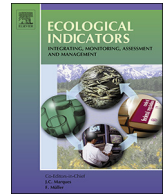




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Original Articles

Intra-annual variation of zooplankton community structure and dynamics in response to the changing strength of bio-manipulation with two planktivorous fishes

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ABSTRACT

Zooplankton is widely used in indicating environmental changes and energy flow efficiency in aquatic ecosystems. Species composition and body size spectrum of zooplankton assemblage are sensitive to the changes of physico-chemical variability and fish feeding stress, and thus have in turn a prime bearing on water quality and cultured fishes. To study the response of zooplankton community to the introduction of planktivorous carps, monthly surveys were conducted in 2015 at six traditionally monitored locations in Miyun Reservoir, the unique surface drinking water of Beijing. There was a decrease in species richness, diversity, density and biomass, suggesting simplification of the community structure. Species diversity, density, and biomass declined significantly through the growth season, illustrating the great pressure imposed on the zooplankton. Regression and canonical correspondence analysis (CCA) showed low relationships between community traits and environmental variables. Zooplankton biomass had a significantly negative relationship with the stocking intensity of the filter-feeding carp. The different responses of the subgroups of Protozoa, Rotifera, Cladocera and Copepoda indicated that they responded differently to environmental stress. Seasonal variations in the density and biomass of the four subgroups and biomass size spectrum (BSS) indicated that planktons with medium and large body sizes were more sensitive and suffered more stress from the filter-feeding carp. The filter feeding by the silver and bighead carp disrupted the natural equilibrium of the zooplankton community, decreased diversity and stocks, altered the seasonal dynamics of all quantitative traits and suppressed the dominance of medium- and large-sized species or functional groups. The impacts of the fishery mode and the responses of different functional groups of zooplankton must be considered in ecological assessments and biomanipulation studies based on the zooplankton community structure and dynamics.

1. Introduction

Zooplankton species composition and community construction are fundamental components of fisheries, environmental evaluations and ecological assessment of freshwater and marine ecosystems. In lentic aquatic ecosystems such as reservoirs and lakes, zooplanktons play an important role in supporting fish production, maintaining community stability and regulating ecosystem resilience of complicated food webs with diverse invertebrates and fish species (Andronikova, 1996; Edmondson and Litt, 1983; Maccann, 2011; Polis and Winemiller, 1998). Because of their small body sizes, short life spans and frequent

species succession, zooplankters are highly sensitive to physico-chemical variability and fish-feeding stress. They also have a strong influence on water quality and fish aquaculture (Gillooly and Dodson, 2000; Gophen et al., 1990; Xie, 2003). The basic features of species richness, species diversity, individual density and community biomass are all good indicators of ecological processes and environmental evolution in routine monitoring studies (Andronikova, 1996; Edmondson and Litt, 1983; Lin et al., 2014).

Besides the traditionally used traits, body size composition and distribution pattern of planktons have been used to describe community construction and ecological efficiency (Lin et al., 2014; Lu et al., 2002).

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The biomass- or density-based size spectrum (BSS or DSS) and their spatio-temporal variation contain valuable information on community structure and functions. These data can help reveal the functional diversity of species within guilds with different body sizes and their differential responses to either bottom-up or top-down processes (Brooks and Dodson, 1965; Santos et al., 2017; Zhou, 2006).

In natural systems with low fish-feeding pressure, crustaceans in large sizes occupy a higher trophic level and maintain community equilibrium with a linear regression coefficient approaching ‘-1’ with respect to the BSS of planktonic particles (Benoît and Rochet, 2004; Santos et al., 2017). Fish-feeding pressure, however, can disturb the zooplankton species composition and reduce the reliability and practicality of zooplankton as bioindicators (Carpenter et al., 2006; Gutierrez et al., 2018; Webber et al., 2005). Following fish introduction, the qualitative and quantitative characteristics of zooplankton community will change in relation to the feeding habits, stocking biomass and biology of the fish species (Chen, 1982; Cremer and Smitherman, 1980). Low-density fish stocking generally favors large-sized zooplanktons, while high-density fish stocking may reduce the populations of large-sized planktons and decrease their dominance. This can result in lower slopes of the BSS regression lines (Cottingham, 1999; Santos et al., 2017).

Zooplankters feed mainly on phytoplankton and other small pelagic organisms (Mavuti, 1990; Zhang and He, 1991), and they represent an important prey for large organisms such as larger sized zooplankters, fish larvae, juveniles and filter-feeding adults in the meantime (Andronikova, 1996; Chen, 1982; Wang et al., 2018). Numerical variations in zooplankters are good indicators of ecological stresses from both lower and higher trophic levels (Maccann, 2011). The relative proportion of planktonic prey to planktivorous fishes influences the levels of inter-specific competition among zooplankters of different body sizes. Zooplankton responses to fish-feeding stress have been well documented, but fewer studies have documented the behavioral differentiation of the zooplankton subgroups under feeding pressure (Yang et al., 2014). This differentiation is necessary to understand the subtle interacting process in the zooplankton community, make accurate scientific assessments, and for practical bio-manipulation.

Silver carp (*Hypophthalmichthys molitrix*) and bighead carp (*Aristichthys nobilis*) are the two most popular planktivorous fishes cultured in the world and subjects of bio-manipulation (Xie, 2003). These two species share a wide food spectrum size range from 10 to 200 μm and larger sized organismic particles, including large-sized phytoplankton, Protozoa, Rotifera and most planktonic crustaceans (Chen, 1982; Wang et al., 2018; Xie, 2003; Yan and Shi, 1995). When the species coexist, silver carp tends to feed on middle- and small-sized planktons, while bighead carp favors larger planktons with body sizes up to, and exceeding, 1000 μm (Xie, 2003). The excellent performance of these carp in reducing harmful algae and promoting ecosystem health has earned them a good reputation, and they have been introduced into reservoirs, lakes and other water bodies worldwide (Xie, 2003). In China, these two species have been introduced into almost all freshwater bodies, including the Miyun Reservoir of this study, to control blue algae, regulate community equilibrium and improve water quality (Jia et al., 2015).

Miyun Reservoir is the unique surface drinking water for Beijing. It is located in the rural county of Miyun. Reservoir water quality was formerly oligotrophic before the middle 1980s, and deteriorated thereafter due to increased pollutant inflows and the cage culture of cyprinoids (Ma et al., 2010). By 1999, the water quality was mesotrophic or moderately polluted (Li et al., 2015; Zhao et al., 2001). After 1999, the water level declined, and this aggravated the pollution and eutrophication. Cyanobacteria blooms occurred in the fall at some localities during the early 2000s (Su et al., 2014).

