

Available online at www.sciencedirect.com ScienceDirect

Limnologia 37 (2007) 242–249

LIMNOLOGICA

www.elsevier.de/limno

Crustacean zooplankton distribution patterns and their biomass as related to trophic indicators of 29 shallow subtropical lakes

Songbo Wang, Ping Xie*, Shikai Wu, Aiping Wu

Donghu Experimental Station of Lake Ecosystems, State Key Laboratory for Freshwater Ecology and Biotechnology of China, Institute of Hydrobiology, The Chinese Academy of Sciences, Wuhan 430072, PR China

Received 8 October 2006; received in revised form 16 January 2007; accepted 21 February 2007

Abstract

A comparative limnological study was carried out to present a snapshot of crustacean zooplankton communities and their relations to environmental factors to test whether there is a consistent relationship between crustacean biomass and trophic indicators among lake groups with similar trophic conditions. The study lakes showed a wide range of trophic status, with total phosphorus (TP) ranging from 0.008 to 1.448 mg L⁻¹, and chlorophyll *a* from 0.7 to 146.1 µg L⁻¹, respectively. About 38 species of Crustacea were found, of which Cladocera were represented by 25 taxa (20 genera), and Copepoda by 13 taxa (11 genera). The most common and dominant species were *Bosmina coregoni*, *Moina micrura*, *Diaphanosoma brachyurum*, *Cyclops vicinus*, *Thermocyclops taihokuensis*, *Mesocyclops notius* and *Sinocalanus dorrii*. *Daphnia* was rare in abundance. Canonical correspondence analysis showed that except for four species (*D. hyalina*, *S. dorrii*, *C. vicinus* and *M. micrura*), almost all the dominant species had the same preference for environmental factors. Temperature, predatory cyclopoids and planktivorous fishes seem to be the key factors determining species distribution. TP was a relatively better trophic indicator than chlorophyll *a* to predict crustacean biomass. Within the three groups of lakes, however, there was no consistent relationship between crustacean biomass and trophic indicators. The possible reason might be that top-down and bottom-up control on crustaceans vary with lake trophic state. The lack of significant negative correlation between crustacean biomass and chlorophyll *a* suggests that there was little control of phytoplankton biomass by macrozooplankton in these shallow subtropical lakes.

© 2007 Elsevier GmbH. All rights reserved.

Keywords: Species composition; CCA; Predation; Temperature

Introduction

Crustacean zooplankton species composition and distribution patterns in lakes have been studied intensively. Previous studies mainly focused on species composition, abundance and their occurrence (e.g. Arcifa, 1984; Patalas, 1971, 1972; Watson & Carpenter,

1974). Afterwards, studies on zooplankton occurrence and their interactions with environmental factors were conducted extensively. As zooplankton differ in their preference for biotic and abiotic factors, they can be grouped according to those factors by statistical analysis (e.g. Hessen, Faafeng, & Andersen, 1995; Swadling, Pienitz, & Nogrady, 2000; Tackx et al., 2004). Some species are suggested to be good indicators of lake trophic status (Attayde & Bozelli, 1998; Pejler, 1983). Subtropical lakes are different from temperate lakes in

*Corresponding author. Tel./fax: +86 27 68780622.

E-mail address: xieping@ihb.ac.cn (P. Xie).

many aspects. They tend to be shallow, with high thermal stress (Wang & Dou, 1997), do not contain abundant *Daphnia* (Havens et al., 2000), but support high densities of filter-feeding fish (Bachmann et al., 1996). All these factors are of great importance to the zooplankton community structure. Havens et al. (2000) gave some general information on subtropical macrozooplankton, based on results from Florida lakes. However, little information is available about crustacean species composition and their distribution patterns in relation to environmental factors in other subtropical regions.

Models relating zooplankton biomass to trophic indicators have been developed for both temperate and subtropical lakes (e.g. Bays & Crisman, 1983; Pace, 1986). Total phosphorus (TP) is suggested to be a powerful predictor (Pinto-Coelho, Pinel-Alloul, Méthot, & Havens, 2005). Nutrient-rich lakes are usually characterized by more food resources and higher planktivorous fish predation pressure (Auer, Elzer, & Arunt, 2004; Bachmann et al., 1996; Jeppesen, Lauridsen, Mitchell, Christoffersen, & Burns, 2000). Also, zooplankton control of phytoplankton biomass varies with trophic status (Benndorf, Böing, Koop, & Neubauer, 2002; Elser & Goldman, 1991). Therefore, the major crustacean zooplankton groups may respond differentially to trophic indicators (Pinto-Coelho et al., 2005). If lakes are grouped with similar trophic conditions, we might gain more insight into the trophic cascade interactions of zooplankton to phytoplankton.

