Crustacean zooplankton communities in 13 lakes of Yunnan-Guizhou plateau: Relationship between crustacean zooplankton biomass or size structure and trophic indicators after invasion by exotic fish

Nichun Guo, Min Zhang, Yang Yu, Shanqing Qian, Daming Li and Fanxiang Kong*

State Key laboratory of Lake Science and Environment, Nanjing Institute of Geography and Limnology, Chinese Academy of Sciences, Beijing East Road 73, Nanjing 210008, P. R. China

Abstract – We investigated crustacean zooplankton communities and their relationships to environmental factors in 13 lakes of Yunnan-Guizhou plateau to determine whether there is a consistent relationship between trophic indicators and crustacean zooplankton biomass or size structure. The lakes showed a wide range of trophic status, with total phosphorus (TP) ranging from 0.013 to 0.268 mg.L^{-1}, and chlorophyll *a* from 0.9 to 76.26 µg.L^{-1}. Continuous stocking with exotic planktivorous fish had taken place on a wide scale in these plateau lakes. About 36 species of Crustacea were found, of which Cladocera were represented by 20 taxa (12 genera), and Copepoda by 16 taxa (13 genera). Canonical correspondence analysis partitioned these species into two clusters. Physicochemical features and food-webs of different lakes seemed to be the key factors determining zooplankton species composition and distribution patterns. Between the 13 lakes, there was no significant relationship between cladocerans and chlorophyll *a* suggesting phytoplankton biomass was little controlled by macrozooplankton. The positive correlation between chlorophyll *a* and copepods suggested the high copepods biomass or size structure caused by the invasion of exotic planktivorous fish had a negative effect on water quality.

Key words: Zooplankton communities / CCA / cladocerans / copepods

Introduction

Crustacean zooplankton species composition and distribution patterns have been studied from oligotrophic to hypertrophic lakes over the last fifty years (Hairston *et al.*, 1960; Patalas, 1971; Amarasinghe *et al.*, 1997; Swadling *et al.*, 2000). Previous studies have investigated zooplankton species composition, abundances and their interactions with environmental factors (Elser and Goldman, 1991; Currie *et al.*, 1999). Other studies have related crustacean biomass and size structure to trophic indicators in different lakes (Pace, 1986; Taylor and Carter, 1997; Wang *et al.*, 2007b). Although particular species have been suggested as good indicators for trophic status (Attayde and Bozelli, 1998), major crustacean zooplankton groups respond differently to trophic conditions (Benndorf *et al.*, 2002; Pinto-Coelho *et al.*, 2005). Different relationships between zooplankton and tropic status have been attributed to the different physical-chemical features (Tessier and Horwitz, 1990). Ecological processes and food-webs in different lakes can also greatly influence the relationships (Mazumder, 1994; Havens, 2002; Auer *et al.*, 2004).

A mechanistic understanding of the ecological processes and food-web is necessary to explain the interactions between the zooplankton community and trophic indicators (Elser and Goldman, 1991). Hypotheses for studying the food-web for the management of reservoirs and lakes (Hairston *et al.*, 1960; Benndorf *et al.*, 2002), include the "Cascading Trophic Interactions" hypothesis (Carpenter *et al.*, 1985) and the "bottom-up: top-down" hypothesis (McQueen *et al.*, 1986). Many studies emphasize the "top-down" forces on phytoplankton biomass, suggesting significant influence by the biomass and size structure of herbivorous cladocerans (Brooks and Dodson, 1965; McCauley and Kalff, 1981; Stemberger and Miller, 2003; Wang *et al.*, 2007b). In order to reduce the phytoplankton biomass and improve water quality, a lower biomass of planktivorous fish is necessary to allow

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*Corresponding author: fxkong@niglas.ac.cn

high macrozooplankton biomass in mesotrophic and slightly eutrophic lakes (Shapiro *et al.*, 1975; Carpenter *et al.*, 1985; Benndorf, 1987).

Since the 1950s, exotic planktivorous fish have been found and studied in all 13 lakes of Yunnan-Guizhou plateau (Xie and Chen, 2001). Two planktivorous fish, bighead and silver carp, were introduced to Lake Xingyun in the early 1950s for the purpose of aquaculture (Xie and Chen, 2001), and another planktivorous fish, *Neosalanx taihuensis*, was introduced to Lake Xingyun and Lake Dianchi in the 1980s for the same purpose (Zhuang *et al.*, 1996). A high production of *N. taihuensis* was soon observed in many lakes of this plateau (Zhuang *et al.*, 1996). Introduction of exotic planktivorous fish has led to significant ecological consequences in the lake ecosystems (Zhang *et al.*, 2005). However, little is known about the relationship between the crustacean zooplankton community and water quality after invasion by exotic fish (Zhang *et al.*, 2005). Mehner *et al.* (2008) found a strong correlation between planktivorous fish and the proportion of copepods in the crustacean zooplankton community. Liu (2001) also found the high grazing pressure of *N. taihuensis* led to an obvious reduction in the abundance of small bodied calanoids, with an increase in the abundance of a large bodied calanoid *Neodiaptomus schmackeri* (Z.R. Wang, private communication). The increase of copepod biomass and change in size structure caused by the invasion of planktivorous fish in these lakes would alter the lake ecosystems to some extent and may influence water quality.

