PRIMARY RESEARCH PAPER

Niche processes shape zooplankton community structure in a sediment-laden river basin

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Abstract Zooplankton play a key role in freshwater ecosystems; however, their community succession and responses to environmental stress remain poorly understood. To fill this gap, zooplankton community dynamics in the main stream, five tributaries and three reservoirs of the Yanhe River Basin (China) were studied in spring and autumn at the zooplankton functional group (ZFG) level. Principal component analysis and non-metric multidimensional scaling were used to reveal the spatiotemporal characteristics of aquatic environmental and zooplankton community structure (ZCS), respectively. Subsequently, redundancy analysis and niche measures were conducted to explore the effects of environmental factors and biotic interactions on ZCS. Significant spatiotemporal heterogeneity in both aquatic environment and ZCS were found. Turbidity, total nitrogen, nitrite-nitrogen,

chemical oxygen demand, pH, water depth, water temperature, and chlorophyll *a* emerged as primary environmental drivers of ZCS. Regarding biotic interactions, weak competition in spring contributed to the positive community succession, while in autumn, intense competition and predation between ZFGs, along with elimination of vulnerable groups, led to community instability. Niche processes emerged as significant shaping factors in the Yanhe River Basin' ZCS. Our study provides valuable insights into zooplankton community response to environmental changes and offers potential applications for understanding other aquatic organisms and ecosystems.

Keywords Zooplankton · Niche process · Functional group · Biotic interactions · Yanhe River Basin · Check dams

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Introduction

Zooplankton play key roles in material circulation, energy flows and signal transmission in aquatic ecosystems (Thompson et al., 2015). Zooplankton have a short generation time and exhibit rapid responses to physical, chemical, and biological changes in the environment. Consequently, zooplankton are widely used as indicators in environmental assessments, with great application potential in water quality monitoring and ecological research (Paturej & Goździejewska, 2005). In particular, zooplankton

community structure (ZCS) has been commonly used to assess changes in the trophic status of freshwater water bodies (Pinto-Coelho et al., 2005; Anton-Pardo et al., 2013).

In recent decades, due to increased human intervention in rivers (such as damming), reservoirs/dams have obstructed natural river flows. The resulting semi-hydrostatic or hydrostatic habitats are distinct from the flowing rivers (Baxter, 1977) and exhibit lake-like characteristics (Ko et al., 2022). Differences in hydraulic conditions and lacustrine characteristics lead to shifts in the structure and distribution patterns of zooplankton communities between rivers and reservoirs (or dams and lakes) (Portinho et al., 2016). Ko et al. (2022) observed that damming increased the species richness of the zooplankton community, but decreased its longitudinal similarity in species number and population density along the direction of river flow. In addition, Wu et al. (2022) demonstrated remarkable spatial variation in ZCS between different types of water bodies (lakes and rivers). Furthermore, Zhao et al. (2017) observed that environmental factors were more important than spatial factors in driving ZCS in habitats such as rivers.

Despite the importance of environmental factors, biotic interactions have to be considered when studying zooplankton community succession, as the resource availability and biotic interactions are equally important as environmental factors (Verity & Smetacek, 1996). Zooplankton community structure and dynamics can be better explained by taking into account biotic interactions within the community, rather than focusing solely on its relationship with environmental factors (Wu et al., 2022). Both environmental factors and biotic interactions are deterministic processes, and niche processes suggests that biological communities are determined by deterministic abiotic factors (such as pH, temperature, etc.) and biotic factors (species interactions like competition, predation, etc.) (Coz et al., 2018), attributed to the varying habitat preferences and adaptive capabilities of organisms (Hutchinson, 1957). The species niche can be defined as an n-dimensional set of abiotic and biotic conditions (Carscadden et al., 2020). In contrast, according to the neutral theory, random processes, such as birth, death, migration and limited dispersal, shape biotic communities (Hubbell, 2001). Hence, neutral theory suggests that community

similarity decreases with increasing distance between communities (Soininen et al., 2007).

Niche theory has been used extensively to study community structure, species diversity, interspecific relationships and population succession (Keddy, 1992). In a specific environment, the competitiveness, richness, and distribution of species are primarily expressed through niche breadth and overlap (Bates et al., 2020). Niche breadth measures the ability of species to utilize environmental resources in a specific habitat (Manlick & Pauli, 2020), while niche overlap estimates the extent to which two species/populations share a common set of resources or utilize the same portion of the environment (Ofomata et al., 1999). Research into interspecific relationships can quantify the biotic interactions and further decipher the mechanisms of community development and succession (Gu et al., 2019). Therefore, the combination of niche measures and interspecific relationships can effectively reflect the basic structure and function of communities (Tarjuelo et al., 2017). In addition, zooplankton niche differentiation can reportedly reduce interspecific competition and promote species co-existence (Lindegren et al., 2020).

Although zooplankton are sensitive environmental indicators, their species composition alone cannot provide a stable and accurate indicator of environmental change (Neto et al., 2014). Compared with species characteristics, functional group characteristics are more stable, which can effectively eliminate seasonal disturbances (Wu et al., 2022). Functional groups are classified by combining species with similar characteristics or behaviors in the ecosystem as much as possible (Pomerleau et al., 2015). Functional groups emphasize the ecological functions of the whole group whose responses are closely related to environmental changes, and this may help to reduce the complexity of dealing with many species, while still retaining enough information to understand community selection pressures and environmental driving factors (Litchman et al., 2013). Therefore, classifying aquatic organisms into functional groups can facilitate the understanding of their community succession (Hébert et al., 2017).

The Yanhe River, located in the heart of the Loess Plateau, is a major sediment transport tributary of the Yellow River (Yue et al., 2014). Over-cultivation and severe erosion in this area have a significant impact on the ecological health of the middle reaches of the

Yellow River and the Loess Plateau region, highlighting its importance (Gao et al., 2015). The Chinese government has made significant investments in soil and water conservation measures in this watershed, including the construction of thousands of check dams (a type of dam for sediment retention) since the 1960s (Wang, 2020). Check dams play a crucial role in reducing soil erosion within the watershed. However, the construction of these dams has also decreased the connectivity of river habitats and fragmented aquatic ecosystems (Raabe & Hightower, 2014). Therefore, check dams are an integral component of the aquatic ecology in the Yanhe River Basin. However, previous studies on the zooplankton in the Yanhe River Basin have not focused specifically on check dams as representative water bodies (Li et al., 2014; Wang et al., 2022; Xie et al., 2022). Thus, this study conducted aquatic ecological investigations on zooplankton of the Yanhe River Basin. Specifically, we investigated the dynamics of ZCS and ZFGs in three types of water bodies (main stream, tributaries, and reservoirs) during two different seasons (spring and autumn). By utilizing the characteristics of ZFGs to help reveal the distribution patterns and succession processes of zooplankton communities. Considering that ecological barriers caused by dams reduce connectivity of aquatic systems (Cote et al., 2009; Zhao et al., 2017), we hypothesize that niche processes are the primary processes that influence the zooplankton community structure in different water bodies within the Yanhe River Basin.

