



Experimental observation on the effects of bighead carp (*Hypophthalmichthys nobilis*) on the plankton and water quality in ponds

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Abstract

It is a common practice to improve the water environment of rivers and lakes in China by the enhancement and releasing (EAR) of silver carp (*Hypophthalmichthys molitrix*) and bighead carp (*Hypophthalmichthys nobilis*) for biomanipulation. However, the quantity of bighead carp and its effect on water quality and plankton community have been the focus of debate among ecologists. Herein, in order to more accurately simulate the environmental conditions of lakes, we selected earthen ponds with large areas adjacent to Lake Qiandao from May to August in 2016 to study the responses of water quality condition and plankton community to a gradient of bighead carp stocked alone. Experimental groups with different densities of carp stocked were set as follows: 12.1 (LF), 23.5 (MF), and 32.5 g/m³ (HF), and a control group with no fish (NF). Results showed that total phosphorus (TP) in the fish-containing groups considerably decreased, and the lowest chlorophyll-*a* concentration (chl-*a*) was detected in the MF group. The biomass accumulation of the crustacean zooplankton was suppressed after carp was introduced, but the diversity, richness, and evenness of the crustacean zooplankton were weakly affected, except in the HF group. Phytoplankton biomass especially that of cyanobacteria was grazed rapidly by fish in the MF and HF groups and biodiversity indices were considerably increased in the fish-containing groups, especially in the late stages of the experiment. At a fish stocking density of 23.5–38.8 g/m³, the highest efficiency in controlling cyanobacteria and promoting water condition was achieved, and the impact on zooplankton diversity was weak. Our results indicated that bighead carp can be included in the EAR of lakes and reservoirs, but the optimal density of bighead carp stocking should be carefully considered.

Keywords Biomanipulation experiment · Earthen ponds · Bighead carp · Water quality condition · Plankton community · Optimal density

Introduction

Biomanipulation, originally proposed by Shapiro et al. (1975), is a method for effectively controlling the amount of nuisance algae in lakes or reservoirs by reducing the predation pressure of planktivores on zooplankton and

increasing zooplankton biomass. This method involves the use of piscivorous fish in controlling planktivorous fish or other fish-killing measures. It has been considered one of the most effective approaches for improving water quality in many eutrophic lakes and reservoirs (Gulati et al. 1990; ter Heerd and Hootsmans 2007; McQueen 2010) and has now become a routine technique for managing lakes in Europe, Australia, and North America (Benndorf 1990; Mehner et al. 2004; Sierp et al. 2009; Jeppesen et al. 2012; Gophen and Snovsky 2015). However, the effectiveness of using traditional biomanipulation in controlling nuisance algae is often questioned because of the inefficient grazing of zooplankton on cyanobacteria or difficulty in sustaining high zooplankton biomass for long periods in complex lake ecosystems (Zhang et al. 2008; McQueen 2010; Jeppesen et al. 2012).

A similar but different approach is nontraditional biomanipulation, which was suggested by Xie and Liu (2001);

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this approach involves the use of filter-feeding planktivorous carps (i.e., bighead carp, *Hypophthalmichthys nobilis*, and the silver carp, *Hypophthalmichthys molitrix*) in directly controlling algal overgrowth. Nontraditional biomanipulation has attracted considerable interest and has been widely tested for its feasibility in algal control in China (Wang et al. 2009; Xiao et al. 2010; Yi et al. 2016a; Liu and Zhang 2016; Chen et al. 2020) and other countries (Zubcov et al. 2021; Mohammad and Haque, 2021). In fact, long before the concept of nontraditional biomanipulation had been proposed, the effects of using two species of carps on plankton community and water quality have been extensively studied worldwide (Leventer and Teltsch 1990; Starling 1993; Domaizon and Dévaux 1999; Post and McQueen 1987); meanwhile, silver and bighead carps have been used as core elements in aquatic environment protection-oriented lake fishery practices in many reservoirs and lakes, such as Lake Qiandao in China (Liu 2005). However, studies on the use of two filter-feeding carps in controlling algal overgrowth presented conflicting results (Zeng et al. 2010; Yi et al. 2016b), which have created many controversies over the feasibility of non-traditional biomanipulation. After carefully comparing and analyzing different studies, Liu and Zhang (2016) found that the seemingly different results were actually not contradictory to one another as previously believed. The different results might be attributed to differences in experimental designs or protocols. They found that the results showing the successful control of algae with carps are mostly from studies conducted in experimental systems with natural bottoms (Tan et al. 1995; Wang et al. 2009; Zhou et al. 2011), such as the natural lakes, ponds, and enclosures without artificial bottoms (i.e., with the natural bottoms of water bodies), whereas results showing failure in controlling algae with carps were from studies conducted in concrete or glass tanks or enclosures with artificial bottoms. Nevertheless, this finding has not convinced some researchers, who performed statistical analysis on many lakes either in the middle and lower reaches of the Yangtze River or in the Pearl River Delta region and found that high chlorophyll-*a* (chl-*a*) concentration in areas with high carp biomass and thus reached an opposite conclusion (Wang et al. 2008; Lin et al. 2020). Other researchers found that planktivorous carps reduce zooplankton biomass and even increase phytoplankton biomass, presenting results predicted by studies on traditional biomanipulation (Yi et al. 2016a, Shen et al. 2021). The effectiveness of stocking with bighead carps in lakes and reservoirs has been questioned because bighead carps predominantly feed on zooplankton (Cremer and Smitherman 1980; Burke et al. 1986; Dong and Li 1994; Li et al. 2018a) and silver carp mainly feed on phytoplankton (Xie 2003), although bighead carps are effective biological control agents for algal blooms (Cremer and Smitherman 1980; Xie 2001) and played an important role in the trophic dynamics of aquatic

ecosystems during top-down and bottom-up processes (Carpenter et al. 1992; Schindler et al. 2001; Jeppesen et al. 2010). The view that bighead carps are ineffective algal control agents is supported by the fact that the mesh size of the gill raker of a bighead carp (with a relatively wide spacing of less than 20 μm) is considerably larger than that of a silver carp (with filtering particles of less than 12 μm) (Opuszynski and Shireman 1993; Vörös 2000). However, evidence of the successful use of bighead carps in manipulation has been presented as well (Xie 1999, 2001; Ke et al. 2007; Chen et al. 2011; Jayasinghe et al. 2015; Nistor et al. 2018).

Bighead carps have been stocked in lakes and reservoirs for long times because of their high economic value and this method have yielded practical results (which often mean good growth; FAO 2018). Along with the silver carp, the bighead carp has become a dominant fish species in lakes and reservoirs in China and has thus exerted considerable impact on lake ecosystems; thus, its effects on plankton should be assessed. Moreover, experiments using bighead carp alone in investigating their effects on aquatic environments and plankton communities are necessary because whether or not bighead carps can be used in controlling nuisance algae is unclear. Some of the questions considered in the present study were as follows: (1) What are the real effects of bighead carp on plankton structures and nutrients in experimental water bodies; (2) can bighead carp yield a positive effect on water quality or phytoplankton; and what is the optimum stocking density for bighead carp? Previous studies that investigated the effects of using two species of carps on phytoplankton in lakes are often conducted in small enclosures (e.g., enclosures with sizes of approximately 10–50 m^2) (Zhao et al. 2013, 2016; Li et al. 2018b). In such small systems, the walls of enclosures are conducive to the growth of epiphytes (Dickman 1968; Martin et al. 1992), which exert a huge impact on nutrient level and phytoplankton. Furthermore, environmental conditions in small experimental systems (e.g., enclosures) readily fluctuate and different (in comparison with the conditions in large experiment systems) from those in real scenarios (lakes or reservoirs) and might thus lead to large errors. Hence, in this study, we adopted large earthen ponds for the control study. We hope that by using larger experimental systems, we can eventually obtain the results closer to those obtained in actual situations in which bighead carp are stocked in lakes and reservoirs.

