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Research Article

Seasonal dynamics of Zooplankton functional groups in relation to environmental variables in Xiquanyan Reservoir, Northeast China

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Abstract – In this study, the concept of functional feeding groups was used to classify and model the seasonal variation of zooplankton functional groups in relation to environmental variables. A total of 48 zooplankton species were observed in the reservoir and grouped into 8 functional groups. Both environmental variable and the biomass of zooplankton functional groups vary spatially and seasonally. Water temperature, water transparency, total nitrogen and nitrates were significantly higher in summer, while chlorophyll-*a* and ammonium were higher in autumn and spring, respectively. Biomass of zooplankton was significantly higher in summer (245.81 μg/L), followed by autumn (196.54 μg/L) and spring (54.25 μg/L). Group RF (rotifer filter feeders) dominated in spring, accounting for 80% of the total biomass. In summer and autumn, group RC (rotifer carnivore) and SCF (small copepods and cladocerans filter feeders) were the dominant, respectively. Total nitrogen, total phosphorus, ammonium, chlorophyll-*a* and water transparency were the major factor influencing zooplankton community. Group RF was positively influenced by ammonium and total phosphorus, while RC, SCF and MCF (middle copepods and cladocerans filter feeders) were positively correlated with chlorophyll-*a*. Top-down control of phytoplankton by groups RC, SCF and MCF in Xiquanyan reservoir is not strong enough to produce negative effect. Increase in predator size biomass did not strengthen top-down control on prey. It is quite clear that the zooplankton function groups of Xiquanyan reservoir followed a predictable seasonal pattern. This therefore highlights the significance of environmental variables in structuring plankton composition in the reservoir.

Keywords: zooplankton / functional groups / biomass / seasonal / spatial / environmental variables

1 Introduction

Water is an important resource in any scene that involves life. As a result of socio-economic and population growth, the global water demand has been rising steadily and is projected to continue to increase in the near future. In order to meet the increasing demand of water, human beings have been intervening in the natural water cycles to make more water available. For instance, dams and reservoirs have been constructed to supply water for irrigation and other anthropogenic users. Construction of reservoirs along rivers for water supplies has altered the natural flow pattern, linkages with floodplain lead to the discontinuity of river physical structures which may cause the reduction of ecological diversity of river communities such as zooplankton (Martinet *et al.*, 2014; Shen *et al.*, 2014).

Zooplanktons are among the top most important organisms in aquatic systems. They have been documented to actively transport particles to deeper part of aquatic systems through vertical migration (Jónasdóttir *et al.*, 2015). By feeding on particle aggregates, zooplanktons play a major role in breaking down organic matter, and thus are involved in nutrients' cycling (Schneider-Olt and Adrian, 2001; Turner, 2015). Additionally, as grazers in reservoirs and lakes, zooplanktons may influence phytoplankton dynamics and hence the relationship between nutrients and chlorophyll (Tessier *et al.*, 2001). Changes in zooplankton diversity and abundance have been used as indicator for human and climate variability effect on the functioning of the ecosystem (Auer *et al.*, 2004; Benedetti *et al.*, 2018). Recently, the use of functional traits to model variation in zooplankton biomass in aquatic systems has gained much attention (Araújo *et al.*, 2006; Kishi *et al.*, 2007;

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Benedetti *et al.*, 2015). Functional traits are the behavioral, morphological or phonological characteristics of organisms that impact their ecological role and fitness in their niches (Araújo *et al.*, 2006; Benedetti *et al.*, 2015). Initially, the functional traits approach of classifying zooplankton relied on limited number of size classes only, which poorly captured the dynamics of zooplankton community (Quere *et al.*, 2005; Litchman *et al.*, 2013). Several trait-based approaches such as the use of morphological traits (body size/length) and life-history traits (mode of feeding) have been proposed and used to classify and asses zooplankton dynamics in marine, lakes and large river ecosystems (Araújo *et al.*, 2006; Sun *et al.*, 2010). However, the functional trait approach remains to be used in classifying and assessing the variations of zooplankton community in relation to environmental variables in reservoirs such as Xiquanyan.

Xiquanyan Reservoir was built in 1992 with the main objective of supplying drinking water to the millions of people living in Harbin city and Heilongjiang province. The main sources of water to the reservoir are Ashihe river, Huangni river and Erdao river. While assessing the phytoplankton community structure and trophic status of Xiquanyan reservoir, Ma and Yu (2013) revealed that the reservoir is mesotrophic and the phytoplankton community varies seasonally as a result of changes in environmental factors, mainly nutrients. This seems to be the only existing published study on Xiquanyan reservoir despite its importance. In this study, the concept of functional feeding groups was used to model the seasonal variation of zooplankton functional groups in relation to environmental variables in Xiquanyan reservoir. Understanding the variation of the biomass of zooplankton functional groups in relation to environmental variables is very important to (1) develop more realistic models and (2) better understand the environmental variables that significantly structure the zooplankton community in the reservoir. This will form an important source of information to be used in implementing correct management practices in order to maintain water quality of the reservoir in a perspective of multiple-use approach. This study aims (1) at identifying and classifying zooplankton species of Xiquanyan reservoir into functional group and (2) to determine the seasonal and spatial dynamics of the biomass of zooplankton functional groups and their relationship to environmental variables. We hypothesized that seasonal and spatial change in biomass of zooplankton functional groups will be strongly influenced by environmental variables.

2 Methods

2.1 Study area

Xiquanyan Reservoir (127°16′−127°22′ E, 45°11′−45°15′ N) is situated at about 84 km southeast of Acheng District in Harbin of Heilongjiang province Northeastern China (Fig. 1). The region is under the influence of continental monsoon with a mean annual temperature and rainfall of about 3.9 °C and 540 mm, respectively. During winter season, the entire surface of the reservoir is covered by ice. The reservoir was constructed in 1992 and is used, among many other purposes, to supply water to the Harbin city, which has about 10 million inhabitants. Xiquanyan Reservoir has a surface area of 40.86 km^2, a capacity of 4.7×10^8 m^3 and an average depth of 11.6 m. The reservoir is classified as mesotrophic (Ma and Yu, 2013) and it receives water from Ashihe river, Huangni river and Erdao river with about 68% of the flow occurring from June to September.

2.2 Field sampling and analysis

2.2.1 Sample collection

Based on the shape of the reservoir, sampling sites were selected taking into consideration the maximum representation of the reservoir. Samples were collected (0.5 m from the surface water) on monthly basis (April, May, July, August, September and October) from 9 georeferenced sites (S1–S9) inside the Xiquanyan Reservoir (Fig. 1). April and May were clustered for spring, July and August for summer and September and October for autumn. Sites S1–S4 were located near the discharge point of the rivers into the reservoir (upstream of the reservoir), sites S5– S8 were located at the middle of the reservoir and site S9 was located near the outflow of the reservoir (downstream of the reservoir). At every sampling site, water temperature, pH, conductivity and dissolved oxygen was measured in the field using a portable multiprobe (YSI 6600, YSI Inc., USA). Water transparency and turbidity were measured using Secchi disk and turbidimeter, respectively.