A central area of freshwater shallow lakes in China is found along the middle and lower reaches of the Yangtze River. Most of these lakes are mesotrophic or eutrophic (Qin, 2002). Although there exists some studies on crustacean zooplankton, they are either out of date, giving inadequate physical–chemical data, or are not representative of a broad spectrum of lakes in this region. In this paper, we presented the results of the first comprehensive survey in this subtropical region. The main goals of our study were first to present a snapshot of crustacean zooplankton communities and their relations to environmental factors, and then to test whether there is a consistent relationship between crustacean biomass and trophic indicators among lake groups with similar trophic conditions.

Material and methods

Study site

A total of 29 lakes, located along the middle and lower reaches of the Yangtze River, were selected for this study. These lakes ranged from 100 to 34,800 ha in area and from 0.94 to 7.61 m in mean depth. Secchi disk

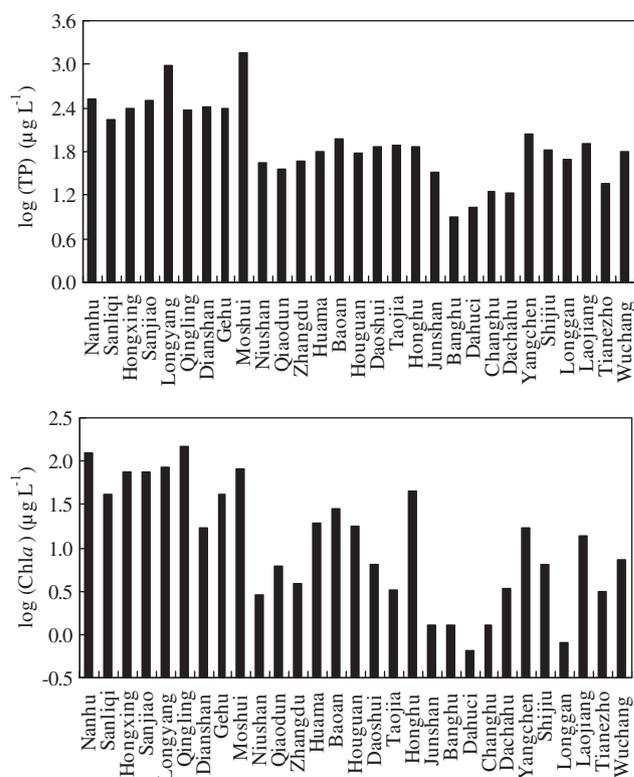


Fig. 1. Total phosphorus (TP) and chlorophyll *a* (Chl *a*) in the 29 lakes during the summer sampling (from June 20 to September 12).

visibility (SD) measured in spring varied from 0.33 to 2.60 m. Temperature ranged from 16 to 28.5 °C in spring, with an average of 21.3 °C, and from 24–33 °C, with an average of 29.1 °C in summer. TP ranged from 0.008 to 1.448 mg L⁻¹ and chlorophyll *a* (Chl *a*) from 0.7 to 146.1 µg L⁻¹ (Fig. 1). More information on limnological characteristics of the lakes is provided in detail in Wang, Xie, Wu, and Wang (2007). Every lake was sampled at least twice seasonally, but only data from spring and summer were analyzed in the present study.

Sampling and sample processing

Field sampling was conducted from April 2003 to September 2004. Zooplankton samples were taken during the daylight hours by a series of hauls 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 preserved with 5% formalin. In addition, qualitative samples for species identification were collected by pulling a 112 µm plankton net through the water column.

Counting was undertaken in the laboratory using a compound microscope (at a magnification of 100 ×). A whole sample was used and most crustaceans were identified and counted at species level. Cladocera were

identified according to Chiang and Du (1979), and Copepoda according to Shen (1979). The biomass of crustaceans was estimated from body length–weight regression equations described in Huang (1999). Size of Cladocera was measured from the top of the head to the base of the tail spine. Size of Copepoda was measured from the top of the head to the end of the furca. Species more abundant than 5% of the total crustacean density were considered as “dominants”.

Water sampled from 0.5 m below the water surface and 0.5 m above the lake bottom was combined and taken for measurement of Chl *a*, nutrient concentrations and particulate organic carbon (POC). Chl *a* was measured using a spectrophotometer and the standard acetone extraction method. Total nitrogen (TN) was digested with alkaline potassium persulfate and absorbance measured at 220 nm. TP was analyzed according to the ammonium molybdate method after oxidation with potassium persulfate under pressure. Ammonium-N (NH_4^+) was analyzed by colorimetry with Nessler's reagent. Nitrate (NO_3^-) was analyzed using the automated Korolev/cadmium reduction method. All of the above methods are described in detail in Huang (1999). The concentration of POC was determined with a total organic carbon analyzer (TOC-1010, OI Analytical).