The 13 lakes of this study, located in southwest China, are mainly mesotrophic or slightly eutrophic (Liu, 2001; Zhang *et al.*, 2005). A deep water refuge for crustacean zooplankton (Wissel *et al.*, 2000) is available in most of these lakes. This may induce a top-down control on phytoplankton biomass. The main goals of our study were twofold: First, to present a snapshot of crustacean zooplankton communities and their relationship to environmental factors in these lakes. Second, to test whether there is a consistent relationship between the biomass or size of crustaceans and trophic state among lakes with similar trophic conditions, after invasion by exotic fish.

Material and methods

Study site

A total of 13 lakes, located in southwest China, were selected for this study (Table 1). These lakes ranged from 10.7 to 297.9 km^2 in area and from 5 to 155 m in maximum lake depth. Secchi disk visibility (SD) measured in summer varied from 0.36 to 10.06 m. Temperature in winter ranged from 13.0 to 15.8 °C, with an average of 15.2 °C, and in summer, from 18.4 to 26.6 °C, with an average of 21.9 °C. Total phosphorus (TP) ranged from 0.013 to 0.268 mg.L^{-1} and chlorophyll *a* (Chl *a*) from 0.9 to 76.26 µg.L^{-1} (Fig. 1).

Sampling and sample processing

Water sampling at 3–7 stations in each of the 13 lakes was conducted in November 2007 and July 2008 (Tables 1 and 2). Zooplankton samples were taken during daylight hours from near the lake bottom to the surface using a modified 5-L Patalas sampler. Quantitative samples of crustaceans were collected by sieving 10 or 20 L water samples through a 64 µm plankton net and were stored in 50 mL plastic bottles fixed with 5% formalin solution. In addition, a 112-µm plankton net was used through the water column to collect qualitative samples for species identification. Crustaceans were identified to species level and counted using a compound microscope (at a magnification of 100×). Cladocera were identified according to Chiang and Du (1979), and Copepoda according to Shen (1979). Wet weights of crustacean zooplankton were estimated according to the weight-body size regression of Huang (1999). Cladocera were measured from the top of the head to the base of the tail spine. Copepoda were measured from the top of the head to the end of the furca. Species comprising more than 5% of the total crustacean abundance were considered as 'dominants'.

For measurement of Chl *a* and nutrient concentrations, we combined water sampled from the water surface and the bottom. Total nitrogen (TN) was measured by alkaline potassium persulfate oxidation and absorbance measured at 220 nm. After oxidation with potassium persulfate under pressure, the ammonium molybdate method was used to analyze total phosphorus (TP). The Nessler colorimetry method was used to analyze Ammonium-N (NH$_4^+$). The automated Korolev/cadmium reduction method was used to analyze nitrate (NO$_3^-$). All of the above methods are described in detail in Huang (1999). Each lake was sampled at least twice yearly, but only data from winter and summer were analyzed in the present study.

Statistical analysis

Canonical correspondence analysis (CCA) was used to partition lake groups and to analyze the relationship between species distribution patterns and environmental factors. All data were analyzed using the CANOCO 4.53 package (Ter Braak, 2004). Correlation analysis was used to demonstrate the relationship between crustacean biomass and trophic indicators, using SPSS 10.0. The data were tested for normality with the Kolmogorov–Smirnov one-sample test and log$_{10}$-transformed before analysis. Only those taxa which were considered as 'dominants' in more than 10% of the 13 lakes were included in the crustacean species data matrix (11 of the 36 enumerated taxa). A set of explanatory variables was created, which contained all measured environmental factors (lake depth, area, dissolved oxygen (DO), Secchi disk visibility (SD), pH, TN, TP, TN/TP, Chl *a* and temperature). The original data were used for the partitioning of lake groups. After a forward selection and down weighting of rare species, final variables were obtained by CCA. The crustacean

Table 1. Limnological characteristics of the studied lakes.

