/L, *Daphnia carinata* could not complete its growth and development (Deng et al., 2008). The competition experiments carried out by Chen et al. (2003, 2007) indicated that the colony size and biomass of *Microcystis* determined the outcome of competition between *Daphnia carinata* and small-bodied cladocerans. During May–October 2010, the colony and filamentous algae densities in Erhai Lake were high, ranging from 2.37×10^7–4.19×10^7 colonies + filaments/L. The dominant colonial species were *Microcystis* and *Dictyosphaerium pulchellum*, and the filamentous *Ulothrix* and *M. granulata*, forming a thin bloom on the surface of the northern regions in September. In contrast, some small-bodied crustacean zooplankton (e.g. *Bosmina*, *C. quadrangula* and cyclops) were mostly dominant when the colony or filamentous algae became dominant in Erhai Lake, while large-bodied cladoceran (e.g. *D. galeata*) population density was low to nil. However, the bio-volume of small algae declined quickly from November 2010 to April 2011 and remained at a lower level in winter and spring, while *D. galeata* density was higher. Redundancy analysis (RDA) revealed that the relationship between *D. galeata* density and the bio-volume of small algae was negatively significant. When filamentous cyanobacteria density reached 8×10^7 filaments/L, *D. magna* stopped growing and its population density reduced significantly (Dawidowicz et al., 1988). Hambright et al. (2001) observed that small-bodied grazers (e.g. *Ceriodaphnia* and *Bosmina*) avoided the inhibiting effect of filamentous algae more easily than large-bodied *D. magna* in Lake Kinneret. In Lake Valencia, when *Lyngbya* and *Oscillatoria* densities exceeded 9×10^7 filaments/m^2, all cladocerans disappeared (Infante and Riehl, 1984). Therefore, the combined effects of small and large algae were important factors in the seasonal succession of crustacean zooplankton community structure in Erhai Lake.

The dominant cladoceran and copepod species in Erhai Lake has changed hugely since 1957 (Table 4). From 1957 to 1980, smaller-bodied species (e.g. *Neutrodiaptomus mariadviagae mariadviagae* and *Daphnia longispina*) were dominant, while other small-bodied species (e.g. *Bosmina*, *C. quadrangular*, and *M. leuckarti*) and the larger-bodied *D. galeata* were dominant in 2010 to 2011. During the past 50 years, cladoceran and copepod densities in Erhai Lake decreased at first and then increased (Table 4). From 1957 to 2011, with increased eutrophication, the dominant phytoplankton species changed from small-bodied species (such as small green alga and diatom) to large-bodied species (such as colony *Microcystis* and filamentous algae), but the biomass of small-size algae gradually increased. Therefore, the variations in community structure and phytoplankton biomass might affect the historical succession of crustacean zooplankton structure in Erhai Lake.

Table 4 Historical changes in the crustacean zooplankton community and phytoplankton of Erhai Lake

Years	Crustacean zooplankton			Phytoplankton		Sources
	Cladoceran density (ind./L)	Copepod density (ind./L)	Dominant species	Biomass (mg/L)	Dominant species	
1957	10	120	*Neutrodiaptomus mariadvigae* *Daphnia longispina*	0.55	*Pediastrum simpler* *Cyclotella* *Aphanizomenon flos-aquae*	Li et al., 1963
1980	80	150	*N. mariadvigae*, *D. longispina*	1.01	*A. flos-aquae*, *Cyclotella*	Wu and Wang, 1999
1992	17	62.3		1.13		Wu and Wang, 1999
1997	5.4	8.7		4.66	*Microcystis*, *Anabaena* *A. flos-aquae*	Wu and Wang, 1999
2010–2011	48.7	18.1	*Bosmina*, *D. galeata* *C. quadrangular* *M. leuckarti*	2.31	*Ulothrix* sp., *Microcystis* *Melosira*, *C. meneghiniana*	This paper

N. tangkahkeii taihuensis are inclined to feed on large-bodied species (Liu and Zhu, 1994; Guo, 2005). In Lake Dianchi, Yunnan Province, *N. tangkahkeii taihuensis* fed mainly on large-bodied *Daphnia longispina* and *Diaptomus* sp. (Liu and Zhu, 1994). In Lake Chaohu, when there are large-bodied cladocerans, *N. tangkahkeii taihuensis* preferentially fed on *Daphnia* and *Leptodora*, and fed on medium-size species (e.g. *Moina* and calanoida) when large-bodied ones were lacking (Guo, 2005). In Erhai Lake, the *N. tangkahkeii taihuensis* population was about 848 t in 2010 (unpublished data, Erhai Management Bureau). Therefore, selective predation by *N. tangkahkeii taihuensis* might regulate crustacean zooplankton structure in Erhai Lake.

5 CONCLUSION

Eleven species of crustacean zooplankton were recorded in Erhai Lake; the dominant species were *Daphnia galeata*, *Ceriodaphnia quadrangular*, *Bosmina fatalis*, *Chydorus sphaericus*, *Mesocyclops leuckarti*, and *Phyllodiaptomus tunguidus*. Crustacean zooplankton density ranged from 24.3–155.4 ind./L.

In winter and spring, the large-bodied cladocerans (*D. galeata*) dominated the crustacean plankton community. When the colonial or filamentous algae dominated the phytoplankton communities, small-bodied cladoceran species (e.g. *Bosmina*, *C. quadrangular*, and cyclops) replaced the large-bodied ones. The variation in both phytoplankton structure and environmental variables were important factors in the seasonal succession of crustacean zooplankton structure in Erhai Lake.

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