Zooplankton Size Structure in Relation to Environmental Factors in the Xiangxi Bay of Three Gorges Reservoir, China

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Abstract

Body size is sensitive to environmental changes and recognized as one of the fundamental traits linking ecological functions. Recently, size structure has been suggested as a useful indicator for environmental monitoring and assessment in aquatic ecosystems. However, the organisms' size structure and the relationship with environmental factors remain seldom addressed in reservoir ecosystems. In this study, firstly, we investigated the zooplankton community composition and size structure, including the slope of the normalized biomass size spectrum (NBSS) and size diversity in the Xiangxi Bay of Three Gorges Reservoir, China. Then we analyzed how the environmental factors affect the zooplankton abundance and size structure (NBSS slope and size diversity) by using the structural equation model (SEM). In terms of the community composition, rotifers were the predominant zooplankton group in the Xiangxi bay during the whole research period, which abundance is significantly higher than protozoan, cladoceran, and copepod (Mann-Whitney U tests, $P < 0.001$). For the size structure, both the slope of NBSS and size diversity showed high spatiotemporal dynamics. The slope of NBSS ranged from − 2.201 to -0.097, and the size diversity ranged from 0.631 to 3.291. And lowest values of NBSS slope and size diversity were observed in the upstream areas of Xiangxi Bay. Further analyses based on SEMs found a clear pathway revealing how nutrient variables affect the zooplankton abundance and size structure. That is, dissolved inorganic nitrogen had an indirect effect on the zooplankton abundance, NBSS slope, and size diversity by affecting the phytoplankton biomass. In addition, SEM found that water temperature had a significant negative effect on the size diversity but had nonsignificant effects on zooplankton abundance and NBSS slope. This finding suggests that size diversity is a useful index in measuring the zooplankton size structure. Our study highlights that size diversity is a robust indicator for environmental monitoring and assessment, especially in complex and dynamic reservoir ecosystems.

Introduction

Zooplankton is an essential component in aquatic ecosystems and plays a fundamental role in energy flow and material cycle in the ecosystem (Ju et al. 2019; Eddy et al. 2020). Zooplankton is the crucial linking of the primary producer to high trophic organisms, which is recognized as essential information in understanding pelagic food webs dynamics (Fenchel 1988; Eddy et al. 2020). Because of their small size and short lifecycle, zooplankton is very sensitive to environmental changes and has a wide distribution in aquatic ecosystems (Whitman et al. 2004; García-Comas et al. 2014; Chiba et al. 2018). These characteristics make zooplankton become a good indicator for water quality monitoring and environmental change assessment in aquatic ecosystems (García-Comas et al. 2014; Hamil et al. 2020; Venello et al. 2021).

Body size has long been considered as a fundamental functional trait in determining community structure and functions and indicating environmental changes (Daufresne et al. 2009; Stouffer et al. 2011; Ye et al. 2013; Verberk et al. 2021). The normalized biomass size spectrum (NBSS) and size diversity are the two widely used metrics representing community size structure (Yvon-Durocher et al. 2011; Ye et al. 2013; Sprules and Barth 2016). Specifically, the slope of the NBSS represents the relative distribution of individual sizes; a steeper slope indicates a higher contribution of small organisms to the total biomass of a community (García-Comas et al. 2014). Size diversity was adapted from the Shannon diversity expression to quantify the continuous size distribution in a community (Quintana et al. 2008). Although many researchers have reported that zooplankton size structure is sensitive to climate change and anthropogenic activities in marine ecosystems (Daufresne et al. 2009; García-Comas et al. 2014; Venello et al. 2021), how zooplankton size structure response to environmental factors remains seldom addressed in reservoir ecosystems (Gao et al. 2019).

Different from many other natural water bodies, reservoir ecosystems are a kind of unique ecosystem between river ecosystems and lake ecosystems and generally have a high spatial heterogeneity of physicochemical and biological conditions (Straškraba and Tundisi 1999; Ye and Cai 2011; Shen et al. 2014). According to the hydrodynamic characteristics, the flooded area of reservoirs can divide into a riverine zone, transition zone, and lacustrine zone from the backwater area to the dam (Straškraba and Tundisi 1999), which make reservoir ecosystems have a high spatial heterogeneity (Ye and Cai 2011; Shen et al. 2014). For example, Ye and Cai (2011) reported that the nitrogen and phosphorus a clear inverse pattern in the Xiangxi Bay, with tendencies for a decrease of nitrogen and an increase of phosphorus from the mouth to the upstream region of the bay. Obviously, this kind of nutrient gradients provides a natural experiment site to investigate how zooplankton size structure responds to nutrient enrichment in aquatic ecosystems.

