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

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A B S T R A C T

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.

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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

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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 km² 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 (Yellow Springs, 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 (JY98-II, Scientz, 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 CX21 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 (Br léak 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 Rotifer, small cladocera, medium cladocera, large cladocera, Calanoida, and Cyclopoidea. 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 better 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 Cyclopoidea to Calanoida (Cyclopoidea/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, Simecephalus and Leptodora) (small cladocera/other cladocera) respectively. The linear regression was implemented in R using the car package; a leverage plot was produced (Sall, 1990).
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 accounted 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).

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.
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 Rotiferia 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 differences 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. Rotifer 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 differences between lakes with the low nutrient (1L) and the high nutrient (1H) (ANOVA, \(p > 0.05\)). For the type 1H, fish yield was significantly higher than that of the type 1L (ANOVA, \(F = 162.683, p < 0.001\), Fig. 2A). The mean value of the fish yield was 7.5 kg ha\(^{-1}\) (ranges from 1.06 kg ha\(^{-1}\) to 115.38 kg ha\(^{-1}\)) in the type 1L and 31.36 kg ha\(^{-1}\) (ranges from 27.04 kg ha\(^{-1}\) to 115.38 kg ha\(^{-1}\)) in the type 1H.
However, some nutrient-dependent differences were also observed. For instance, higher TN was associated with higher fish yield in the low nutrient conditions (Fig. 2A). TN and cyanobacteria negatively correlated with fish yield (Fig. 2B). Conversely, TP showed a positive correlation with fish yield (Fig. 2C). The SD of phytoplankton biomass was negatively related to fish yield (Fig. 2D). Cyanobacteria concentration was significantly higher in the high nutrient conditions (Fig. 2E). For phytoplankton, a higher concentration was associated with low nutrient conditions (Fig. 2F).

**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.

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

<table>
<thead>
<tr>
<th>Response variable</th>
<th>R²</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rotifera/crustacean zp</td>
<td>0.1966</td>
<td>6.771</td>
<td>0.0004</td>
</tr>
<tr>
<td>Cyclopoidea/Calanoida</td>
<td>0.0926</td>
<td>2.959</td>
<td>0.0367</td>
</tr>
<tr>
<td>small cladocera/others cladocera</td>
<td>0.1358</td>
<td>4.555</td>
<td>0.0052</td>
</tr>
</tbody>
</table>

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 Cyclopoidea to Calanoida (Cyclopoidea/Calanoida) and the relative biomass of small cladocera to others cladocera (small cladocera/others cladocera).

**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 Cyclopoidea 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 longitude (Fig. 4). Linear regression showed that fish yield and cyanobacteria had significant effects on Rotifera/crustacean zooplankton (the model parameters: $R^2 = 0.1966$, $F = 6.771$, $p = 0.0004$), Cyclopoidea/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 ($p = 0.0382$); Cyclopoidea/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 Cyclopoidea, while a decline of Daphnia spp. and Calanoida in lakes (Hansson et al., 2007). The effects of eutrophication on zooplankton 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...
zoo plankton 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.
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. Hypothalaschitina 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 Hypothalaschitina 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.ecoiol.2016.11.040). This might result 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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