Triplicates unfiltered water samples for measurements of nutrients, chlorophyll-*a* and zooplankton were collected at 0.5 m from the surface using a calibrated van Dorn sampler. Water samples for nutrients analysis were put on acid-washed plastic bottles, placed in ice box and transported to laboratory for analysis. The nutrients analysis (total nitrogen, ammonium, nitrate, and total phosphorus and chemical oxygen demand) was done according to the environmental quality standards for surface water of China (MEP, Ministry of Environmental Protection, 2002). Biomass of phytoplankton in terms of chlorophyll-*a* concentration was determined according to the protocols for standard observation and measurement in aquatic ecosystems by filtering 100 mL of water through a GF/C whatman filter and the filters were put in a dark cooler and placed in ice box until analysis (Cai *et al.*, 2007; Shen *et al.*, 2014). Pigments extraction was done in 90% aqueous solution of acetone, and chlorophyll-*a* concentrations were measured spectrometrically.

Zooplankton samples (10 L of water filtered through 64 mm mesh size) were fixed using formaldehyde solution (4% final concentration). The concentrated samples were allowed to sediment in a 1-L jar for at least 24 h. Supernatant water was carefully decanted and the residual collected and made to a known volume 50 mL as described in literature (Huang, 1981; Thompson *et al.*, 2013). Triplicates subsamples of 10 mL aliquot of the condensed sample were counted when zooplankton abundance was very high; otherwise, the whole condensed sample was analyzed. Identification of the zooplankton species was done using an inverted microscope at 400× magnification following the species keys (Chen, 1974; Haney *et al.*, 2013; Kotov *et al.*, 2013). The biomass of the zooplankton functional groups was computed by dividing dry weight (mg) obtained from length–weight relation of the species to the volume of water (L) filtered (McCauley, 1984; Sun *et al.*, 2010).

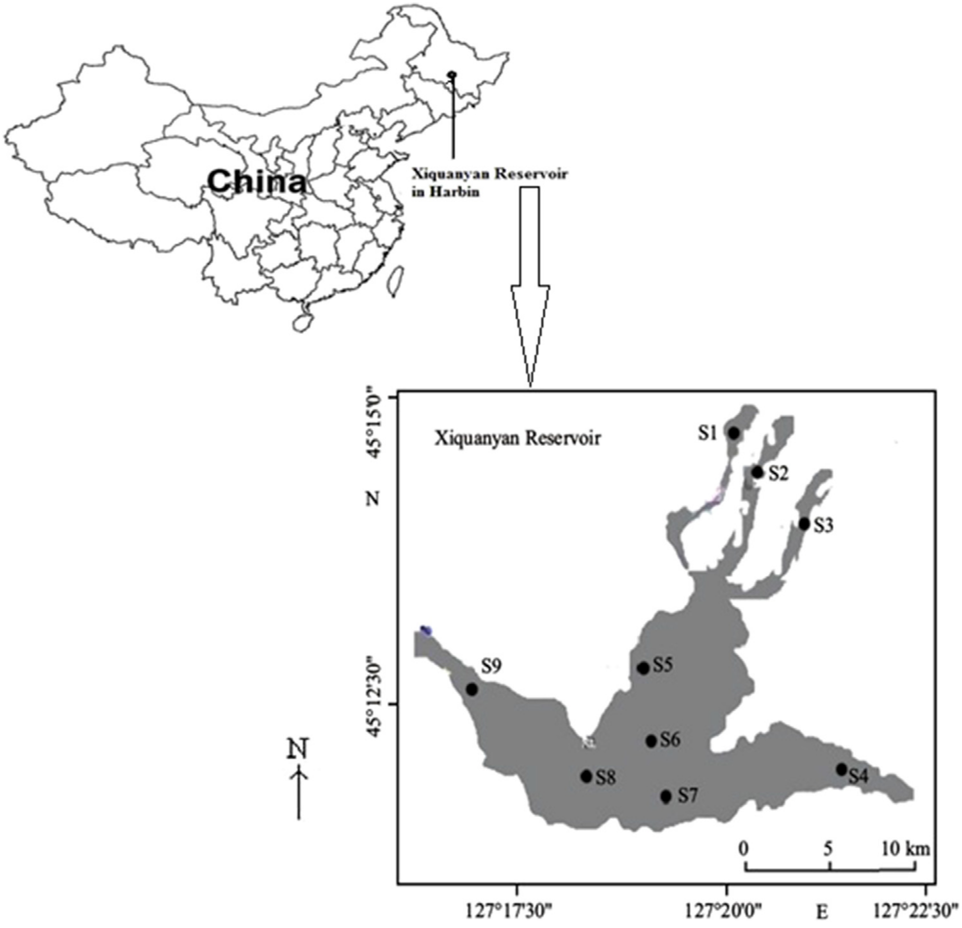

Fig. 1. Map of China with insert of Xiquanyan Reservoir in the Northeast China showing the distribution of sampling sites (S1–S9).

2.2.2 Classification of zooplankton functional group

The sampled zooplankton species in Xiquanyan Reservoir were classified into eight functional groups based on their body size/length and mode of feeding (Benedetti *et al.*, 2018; Ma *et al.*, accepted for publication). The eight functional groups are protozoa filter feeders (PF), protozoa carnivore (PC), rotifer filter feeders (RF), rotifer carnivore (RC), small copepods and cladocerans filter feeders (SCF), middle copepods and cladocerans filter feeders (MCF), middle copepods and cladocerans carnivore (MCC) and large copepods and cladocerans carnivore (LCC). PF and RF are passive filter feeders feeding on organic detritus, bacteria and algae. RC and PC are ambush feeders that target small motile prey (other zooplanktons). RC group was mainly dominated by *Asplanchna priodonta* and *Asplanchna girodi* (Tab. 2). Functional group SCF included those species with body size <0.7 mm that mostly feed through filter-feeding on bacteria, algae, organic detritus and protozoa. This group was mainly represented by *Bosmina coregoni* and *Microcyclops javanus.* Group MCF included those zooplankton individuals with body length in the range of 0.7–1.5 mm. Just like SCF, MCF is a filter-feeder feeding on bacteria, algae, organic detritus and protozoa. Ecologically, MCF plays a major role as a food source for fish and also can control algal blooms. Species in MCF group included *Microcyclops inchoatus, Paracyclops affims, Paracyclops fimbrtatus, Diaphanosoma leuchtenbergianum* and *Alona Baird* sp. MCC consists of middle copepods and cladocerans of body size in the range of 0.7–1.5 mm that mainly feed through ambush tactics. This group mainly feeds on rotifer, oligochaeta, chironomidae larvae and other cladoceran, thereby competing with fish for food resources in the aquatic systems. Group MCC was represented by only four species: M*acrocyclops albidus, Thermocyclops dybowskii, Thermocyclops vermifer* and *Acanthocyclops vernalis*. Functional group LCC constitutes carnivore copepods and cladocerans of body length greater than 1.5 mm and was composed by *Leptodora kindti* and *Cyclops furcifer*. LCC group feeds on other zooplankton and it forms an important food source for fish (Meerhoff *et al.*, 2007).