Material and methods

Experimental design

The experiment was conducted in eight earthen ponds with the depth of 2 m adjacent to a lake shore in the southwest portion of Lake Qiandao (118°38'58.70" E, 29°26'1.57"

N) (Fig. 1). The experiment lasted for 102 days from May 6 to August 16, 2016. Before the experiment, we removed the sediment (approximately 5 cm) to minimize initial interference from variations during treatment, and the earthen ponds were filled with lake water from Lake Qiandao at a depth of 1.5 m. We ensured that the water remained stagnant for more than 2 weeks for the sedimentation of inorganic suspended solids, which may affect initial conditions in all treatments. Bighead carps were obtained from a nearby fish hatchery and acclimatized in a net cage in Lake Qiandao 12 days before the start of the experiment. We captured fish by using a basic seining net and minimized the handling of mortality by a short time before the carps were transferred to the earthen ponds. On May 6, six fish-containing ponds were selected randomly, as presented in Fig. 1. The average standing biomass of carp in Lake Qiandao was around 28.30 g/m^2 (Li, 2016). However, earthen pond conditions could not fully represent the actual condition of the lake. Therefore, the three gradients set in the experimental groups included the carp density of the lake. The detailed information of the three gradients and earthen pond areas was shown as follows: LF (12.1 g/m^3 , $2980\text{--}3056 \text{ m}^2$), MF (23.5 g/m^3 , $3012\text{--}3056 \text{ m}^2$), HF (32.5 g/m^3 , $2998\text{--}3067 \text{ m}^2$), and a control group with no fish (NF, $3000\text{--}3100 \text{ m}^2$), with two replicates each (Fig. 1). The mean individual weight (\pm

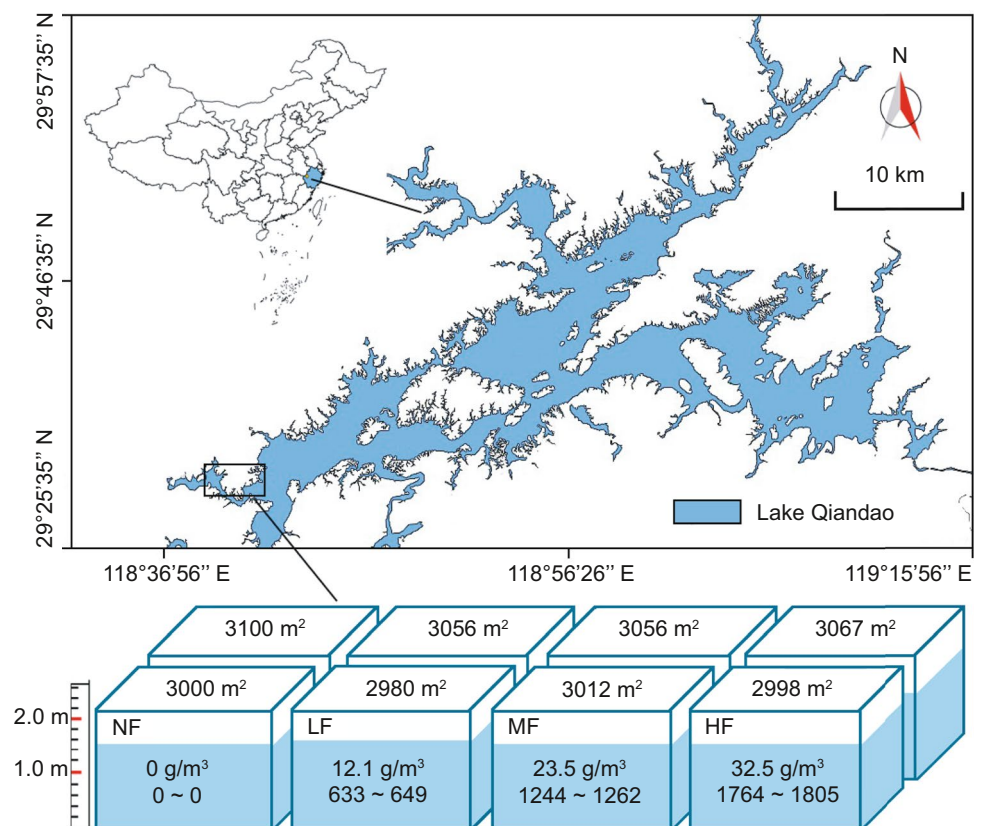
S.E.) and body length (\pm S.E.) of the carp stocked were $85.38 \pm 1.44 \text{ g}$ and $16.0 \pm 0.1 \text{ cm}$, respectively.

Sampling and measurement

The earthen ponds were sampled on May 6 before the experiment for the assessment of pretreatment conditions, and the samples were taken at 10-day intervals until 16 August. Integrated water samples were collected using a 5 L modified Patalas bottle sampler from the surface (20 cm below the surface) and from the bottom layers (approximately 20 cm above the sediment to minimize disturbance) in each treatment on each sampling occasion. Water temperature (W_T), transparency (W_{SD}), dissolved oxygen (DO), pH, total nitrogen (TN), total phosphorus (TP), nitrate-N ($\text{NO}_3\text{-N}$), nitrite-N ($\text{NO}_2\text{-N}$), ammonia-N ($\text{NH}_3\text{-N}$), chemical oxygen demand (COD_{Mn}), chl-*a*, and plankton communities were investigated for the comparison of the ability of fish to interfere with the characteristics of water environments.

The W_{SD} value was measured with a 20 cm diameter Secchi's disk, and DO, W_T , and pH were determined with a YSI Professional Plus Water Quality Monitor (YSI Inc., Yellow Springs, Ohio, USA). Chl-*a* was tested using a new submersible probe (FluoroProbe, bbe-Moldaenke), which is widely used in limnology study (Garrido et al. 2019). Chl-*a* and physical factors were determined on the spot. In

Fig. 1 The location of the experimental ponds on Lake Qiandao, design and assignment of each pond, including the characteristics of each experimental pond, the number of stocked fish and the initial densities in all treatments



the laboratory, 500 mL of integrated water was collected for the testing of chemical parameters, including TN, TP, $\text{NO}_3\text{-N}$, $\text{NO}_2\text{-N}$, $\text{NH}_3\text{-N}$, and COD_{Mn} , with spectrophotography methods according to SEPA (2002). All water samples were analyzed within 24 h.

Pretreated samples (50 mL) of crustacean zooplankton, including Cladocera and Copepoda, were collected by filtering 10 L of integrated water samples through a 64 μm mesh plankton net, which collected from the surface (20 cm below the surface) and from the bottom layers (approximately 20 cm above the sediment to minimize disturbance), and immediately preserved with a 5% final concentration of formaldehyde in glass bottles (Jin and Tu 1990). Entire samples of zooplankton were used in identifying species under a dissecting microscope with an ocular micrometer. Copepoda was identified according to Sheng (1979), and Copepoda volumes (copepodid and adult) were estimated using the geometric figures of their approximate shapes (Lawrence et al. 1987). Copepoda nauplii were counted without further taxonomic distinction. Cladocera was identified according to the method of Chiang and Du (1979), and biomass was estimated according to the method of Huang and Hu (1986). Rotifera was counted directly from the phytoplankton samples at 100 \times magnification (at least 100 individuals of the most abundant taxa), and enumerating sorted counting was performed according to the methods of Wang (1961) and Ruttner-Kolisko (1977). We calculated the body volume according to the geometric shapes provided by McCauley (1984). The dry weight of each Rotifera species was obtained by assuming a specific gravity of 1 and a dry weight/wet weight ratio of 0.1 (McCauley 1984).

A 1 L portion of water sampled was preserved with 1% of acidified Lugol's iodine solution and concentrated to 50 mL after 48 h of sedimentation (Jin and Tu 1990). After mixing, 0.1 mL of concentrated samples was counted directly with a 0.1 mL counting chamber and a microscope at 400 \times magnifications. Phytoplankton taxonomy was identified at the species level (whenever possible) and enumerated using a compound microscope according to the method of Hu and Wei (2006). For phytoplankton biomass (wet weight) measurement, algal cells were considered to have equivalent geometric shapes (Hillebrand et al. 1999) and uniform specific gravity. Each subsample was counted, and the average of the three counts was used for statistical analysis (Zhang and He 1991). Measurements were made for 10–30 individuals per species in each sample.

Data analysis

The effects of fish biomass level on the water quality condition and chl-*a* were analyzed using one-way repeated-measures ANOVA performed in SPSS statistics 19.0 for windows (Statistics Product and Service Solutions, IBM Inc., USA)

excluding first sampling (D1). Because fish were stocked after first sampling, data from D1 were excluded from the analysis. For low replication and statistical power, we choose a probability level of $\alpha < 0.10$ to reduce the chance of making the type II error of failing to reject a false null hypothesis. We employed the Presence/Absence (P/A) methods to evaluate the effects of TN, TP, and plankton communities on fish stocks (Compte et al. 2012). The P/A values were calculated as follows: $\log_{10}(X_{\text{Presence}}/X_{\text{Absence}})$, where X_{Presence} and X_{Absence} are the values of fish presence and fish absence groups for all sampling dates, respectively. If the P/A values were positive, it means the indicators in fish presence groups were higher than those in the fish absence groups, whereas a negative log ratio values indicated the opposite. Values close to 0 implied that the characteristics were unaffected by fish stocks.

Plankton diversity in all treatments was assessed using the Shannon-Wiener diversity index (Shannon 1948), Margalef's richness index (Legendre and Legendre 1998), and Pielou evenness index (Pielou 1966). The dominant species of plankton in different treatments were ascertained using the McNaughton dominance index (McNaughton 1967).

The calculation formula of the dominance index (Y) is

$$Y = \frac{n_i f_i}{N}$$

The calculation formula of Shannon-Wiener diversity index (H') is

$$H' = - \sum \frac{n_i}{N} \ln \frac{n_i}{N}$$

The calculation formula of Margalef's richness index (R) is

$$R = (S - 1) / \ln N$$

The calculation formula of Pielou evenness index (J) is

$$J = H' / \ln S$$

where n_i represents the number of i th species, N represents the total amount of all species, S is the number of the species observed, and f_i represents the appearance frequency of certain species at all sampling sites. Taxa with a $Y_i \geq 0.02$ were selected as dominant species (Deng et al. 2016).

