



Benthic assemblages in relation to planktonic assemblages in a eutrophic, thermally stratified reservoir

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ABSTRACT: Few studies have explored the relationship between benthic and planktonic assemblages in reservoirs, despite their role in food chains and maintaining ecological functions. Macroinvertebrates play a crucial role in food webs and contribute about 42% of whole-lake secondary productivity. Therefore, their status is vital for maintaining good ecological functions. In this study, we selected Nanwan Reservoir, a eutrophic thermally stratified reservoir in China, to evaluate the community of macroinvertebrates in different seasons and explore the relationships between macroinvertebrate assemblages and different planktonic groups, including phytoplankton, protozoans, rotifers, and planktonic crustaceans. Cyanophyta and Bacillariophyta dominated the phytoplankton assemblages, and their proportions varied with seasons. The bad community of macroinvertebrates in summer, autumn, and winter could be attributed to the excessive growth of Cyanophyta or other phytoplankton. Based on the results of partial least squares regression, an algorithm used for prediction, we determined that the excessive growth of algae, crustaceans, protozoans, and Cyanophyta was detrimental to the development of macroinvertebrates, and was indicative of high nutrient loads in the reservoir. However, the growth of Bacillariophyta, Chrysophyta, and Euglenophyta was advantageous to macroinvertebrate assemblages and indicated a better ecological condition of the reservoir. The results of partial least squares structural equation modeling demonstrated close associations between phytoplankton and both zooplankton and macroinvertebrates, indicating their interdependence in this reservoir system. Our study results imply that the status of macroinvertebrates can be predicted by the abundance of some planktonic assemblages, and cost savings from selecting one of the planktonic groups to monitor ecological conditions could be accomplished in future studies.

KEY WORDS: Benthic and planktonic assemblages · Ecological condition · Congruence · Excessive growth · Eutrophication · Thermal stratification · Reservoir

1. INTRODUCTION

Reservoirs are man-made aquatic systems that are regulated by humans. They are widely distributed in the world, particularly in regions with relatively few natural lakes (Lin & Han 2001, Lin et al. 2003). These systems have 2 main food chains: the grazing food chain and the detrital food chain. In the grazing food

chain, phytoplankton serve as primary producers, and zooplankton as secondary producers; filter-feeding and omnivorous fish feed on the primary and secondary producers (Amaral et al. 2021), and carnivorous fish prey on the filter-feeding and omnivorous fish. In the detrital food chain, macroinvertebrates feed on detritus and are preyed upon by omnivorous fish, while carnivorous fish prey on the omnivorous fish.

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These 2 key food chains are short and interconnected, forming simple food webs in reservoir systems (Wu et al. 2012). Phytoplankton, zooplankton, and macroinvertebrates are crucial components of energy flow and nutrient recycling through the food webs in reservoir systems. They are also commonly considered to be excellent indicators of environmental changes in these systems (Sousa et al. 2008, Pinto et al. 2014).

In aquatic ecosystems, top-down effects refer to the impacts of predators on the lower trophic levels of the food web, and bottom-up effects refer to the influence of the lower trophic levels of the food web (limited by resource availability) on the higher trophic levels (Rettig & Smith 2021, Karpowicz et al. 2023, Zhang et al. 2023). There are strong interactive relationships between phytoplankton and zooplankton in aquatic ecosystems. The main systematic groups of zooplankton, encompassing many taxa, feed on phytoplankton and affect the structure of phytoplankton assemblages through selective grazing; these are considered top-down effects in aquatic systems (Li et al. 2020). In turn, changes in phytoplankton assemblages influence the taxonomic composition and dominance of zooplankton through food chains, and are considered bottom-up effects in aquatic systems (Jeppesen et al. 2002, Scheffer & Nes 2007, Utete et al. 2017). For example, copepods and cladocerans can control large algal species such as diatoms, Cyanophyta, and Chlorophyta, while rotifers, as filter feeders, can exert strong predation pressure on smaller algal species (Kozak & Goldyn 2004). Research has shown that Cyanophyta negatively impact the feeding, development, and abundance of large cladocerans, leading to declines in the cladoceran community due to its morphological complexity (Kozak & Goldyn 2004, Utete et al. 2017). Filtration or grazing of macrozooplankton, such as cladocerans and calanoids, controls the development of small organisms or microplankton and stimulates the development of large phytoplanktonic organisms (Gutierrez et al. 2020). Similarly, microzooplankton, such as rotifers and nauplii, exert predation pressures on micro- and nanophytoplankton, and there is a positive correlation between them (Kozak & Goldyn 2004). Overall, zooplankton can restrict the development of phytoplankton and microbes in aquatic ecosystems by top-down effects (Gao & Chen 2008), but the abundance of zooplankton during the annual cycle oscillates with that of the phytoplankton by bottom-up effects (Mukherjee et al. 2010).

Additionally, there are strong interactive relationships between macroinvertebrates and zooplankton due to predator–prey interactions by top-down and bottom-up effects (Kübar et al. 2005, Liu & Wang

2008). In lakes or reservoirs, macroinvertebrate predators play a central role in the food web by preying on smaller organisms such as cladocerans while also serving as prey for fish, thus mediating cascading effects to lower levels (Arnér et al. 1998, Zimmer et al. 2001). For example, in small, boreal-shield, fishless lakes, crustacean zooplankton assemblages are often regulated by macroinvertebrate predators such as *Buena macrotibialis* and *Chaoborus punctipennis* (MacPhee et al. 2011). Furthermore, some taxa of macroinvertebrates use phytoplankton as their food source, such as bivalves, which filter phytoplankton, bacteria, and particulate organic matter from the water column and control primary production when their biomass is large relative to the water volume and the hydrologic residence time is long (Vaughn & Hakenkamp 2001, Sun et al. 2022, Du et al. 2023). Research has shown that macroinvertebrates feed mainly on detritus but also consume large amounts of plankton, and benthic food webs appear to be based on detritus and primary production in shallow lakes (Liu et al. 2006, Liu & Wang 2008).