2.3 Data analysis

Before analysis, all the environmental variables and biomass of zooplankton functional groups were tested for normality using Kolmogorov–Smirnov test and homogeneity of the data was tested using Bartlett test. Environmental variables and biomass of zooplankton functional groups which were found to be skewed were log(x+1) transformed to satisfy

Table 1. Means values ± standard error ($n = 43$) of environmental variables of the Xiquanyan reservoir. Differences between the seasons were tested by Tukey HSD ANOVA. Values with same superscripts in each column are not significantly different.

	Spring	Summer	Autumn	*p*-value
Water temperature (°C)	6.31 ± 0.28^{a}	24.31 ± 0.18^{b}	12.69 ± 0.30^{c}	0.000
pH	7.14 ± 0.07^{a}	9.16 ± 0.11^{b}	7.75 ± 0.10^{c}	0.000
Dissolved oxygen(mg/L)	7.40 ± 0.40^{a}	6.67 ± 0.27^{a}	6.96 ± 0.23^{a}	0.354
Conductivity (mS/m)	0.09 ± 0.00^{a}	0.14 ± 0.01^{b}	$0.12 \pm 0.00^{a,b}$	0.002
Water transparency (m)	0.46 ± 0.09^{a}	$0.84 \pm 0.04^{b,c}$	$0.78 \pm 0.07^{b,c}$	0.000
Turbidity (NTU)	58.42 ± 18.41^{a}	$21.99 \pm 3.89^{b,c}$	$23.83 \pm 1.33^{b,c}$	0.006
Chloride (mg/L)	3.63 ± 0.43^{a}	$7.73 \pm 0.62^{b,c}$	$6.42 \pm 0.62^{b,c}$	0.000
Total nitrogen (mg/L)	0.66 ± 0.02^{a}	$0.91 \pm 0.0\ ^{a}$	0.69 ± 0.02^{a}	0.150
Ammonium (μg/L)	8.78 ± 1.04^{a}	$1.82 \pm 0.24^{b,c}$	$3.00 \pm 0.69^{b,c}$	0.000
Nitrate (mg/L)	0.26 ± 0.04^{a}	$0.55 \pm 0.11^{a,b}$	$0.22 \pm 0.02^{a,c}$	0.014
Total phosphorus (mg/L)	0.11 ± 0.03^{a}	$0.07 \pm 0.01^{a,b}$	$0.13 \pm 0.03^{a,c}$	0.013
Chemical oxygen demand (mg/L)	4.73 ± 0.18^{a}	4.96 ± 0.23^{a}	5.04 ± 0.17^{a}	0.838
Chlorophyll-*a* (μg/L)	3.32 ± 0.53^{a}	$17.54 \pm 2.32^{b,c}$	$19.03 \pm 2.07^{b,c}$	0.000

the normality and variance assumption before conducting analysis. Principal component analysis (PCA) was used to assess the possible relations between environmental variables. PCA is an ordination method used to reduce the dimensionality of multivariate data sets and enable graphical representation of relationship between variables (Sharma *et al.*, 2017). Variance analysis (two-way ANOVA) with sites and seasons as main factors was used to determine the seasonal and spatial variations of environmental variables and the biomass of zooplankton functional groups. A Post Hock Tukey HSD test was applied to identify sources of variation if there were statistically significant difference detected among seasons or sites using ANOVA. A detrended corresponding analysis of the eight zooplankton functional groups indicated that the gradient length of the four axes was 2.17. Therefore, linear ordination method of the redundancy analysis (RDA) was used to test the relationship between environmental variables and the biomass of zooplankton functional groups (Shen *et al.*, 2014; Šmilauer and Lepš, 2014). This was done through a stepwise forward selection procedure based on *p* values from 999 Monte Carlo permutation test. Pearson correlation analysis was done to confirm the significant relationships between environmental variables and the biomass of zooplankton functional groups. Figures were drawn using Microsoft Excel and R software (version 3.4.1) (Team, 2014). Unless otherwise indicated, the results are reported as mean value ± standard error (SE).

3 Results

3.1 Environmental variables

The average seasonal values of environmental variables recorded among the sampling sites within the Xiquanyan reservoir are shown in Table 1. Most of the variables revealed statistically significant variations with respect to seasons (two-way ANOVA and Tukey HSD test); $p < 0.05$. However, dissolved oxygen, total nitrogen and chemical oxygen demand were not statistically significant difference among the seasons. According to Badsi *et al.* (2010), water temperature is one of the essential factors that regulate the growth of zooplankton in aquatic systems. From our results, water temperature depicted a significant seasonal variation ($F_{(2,\ 34)} = 1276.24$, $p < 0.001$) with higher significant mean value recorded in summer (24.31 °C) than in autumn (12.69 °C) and spring (6.31 °C). Spatially, no significant difference was observed for water temperature among the sites. Statistically significant differences among seasons were observed for pH ($p = 0.000$), with the highest value occurring in summer (9.16) and lowest in spring (7.14). Just like pH, the highest values of conductivity and chloride were observed in summer of 0.14 ms/m and 7.73 mg/L, respectively (Tab. 1). Although relatively higher mean dissolved oxygen was recorded in spring, no statistically significant variations were observed among the seasons ($F_{(2,\ 34)} = 1.072$ $p = 0.354$). Significant differences among seasons and sites were observed for both water transparency and turbidity (Tab. 1; Figs. 2b and 2c). Higher water transparency was observed in summer when turbidity was low. Spatially, sites located upstream of the reservoir recorded higher turbidity and low water transparency than those located middle and downstream of the reservoir. In relation to nutrients, the mean total nitrogen measured in summer was higher than for the other seasons; however, no distinct seasonal variations pattern in total nitrogen was observed. Tukey HSD test indicated that ammonium determined in spring, nitrate in summer and total phosphorus in autumn season were significantly higher than in the other seasons. Total phosphorus did not show any significant differences spatial. However, ANOVA revealed a significant difference in total phosphorus among the seasons. Tukey HSD Post hoc test indicated that the mean total phosphorus determined in summer was significantly lower that than in autumn. The overall mean biomass of phytoplankton in terms of chlorophyll-*a* was 15.00 μg/L (Tab. 1), with the highest value (19.03 μg/L) observed during autumn. Tukey HSD test revealed that the mean chlorophyll-*a* in spring was statistically significantly lower (3.32 μg/L) compared to that of autumn (19.03 μg/L) and summer (17.54 μg/L). Based on the chlorophyll-*a* concentrations values, Xiquanyan reservoir