Canonical correspondence analysis (CCA) and correlation coefficients were used in verifying the relationship between plankton species and environmental variables. CCA was performed using the CANOCO program (version 5.0). The model achieved was tested using Monte-Carlo permutation (ter Braak 1994). Environmental factors and dominant plankton species were transformed using $\log_{10}(x + 1)$; except pH) for increasing the importance of small values and achieving a normalized distribution. Environmental

variables were selected according to significant statistical level in the forward selection ($p < 0.05$). The figures were devised with Origin 2019b (Origin Lab Corporation, USA).

Results

Effects of fish on environmental parameters

The W_T varied from 24.5 to 33.8 °C (no difference was detected among the groups). Initially, all groups had similar W_{SD} values, which ranged from 70.0 to 92.5 cm. Significant differences of W_{SD} were observed among the groups (except NF vs. LF, Fig. 2, Table 1) after the fish stocking. No significant difference of DO was detected (Fig. 2, Table 1). The pH values in the MF group showed markedly lower than other groups (Fig. 2, Table 1). The concentration of nutrients and chl-*a* are shown in Fig. 3. Differences in NO_3 -N, NO_2 -N, and NH_3 -N were not observed among all groups. COD_{Mn} in the MF group was lower than that in LF and HF groups (Table 1). The TP value in the MF group showed lowest concentration compared with other groups, and almost showed

notably difference among all the groups (except LF vs. HF, Table 1). Chl-*a* was significantly lower in the MF group than that in the NF, LF and HF groups.

The ratios of TN and TP values (P/A values) between the fish presence and absence groups are shown in Fig. 4. The two curves showed downward trends as sampling time increased, and both parameters varied by sampling time. All groups had similar patterns of fluctuation. The P/A values of TN and TP, respectively, became negative after the fourth sampling (D4, June 8) and the third sampling point (D3, May 27). The REG2 curve of TP showed the lowest level.

Effects of fish on zooplankton community

In this study, the composition of zooplankton and its biomass (including Cladocera, Copepoda, and Rotifera) were identified and calculated for each treatment. A total of 97 zooplankton species were recorded in all treatments over the entire experimental period, including 30 Cladocera species, 36 Copepoda species, and 31 Rotifera species. The NF group showed the highest number of species in all treatments, containing 77 species (20 Cladocera species, 32

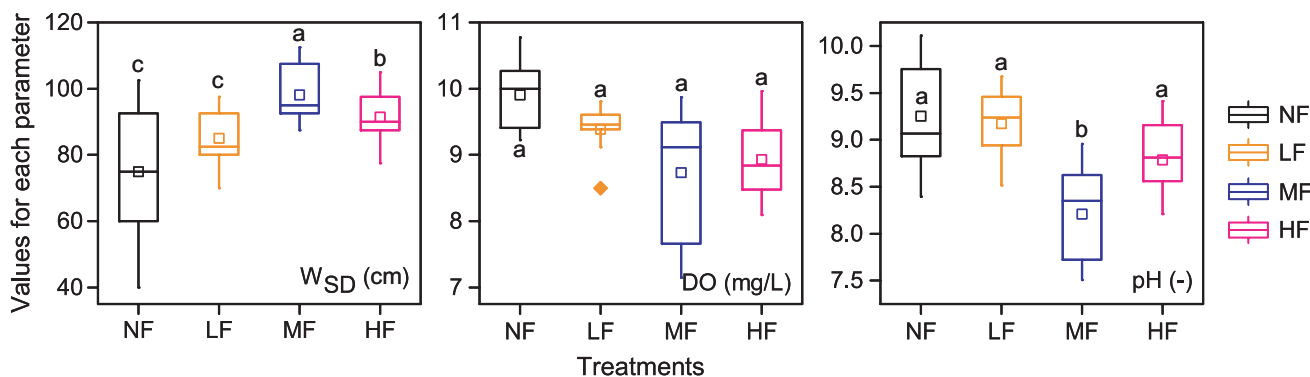


Fig. 2 Mean values (hollow square symbol “white square”) for W_{SD} (cm), DO (mg/L), and pH (–) for each sample. Abnormal values are marked using the solid rhombus symbol “black diamond”. Dif-

ferent letters indicate significant differences in all treatments at $p < 0.1$, as determined by the post-hoc test (LSD) of the variance analysis (ANOVA). Treatments were treated as fixed factors

Table 1 Differences of water quality and chl-*a* concentration among four treatments (p value)

Parameters	NF vs. LF	NF vs. MF	NF vs. HF	LF vs. MF	LF vs. HF	MF vs. HF
W_{SD}	0.803	0.034**	0.079*	0.038**	0.042**	0.058*
DO	0.988	0.666	0.614	0.584	0.563	0.992
pH	0.964	0.008**	0.391	0.004**	0.297	0.005**
NH_3 -N	0.982	0.677	0.962	0.933	0.951	0.959
NO_2 -N	0.977	0.966	0.961	0.949	0.939	0.961
NO_3 -N	0.966	0.958	0.943	0.974	0.971	0.972
COD_{Mn}	1.000	0.998	0.989	0.058*	0.965	0.034**
TN	0.956	0.993	0.995	0.032*	0.172	0.966
TP	0.033**	0.001**	0.042**	0.058*	0.142	0.053*
Chl- <i>a</i>	0.459	0.068*	0.697	0.082*	0.816	0.072*

* $p < 0.1$; ** $p < 0.05$

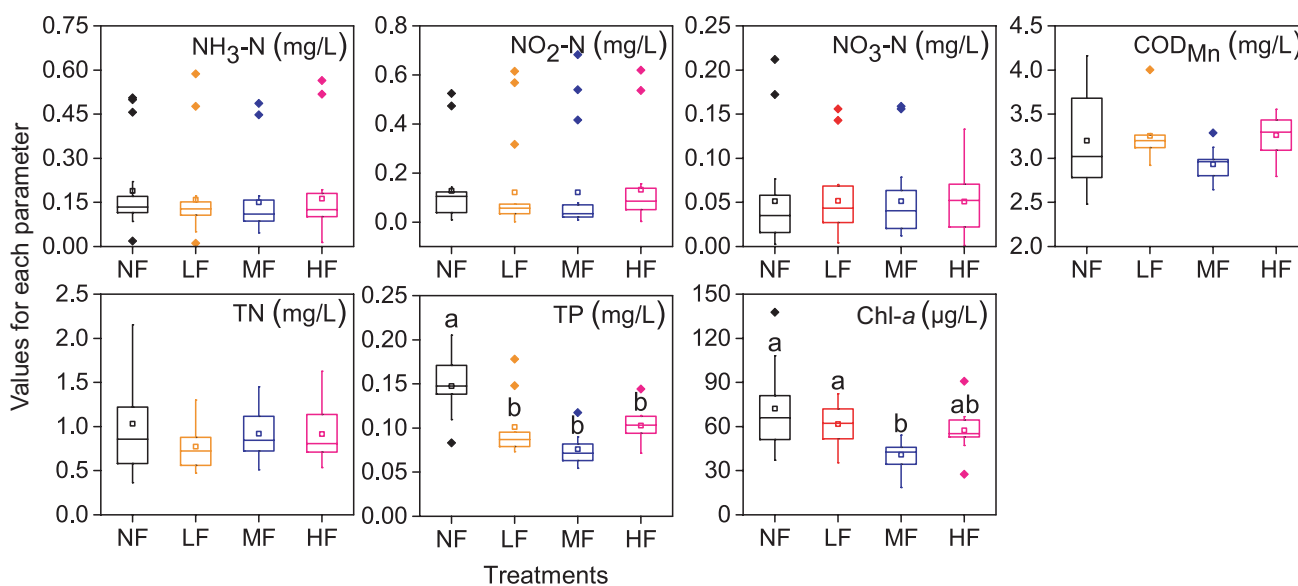
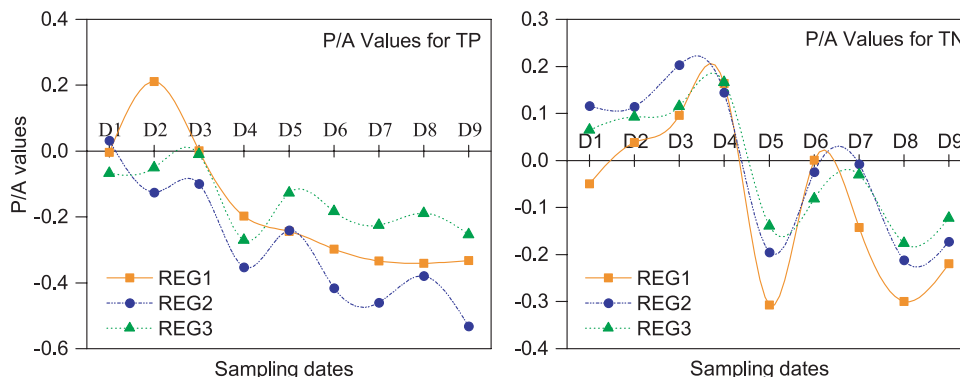


Fig. 3 Mean values (hollow square symbol “white square”) for NH₃-N (mg/L), NO₂-N (mg/L), NO₃-N (mg/L), COD_{Mn} (mg/L), TN (mg/L), TP (mg/L), and Chl-a (µg/L) in the experiment period (except first sampling). Abnormal values are marked using the solid

rhombus symbol “black diamond”. Different letters indicate significant differences in all treatments at $p < 0.1$, as determined by the post-hoc test (LSD) of the variance analysis (ANOVA). Treatments were treated as fixed factors