| Lakes	Samples	Area (km^2)	Depth (m)	SD (m)	pH	TN (mg.L^{-1})	TP (mg.L^{-1})	Chl *a* (μg.L^{-1})
Dianchi	5	297.9	5.87	0.56	9.18	3.13	0.138	58.78
Fuxian	5	211	155	4.35	8.87	0.85	0.025	3.32
Xingyun	4	34.7	11	0.81	8.67	2.30	0.181	45.68
Yangzonghai	3	31.7	30	2.62	9.22	0.77	0.058	2.17
Qilu	3	36.9	6.8	1.10	8.34	3.65	0.069	42.24
Yilong	3	38	6.2	0.95	9.17	1.62	0.048	13.54
Erhai	7	249	20.7	1.38	8.40	0.81	0.045	9.81
Caohai	3	25	5	1.23	8.87	0.78	0.034	5.40
Datunhai	3	12.3	5	0.37	9.20	2.43	0.268	76.26
Changqiaohai	3	10.7	5.5	0.60	9.48	3.07	0.055	33.48
Chenghai	7	77.2	35.1	1.42	9.34	0.86	0.041	9.38
Qionghai	5	31	34	1.32	7.41	0.61	0.029	2.95
Lugu	5	48.5	93.5	10.06	8.39	0.17	0.013	0.90
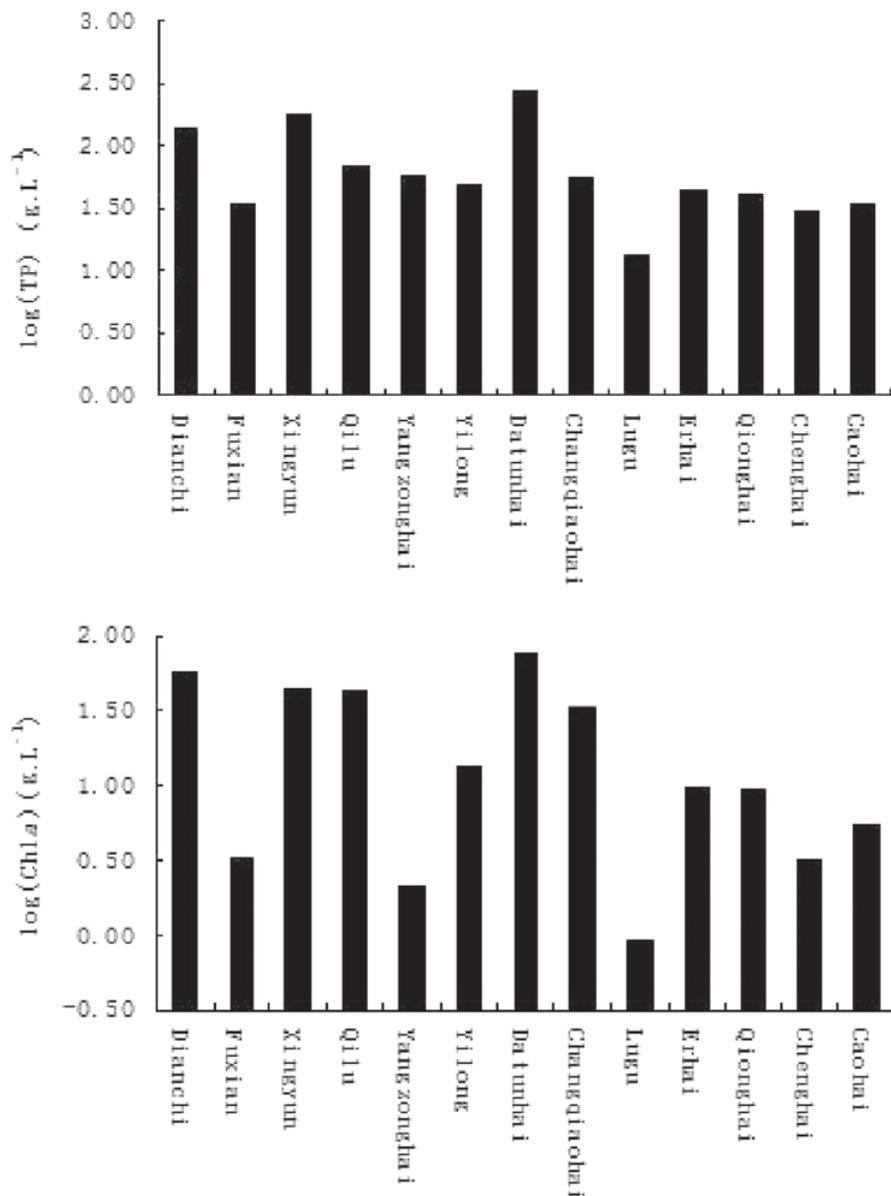
Fig. 1. Total phosphorus (TP) and chlorophyll *a* (Chl *a*) in the 13 lakes during the summer sampling (from June 18 to August 6).

Table 2. Production of *Neoslanx taihuensis* in different lakes (t/a).

Year	Dianchi	Xingyun	Fuxian	Qilu	Erhai	Chenghai	Total
1980	0.5						0.5
1981	6.5						6.5
1982	1200						1200
1983	2000						2000
1984	3500						3500
1985	360	78					438
1986	2200	200					2400
1987	3203	400	70				3673
1988	2300	400	190				2691
1989	2500	300	334				3134
1990	1100	100	1155				2355
1991	500	405	963		500	3	2371
1992	355	420	1181	50	750	48	2804
1993	400	350	1313	20	250	400	2733
1994	200	-	-	-	-	580	780
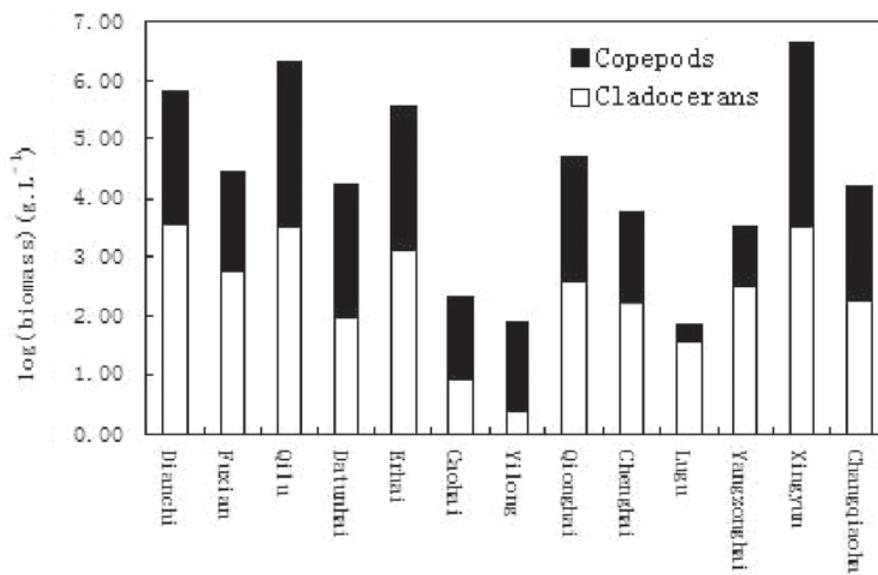
Fig. 2. Biomass composition of crustacean zooplankton in summer in the 13 lakes.

abundances and environmental variables were log $(x + 1)$ transformed before analysis to obtain normality of variance in the datasets.