Studies have shown that thermal stratification is a common characteristic of deep-water lakes and reservoirs, significantly affecting the vertical distribution of dissolved oxygen concentration and plankton populations (Jones et al. 2011, Zhang et al. 2015, Niu et al. 2016, Qiu et al. 2016, Novais et al. 2019). The formation of thermal stratification can deteriorate water quality and accelerate the consumption of dissolved oxygen in the bottom water (Lu & Li 2014). Thermal stratification also affects the vertical distribution of phytoplankton populations, resulting in higher abundances in surface water than in the bottom water and sharp declines in biomass below the thermocline (Lin et al. 2010, Niu et al. 2016). The vertical distribution of zooplankton is related to temperature and oxygen decreases, with scarce populations in the hypolimnion and abundant populations in the epilimnion and metalimnion (Pinel-Alloul et al. 2004, Kübar et al. 2005). Overall, the scarcity of plankton assemblages in the hypolimnion likely results in a lack of food resources for macroinvertebrates in deep reservoirs. This scarcity becomes a limiting factor for the development of benthic assemblages when reservoirs are in a state of eutrophication and experience long periods of thermal stratification.

In China, many reservoirs have been investigated to calculate fish productivity when considering the utilization of fishery resources. Plankton and macroinvertebrates have been studied, as these assemblages provide significant food sources for fish. However, the relationships between benthic and planktonic assem-

blages such as macroinvertebrates and plankton have not been extensively explored, despite playing key roles in food chains and maintaining ecological functions in man-made systems (Dong et al. 1986, Wang et al. 1994, Peng 1995, Kuang & Xia 1996, Yang et al. 1996). In contrast, the relationships between macroinvertebrates and abiotic factors have been relatively more explored in reservoirs (Li et al. 2013, Lu et al. 2013, Jiang et al. 2014). Research has shown that about 30% of energy in lake systems is derived from plankton, such as cyanobacteria, protozoans, and rotifers (Liu & Wang 2008). Additionally, macroinvertebrates contribute approximately 42% of whole-lake secondary productivity (Vadeboncoeur et al. 2002, Liu et al. 2006), highlighting the importance of macroinvertebrate assemblages in food webs and the maintenance of good ecological functions.

Studies based on bottom-up and top-down effects are mostly based on shallow lakes, but relatively few on deepwater reservoirs with thermal stratification. In this study, we investigated the relationships of different planktonic groups (phytoplankton, protozoans, rotifers, and planktonic crustaceans) with macroinvertebrates in a thermally stratified reservoir with eutrophication, to understand the responses of benthic macroinvertebrate assemblages to the abundance of plankton, and to further test the following hypothesis: abundant plankton cannot be fully utilized by macroinvertebrates in deep reservoirs with thermal stratification, and their relationship is inconsistent with the expectation that abundant food resources can promote the development of benthic assemblages in shallow lakes. Thus, we selected a deepwater reservoir with thermal stratification in China, evaluated the community status of macroinvertebrates in different seasons, and explored the relationships between the macroinvertebrate community status and plankton to test whether abundant plankton can promote the development of benthic macroinvertebrate assemblages in such a reservoir system. In this study, we extend the relationship between macroinvertebrates and abiotic factors to biotic factors, which helps us better understand the effects of abiotic factors on the state of benthic communities.

2. MATERIALS AND METHODS

2.1. Study area

The Nanwan Reservoir is located in a transition zone with a monsoon climate ranging from subtropical to warm temperate in Henan Province of China. The re-

gion experiences 4 distinct seasons, with abundant rainfall in spring, frequent heavy rains in a hot summer, moderate rainfall in a cool autumn, and synchronous rain and snowfall in a short and cold winter, resulting in significant seasonal variation in precipitation. The reservoir covers an area of about 28.965 km², with a width of 2–3 km and a length of 70 km. It has a catchment area of 1100 km², a total capacity of approximately 1.63 × 10⁹ m³, and an average depth of 17.4 m. The maximum depth of this reservoir reaches up to 38 m. The inundation area is mainly composed of 50% mountains, 28% hills, 18% farmland, and 1% river channels, which are part of the reservoir region. In the region, the annual average sunshine time is 2180 h, the average transparency (Secchi depth) is around 1.5 m, the annual average temperature is 16.3°C, and the average rainfall is approximately 1140 mm. Rainfall mainly occurs between June and September. The annual average evaporation for the whole lake is about 935 m³, and the water exchange coefficient is 0.95. The reservoir serves multiple purposes, including flood control, power generation, aquaculture, tourism, and urban water supply (Xin 2003). Historical data show that the reservoir has been eutrophic since 2007, with a thermal stratification phenomenon (Chen et al. 2009). The reservoir is divided into 9 areas according to the function zoning of the reservoir, watershed soil type, vegetation, and land use in the basin. A total of 9 sampling sites were set up within the reservoir to collect biological samples, based on the principle of having 1 sampling station in each area (Fig. 1).