To help restore ecosystem health and reduce water pollution, caged cyprinoid culture was banned and filter-feeding silver and bighead carp have been introduced since 2004. To 2015, the levels of released larvae

and juveniles of silver and bighead carp were 0.54 g/m^3 in the spring, and the abundances of these two carp species were estimated to be 2.0 g/m^3 at the end of the growing season in late autumn (Jia et al., 2015; Ke et al., 2008; Yan et al., 2007). Feeding pressure from the carp effectively controlled cyanobacteria after 2010 (Su et al., 2014). The influence on zooplankton community, however, has not been documented (Zeng et al., 2016; Zhou et al., 2013).

To understand the effects of carp introduction on zooplankters, we conducted a monthly survey on zooplankton community structure and seasonal dynamics in Miyun Reservoir in 2015. We studied the characteristics and distribution patterns of zooplankton, paying special attention to the inter-group relationships of Protozoa, Rotifera, Cladocera and Copepoda. We hypothesized that the introduction of filter-feeding carp has had variable effects on the zooplankters with different body sizes. The middle- and large-sized planktonic species have a direct response to increased feeding stress, whereas the over-stressed fishery will produce opposite effects on zooplankton composition and community stability. Our results contribute to an integrated assessment of ecosystem health and fishery influences and will help improve managerial decisions on the bio-manipulation of filter-feeding carp in temperate fresh waters.

2. Methods and materials

2.1. Study area

Miyun Reservoir, situated at 40°27′–40°34′N and 116°50′–117°03′E and an elevation of 147 m, is a deep reservoir with a 4.3 billion m^3 water capacity, 188 km^2 surface area and 43.5 m depth. Its current storage is only 1.0 billion m^3 with a greatest depth of 32.5 m. The reservoir is the source of drinking water for the suburbs of Beijing, and it supplies 200–500 million m^3 water to Beijing yearly. This reservoir is located in a warm temperate semi-humid monsoonal climate with a mean annual air temperature of 10.5 °C. Annual precipitation averages 640 mm with a wet season from late June to early August. During the winter (December to March), the reservoir has thick ice on the surface. Zooplankton and fish stop feeding through the cold winter and resume activity in May.

2.2. Sampling methodology

We chose six sites for monthly zooplankton surveys and used sampling protocols based on monitoring studies by Qiu (1981), Zhao et al. (2001), Liu et al. (2004) and Lin et al. (2014, Fig. 1). Sites CE and BE were located at the estuaries of two inflowing rivers (Chaohe and Baihe). Sites CD and BD were located at the deep areas of the reservoir near Chaohe Dam and Baihe Dam, respectively. Sites JG and YL were shallow areas located in the center and northern bay of the reservoir (Fig. 1). These six sites covered the main habitat types of the Miyun Reservoir and represented the distribution pattern of the zooplankton community.

Zooplanktons were sampled monthly at depths of 0.5, 13 and 25 m (1.0 m above the bottom) at CD and BD. Only surface samples (0.5 m below the surface) were taken for CE, BE, JG and YL (Fig. 1). Sampling sites were located with a GPS navigator (Garmin, Olathe, KS, USA). Five-liter samples were taken by a plexiglass sampler for each sampling unit. All samples were fixed with Lugol's solution according to Sherr and Sherr (1993) and Su et al. (2014). After 48 h settling and supernatant siphoning, zooplankton was concentrated to a 30 mL volume and preserved with formalin at a final concentration of 5.0% in glass bottles. Zooplankton identification and enumeration was accomplished with a digital microscope (Olympus BX 53, Japan) with three 1.0 mL subsamples according to Su et al. (2014). In the counting experiment, each subsample was counted and the average of the three counts was used for the statistical analysis (Zhang and He, 1991).

Species identification followed Jiang and Du (1979), Shen et al.

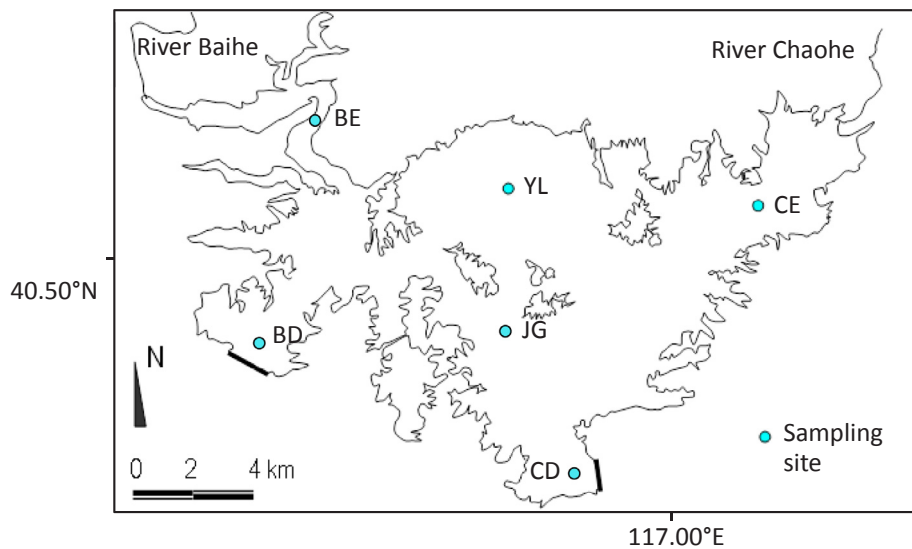


Fig. 1. Map of the Miyun Reservoir and sampling sites. CE and BE were located at the two estuaries of the inflow rivers of Chaohe and Baihe, JG was located near the core area of Jingyou island, YL was located at the north shallow bay of Yanluo, and CD and BD were located at the deep water near the Chaohe and Baihe dams.

(1979) and Su et al. (2014) with help from Algae C software (Wanshen, China). Microscopic pictures were taken at $100\times$ or $400\times$ field by BX53 Olympus microscopes. Body length, width, and biovolume were measured and calculated with Algae C software following Hillebrand et al. (1999). When possible, 30–50 individuals of each species were randomly measured, and the mean sizes were applied to subsequent biomass calculation and BSS analysis. Wet body mass was calculated using the following equation: $1\ \mu\text{m}^3 = 1 \times 10^{-6}\ \mu\text{g}$ (Cottingham, 1999).