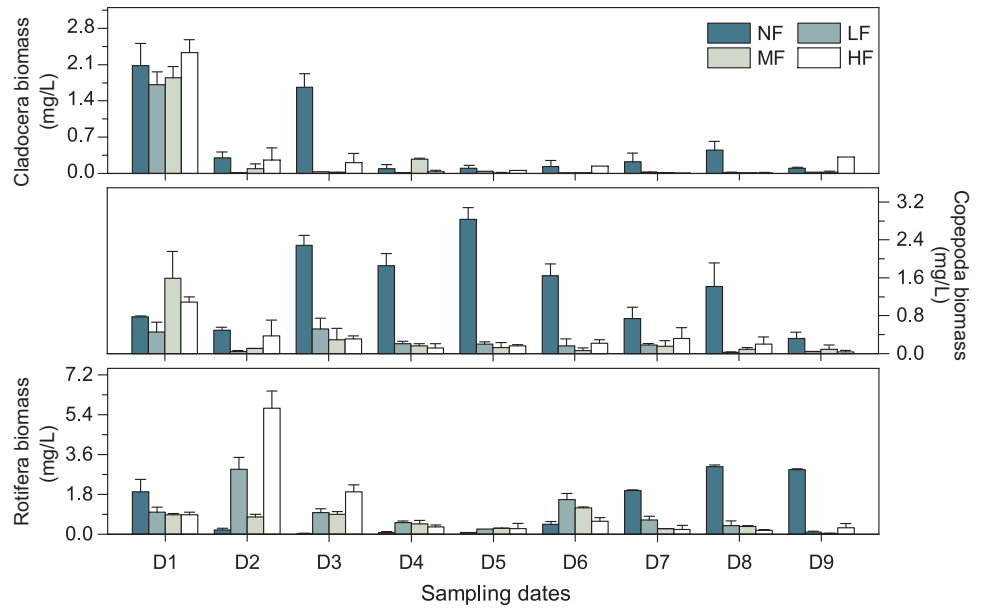
Fig. 4 P/A values ($\log_{10}(X_{\text{Presence}}/X_{\text{Absence}})$) of TN and TP for all samples in the fish presence groups. REG1, REG2, and REG3 are shown for the ratios of the values between LF, MF, HF and NF respectively



Copepoda species, and 25 Rotifera species), whereas the LF group had the least number of zooplankton, containing 59 species (14 Cladocera species, 25 Copepoda species, and 20 Rotifera species). In addition, 64 species of zooplankton (18 Cladocera, 25 Copepoda, and 21 Rotifera species) were found in the MF group, and 70 zooplankton species were found in the HF group (19 Cladocera, 28 Copepoda, and 23 Rotifera species). The detailed composition of zooplankton in each experimental group was shown in Electronic Supplementary Material 1. All experimental groups had the same dominated species, *Phyllodiaptomus tunguidus*. NF group was mainly dominated by Cladocera and Copepoda, including *Moina rectirostris*, *P. tunguidus*, *Neodiaptomus schmackeri*, etc., whereas LF group was mainly Rotifera, such as *Ploesoma hudsoni*, *Polyarthra trigla*. MF and HF groups had similar distributions, including *M. rectirostris*, *P. tunguidus*, *P. trigla*, etc.

Figure 5 shows the changes in the biomass of zooplankton in each experimental group at different sampling times. The biomass of crustacean zooplankton was much higher in the NF group than in the fish-containing groups (Fig. 5, $p = 0.012$). The biomass of Cladocera, Copepoda, and Rotifera in all treatments was similar at the start of the experiment. The status was broken after bighead carp was stocked. The fish absence groups showed higher Cladocera and Copepoda biomass than those in LF ($p = 0.044$), MF ($p = 0.021$), and HF groups ($p = 0.010$). Cladocera biomass showed a rapidly decreasing trend in all treatments. Meanwhile, Copepoda biomass remained high in the fish absence groups, and Copepoda biomass growth was inhibited in the fish presence groups. The Rotifera biomass in the fish absence groups was lower than that in the fish presence groups at the early stage of the experiment (before D6, $p = 0.104$), but an opposite result was obtained

Fig. 5 Mean biomass of Cladocera, Copepoda, and Rotifera for all treatments at all sampling dates



at the late stage ($p = 0.041$). Over the entire period, crustacean zooplankton contributed to the majority of biomass in the NF group, consisting of approximately 65.5% of wet weight of zooplankton. The proportions of Rotifera biomass in the LF and HF groups were 74.6% and 73.8%, respectively, and the proportion of crustaceans in the MF group was 54.8%.

The Shannon-Wiener diversity index, Pielou evenness index, and Margalef's richness index of the zooplankton community were calculated over the entire experimental period (Fig. 6). The indices of the fish absence groups were higher than those of the presence groups. And the zooplankton community was more significantly inhibited by the introduction of bighead carp, and the diversity, evenness, and

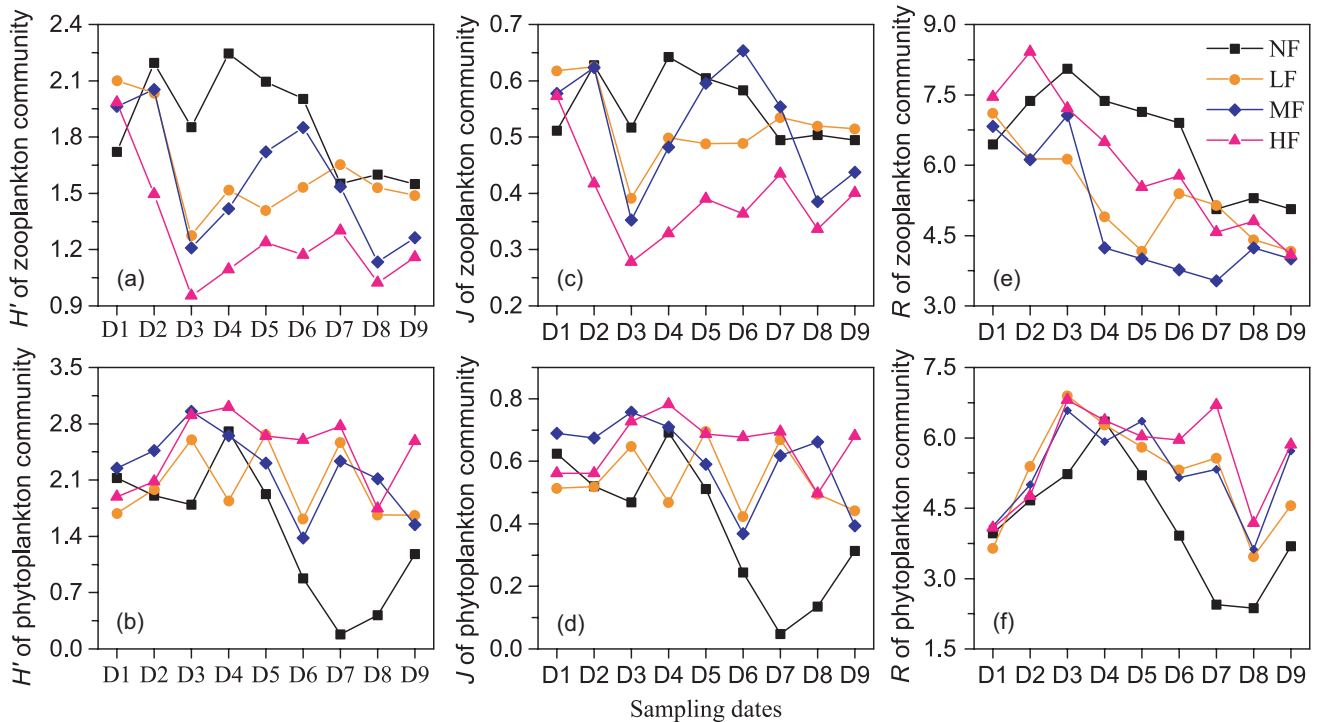


Fig. 6 Changes in the mean values of Shannon-Wiener diversity index (H' , **a** and **b**), Pielou evenness index (J' , **c** and **d**), and Margalef's richness index (R , **e** and **f**) of the plankton communities in all treatments

richness showed a more obvious downward trend compared with the fish absence groups.

To investigate differences in each treatment, we calculated the natural logarithmic ratios of the three zooplankton catalogs and compared the results from the fish presence and the absence groups (Fig. 7). Cladocera ratios in all the fish presence groups were negative at all sampling times (except in MF at D1 and HF at D9). Copepoda ratios in the fish presence groups were also negative (except in MF and HF at D1). Rotifera ratios in the fish presence groups present were positive from D2 to D6, when the early stages of the experiment were performed, and a negative proportion was observed from D7 to the end of the experiment. Different distributions of dominated species were found among treatments, as shown in Table 2. The NF group had six species,

which were mainly from the Cladocera and Copepoda. The LF group included five predominant species, mainly from Rotifera. Macrozooplankton biomass decreased, and a similar phenomenon was observed in the HF group. The MF group was involved in five dominant species, mainly Cladocera and Rotifera.