Results

Crustacean zooplankton community and species dominance

Crustacean zooplankton communities were quite different between winter and summer. In winter, the community was mainly composed of *D. hyalina*, *B. coregoni*, *C. vicinus* and *S. dorrii*. In summer, the community was mainly composed of *B. coregoni*, *C. sphaericus*, *T. taihokuensis* and *P. tunguidus*. From oligotrophic to hypertrophic lakes, the diminishing significance of large herbivorous cladocerans (*Daphnia*) was accompanied by the increasing predominance of cyclopoids (*Cyclops*, *Thermocyclops*) and small cladocerans (*Chydorus*, *Bosmina*). Crustacean zooplankton species composition, frequency of occurrence and percentage as a dominant in the 13 lakes are shown in Table 1. About 36 taxa were identified. Cladocera were represented by 20 taxa (12 genera) and Copepoda by 16 taxa (13 genera). Of the 36 species, about 60% were littoral species of low abundance. The most common species were *B. coregoni*, *C. sphaericus* and *T. taihokuensis*. They were found in 85%, 60% and 63%, respectively, of all the lakes sampled. *E. serrulatus*, *T. taihokuensis*, *B. coregoni* and *D. hyalina* occurred in 25–85% of these lakes. None of the remaining species occurred in more than 25% of these lakes. The following species dominated the crustacean plankton of the lakes sampled: *B. coregoni* (17% of total abundance),

Table 3. Zooplankton species, frequency of occurrence (F) and percentage as a dominant (D) (> 5% of the total crustacean density) in the 13 lakes.

Species	F (%)	D (%)	Species	F (%)	D (%)
Chydorus sphaericus	60	10	*Acroperus harpae*	5	0
Daphnia hyalina	48	14	*Bosminopsis*	5	0
Diaphanosoma brachyurun	28	5.2	*Sinocalanus dorrii*	5	0
Simocephalus vetulus	8	0	*Schmackeria forbesi*	5	0
Simocephalus spp.	5	0	*Neodiaptomus mariadvigae mariadvigae*	20	1.3
Bosmina coregoni	85	17	*Neodiaptomus yangtsekiangensis*	31	3.4
Ceriodaphnia pulchella	15	4.2	*Neutrodiaptomus alatus*	5	0
C. quadrangula	25	17.5	*Tropodiaptomus oryzanus*	2	0
C. cornuta	9	0	*Cyclops vicinus*	9	6.5
C. hamata	9	0	*Thermocyclops taihokuensis*	63	11.5
Moina macrocopa	9	0	*Thermocyclops hyalinus*	31	10.3
Moina spp.	6	0	*Eodiaptomus sinensis*	2	0
Pleuroxus	9	0	*Eucylops serrulatus*	29	18.1
Scapholeberis mucronata	5	0	*Eucylops euacanthus*	8	0
Daphnia cucullata	6	0	*Elaphoidella*	6	0
Alona	5	0	*Phyllodiaptomus tunguidus*	22	16.7
Daphnia longispina	11	0	*Paracyclops affinis*	11	0
Daphnia pulex	2	0	*Sinodiaptomus sari*	15	2.1

D. brachyurum (5.2%), *T. taihokuensis* (11.5%), *E. serrulatus* (18.1%), *C. vicinus* (6.5%) and *P. tunguidus* (16.7%). The biomass of cladocerans and copepods both showed a wide range in summer, with small cladocerans being dominant in most of the lakes (Fig. 2, Table 3).

The two-dimensional plot of CCA partitioned the species into two clusters (Fig. 3a). The physicochemical variables explained 82.1% of the total variance of species distribution (Table 4). Species in cluster I included: *D. hyalina*, *B. coregoni*, *E. serrulatus*, *T. hyalinus* and *C. sphaericus*; species in cluster II included: *T. taihokuensis*, *C. vicinus* and *D. brachyurun*. The two clusters showed different preference for trophic state and physical conditions (Fig. 3a). *B. coregoni*, *C. sphaericus* peaked in lakes with relatively high nutrient loading, low SD and shallow depth, while *C. vicinus* and *D. brachyurun* usually peaked in deeper lakes with low trophic state and low SD. In addition, the biplot of the CCA analysis showed that cladocerans like *B. coregoni*, *C. sphaericus* deviated from the calanoids (*N. yangtsekiangensis*, *P. tunguidus*), but predatory cyclopoids (*T. hyalinus* and *E. serrulatus*) peaked with them. Moreover, pH seemed to be an important factor determining the dominance of *C. vicinus*, and *D. brachyurun*.