2.2. Data collection

Four seasonal investigations were carried out in the Nanwan Reservoir, with sampling taking place in March 2016 (spring), July 2016 (summer), September 2016 (autumn), and November 2015 (winter). We collected biological samples from phytoplankton, zooplankton, and macroinvertebrates simultaneously. Macroinvertebrate samples were collected using a modified Peterson grab (area 0.0625 m²). The quantitative samples of phytoplankton, protozoa, and rotifers were collected from 1.5 l of water, fixed with 25 ml Lugol's solution for 48 h, and siphoned to 30 ml twice for microscopic examination. The quantitative samples of planktonic crustaceans from 10 l of water were filtered by a plankton net with a mesh size of 65 µm and concentrated into 100 ml for microscopic examination. In quantitative sampling, water samples from different water layers were mixed and sampled. Detailed biological sample collection, preservation,

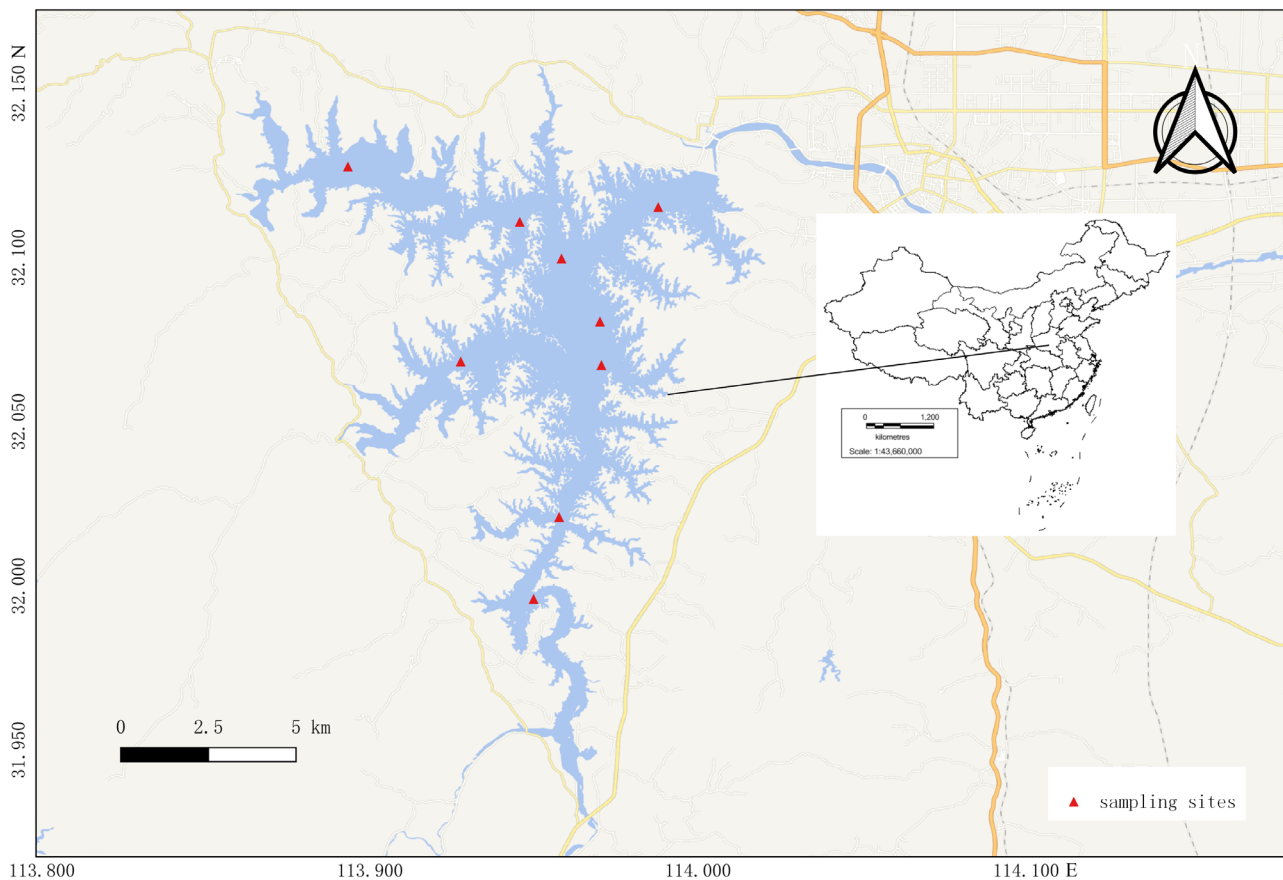


Fig. 1. Sampling locations in Nanwan Reservoir, China

and identification were undertaken by referring to available literature (Jiang & Du 1979, Shen 1979, Hu 1980, Shen et al. 1990, Morse et al. 1994, Zhuge 1997). For macroinvertebrates, mollusks were identified to the species level, aquatic insects and oligochaetes were identified to the genus level, while others were identified to possible levels. For phytoplankton and zooplankton, samples were identified to the species level. The biomass of macroinvertebrates was measured by an electronic balance with an accuracy of 0.0001 g.

2.3. Data analysis

The status of benthic assemblages in the Nanwan Reservoir was evaluated using the integral index of community state (IICS). This rank index combines 4 characteristics of the community: population N (species m^{-2}), biomass B ($g\ m^{-2}$), species number per site S , and species diversity H evaluated by the Shannon-Wiener index. The formula for IICS is as follows:

$IICS = (RN + 2RB + RS + RH)/5$, where RN , RB , RS , and RH are the ranks of the site in terms of N , B , S , and H , respectively. In practice, rank 1 corresponds to the maximum values of individual indices. The better the abundance and diversity of the organisms, the lower the IICS value, indicating a better community status (Bakanov 2003). In total, the IICS can fully characterize the community state of benthic macroinvertebrate communities.

