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Effects of filter-feeding planktivorous fish and cyanobacteria on structuring the zooplankton community in the eastern plain lakes of China

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ABSTRACT

To explore the changes of the zooplankton community in response to excessive interferences of anthropogenic eutrophication and aquaculture on aquatic ecosystem, we performed a survey to determine the variations in these communities in 100 eastern plain lakes of China in summer. Our results showed that when filter-feeding planktivorous fishes were in high yield, Rotifera and medium cladocera accounted for a large proportion of the community; when they were in low yield, small cladocera increased with the increased nutrient level. The detrended correspondence analysis demonstrated that planktivorous fish and cyanobacteria were important factors influencing the zooplankton community. The linear regression analysis showed that the fraction of Rotifera increased and Calanoida decreased with the increasing fish yield; the fraction of small cladocera increased with the increasing cyanobacteria. The results implied that zooplankton community succession was strengthened by the combined effects of planktivorous fish and cyanobacteria. The effects of filter-feeding planktivorous fish on zooplankton depend on the survival ability of different zooplankton species as well as the size. With the combined effects of planktivorous fish culture and eutrophication, the zooplankton community tend to be dominated by r-strategy species and good escape ability species.

1. Introduction

Zooplankton are studied widely as indicator of ecological change due to their sensitive response to environmental variation (Hessen et al., 1995; Jeppesen et al., 2011) and their specific biological properties, such as, geographically widespread, having short reproduction cycles, and occupying a central position in aquatic food webs (Lampert, 2006). A large body of studies have documented that excessive interferences of anthropogenic eutrophication and aquaculture seriously influence aquatic ecosystem all over the world (Smith et al., 1999; Naylor et al., 2000; Jackson et al., 2001; Smith, 2003; Smith and Schindler, 2009), leading to collapse of vascular plant communities, increased proportion of inedible phytoplankton, increased fish production with alteration of fish community (Smith et al., 1999; Smith, 2003). These effects strongly influenced the zooplankton community by eutrophication of cyanobacterial blooms (Sun et al., 2012) and strong fish predation (Zhang et al., 2013).

Eutrophication is a global problem among oceans, rivers, and lakes (Smith, 2003; Smith and Schindler, 2009; Azevedo et al., 2015; Snickars et al., 2015). Cyanobacterial blooms is the key symptom of eutrophication, which is mainly caused by the increase of total nitrogen (TN) and total phosphrous (TP) nutrients (Elser et al., 2007; Conley et al., 2009; Paerl et al., 2011). Basically the cycles of the key nutrient elements of nitrogen and phosphorus have been massively altered by anthropogenic activities (Smith et al., 1999; Smith, 2003), followed by water environmental degradation with low dissolved oxygen, unpleasant smell, and algal toxins et al. (Smith et al., 1999; Codd et al., 2005), and these may negatively affect trophic structure through food web (de Figueiredo et al., 2004; Malbrouck and Kestemont, 2006). Eutrophication of cyanobacteria blooms leads to the succession of the zooplankton community to more tolerant species (Ghadouani et al., 2003; Sun et al., 2012). What is more, in many freshwater ecosystems, the

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decrease of piscivorous fishes and the increase of planktivorous fishes reduced the strength of top-down effects on phytoplankton as the loss of effective predator of zooplankton (Andersson et al., 1978; Christoffersen et al., 1993; Vanni and Layne, 1997; Osterblom et al., 2007). Previous study experimentally showed that the zooplankton community changed much with the increasing filter-feeding planktivorous fishes. On the one hand, the gizzard shad (filter feeder) directly reduced zooplankton via predation; on the other hand, they indirectly affected zooplankton by reducing edible phytoplankton abundance to zooplankton (DeVries and Stein, 1992). However, the large scale study of the combined effects of eutrophication and filter-feeding planktivorous fish culture on the zooplankton community is few.

In this study, 100 eastern plain lakes were surveyed to explore the effects of filter-feeding planktivorous fish and cyanobacteria on the zooplankton community, covering about 16900 km^2 and accounting for nearly 20% of the total lake area in China. We investigated the zooplankton community composition of these lakes and then analyzed the changes in the structure of these communities in response to the combined effects of planktivorous fish and cyanobacteria.

2. Sampling and analyses

2.1. Study area

100 subtropical and shallow lakes (mean depth, <3 m) along the eastern plain areas of China were studied from 2008 to 2009 (Fig. 1). The longitudes and the latitudes of studied lakes range from 111.7° E to 121.7° E and 28.5° N to 38.9° N respectively. Most lakes have been interfered by human activities, like aquaculture and eutrophication. Due to the regional difference of aquaculture, these lakes can be divided into two types according to the result of K-Means Cluster with planktivorous fish yield as the parameter for clustering (type 1: low fish yield, type 2: high fish yield). The aquacultural planktivorous fishes were *Hypophthalmichthys molitrix* and *Aristichthys nobilis* in these lakes, which are filter-feeding feeders.

2.2. Sampling and analyses

For 100 lakes of the eastern plain of China, sampling sites were evenly distributed for each lake, of which the numbers set for each lake changed with the surface area from 1 to 30. All sites were sampled once during June to August of 2008–2009. In this study, to understand the relationships among the trophic status, cyanobacteria, zooplankton, and fish, all parameters of the eastern plain lakes of China were represented by the mean values of the summer. The eight lakes with incomplete data were excluded from the study, and a total of 92 lakes with summer samples were used.

Water temperature (T), pH value, dissolved oxygen (DO), conductivity (COND) were measured in 0.5 m below the water surface in situ by multi-parameter water quality meter YSI ProPlus (YellowSprings, OH, USA). Secchi depth (SD) was surveyed by a black and white Secchi disk (20 cm) to determine water transparency. Water samples from each site were collected at the upper (i.e., 0.5 m below the water surface), middle (midway between the surface and the bottom), and lower (i.e., 0.5 m above the sediment surface) parts of the water column using a 5-L Schindler sampler respectively and then mixed together for subsequent analyses. Hydrochemical parameters and biotic samples were disposed and measured for each sample in the laboratory according to the methods described in detail by Yang et al. (2005).