Materials and methods

Study area and sampling locations

The Yanhe River (36° 21′–37° 19′ N and 108° 38′–110° 29′ E) is a primary tributary (286.9 km long) in the middle reach of the Yellow River and flows through the Loess Plateau region, China (Lian et al., 2021). The river basin, with a total area of 7687 km², is part of the temperate semi-arid monsoon climate, where rainfall is concentrated in summer (Yang & Lu, 2018). It is a typical hilly and gully area and soil erosion is severe, the terrain is crisscrossed with ravines, and the ecological environment is fragile (Xie et al., 2009), leading to the construction of numerous check dams for sediment management. Check dams

serve a dual purpose: they can store water and sediment, reducing sediment discharge from the river, and when filled with silt, they can be converted into productive farmland (Shi, 2019).

In the Yanhe River basin, annual flooding occurs in summer, during which large amounts of precipitation and silt input into the rivers. As zooplankton lack the ability to withstand water flow and turbidity (Marques et al., 2006; Kamboj & Kamboj, 2020), such an environment will severely disturbs ZCS. Moreover, during winter, low temperatures cause most areas of the Yanhe River Basin to freeze, which presents challenges for investigations. Therefore, the main stream of Yanhe River, five typical tributaries (Pingqiao River, Xingzi River, Xichuan River, Nanchuan River, and Panlong River), and three reservoirs (Wangyao reservoir, Majiagou check dam, and Liujiapan check dam) were investigated in spring (April) and autumn (October) of 2021. According to the Beijing Technological Regulations of Hydrobiological Investigation (DB11T1721-2020, in Chinese) and field conditions, 10 sampling segments were selected in the main stream and three sampling segments selected in each tributary (excluding Nanchuan River, with two sampling segments). Additionally, we sampled one segment at the head, middle, and tail of each reservoir, totaling three segments per reservoir. A total of 33 sampling segments were sampled (Fig. 1); however, Liujiapan was not sampled in autumn due to weather-related factors.

Water quality analysis

A YSI 6600V2 analyzer (Xylem, USA) was used for temperature (WT), dissolved oxygen (DO), and pH. Turbidity (Turb) was analyzed in the field using a 2100Q portable turbidity meter (Hach, Loveland, CO, USA), and flow was measured using a FP211 direct-reading current meter (Global Water Instrumentation, Sunnyvale, CA, USA). Water depth was determined with a calibrated rod for the river and an SM-5A echosounder (SPEEDTECH, USA) for the reservoir. Physical water environmental factors included these above field-obtained measurements, except for pH. Mixed surface (0.5 m below the surface) and bottom (0.5 m above the bottom) water samples were stored in 1-L polyethylene bottles and transported to the laboratory under dark conditions. Total nitrogen (TN), ammonium-nitrogen (NH_4-N), nitrite-nitrogen

Fig. 1 Map of Yanhe River Basin and the distribution of sampling locations. *WY* Wangyao Reservoir, *MJG* Majiagou check dam, *LJP* Liujiapan check dam (1–10 were sampling segments on the main stream; 11–24 were sampling segments on the tributaries; WY, MJG, and LJP were reservoir sampling segments)
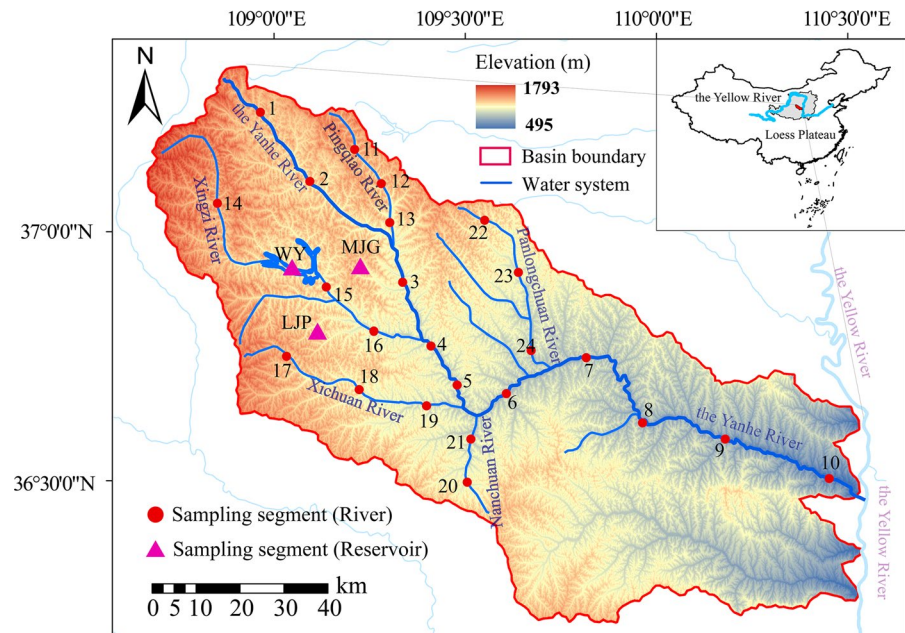
(NO$_2$-N), total phosphorous (TP), and chemical oxygen demand (COD) were determined according to the Water and Wastewater Detection and Analysis Methods (Ministry of Ecology and Environment of the People's Republic of China, 2002). Chlorophyll a (Chl-*a*) was extracted with hot ethanol (Chen et al., 2006) and quantified using a DR-6000 ultraviolet spectrophotometer (Hach, Loveland, CO, USA).