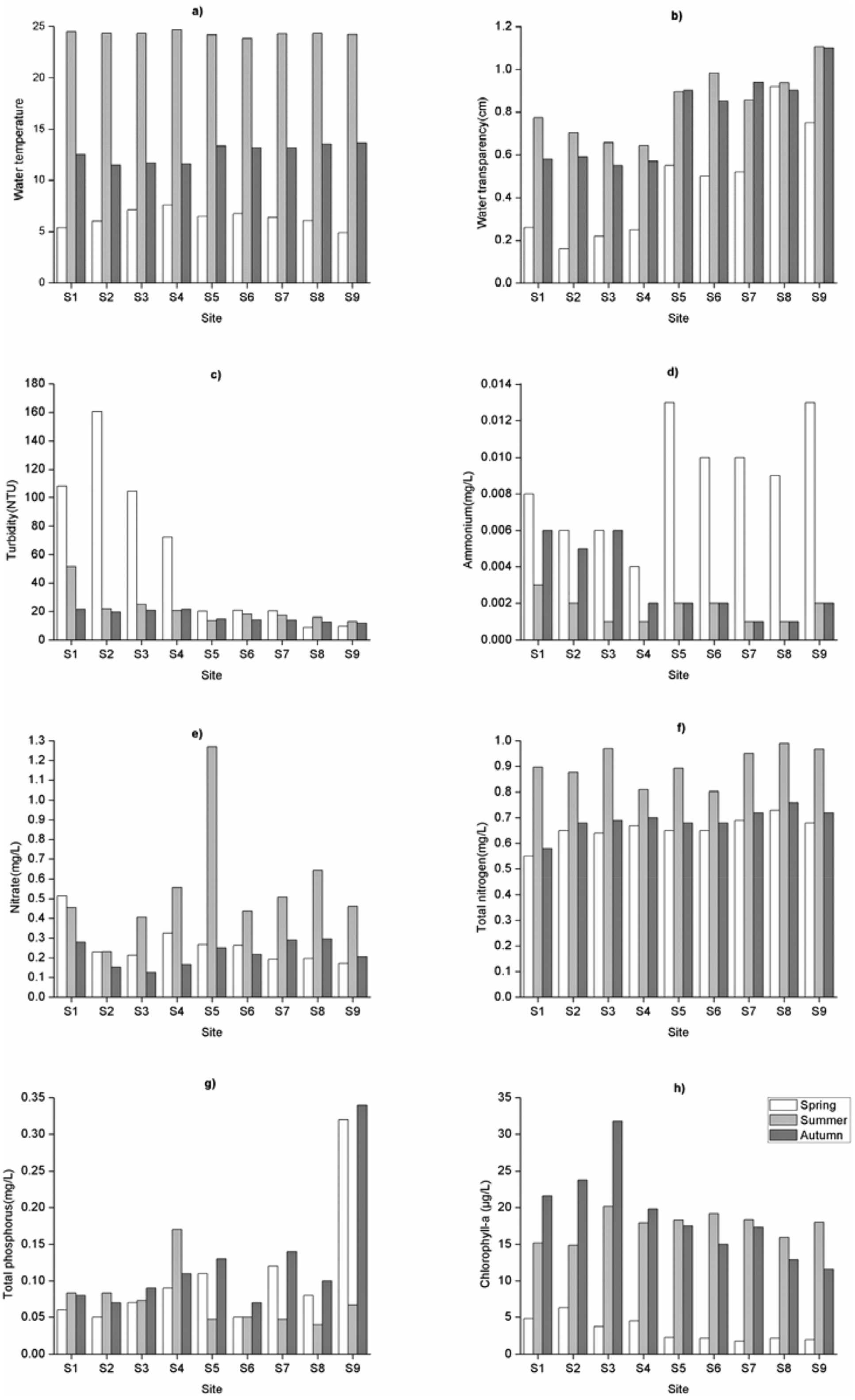

Fig. 2. Spatial variations of selected environmental variables of the Xiquanyan reservoir in different seasons.

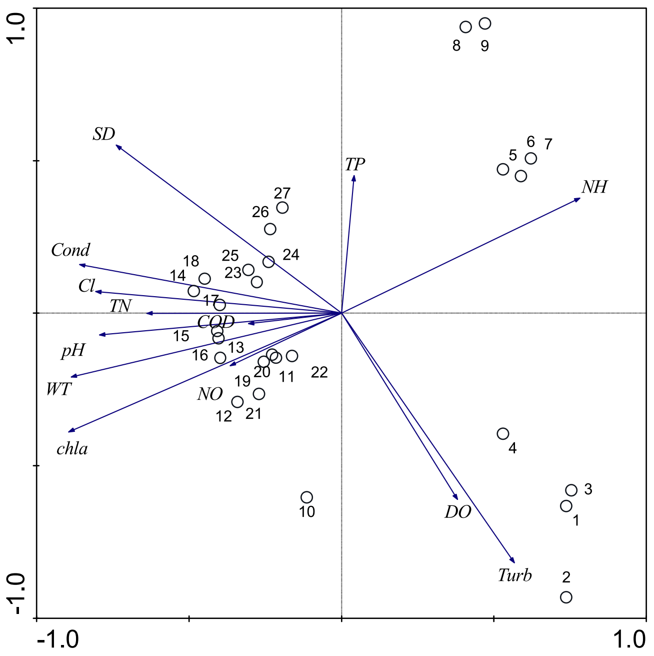

Fig. 3. Principal component analysis (PCA) for the environmental variables of the Xiquanyan reservoir. Circle numbers 1–9, 10–18 and 19–27 indicate sampling in spring, summer and autumn, respectively. Environmental variables: DO = dissolved oxygen; Cond = conductivity; SD = water transparency; Turb = turbidity; Cl = chloride; TN = total nitrogen; NH = ammonium; NO = nitrate; TP = total phosphorus; COD = chemical oxygen demand; Chla = chlorophyll-*a*.

can be categorized as of mesotrophic system during spring season and slightly eutrophic system in summer and autumn seasons (Klapper, 1991). Spatially, sites located upstream of the reservoir had a relative high mean value for chlorophyll-*a* (Fig. 2h).

The principal components analysis (PCA) using 13 environmental variables explained 71.22% of data variability in the first two components (component 1 = 52.41%; component 2 = 18.81%) (Fig. 3). In component 1, the most important environmental variables were water temperature (0.926), conductivity (0.924), pH(0.922), chloride (0.877), ammonium (−0.843), total nitrogen (0.830), water transparency (0.785), chlorophyll-*a* (0.704), nitrate (0.567), turbidity (−0.564) and dissolved oxygen (−0.513). With respect to component 2, the most important environmental variable for its ordination were total phosphorus (−0.812), turbidity (0.681) and dissolved oxygen (0.678). The PCA results revealed that component 1 reflected higher warming gradient, redox potential gradient, increased trophic status and water clarity in the seasons of summer and autumn. Positively, component 1 (sampling units of summer and autumn seasons) was correlated with water temperature, conductivity, pH, chloride, total nitrogen, water transparency, chlorophyll-*a* and nitrates and negatively correlated with ammonium, turbidity and dissolved oxygen. On its positive side, the sampling units in spring were correlated with turbidity and dissolved oxygen and negatively correlated with total phosphorus.