Fish effects on phytoplankton community

Eight types of phytoplankton, including Cyanophyta, Chlorophyta, Bacillariophyta, Cryptophyta, Pyrroptata, Euglenophyta, Xanthophyta, and Chrysophyta, were observed. A total of 148 phytoplankton species were recorded in all treatments during the entire sampling period, and 118 species of phytoplankton belonging to 62 genera were found

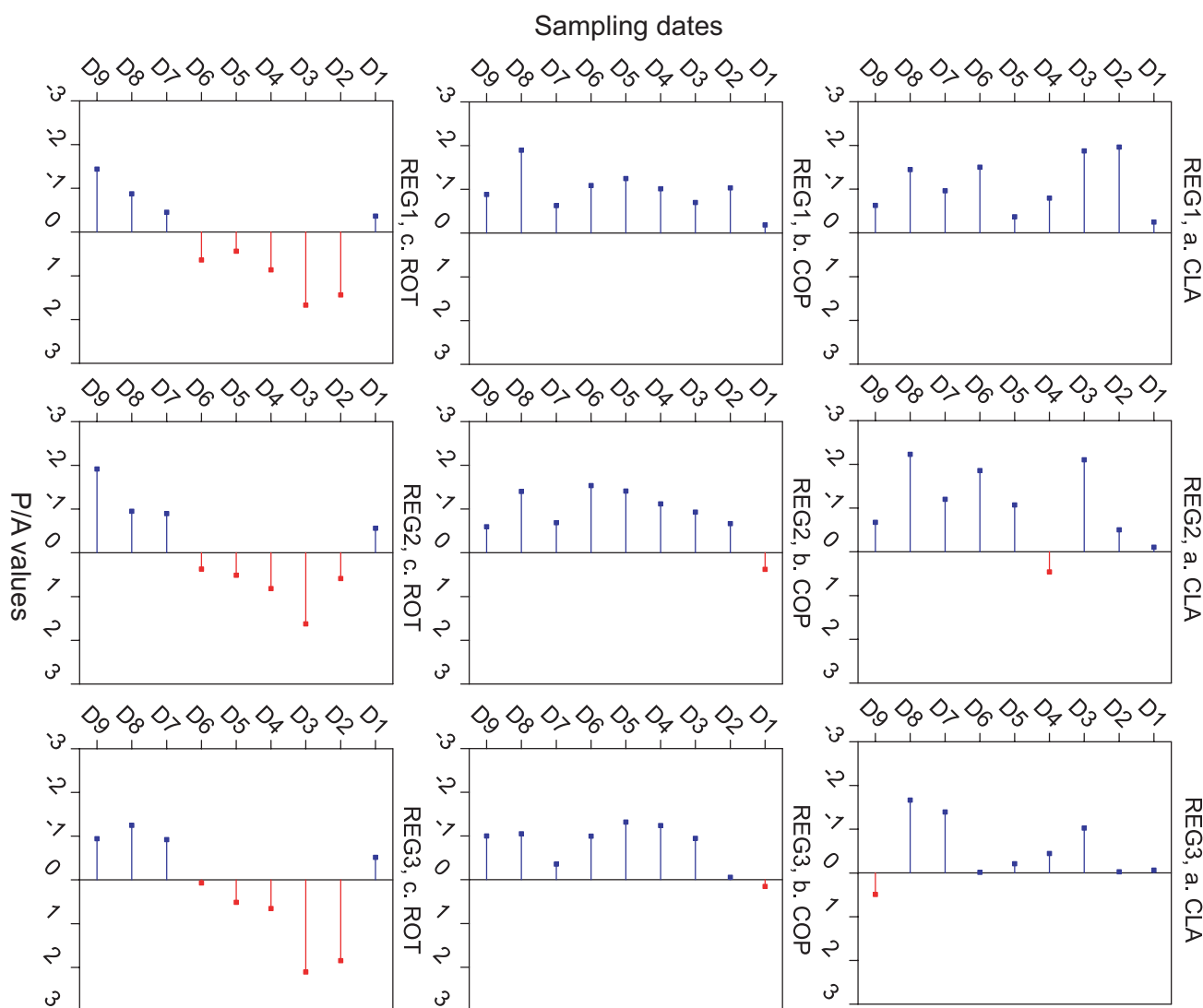


Fig. 7 P/A values ($\log_{10} (X_{\text{Presence}}/X_{\text{Absence}})$) for CLA (Cladocera), COP (Copepoda), and ROT (Rotifera) for all samplings in each treatment, where REG1, REG2, and REG3 are shown for the ratios of the

values between LF, MF, HF, and NF, respectively. A blue line with a blue dot means P/A value < 0 (left to the dashed line) and a red line with a red dot means P/A value > 0 (right to the dashed line)

Table 2 Dominated species of zooplankton and their biomass (mean \pm SD, mg/L) in all treatments

Catalog	Genus–Species	NF	LF	MF	HF				
Cladocera	<i>Bosmina longirostris</i>	○	0.34 \pm 0.16		○	0.05 \pm 0.02			
	<i>Lathonura rectirostris</i>	○	0.87 \pm 0.12		○	0.45 \pm 0.11	○	0.57 \pm 0.13	
Copepoda	<i>Nauplii</i>			○	0.04 \pm 0.01				
	<i>Phyllodiaptomus tunguidus</i>	○	0.62 \pm 0.17	○	0.07 \pm 0.01	○	0.13 \pm 0.04	○	0.12 \pm 0.03
	<i>Neodiaptomus schmackeri</i>	○	0.49 \pm 0.12						
	<i>Thermocyclops hyalinus</i>	○	0.23 \pm 0.09						
Rotifera	<i>Ploesoma hudsoni</i>	○	0.50 \pm 0.11	○	0.87 \pm 0.21			○	1.80 \pm 0.33
	<i>Pelyarhtra trigla</i>			○	0.16 \pm 0.04	○	0.22 \pm 0.08	○	0.14 \pm 0.06
	<i>Trichocerca rousseleti</i>			○	0.07 \pm 0.02	○	0.07 \pm 0.02		

“○” represented the dominant species of zooplankton, which was determined to be $Y \geq 0.02$

in the fish absence groups, 124 species belonged to 63 genera in the LF group, 110 species belonged to 62 genera in the MF group, and 117 species belonged to 65 genera in the HF group. The detailed composition of phytoplankton in each experimental group was shown in Electronic Supplementary Material 2. The most frequent phytoplankton taxa in all treatments were Cyanophyta, Chlorophyta, and Bacillariophyta (Fig. 8). The biomass of these three types of algae accounted for the largest proportion of phytoplankton. The NF group had 98.23%, LF had 94.98%, MF had 82.17%, and HF had 90.02%. Changes in phytoplankton biomass in the NF and LF groups showed different trends compared with the MF and HF groups (Fig. 9). The different stocking densities of bighead carp had different control pressures on the main population of phytoplankton (Fig. 10). The MF and HF groups had different inhibitory effects on blue-green algae (except at D2), and the control effects increased gradually with sampling time. The LF group presented positive values at the former stage and

negative values at the late stage. The green algal ratios in all the fish presence groups showed no apparent effects before D4 and then had a positive increase during the rest of the experiment. Overall, the P/A values of diatoms were positive in all the fish presence groups.

Bighead carp stocking not only affected the biomass of the main phytoplankton population but also the community structure (Fig. 6). In the fish absence groups, phytoplankton diversity, evenness, and richness were lower than those in the fish presence groups, especially after D5. The compositions of the dominant phytoplankton species varied among the treatments (Table 3). The NF group consisted mainly of the phytoplankton of cyanobacteria, including *Microcystis incerta* ($Y = 0.128$), *Anabaena circinalis* ($Y = 0.066$), and *Anabaena smithii* ($Y = 0.161$). As the density of stocked fish increased, the composition of the dominant species in fish presence groups gradually changed to that of Chlorophyta species.