Total nitrogen (TN) and total phosphorus (TP) were measured for each sample in the laboratory according to the methods described in detail by Huang et al. (1999). 1L water sample was preserved in acetic Lugol's solution and concentrated to 50 mL after sedimentation for 48 h for analysis of phytoplankton and rotifers (Huang et al., 1999). Phytoplankton were counted and measured under 400× magnification using an Olympus BX41 microscope (Olympus, Tokyo, Japan). For *Microcystis* colonies, an ultrasonic crusher (JY88-II, Scientiz, Ningbo, Zhejiang, China) was used to separate and count the single cells. Taxonomic identification of phytoplankton was performed according to Hu (2006). Rotifers were counted and measured under 200× magnification using an Olympus CX 21 microscope (Olympus, Tokyo, Japan) and identified according to Voigt and Koste (1978). For crustacean zooplankton, 10 L water samples were sieved through 64 μm plankton nets and preserved with 5% formalin for further analysis (Huang et al., 1999). In the crustacean zooplankton samples, all individuals were counted and, if possible, the body of at least 30 individuals of each species were measured under 40× magnification by using an Olympus CX 21 microscope (Olympus, Tokyo, Japan). Crustacean zooplankton were identified according to Shen et al. (1979) and Chiang and Du (1979). The biomass of each plankton species was calculated using methods described by Huang et al. (1999). Fish yield data were obtained from the fishery management committee of each lake. To isolate the effects of planktivorous fishes on the zooplankton community, we used fish yield of planktivorous fishes for analysis.

2.3. Statistical analyses

First, K-Means Cluster was conducted to separate the different trophic status in two types of lake respectively with TN, TP and SD as the trophic status parameters for clustering. Each type can be divided into high nutrient level and low nutrient level. Thus there are four gradients of the eastern plain lakes of China as follows: low fish yield with low nutrient (1L, the number of lakes (n) = 36), low fish yield with high nutrient (1H, n = 31), high fish yield with low nutrient (2L, n = 7), and high fish yield with high nutrient (2H, n = 18). Second, differences in the nutrient level and biotic parameters among gradients of the eastern plain lakes of China were tested with one-way analysis of variance (ANOVA). Least significance difference test (LSD) was used for variables with constant variances and Games-Howell (A) was used for variables with unequal variances. The analysis was carried out with IBM SPSS Statistics v. 19 for Windows software (SPSS, Inc., Chicago, IL, USA). Third, a detrended correspondence analysis (DCA) was performed using CANOCO 5.0 (Braak and Šmilauer, 2002) to assess the effects of the environmental variables on the zooplankton community (biomass) with a short gradient length. The assessed environmental variables were lake area, longitude, latitude, T, TN, TP, TN: TP ratio, DO, SD, pH, COND, total phytoplankton biomass, *Microcystis* biomass, and fish yield. The dependent variables were the biomass of Rotifera, small cladocera, medium cladocera, large cladocera, Calanoida, and Cyclopoida. After forward selection, only the significant independent variables ($p < 0.05$) were included in the final DCA ordination. Last, a linear regression analysis was employed to gain a greater understanding of the linkage between the zooplankton community composition and the most important influencing variables. The independent variables were fish yield and cyanobacteria; the dependent variables were the relative biomass of Rotifera to crustacean zooplankton (Rotifera/crustacean zp), the relative biomass of Cyclopoida to Calanoida (Cyclopoida/Calanoida) and the relative biomass of small cladocera (Ceriodaphnia, Bosminidae, Chydoridae and Macrothricidae) to others cladocera (medium cladocera, Diaphanosoma, Moina and Sida; large cladocera, Daphnia, Simocephalus and Leptodora) (small cladocera/others cladocera) respectively. The linear regression was implemented in R using the car package; a leverage plot was produced (Sall, 1990).

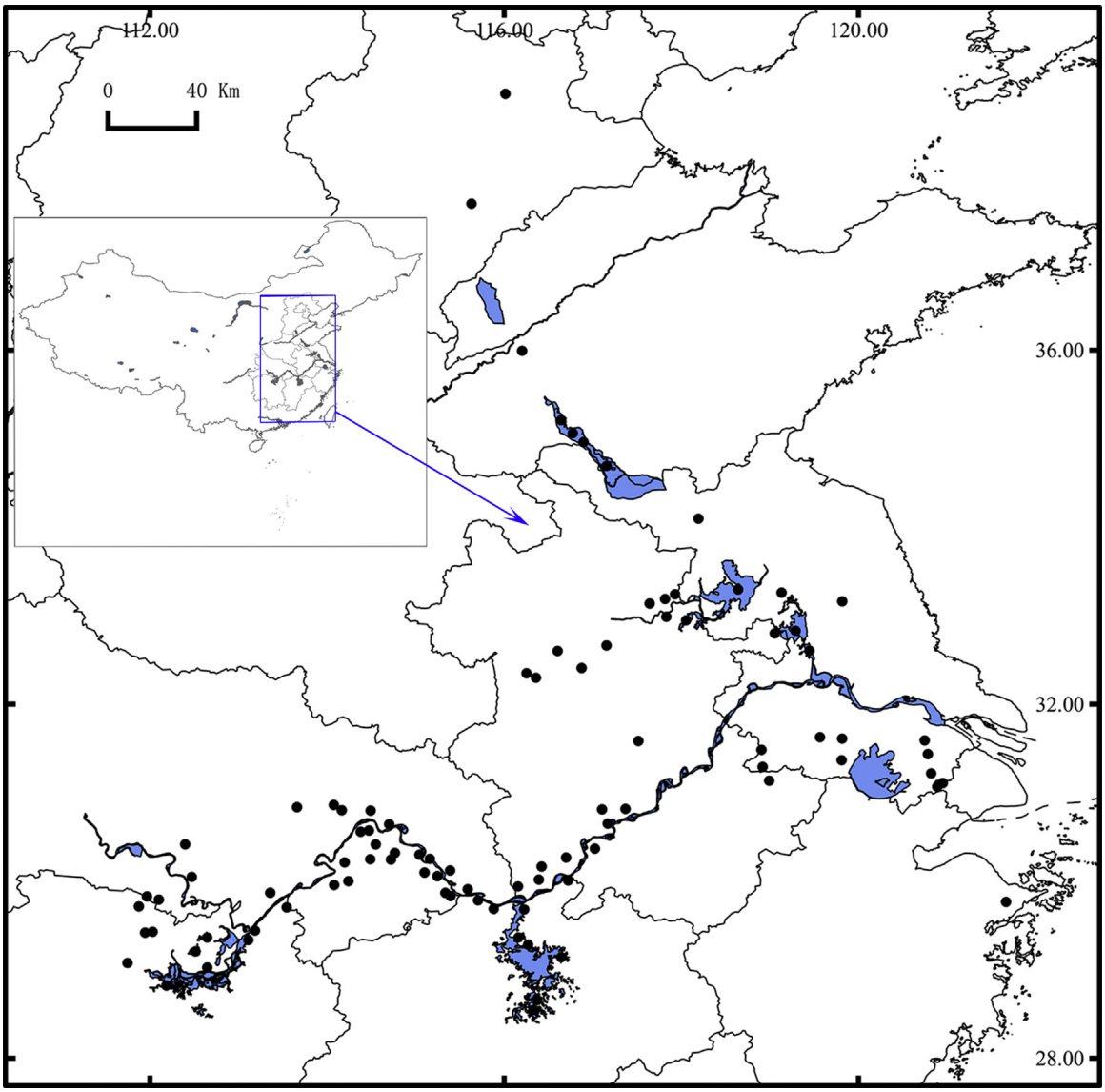

Fig. 1. Distribution of the studied eastern plain lakes of China.