3.2 Zooplankton community in Xiquanyan reservoir

During the study period, 48 zooplankton species belonging to four taxonomic categories: protozoans, rotifers, copepods and cladocerans were observed in the Xiquanyan reservoir (Tab. 2). Rotifers were composed of 19 species equivalent to 39.58%, followed by protozoans with 14 (29.17%), copepods 8 (16.67%) and cladocerans 4 (8.33%). The highest number of species collected was in summer (41 species) followed by autumn (28 species) and spring (7 species). In summer, group RC was mainly represented by *A. priodonta* and *A. girodi,* while functional group MCC was represented by *M. albidus*, *T. dybowskii*, *T. vermifer* and *A. vernalis*. Small copepods and cladocerans filter feeders (SCF) were represented by *B. coregoni* and *M. javanus*. In autumn, group RC was mainly dominated by *A. priodonta*, while group MCC was represented by *T. dybowskii*, *M. albidus* and *A. vernalis.* Group LCC was represented only by *L. kindti.*

3.3 Seasonal and spatial variation of zooplankton functional groups

The mean biomass of all zooplankton functional group differed significantly among the seasons as determined by two-way ANOVA ($F_{(2,\ 43)} = 3.654$ $p = 0.041$). A Tukey HSD test showed that the total mean biomass was statistically significantly lower in spring (54.25 ± 40.22 μg/L) compared to that in autumn (196.54 ± 53.56 μg/L) and summer (245.81 ± 58.02 μg/L). In spring, functional group RF, dominated mainly by *Gastropus stylifer,* was dominant with a mean biomass of 43.42 ± 37.88 μg/L, which corresponded to about 80% of the total biomass (Fig. 4). Functional group MCC also accounted for about 8.36% (mean biomass 4.54 ± 1.75 μg/L) of the total biomass in spring. With exception of site S2, all the sites were dominated by group RF (Fig. 5a). In summer, functional group RC accounted the highest mean biomass of 91.25 μg/L (35.81%) followed by MCC 36.27 μg/L (14.75%), SCF 34.66 μg/L (14.10%), LCC 27.22 μg/L (11.07%) and PF 23.56 ± 11.92 μg/L (9.58%) (Fig. 4). The mean biomass contribution by groups RF and PC in summer was less than 10 μg/L. Spatially, groups RC, SCF, MCC and MCF were present in almost all sites in summer. However, functional group LCC contributed large percentage of biomass in sites located middle and downstream of the reservoir (Fig. 5b). In autumn, the relative biomass contribution by groups SCF, RC, MCC and LCC were almost similar (Fig. 4). Group SCF, mainly represented by *B. coregoni,* accounted for about 52.68 ± 27.40 μg/L (26.80%) of the total biomass. Groups RC, MCC and LCC accounted for 48.41 ± 38.03 μg/L (24.63%), 47.44 ± 21.10 μg/L (24.18%) and 38.88 ± 15.91 μg/L (19.78%) of the total biomass in autumn, respectively. Spatially, sites located upstream (S1–S4) were dominated by group RC, while groups SCF, MCC and LCC co-dominated in sites located middle and downstream of the reservoir (Fig. 5c).

3.4 Environmental variables related to the biomass of zooplankton functional groups

The RDA ordination of the biomass of zooplankton functional groups with respect to environmental variables are

Table 2. Zooplankton species composition observed in Xiquanyan reservoir listed according to their functional groups and their percentage contribution to their total biomass (*) = present.

Taxonomic group	Species	Functional groups	Spring	Summer	Autumn	% Biomass
Protozoa	*Difflugia globulosa*	PF		*		0.03
	Difflugia avellana	PF		*		5.34
	Difflugia gramen	PF		*		0.03
	Cucurbitella mespiliformis	PF		*		1.26
	Acanthocystis aculeate	PF		*		0.02
	Paramecium bursaria	PF		*	*	0.09
	Paramecium caudatum	PF		*	*	0.08
	Vorticella microstoma	PF	*	*		0.01
	Tintinnopsis wangi	PF		*	*	0.06
	Askenasia volvox	PC	*	*	*	0.01
	Lacrymaria olor	PC		*	*	0.09
	Spathidium sp	PC			*	0.08
	Didinium balbianiinanum	PC		*	*	0.01
	Podophrya maupasi	PC		*		0.01
Rotifera	*Brachionus angularis*	RF		*	*	0.34
	Brachionus budapestiensis	RF		*	*	1.62
	Brachionus calyciflorus	RF		*	*	0.10
	Brachionus forficula	RF		*		0.02
	Gastropus stylifer	RF	*			4.45
	Keratella cochlearis	RF		*	*	0.01
	Monostyla pyriformis	RF		*		0.04
	Filinia longiseta	RF		*		0.44
	Pompholyx xcomplanata	RF		*	*	0.13
	Asplanchna girodi	RC		*		2.85
	Asplanchna priodonta	RC		*	*	44.51
	Diurella dixon-nuttalli	RC		*	*	0.01
	Diurella rousseleti	RC		*	*	0.03
	Diurella stylata	RC		*	*	0.11
	Trichocerca similis	RC		*	*	0.07
	Polyarthra minor	RC		*	*	2.08
	Synchaeta stylata	RC		*	*	0.01
	Collotheca ambizua	RC		*	*	0.28
Cladoceran	*Daphnia cristata*	SCF			*	0.02
	Bosmina coregoni	SCF		*	*	9.23
	Alona Baird sp	MCF		*		0.02
	Diaphanosoma leuchtenbergianum	MCF		*		0.24
	Leptodora kindti	LCC		*	*	9.47
Copepoda	*Cyclops furcifer*	LCC	*			0.10
	Thermocyclops vermifer	MCC		*		0.49
	Thermocyclops dybowskii	MCC	*	*	*	3.09
	Paracyclops fimbrtatus	MCF		*		0.08
	Paracyclops affims	MCF		*		0.01
	Macrocyclops albidus	MCC	*	*	*	6.12
	Acanthocyclops vernalis	MCC			*	0.18
	Microcyclops javanus	SCF	*	*	*	0.86
	Microcyclops inchoatus	MCF		*	*	5.86

presented in Figure 6. The first two RDA axes explained 61.7% (axis 1: 47.2%; axis 2: 14.5%) of the variation in the biomass of zooplankton functional groups data and 76.3% (axis 1: 58.4%; axis 2: 17.9%) of the functional groups–environment variables relationship. Using the function ordistep from the vegan package to conduct forward selection and screening of the environmental variables yielded five variables that were significant to the model. These five variables are total nitrogen ($F = 5.299$, $P = 0.010$), total phosphorus ($F = 4.37$, $P = 0.031$), ammonium ($F = 6.635$, $P = 0.010$), chlorophyll-*a* ($F = 5.567$, $P = 0.005$) and water transparency ($F = 9.582$, $P = 0.005$). These five variables accounted for 66.7% of the total variance