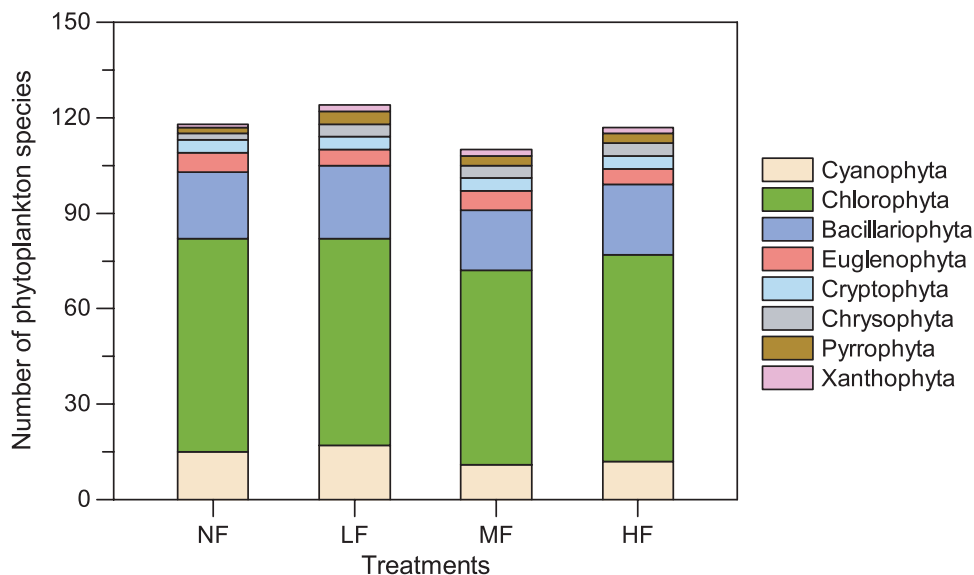
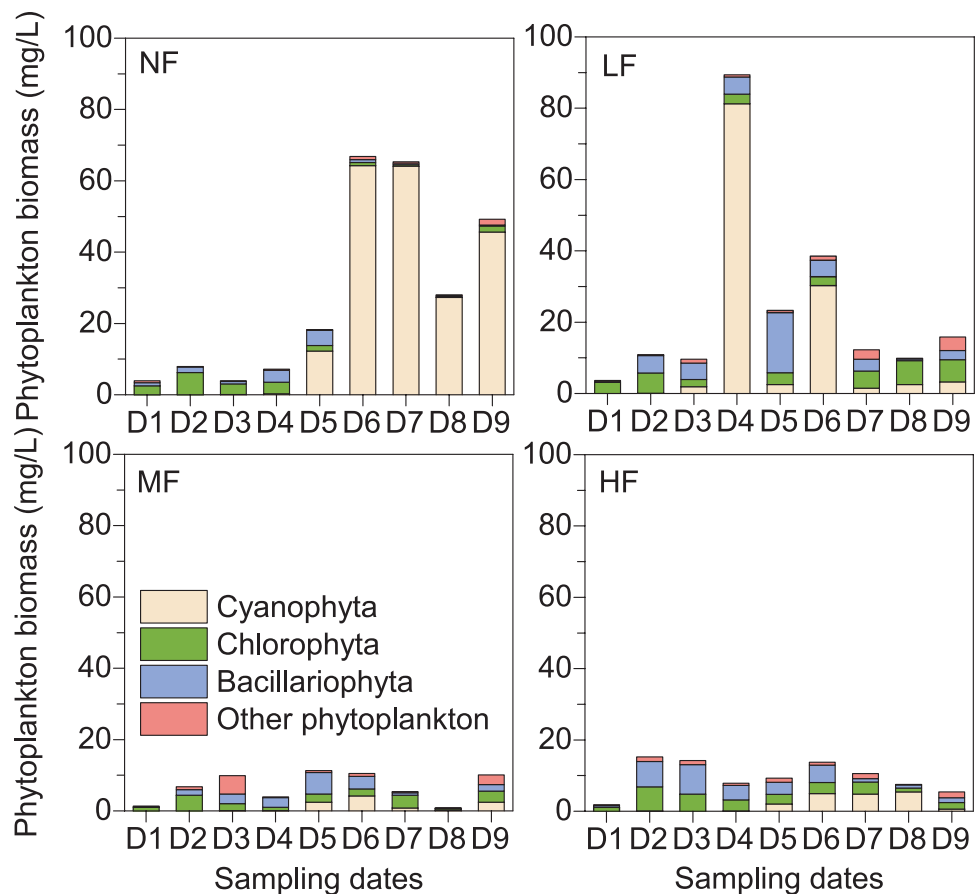
Fig. 8 Number of phytoplankton species in each treatment during the experiment

Fig. 9 Changes of phytoplankton biomass in all treatments at all sampling dates



Canonical correspondence analysis of dominant species of plankton and environmental factors

Multivariate statistical approaches were used in assessing the relationship of dominant zooplankton or phytoplankton species with environmental variables in different fish stocks. The results of the DCA analysis indicated a good dispersion of plankton species on axes with high gradient length (> 3), which is suitable for unimodal methods, such as CCA (Šmilauer and Lepš 2014). CCA was performed to explore the relationship between environmental factors (predictor variables) and phytoplankton or zooplankton species (response variable) in the experimental ponds (Fig. 11). The dominant species of phytoplankton were apparently affected by the environmental factors (Fig. 11a). A total of 54.3% of cumulative variance in species was explained by the first two CCA axes, and over 90% of correlation was found between environmental factors and phytoplankton assemblies. The application of forward selection using the Monte-Carlo test confirmed that the first two axes were highly significant ($p = 0.002$; Table 4). Multiple environmental variables (e.g., TP, DO, pH, TN, W_T , and fish biomass) played significant roles in driving the succession of species (Table 5). Cyanophyta showed a significant suppression by fish, and positive

correlations with pH, DO, and nutrient level. Responses of dominant zooplankton species to environmental variables have been observed in Fig. 11b. The detailed results of the coordinate were shown in Table 4 and Table 5. A total of 40.8% of cumulative variance in species was explained by the first two CCA axes, and over 89.6% of correlation was found between environmental variables and zooplankton assemblies. Environmental variables (chl-*a*, TP, pH, W_T , fish biomass, and W_{SD}) exerted considerable impacting on zooplankton community (Table 5). Fish biomass showed the inhibition of crustacean zooplankton, and an opposite result was obtained in Rotifera. Copepoda showed a positive relationship with chl-*a*.

Discussions

Trophic cascade of bighead carp on plankton community structure and water environment

Phosphorous transferred to the pelagic zone via the feeding of fish is an important flux in lakes (Carpenter et al. 1992). Filter-feeding fish plays an important role in “phosphorus pumps” in many lakes and accounted for 70% of the

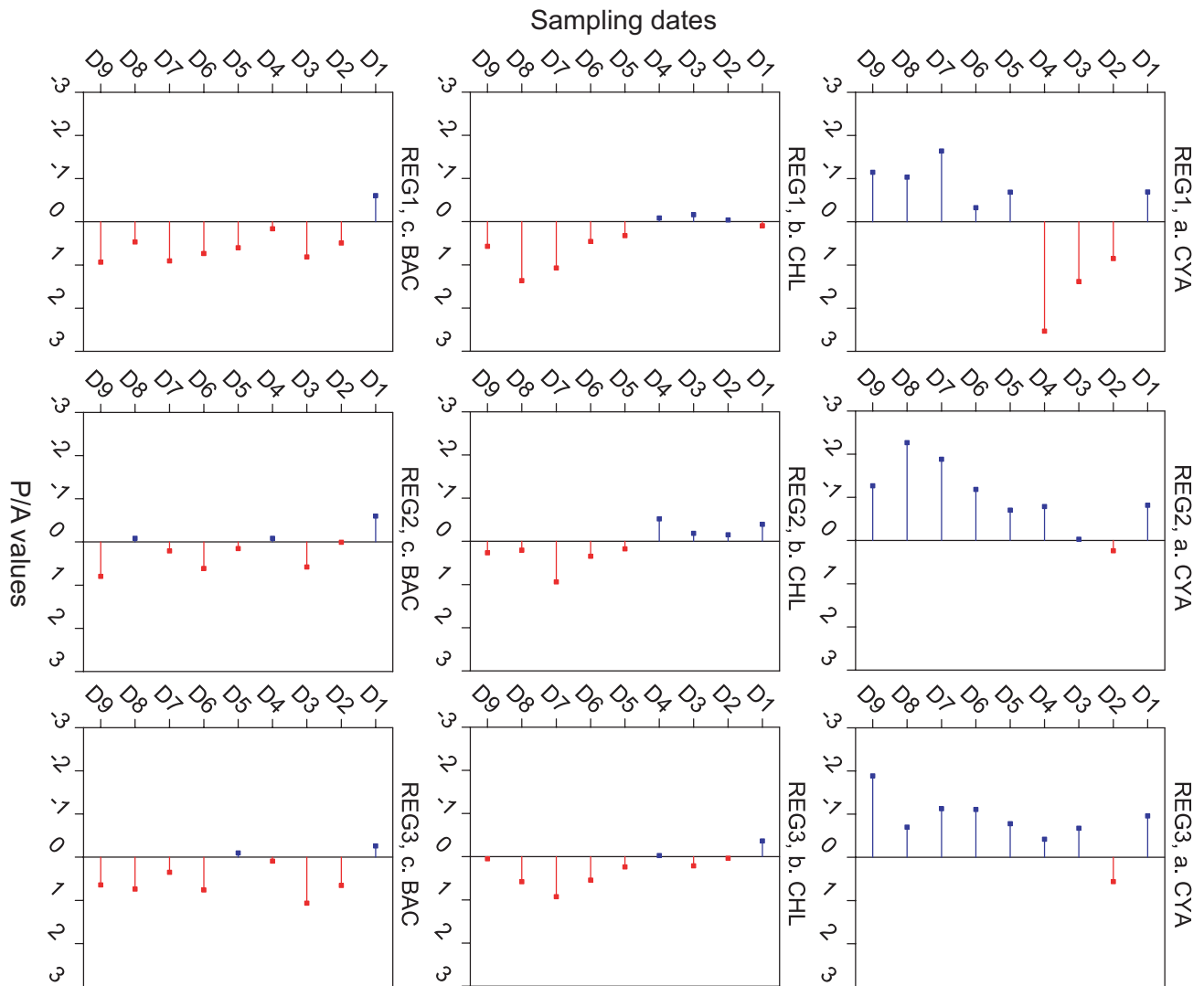


Fig. 10 P/A values ($\log_{10} (X_{\text{Presence}}/X_{\text{Absence}})$) for CYA (Canophyta), CHL (Chlorophyta), and BAC (Bacillariophyta) for all samples in each treatment, where REG1, REG2, and REG3 are shown for the ratios of the values between LF, MF, HF, and NF, respectively. A blue