In this study, the Spearman test and partial least squares regression (PLSR) were simultaneously used to explore the correlations between the IICS and the densities of planktonic assemblages, including protozoans, rotifers, planktonic crustaceans, phytoplankton, and orders of phytoplankton, for enhancing the reliability of the results. In the PLSR model, IICS was considered the dependent variable, while all other parameters were predictor variables. Predictor variables with weights greater than 0.20 were considered influential in the model (Malmqvist & Hoffsten 1999). The Spearman test and PLSR were conducted using SPSS version 20.

We used partial least squares structural equation modeling (PLS-SEM) to investigate the connections between plankton and macroinvertebrate assemblages by constructing a proposed research model. The analysis offers parameter estimates linked to specific pathways, along with measures of direct, indirect, and total effects. These estimates provide valuable insights into the strength and significance of the relationships between variables within the model (dos Santos et al. 2020). In the PLS-SEM model, 3 latent variables were created to represent the status of phytoplankton, zooplankton, and macroinvertebrate assemblages, respectively. The plankton status was assessed by the densities of each broad taxonomic group, while the macroinvertebrate status was measured using the IICS index and the 4 community characteristics (N, B, S, and H). In the PLS-SEM model, the outer loadings concerning the relationship between latent variables, and their corresponding observed indicators, along with the path coefficients among latent variables, and the adjusted R-square values, were all calculated. The PLS-SEM is a non-parametric analysis method that does not depend on distributional assumptions. This approach is well-suited for examining intricate causal models with limited sample sizes, and imposes fewer strict assumptions regarding the normality of data compared to other methods (Wong 2013, Afthanorhan 2014). The PLS-SEM analyses were performed using SmartPLS version 4.0 software.

3. RESULTS

3.1. Planktonic assemblages

In the 4 seasonal investigations, a total of 176 taxa of phytoplankton were collected (Table S1 in the Supplement at www.int-res.com/articles/suppl/b033p055_supp.pdf), including 73 taxa of Chlorophyta, 34 taxa of Bacillariophyta, 42 taxa of Cyanophyta, 3 taxa of Chrysophyta, 6 taxa of Cryptophyta, 7 taxa of Pyrrophyta, and 11 taxa of Euglenophyta. The total average density was 8.8×10^6 cells l^{-1} . In spring, the average density was 2.5×10^6 cells l^{-1} , with the percentages of Cyanophyta, Bacillariophyta, Pyrrophyta, Euglenophyta, and Chrysophyta being 18.70, 48.27, 7.66, 5.52, and 2.72%, respectively. In summer, the average density was 7.37×10^6 cells l^{-1} , with the percentages of Cyanophyta, Bacillariophyta, Cryptophyta, Chlorophyta, Pyrrophyta, Euglenophyta, and Chrysophyta being 80.75, 5.60, 9.41, 3.76, 0.37, 0.08, and 0.03%, respectively. In autumn, the average den-

sity was 12.95×10^6 cells l^{-1} , and percentages of Cyanophyta, Bacillariophyta, Pyrrophyta, Chrysophyta, Chlorophyta, Euglenophyta, and Cryptophyta were 98.03, 0.80, 0.01, 0.02, 0.70, 0.05, and 0.39%, respectively. In winter, the average density was 12.4×10^6 cells l^{-1} , and percentages of Bacillariophyta and Cyanophyta, the dominant taxa, were 19.35 and 62.52%, respectively (Fig. 2).

A total of 69 taxa of protozoans were collected in the 4 surveys (Table S2), and the total average density was 30 770.67 ind. l^{-1} . The average densities in spring, summer, autumn, and winter were 12 414, 32 733.33, 50 333, and 27 602 ind. l^{-1} , respectively. We collected 42 taxa of rotifers, and the total average density was 1501.67 ind. l^{-1} . The densities in spring, summer, autumn, and winter were 1108, 1960, 2600, and 338.67 ind. l^{-1} , respectively. A total of 15 taxa of planktonic crustaceans were collected, including 6 taxa of cladocerans and 9 taxa of copepods. The total average density was 92.20 ind. l^{-1} , with the spring, summer, autumn, and winter average densities of 38.30, 68.60, 221.00, and 33.90 ind. l^{-1} , respectively (Fig. 3).

3.2. Benthic assemblages

The 4 seasonal investigations collected a total of 20 taxa of macroinvertebrates (Table S3), including 12 taxa of aquatic insects, 7 taxa of oligochaetes, and 1 taxon of others. The dominant taxa were *Procladius* sp., *Tokunagayusurika* sp., and *Limnodrilus hoffmeisteri*. The average density and biomass in spring were 400.89 ind. m^{-2} and 1.4901 g m^{-2} , respectively. The average density and biomass in summer were, respec-