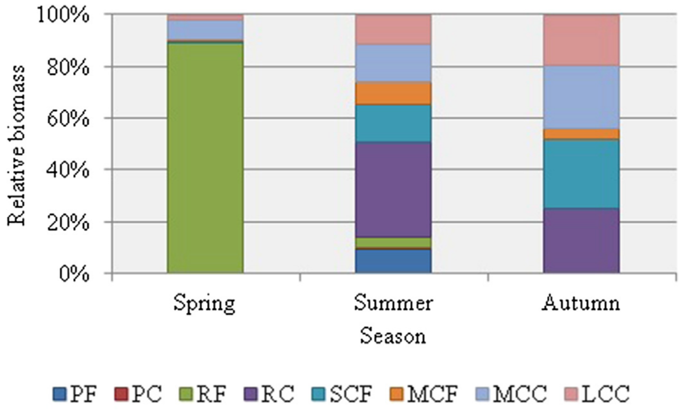

Fig. 4. Seasonal variation in the relative biomass of zooplankton functional groups in Xiquanyan reservoir. Protozoa filter feeders (PF), protozoa carnivore (PC), rotifer filter feeders (RF), rotifer carnivore (RC), small copepods and cladocerans filter feeders (SCF), middle copepods and cladocerans filter feeders (MCF), middle copepods and cladocerans carnivore (MCC) and large copepods and cladocerans carnivore (LCC).

in the biomass of zooplankton functional groups. The first RDA axis was positively correlated to conductivity (0.866), chloride (0.866), water temperature (0.855), pH (0.810), water transparency (0.755), total nitrogen (0.728), and chlorophyll-*a* (0.714) and negatively to ammonium (−0.924), and turbidity (−0.535). Axis 2 was negatively correlated with chlorophyll-*a* (−0.672).

The biomass of functional group PF was positively correlated with water temperature, pH, conductivity, total nitrogen, chloride and nitrate (as indicated by the similar directions of their arrows in Fig. 6). A multiple forward stepwise regression indicated that total nitrogen was the most important variable related to the biomass of group PF (Biomass of PF = 1.060 + 2.482 total nitrogen, $F_{(2,\ 43)} = 27.37$, $p = 0.000$, $R^2 = 0.523$). Group RF, which accounted for about 80% of the total biomass in spring, was positively associated with ammonium and total phosphorus the gradient of trophic status and negatively related by water temperature, chlorophyll-*a* and pH (as indicated by the directions of the arrows). Group RC had a positive relationship with chlorophyll-*a*, water temperature, pH, total nitrogen and conductivity with about 76.9% of its biomass variation explained by chlorophyll-*a* and total nitrogen (RC = −0.026+0.657 chlorophyll-*a* + 1.625 total nitrogen $F_{(2,\ 43)} = 39.88$, $p = 0.010$, $R^2 = 0.769$). Groups SCF, MCC, MCF and LCC were positively related to water transparency, water temperature, pH, conductivity, chloride and total nitrogen and negatively to turbidity, dissolved oxygen and ammonium. Forward stepwise regression selection with the biomass of SCF as response variable revealed ammonium and total phosphorus as important variables with a significant *F*-value that significantly increase the regression sum of squares (SCF = −2.584–0.766 ammonium + 0.415 total phosphorus, $F_{(2,\ 43)} = 34.163$, $p = 0.010$, $R^2 = 0.74$). Approximately 76.1% of the variation in the biomass of MCC could be explained by ammonium, turbidity and chlorophyll-*a* according to the model (MCC = −1.69–0.755 ammonium, −0.276 turbidity, −0.319 chlorophyll-*a*, $F_{(2,\ 43)} = 24.364$, $p = 0.000$, $R^2 = 0.761$). On the other hand, the biomass of LCC group was significantly influenced by water transparency (LCC = 1.068 + 0.997 water transparency, $F_{(2,\ 43)} = 13.63$, $p = 0.001$, $R^2 = 0.353$). From the Pearson correlation analysis (Tab. 3), group RF was negatively correlated with chlorophyll-*a,* while groups PC, RC and SCF were positively correlated. Functional group PF was strongly positively correlated with groups PC and RC, and weakly but positively correlated with MCF and MCC. Groups SCF, MCf, MCC and LCC were positively correlated.

4 Discussion

4.1 Zooplankton functional group

According to Benedetti *et al.* (2015), Violle *et al.* (2007) and Reynolds *et al.* (2002), functional traits are the behavioral, morphological or phonological characteristics of organisms that impact their ecological role and fitness in their niches. In plankton communities, for instance, these traits include body size, shape, motility, tolerance and sensitivity to environmental conditions among many others (Reynolds *et al.*, 2002; Litchman *et al.*, 2013; Benedetti *et al.*, 2018). For sometimes now, classification of aquatic organisms into functional groups has been proposed to be the best way of understanding their ecological interaction (Hébert *et al.*, 2016). Sun *et al.* (2010) classified zooplankton species of the continental shelf of yellow sea into six functional groups based on size spectrum and food preference. While modeling food web interaction in Western English channel ecosystem, Araújo *et al.* (2006) came up with three functional groups of macrozooplankton, mesozooplankton and microzooplankton. Recently, the functional traits including feeding mode, maximum body length, trophic group and spawning strategy have been used to classify plankton copepods (Benedetti *et al.*, 2018). This approach has proved it worth when it comes to addressing the question at hand. Based on body size/length and mode of feeding, zooplankton species observed in the Xiquanyan reservoir were classified into eight functional groups PF, PC, RF, RC, SCF, MCF, MCC and LCC. Body size and mode of feeding are regarded as “master traits” that not only scale with different traits related to ecosystem processes such as secondary production and nutrients and carbon cycling but also describe the main food source of an organism, hence its role in aquatic food-web dynamics (Pomerleau *et al.*, 2015; Hébert *et al.*, 2016).