Six environmental variables that commonly used in interpreting zooplankton composition were monitored (Gutierrez et al., 2018). Water temperature and dissolved oxygen (DO) were measured with a DO detector (YSI ProODO, USA). Transparency (SD), pH and chlorophyll-a concentration (Chla) were measured with a Secchi disc (Shuisheng DC20, China), pH meter (LEICI PHS3E, China) and portable chlorophyll fluorometer (Seabird, USA), respectively. Another 2 L of water was taken from each sample layer and stored at a pH < 2.0 before returning it to the lab for testing the permanganate index (COD_{Mn}). COD_{Mn} was tested with a multifunctional water quality detector (HACH DRB200, USA) within 24 h after sampling.

2.3. Data analysis

Species richness, individual density, and biomass were measured to describe intra-annual structure and dynamics of the zooplankton community. To study changes within the zooplankton community, four subgroups of Protozoa, Rotifera, Cladocera and Copepoda were considered separately as well as integrated as a whole in the data analysis. Species richness of total zooplankton and its four subgroups were accumulated counts of the corresponding samples in the same months. To calculate zooplankton density and biomass, the mean value of the six sites was used. All data from different sampling layers were previously averaged to represent the density and biomass of the corresponding site.

The Shannon–Wiener index (H') was used to calculate species diversity of the zooplankton community. For the subgroups, we used cumulative data before calculating total zooplankton diversity. The integrated diversity index of each month was calculated on the general averaged density using the following equation: $H' = -\sum(P_i \cdot \ln P_i)$, where P_i is the relative abundance of species i .

Species dominance (Y) was calculated for each of the sample months using the equation $Y_i = (n_i/N) \cdot f_i$, where n_i and N were

individual density of species i and the total zooplanktons, respectively, and f_i was the occurring incidence of species i among the six sites of each month or 42 sampling units of the whole sampling period. Dominant species were defined by index $Y \geq 0.02$.

The analysis of variance (ANOVA) was used to test the variation among surveys for the 42 sample units (contained in six sites) during the seven months. When significant differences were indicated, multiple comparisons (Duncan's SSR test) were used to specify the sample pairs showing significant differences. Stepwise regression analysis was used to test relationships between total zooplankton and the four subgroups, and between community characteristics and environment variables based on the 42 sampling units. The data of the 42 sampling units were also used to perform the regression analysis on the relationships between the four subgroups on the indexes of species diversity (H') and biomass (B). Due to nonsignificant variation of richness, density, and biomass among sampling sites, inter-location variation is not discussed in this report.

The biomass size spectrum covered all plankton species, which were divided into different body size groups by their equivalent spherical diameter (ESD). ESD was calculated by the regular volume of a sphere $V = (\pi/6) \cdot (\text{ESD})^3$ (Santos et al., 2017). To obtain a reasonable spectrum pattern, particles that occurred in the same size range with focused organisms were integrated (Zhou, 2006). In this study, phytoplanktons in ESD sizes ranging from 8 to $64\ \mu\text{m}$ were integrated into corresponding size groups of zooplankton beforehand for better fitting to the BSS model.

The geometric mean of ESD of a given size range was assigned as the nominal point of the taxonomic group (Santos et al., 2017; Zhou, 2006). Summary biomass of each taxonomic group was normalized by dividing the ESD amplitude ($\text{ESD}_{\text{max}} - \text{ESD}_{\text{min}}$) of the corresponding size range. The \log_2/\log_2 plot of the normalized biomass to the nominal ESD point depicts the BSS. Parameters of the regression lines, e.g. slope, intercept and determinant coefficient (R^2), to each BSS were estimated.

Lacking data records for most historical periods, the historical changes of zooplankton biomass were analyzed with data from the years 1980, 1996 and 2002 (Li et al., 2007; Liu et al., 2004; Qiu, 1981; Zhao et al., 2001). Historical records of the stocked filter-feeding carp were not available for most years. Considering that the carp released in spring were harvested from the reservoir after the growing season (in autumn and winter) every year, the carp stocks in Miyun Reservoir were mainly determined by the number of juveniles released in the corresponding spring. We therefore used the historical number of

released juveniles for regression analysis of the influence of carp stocking to zooplankton biomass.

All statistics analyses were conducted with MS excel 2010 and SPSS 20.0 for windows (SPSS Inc., USA), with significance at 0.05 occurrence probability. CCA analysis on zooplankton species relationships with environmental variables was conducted with Canoco 4.5 (Netherlands).

3. Results

3.1. Structure and seasonal dynamics of zooplankton characteristics

3.1.1. Species richness

There were 54 species of zooplankton identified, including 19 Protozoa, 16 Rotifera, 10 Cladocera and 9 Copepoda species. The small sized forms of Protozoa and Rotifera had significantly higher richness ($t = 12.858$, $df = 41$, $P < 0.001$) than the large sized Cladocera and Copepoda.

Seasonal dynamics of species richness (S) showed a significant variation (ANOVA, $F_{6,35} = 6.147$, $P < 0.001$) among sampling months, ranging in 13–24 species and averaging to 19 ± 3 (\pm S.D.) species per month. Multiple comparisons with Student-Newman-Keuls (S-N-K) revealed that the variation significance stemmed mainly from season-transition months, e.g. May/June, August/September and October/November.

There was significant monthly variation of S for Protozoa ($F_{6,35} = 3.224$, $P = 0.013$) and Rotifera ($F_{6,35} = 9.320$, $P < 0.001$), while Cladocera and Copepoda had non-significant ($P > 0.05$) S variation (Fig. 2). The seasonal variation of Rotifera richness made a significant ($F_{1,5} = 7.863$, $P = 0.038$) contribution to the entire zooplankton community.

3.1.2. Species diversity

The Shannon–Wiener index (H') illustrated low diversity levels through the monitoring period with a significant difference ($F_{6,35} = 3.939$, $P = 0.004$) between May (2.24) and June (1.35) and an average of 1.89 ± 0.28 . During the carp growing season of May to October, H' generally declined with an exception of June. By late November, species diversity rebounded with increases in the Protozoa and Cladocera groups (Fig. 3).