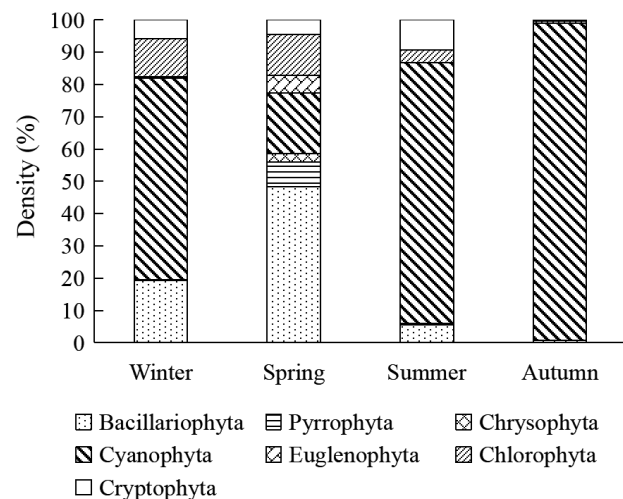


Fig. 2. Seasonal composition of phytoplankton in Nanwan Reservoir

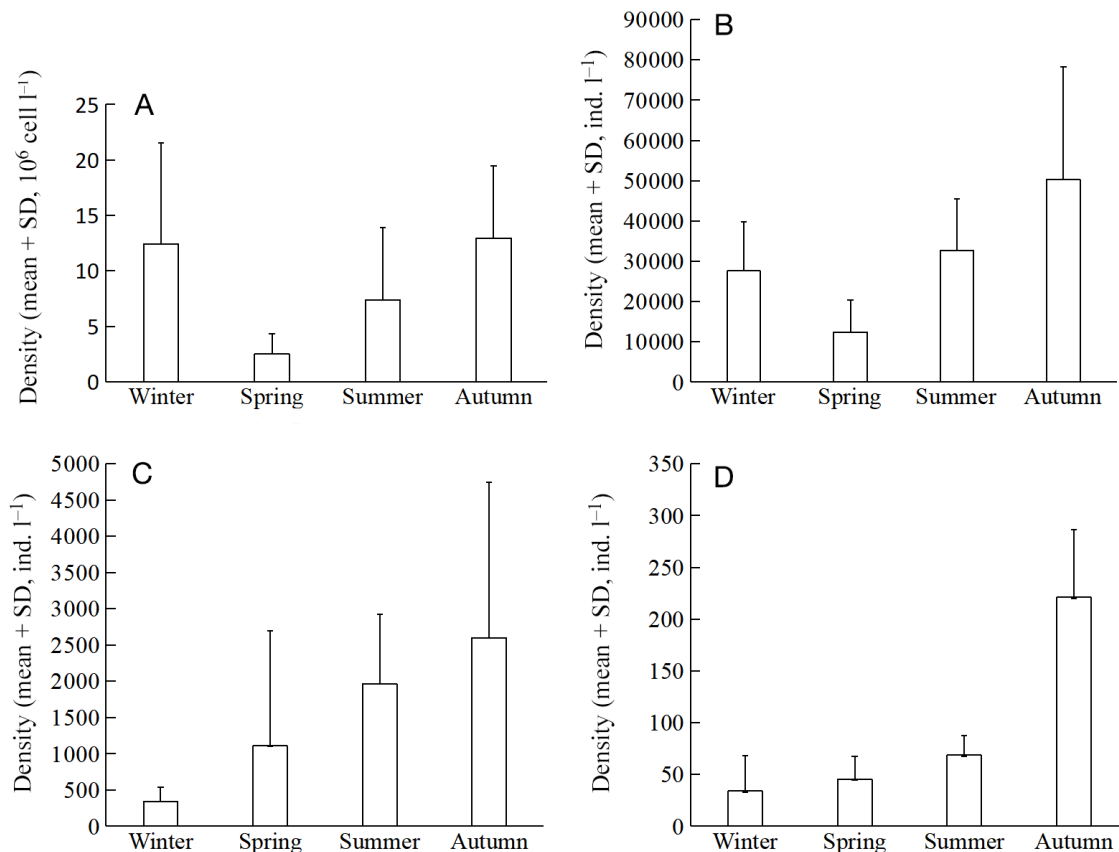


Fig. 3. Densities of planktonic assemblages in different seasons. (A) Phytoplankton, (B) protozoa, (C) rotifers, (D) planktonic crustaceans

tively, 74.67 ind. m⁻² and 0.2162 g m⁻²; in autumn 74.96 ind. m⁻² and 0.0836 g m⁻² and in winter 124.44 ind. m⁻² and 0.1917 g m⁻². The taxa per site and Shannon-Wiener index were 4.8 and 0.8948 in spring, 2.3 and 0.6163 in summer, 1.8 and 0.3275 in autumn, and 3.0 and 0.7912 in winter, respectively.

Among the 4 seasons, the value of IICS was the lowest in spring, indicating that the status of the macroinvertebrate community in this season was the best. On the other hand, the IICS value was the highest in autumn, indicating that the macroinvertebrate community status in this season was the worst. Overall, the status of the macroinvertebrate community was ranked as spring > winter > summer > autumn (Fig. 4).

3.3. Relationships between benthic and planktonic assemblages

The Spearman test results indicated that the densities of protozoans, Cyanophyta, and phytoplankton had positive correlations with IICS (correlation coefficient of 0.504, 0.607, and 0.506, respectively), while

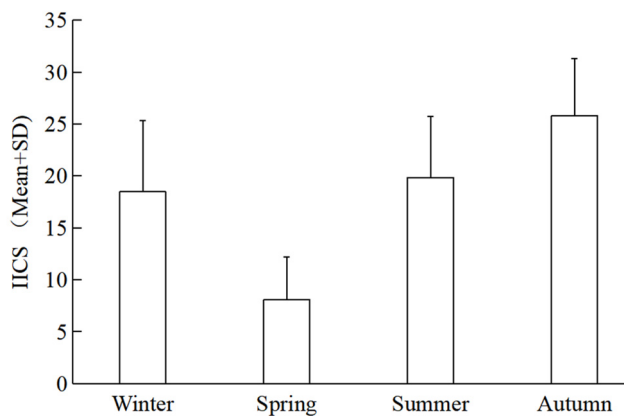


Fig. 4. Values of the integral index of the community state (IICS) in different seasons

the densities of Bacillariophyta and Euglenophyta had negative correlations with IICS (correlation coefficient of -0.416 and -0.612 , respectively). Conversely, the augmentation of Bacillariophyta and Euglenophyta densities contributed to the enhancement of macroinvertebrate community status. Among