Statistical analysis

Species distribution patterns in relation to environmental factors, as well as the partition of lake groups, were analyzed using canonical correspondence analysis (CCA) within the CANOCO 4.53 package (Ter Braak,

2004). CCA is a multivariate direct gradient analysis method that has been widely used in ecology. As the name suggests, this method is derived from correspondence analysis, but it has been modified to allow environmental data to be incorporated into the analysis. To illuminate the relationships of crustacean biomass to trophic indicators, correlation analysis was done using SPSS 10.0. The data were tested for normality with Kolmogorov–Smirnov one-sample test and \log_{10} -transformed before analysis. In the crustacean species data matrix, only those taxa were included which dominated 10% of the 29 lakes. Thus, 11 of 38 enumerated taxa were met. Additionally, Diaptominae was incorporated into the analysis. A set of explanatory variables was built, which contained all measured environmental factors (including latitude, longitude, lake area, depth, SD, pH, TN, NO_3^- , NH_4^+ , TP, TN/TP, Chl *a*, POC and temperature). The final variables contained in the analysis were obtained by CCA after a forward selection and downweighting of rare species. The crustacean abundances and environmental variables were $\log(x+1)$ transformed before analysis to obtain normality of variance in data. In the partition of lake groups, however, the original data were used.

Results

Species composition and dominance

Crustacean zooplankton species composition, frequency of occurrence and percentage as a dominant in

Table 1. Zooplankton species, frequency of occurrence (*F*) and percentage as a dominant (*D*) (>5% of the total crustacean density) in the 29 lakes

Species	<i>F</i> (%)	<i>D</i> (%)	Species	<i>F</i> (%)	<i>D</i> (%)
<i>Leptodora kindtii</i>	24	0	<i>Graptoleberis testudinaria</i>	28	0
<i>Sida crystallina</i>	41	0	<i>Disparalona rostrata</i>	7	0
<i>Diaphanosoma brachyurum</i>	86	79	<i>Rhynchotulona falcata</i>	3	0
<i>Daphnia carinata</i>	7	0	<i>Pleuroxus</i>	28	0
<i>Daphnia hyalina</i>	48	17	<i>Chydorus</i>	62	3
<i>Daphnia pulex</i>	31	0	<i>Pseudochydorus globosus</i>	7	0
<i>Scapholeberis mucronata</i>	7	0	<i>Sinocalanus dorrii</i>	72	34
<i>Simocephalus vetulus</i>	10	0	<i>Schmackeria forbesi</i>	41	17
<i>Simocephalus vetuloides</i>	3	0	<i>Neodiaptomus schmackeri</i>	10	3
<i>Simocephalus serrulatus</i>	3	0	<i>Neodiaptomus yangtsekiangensis</i>	17	0
<i>Ceriodaphnia quadrangula</i>	14	0	<i>Neutrodiaptomus alatus</i>	7	0
<i>Ceriodaphnia cornuta</i>	28	10	<i>Tropodiaptomus oryzanus</i>	14	0
<i>Moina micrura</i>	83	31	<i>Cyclops vicinus</i>	31	28
<i>Bosmina coregoni</i>	76	55	<i>Mesocyclops notius</i>	69	52
<i>Bosminopsis deitersi</i>	41	10	<i>Thermocyclops taihokuensis</i>	59	38
<i>Ilyocryptus agilis</i>	14	0	<i>Thermocyclops hyalinus</i>	31	0
<i>Alona</i>	83	0	<i>Eodiaptomus sinensis</i>	31	7
<i>Camptocercus rectirostris</i>	14	0	<i>Eucylops serrulatus</i>	34	0
<i>Leydigia leydigii</i>	14	0	<i>Eucylops euacanthus</i>	3	0

the 29 lakes are shown in Table 1. About 38 taxa were identified. Cladocera were represented by 25 taxa (20 genera), and Copepoda by 13 taxa (11 genera). Of the 38 species, about 48% were littoral species and were scarcely found in abundance. The most common species were *Bosmina coregoni*, *Moina micrura* and *Diaphanosoma brachyurum*. They were found in 76%, 83% and 86%, respectively, of all the lakes sampled. *Mesocyclops notius*, *Thermocyclops taihokuensis*, *Sinocalanus dorrii* and *Daphnia hyalina* occurred in 48–72% of these lakes. None of the remaining species occurred in more than 45% of these lakes. Based on density, *B. coregoni* (55%), *D. brachyurum* (79%), *M. micrura* (31%), *M. notius* (52%), *S. dorrii* (34%), *T. taihokuensis* (38%) and *Cyclops vicinus* (28%), respectively, dominated the crustacean plankton of the lakes sampled. The biomass of cladocerans and copepods in summer both showed a wide range, with cladocerans being dominant in most of the lakes (Fig. 2).