Zooplankton sample preparation and functional group classification

Qualitative samples of zooplankton were collected by filtering the upper water column with a No. 25 plankton net (mesh size 64 μm) for 3–5 min. The filtered samples were placed into a 100-mL sample vial and fixed with 5% formaldehyde solution. For quantitative analysis of protozoa and rotifers, 3-L water samples were collected in each segment and fixed with 15 mL Lugol reagent in the field. The samples were transported to the laboratory and left to stand for 48 h. Subsequently, the supernatant of each sample was siphoned smoothly and slowly every 24 h, concentrated to 50 mL by siphoning twice, and then fixed with 4% formaldehyde solution in a 100-mL sample vial. For quantitative analysis of cladocera and copepods, 20 L of mixed water sample was obtained with a 5-L water collector, filtered through the No. 25

plankton net, and fixed with 5% formaldehyde solution in a 100-mL sample vial. Prior to identification, preprocessing of zooplankton samples is required by removing the supernatant fluid from the stationary samples via siphoning. This concentrates the sample volume to 40 ml, facilitating calculations.

Zooplankton species were identified and counted using an Axio Imager 4.2 microscope (Zeiss, Germany) at ×100–400 magnification (Wang, 1961; Jiang & Du, 1979; Shen 1979; Zhang & Huang, 1991). Protozoa and rotifers were counted in full slices in a 1-mL counting frame, and the mean value of two slices was taken for each sample. Cladocera and copepods were counted several times with a 5-mL counting frame.

According to previous studies (An et al., 2017; Ma et al., 2019; Wu et al., 2022), zooplankton were divided into 10 ZFGs based on their size and feeding habits (Table S1): protozoa filter feeders (PF), protozoa carnivora (PC), rotifer filter feeders (RF), rotifer carnivora (RC), small copepod and cladocera filter feeders (SCF), small copepod and cladocera carnivora (SCC), middle copepod and cladocera filter feeders (MCF), middle copepod and cladocera carnivora (MCC), large copepod and cladocera filter feeders (LCF), and large copepod and cladocera carnivora (LCC). The division of ZFGs in the Yanhe River basin is shown in Table S2.

Data analysis

ArcGIS v10.7 (ESRI Inc., Redlands, CA, USA) was used to generate the sampling map of Yanhe River Basin. The 'factoextra' package (Kassambara & Mundt, 2020) in software *R*, version 4.3.0 (R Core Team, 2023) was used to perform a principal component analysis (PCA) based on all environmental factors to characterize the aquatic environmental characteristics of different water bodies. The Kruskal–Wallis nonparametric test was performed in SPSS v25.0 (IBM Corp., Armonk, NY, USA) because data did not follow a normal distribution and heterogeneity of residuals. Pairwise comparisons were performed using the Wilcoxon test, with *p* values adjusted using Bonferroni correction. The 'vegan' package (Oksanen et al., 2022) in *R* was used to conduct non-metric multidimensional scaling (NMDS), analysis of similarities (ANOSIM), redundancy analysis (RDA), and variance partition analysis (VPA). NMDS and ANOSIM were used based on density of ZFGs to analyze differences in ZFGs structure in different types of water bodies, while RDA was performed using density of ZFGs and water environment factors to examine the impact of environmental factors on ZFGs. During the process of RDA, we eliminate all explanatory variables whose variance inflation factors (VIF) are more than 10 in order to avoid collinearity amongst environmental indicators (Ding et al., 2021). Subsequently, significant factors were selected by the forward selection with Monte Carlo permutation tests ($N = 999$) for further analysis. VPA was employed to assess the proportion of the zooplankton community variation that could be explained by environmental factors.

The 'spaa' (Zhang et al., 2016) package in *R* was used to calculate the niche breadth, niche overlap, overall association, and association coefficient (*AC*) by using density of ZFGs, and also conducted the diagrams of niche overlap and association coefficient (*AC*), for assessing their environmental adaptation and biotic interactions. Venn diagram of zooplankton species, biaxial diagram of ZFGs density and biomass, diagram depicting the nonparametric test results for environmental factors and diagram of niche breadth were conducted using a freely available online data analysis platform (https://www.genescloud.cn). The density of each ZFG was calculated by summing the density of the zooplankton species

within it, while the biomass of each ZFG was determined by calculating the individual wet weight of each species given by Zhao (2015). All data entered into analysis were transformed into the log $(x + 1)$ format, except for the pH values.

The niche breadth (Eq. 1) was calculated using the formula proposed by Levins (1968):

$$B_i = \frac{1}{\sum_{j=1}^{R} \left(P_{ij} \right)^2} \tag{1}$$

where B_i is the niche breadth of the *i*th ZFG and ranges from 1 to a maximum value that varies depending on the dataset. *R* is the total number of sampling sites, and P_{ij} represents the proportion of the number of groups *i* in the *j*th sampling site to the number of ZFGs.

The Pianka index (Eq. 2) was used to characterize the niche overlap between ZFGs (Pianka, 1973):

$$Q_{ik} = \sum_{j=1}^{R} \left(P_{ij} P_{kj} \right) \Bigg/ \sqrt{\sum_{j=1}^{R} P_{ij}^2 \sum_{j=1}^{R} P_{kj}^2} \tag{2}$$

where Q_{ik} is the overlap value and ranges from 0 (no overlap) to 1 (fully overlap). P_{ij} and P_{kj} represent the proportions of groups *i* and groups *k* in the *j*th site to the number of ZFGs, respectively. *R* is the total number of sampling sites.

The variance ratio (*VR*, Eqs. 3–5) based on species presence or absence was used to gain insight into the overall association among different species (Schluter, 1984). The statistical quantity *W* (Eq. 6), a modification of *VR* when *N* is too small, was calculated to test the significance of association:

$$\sigma_T^2 = \sum_{i=1}^{s} P_i \left(1 - P_i \right)^2 \tag{3}$$

$$S_T^2 = \frac{1}{n} \sum_{i=1}^{n} \left(T_j - t \right)^2 \tag{4}$$

$$VR = S_T^2 / \sigma_T^2 \tag{5}$$

$$W = VR \cdot n \tag{6}$$

where σ_T^2 variance of total sample locations, *S* is the sum of ZFGs in the study area, and $P_i = n_i/n$, *n* is the sum of sampling locations, and n_i is the number

of locations with ZFG i; S_T^2 is the variance of total number of ZFGs, T_j is the total number of ZFGs present at location j, and t is obtained by rounding the mean number of all ZFGs present in the corresponding location. Under the null hypothesis of independence, the expected value of VR is 1, $VR < 1$ indicates a negative overall association, $VR = 1$ meets the null hypothesis that all ZFGs are unrelated, and $VR > 1$ implies a positive overall association. The statistical quantity W was used to test the significance of deviation of VR from 1, if there is no significant overall association between ZFGs, the probability of $(\chi^2_{0.95N} < W < \chi^2_{0.05N})$ is 90%. The chi-square (χ^2) statistics based on a 2×2 contingency table (Eq. 7) was used to examine the associations (Chai et al., 2016):

$$\chi^2 = \frac{n[|ad - bc| - 0.5n]^2}{(a+b)(a+c)(b+d)(c+d)} \quad (7)$$

where n is the number of total sampling locations, a is the number of locations where both groups occurred between ZFG pairs, b and c are the numbers of locations where only one group occurred, and d is the number of locations with no occurrence of either group between ZFG pairs.