Table 1. Correlation coefficients between variables related to densities of benthic and planktonic assemblages in Nanwan Reservoir based on Spearman correlation analysis (*p < 0.05, **p < 0.01). IICS: integral index of community state

	IICS	Crustaceans	Rotifers	Protozoans	Bacillariophyta	Pyrrhophyta	Chrysophyta	Cyanophyta	Euglenophyta	Chlorophyta	Cryptophyta
Crustaceans	0.325	1									
Rotifers	0.331	0.355*	1								
Protozoans	0.504**	0.535**	0.695**	1							
Bacillariophyta	-0.416*	-0.697**	-0.318	-0.268	1						
Pyrrhophyta	-0.082	-0.145	0.377*	0.083	0.169	1					
Chrysophyta	-0.245	-0.039	0.204	-0.024	-0.016	-0.016	1				
Cyanophyta	0.607**	0.389*	0.462**	0.725**	-0.211	-0.142	-0.212	1			
Euglenophyta	-0.612**	-0.542**	-0.304	-0.529**	0.565**	0.16	0.255	-0.597**	1		
Chlorophyta	-0.277	-0.618**	-0.333	-0.236	0.768**	0.200	-0.137	0.013	0.355*	1	
Cryptophyta	-0.212	-0.361*	-0.083	0.02	0.519**	0.447**	0.002	0.059	0.147	0.746**	1
Phytoplankton	0.506**	0.294	0.424*	0.688**	-0.025	-0.055	-0.164	0.964**	-0.420*	0.173	0.194

the variables of planktonic assemblages, the densities of rotifers, crustaceans, and Cyanophyta exhibited strong correspondence. Additionally, an increase in the density of phytoplankton facilitated the rise of rotifer and protozoan densities (Table 1).

In the PLSR model, the latent factor 1 accounted for 42.80% of the variance of IICS, while the remaining latent factors explained less than 8% of the variance, which implies that latent factor 1 served as a robust independent variable for predicting the dependent variable (Table 2). The absolute values of weights in latent factor 1 of abiotic factors such as densities of crustaceans, protozoans, phytoplankton, and the phytoplankton orders Bacillariophyta, Chrysophyta, Cyanophyta, and Euglenophyta, were higher than 0.20 (Table 3).

In the PLS-SEM model, the outcomes of path coefficients indicated a close association between phytoplankton and zooplankton, and between phytoplankton and macroinvertebrates. For instance, the primary producer (phytoplankton) had a negative impact on the secondary producer (zooplankton) (-0.561), while simultaneously having a positive influence on the benthic settlers (macroinvertebrates) (0.531). Moreover, there was a negligible impact of zooplankton on macroinvertebrates (-0.198). Combining the outer loadings of each latent variable and path coefficients between latent variables demonstrated that the abundance of phytoplankton and Cyanophyta had a positive correlation with IICS, but exhibited a negative relation with density, biomass, species richness per site, and Shannon-Wiener index. However, Chlorophyta abundance showed the opposite trend. The abundance of phytoplankton and Cyanophyta had a positive impact on the growth of the zooplankton population (Fig. 5).

Table 2. Results of partial least squares regression analysis for independent (x) and dependent (y) variables, including the proportion of variance (x and y) explained by each factor, and the cumulative proportion of variance (y) explained. Note: R_x^2 is the proportion of the variance in the independent variable matrix used in the model, R_y^2 is the proportion of the variance which can be predicted by the model

Latent factors	R_x^2	R_y^2	Cumulative y variance (R^2)	Adjusted R^2
1	0.291	0.445	0.445	0.428
2	0.190	0.052	0.498	0.465
3	0.111	0.072	0.570	0.527
4	0.090	0.032	0.603	0.548
5	0.132	0.013	0.615	0.547

Table 3. Weights of independent variables in the latent factors in the partial least squares regression model. Note: the variables with absolute weight value higher than 0.2 are marked in **bold**

Variables	Latent factors				
	1	2	3	4	5
Crustaceans	0.418	0.031	-0.172	-0.272	-0.142
Rotifers	0.157	-0.262	-0.505	-0.018	-0.653
Protozoans	0.335	-0.200	-0.183	0.377	0.233
Bacillariophyta	-0.246	-0.027	0.547	0.423	0.587
Pyrrophyta	-0.193	0.510	0.986	0.566	-0.183
Chrysophyta	-0.278	-0.277	-0.392	0.277	0.151
Cyanophyta	0.427	0.039	0.327	-0.063	-0.191
Euglenophyta	-0.453	-0.368	-0.713	-0.761	-0.796
Chlorophyta	-0.165	-0.585	-0.483	-0.628	-0.657
Cryptophyta	-0.062	-0.317	-0.091	0.155	0.268
Phytoplankton	0.309	-0.055	0.336	-0.032	-0.133

4. DISCUSSION

The composition of phytoplankton assemblages in reservoirs can vary depending on nutrient levels. In low-nutrient reservoirs, phytoplankton may mainly include Bacillariophyta–Pyrrophyta, Bacillariophyta–Chlorophyta, or Chrysophyta–Bacillariophyta, whereas high-nutrient reservoirs may have mainly Cyanophyta–Bacillariophyta or Cyanophyta–Chlorophyta (Lin et al. 2003). In Nanwan Reservoir, phytoplankton assemblages were mainly dominated by