4.2 Variation in zooplankton functional groups

According to Shi *et al.* (2015), biomass is one of the most important variable when modeling temporal and spatial variation of zooplankton functional groups in aquatic systems. However, it has been applied sparingly for modeling zooplankton community structure in oligo-mesotrophic reservoir (Beaver *et al.*, 2013; Sellami *et al.*, 2016) such as Xiquanyan. In this study, the biomass of zooplankton functional groups varied significantly among seasons and sites. The average biomass recorded in spring (54.25 µg/L), summer (245.81 µg/L) and autumn (196.54 µg/L) was much lower compared to those reported by Ma *et al.*(accepted for

a) Spring

b) Summer

c) Autumn

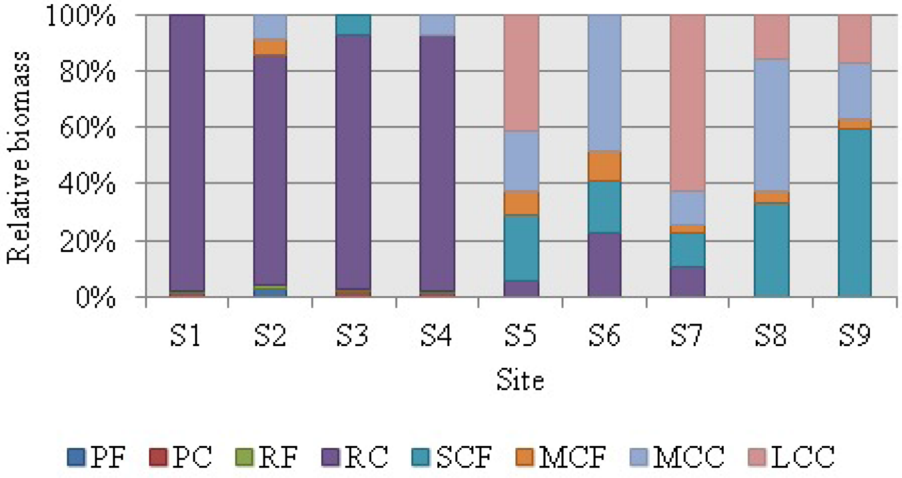

Fig. 5. Spatial variations biomass of zooplankton functional groups in Xiquanyan reservoir: (a) spring, (b) summer, (c) autumn.

publication) for Small Xingkai Wetland Lake of autumn (0.72 mg/L), summer (5.11 mg/L) and spring (0.28 mg/L). During spring season, zooplankton biomass was dominated by RF mainly composed of *G. stylifer* accounting for about 80% of the total biomass. Spatially, this group was found in all sites except site S2. Higher biomass of RF group in spring coincided with higher ammonium and total phosphorus and very low temperature (mean value 6.31 °C) and chlorophyll-*a* (<4 μg/L). Such observations are not strange, because RF species are filter-feeders feeding on bacteria-detritus suspension which could have been favored by the occurrence of higher concentrations of total phosphorus and total nitrogen (Duggan *et al.*, 2001; Špoljar *et al.*, 2005). While assessing spatial–temporal dynamics of planktonic rotifers in the Elbe Estuary, Germany, Holst *et al.* (1998) established that rotifers grazed predominantly on heterotrophic components of the microbial food-web, such as bacteria, detritus and heterotrophic flagellates in spring. Apart from food, water temperature is an important environmental variable that affects rotifer population abundance and seasonal succession (Dumont, 1983; Berzinš and Pejler, 1989; Yin *et al.*, 2017). Several studies have found strong positive relationship between rotifers biomass and temperature (Galkovskaja, 1987). However, our results revealed that the biomass of RF was high in spring despite the fact that temperature was very low. This observation could be explained by (i) low temperature created hostile and unpredicted environment which allows rotifers an opportunistic and r-strategist organisms to flourish by eliminating other resource species competitor, (ii) high temperature has been reported to have negative effect on some species of rotifers. For example, Persaud and Williamson (2005) observed that exposure to ultraviolet light and high temperature had a remarkable effect on the reproduction and abundance of four rotifer species: *G. stylifer*, *Kellicottia bostonensis*, *Kellicottia longispina*, *Keratella* spp. Therefore, the dominance of *G. stylifer,* the only representative of RF group in spring, could be attributed by the favorable low temperatures. In fact *G. stylifer* was not found in summer or autumn when the temperature was relatively higher. Note, however, that, in their study, Pinese *et al.* (2015) and Yin *et al.* (2017) cautions that the concept of rotifer seasonal occurrence should be separated from the great dependence of changes in temperature since these processes among the zooplankton species are difficult to systematize due to the variety of interactions involved. Therefore, it is possible that other factors such as lack of exploitive competition from other filter feeders such as SCF and MCF and predation from MCC and LCC lead to the general high biomass of RF in spring (Fussmann, 1996; Brandl, 2005; Gilbert, 2014).

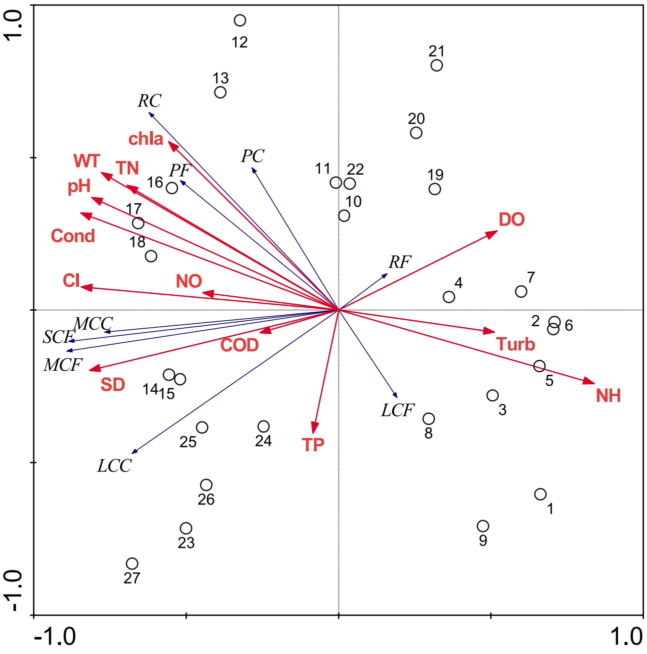

Fig. 6. Redundancy analysis (RDA) ordination diagram of zooplankton functional groups (blue lines with black letters) and environmental variables (red lines with red letters) in Xiquanyan reservoir.

Rotifer carnivore (RC) an ambush feeder group that targets small motile 536 prey dominated zooplankton biomass during summer (35.81%) followed by MCC (14.75%), SCF (14.10%) and LCC (11.07%). Group RC was mainly represented by genus *A. priodonta,* a common rotifer distributed from tropical to temperate waters (Fernando *et al.*, 1990). According to Chang *et al.* (2010), *A. priodonta* is an omnivore rotifer that feeds on phytoplankton dominated by dinoflagellates and protozoa prey such as *Codonella* spp. and *Difflugia* spp. It is

Table 3. Pearson correlation coefficients between zooplankton functional groups and with the biomass of phytoplankton in terms of chlorophyll-*a*; $*p < 0.05$; $**p < 0.01$.