The association coefficient (*AC*) (Eqs. 8–10) was used to test and quantify the association of each ZFGs pair, and further verify the results of overall association (Chai et al., 2016):

$$AC = (ad - bc)/(a+b)(b+d), (if ad \geq bc) \quad (8)$$

$$AC = (ad - bc)/(a+b)(a+c), (if ad < bc, d \geq a) \quad (9)$$

$$AC = (ad - bc)/(b+d)(d+c), (if ad < bc, d < a) \quad (10)$$

where AC ranges from -1 to 1. $AC = 0$ suggests that the ZFG pairs are completely independent. An AC value closer to 1 indicates a higher positive association between ZFGs, and an AC value closer to -1 indicates a stronger negative association between ZFGs.

Results

Spatiotemporal variation in aquatic environment

The first two axes of PCA based on all environmental factors explained 23.4% and 15.6%, respectively, of the total variation in spring (Fig. 2a), while in autumn, they explained 38.4% and 19.8%, respectively (Fig. 2b). The PCA based on seasonal data explained 36.1% and 17.3% of variation with the first and second axis, respectively (Fig. 2c). According to PCA, the areas of distribution of the main stream and tributaries water samples overlapped completely in both spring and autumn, but were basically separated from those of reservoirs (Fig. 2a, b). The overall distribution area of spring and autumn water samples overlapped slightly (Fig. 2c).

Based on the PCA results, the main stream and tributary were grouped together for comparison
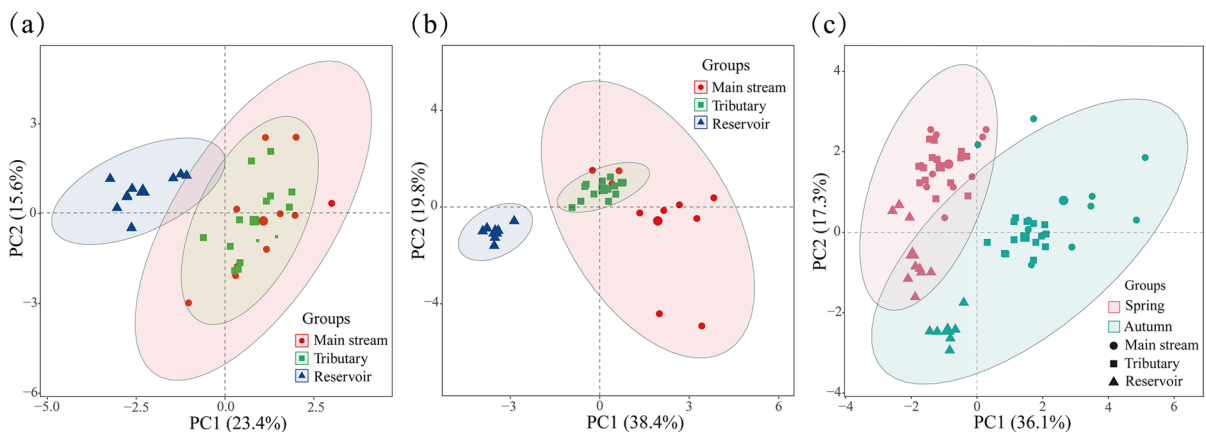

Fig. 2 Principal Component Analysis (PCA) of aquatic environment in three types of water bodies in **a** spring, **b** autumn, and **c** the two seasons. (Ellipses means 95% confidence interval around the centroid)

with reservoir based on specific environmental factors (Fig. 3). In addition to flow and water depth, at the spatial scale, TN and NO_2-N concentrations in river samples were significantly higher than those in reservoir samples during spring. Similar trends were observed for TP and NO_2-N concentrations,