Relationship between crustacean zooplankton and trophic indicators

The biomass of crustacean zooplankton in the 13 lakes ranged from 34.39 to 4554.39 μg.L^{-1}, the average being 1234.33 μg.L^{-1} (Fig. 2). The crustacean biomass showed a weak correlation with the trophic indicators Chl *a* ($r^2 = 0.21$, $P < 0.05$) and TP ($r^2 = 0.15$, $P < 0.05$) (Fig. 4). The mean body length of crustacean zooplankton (including copepod nauplii) in the lakes ranged from 0.248

to 0.553 mm, the overall average for zooplankton being 0.348 mm. The mean body length of crustacean zooplankton showed no correlation with Chl *a* ($r^2 = 0.02$, $P > 0.05$) or TP ($r^2 = 0.01$, $P > 0.05$). The largest animals in our samples were *D. hyalina*, found in winter, always being greater than 1 mm in body length. The most abundant crustaceans were mainly omnivorous, such as *B. coregoni* and *T. taihokuensis*. Biomass of cladocerans did not show significant correlations with Chl *a* ($r^2 = 0.03$, $P > 0.05$) or TP ($r^2 = 0.04$, $P > 0.05$). However, biomass of copepods showed significant correlations with Chl *a* ($r^2 = 0.46$, $P = 0.000$) and TP ($r^2 = 0.25$, $P < 0.05$) (Fig. 5). In all 13 lakes, Chl *a* and TP were strongly correlated in summer ($r^2 = 0.72$, $P = 0.000$), suggesting that phytoplankton biomass was mainly controlled by nutrient resources, with crustacean zooplankton having a minor effect.

Between the two types of lakes (Group I and Group II) (Fig. 3b), mean body length of crustacean zooplankton was 0.368 mm and 0.327 mm, TP was 0.111 and 0.053 mg.L^{-1}, and Chl *a* was 26.93 and 19.37 μg.L^{-1}, respectively. A significant relationship between copepods and cladocerans was found in the Lake Group II. Copepod biomass of Lake Group II was positively related to cladoceran biomass ($r^2 = 0.65$, $P = 0.000$), and to cladoceran size structure ($r^2 = 0.76$, $P = 0.000$). In summer, the mean body length of copepods was also positively related to cladoceran biomass ($r^2 = 0.36$, $P = 0.000$) and to cladoceran size structure ($r^2 = 0.42$, $P = 0.000$) (Fig. 6). The mean body length of copepods was positively related to Chl *a* ($r^2 = 0.16$, $P < 0.05$) and TP ($r^2 = 0.61$, $P = 0.000$) (Fig. 7). We examined the effect of crustacean zooplankton biomass on water quality indicators, and found that copepod biomass in Lake Group II had a significant effect on the Chl *a* and SD (Table 5).
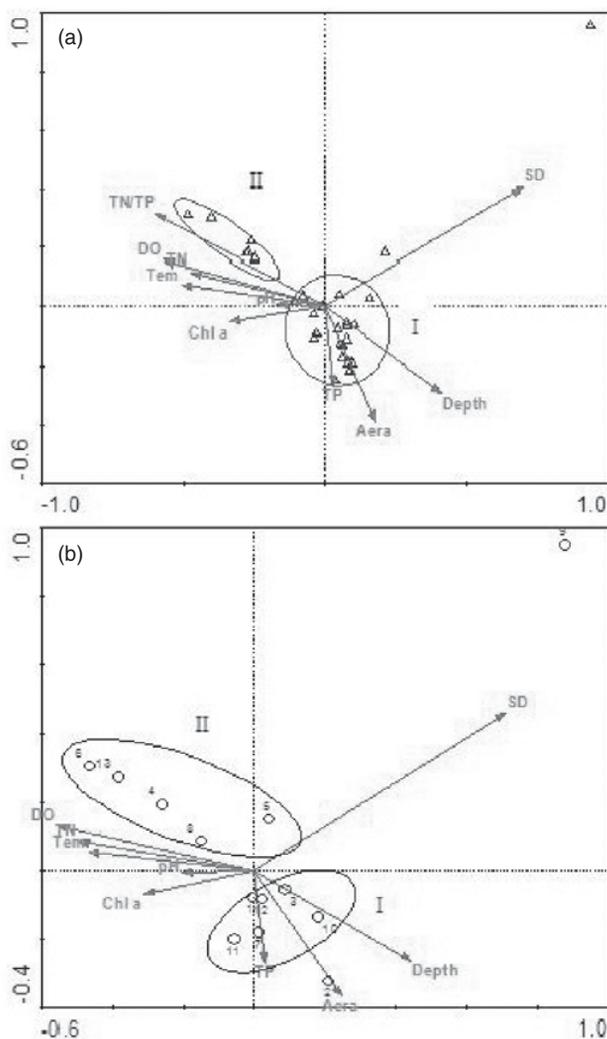
oligotrophic lakes (Zhang *et al.*, 2005). In the present study, *Daphnia* was only dominant in five lakes during winter. The three dominant cladocerans had relatively high occurrence and dominance in this study, despite possible predation by other invertebrates (Blumenshine and Hambright, 2003). According to the PEG-model (Sommer *et al.*, 1986), temperature, food resources and fish predation explain the structure of zooplankton communities. Studies have shown that *Bosmina* and *Ceriodaphnia* to be inefficient consumers of phytoplankton biomass, while *Daphnia* are efficient phytoplankton consumers in many lakes (Brooks and Dodson, 1965; Benndorf *et al.*, 2002). On the other hand, predation by cyclopoid copepods would result in great mortality of herbivorous zooplankton (Blumenshine and Hambright, 2003). The biplot of the CCA analysis showed that cladocerans like *B. coregoni* and *C. sphaericus* deviated from the calanoids (*N. yangtsekiangensis*, *P. tunguidus*), while the small predatory invertebrates, *T. hyalinus* and *E. serrulatus*, peaked with them. Thus, disappearance of *Daphnia* and the increasing dominance of invulnerable copepods might be an outcome of combined predation by large predatory invertebrates and planktivorous fish.