line with a blue dot means P/A value < 0 (left to the dashed line) and a red line with a red dot means P/A value > 0 (right to the dashed line)

phosphorus excreted from pelagic fish in filter-feeding fish-dominated lakes (Carpenter et al. 1992; Sterner and George 2000). Studies on the nutrient budget mediated by filter-feeding fish revealed their regulatory effects on nutrients in experimental water bodies. Chen et al. (1991) showed that the amounts of nutrients released by filter-feeding fish in Lake Donghu were lower than the optimal algal production requirements (Chen et al. 1991), suggesting that the excretion of nutrients by fish in eutrophic environments is not critical to algal growth (Lu et al. 2002). Research on the ecological stoichiometry of filter-feeding fish and their driven nutrient recycling in Lake Qiandao showed similar results. The nitrogen and phosphorus released by the excretion of filter-feeding fish only accounted for 0.237% and

0.788% of algal primary production needs, respectively (Li 2010). Therefore, the nutrients released by filter-feeding fish were insignificant compared with those required by algae in Lake Qiandao (Li 2010). Given that the N/P ratio of big-head carp is much higher than that of other food organisms, excess nitrogen is discharged, and phosphorus is fixed, and thus homeostasis of its element composition is sustained (Li 2010). At the end of the current experiment, the weights of bighead carp in the LF, MF, and HF groups were 1.78, 1.55, and 1.58 times those of their respective initial weights. Li (2010) concluded that the contents of N and P in bighead carp were $9.99 \pm 0.07\%$ and $3.70 \pm 0.09\%$, respectively. According to these proportions, the effective preservation of N and P of the current treatments was calculated as

Table 3 Dominant species of phytoplankton and their biomass (mean ± SD, mg/L) in all treatments

Phylum	Genus–Species	NF	LF	MF	HF
Cyanophyta	<i>Microcystis incerta</i>	○	2.80 ± 0.88	○	0.01 ± 0.03
	<i>Anabaena circinalis</i>	○	19.69 ± 2.21	○	1.04 ± 0.24
	<i>Anabaena smithii</i>	○	8.07 ± 1.62		
	<i>Merismopedia punctata</i>				○
Chlorophyta	<i>Scenedesmus quadricauda</i>		○	0.24 ± 0.08	○
	<i>Scenedesmus carinatus</i>		○	0.11 ± 0.03	○
	<i>Scenedesmus bijuga</i>			○	0.22 ± 0.08
	<i>Scenedesmus bicaudatus</i>			○	0.07 ± 0.02
	<i>Coelastrum microporum</i>	○	0.87 ± 0.20	○	0.21 ± 0.06
	<i>Chlorella vulgaris</i>			○	0.27 ± 0.11
	<i>Westlopsiopsis linearis</i>			○	0.25 ± 0.07
Bacillariophyta	<i>Synedra acus</i>		○	3.29 ± 0.19	
	<i>Melosira sulcata</i>				○

“○” represented the dominant species of phytoplankton, which was determined to be $Y \geq 0.02$

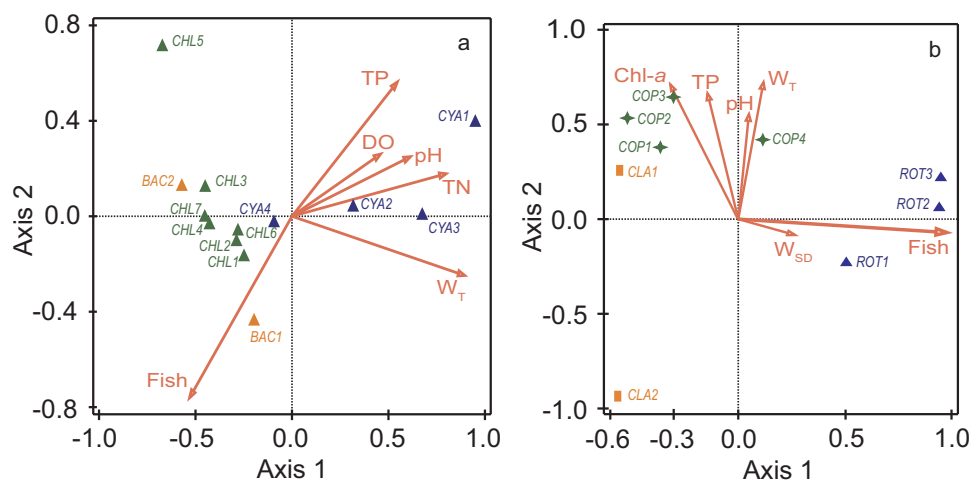


Fig. 11 Ordination diagram of canonical correlation analysis (CCA) shows dominant species of phytoplankton (a) and zooplankton (b) and environmental characteristics (arrows) in all treatments. Abbreviated names are as follows: TN total nitrogen, TP total phosphorus, DO dissolved oxygen, pH, WT water temperature, Fish fish biomass in various groups, Chl-a chlorophyll-a, CLA1 *B. longirostris*, CLA2 *L. rectirostris*, COP1 *P. tunguidus*, COP2 *N. schmackeri*, COP3 *T.*

hyalinus, COP4 Nauplii (Copepoda), ROT1 *P. hudsoni*, ROT2 *P. trigla*, ROT3 *T. rousseleti*, CYA1 *M. incerta*, CYA2 *A. circinalis*, CYA3 *A. smithii*, CYA4 *M. punctata*, CHL1 *S. quadricauda*, CHL2 *S. carinatus*, CHL3 *S. bijugatus*, CHL4 *S. bicaudatus*, CHL5 *C. microporum*, CHL6 *C. vulgaris*, CHL7 *W. linearis*, BAC1 *S. acus*, BAC2 *M. sulcata*

follows: LF, N 4211.34–4317.78 g, P 1559.75–1599.18 g; MF, N 5835.86–5920.30 g, P 2161.43–2192.70 g; HF, N 8726.66–8929.49 g, and P 3232.10–3307.22 g. TP in each treatment group was significantly lower than that in the control group, and the effect intensity gradually increased with experimental time, mainly showing a downward trend in the P/A curve (Fig. 4). The inhibition intensity of TN fluctuated greatly with sampling time. Therefore, the bighead carp played a key role in the phosphorus sink in the experimental pond. Meanwhile, bighead carp improved the W_{SD} and maintained the stability of the pH value. As mentioned in

the introduction, experiments were carried out using earthen ponds rather than enclosures or concrete ponds (without natural bottom) will directly determine the final results of the experiment.

Some studies directly or indirectly emphasized that big-head carp is selective in phytoplankton feeding and shows no interest in cyanobacteria (Brooks and Dodson 1965; Cremer and Smitherman 1980). The results of other studies concluded that the sparser gill rakers of bighead carp automatically filter out the flow of small algae and therefore opportunistically “select” relatively large particles, such as

Table 4 Main results of canonical correspondence analysis (CCA) using the Monte-Carlo permutation test for plankton species–environmental variables relationship

Response variable	Phytoplankton					Zooplankton				
	Axis1	Axis2	Axis3	Axis4	Total inertia	Axis1	Axis2	Axis3	Axis4	Total inertia
Eigenvalues	0.542	0.203	0.044	0.015	1.372	0.417	0.313	0.166	0.055	1.790
Species–environment correlations	0.936	0.842	0.714	0.580		0.896	0.863	0.637	0.665	
Cumulative percentage variance										
Of species data	39.5	54.3	57.5	58.6		23.3	40.8	50.1	53.1	
Of species–environment relation	66.1	90.8	96.2	98.1		43.4	76.1	93.4	99.1	
Sum of all eigenvalues:					1.372					1.790
Sum of all canonical eigenvalues					0.820					0.960
<i>F</i> -ratio		<i>F</i> -ratio = 4.1, <i>p</i> = 0.002					<i>F</i> -ratio = 3.8, <i>p</i> = 0.002			

Table 5 Correction coefficients of dominant species of plankton and environmental variables in the CCA analysis

Phytoplankton					Zooplankton				
Variables	Explains %	Contributions %	<i>F</i> value	<i>p</i> value	Variables	Explains %	Contributions %	<i>F</i> value	<i>p</i> value
Fish	19.9	28.0	8.4	0.002	Fish	22.4	32.4	9.8	0.002
TN	17.4	24.6	9.2	0.002	pH	8.3	12.0	4.0	0.004
pH	5.2	7.3	2.9	0.036	W_T	9.1	13.1	4.8	0.004
TP	5.0	7.1	3.0	0.032	W_{SD}	5.1	7.3	2.9	0.018
W_T	9.0	12.7	6.2	0.002	TP	4.2	6.1	2.5	0.030
DO	3.3	4.6	2.4	0.032	Chl- <i>a</i>	4.6	6.6	2.9	0.008