Crustacean zooplankton community

Crustacean zooplankton communities were quite different between spring and summer. In spring, the community was mainly composed of one or two cladocerans (*B. coregoni* and *D. hyalina*), one cyclopoid (*C. vicinus*) and one calanoid (*S. dorrii*). However, in summer the community was mainly composed of one or two cladocerans (*B. coregoni* or *D. brachyurum* or *M. micrura*), one cyclopoid (*M. notius* or *T. taihokuensis*) and one calanoid (*S. forbesi*). A general trend was to be seen from mesotrophic to hypertrophic lakes. The diminishing significance of large herbivorous cladocerans (*Daphnia*) was accompanied by the increasing predominance of cyclopoids (*Cyclops*, *Thermocyclops* and *Mesocyclops*) and small cladocerans (*Moina*, *Diaphanosoma*).

The two-dimension graph of CCA did not clearly partition the species into different clusters (Fig. 3a), although the physico-chemical variables explained

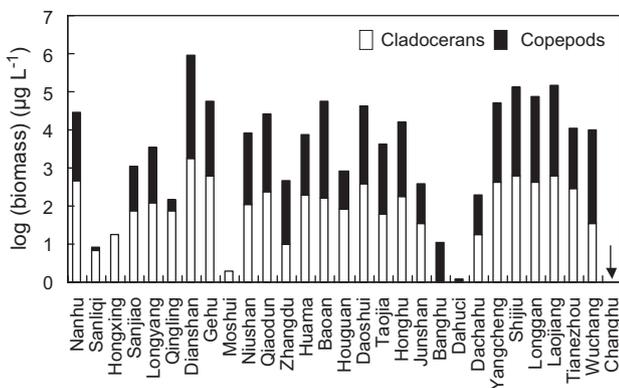


Fig. 2. Biomass composition of crustacean zooplankton in summer in the 29 lakes. Arrow indicates missing data.

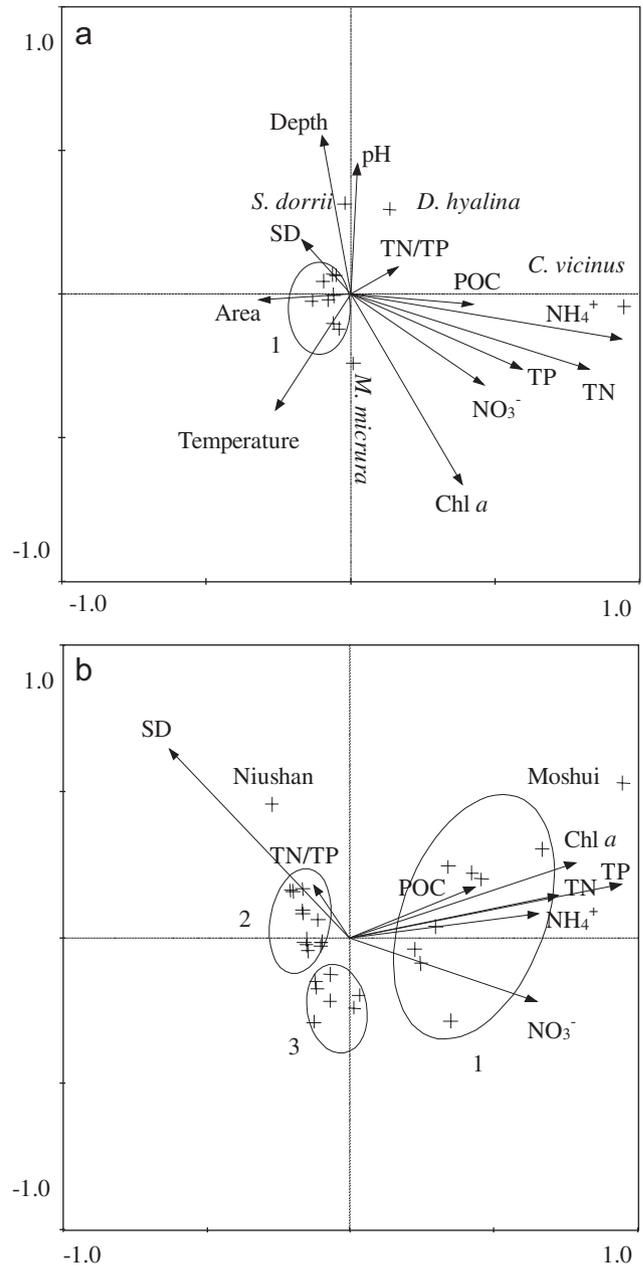


Fig. 3. The biplot of the first two axes of CCA analysis for (a) species association with the environmental factors. Cluster 1 in (a) includes: *D. brachyurum*, *M. notius*, *T. taihokuensis*, *S. forbesi*, *B. coregoni*, *B. deitersi*, *C. cornuta* and Diaptominae. (b) partition of lake groups.