All of the data were tested for homogeneity and normality and the data were log10-transformed prior to performing the statistical analysis when these assumptions were violated.

3. Results

3.1. Zooplankton community composition and their difference among different types of lake

In this study, we identified 58 rotifer taxa and 41 crustacean zooplankton taxa in total. Rotifera accounted for a large proportion of the community (Fig. 2) and the dominant genus included *Polyarthra*, *Keratella* and *Brachionus*. Cladocera dominated the crustacean zooplankton community (Fig. 2) and the dominant cladocerans species were *Diaphanosoma brachyurum* (*D.brachyurum*) and *Moina micrura* (*M.micrura*). The main copepod species were *Mesocyclops leuckarti* and *Thermocyclops taihokuensis*. Large cladocera and Calanoida accouted for only a small proportion of the zooplankton community in this study and showed no difference in different nutrient levels of both the two types of lake (Fig. 2).

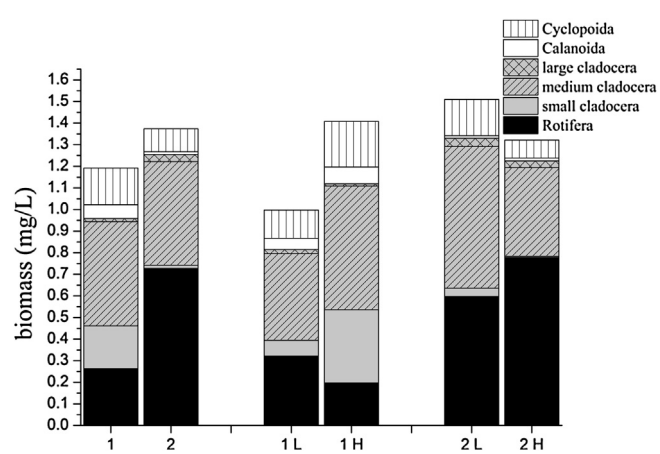

Fig. 2. Zooplankton communities of the eastern plain lakes of China. 1, low fish yield; 2, high fish yield. 1L, low fish yield with low nutrient; 1H, low fish yield with high nutrient. 2L, high fish yield with low nutrient; 2H, high fish yield with high nutrient.

Table 1
Mean values and ranges of abiotic and biotic parameters in the different types of the eastain plain lakes of China.

	1 mean (range)	2 mean (range)	1L mean (range)	1H mean (range)	2L mean(range)	2H mean (range)
Longitude	116.47 (119.97–121.67)	115.23(111.75–119.81)	115.38(111.97–119.82)	117.74(113.36–121.67)	112.63(111.75–114.38)	116.23(111.87–119.81)
Latitude	31.36 (28.54–38.89)	30.56 (28.65–34.96)	30.62 (28.54–35.99)	32.22 (29.28–38.89)	29.50 (29.08–30.56)	30.97 (28.65–34.96)
Area (km^2)	233.1 (11.8–2933.0)	49.3 (10.3–316.0)	166.3 (11.8–2423.0)	310.7 (12.9–2933.0)	38.6 (12.3–114.2)	53.4 (10.3–316.0)
Depth (cm)	252 (93–639)	268 (44–545)	272 (102–639)	229 (93–523)	266 (150–350)	268 (44–545)
TN ($mg\,L^{-1}$)	1.17 (0.30–3.16)	1.15 (0.39–1.62)	0.67 (0.30–1.25)	1.76 (1.18–3.16)	0.65 (0.39–0.97)	1.35 (1.06–1.62)
TP ($mg\,L^{-1}$)	0.114 (0.022–0.486)	0.147 (0.035–0.329)	0.059 (0.022–0.221)	0.179 (0.066–0.486)	0.150 (0.065–0.200)	0.145 (0.035–0.329)
SD (cm)	64 (20–269)	46 (26–65)	78 (20–269)	47 (20–90)	44 (26–58)	47 (27–65)
T (°C)	28.7 (24.4–33.1)	29.3 (24.3–32.2)	29.2 (25.1–33.1)	28.0 (24.4–32.6)	29.4 (27.9–30.5)	29.2 (24.3–32.2)
TN: TP ratio	13 (4–28)	8 (2–12)	14 (4–28)	12 (4–24)	5 (2–8)	9 (5–12)
pH	8.6 (7.5–9.8)	8.8 (8.1–9.5)	8.4 (7.5–9.4)	8.6 (7.5–9.8)	9.0 (8.2–9.5)	8.7 (8.1–9.3)
DO ($mg\,L^{-1}$)	7.3 (4.2–9.8)	9.3 (6.9–15.9)	7.2 (4.2–9.8)	7.3 (5.6–9.5)	10.1 (7.4–15.9)	9.0 (6.9–10.9)
COND ($\mu s\,cm^{-1}$)	402.8 (61.7–1524.7)	379.6 (74.6–1291.6)	276.4 (61.7–891.8)	549.6 (92.2–1524.7)	333.3 (179.4–461.4)	397.7 (74.6–1291.6)
fish yield ($kg\,ha^{-1}$)	47.1 (0.01–283.3)	291.2 (34.8–882.5)	52.5 (0.01–215.3)	40.9 (0.02–283.3)	332.4 (43.8–882.5)	275.2 (34.8–589.1)
phytoplankton ($mg\,L^{-1}$)	5.51 (0.65–21.09)	9.33 (1.27–28.89)	3.51 (0.65–9.73)	7.84 (0.94–21.09)	10.55 (4.14–28.89)	8.86 (1.27–28.31)
cyanobacteria ($mg\,L^{-1}$)	1.61 (0.02–7.20)	1.86 (0.27–4.31)	0.87 (0.02–5.36)	2.48 (0.07–7.20)	2.39 (0.90–4.31)	1.65 (0.27–4.00)
cyanobacteria (%)	27.04 (0.98–82.62)	25.78 (3.11–74.10)	22.29 (0.98–82.62)	32.56 (0.98–80.33)	34.85 (3.11–74.10)	22.26 (5.25–45.41)
zooplankton ($mg\,L^{-1}$)	1.23 (0.06–5.81)	1.40 (0.32–3.10)	1.04 (0.11–4.33)	1.45 (0.06–5.81)	1.55 (1.04–3.00)	1.35 (0.32–3.10)

Note: TN, total nitrogen; TP, total phosphorus; SD, Secchi depth; T, water temperature; TN: TP ratio, total nitrogen to total phosphorous ratio; DO, dissolved oxygen; COND, conductivity; fish yield, the yield of filter-feeding planktivorous fishes; cyanobacteria (%), the relative biomass of cyanobacteria to phytoplankton.