The Three Gorges Reservoir (TGR) is the most giant strategic freshwater resource reservoir in China, with a storage capacity of 39.3×10^9 m^3 (Ye et al. 2016). A previous study showed that the nutrient variables have clear gradients in the Xiangxi Bay of TGR (Ye and Cai 2011). And spring and summer phytoplankton blooms were frequently observed in the tributaries after the impoundment of TGR (Wang et al. 2011; Ye and Cai 2011). For the above reasons, the main purposes of this study are to investigate i) the size structure of zooplankton community in the Xiangxi Bay of TGR during the spring and summer phytoplankton bloom periods, ii) the relationships between zooplankton size structure and the environmental factors, and iii) whether the NBSS slope or size diversity is more sensitive to the environmental changes.

Materials And Methods

Study area and field sampling

The field study was carried out in the Xiangxi Bay of Three Gorges Reservoir (Fig. 1). The Xiangxi Bay, located about 32 km in upstream of Three Gorges Dam, is the former Xiangxi River before the impoundment of TGR. After the TGR had been filled into the altitude of 175 m above sea level in October 2010, about 28 km downstream of the Xiangxi River was flooded and formed the bay zone. Previous research showed that this bay is facing severe eutrophication problems (Ye et al. 2014) with clear nitrogen and phosphorus gradients (Ye and Cai 2011). This distinct environmental condition provided a good research area to investigate the relationships of zooplankton size structure with nitrogen and phosphorus in aquatic ecosystems.

The field sampling was carried out monthly in the spring and summer blooms period, from March to August in the year 2014. A total of 9 sites were distributed from the mouth of Xiangxi Bay to its upstream (Fig. 1). Due to the water level dropping in the summer (June to August), sites XX10 and XX12 became running water and were neglected in the field sampling in the summertime. Zooplankton samples were collected by filtering the 20L water sample with a plankton net (~60 μm in mesh size) at each sampling site. All filtered zooplankton samples were fixed and preserved in the formalin solution with a final concentration of 4% immediately. Following Wong et al. (2017), the FlowCAM integrated system was used to obtain the size information of each zooplankton individual in the samples. Specifically, the FlowCAM was used to digitized and extract the size information (equivalent spherical diameter, ESD) of all particles in the zooplankton samples. Then, the particles were classified into different groups of rotifers, protozoans, cladocerans, copepods, zooplankton egg, and non-zooplankton particles by the taxonomic expert manually for the research.

At the same time, the water quality parameters of each sample site were measured to analyze the potential environmental driving the zooplankton size structure in the Xiangxi Bay. Specifically, the water temperature (WT) was measured *in situ* by the multi-parameter water quality sonde (YSI 6600, USA). About 300 ml water sample in the surface layer (0.5m in depth) of each site was collected for water chemistry analyses, including dissolved inorganic nitrogen (DIN, the sum of the ammonia nitrogen, nitrite nitrogen, and nitrate nitrogen), phosphate phosphorus (PO_4P), and dissolved silicate (DSi). The above chemical variables were analyzed by the segmented flow analyzer (Skalar SAN^{++}, Netherlands), according to the user manual of Skalar. Meanwhile, the concentration of chlorophyll *a* (Chl-*a*) was used to estimate the phytoplankton biomass. To measure the concentration of Chl-*a*, 615 ml water sample collected in each site was filtered through a micro-filter (~1.2 μm, GF/C Waterman) and stored in the dark at -20 ℃ until the analysis. The concentration of Chl-*a* was measured with a spectrophotometer (Shimadzu UV-1800, Japan) with the standard method of American Public Health Association (1998).

Zooplankton size structure

The normalized biovolume size spectrum (NBSS) and size diversity were used to quantify the changes in zooplankton size structure. The NBSS and size diversity were calculated by following García-Comas et al. (2014). In simple terms, in calculations of the NBSS and size diversity, the width of each size class was doubled with respect to the previous one (geometric 2^n series). In our study, the biovolume of each zooplankter was estimated as a sphere with the ESD (Zhou et al. 2015). Specifically, the biovolumes of zooplankton in our study ranged from 0.00011 to 0.62287 mm^3 which divided a total of 13 size groups. With the divided size groups, NBSS was constructed by linear regression for each site. The zero data in the NBSS were treated as empty size groups in the linear regression analysis. The slope of linear regression is used to describe the relative abundance of different size individuals in the community. The linear fit (R^2) reflects the stability of the community structure, and values near to 1 mean community close to steady-state equilibrium (Sourisseau and Carlotti 2006).

Size diversity (μ) is adapted from the Shannon-Wiener index that is commonly used for species diversity (Ye et al. 2013). Here, the size diversity was computed based on size classes divided in the calculating of size spectra:

$$\mu = -\sum_{i}^{S} p_i \log p_i$$

Where μ is the size diversity, and pi is the probability that zooplankter belongs to a specific size class.