38.4% of the total variance of species distribution (Table 2). Species in cluster 1 (including *D. brachyurum*, *M. notius*, *T. taihokuensis*, *S. forbesi*, *B. coregoni*, *B. deitersi*, *C. cornuta* and Diaptominae) showed the same preference for trophic state and physical conditions (Fig. 3a). In four species, however, a remarkable different pattern was found. While *M. micrura* and *C. vicinus* usually peaked in lakes with high trophic state and low SD and depth, *S. dorrii* and *D. hyalina* peaked in lakes with relatively low nutrient loading and high

SD, depth and pH. In addition, *Daphnia* deviated from the predatory cyclopoids (*C. vicinus*, *T. taihokuensis* and *M. notius*) but *Bosmina*, *Moina* and *Diaphanosoma* peaked with them. Moreover, temperature seemed to be an important factor determining the dominance of *C. vicinus*, *S. dorrii*, *D. hyalina* and *M. micrura*.

Relationship between crustacean biomass and trophic indicators

According to the results of CCA (Table 2), the 29 lakes were divided into three groups, with the exception of highly eutrophic Lake Moshui and Lake Niushan with relatively good water quality (Fig. 3b). The first eight lakes were classified as group 1, the last seven lakes group 3 and the left as group 2 (Fig. 1). The biomass of different crustacean groups in the three groups of lakes was correlated with trophic indicators (Table 3). The pooled data of crustaceans (TB) showed a weak but significant correlation with TP ($r = 0.268$, $p < 0.01$) but not with Chl *a* ($r = 0.146$, $p > 0.05$). The same was found for the pooled data of cladocerans and copepods. Cladocerans and copepods in the second group were both significantly related to trophic indicators ($0.495 < r < 0.610$, $p < 0.01$). In addition, copepods were significantly correlated with Chl *a* in the first group ($r = -0.595$, $p < 0.01$), and with TP in the third group ($r = 0.339$, $p < 0.05$).

Discussion

Crustacean zooplankton taxonomic structure

Korovchinsky (2000) reported that pelagic cladocerans of large lakes in the eastern hemisphere were mainly composed of *Diaphanosoma*, *Daphnia*, *Ceriodaphnia*, *Bosmina* and *Moina*. These genera have a great significance in terms of occurrence and biomass in our study lakes. They are also common genera in temperate and tropical waterbodies (Arcifa, 1984; Gulati, 1990; Pinto-Coelho et al., 2005; Patalas, 1972). With respect to community structure, Patalas (1972) found in St. Lawrence Great Lakes that cyclopoids (*Cyclops*, *Mesocyclops*) and cladocerans (*Daphnia* and *Bosmina*) dominated eutrophic lakes. Although cyclopoids were the dominant copepods in our lakes, the dominant cladocerans differed from the Great Lakes. The cladocerans in most of our lakes were dominated by *Bosmina*, *Moina* and *Diaphanosoma*. *Daphnia* was only dominant in five lakes in spring. The three dominant cladocerans had relatively high occurrence and dominance in our lakes, although being less competitive in exploiting resources than *Daphnia* (Matveev, Matveeva, & Jones, 2000). Sommer, Gliwicz, Lampert, and Duncan (1986) demonstrated in the PEG-model that temperature, food resources and fish predation had great importance in structuring the zooplankton community. There are studies showing that *Bosmina*, *Moina*

Table 2. Summary of CCA analysis for the first two axes between environmental factors and species as well as lakes

Axes	Species		Lakes	
	1	2	1	2
Eigenvalues	0.676	0.257	0.892	0.726
Species–environment correlations	0.877	0.685	0.945	0.852
Cumulative percentage variance of species data	20.5	28.4	3.2	5.9
Of species–environment relation	53.5	73.8	24.6	44.6
Sum of all eigenvalues	3.291		27.500	
Sum of all canonical eigenvalues	1.264		3.627	
Variance explained	38.4%		13.2%	

Table 3. Coefficients of the Pearson correlation between crustacean biomass and trophic indicators in the three groups of lakes. The data were log transformed

	TP				Chl <i>a</i>			
	1	2	3	Total	1	2	3	Total
TB	0.342	0.734**	0.137	0.268**	-0.284	0.724**	0.185	0.146
Cladocerans	0.334	0.498**	-0.016	0.182*	-0.253	0.609**	0.085	0.090
Copepods	0.085	0.576**	0.339*	0.211*	-0.595**	0.571**	0.174	0.038