Cyanophyta and Bacillariophyta, with varying proportions across seasons. During summer, autumn, and winter, Cyanophyta demonstrated overwhelming dominance (Fig. 2), indicating eutrophication or high nutrient levels in those seasons. Eutrophication in aquatic systems is characterized by excessive phytoplankton growth and algae blooms. The presence of direct sunlight leads to supersaturation of dissolved oxygen in the upper water zone, as a result of intense photosynthesis by algae. However, in the lower water zone, the high density of phytoplankton obstructs light penetration, resulting in weak light areas. This phenomenon, along with respiration by algae and decomposition of organic matter by heterotrophic bacteria, causes the water body to become anoxic (Liu 2004, Xu et al. 2007). Studies demonstrate that anoxic conditions in the lower layer of a waterbody are detrimental to the growth and reproduction of benthic macroinvertebrate assemblages (Pavela et al. 1983). In our study, poor macroinvertebrate status during the summer, autumn, and winter seasons could be attributed to excessive growth of Cyanophyta or phytoplankton (Figs. 2 & 3A). Research has shown that the

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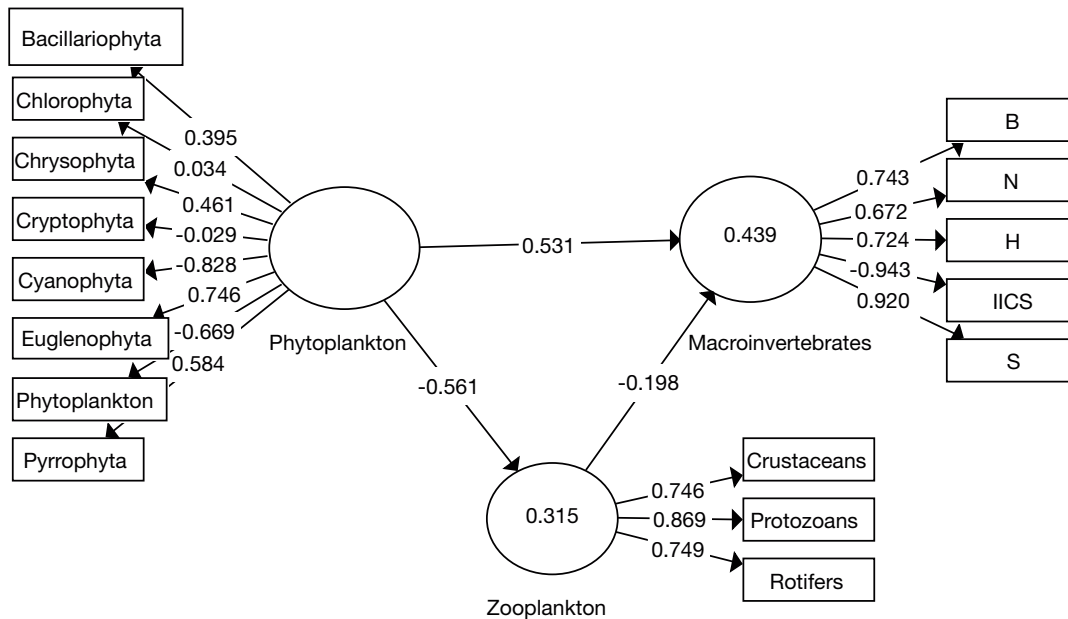


Fig. 5. Path diagram of the structural equation model. Circles represent latent variables; boxes represent observed variables (B: biomass; N: population, species m⁻²; H: species diversity; IICS: integral index of community state; S: species number per site). Arrows represent predicted effects. Values within the arrows between observed variables and latent variables represent outer loadings. Values within the arrows between latent variables represent path coefficients. The values within the circles are adjusted R²

numbers of phytoplankton and macroinvertebrate taxa decrease, while the densities of both assemblages increase during the transformation process from mesotrophication to eutrophication (Kuang & Xia 1996, Liu 2004). Based on the percentages of Cyanophyta in different seasons, it can be inferred that the eutrophication in spring was better than in other seasons. The response of macroinvertebrates in Nanwan Reservoir differed from the previously observed experience, where the density typically increases during the process of eutrophication.

In this study, the dominant taxa, namely *Procladius* sp., *Tokunagayusurika* sp., and *Limnodrilus hoffmeisteri*, were indicators of eutrophication (Iwakuma 1992, Gong et al. 2001), with *Tokunagayusurika* sp. being widely distributed in eutrophic lakes and reservoirs in northern and southern China (Ma et al. 2004, Chen et al. 2012). In a lake system, some macroinvertebrate taxa, such as oligochaetes and chironomids, are considered to be useful indicators of oxygen condition and trophic status. Different species of these taxa prevail depending on the trophic status, which reflects the quality and quantity of food and oxygen status. When the environmental conditions are not too severe, food is the primary factor influencing the community composition. However, in the case of intense organic pollution, it is the oxygen concentration that limits species survival and community composition (Rossaro et al. 2007). In Nanwan Reservoir, the quality and quantity of food did not seem to be limiting factors in improving the community status of macroinvertebrates, as the plankton, being their potential food source, was abundant. It is likely that the oxygen concentration in the lower water layer was the limiting factor in the development of macroinvertebrates. This could be related to the formation of persisting water temperature stratification, hindering the exchange of oxygen between the upper and lower water layers.