Statistical analysis

Structural equation model (SEM) was used to investigate the effects of environmental variables on zooplankton size structure and the affecting paths (DiLalla 2000). Based on the known relationship between zooplankton and environmental variables, we assumed that water temperature and nutrient variables (DIN, PO_4-P, DSi) would affect the zooplankton size community (abundance, size diversity, and NBSS slope) directly and indirectly by affecting the phytoplankton. To fit the requirement of the SEM, the zooplankton abundance and Chl-*a* were $\log_2$ transformed in the SEM analyses (Kang et al. 2013). The favorable model fit in SEMs was selected by the root of mean square error of approximation (RMSEA, $\leq$ 0.05), the comparative fit index (CFI, $\geq$ 0.95), and the standardized root-mean-squared residual (SRMR, $\leq$ 0.08) (Hu and Bentler 1998, 1999). The SEM analysis was performed using the “lavaan” package (Rosseel 2012) in R (4.0.4) software (R Core Team 2021).

Results

Environmental factors

The statistical summaries of the selected environmental factors are presented in Table 1. The Chl-*a* concentration ranged from 1.13 to 152.42 μg/L, with a mean value of 39.39 μg/L. Water temperature ranged from 12.99 to 25.53 °C, with a gradual rise process from the early spring to later summer. The concentrations of DIN, PO_4P, and DSi during the research period ranged from 0.19 to 2.07 mg/L, 0.02 to 0.48 mg/L, and 0.07 to 3.28, respectively.

Table 1

Descriptive statistics of environmental factors measured in the Xiangxi Bay of Three Gorges Reservoir

Statistic value	Environmental variables				
	Chlorophyll *a* (μg/L)	WT (°C)	DIN (mg/L)	PO_4-P (mg/L)	DSi (mg/L)
Max	152.42	25.53	2.07	0.48	3.28
Min	1.13	12.99	0.19	0.02	0.07
Mean	39.39	19.73	1.33	0.12	1.93
SD	37.40	3.38	0.52	0.08	0.88

Boxplot showed that a clear spatial pattern of nutrient variables in the Xiangxi Bay (Fig. 2). Specifically, a high concentration of DIN was observed in the mouth of the bay, and the concentration of DIN decreased from the mouth to the upstream of the bay. On the contrary, the PO_4P had the reverse spatial pattern comparing to the DIN, that is, low concentration of PO_4P was observed in the mouth of the bay, and the concentration of PO_4P increased from the mouth to the upstream of the bay. The DSi had a similar spatial pattern with DIN in the Xiangxi Bay.

Zooplankton composition and size structure

We found that rotifer is the predominant zooplankton group in the Xiangxi bay in the whole research period (Fig. 3). The mean abundance of rotifer among all sites is 63.5 ind./L, which is significantly higher than protozoan (mean abundance is 7.0 ind./L), cladoceran (1.4 ind./L), and copepod (4.2 ind./L) by the Mann-Whitney U tests ($P < 0.001$). The high abundance of rotifer was observed in March and April, with the highest value of 571.9 ind./L observed in XX05 in April. The high abundance of protozoan was generally observed in the region from the mouth of Xiangxi Bay (XX00) to the middle reach (XX05) in March and May (Fig. 3). Copepod has a high relative abundance in the summer (June, July, and August), and cladoceran has a low ratio in the whole research period.

The NBSS slope ranged from -2.201 to -0.097 during the research period, with an acceptable linear fit for most samples (Fig. 4b). In terms of temporal dynamics, the NBSS slopes in August are significantly higher than in other months (Mann-Whitney U tests, $P < 0.05$). In spatial variations, the lower NBSS slopes were generally observed in the upstream sites XX10 and XX12, with an average value of -1.601 and -1.370. The size diversity ranged from 0.631 to 3.291. The highest value of size diversity was observed in XX07 in May, and the lowest value was observed in XX12 in April. The spatial pattern of size diversity is similar to the NBSS slope (Fig. 4). That is, low values of size diversity were generally observed in upstream sites XX10 and XX12. In temporal dynamics, low values of size diversity were generally observed in March and April, with mean values of 1.963 and 2.015.

Factors driving zooplankton abundance and size structure

The SEMs found a clear pathway that how nutrient variables affect the zooplankton size structure, and all 3 models had good favorable fit degree (Fig. 5). SEM found that DIN had an indirect effect on the zooplankton abundance, NBSS slope, and size diversity by affecting the Chl-*a*. The explanation power of SEM for the zooplankton abundance, NBSS slope, size diversity was 60%, 52%, and 57%. The coefficient between DIN and Chl-*a* was -0.90 ($P < 0.001$). The coefficient of Chl-a with zooplankton abundance, NBSS slope, and size diversity was 0.22 ($P = 0.083$), -0.57 ($P < 0.001$), and -0.45 ($P = 0.001$). SEM found that water temperature had a significant negative effect on the size diversity but no significant effects on the zooplankton abundance and NBSS slope (Fig. 5).