Table 2
Differences in the nutrient level and biotic parameters among different types of the eastern plain lakes of China were tested with one-way analysis of variance (ANOVA). Least significance difference test (LSD) was used for variables with constant variances and Games-Howell (A) was used for variables with unequal variances.

	ANOVA (type1, 2) 2)2Type2)		ANOVA (1L, 1H)		ANOVA (2L, 2H)	
	F	*p*	F	*p*	F	*p*
TN	0.023	>0.05	**162.683**	**<0.001**	**63.098**	**<0.001**
TP	2.403	>0.05	**38.308**	**<0.001**	0.026	>0.05
SD	3.897	>0.05	**10.334**	**0.002**	0.520	>0.05
fish yield dedensitydensity	**67.001**	**<0.001**	0.566	>0.05	0.322	>0.05
phytoplankton	9.253	**0.003**	**20.543**	**<0.001**	0.262	>0.05
zooplankton	0.559	>0.05	2.539	>0.05	0.262	>0.05
cyanobacteria	0.331	>0.05	**13.383**	**0.001**	1.839	>0.05
cyanobacteria (%)	0.060	>0.05	3.386	>0.05	2.659	>0.05
Rotifera	22.977	**<0.001**	2.801	>0.05	0.421	>0.05
Cladocera	0.729	>0.05	3.779	>0.05	2.490	>0.05
Copepoda	5.952	**0.017**	4.791	**0.032**	1.580	>0.05
small cladocera	3.806	>0.05	5.682	**0.020**	1.964	>0.05
medium cladocera cladocerans	0.000	>0.05	1.532	>0.05	2.233	>0.05
large cladocera	1.774	>0.05	1.046	>0.05	0.025	>0.05
Calanioda	4.562	**0.035**	0.788	>0.05	0.016	>0.05
Cyclopoida	2.878	>0.05	4.143	**0.046**	2.174	>0.05

Note: Significant effects are indicated in bold.

The mean biomass of zooplankton showed no difference between the type 1 and type 2 lakes and the value was 1.23 $mg\,L^{-1}$ (ranges from 0.06 $mg\,L^{-1}$ to 5.81 $mg\,L^{-1}$) in the type 1 lakes and 1.40 $mg\,L^{-1}$ (ranges from 0.32 $mg\,L^{-1}$ to 3.10 $mg\,L^{-1}$) in the type 2 lakes (Table 1). Zooplankton community composition varied between the type 1 and the type 2 lakes. Zooplankton community of the type 2 had Rotifera significantly higher than that of the type 1 (ANOVA, F = 22.977, $p < 0.001$) and Copepoda significantly lower than that of the type 1 (ANOVA, F = 5.952, $p = 0.017$) (Fig. 2, Table 2). The type 2 had Calanoida significantly lower than that of the type 1 (ANOVA, F = 4.562, $p = 0.035$) whereas Cyclopoida with no difference between the two types (ANOVA, $p > 0.05$) (Fig. 2). Both Cladocera biomass and Cladocera groups showed no difference between the type 1 and the type 2 lakes (ANOVA, $p > 0.05$).

For the type 1 lakes, no difference was shown for zooplankton biomass, Rotifera and Cladocera between lakes with the low nutrient (1L) and the high nutrient (1H) (ANOVA, $p > 0.05$). However, Copepoda of the type 1H was significantly higher than that of the type 1L (ANOVA, F = 4.791, $p < 0.05$). The type 1H had a significantly higher Cyclopoida (ANOVA, F = 4.143, $p < 0.05$) and small cladocera (ANOVA, F = 5.682, $p < 0.05$) (Fig. 2); the small cladocerans were mainly *Ceriodaphnia* (ANOVA, F = 5.964, $p < 0.05$) and *Bosmina* (ANOVA, F = 4.149, $p < 0.05$). For the type 2 lakes, zooplankton biomass and zooplankton groups did not show significant difference between the type 2L and the type 2H (Fig. 2, Table 2).

3.2. Changes of abiotic and biotic parameters

The change of abiotic and biotic parameters in the eastain plain lakes of China was shown in Table 1. The fish yield of the type 2 lakes was significantly higher than that of the type 1 lakes (ANOVA, F = 67.001, $p < 0.001$, Fig. 3A). The mean value of the fish yield was 47.1 $kg\,ha^{-1}$ (ranges from 0.01 $kg\,ha^{-1}$ to 283.3 $kg\,ha^{-1}$) in the type 1 lakes and 291.2 $kg\,ha^{-1}$ (ranges from 34.8 $kg\,ha^{-1}$ to 882.5 $kg\,ha^{-1}$) in the type 2 lakes. Mean values of TN, TP, and SD showed no difference between the type 1 and the type 2 lakes (ANOVA, $p > 0.05$). Cyanobacteria biomass also showed no difference between the type 1 and the type 2 lakes (ANOVA, $p > 0.05$).

For the type 1 lakes, fish yield showed no difference between lakes with the low nutrient (1L) and the high nutrient (1H) (ANOVA, $p > 0.05$) (Fig. 3A). The type 1H had significantly higher TN (ANOVA, F = 162.683, $p < 0.001$), TP (ANOVA, F = 38.308, $p < 0.001$), and lower SD (ANOVA, F = 10.334, $p = 0.002$) than that of the type 1L (Fig. 3B–D). The type 1H had a significantly higher phytoplankton biomass (ANOVA, F = 20.543, $p < 0.001$) and cyanobacteria biomass (ANOVA, F = 13.383, $p = 0.001$) than that of the type 1L