	PF	PC	RF	RC	SCF	MCF	MCC	LCC
Chlorophyll-*a*	0.380	0.400*	−0.528**	0.832**	0.558**	0.511**	0.357	0.262
PF	1	0.672**	0.307	0.668**	0.321	0.446*	0.395*	0.056
PC		1	0.131	0.698**	0.094	0.097	0.258	−0.049
RF			1	−0.123	−0.195	−0.110	0.126	−0.281
RC				1	0.407*	0.415*	0.429*	−0.039
SCF					1	0.836**	0.798**	0.609**
MCF						1	0.687**	0.685**
MCC							1	0.446*
LCC								1

documented that the abundance and biomass of *A. priodonta* in a habitat is often influenced primarily by food source rather than predation pressure (Fernando *et al.*, 1990; Yoshida *et al.*, 2003). This agrees with our study since *A. priodonta* was found to be positively correlated with phytoplankton biomass in terms of chlorophyll-*a*. Spatially, group RC accounted for more than 50% of the total biomass in sites located upstream of the reservoir where chlorophyll-*a* was very high. Group SCF mainly composed by *B. coregoni* depicted almost similar distribution pattern to that of RC (*A. priodonta*) with relative high biomass values observed in sites located upstream of the reservoir coinciding with higher chlorophyll-*a* values. This observation is not surprising since other studies have shown *B. coregoni* to be efficient filter feeder of phytoplankton biomass (Guo *et al.*, 2009). On the other hand, the low biomass contribution by RC in sites located middle and downstream of the reservoir can be probably explained by predation from MCC and LCC.

Almost similar biomass contribution pattern by the zooplankton functional group to that of summer were observed in autumn. However, unlike in summer, the biomass contribution by the SCF, RC, MCC and LCC were almost similar in autumn which led to the question: Is there any competitive interaction between those functional groups in this reservoir during autumn? Since these functional groups have different ecological requirement and resource utilization, we may think that competitive interaction was probably avoided. Furthermore, coexistence of the groups does not ensure competition because, in general, species explore different ecological niches and resources are not always limiting. In fact, our results revealed that group RC preferred sites located upstream of the reservoir where water transparency was very low and there were no SCF, MCC or LCC groups. Probably group RC was avoiding competition interaction especially from SCF group or predation from MCC and LCC groups. The evidence that rotifers (such as RC group species) could be preyed by copepods and cladocerans carnivore is pointed out by Brandl (2005). In the site located middle and downstream of the reservoir, the biomass contribution by SCF, MCC and LCC was almost similar probably because of their different morphological mechanisms for food resource exploitation. Protozoa, which are the main contributors to PF and PR functional groups in the reservoir investigated, exhibited no obvious seasonal and spatial variation and their contribution to the total biomass was very minimal. This could have been attributed by depressed exploitative competition for food resources from other functional groups such as MCF, RF and SCF as well as predation.

4.3 Zooplankton functional groups driving factors in Xiquanyan reservoir

Different studies have established that water temperature, food resources, predation, water transparency, nutrients and hydrology are important drivers that influence structuring of zooplankton community (Sommer *et al.*, 1986, 2012; Shi *et al.*, 2015; Sharma *et al.*, 2017). Similarly, this current study has revealed that the zooplankton functional groups are influence by environmental variables that vary with season in Xiquanyan reservoir. From the RDA results, group RF was positively influenced by ammonium and total phosphorus. This relation may be the indirect result of food availability in the form of bacteria-detritus suspension, which have been documented to be strongly influenced by higher concentration of nutrients (Špoljar *et al.*, 2005). The biomass of RF group was negatively correlated with chlorophyll-*a*. This may be explained in different ways: (i) strong top-down control on phytoplankton by RF group, which is contrary to what is documented in other studies that zooplankton are ineffective in controlling phytoplankton in reservoir (von Rückert and Giani, 2008; Okuku *et al.*, 2016), (ii) high chlorophyll-*a* concentration could be attributed to blue-green algae and green algae that contain some toxic extracellular substance which can cause decline in number and reproduction rate of rotifers (Arnold, 1971; Ger *et al.*, 2014), and (iii) some studies have shown that rotifers (macrofilter-feeders species) abundance were negatively correlated with algal bloom in Oligo-mesotrophic Nabhana Reservoir because algal bloom eliminated the fine micro-algae which serve as food of micro-filter feeders (Sellami *et al.*, 2016).

The fact that the biomass of groups RC, SCF and MCF were positively correlated with chlorophyll-*a* could mean that the top-down control was not strong enough to produce negative effect on phytoplankton production. This also suggests that phytoplankton have an important role in energy transfer along the Xiquanyan reservoir food web, and phytoplankton particles are probably edible to the zooplankton functional groups. Similar observations were reported by Ismail and Adnan (2016) in two small man-made lakes in Malaysia. This observation has implications for the quantification of phytoplankton biomass in terms of chlorophyll-*a* within Xiquanyan reservoir, as it appears that groups RC, SCF and MCF may be equally as significant in utilizing chlorophyll-*a* directly. Moreover, groups RC and MCF were positively correlated with groups PF and PC, which could imply that these protozoans served as important additional food for these functional groups probably at a time with limited supply of edible algae. In fact, Adamczuk *et al.* (2015) and Marzolf (1990) noted that phytoplankton alone does not satisfy all of the nutritional requirements of zooplankton. Top-down control of SCF, MCF and MCC by LCC seems to be not as important as indicated by their positive correlation. This could mean that increasing predator size biomass in reservoir does not strengthen top-down control on prey.

5 Conclusion

In this current study, a total of 48 zooplankton species belonging to four taxonomic categories (protozoans, rotifers, copepods and cladocerans) were identified and grouped into eight functional groups PF, PC, RF, RC, SCF, MCF, MCC and LCC. Both environmental variable and the biomass of zooplankton functional groups in Xiquanyan reservoir vary spatially and seasonally. Water temperature, water transparency, total nitrogen and nitrates were significantly higher in summer, while chlorophyll-*a* and ammonium were higher in autumn and spring, respectively. The biomass of zooplankton functional groups was significantly higher in summer (245.81 μg/L), autumn (196.54 μg/L) and spring (54.25 μg/L). In spring group, RF was the dominant functional group accounting for about 80% of the total biomass. In summer and autumn, group RC and SCF were the dominant, respectively. Nutrients, mainly total nitrogen, total phosphorus and ammonium, chlorophyll-*a* and water transparency were identified as the major factors influencing zooplankton functional groups in Xiquanyan reservoir. Group RF was positively influenced by ammonium and total phosphorus, while RC, SCF and MCF were positively correlated with chlorophyll-*a*. This clearly shows that the top-down control of phytoplankton by groups RC, SCF and MCF in Xiquanyan reservoir is not strong enough to produce negative effect. Moreover, increase in predator size biomass (e.g. LCC) does not strengthen top-down control on prey. Even though our study may not be conclusive as such, it is quite clear that the zooplankton functional groups of Xiquanyan reservoir followed a predictable seasonal pattern. This, therefore, highlights the significance of environmental variables in structuring plankton composition in the reservoir.

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