** $p < 0.01$, * $p < 0.05$. TB = total crustacean biomass, the sum of cladocerans and copepods.

and *Diaphanosoma* are all resistant to planktivorous fish predation (Hanazato & Yasuno, 1989; Ślusarczyk, 1997; Xie & Wu, 2002). However, it was not the case for *Daphnia* (Brooks & Dodson, 1965). On the other hand, cyclopoid copepods, despite having much lower biomass, can also account for a greater portion of the predation mortality on herbivorous zooplankton than planktivorous fish (Blumenshine & Hambright, 2003). The biplot of the CCA analysis showed that *Daphnia* deviated from the predatory cyclopoids (*C. vicinus*, *T. taihokuensis* and *M. notius*) but *Bosmina*, *Moina* and *Diaphanosoma* peaked with them. Thus, the disappearance of *Daphnia* and the increasing dominance of invulnerable cladocerans might be an outcome of combined predation arising from predatory copepods and planktivorous fishes.

In addition, *D. hyalina*, *S. dorrui* and *C. vicinus* peaked at low temperature, while other species at relatively high temperature. In our lakes, the above three species and *M. micrura* were found at an average temperature of 20.0, 21.9, 17.9 and 28.7 °C, respectively. Chiang and Du (1979) observed that *D. hyalina* occurred below a temperature of 20 °C and the population could survive in winter but disappeared in May or June. Havens et al. (2000) also found temperature played a role in determining the dominance of daphnids in subtropical Florida lakes. *C. vicinus* was a predominant early spring species in eutrophic lakes and was replaced by two typical thermophilic species, *T. taihokuensis* and *M. notius*. Yang, Huang, and Liu (1999) documented that *C. vicinus* preyed on *M. notius* and even replaced it to be dominant in winter and spring. Moreover, *C. vicinus* has a higher rate of development at a temperature below 25 °C (Maier, 1989). Therefore, the seasonal temperature changes may be another reason responsible for the shift of crustacean community (Tackx et al., 2004).

In the present study, the measured environmental factors only explained 38.4% of the total variance of crustacean species distribution, suggesting that many other undetermined factors within lakes are also of great importance in structuring the crustacean community. These undetermined factors might include bacteria (Havens, 2002), invertebrate predator such as *Chaoborus* (Hanazato, 1991), and planktivorous fishes (Havens, 2002; Hessen et al., 1995).

Response of crustacean biomass to trophic indicators

TP was a relatively better predictor of the biomass of crustacean groups than chlorophyll *a* in our study, as suggested by Pinto-Coelho et al. (2005). However, in the study of Pinto-Coelho et al. (2005), the ability of TP to predict crustacean biomass in subtropical region was only based on the significant relationship between cladocerans

and TP in five Florida lakes. The number of lakes included in the study was low. Therefore, the conclusion needs to be further justified. In our 29 subtropical lakes, the pooled biomass of crustaceans, cladocerans and copepods were all significantly correlated with TP but not with chlorophyll *a*. Therefore, our study supplied a more comprehensive evidence to support the power of TP in predicting zooplankton biomass. TP is also considered to be better for reflecting the total food materials edible than chlorophyll *a* (Yan, 1986).

In the three groups of lakes, however, only a few strong correlations were found. Some studies also fail to find significant relationships, and the possible reason is attributed to differences in predation pressure exerted by fishes or invertebrates (Amarasinghe, Vijverberg, & Boersma, 1997), or the lack of nannoplanktonic food resources (McCauley & Kalff, 1981). The different response of lake groups to trophic indicators suggests that top-down and bottom-up control on crustaceans also varied with trophic state in our lakes. The second group of lakes was associated with better prediction of crustacean biomass, suggesting that crustacean biomass may be bottom-up controlled. The first group of lakes was highly eutrophic and seven of the eight lakes were stocked with abundant filter-feeding fishes (Wang et al., 2007). Exceptionally, copepods were negatively correlated with phytoplankton biomass. Although studies exist showing that copepods have a strong impact on the size structure of phytoplankton, they show no impact on the decline of phytoplankton biomass (e.g. Sommer et al., 2001). Thus, the most probable explanation for the negative interaction might be fish predation, which depresses copepod biomass to a low level but is associated with high phytoplankton biomass (Radke & Kahl, 2002). Anyhow, no consistent relationship between crustacean biomass and trophic indicators was found among the three lake groups.

In the present study, the lack of significant negative correlation between crustacean biomass and chlorophyll *a* suggests that there is little control of phytoplankton biomass by macrozooplankton, as found in subtropical Florida lakes (Crisman & Beaver, 1990; Havens et al., 2000). Havens (2002) demonstrated that phytoplankton biomass in south Florida lakes was controlled by bottom-up, rather than top-down forces. Another study in our lakes also provided evidence for the above conclusion that nutrients are more important than crustacean zooplankton in controlling the phytoplankton biomass in shallow subtropical lakes (unpublished data).