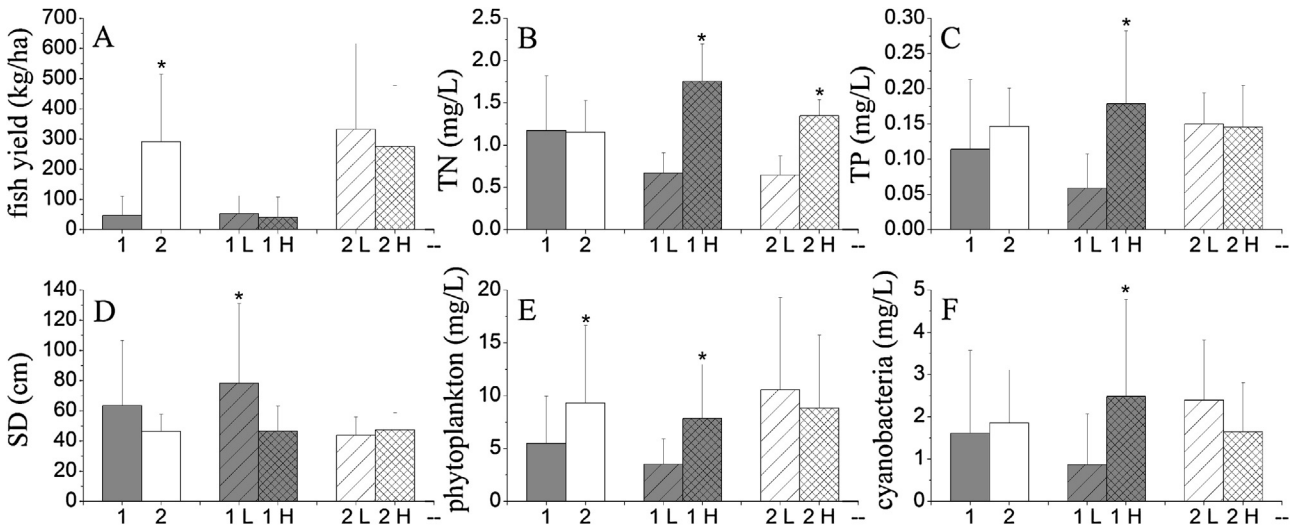

Fig. 3. Mean values of fish, TN, TP, SD, phytoplankton and cyanobacteria of the eastern plain lakes of China. 1, low fish yield; 2, high fish yield. 1L, low fish yield with low nutrient; 1H, low fish yield with high nutrient. 2L, high fish yield with low nutrient; 2H, high fish yield with high nutrient.

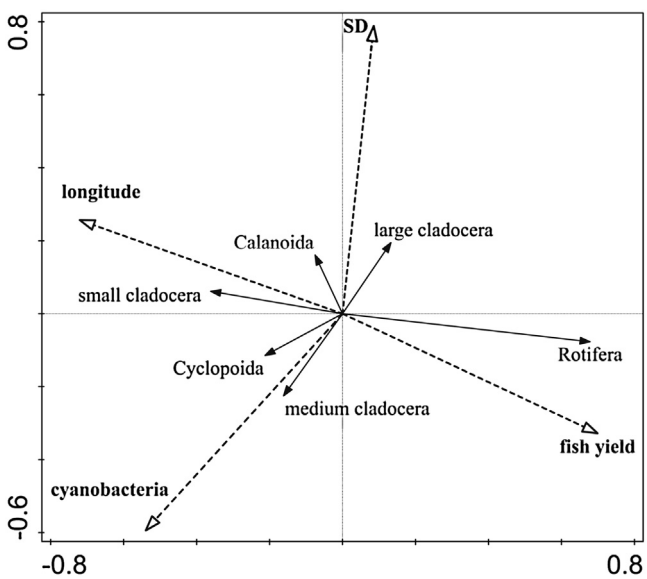

Fig. 4. Detrended correspondence analysis (DCA) ordination of significantly independent influencing variables and the zooplankton community.

(Fig. 3E, F). For the type 2 lakes, fish yield also showed no difference between lakes with the low nutrient (2L) and the high nutrient (2H) (ANOVA, $p > 0.05$). The type 2H had a significantly higher TN (ANOVA, $F = 162.683$, $p < 0.001$) than that of the type 2L (Fig. 3C). However, TP and SD showed no difference between the type 2L and the type 2H (ANOVA, $p > 0.05$). In addition, phytoplankton and cyanobacteria did not show significant difference between the type 2L and the type 2H (Fig. 3E, F, Table 2).

3.3. Results of the statistical analysis

The DCA showed that fish yield and cyanobacteria were the most important factors influencing the zooplankton community composition. Fish yield was positively related to Rotifera and negatively related to Calanoida and small cladocera. Cyanobacteria was positively related to small cladocera, medium cladocera, and Cyclopoida and negatively related to large cladocera (Fig. 4). Fish yield was associated with the culture area in the eastern plain of China and was shown related to the longtitude (Fig. 4). Linear

Table 3
Model parameters of linear regression of the zooplankton community and influencing factors.

Response variable	R^2	F	*p*
Rotifera/crustacean zp	0.1966	6.771	**0.0004**
Cyclopoida/Calanoida	0.0926	2.959	**0.0367**
small cladocera/others cladocera	0.1358	4.555	**0.0052**

Note: Significant effects are indicated in bold. The independent variables, fish yield and cyanobacteria; the response variables, the relative biomass of Rotifera to crustacean zooplankton (Rotifera/crustacean zp), the relative biomass of Cyclopoida to Calanoida (Cyclopoida/Calanoida) and the relative biomass of small cladocera to others cladocera (small cladocera/others cladocera).

regression showed that fish yield and cyanobacteria had significant effects on Rotifera/crustacean zooplankton (the model parameters: $R^2 = 0.1966$, $F = 6.771$, $p = 0.0004$), Cyclopoida/Calanoida (the model parameters: $R^2 = 0.0926$, $F = 2.959$, $p = 0.0367$) and small cladocera/others cladocera (the model parameters: $R^2 = 0.1358$, $F = 4.555$, $p = 0.0052$) (Table 3). The results showed that Rotifera/crustacean zooplankton was positively related to fish yield ($p = 0.0234$) and cyanobacteria ($p = 0.0382$); Cyclopoida/Calanoida was positively related to fish yield ($p = 0.0056$); small cladocera/others cladocera was positively related to cyanobacteria ($p = 0.02596$) (Fig. 5).

4. Discussion

4.1. Cyanobacteria had a dominant effect on zooplankton community succession

Previous study showed that eutrophication effects of cyanobacteria blooms lead to higher abundance of Rotifera, small cladocera, and Cyclopoida, while a decline of *Daphnia* spp. and Calanoida in lakes (Hansson et al., 2007). The effects of eutrophication on zooplankotn communities in this study were consistent with previous study. The abundant phytoplankton in eutrophic lakes benefit zooplankton by providing high food availability on the one hand and inhibit large cladocerans on the other hand, because nutritionally poor and harmful species accounted for a large proportion (Tillmanns et al., 2008; Domis et al., 2014; Filstrup et al., 2014). Our study showed that when the filter-feeding planktivorous fish was not abundant, the cyanobacteria was higher in high nutrient level lakes than in low nutrient level lakes (Fig. 3F); the crustacean