Among the four subgroups, the H' of small forms of Protozoa and Rotifera was significantly ($t = 15.049$, $df = 6$, $P < 0.001$) greater than the large forms of Cladocera and Copepoda (Fig. 3). Monthly dynamics of Protozoa and Cladocera diversity were similar, first declining and then gradually recovering after June. For Rotifera and Copepoda, H' increased first, but declined after peaking in the summer months (Fig. 3). Stepwise regression showed a non-significant ($P > 0.05$) relationship between zooplankton and the four subgroups.

3.1.3. Dominant species

Twelve species were dominant ($Y \geq 0.02$) in at least one month.

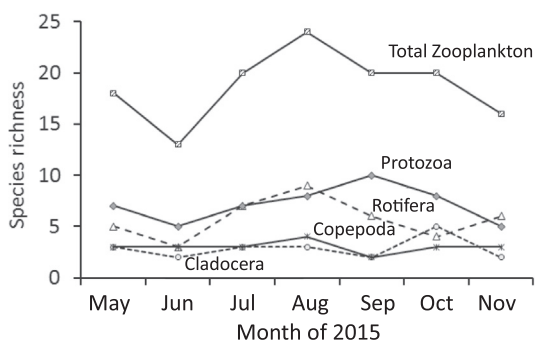


Fig. 2. Monthly fluctuations of species richness of total zooplankton and four subgroups.

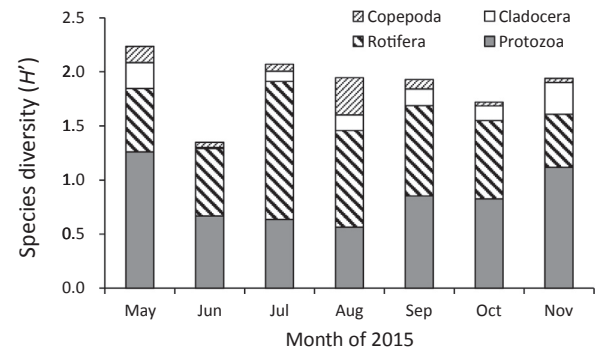


Fig. 3. Seasonal dynamics of Shannon-Wiener diversity index (H') of zooplankton community and the four subgroups.

The number of dominants ranged from three to seven species in each month (Table 1). Small sized forms of Protozoa (6) and Rotifera (4) had more dominants than larger forms of Cladocera (1) and Copepoda (1). Their dominance indexes showed higher predominance than crustacean species. For example, *Tintinnopsis wangi* (Protozoa) and *Keratella cochlearis* and *Polyarthra trigla* (Rotifera) were the top two dominant species for each month during the sampling period (Table 1).

The Bray-Curtis dissimilarity index indicated that the dominants transition rate was higher between the season-transition months of May and June (88.8%), and September and October (57.1%).

3.1.4. Individual density

Individual density varied between 54 and 1627 ind./L among the seven months, with an average of 582 ± 579 (\pm SD) ind./L per sample. The highest densities occurred in Rotifera (343 ± 655 ind./L), and Protozoa (208 ± 355 ind./L), while Cladocera and Copepoda occurred at lower densities (16 ± 32 and 14 ± 28 ind./L, respectively, Fig. 4). Zooplankton density was significantly determined by Protozoa and Rotifera (stepwise regression, $R^2 = 0.999$, $F_{2,6} = 1789.4$, $P < 0.001$, Fig. 4).

Seasonal density of zooplankton rapidly increased to a peak density (1627 ind./L) in late July, then it declined (Fig. 4). The temporal variation of protozoans, rotifers and copepods were all similar to total zooplankton except for different peak times in June, July and August, respectively. Cladoceran density remained relatively stable through the growing period (Fig. 4). Variation of monthly density was significant for total zooplankton ($F_{6,35} = 3.919$, $P = 0.004$), rotifers ($F_{6,35} = 2.583$, $P = 0.035$) and copepods ($F_{6,35} = 4.218$, $P = 0.003$), while not significant for the other two subgroups ($P > 0.05$). Multiple comparisons revealed that the significant variations all existed between the peak month and the other months (Fig. 4).

3.1.5. Biomass and biomass size spectrum (BSS)

Zooplankton biomass was lower than 0.60 mg/L through the entire seven-month survey period with a monthly average of 0.25 ± 0.21 mg/L. After peaking in summer, biomass for all taxa declined through autumn until early winter, when biomass increased slightly for all taxa except for Rotifera (Fig. 5). Non-significant variation ($P > 0.05$) was tested among the sampling months for total zooplanktons and the subgroups, except for Copepoda ($F_{6,35} = 3.643$, $P = 0.006$).

Lower biomass was observed for Protozoa (0.010 ± 0.009 mg/L) and Rotifera (0.067 ± 0.072 mg/L) than for the large forms of Cladocera (0.073 ± 0.077 mg/L) and Copepoda (0.104 ± 0.136 mg/L) in the sampling period (Fig. 5).

Seasonal biomass variation of different taxa of planktons was best illustrated among different size groups. Based on the equivalent spherical diameter (ESD), planktons were divided into seven size groups, that is, 2^3 – 2^9 μm , respectively (Fig. 6). The different size groups showed

Table 1

Monthly succession of dominant species ($Y \geq 0.02$), with equivalent spherical diameter (ESD) illustrated. ESD – equivalent spherical diameter used in biomass size spectrum analysis.

Dominant species	Dominance index (Y)								ESD μm
	May	Jun	Jul	Aug	Sep	Oct	Nov	Year	
<i>Tintinnopsis wangi</i>	0.099	0.387	0.163	0.081	0.068	0.127	0.273	0.262	45
<i>Hemiphrys procera</i>	0.076					0.075	0.041	0.020	45
<i>Diffugia urceolata</i>			0.038	0.107	0.204			0.038	46
<i>Vorticella microstoma</i>	0.040				0.034		0.173	0.029	50
<i>Strombidium viride</i>	0.024						0.092		36
<i>Trachelius ovum</i>	0.028								35
<i>Keratella cochlearis</i>	0.191		0.076	0.420	0.329	0.186	0.183	0.159	68
<i>Polyarthra trigla</i>		0.347	0.330	0.136	0.212	0.215	0.029	0.356	78
<i>Trichocerca lophoessa</i>		0.069	0.099	0.023				0.053	52
<i>Trichocerca cylindrica</i>			0.072						43
<i>Bosmina longirostris</i>	0.027				0.051				164
<i>Tropocyclops jerseyensis</i>				0.026					286

Note: Bold characters indicate the top two dominant species in each month.