as well as Turb in autumn. In terms of time scale, Chl-a, DO, and WT values in river samples and DO in reservoir samples were all higher in spring than in autumn. In contrast, TP, NH_4-N, pH, and Turb values in river samples were significantly higher in autumn than in spring, similar to pH in reservoir
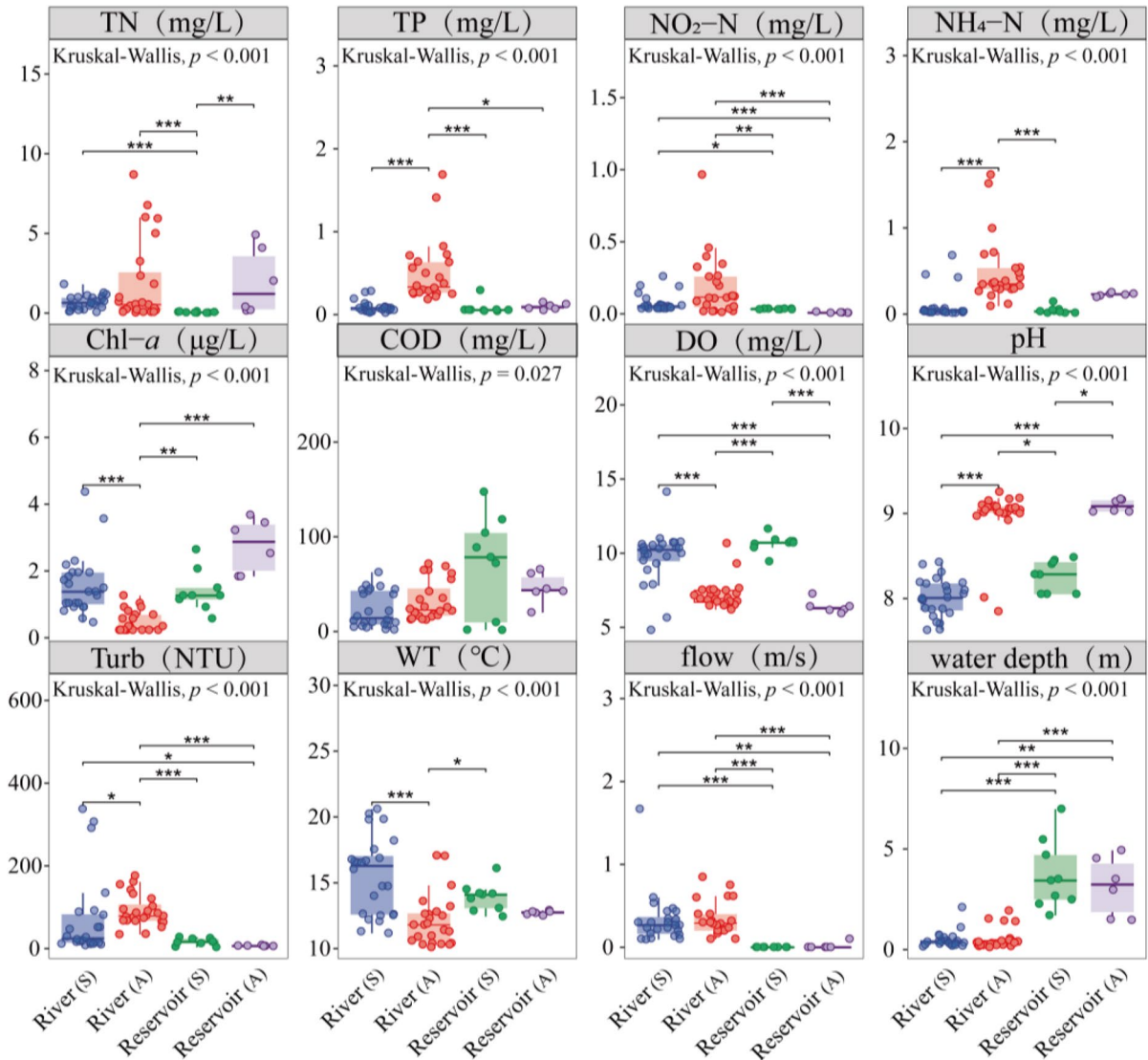

Fig. 3 Water environmental factors between rivers and reservoirs. ('S' represents spring and 'A' represents autumn. The Kruskal–Wallis test detects overall differences among four groups, while Wilcoxon compares pairwise differences. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; Wilcoxon test. *TN* total nitrogen, *TP* total phosphorus, *NO_2-N* nitrite-nitrogen, *NH_4-N* ammonium-nitrogen, *Chl-a* chlorophyll a, *COD* chemical oxygen demand, *DO* dissolved oxygen, *Turb* turbidity, *WT* water temperature. The top edge of the box plot, horizontal line in the box and the bottom edge of the box plot represent the 75%, 50% and 25% quartiles, respectively. The vertical bar above the box represents the range of values from the 75% quartile to the maximum value, and the vertical bar below the box represents the range of values from the minimum value to the 25% quartile)

samples ($P < 0.05$). COD showed no evident spatiotemporal differences.

Spatiotemporal patterns of zooplankton communities

Zooplankton community composition

A total of 114 zooplankton species were identified during the two seasons (Table S2), and there were 37 protozoa (32.46%), 57 rotifers (50.00%), 10 cladocera (8.77%), and 10 copepods (8.77%). In spring, we identified 87 zooplankton species, with the highest number of species found in the main stream (70), followed by tributaries (56) and the reservoir (44). Among these, 48 species were shared between the main stream and tributaries, 33 species between the main stream and reservoir, and 24 species between tributaries and reservoirs. Additionally, 22 species were present in all three water body types (Fig. 4a). During autumn, a total of 61 zooplankton species were identified, with the main stream having the highest species count (35), followed by the reservoir (25) and tributaries (23). Only 8 species were shared between the main stream and tributaries, 9 species between the main stream and reservoir, and 11 species between
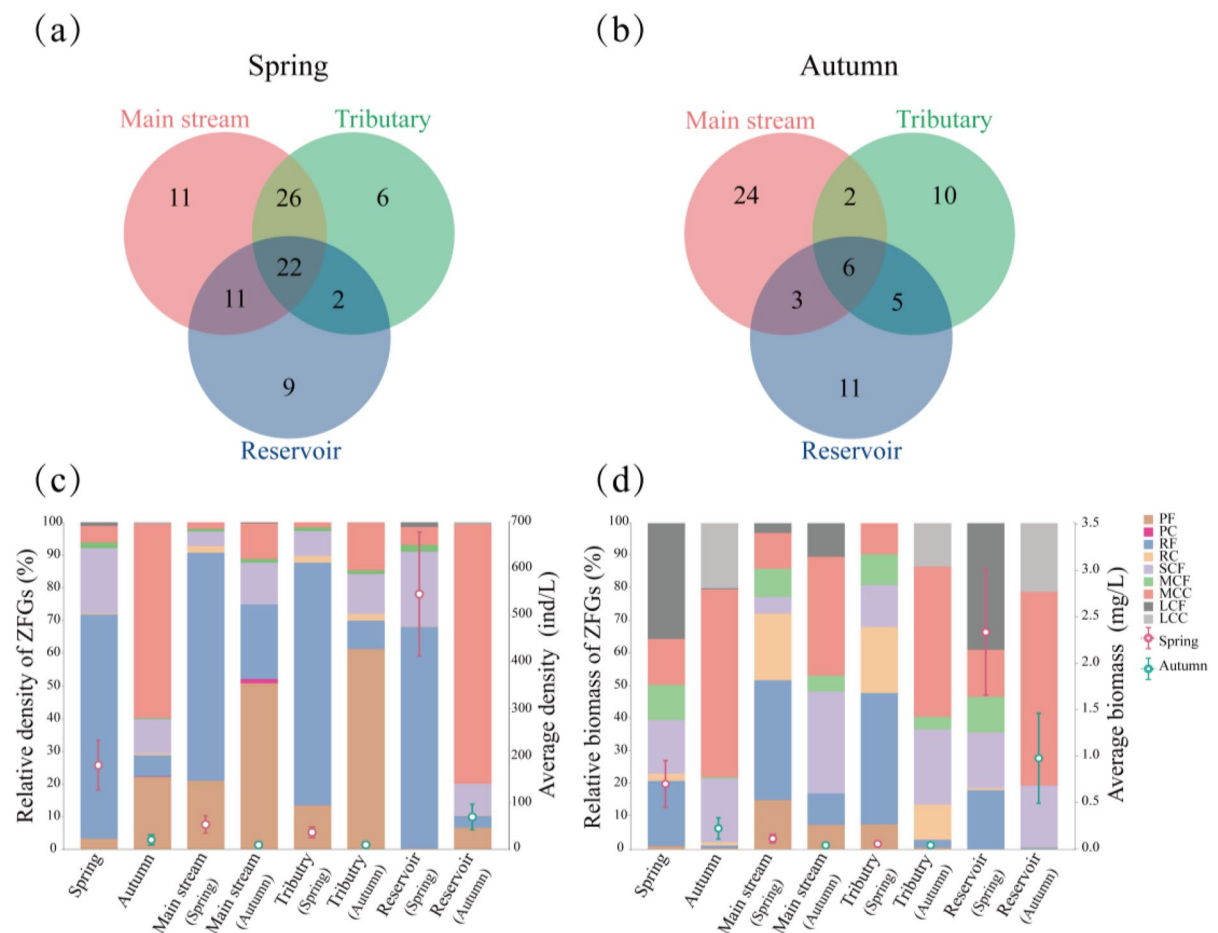