Discussion

Zooplankton composition and size structure

Our study found that the small body size zooplankton rotifer is the dominant group in the Xiangxi Bay of TGR (Fig. 3). This finding is widely observed in reservoirs because of the high reproduction rate of rotifers and their adaptability to the environment (Segers 2008; Goswami and Mankodi 2012; Gu et al. 2021). However, because the swimming ability of planktonic rotifers was significantly weaker than that of copepods and cladocerans, the growth of rotifers will be inhibited in the environment with fast water exchange rate or high flow velocity (Holst et al. 1998). This may be the reason explaining why the relative abundance of rotifer decreased in the summertime (June, July, and August). For flood control, the water level of TGR needs to be dropped to 145 m above sea level in June. As a comprehensive effect of a large amount of inflow water and water level control in the flood season, the water exchange rate in the summertime is very high. Because of the high hydrological disturbances, the relative abundance of rotifer decreased in the summertime.

For the size structure, we found that the NBSS slopes of most sites in our study are higher than the theoretical NBSS slope (-1.0) of multi-trophic communities (Mehner et al. 2018). The average NBSS slope in our study is -0.82, which is almost the same as the reported value in the East China Sea (García-Comas et al. 2014). This suggested that a relatively high trophic transfer efficiency among the zooplankton community in the Xiangxi Bay of TGR (Mehner et al. 2018). In terms of the spatial distribution, the upstream sites have a steeper NBSS slope (Fig. 4). The is mainly because the upstream areas are vulnerable to hydrological disturbances and anthropogenic activities, which generally lead to a steeper NBSS slope (Dickerson et al. 2010; Ma et al. 2014; Medellin-Mora et al. 2018). Comparing to García-Comas et al. (2014), we found that the zooplankton size diversity in the Xiangxi Bay (mean value is 2.25) is slightly higher than that (mean value is 1.57) in the East China Sea. This suggests that the zooplankton community in the Xiangxi Bay has relatively high efficiency in predating phytoplankton because higher zooplankton size diversity is supposed to have a stronger predation effect on phytoplankton (Ye et al. 2013).

How nutrients affecting zooplankton community

Our study found that DIN can affect the zooplankton abundance and size structure by influencing the phytoplankton biomass (Fig. 5). This finding provided a mechanistic understanding of how environmental factors affecting the zooplankton community in Xiangxi Bay of TGR. We found that DIN had a significant negative correlation with the Chl-*a* concentration, suggesting that the growth of phytoplankton will uptake the nitrogen and therefore decreased the DIN concentration. Actually, the consumption of nitrogen by phytoplankton was usually observed in the Xiangxi Bay (Ye et al. 2007) and other water bodies (Gu et al. 1997). As the primary food source for zooplankton, phytoplankton can support the standing stock of zooplankton (Yuan and Pollard 2018). Therefore, we observed a significant positive relationship between Chl-*a* concentration and zooplankton abundance in the Xiangxi Bay.

In contrast, we found that the sites with higher phytoplankton biomass tended to have lower size diversity and steeper size spectra (negative relationships in Fig. 5). To explain this opposite finding, we investigated the effects of increasing of phytoplankton biomass on the abundance of different groups of zooplankton (Table 2). Interestingly, we found that the increase phytoplankton biomass only promotes the abundance of parts of small body-size zooplankters (eggs and rotifer). This suggests that high phytoplankton abundance will promote the abundance of small body size zooplankters and result in a steep NBSS slope and low size diversity. A previous study carried out in the East China Sea also found a similar pattern that increasing food availability increased zooplankton abundance, and more importantly, this increase was due to small body size zooplankton (García-Comas et al. 2014).

Table 2

The mean equivalent spherical diameter (ESD) of each zooplankton group and the results of linear regression analyses between different zooplankton groups and phytoplankton biomass (chlorophyll *a*) in the Xiangxi Bay of Three Gorges Reservoir.

	Mean ESD (μm)	Regression coefficient	intercept	R^2	P value
Cladoceran	301.0	-0.017	2.105	0.016	0.385
Copepod	207.2	-0.019	4.918	0.013	0.449
Protozoan	94.4	0.065	4.451	0.045	0.149
Rotifer	99.2	1.059	21.811	0.122	0.015
Egg	94.9	0.059	-0.552	0.177	0.003

Size diversity is a good indicator for climate change

It is worth mentioning that our study found that size diversity is more sensitive to temperature changes than the NBSS slope (Fig. 5). Our study suggests that zooplankton size diversity may be a good indicator for climate change related research. Despite the widespread use of the NBSS slope as the primary indicator of size structure, we found that the NBSS slope had a nonsignificant relationship with the water temperature in the Xiangxi bay. This nonsignificant relationship could be attributed to the NBSS in some sites were nonlinear (García-Comas et al. 2014), and the linear estimation of NBSS slopes may bring some uncertainties. In fact, the low fitness of the linear estimation of NBSS slopes in some sites in our study confirmed this point in the other aspect. Thus, the application of NBSS in quantifying size structure of dynamic ecosystems should be aware of the nonlinearity. On the contrary, size diversity measures the continuous analogue of size structure (Ye et al. 2013). For this reason, whether the zooplankton community is stable or not will not affect the accuracy in estimating size diversity. Therefore, we suggested that size diversity is a robust index in measuring the size structure.