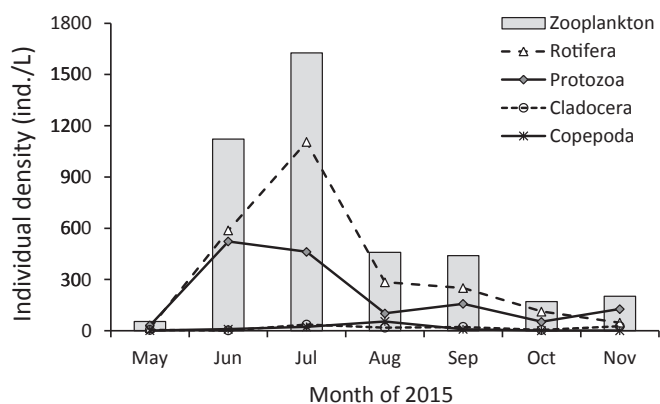


Fig. 4. Seasonal dynamics of monthly mean density of zooplankton and its subgroups.

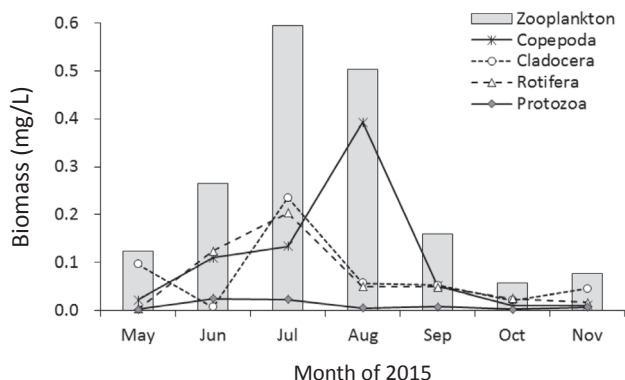


Fig. 5. Seasonal dynamics of monthly mean biomass of zooplankton and its subgroups.

different stability through the sampling months. Small sized guilds (2^3 – $2^4 \mu\text{m}$) were more consistent with a low CV (coefficient of variance) of 9.4%–18.2%, large sized guilds (2^8 – $2^9 \mu\text{m}$) showed higher fluctuation (CV = 34.1%–51.8%), and the middle large sized guilds (2^5 – $2^7 \mu\text{m}$) fluctuated the most (CV = 124.5%–204.2%, Fig. 6). An important observation was the time of the decrease of seasonal biomass dynamics curves. The smaller size planktons began declining later in the season, while the larger planktons declined earlier. This suggested a greater sensitivity of larger sized planktons to carp feeding pressure than smaller planktons (Fig. 6).

Normalized zooplankton biomass also negatively related to body

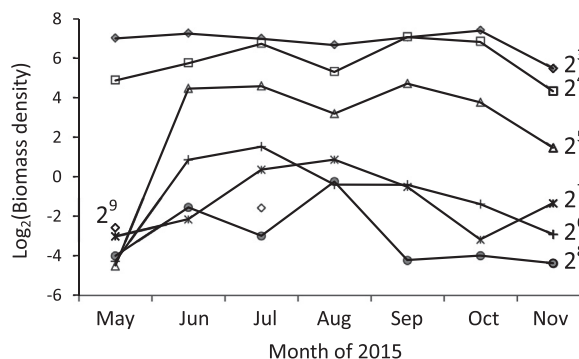


Fig. 6. Monthly variation of biomass densities of each ESD groups of planktons. ESD is equivalent spherical diameter (μm) of plankton species. Biomass density or normalized biomass is calculated by dividing the sum biomass of one ESD group with its correspondence ESD amplitude.

size, providing a good fit to the linear BSS model (Fig. 7). Slopes and intercepts of the regression lines were all statistically significant ($P < 0.01$) with high determination coefficient ($R^2 > 0.855$) in every month. The regression intercepts were higher in summer months (7.72–10.80) than in May (5.51) and November (7.52). This indicated higher production in summer than in the other seasons. All slopes of the regression lines were lower than -1.0 , (-2.6342 to -1.4722), indicating that the community deviated from equilibrium state with less common, large-sized zooplanktons. High production and low populations of large-sized planktons implied higher feeding stress and the removal of the large sized planktons in Miyun Reservoir. The monthly biomass variation of the middle and large sized planktons (32 – $256 \mu\text{m}$ ESD) was greatest, indicating their more sensitive response to carp feeding pressure compared to the other size groups.

3.2. Relationships among zooplankton subgroups

Regression on the relationships of the diversity index (H') and biomass (B) between and among subgroups revealed a negative relationship with H' , and positive relationships with B (Table 2). Rotifera (H_{rot}) diversity contributed negatively to Protozoa (H_{pro}) and related negatively to Protozoa (H_{pro}) and Cladocera (H_{cla}). Rotifera (B_{rot}) biomass contributed positively to the biomass of Protozoa (B_{pro}) and Copepoda (B_{cop}), respectively, and was negatively related to the diversity of Protozoa (H_{pro}) and Copepoda (H_{cop} , Table 2). Cladocera and Copepoda showed no significant relationships with any other group in either biomass or diversity (Table 2).