Fig. 4 Venn diagram of zooplankton species number (**a** spring; **b** autumn) and biaxial diagram of ZFGs density (**c**) and biomass (**d**) in spring and autumn in Yanhe River Basin (*PF* protozoa filter feeders, *PC* protozoa carnivore, *RF* rotifer filter feeders, *RC* rotifer carnivore, *SFC* small copepod and cladocera filter feeders, *SCC* small copepod and cladocera carnivore, *MCF* middle copepod and cladocera filter feeders, *MCC* middle copepod and cladocera carnivore, *LCF* large copepod and cladocera filter feeders, *LCC* Large copepod and cladocera carnivora. The average density and biomass are expressed by means ± standard error)

tributaries and reservoirs. There were only 6 species distributed across all three water body types (Fig. 4b).

The zooplankton species identified in spring were divided into seven zooplankton functional groups (ZFGs). All the groups existed in the main stream and reservoirs, excluding group LCF, which was not found in the tributaries. In autumn, the zooplankton species were divided into nine ZFGs, and all the groups occurred in the main stream. Groups PC and LCF were not found in the tributaries, whereas PC, MCF, and LCF populations were absent in the reservoirs. In addition, predator groups PC and LCC were only found in autumn. In terms of density (Fig. 4c), RF had the highest density proportion in spring, while PF and MCC had the highest density proportion in rivers and reservoirs in autumn. In addition, the average density of ZFGs in reservoirs is generally higher than that in rivers, and the average density of ZFGs in spring is highter than autumn. In terms of biomass (Fig. 4d), the proportion of ZFGs was balanced in spring, RF dominanted as biomass in river water, while LCF dominanted as biomass in reservoir. However, in autumn, the biomass proportion of MCC was the highest in both rivers and reservoirs, followed by SCF. In addition, the average biomass follows the same pattern as the average density.

Zooplankton functional group dynamics

The NMDS for ZFG structure in the three types of water bodies showed that the main stream and tributary had a high degree of overlap in both seasons (Fig. 5a, b). The reservoirs were relatively independent in spring (Fig. 5a), whereas a high degree of overlap was observed between the reservoirs and rivers in autumn (Fig. 5b). ANOSIM (Fig. S1) results confirmed the results of NMDS. In addition, the ZFGs structure characteristics also showed significant seasonal differences (Fig. 5c; Fig. S1).

The results of NMDS and ANOSIM analyses in spring were similar to those of PCA analysis, but the difference was that the structural differences of ZFG between the three types of water bodies were no longer significant in autumn. Therefore, the main stream and the tributaries were grouped together, while the reservoirs formed one group in the subsequent analyses. The two groups were used to explore the deterministic factors that led to changes in ZFG structure.

Influence of environmental factors

The RDA results revealed that Turb, TN, NO_2-N, COD, pH, water depth and WT were the most significant environmental factors in spring (Fig. 6a; Table S3), accounting for 56.86% and 5.62% of the ZFGs community variance in RDA axis 1 and axis
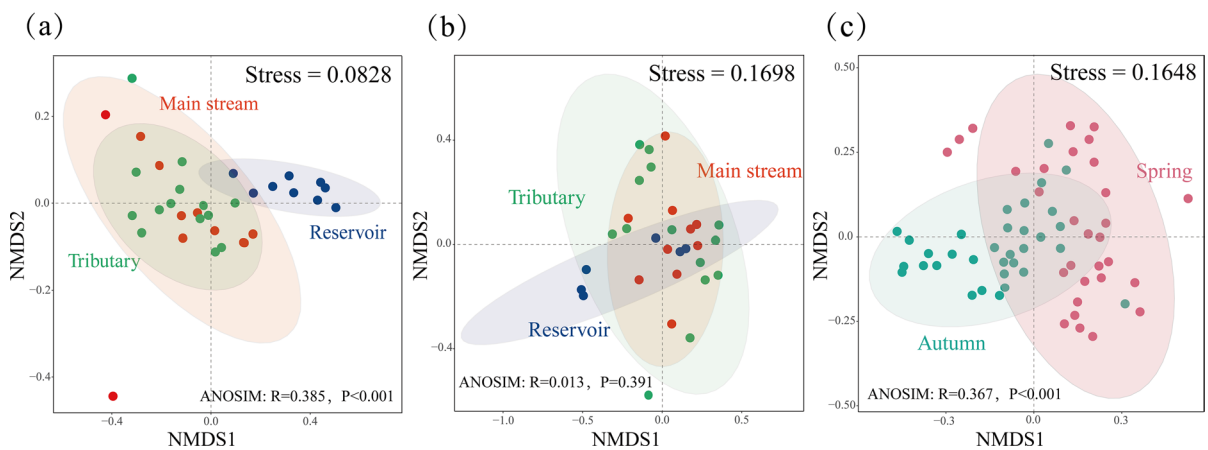

Fig. 5 Non-metric Multidimensional Scaling (NMDS) biplot showing differences in zooplankton functional group structure in different types of water bodies in the Yanhe River Basin (**a** spring; **b** autumn; **c** two seasons. Ellipses means 95% confidence interval around the centroid)