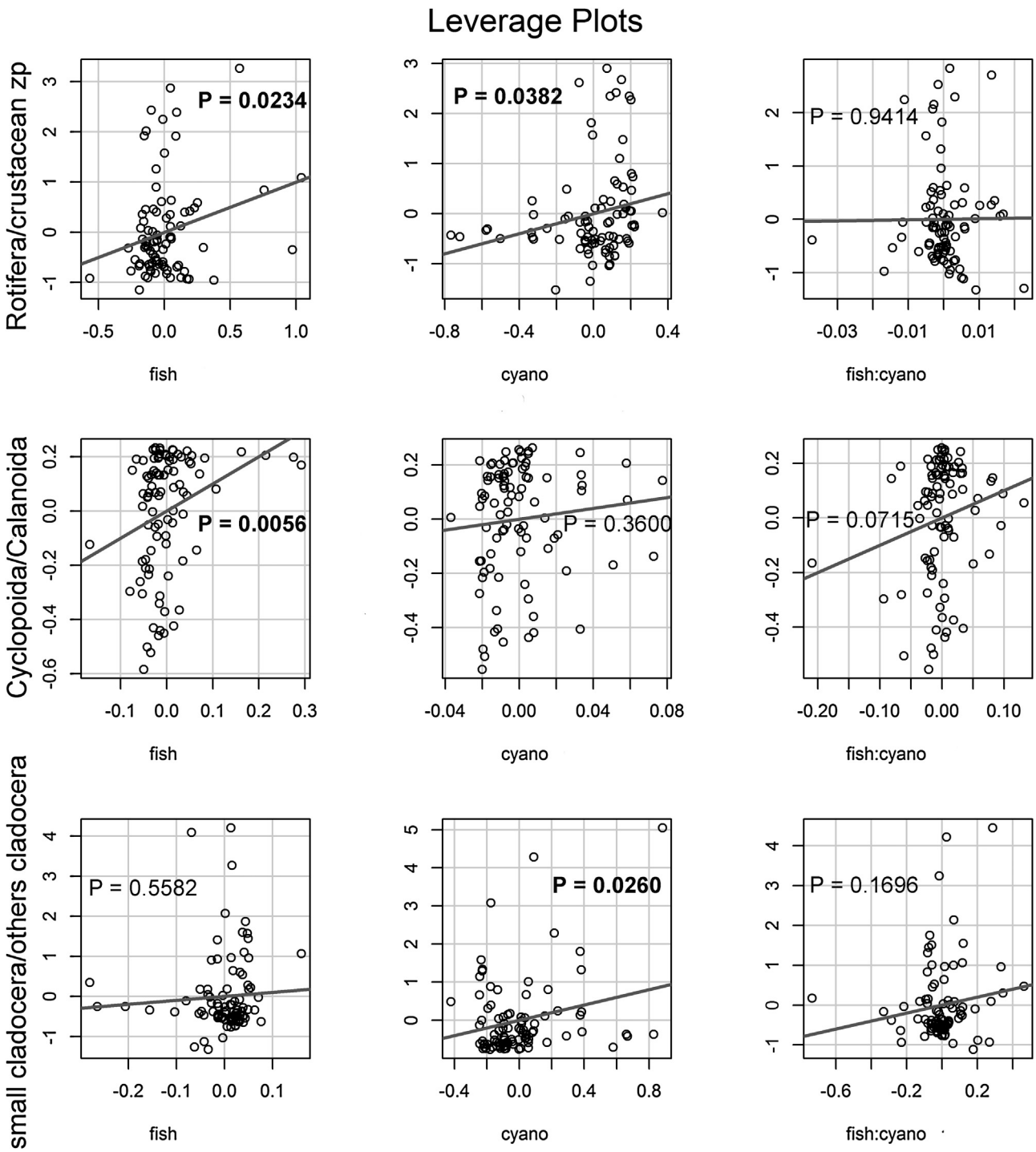

Fig. 5. Leverage plots of the linear regressions of fish yield and cyanobacteria on the zooplankton community. The effect leverage plot for X is type of scatterplot of the X-residuals against the Y-residuals. Y-axis, the residuals of the relative biomass of Rotifera to crustacean zooplankton (Rotifera/crustacean zp), the relative biomass of Cyclopoida to Calanoida (Cyclopoida/Calanoida), and the relative biomass of small cladocera to others cladocera (small cladocera/others cladocera) regressed on all of the predictors except X; X-axis, the residuals of fish yield, cyanobacteria, and fish: cyanobacteria regressed on all of the other predictors in the model. Cyano, cyanobacteria; fish: cyano, the interaction of fish yield and cyanobacteria.

zooplankton was more abundant in high nutrient level lakes. However, the high nutrient level lakes only showed higher biomass of small cladocera and Cyclopoida. No significant difference of other categories was shown between the high nutrient level lakes and the low nutrient level lakes. Moreover, the fraction of small cladocera increased with the increasing cyanobacteria (Fig. 5). The results meant that the abundant phytoplankton in high nutrient lakes (Fig. 3E) benefited small cladocerans by supporting more food but did not benefit the relative increase of other categories. Sun et al. (2012) also showed that *Microcystis* promoted a shift in composition of zooplankton, resulting in a higher fraction of small cladocerans. Nanazato and Yasuno (1985) suggested that the highest cladoceran biomass (primarily small cladocerans) coincided with the highest cyanobacterial production. However, the larger cladocerans and Calanoida had a larger food size spectra (Geller and Müller, 1981) and were easily influenced by cyanobacteria. The

large proportion of inedible cyanobacteria would weaken the larger cladocerans and Calanoida by their low nutrition, large filamentous or colonies, and toxic secondary metabolite (Hansson et al., 2007; Tillmanns et al., 2008; Domis et al., 2014; Filstrup et al., 2014). Our results also showed that cyanobacteria was positively related to the Rotifera/crustacean zooplankton ratio which meant cyanobacteria benefit the dominance of Rotifera (Fig. 5). The rotifers and small cladocerans could be benefited by the abundant food source of bacteria during cyanobacteria blooms (Sanders et al., 1989; Sun et al., 2012).

Hence, cyanobacteria had positive effects on Rotifera and small cladocera which led to the change of zooplankton community composition.

4.2. Filter-feeding planktivorous fish strengthened zooplankton community succession

Predation of planktivorous fish would strengthen zooplankton community succession combined with eutrophication. *Hypophthalmichthys molitrix* and *Aristichthys nobilis* are the main planktivorous fishes in the eastern plain lakes of China filtering on both phytoplankton and zooplankton (Cremer and Smitherman, 1980; Spataru and Gophen, 1985; Dong and Li, 1994; Xie and Liu, 2001). The effects of filter-feeding planktivorous fishes on the succession of the zooplankton community not only resulted from the direct feed on zooplankton but also the indirect effects on phytoplankton (DeVries and Stein, 1992).