Conclusion

This study reported the zooplankton size structure and its relationship with the environmental factors in the Xiangxi Bay of TGR during the spring and summer phytoplankton bloom periods. Our results demonstrated that the rotifers were the predominant zooplankton group in the Xiangxi Bay during the whole research period. Both the NBSS slope and size diversity showed high spatiotemporal dynamics with values ranged from -2.201 to -0.097 and 0.631 to 3.291. Comparing the values reported in the East China Sea, we found that the Xiangxi Bay has relatively high values of zooplankton NBSS slope and size diversity. This suggests a relatively high trophic transfer efficiency and stable zooplankton community in the Xiangxi Bay of TGR. Further analyses based on SEMs revealed a clear pathway that DIN had an indirect effect on the zooplankton abundance, NBSS slope, and size diversity through affecting the Chl-*a*. Besides, SEM found that water temperature has a significant relationship only with the size diversity, but not zooplankton abundance or NBSS slope. This finding highlights that size diversity is a robust indicator for environmental monitoring and assessment in reservoirs as well as other similar water bodies.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Availability of data and materials

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

Competing interests

The authors declare that they have no competing interests.

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Authors’ contributions

Li HR: formal analysis, writing - original draft, visualization. Gu Y: field investigation, sample analysis. Cai QH: conceptualization. Dong XW: methodology, sample analysis. Ye L: supervision, conceptualization, methodology, project administration, writing-review & editing. All authors read and approved the final manuscript.