Acknowledgments

This research was supported by a National Natural Science Foundation of China (Grant No. 30225011).

Great thanks are given to Baozhu Pan, Haijun Wang and Xiaomin Liang for their generous helps in the field sampling. The authors are also grateful to two anonymous reviewers for their valuable comments on this manuscript.

References

- Amarasinghe, P. B., Vijverberg, J., & Boersma, M. (1997). Production biology of copepods and cladocerans in three south-east Sri Lankan low-land reservoirs and its composition to other tropical freshwater bodies. *Hydrobiologia*, *350*, 145–162.
- Arcifa, M. S. (1984). Zooplankton composition of ten reservoirs in southern Brazil. *Hydrobiologia*, *113*, 137–145.
- Attayde, J. L., & Bozelli, R. L. (1998). Assessing the indicator properties of zooplankton assemblages to disturbance gradients by canonical correspondence analysis. *Canadian Journal of Fisheries and Aquatic Sciences*, *55*, 1789–1797.
- Auer, B., Elzer, U., & Arunt, H. (2004). Comparison of pelagic food webs in lakes along a trophic gradient and with seasonal aspects: Influence of resource and predation. *Journal of Plankton Research*, *26*(6), 697–709.
- Bachmann, R. W., Jones, B. L., Fox, D. D., Hoyer, M., Bull, L. A., & Canfield, D. E., Jr. (1996). Relations between trophic state indicators and fish in Florida (USA) lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, *53*, 842–855.
- Bays, J. S., & Crisman, T. L. (1983). Zooplankton and trophic state relationships in Florida lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, *40*, 1813–1819.
- Benndorf, J., Böing, W., Koop, J., & Neubauer, I. (2002). Top-down control of phytoplankton: The role of time scale, lake depth and trophic state. *Freshwater Biology*, *47*, 2282–2295.
- Blumenshine, S. C., & Hambright, K. D. (2003). Top-down control in pelagic systems: A role for invertebrate predation. *Hydrobiologia*, *491*, 347–356.
- Brooks, J. L., & Dodson, S. I. (1965). Predation, body size, and composition of plankton. *Science*, *150*, 28–35.
- Chiang, S. C., & Du, N. S. (1979). *Fauna Sinica, Crustacea, freshwater Cladocera*. Beijing: Science Press, Academia Sinica.
- Crisman, T. L., & Beaver, J. R. (1990). Applicability of biomanipulation for managing eutrophication in the subtropics. *Hydrobiologia*, *200*, 177–185.
- Elser, J. J., & Goldman, C. R. (1991). Zooplankton effects on phytoplankton in lakes of contrasting trophic status. *Limnology and Oceanography*, *36*(1), 64–90.
- Gulati, R. D. (1990). Zooplankton structure in the Loosdrecht lakes in relation to trophic status and recent restoration measures. *Hydrobiologia*, *191*, 173–188.
- Hanazato, T. (1991). Effects of repeated application of carbaryl on zooplankton communities in environmental ponds with or without the predator *Chaoborus*. *Environmental Pollution*, *74*(4), 309–324.
- Hanazato, T., & Yasuno, M. (1989). Zooplankton community structure driven by vertebrate and invertebrate predators. *Oecologia*, *81*, 450–458.
- Havens, K. E. (2002). Zooplankton structure and potential food web interactions in the plankton of a subtropical chain-of-lakes. *The Scientific World Journal*, *2*, 926–942.
- Havens, K. E., East, T. L., Marcus, J., Essex, P., Bolan, B., Raymond, S., et al. (2000). Dynamics of the exotic *Daphnia lumholtzii* and native macro-zooplankton in a subtropical chain-of-lakes in Florida, USA. *Freshwater Biology*, *45*, 21–32.
- Hessen, D. O., Faafeng, B. A., & Andersen, T. (1995). Replacement of herbivore zooplankton species along gradients of ecosystem productivity and fish predation pressure. *Canadian Journal of Fisheries and Aquatic Sciences*, *52*, 733–742.
- Huang, X. F. (1999). *Survey, observation and analysis of lake ecology*. Beijing: Standards Press of China.
- Jeppesen, E., Lauridsen, T. L., Mitchell, S. F., Christoffersen, K., & Burns, C. W. (2000). Trophic structure in the pelagial of 25 shallow New Zealand lakes: Changes along nutrient and fish gradients. *Journal of Plankton Research*, *22*, 951–968.
- Korovchinsky, N. M. (2000). Species richness of pelagic Cladocera of large lakes in the eastern hemisphere. *Hydrobiologia*, *434*, 41–54.
- Maier, G. (1989). The seasonal cycle of *Thermocyclops crassus* (Fischer 1853) (Copepoda: Cyclopoida) in a shallow, eutrophic lake. *Hydrobiologia*, *178*, 43–58.
- Matveev, V., Matveeva, L., & Jones, G. J. (2000). Relative impacts of *Daphnia* grazing and direct stimulation by fish on phytoplankton abundance in mesocosm communities. *Freshwater Biology*, *44*, 375–385.
- McCauley, E., & Kalf, J. (1981). Empirical relationships between phytoplankton and zooplankton biomass in lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, *38*, 458–463.
- Pace, M. L. (1986). An empirical analysis of zooplankton community size structure across lake trophic gradients. *Limnology and Oceanography*, *31*, 45–55.
- Patalas, K. (1971). Crustacean plankton communities in forty-five lakes in the Experimental Lakes Area, northwestern Ontario. *Journal of the Fisheries Research Board of Canada*, *28*, 231–244.
- Patalas, K. (1972). Crustacean plankton and the eutrophication of St. Lawrence Great Lakes. *Journal of the Fisheries Research Board of Canada*, *29*, 1451–1462.
- Pejler, B. (1983). Zooplanktonic indicators of trophy and their food. *Hydrobiologia*, *101*, 111–114.
- Pinto-Coelho, R. P., Pinel-Alloul, B. P., Méthot, G., & Havens, K. E. (2005). Crustacean zooplankton in lakes and reservoirs of temperate and tropical regions: Variation with trophic status. *Canadian Journal of Fisheries and Aquatic Sciences*, *62*(2), 348–361.
- Qin, B. Q. (2002). Approaches to mechanisms and control of eutrophication of shallow lakes in the middle and lower reaches of the Yangtze River. *Journal of Lake Sciences*, *14*(3), 193–202.
- Radke, R., & Kahl, U. (2002). Effects of a filter-feeding fish [silver carp, *Hypophthalmichthys molitrix* (Val.)] on phyto- and zooplankton in a mesotrophic reservoir: Results from an enclosure experiment. *Freshwater Biology*, *47*, 2337–2344.