On the one side, planktivorous fishes have less impact on the small species of zooplankton than on the large-bodied species because of their size-selective predation on zooplankton (Brooks and Dodson, 1965; Drenner, 1977). Brooks and Dodson (1965) showed that the planktivorous fish was primarily feeding on large zooplankton and would decrease the size of zooplankton. Many other studies further proved the negative effects of abundant planktivorous fish on zooplankton, resulting in small size of zooplankton and the dominance of rotifers, small cladocerans and cyclops (Andersson et al., 1978; Christoffersen et al., 1993; Vanni et al., 1997). But *Hypophthalmichthys molitrix* and *Aristichthys nobilis* are filter-feeding not size-selective feeders (Cremer and Smitherman, 1980; Lazzaro, 1987). Their effects on zooplankton might depend on the survival ability of different zooplankton species as well as the size. In this study, Rotifera accounted for a large proportion of zooplankton, especially in lakes with high fish yield. The biomass ratio of Rotifera to crustacean zooplankton was positively related to fish yield. Furthermore, cladocerans of these lakes were dominated by *D. brachyurum* and *M. micrura* (Supplementary Fig. S1 in the online version at DOI: http://dx.doi.org/10.1016/j.ecoleng.2016.11.040). This might reslut from that rotifers were more tolerant to fish predation due to their r-strategy related growth pattern (Geng et al., 2005), and *D. brachyurum* and *M. micrura* were more adaptable to high fish predation pressure due to their good escape ability (Zhang et al., 2013). Moreover, our results showed that Calanoida decreased with the increased fish yield. The planktivorous fish resulted in higher predation pressure on Calanoida, because of their weaker escape ability compared with that of Cyclopoida (Brooks and Dodson, 1965; Drenner et al., 1978; Kiorboe, 2011). On the other side, large zooplankton, such as *Daphnia* spp., were easily influenced by planktivorous fishes according to their large size and weak escape ability (Brooks and Dodson, 1965; Drenner et al., 1978). Daphnia can efficiently prey on phytoplankton, even some cyanobacteria, that their shortage will lead to the increase of phytoplankton and even cyanobacterial blooms in eutrophic lakes (Andersson et al., 1978; Christoffersen et al., 1993; Vanni et al., 1997). The cyanobacterial blooms would inhibit large species and benefit small species further. In addition, filter-feeding planktivorous fishes indirectly affected zooplankton by reducing edible phytoplankton abundance to zooplankton, leading to the decrease of zooplankton biomass (DeVries and Stein, 1992).

In summary, filter-feeding planktivorous fish had positive effects on Rotifera and negative effects on Calanoida. Furthermore, the cladocerans were dominated by good escape ability species when the fish yield was high.

5. Conclusion

In conclusion, zooplankton community composition changed with both planktivorous fish and cyanobacteria. Eutrophication effects of cyanobacteria led to the higher abundance of small cladocera and was positively related to the relative biomass of Rotifera. Predation of filter-feeding planktivorous fish mainly influenced the dominance of Rotifera and Calanoida. The fraction of Rotifera increased and Calanoida decreased with the increasing fish yield. Our results implied that the zooplankton community tend to be dominated by r-strategy species and good escape ability species with the increasing filter-feeding planktivorous fishes. The succession of the zooplankton community will be strengthened by the combined effects of both planktivorous fish culture and eutrophication.

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References

Andersson, G., Berggren, H., Cronberg, G., Gelin, C., 1978. Effects of planktivorous and benthivorous fish on organisms and water chemistry in eutrophic lakes. Hydrobiologia 59, 9–15.
Azevedo, L.B., van Zelm, R., Leuven, R.S.E.W., Hendriks, A.J., Huijbregts, M.A.J., 2015. Combined ecological risks of nitrogen and phosphorus in European freshwaters. Environ. Pollut. (Barking, Essex : 1987) 200, 85–92.
Braak, C.t., Šmilauer, P., 2002. CANOCO reference manual and CanoDraw for Windows user's guide: software for canonical community ordination (version 4.5). In: Section on Permutation Methods. Microcomputer Power, Ithaca, New York.
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. Academia Sinica (in Chinese).
Christoffersen, K., Riemann, B., Klysner, A., Sondergaard, M., 1993. Potential role of fish predation and natural populations of zooplankton in structuring a plankton community in eutrophic lake water. Limnol. Oceanogr. 38, 561–573.
Codd, G.A., Morrison, L.F., Metcalf, J.S., 2005. Cyanobacterial toxins: risk management for health protection. Toxicol. Appl. Pharmacol. 203, 264–272.
Conley, D.J., Paerl, H.W., Howarth, R.W., Boesch, D.F., Seitzinger, S.P., Havens, K.E., Lancelot, C., Likens, G.E., 2009. Ecology controlling eutrophication: nitrogen and phosphorus. Science 323, 1014–1015.
Cremer, M.C., Smitherman, R.O., 1980. Food-habits and growth of silver and bighead carp in gages and ponds. Aquaculture 20, 57–64.
DeVries, D.R., Stein, R.A., 1992. Complex interactions between fish and zooplankton: quantifying the role of an open-water planktivore. Can. J. Fish. Aquat.Sci. 49, 1216–1227.
Domis, L.N.D., Van de Waal, D.B., Helmsing, N.R., Van Donk, E., Mooij, W.M., 2014. Community stoichiometry in a changing world: combined effects of warming and eutrophication on phytoplankton dynamics. Ecology 95, 1485–1495.
Dong, S.L., Li, D.S., 1994. Comparative-studies on the feeding selectivity of silver carp Hypophthalmichthys-molitrix and bighead carp Aristichthys-nobilis. J. Fish Biol. 44, 621–626.
Drenner, R.W., Strickler, J.R., O'Brien, W.J., 1978. Capture probability: the role of zooplankter escape in the selective feeding of planktivorous fish. J. Fish. Board Canada 35, 1370–1373.
Drenner, R.W., 1977. The Feeding Mechanics of the Gizzard Shad (Dorosoma Cepedianum). University of Kansas.
Elser, J.J., Bracken, M.E.S., Cleland, E.E., Gruner, D.S., Harpole, W.S., Hillebrand, H., Ngai, J.T., Seabloom, E.W., Shurin, J.B., Smith, J.E., 2007. Global analysis of

nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. Ecol. Lett. 10, 1135–1142.
Filstrup, C.T., Hillebrand, H., Heathcote, A.J., Harpole, W.S., Downing, J.A., 2014. Cyanobacteria dominance influences resource use efficiency and community turnover in phytoplankton and zooplankton communities. Ecol. Lett. 17, 464–474.
Geller, W., Müller, H., 1981. The filtration apparatus of Cladocera: filter mesh-sizes and their implications on food selectivity. Oecologia 49, 316–321.
Geng, H., Xie, P., Deng, D.G., Zhou, Q., 2005. The rotifer assemblage in a shallow, eutrophic Chinese lake and its relationships with cyanobacterial blooms and crustacean zooplankton. J. Freshw. Ecol. 20, 93–100.
Ghadouani, A., Pinel-Alloul, B., Prepas, E.E., 2003. Effects of experimentally induced cyanobacterial blooms on crustacean zooplankton communities. Freshw. Biol. 48, 363–381.
Hansson, L.A., Gustafsson, S., Rengefors, K., Bomark, L., 2007. Cyanobacterial chemical warfare affects zooplankton community composition. Freshw. Biol. 52, 1290–1301.
Hessen, D.O., Andersen, T., Faafeng, B.A., 1995. Replacement of herbivore zooplankton species along gradients of ecosystem productivity and fish predation pressure. Can. J. Fish. Aquat.Sci. 52, 733–742.
Hu, H., 2006. The Freshwater Algae of China: Systematics, Taxonomy and Ecology. Science Press (in Chinese).
Huang, X., Chen, W., Cai, Q., 1999. Survey, Observation and Analysis of Lake Ecology. Standard Methods for Observation and Analysis in Chinese Ecosystem Research Network, Series V. Standards Press of China, Beijing (in Chinese).
Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J., Bradbury, R.H., Cooke, R., Erlandson, J., Estes, J.A., Hughes, T.P., Kidwell, S., Lange, C.B., Lenihan, H.S., Pandolfi, J.M., Peterson, C.H., Steneck, R.S., Tegner, M.J., Warner, R.R., 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293, 629–638.
Jeppesen, E., Noges, P., Davidson, T.A., Haberman, J., Noges, T., Blank, K., Lauridsen, T.L., Sondergaard, M., Sayer, C., Laugaste, R., Johansson, L.S., Bjerring, R., Amsinck, S.L., 2011. Zooplankton as indicators in lakes: a scientific-based plea for including zooplankton in the ecological quality assessment of lakes according to the European Water Framework Directive (WFD). Hydrobiologia 676, 279–297.
Kiorboe, T., 2011. What makes pelagic copepods so successful? J. Plankton Res. 33, 677–685.
Lampert, W., 2006. Daphnia: model herbivore, predator and prey. Polish J. Ecol. 54, 607–620.
Lazzaro, X., 1987. A review of planktivorous fishes -their evolution, feeding behaviors, selectivities, and impacts. Hydrobiologia 146, 97–167.
Malbrouck, C., Kestemont, P., 2006. Effects of microcystins on fish. Environ. Toxicol. Chem. 25, 72–86.
Nanazato, T., Yasuno, M., 1985. Population dynamics and production of cladoceran zooplankton in the highly eutrophic Lake Kasumigaura. Hydrobiologia 124, 13–22.
Naylor, R.L., Goldburg, R.J., Primavera, J.H., Kautsky, N., Beveridge, M.C., Clay, J., Folke, C., Lubchenco, J., Mooney, H., Troell, M., 2000. Effect of aquaculture on world fish supplies. Nature 405, 1017–1024.
Osterblom, H., Hansson, S., Larsson, U., Hjerne, O., Wulff, F., Elmgren, R., Folke, C., 2007. Human-induced trophic cascades and ecological regime shifts in the Baltic sea. Ecosystems 10, 877–889.
Paerl, H.W., Xu, H., McCarthy, M.J., Zhu, G.W., Qin, B.Q., Li, Y.P., Gardner, W.S., 2011. Controlling harmful cyanobacterial blooms in a hyper-eutrophic lake (Lake Taihu, China): the need for a dual nutrient (N & P) management strategy. Water Res. 45, 1973–1983.
Sall, J., 1990. Leverage plots for general linear hypotheses. Am. Stat. 44, 308–315.
Sanders, R.W., Porter, K.G., Bennett, S.J., DeBiase, A.E., 1989. Seasonal patterns of bacterivory by flagellates, ciliates, rotifers, and cladocerans in a freshwater planktonic community. Limnol. Oceanogr. 34, 673–687.
Shen, J., Tai, A., Zhang, C., Li, Z., Song, D., Chen, G., 1979. Fauna Sinica, Crustacea, Freshwater Copepoda. Institute of Zoology, Academia Sinica, Beijing (in Chinese).
Smith, V.H., Schindler, D.W., 2009. Eutrophication science: where do we go from here? Trends Ecol. Evol 24, 201–207.
Smith, V.H., Tilman, G.D., Nekola, J.C., 1999. Eutrophication: impacts of excess nutrient inputs on freshwater, marine, and terrestrial ecosystems. Environ. Pollut. 100, 179–196.
Smith, V.H., 2003. Eutrophication of freshwater and coastal marine ecosystems - a global problem. Environ. Sci. Pollut. Res. 10, 126–139.
Snickars, M., Weigel, B., Bonsdorff, E., 2015. Impact of eutrophication and climate change on fish and zoobenthos in coastal waters of the Baltic Sea. Mar. Biol. 162, 141–151.
Spataru, P., Gophen, M., 1985. Feeding behaviour of silver carp Hypophthalmichthys molitrix Val. and its impact on the food web in Lake Kinneret, Israel. Hydrobiologia 120, 53–61.
Sun, X.X., Tao, M., Qin, B.Q., Qi, M., Niu, Y., Zhang, J., Ma, Z.M., Xie, P., 2012. Large-scale field evidence on the enhancement of small-sized cladocerans by Microcystis blooms in Lake Taihu, China. J. Plankton Res. 34, 853–863.
Tillmanns, A.R., Wilson, A.E., Pick, F.R., Sarnelle, O., 2008. Meta-analysis of cyanobacterial effects on zooplankton population growth rate: species-specific responses. Fundam. Appl. Limnol. 171, 285–295.
Vanni, M.J., Layne, C.D., 1997. Nutrient recycling and herbivory as mechanisms in the top-down effect of fish on algae in lakes. Ecology 78, 21–40.
Vanni, M.J., Layne, C.D., Arnott, S.E., 1997. Top-down trophic interactions in lakes: effects of fish on nutrient dynamics. Ecology 78, 1–20.
Voigt, M., Koste, W., 1978. Rotatoria: die radertiere mitteleuropas Rotatoria: die radertiere mitteleuropas. Gebruder Borntraeger.
Xie, P., Liu, J., 2001. Practical success of biomanipulation using filter-feeding fish to control cyanobacteria blooms: a synthesis of decades of research and application in a subtropical hypereutrophic lake. Sci. World J. 1, 337–356.
Yang, Y.F., Huang, X.F., Liu, J.K., Jiao, N.Z., 2005. Effects of fish stocking on the zooplankton community structure in a shallow lake in China. Fish. Manage. Ecol. 12, 81–89.
Zhang, J., Xie, P., Tao, M., Guo, L.G., Chen, J., Li, L., Zhang, X.Z., Zhang, L., 2013. The impact of fish predation and cyanobacteria on zooplankton size structure in 96 subtropical lakes. PLoS One 8, 15.
de Figueiredo, D.R., Azeiteiro, U.M., Esteves, S.M., Goncalves, F.J.M., Pereira, M.J., 2004. Microcystin-producing blooms - a serious global public health issue. Ecotox. Environ. Safe. 59, 151–163.