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Figures

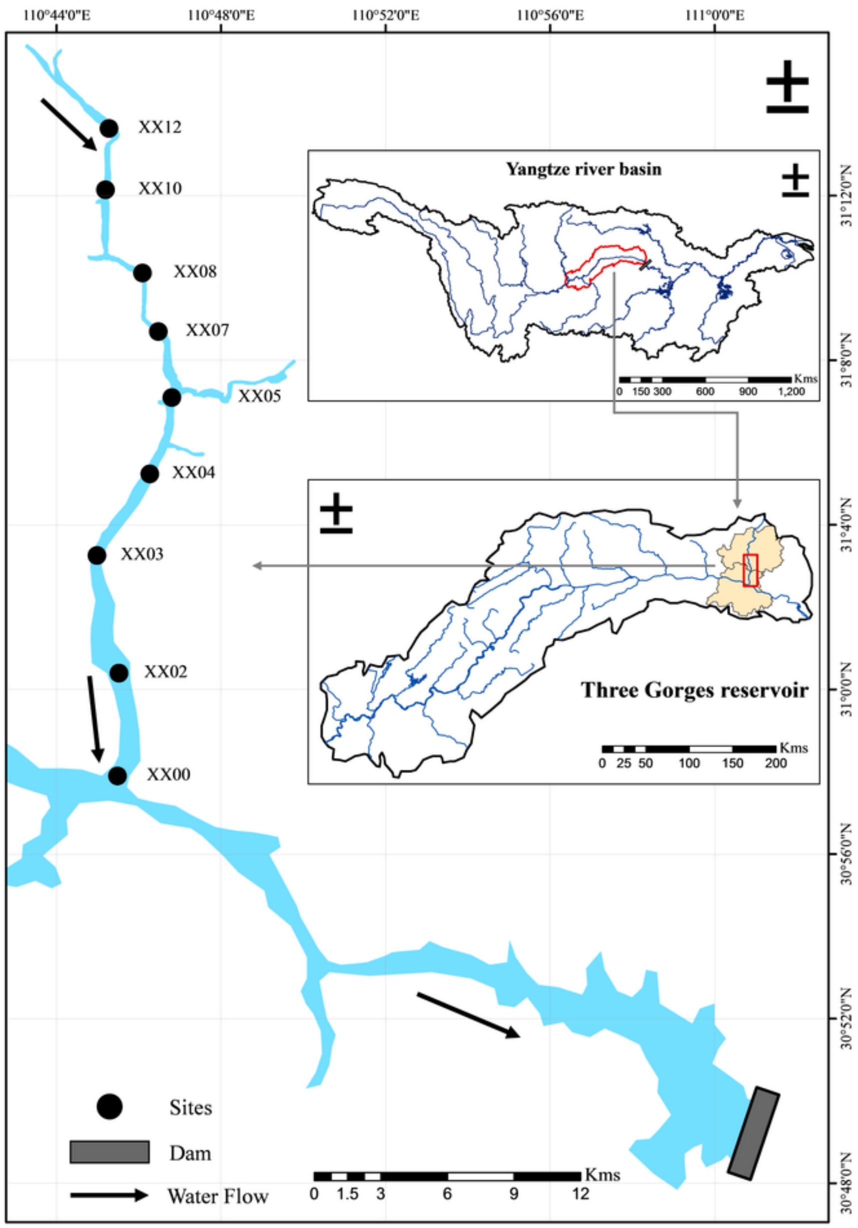

Figure 1

Spatial distribution of the sampling sites in the Xiangxi Bay of Three Gorges Reservoir. Arrows in the figure represent the direction of water flow. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

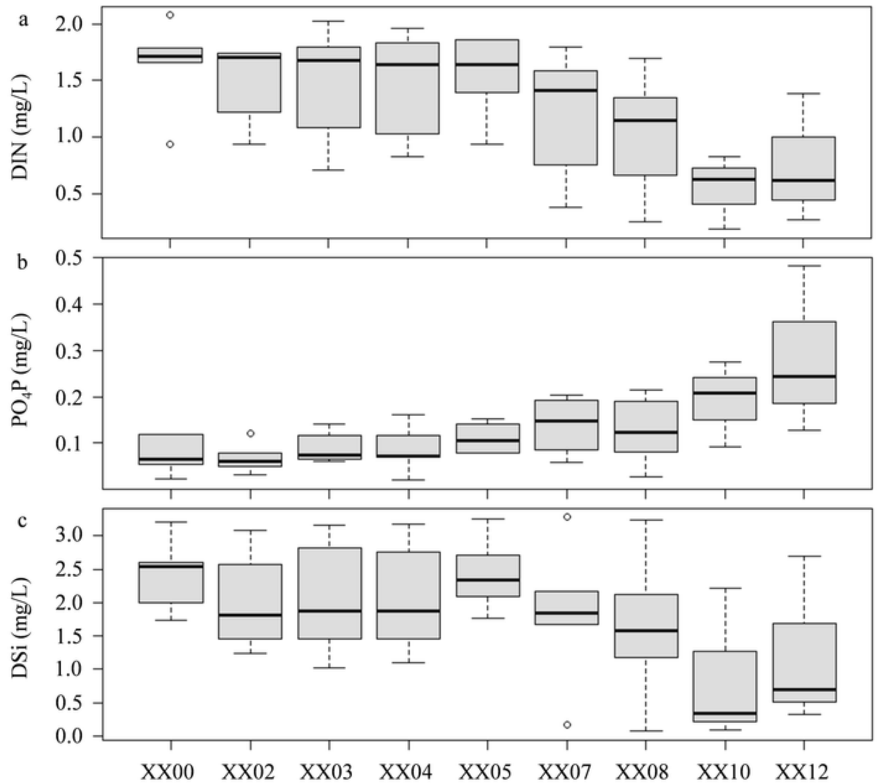

Figure 2

Boxplots showing the spatiotemporal variation of dissolved inorganic nitrogen (DIN, a), phosphate phosphorus (PO4P, b), and dissolved silicate (DSi, c) in the Xiangxi Bay of Three Gorges Reservoir. The sites were arranged by the distance to the mouth of the bay (XX00).