In the present study, the measured environmental factors explained 82.1% of the total variance of crustacean species distribution, suggesting that environmental factors within lakes are important in structuring the crustacean community. Factors such as bacteria (Havens, 2002), the invertebrate *Chaoborus* (Benndorf *et al.*, 2000; Wissel *et al.*, 2000), and planktivorous fish in the food web (Havens, 2002; Wang *et al.*, 2007a) also partly explained variance of crustacean species distribution.

Fig. 3. Biplot of the first two axes of CCA analysis for (a) species association with the environmental factors. Cluster I in (a) includes: *C. sphaericus*, *D. hyalina*, *T. hyalinus*, *E. serrulatus*, *B. coregoni*. Cluster II includes: *T. taihokuensis*, *D. brachyurum*, *C. vicinus* (b) partition of lake groups. Lake group I in (b) including: 1) Dianchi, 3) Xingyun, 7) Datunhai, 10) Chenghai, 11) Qionghai, 12) Erhai. Lake group II in (b) including: 4) Yilonghu, 5) Yangzonghai, 6) Qiluhu, 8) Changqiaohai, 13) Caohai.

Discussion

Crustacean zooplankton taxonomic structure

Swadling *et al.* (2000) reported that lakes in forested catchments were generally deep, and cladocerans in these lakes were mainly composed of *Daphnia* and *Bosmina*. These genera have a great significance in terms of occurrence and biomass in our study lakes and are common in temperate and tropical water bodies (Arcifa, 1984; Gulati, 1990; Pinto-Coelho *et al.*, 2005). With respect to community structure, cyclopoids (*Cyclops*) and cladocerans (*Daphnia* and *Bosmina*) dominated slightly eutrophic lakes (Patalas, 1971), while calanoids (*Phyllodiaptomus*) and cladocerans (*Bosmina*) dominated

Response of crustacean biomass and size structure to water quality indicators

Compared with the crustacean zooplankton biomass found in shallow lakes by Wang *et al.* (2007a), the mean biomass of crustacean zooplankton in these 13 lakes was higher. The probable explanation is that the deep water in these lakes provides refuges for crustacean zooplankton (Wissel *et al.*, 2000). The mean body length of crustacean zooplankton in these lakes was also lower than that found in eutrophic or hypertrophic shallow lakes (Wang *et al.*, 2007a). Such a finding is in accordance with the conclusion of Arcifa (1984). In the 13 lakes, the crustacean biomass showed a weak correlation with the trophic indicators. Cladocerans did not show significant correlations with the trophic indicators, which may be attributed to the unfeasible food web and predation pressure exerted by fishes and invertebrates (Amarasinghe *et al.*, 1997). Our results suggest that deep water refuges for crustacean zooplankton are not favorable for the control of phytoplankton by large-bodied cladocerans, because small cladocerans, such as *Ceriodaphnia*, and large calanoids also had a high biomass in these lakes. These results also support the conclusion that top-down control

Table 4. Summary of CCA analysis for the first two axes between environmental factors and species as well as lakes.