Fig. 6 Redundancy analysis (RDA) of the density of ZFGs and water environmental factors (**a** spring; **b** autumn) and Variance partition analysis (VPA) of all environmental factors (**c** spring; **d** autumn. An acute angle between ZFGs and environmental factors in RDA indicates a positive effect, while an obtuse angle indicates a negative correlation. Physical: Turb, DO, WT, flow, water depth; chemical: pH, TN, TP, NO_2-N, NH_4-N, Chl-*a* and COD. Environmental factors abbreviations are defined in Fig. 3 caption. Functional group abbreviations are defined in Fig. 4 caption)
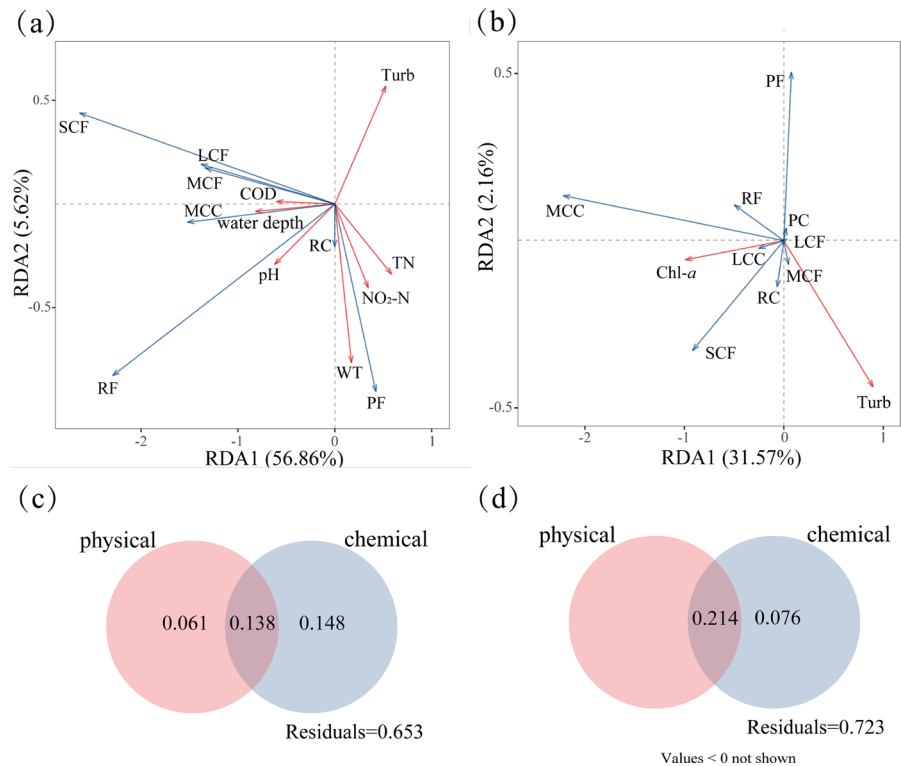
2, respectively. Turb and Chl-*a* were the most crucial environmental factors in autumn (Fig. 6b), explaining 31.57% and 2.16% of the ZFGs community variance in RDA axis 1 and axis 2, respectively. Among these factors, Turb was one of the most powerful influential factors in both seasons and had generally a negative impact on the most ZFGs (Fig. 6a, b). Variance partition analysis (VPA) showed that environmental factors could explain 34.7% of the zooplankton community variance in spring (Fig. 6c). However, in autumn, this proportion decreased to 27.7% and a portion of up to 72.3% could not be explained (Fig. 6d).

Role of biotic interactions

Niche breadth and overlap

The average niche breadth of ZFGs were generally higher in spring than in autumn (Fig. 7). Specifically, during spring, RF (9.59) had the highest niche breadth, closely followed by RC (7.60) and PF (6.98), which all demonstrated relatively high niche breadth. Meanwhile, SCF (5.64) and LCF (5.20), MCF (3.87), and MCC (2.64) exhibited a moderate niche breadth.

During autumn, the niche breadth of ZFGs ranged from 1 to 13.91. Nevertheless, RF (13.91) remained the ZFG with the highest niche breadth, followed by PF (9.56). Additionally, ZFGs such as SCF (5.02), MCF (3.46), MCC (3.36), and LCC (2.48) each exhibited a moderate niche breadth. In comparison, RC (1.59) had relatively narrow niche breadth, PC and LCF were only 1 (minimum). Notably, under the condition of decreased average niche breadth in autumn, RF, PF, and MCC exhibited varying degrees of increase in niche breadth, while LCF' niche breadth has dropped to a minimum ($5.20 \rightarrow 1$) and was even difficult to observe.

In the river during spring, the niche overlaps between filter feeding groups (excluding PF) were generally high (Fig. 8a). Similarly, high niche overlaps were observed between MCC and filter feeding groups (excluding PF). In relatively enclosed reservoirs, niche overlaps among different functional groups were even higher in spring (Fig. 8b). The situations changed in autumn. Specifically, in rivers, SCF, RF, MCC and LCC showed high niche overlaps with each other, while MCF and LCF did not exhibit considerable overlap with them (Fig. 8c), however,