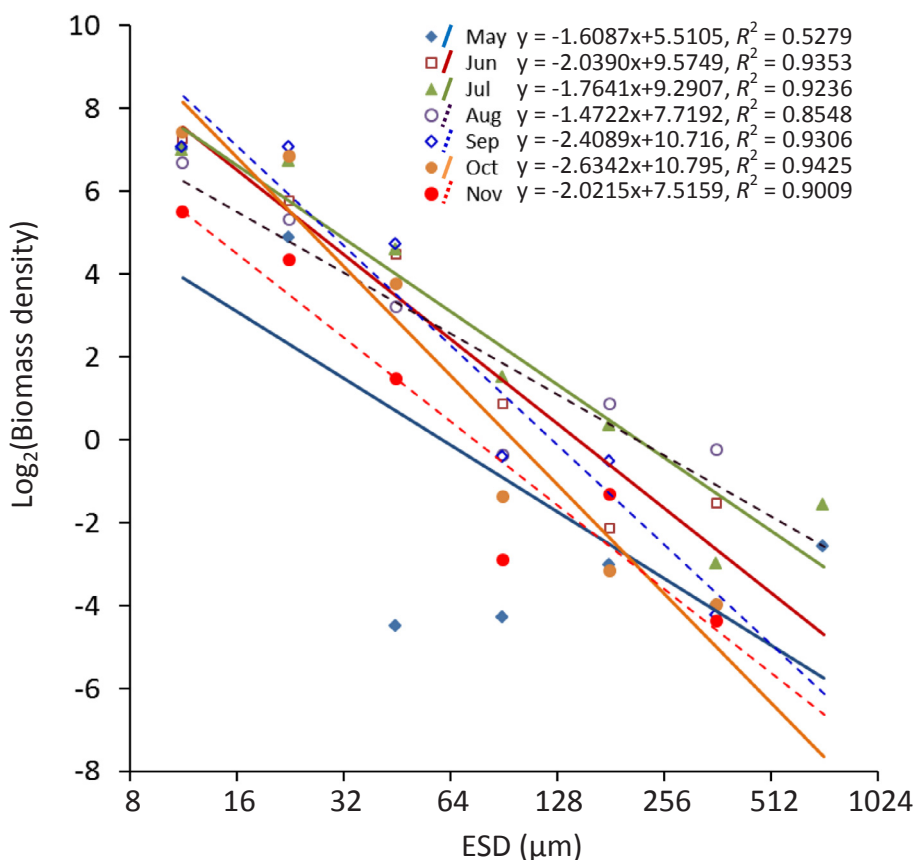


Fig. 7. Biomass size spectra (BSS) of planktons in the Miyun Reservoir. Biomass of each size group was normalized by dividing with ESD amplitude of the corresponding size group and then logarithm transformed before model simulation and mapping.

Table 2

Stepwise regression results of the biomass and diversity index of the four subgroups, illustrating interaction between the subgroups.

Response variable	Explanatory variable	Coef.	S.E.	t-value	Sig.
H_{pro}	H_{rot}	-0.597	0.157	-3.817	< 0.001
B_{pro}	B_{rot}	0.776	0.140	5.551	< 0.001
	H_{rot}	-1.483	0.152	-4.210	< 0.001
H_{rot}	H_{pro}	-0.470	0.101	-4.647	< 0.001
	H_{cla}	-1.178	0.363	-3.245	0.002
	B_{cla}	0.160	0.040	3.942	< 0.001
B_{rot}	B_{pro}	0.425	0.136	3.122	0.003
	B_{cop}	0.448	0.117	3.829	< 0.001
	H_{pro}	-0.942	0.271	-4.032	< 0.001
	H_{cop}	-2.514	0.960	-2.617	0.013
H_{cla}	-	-	-	-	-
B_{cla}	-	-	-	-	-
H_{cop}	-	-	-	-	-
B_{cop}	B_{rot}	0.678	0.201	3.370	0.002

3.3. Relationships of zooplankton diversity and biomass with environmental factors

The monthly distributions of environmental factors were documented in Table S1. Water temperature was 22.8 °C in May, 27.2 °C in late July, decreasing to 5.6 °C in late November. Water transparency, permanganate index, and dissolved oxygen were negatively related to water temperature. Overall, there were lower values in hot summer and higher values in the cooler spring and autumn. The chlorophyll *a* concentration and pH fluctuated without significant tendency through the monitoring period (Table S1).

Regression analysis showed no significant relationships between

Table 3

Stepwise regression on the diversity index (H') and biomass (B) of zooplankton and its subgroups to environmental variables. WT – water temperature, DS – water transparency, COD_{Mn} – permanganate index for chemical oxygen demand, Chla – Chlorophyll *a* and DO – dissolved oxygen. Coefficients and significances were illustrated.

Response variable	Explanatory variable					
	DO	SD	pH	Chla	WT	COD_{Mn}
H_{zoo}	-	-	-	-	-	-
B_{zoo}	-	-	-	-	-	-
H_{pro}	-	-	-	-	-0.018*	-
B_{pro}	-	-0.433**	0.884**	-	-	0.114*
H_{rot}	-	-	-	-	0.013*	-
B_{rot}	-	-0.374*	1.143**	-	-	-
H_{cla}	-	0.114**	-	-	-0.007**	-
B_{cla}	-	-	-	-0.131*	-	-
H_{cop}	-	-	-	-	0.006*	-
B_{cop}	-	-	-	-	0.070**	-

* Significant ($P < 0.05$).

** Highly significant ($P < 0.01$).

diversity and biomass of the total zooplankton and any explanatory variable. Similarly, dissolved oxygen did not have a significant effect on any zooplankton taxa (Table 3).

Among the four subgroups, small forms of Protozoa and Rotifera showed more dependence on the water conditions, while large forms of Cladocera and Copepoda appeared more independent. Water transparency favored Cladocera diversity but inhibited the biomass of Protozoa and Rotifera. Chlorophyll *a* concentration contributed negatively to Cladocera's biomass. Water temperature improved the biomass

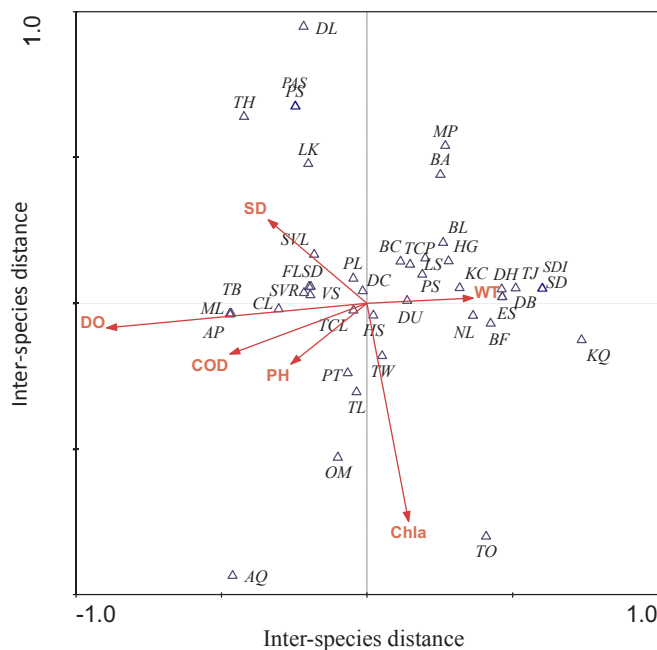


Fig. 8. CCA ordination of the biomass of zooplankton species in Miyun Reservoir. Species and environmental variables are illustrated as triangles and vectors, respectively. Refer to Tables 3 and S2 for abbreviations to environmental variables and zooplankton species.

of Copepoda and diversity of Copepoda and Rotifera, but depressed the diversity of Protozoa and Cladocera. The COD_{Mn} only showed a significant relationship to the biomass of Protozoa.