	Species		Lakes	
Axes	1	2	1	2
Eigenvalues	0.438	0.399	0.423	0.399
Species-environment correlations	0.997	0.998	0.990	0.997
Cumulative percentage variance of species data	14.0	26.7	13.5	26.2
of species-environment relation	17.0	32.5	18.2	35.4
Sum of all eigenvalues		3.135		3.315
Sum of all canonical eigenvalues		2.573		2.322
Variance explained		82.1%		70.0%
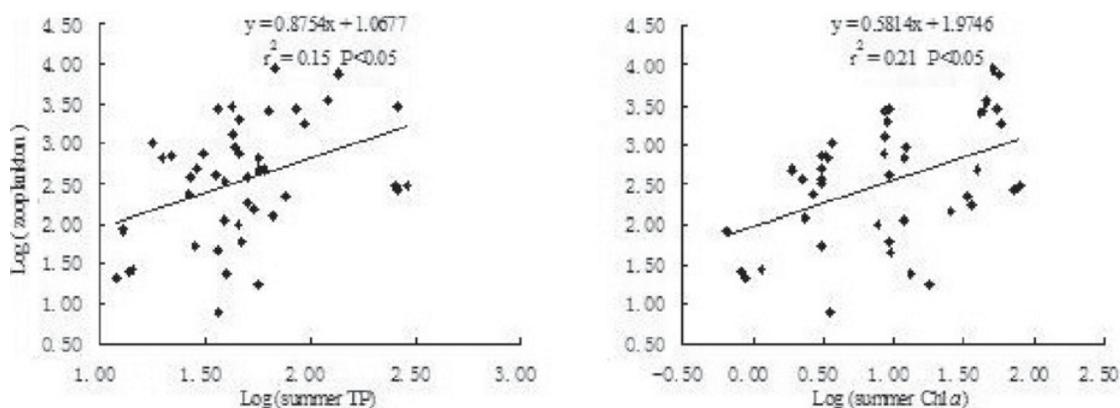
Fig. 4. Relationships between zooplankton biomass and trophic state ($\mu g.L^{-1}$), $n = 41$.
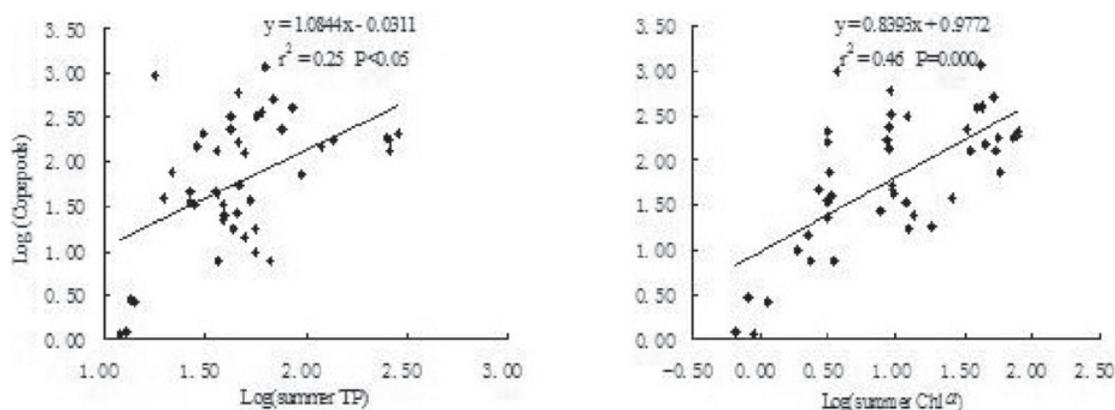
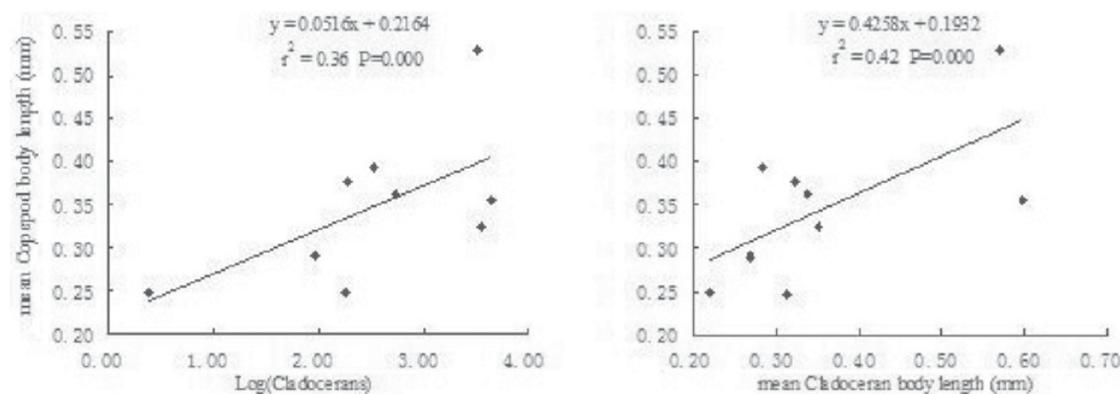**Fig. 5.** Relationships between copepod biomass and trophic state ($\mu g.L^{-1}$), $n = 41$.

Fig. 6. Relationships between mean copepod body length (mm), cladoceran biomass ($\mu g.L^{-1}$), and mean cladoceran body length (mm), $n = 15$.
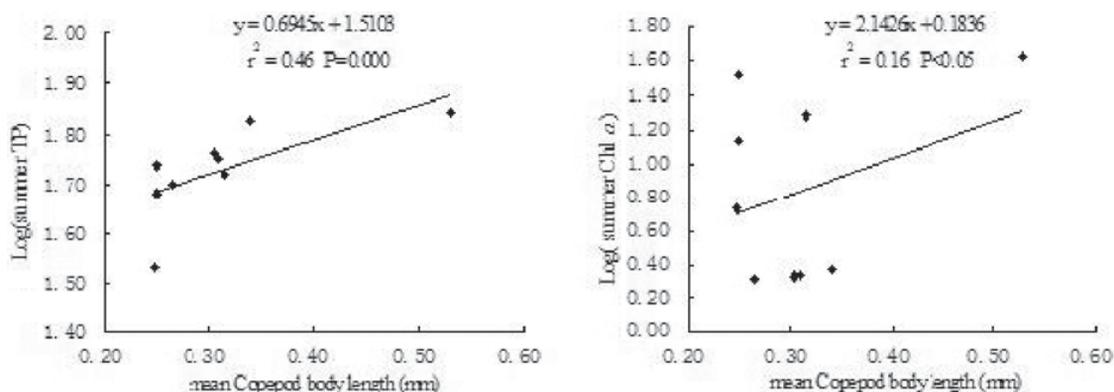
Fig. 7. Relationships between mean copepod body length, biomass, and trophic state ($\mu g.L^{-1}$), $n = 15$.