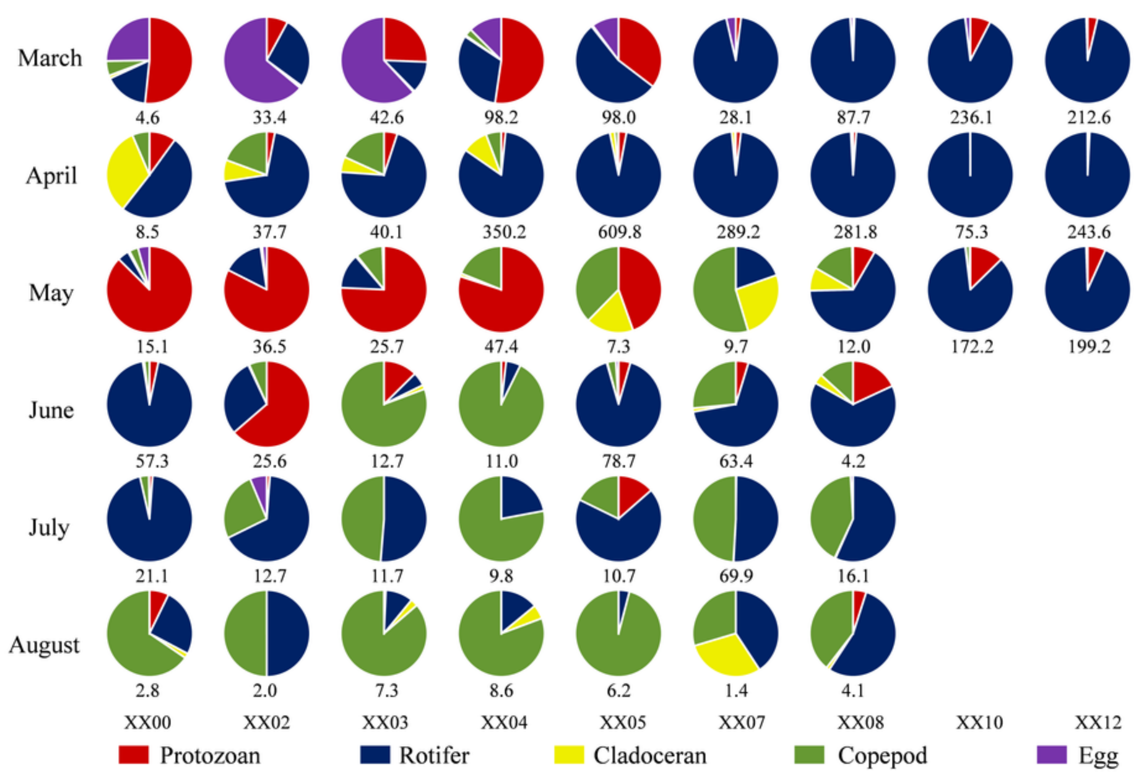

Figure 3

Relative abundance of zooplankton groups in the Xiangxi Bay of Three Gorges Reservoir. Numbers under each pie represent the total abundance (ind./L) for the site.

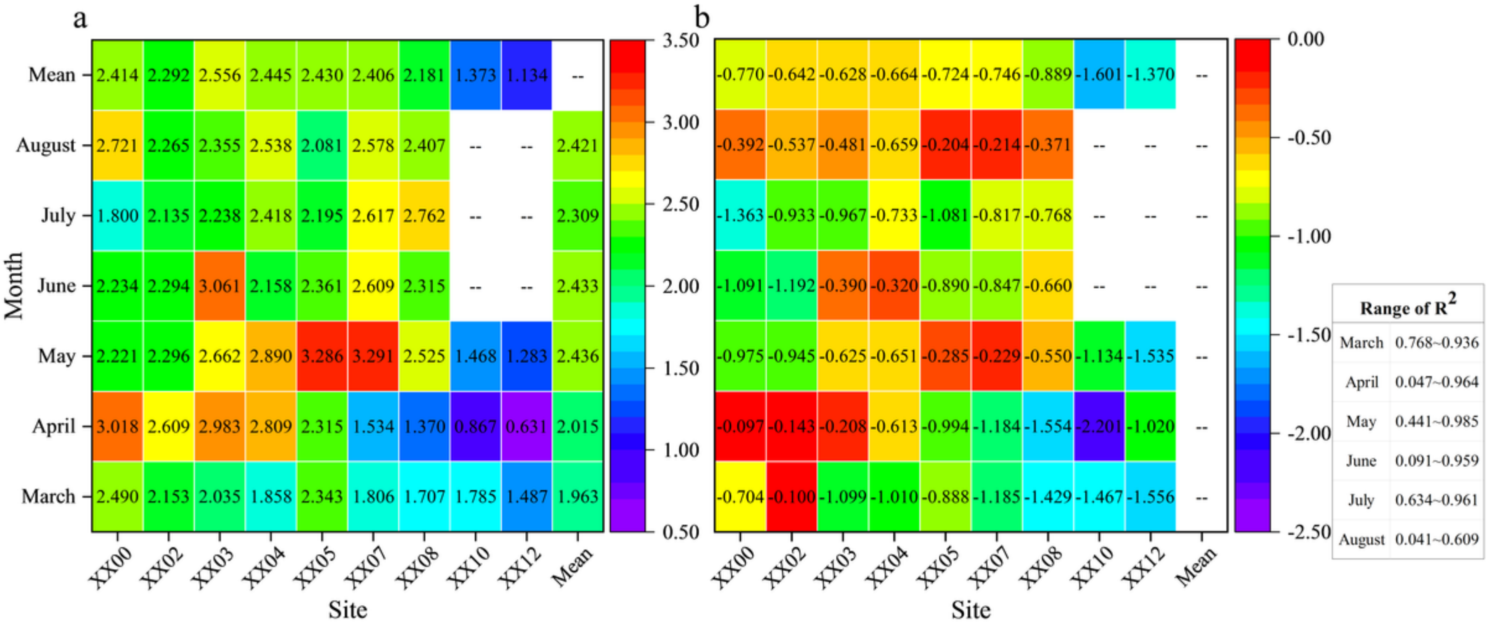

Figure 4

Spatiotemporal variations of zooplankton size diversity (a) and NBSS slope (b) in the Xiangxi Bay of Three Gorges Reservoir. The R2 in the right panel is the fitness of the linear regression analysis in estimating NBSS.