CCA ordination provided an intuitive illustration of the relationships of the 41 species (Table S2). These were sorted on the basis of $P_i > 0.01$ in at least one sample, with environmental variables (Fig. 8). Four axes, drawn from CCA, accounted for 92.8% of biomass variance among the 41 species. Inter-species distance and environmental gradient was best explained by the first two axes. Correlation between the species and the first two axes was greater than 0.80 (Table S3), and vectors of the six factors collectively explained 69.9% of the biomass variation (Fig. 8).

Most zooplankton species, except for *Trachelius ovum*, *Alona quad-rangularis* and *Onychocampus mohammed*, showed weak relationships with Chla, although many rotifers and protozoans projected positively to WT or DO along the first axis. The dominant species in Table 1, except for *T. ovum*, were all located near the crossing point of the two first axes, and showed no obvious orientation to any environmental vector. This distribution pattern implied that the community was occupied by eurytopic species with low dependence on environmental indicators (Fig. 8).

3.4. Relationships of zooplankton biomass with carp stocks

Historical changes of the stocking level of filter-feeding carp and zooplankton biomass showed significantly negative ($R^2 = 0.803$, $F_{1,4} = 12.191$, $P = 0.040$) change tendency (Fig. 9). Before 1980, juvenile carp release was less than $0.216 \pm 0.040 \text{ g/m}^3$. During this period zooplankton biomass remained at 1.0 mg/L (Fig. 9). After 1980, the level of carp release eventually declined to $0.041 \pm 0.013 \text{ g/m}^3$ in 2002, and zooplankton biomass increased to 3.0 mg/L . After 2004, carp release levels increased gradually to $0.540 \pm 0.145 \text{ g/m}^3$ in 2015 and zooplankton biomass has decreased consequently from 3.0 in 2002 to 0.25 mg/L (Fig. 9).

The subgroups of Copepoda, Cladocera, Rotifera and Protozoa all showed negative relationships between their biomass and the variation of carp releases, with regression coefficients of -2.4949 , -1.0793 ,

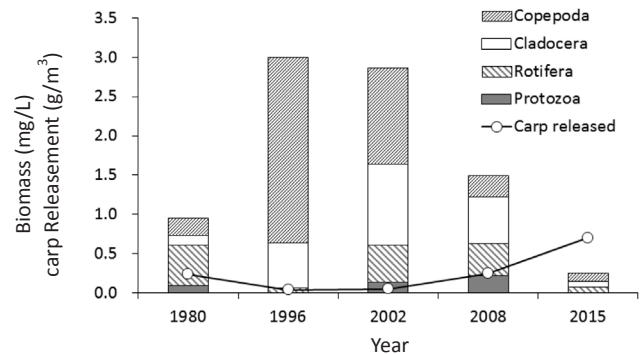


Fig. 9. Historical changes in the biomass of zooplankton and the subgroups related to carp release. Historical data referred to Qiu (1981), Zhao et al. (2001), Liu et al. (2004) and Li et al. (2007).

-0.3261 and -0.0914 , respectively (Fig. 9). The large forms of Copepoda and Cladocera had higher sensitivity to feeding stress variation and showed higher regression coefficients than the smaller forms of Rotifera and Protozoa.

4. Discussion

Community and main zooplankton taxa have typically been studied in relation to environmental changes and the carrying capacity of the associated fishery (Andronikova, 1996; Gophen et al., 1990; Xie, 2003). The different responses of zooplankton functional groups, in different body sizes, to fish-feeding pressure were largely neglected in previous reports, and this additional information was needed to determine the impacts of fishery culture on zooplankton community construction and its ecological significance.

The state, seasonal variation and dynamics of the zooplankton community examined in this study indicated that strong selective pressure has been applied to the zooplanktons in the Miyun Reservoir. Except for species richness, which was similar in historical records, the quantitative traits, such as individual density, biomass and the diversity index, of zooplankton and subgroups have all declined dramatically compared to historical conditions. This has resulted in a more simplified community in 2015 (Liu et al., 2004; Qiu, 1981; Zhao et al., 2001). The yearly mean density (582 ind./L) and biomass (0.25 mg/L) in this study were only 17.3% and 13.7% of these values in 2002 (Li et al., 2007). Compared to other water bodies, the species richness, individual density and biomass in the Miyun Reservoir in 2015 were only 57.4%–75.0%, 13.4%–32.0% and 4.7%–39.7%, respectively, of the values in natural lakes and reservoirs in eastern China (He, 2000; Xie et al., 2005; Yang et al., 2014; Yu et al., 2016) and lower than values in lakes and reservoirs in the temperate zone of other continents (Radke and Kald, 2002; Xie, 2003).

Theoretically, low richness and abundance of zooplankton is a reflection of great selective pressure on the community (Northcote, 1988). Selection pressure might come from bottom-up resource limitation or top-down fish-feeding stress or both (Brooks and Dodson, 1965; Major et al., 2017; Radke and Kald, 2002). However, we found that the weak relationships of the diversity and biomass of total zooplankton and the subgroups with environmental variables in either regression or CCA results failed to explain the unusual community traits presented above. On the contrary, fishery stocks of filter-feeding carp, represented by yearly carp releases, made significant contributions to the dynamics of zooplankton biomass. Therefore, feeding pressure, while not resource limitation, has likely contributed to the simplified community structure of zooplankton in the Miyun Reservoir (Brooks and Dodson, 1965; Hall et al., 1976; Xie et al., 2005).