Table 5. Coefficients of the Pearson correlation between crustacean biomass and water quality indicators in the two groups of lakes. The data were log transformed. ** $P < 0.001$, * $P < 0.05$. TB = total crustacean biomass, the sum of cladocerans and copepods.

	Chl *a*			SD		
	1	2	Total	1	2	Total
TB	0.033	0.221*	0.415*	− 0.242*	− 0.084	− 0.515**
Cladocerans	0.007	0.085	0.033	− 0.175	− 0.180	− 0.180
Copepods	0.106	0.910**	0.431*	− 0.175	− 0.699**	− 0.725**

on phytoplankton is not easily achieved in deep lakes or reservoirs (Benndorf, 1987; Benndorf *et al.*, 2002).

Differing from the conclusion that copepods have strong impact on the structure of phytoplankton (*e.g.*, Sommer *et al.*, 2001), some researchers have found that a high proportion of copepods in the crustacean zooplankton community had a negative influence on the control of phytoplankton biomass and water quality in low-productivity lakes (Benndorf *et al.*, 2000). In the present study, the pooled biomass of crustacean copepods showed significant relationships with trophic indicators such as chlorophyll *a* and TP in all 13 lakes, while size structure only exhibited a relationship with chlorophyll *a* and TP in Lake Group II. Lakes in Group II were mainly mesotrophic or slightly eutrophic. Therefore, high macro-zooplankton biomass possibly reduced phytoplankton biomass and improved water quality in these lakes. In these lakes, cladoceran biomass and size structure were only positively related to the biomass and size structure of copepods and showed no significant correlation with water quality indicators. Earlier studies suggest that herbivorous calanoid copepods can exert little influence on phytoplankton biomasses due to their low overall biomasses, slow growth and low metabolic rates (Mehner *et al.*, 2008). An increase of cyclopoid copepods would result in great mortality of herbivorous zooplankton and have a negative influence on the control of phytoplankton biomass (Blumenshine and Hambright, 2003). The increase of copepod biomass and size structure would result in the increase of inedible algae and a change of phytoplankton community (Zhang *et al.*, 2005). The significant relationship between chlorophyll *a* concentrations and copepods was also suggested by Kasprzak and Koschel (2000).

In accordance with predation by planktivorous fish shifting zooplankton size from large to small in eutrophic and hypertrophic shallow lakes (*e.g.*, Slusarczyk, 1997; Yang *et al.*, 1999; Radke and Kahl, 2002; Xie and Wu, 2002), our studies demonstrated an increase of copepod biomass and size structure caused by an invasion of planktivorous fish. This alleviated the suppression of phytoplankton and resulted in a decrease in water quality.

The ecological consequences of exotic fish to the lake ecosystem

Most studies about the introduction of exotic fish are concerned with the extinction of endemic fish species (Xie and Chen, 2001). Little is known about the changes of zooplankton or phytoplankton communities after invasion by exotic fish (Zhang *et al.*, 2005). Previous studies have suggested that the predation of exotic fish would result in an increase in the proportion of copepods in the crustacean zooplankton community (Qin *et al.*, 2007), and an increase of copepod size structure (Liu, 2001). Zhang *et al.* (2005) found that invasion of *N. taihuensis* had led to a change of the dominant herbivorous zooplankton from small to large calanoids. This has increased the grazing pressure on small edible algae (*e.g.* *Chroomonas* sp.) and indirectly favored the development of the inedible filamentous *Mougeotia* in Fuxian Lake. Our results for Lake Group II show significant relationships between chlorophyll *a* concentrations and the biomass and size structure of copepods in the zooplankton community in accordance with a suggestion proposed by Kasprzak and

Koschel (2000). Currie *et al.* (1999) found that the presence of planktivorous fish also resulted in a significant relationship between copepods and cladocerans. Our results supply more comprehensive evidence to support the idea that copepods were more resistant to the predation of planktivorous fish (Schulz *et al.*, 2003; Iglesias *et al.*, 2008) and the predation of planktivorous fish on cladocerans would result in a decrease of water quality (Benndorf *et al.*, 2002; Radke and Kahl, 2002). Therefore, invasion of exotic fish and consistent high production of these fish in lakes of Yunnan-Guizhou plateau have a negative effect on water quality.

In the present study, there is no consistent correlation between chlorophyll *a* and cladoceran biomass or size structure. This suggests that there is little control of phytoplankton biomass by macrozooplankton, which is consistent with findings in subtropical lakes (Havens *et al.*, 2000; Wang *et al.*, 2007a). It also suggests that phytoplankton biomass in the 13 lakes was controlled by bottom-up, rather than top-down forces. The invasion of exotic planktivorous fish had a negative effect on water quality. In previous studies, lakes stocked with amounts of copepods, and low nutrient are usually associated with planktivorous fish (*e.g.*, Benndorf *et al.*, 2000; Mehner *et al.*, 2008). Other study had also provided evidence supporting the above conclusion that the increase of copepod biomass or size structure, caused by the predation of planktivorous fish, had a negative effect on phytoplankton control and water quality (Blumenshine and Hambright, 2003).

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