Fish fish biomass, *TN* total nitrogen, *pH*, *TP* total phosphorus, W_T water temperature, *DO* dissolved oxygen, W_{SD} transparency, *Chl-a* chlorophyll-*a*

zooplankton, compared with those of silver carp (Opuszynski and Shireman 1993; Xie and Liu 2001). Some researchers found intact and undamaged algae in the excreted feces of bighead carp, which were cytoactive (Xie 2003). Even these algae showed high growth rates and photosynthetic activity (Wang et al. 2014), which provide evidence of the indigestible use of algae by bighead carp. Liu and Zhang (2016) had systematically explained these research results. However, many studies confirmed that bigheaded carp is efficient in controlling total phytoplankton biomass when phytoplankton is dominated by either net phytoplankton or cyanobacteria concentrated in dense blooms or floating mats (Laws and Weisburd 1990; Radke and Kahl 2002; Collins and Wahl 2017). In the current study, no cyanobacterial blooms were observed in the treatment groups. In the control groups, blooms suddenly occurred after the sixth sampling (D6, June 30), and a W_{SD} of 0.40 m was obtained in the worst condition at the last sampling time. The community composition and biomass of Cyanophyta, Chlorophyta, and Bacillariophyta occupied the main proportions of phytoplankton in all the experimental groups (Opuszynski and Shireman 1993; Tang et al. 2002; Yi et al. 2016a). The LF group had the most phytoplankton species, whereas the MF group had the least, suggesting that there was a weak

correlation between the number of phytoplankton species and bighead carp stocks. Strong predation intensity on phytoplankton biomass (in particular, cyanobacteria taxa) was cascaded by bighead carp from the P/A value of phytoplankton and CCA analysis (Fig. 11a), and MF and HF groups displayed greater cyanobacteria reduction rates than that the LF group, and the dominant species transferred to green algae and diatoms. The phytoplankton biomass of the LF group reached its peak at the fourth sampling time (the cyanobacteria biomass accounted for 90.92% of the total biomass) but decreased rapidly thereafter, further indicating that bighead carp stocking had an inhibitory effect on cyanobacteria. The *H'*, *R*, and *J* indices of phytoplankton in the control group were the lowest among the experimental groups possibly because of the blooms that occurred. Therefore, bighead carp can play roles in controlling algae biomass and improving phytoplankton diversity and has the best effect in the MF and HF groups.

Our study found that intense predation by bighead carp reduced the biomass of zooplankton, shifting community structure toward smaller individuals (such as Rotifera and Copepoda nauplii; (Collins and Wahl 2018). The ability of fish to detect and capture a particular prey depends on the conspicuousness and escape behavior of that prey

(Lazzaro 1987; Opuszynski and Shireman 1993). Cladocera is more vulnerable than Copepoda and is easier to be captured by filter-feeding planktivores (Szlauer 1965; Drenner et al. 1978; Drenner et al. 1982; Gophen et al. 1983), but the bighead carp had a strong effect on Cladocera and Copepoda biomass possibly because of the lack of Cladocera in the treatment groups (Yi et al. 2016a). The standing crops of crustaceans and Rotifera showed different changing trends (Fig. 5, Fig. 7) in the different treatment groups with different predation pressures, which was consistent with previous studies (Cremer and Smitherman 1980; Burke et al. 1986; Opuszynski and Shireman 1993; Yi et al. 2016a). In the early stages of the experiment, Rotifera biomass in the treatment groups was higher than that in the control group (Fig. 5), which was consistent with Rosińska et al. (2019). However, when cyanobacterial blooms appeared in the control group, Rotifera biomass increased rapidly. Cyanobacterial blooms severely restrict the growth of macrozooplankton and thus improve the competitiveness of smaller individuals (Lampert 1987; Fulton III and Paerl 1988). In the late stages of the experiment, the crustacean and phytoplankton standing crop of the treatment groups were at low levels. In the current experiment, earthen ponds were used for the control study. The result showed that bighead carp had a faster filter-feeding rate in these earthen ponds than in natural water bodies. Given that large ponds were used, the biomass of small zooplankton, particularly Rotifera, showed a decreasing trend. Filter-feeding fish stocking can lead to phytoplankton miniaturization (Ma et al. 2010), which is conducive to zooplankton feeding. In the ecosystems of natural lakes and reservoirs, filter-feeding fish feed on large phytoplankton, and thus nutrients are effectively used by micro- and nanophytoplankton, which in turn serves a food source for zooplankton. However, although filter-feeding fish may feed on zooplankton, silver and bighead carps and zooplankton have distinct ecological niches in the ecosystems of large or medium natural lakes and reservoirs, which enable zooplankton to thrive in waters without filter-feeding fish (Liu and Zhang 2016). The effect of filter-feeding fish on zooplankton is mainly reflected in the density and biomass of zooplankton rather than in the compositions of their species (Liu 1997; Li et al. 2018a). The findings from our experiment on the HF group showed that the number of zooplankton species was not markedly reduced compared with that in the control group. The H' , R , and J' indices were slightly suppressed in the LF and MF groups compared with those in the controls, and strong inhibition was observed in the HF group. These findings are consistent with those in previous studies (Liu 1997; Mei 2010). Therefore, filter-feeding fish and zooplankton can achieve cooperation in algal control at a reasonable stocking density in natural water bodies.

Optimal density for the management of water environment using bighead carp alone

A study on Lake Taihu suggested that silver and bighead carps in mixed or separate cultures at high densities can be useful in controlling the occurrence of cyanobacterial blooms and the effective density of carp-controlled blooms is between 46 and 50 g/m³ and is based on the current state of a lake (Xie 2003). Ke et al. (2007) predicted that a higher stocking density (more than 40 g/m³) increases the controlling effect on microcystis biomass. Zhang et al. (2008) reviewed many field studies performed on scales from microcosmic to full lakes and concluded that filter-feeding carps reared at 30–70 g/m³ are effective in preventing the rapid growth of algae. A modified minimal model of planktivory by Attayde et al. (2010) presented a unimodal relationship between the biomass of omnivorous filter-feeding fish and phytoplankton biomass, and when the dry weight of the fish was 20 g/m³ (approximately 50 g/m³ wet weight), the plankton community had a stable state. A similar relationship was reported by Liu (2010), who concluded that algal control is effective when the biomass of filter-feeding fish reaches or exceeds the threshold.

Threshold density varies among researchers when the optimal algal density that can be effectively controlled by filter-feeding fish is considered. The interference of the external environment is an important factor that determines the direction of experimental results during in situ experiments. The experiments mentioned above have natural bottoms, and the experimental water body size was controlled. Season, duration, fish stocking density (whether carps stocked achieve threshold density), and the type of nutrition research water or nutritional status affect optimal threshold density and even directly lead to the failure of an experiment. A “Hopf bifurcation” tipping point and alternative stable states in which filter-feeding fish obviously can affect phytoplankton biomass decreasing and without having a significant impact on zooplankton diversity and stability (Attayde et al. 2010).

In this study, although the MF and HF groups can effectively control phytoplankton biomass (especially cyanobacteria), the protection of zooplankton diversity, richness, and evenness, the stocking density of the MF group exerted a higher effect than the HF group, and nutrient reduction (especially TP) was also more pronounced in the MF group. At the beginning of the experiment, the stocking density of the MF group was 23.5 g/m³, and at the end of the experiment, the existing density of bighead carp was 38.8 g/m³. Thus, bighead carp can be included in the EAR of lakes and reservoirs for the control of algal biomass and improvement of the status of water nutrients. However, for the protection of aquatic biodiversity, the amount of bighead carp stocking should be carefully considered.

Conclusion

In the current study, we carried out the experiment in eight earthen ponds, which had larger areas with nature bottoms and were similar to nature water body types, to research the effects of bighead carp stocking alone on eutrophic water columns. The results showed that (1) fish presence groups showed an improvement effect on water quality condition, acting as reductions in TN and TP, promotion in W_{SD} , maintenance of the pH values at a low and stable state; (2) the phytoplankton biomass (especially cyanobacteria) were suppression markedly after carps stocked and different pressures were observed among the treatments, and the MF and HF groups tended to have better controls; (3) the bighead carp showed a clear preference for macrocrustacean zooplankton, especially in the HF group; and (4) the compositions and community structures of plankton showed different changing trends with the H' , R , J' indices of phytoplankton in the fish presence groups and increased compared with those in the control groups, and meanwhile decreasing trends were observed in zooplankton in the HF groups, and no significant decrease in the LF and MF groups was observed. At a fish stocking density of 23.5–38.8 g/m³, after comprehensively comparing the effects of three stocking densities set in this experiment on the water environment indicators and on plankton, the highest efficiency in controlling cyanobacteria and promoting water condition was achieved, and the impact on zooplankton diversity was weak. Our results indicated that bighead carp can be included in the EAR of lakes and reservoirs, but the optimal density of bighead carp stocking should be carefully considered.

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Data availability The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate Not applicable.

Consent for publication The authors declare that they agree with the publication of this paper in this journal.

Competing interests The authors declare no competing interests.

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