The seasonal dynamics of the quantitative features of zooplankton community, including diversity and abundance, illustrate the influences

of the seasonally changing feeding pressure of the released carp on the zooplankton community. Large intercepts of the regression lines in BSS, high values of water temperature and Chl-a in summer months support a high level of primary production in July and August of 2015. These factors should have had positive effects on the energy cascade and increased zooplankton populations. However, we found that the increasing curves of species diversity, density and biomass in the Miyun Reservoir began to decline in the highly productive months of July or August rather than continuing growth through summer to autumn as predicted by the bottom-up hypothesis and which has been seen in other temperate waters (Qiu et al., 2012; Yan and Shi, 1995; Yang et al., 2014; Yu et al., 2016). This unusual change in the dynamics of zooplankton coincided with the growth and feeding rhythm of the cultured carp in Miyun Reservoir, as well as in other temperate zone lakes and reservoirs (Green and Smitherman, 1984; Jia et al., 2015; Nuevo et al., 2004). In temperate waters with ice coverage during winter months, silver and bighead carp begin feeding in late May and stop feeding in middle October (Nuevo et al. 2004; Yan and Shi, 1995; Yan et al., 2007). Accordingly, the growth season for the stocked carp is limited to late May to mid-October in the climate zone where the Miyun Reservoir is located (Jia et al., 2015; Wu et al., 2017). This increase and decrease of filter-feeding stress on the zooplanktons in the Miyun Reservoir can be interpreted in relation to the unusual dynamics of zooplankton features. The temporary rebound in quantitative traits of zooplankton in the colder water of late November occurred immediately after relief from the feeding stress of the filter-feeding carp. This observation supports our feeding stress hypothesis.

Selective predation of fish has been recognized as a major force in shifting competitive relationships among zooplankton species (Cremer and Smitherman, 1980; Maccann, 2011; Stott and Buckley, 1978). Filter-feeding fish feed on large-sized zooplanktons and also compete with them for smaller sized zooplanktons (Brooks and Dodson, 1965; Hrbacek et al., 1961; Northcote, 1988). At low fishery population levels, small body size zooplanktons had low populations under the high feeding stress from both planktonic crustaceans and fish (Cremer and Smitherman, 1980; Lu et al., 2002; Radke and Kald, 2002). When fish population levels increased, however, large crustacean populations decreased as a result of competitive restrictions and feeding depletion from the cultured fish (Bernardi et al., 1987; Edmondson and Litt, 1983; Northcote, 1988). In the Miyun Reservoir, the absolute quantitative dominance of small sized species and the low slopes (less than -1.0) of biomass size spectra in Fig. 7 suggested the strong influence of carp on zooplankton composition. The very low density of large crustacean species illustrated the negative impacts of selective feeding stress and competitive exclusion caused by the carp. However, the relatively higher densities of the small forms of Protozoa and Rotifera must have benefited from the depleted populations of the large planktonic crustaceans (Green and Smitherman, 1984; Jia et al., 2015; Ke et al., 2008; Nuevo et al., 2004).

The abundance fluctuations of zooplankton, particularly the large taxa, may affect energy flow efficiency and algae control (Brooks and Dodson, 1965; Ives and Carpenter, 2007; Radke and Kald, 2002). Larger sized zooplanktons feed on small particles including small sized zooplankters, phytoplankton and other organic particles (Bernardi et al., 1987; Radke and Kald, 2002; Zhang and He, 1991), but their abundance and feeding influence is affected by the populations of filter-feeding carp (Ke et al., 2008). Although zooplankters share some small sized organisms that carp consume, their food spectra covers much smaller sized particles including phytoplankton in less than $10\ \mu\text{m}$ width that carp do not eat (Green and Smitherman, 1984; Hrbacek et al., 1961; Xie, 2003). Therefore, reduced numbers of large zooplankters in an intensively enhanced fishery will likely result in the ecological release of small sized planktons, disequilibrium of the aquatic community and high risk of small-sized algae blooms (Radke and Kald, 2002). The significant relationships between Rotifera density and biomass and Protozoa and Copepoda demonstrated that there is a direct predator-

prey relationship between the large and small sized zooplankters in the Miyun Reservoir (Ke et al., 2008; Lu et al., 2002). This energy cascade within the zooplankton community complicates the trophic relationships and will require additional study to reveal the functional response of zooplankton in different size groups to varied fish-feeding pressure.

Using the body size composition of zooplankton as an indicator of fish culture intensity, carp in the Miyun Reservoir appear to be overstocked. Some reports claim that carp releases of $20\text{--}40\ \text{mg/L}$ are effective in manipulating blue algae and maintaining the stability of plankton assemblages in temperate lakes (Xie, 2003; Xie et al., 2005; Yan and Shi, 1995; Yu et al., 2016) but this suggestion is controversial (Jia et al., 2015; Ke et al., 2008; Nuevo et al., 2004; Qiu et al., 2012; Yang et al., 2014). Our results suggest that the optimal fishery strength must be adaptable to different waters in different climate zones. The fishery strength must be lower in deep boreal reservoirs like the Miyun (Andronikova, 1996). In practice, there may not be a single optimum standard for carp culture intensity.

When applying bio-manipulation using filter-feeding carp, the zooplankton composition and abundance can produce unexpected results (Radke and Kald, 2002; Yu et al., 2016; Zhao et al., 2016). In our scenario, Miyun Reservoir was initially in a mild eutrophication state produced by the zooplankton during our monitoring period). However, several studies have suggested a mesotrophic level of water quality (Li et al., 2015; Wu et al., 2017; Zeng et al., 2016). The bio-indicator approach using zooplankton traits under fish-feeding pressure overestimated the pollution severity or trophic level and indicated that the carp enhancement had impacted the precise assessment of community equilibrium, ecological processes and ecosystem health (Carpenter et al., 2006; Radke and Kald, 2002; Yu et al., 2016). In future studies, scientific strategies must be used for improving the reliability and feasibility of environmental assessment with zooplankton traits by eliminating the impacts of fish feeding.

5. Conclusions

A simplified zooplankton community and a body size diminution of species composition were observed in the Miyun Reservoir. Low richness, diversity, density and zooplankton biomass indicated that the community suffered intensive stress. Unusual dynamics of diversity and abundance occurred. Productivity began to decline in the productive summer months of July and August but temporarily rebounded in late November. These changes coincided with the feeding rhythms of the filter-feeding silver and bighead carps but related only weakly to environmental factors. The significant relationships seen between the historical variation of the biomass of total zooplankton and subgroups with carp release dynamics proved that feeding stress, rather than resource limitation, primarily shaped the zooplankton community structure. When applying bio-manipulation with filter-feeding carp, it is essential to manage the optimal release rate for a specific water body to avoid the deleterious effects, resulting from the overstocked fishes, on zooplankton populations, especially on the large-body-sized crustaceans. To fully understand the ecological effects of fish culture on the structure and energy cascade of the aquatic community, phytoplankton and its relationships with zooplankton and fishes must all be considered.

Declarations of interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2019.01.058>.

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