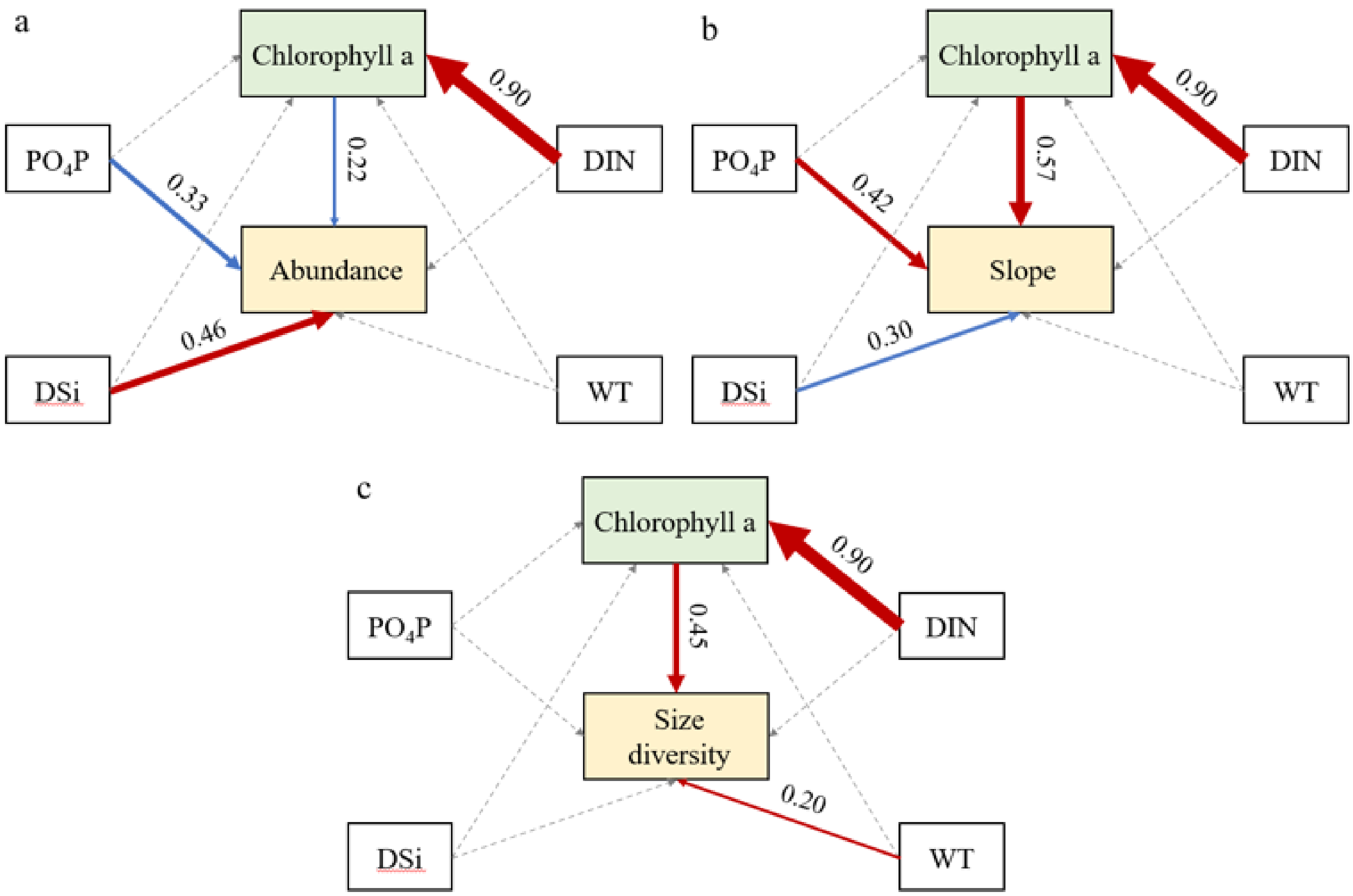

Figure 5

Result of structural equation modeling (SEM) for the direct and indirect effects of the selected environmental variables on zooplankton community (a: Abundance, b: NBSS slope, c: Size diversity). The red solid arrows indicate the negative effects, blue solid arrows indicate the positive effects, and the dashed gray arrows represent non-significant effects. The width of arrows is weighted according to standardized path coefficients.