- Shen, J. R. (1979). *Fauna Sinica, Crustacea, freshwater Copepoda*. Beijing: Science Press, Academia Sinica.
- Ślusarczyk, M. (1997). Impact of fish predation on a small-bodied cladoceran: Limitation or stimulation? *Hydrobiologia*, 342/343, 215–221.
- Sommer, U., Gliwicz, Z. M., Lampert, W., & Duncan, A. (1986). The PEG-model of seasonal succession of planktonic events in freshwaters. *Archiv für Hydrobiologie*, 106, 422–477.
- Sommer, U., Sommer, F., Santer, B., Jamieson, C., Boersma, M., Becker, C., et al. (2001). Complementary impact of copepods and cladocerans on phytoplankton. *Ecology Letters*, 4, 545–550.
- Swadling, K. M., Pienitz, R., & Nogrady, T. (2000). Zooplankton community composition of lakes in the Yukon and Northwest Territories (Canada): Relationship to physical and chemical limnology. *Hydrobiologia*, 431, 211–224.
- Tackx, M. L. M., De Pauw, N., Van Mieghem, R., Azémar, F., Hannouti, A., Van Damme, S., et al. (2004). Zooplankton in the Schelde estuary, Belgium and The Netherlands. Spatial and temporal patterns. *Journal of Plankton Research*, 26(2), 133–141.
- Ter Braak, C. J. F. (2004). *Biometris – quantitative methods in the life and earth sciences*. Plant Research International, Wageningen University and Research Centre, The Netherlands.
- Wang, S. M., & Dou, H. S. (1997). *Lake annals of China*. Beijing: Science Press, Academia Sinica.
- Wang, S., Xie, P., Wu, S., & Wang, H. (2007). Crustacean zooplankton size structure in aquaculture lakes: Is larger size structure always associated with higher grazing pressure? *Hydrobiologia*, 575, 203–209.
- Watson, N. H. F., & Carpenter, G. F. (1974). Seasonal abundance of crustacean zooplankton and net plankton biomass of lakes Huron, Erie, and Ontario. *Journal of the Fisheries Research Board of Canada*, 31, 309–317.
- Xie, P., & Wu, L. (2002). Enhancement of *Moina micrura* by the filter-feeding silver and bighead carps in a subtropical Chinese lake. *Archiv für Hydrobiologie*, 154(2), 327–340.
- Yan, N. D. (1986). Empirical prediction of crustacean zooplankton biomass in nutrient poor Canadian Shield lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, 43, 788–796.
- Yang, Y., Huang, X., & Liu, J. (1999). Long-term changes in crustacean zooplankton and water quality in a shallow, eutrophic Chinese lake densely stocked with fish. *Hydrobiologia*, 391, 195–203.