Studies have shown that the predator–prey relationships between fish and crustaceans could explain the decrease in the average size of crustaceans and the absence of large-bodied forms in shallow and highly eutrophic lakes (Gulati 1990). In 40 lakes in south-central Ontario (Canada), significant concordance patterns in community structure between fish and macroinvertebrates could also be explained by their predator–prey relationships (Jackson & Harvey 1993). However, changes in the thermal structure of lakes have strong and unexpected influences on predator–prey dynamics (MacPhee et al. 2011), resulting in the community congruence between different assemblages varying with study cases (Gre-

nouillet et al. 2008). Community concordance among taxonomic groups is driven by similar responses to environmental gradients and biotic interactions (Jackson & Harvey 1993, Larsen et al. 2012, Padial et al. 2012, Vieira et al. 2015). Due to the special history of each lake or reservoir, significant relationships between different assemblages are not always detected (Paavola et al. 2003, Rossaro et al. 2007, Infante et al. 2009, Doi et al. 2013). In our study, phytoplankton, rotifers, and protozoans had synergistic effects on their respective densities (Table 1). Moreover, rotifers, crustaceans, and Cyanophyta had strong congruency in abundance, which could possibly be explained by their predator–prey relationships. For instance, zooplankton in eutrophic lakes such as Lake Taihu could utilize Cyanophyta detritus as a food source (Yu et al. 2013). In Nanwan Reservoir, higher IICS values were highly related to higher densities of protozoans, Cyanophyta, and phytoplankton, suggesting that the increase in protozoans, Cyanophyta, and phytoplankton densities coincided with the poor status of macroinvertebrate assemblages, while lower IICS values were tied to the densities of Bacillariophyta and Euglenophyta, indicating that the good status of macroinvertebrate assemblages was accompanied by the rise in Bacillariophyta and Euglenophyta.

Considering the weights associated with each variable in latent factor 1 in the PLSR model, it can be reasonably inferred that the densities of crustaceans, protozoans, phytoplankton, and some orders of phytoplankton such as Bacillariophyta, Chrysophyta, Cyanophyta, and Euglenophyta were the most influential factors that affected the community status of macroinvertebrates in this eutrophic, thermally stratified reservoir, and the excessive growth of algae, crustaceans, protozoans, and Cyanophyta was detrimental to the development of macroinvertebrates and also indicated that the reservoir was at a higher nutritional level. However, the excessive growth of Bacillariophyta, Chrysophyta, and Euglenophyta was advantageous to the macroinvertebrate assemblages, which also indicated that the reservoir was in a relatively good ecological condition. The excessive growth of these assemblages was a barometer of the ecological condition of Nanwan Reservoir, which could well predict the status of macroinvertebrate assemblages. The seasonal variation in IICS well reflected changes in ecological conditions, which could also be characterized by changes in the densities of some planktonic assemblages.

In the PLS-SEM model, we found a positive association of some orders of phytoplankton with macro-

invertebrates, such as Pyrrophyta, Euglenophyta, Chrysophyta, Chlorophyta, and Bacillariophyta, and a negative association of Cyanophyta with macroinvertebrates, while the excessive growth of phytoplankton was harmful to the macroinvertebrate community status. All of these were consistent with the results of the PLSR model. We also found a weak association of macroinvertebrates with zooplankton, and a strong association of phytoplankton with zooplankton, which was manifested by the fact that abundant Cyanophyta and algae promoted the growth of zooplankton. Abundant phytoplankton and Cyanophyta were detrimental to the development of macroinvertebrates, resulting in a poor community status, but favorable for the development of zooplankton. Studies have shown that the peak in zooplankton biomass always follows the peak in phytoplankton abundance due to a dependent consumption relationship between herbivorous zooplankton and phytoplankton. For example, seasonal variation in rotifer populations was found to be positively correlated with the abundance of phytoplankton in the Xinan River in China (Tang & Liang 1999); the density and biomass of zooplankton in Donghu Lake in Wuhan were determined by the content of chlorophyll *a* (Cai 1995); and zooplankton abundance in autumn was positively correlated with the abundance of phytoplankton and diatoms in the sea area near the Nanji Islands, China (Wang et al. 1998). In the reservoir system, the interspecies relationships among plankton are similar to those observed in lakes, rivers, and oceans, but the abundance of phytoplankton can deeply affect macroinvertebrates, while zooplankton have a minimal impact.

In aquatic systems, exploring cross-taxon congruence in community structure and selecting indicator groups are used to predict the diversity of another community for cost-effective monitoring of global biodiversity (Qin et al. 2013, Velghe & Gregory-Eaves 2013). The concordance between assemblages of different organism groups has important implications for both theoretical ecology and biodiversity conservation (Grenouillet et al. 2008, Heino et al. 2009, Soininen et al. 2009). In this study, the congruence in abundance between phytoplankton, rotifers, and protozoans, as well as the strong relationships between IICS and the abundance of some planktonic assemblages, implied that the status of macroinvertebrates in this eutrophic, thermally stratified reservoir could be predicted by the abundance of some planktonic assemblages. One of these planktonic assemblages could be selected to monitor ecological conditions in future studies for cost efficiency. The results of PLSR and

PLS-SEM demonstrated a strong association between phytoplankton and macroinvertebrates, but excessive growth of phytoplankton or certain phytoplankton orders had a negative impact on the development of macroinvertebrate assemblages. Even though plankton plays an important role in the food chain of macroinvertebrates, our study indicated that their abundance did not promote the growth of these benthic organisms. This is in contrast to shallow lakes, where plankton can be fully utilized by benthic animals.

5. CONCLUSION

Overall, the results of our study highlight the importance of studying cross-taxon congruence in community structure to understand ecological processes in aquatic systems. The excessive growth of certain planktonic groups, such as cyanobacteria, can negatively impact the development of macroinvertebrate assemblages, and indicate a high-nutrient or eutrophic status of the ecosystem. Assessing the abundance of different planktonic assemblages can serve as a cost-effective approach to monitoring ecological conditions and predicting the status of macroinvertebrate assemblages. It is crucial to closely manage and monitor the growth of different planktonic groups to maintain a healthy and balanced aquatic ecosystem and ensure the well-being of macroinvertebrate assemblages.

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