Fig. 7 Niche breadth of zooplankton functional groups in the Yanhe River Basin (Functional group abbreviations are defined in Fig. 4 caption)
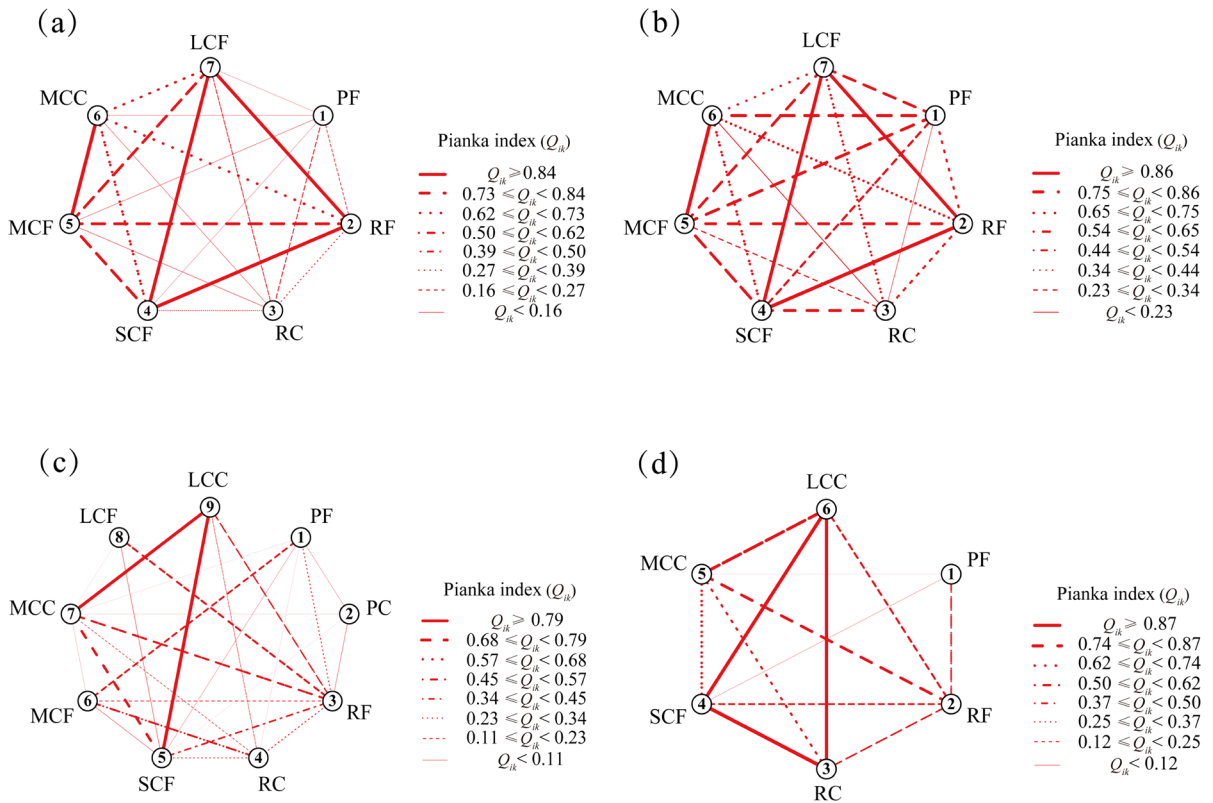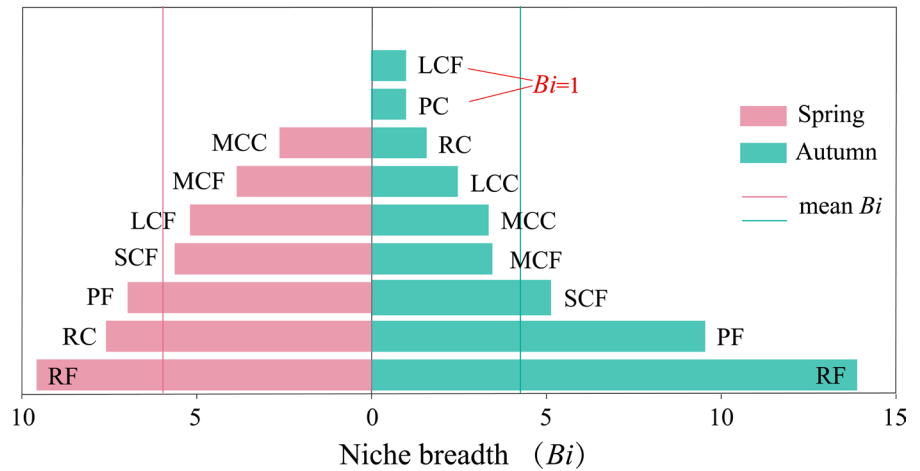

Fig. 8 Niche overlap of zooplankton functional groups in **a** rivers in spring, **b** reservoirs in spring, **c** rivers in autumn, and **d** reservoirs in autumn. Functional group abbreviations are defined in Fig. 4 caption

the MCF and PF showed an increase in overlap. In the reservoir (Fig. 8d), SCF, RF, MCC and LCC, still demonstrated high niche overlaps. However, MCF and LCF were rarely observed even in the reservoirs.

Overall association and AC coefficient

The overall association of ZFGs in two seasons was showed in Table 1. The *VR* values were

Table 1 Overall association of zooplankton functional groups in two seasons

Season	VR	W	df	χ^2	Significance
Spring	1.30	42.85	6	1.64–12.592	Significant positive association
Autumn	0.94	28.10	8	2.73–15.507	Significant negative association

$VR_{spring} = 1.30$ and $VR_{autumn} = 0.94$. The W values were $W_{spring} = 42.85$ and $W_{autumn} = 28.10$, neither were in the interval of χ^2. Therefore, the overall association of ZFGs in spring and autumn showed significant positive association and significant negative association, respectively.

According to AC coefficient of ZFGs (Fig. 9), most of ZFGs (except PF) were positively correlated in spring (Fig. 9a). PF, PC, MCF, and LCF were predominantly negatively correlated with other ZFGs in autumn (Fig. 9b). In spring, 12 pairs of ZFGs exhibited positive associations, with seven pairs showing strong associations ($AC \geq 0.6$). Among the nine pairs with negative associations, only one pair (PF–RF) showed high association ($AC < -0.6$). In autumn, 20 pairs of ZFGs showed positive associations, and only seven pairs showed high associations ($AC \geq 0.6$). Among the 16 pairs showing negative associations, up to 11 pairs showed high associations ($AC < -0.6$), primarily within the group PF, PC, MCF, and LCF. The AC coefficient showed that the positive correlation between ZFGs was more significant in spring, while the negative correlation was more prominent in autumn, which were consistent with the VR results.

Discussion

Spatiotemporal dynamics of aquatic environment and zooplankton communities

This study revealed significant spatiotemporal heterogeneity in the characteristics of the aquatic environment in the Yanhe River Basin. This outcome was expected because the distinct hydrological and limnological characteristics of rivers and reservoirs lead to significant difference in their aquatic environment characteristics (Petts & Gurnell, 2005). 87 zooplankton species of seven ZFGs were identified in spring, while 61 species of nine ZFGs were identified in autumn. The results of this study are similar to previous findings of Li et al. (2014) at the main stream of Yanhe River (in May 2012), where the most common zooplankton species were rotifers. However, Xie et al. (2022) reported that protozoa exhibited the highest species diversity in the wet season (In July 2019) of the Yanhe River. This difference was attributed to the distinct environmental conditions that steer the development of zooplankton communities in varying directions at different times of year (Sarma et al., 2005; Li et al., 2019), furthermore, fixation with Lugol may also lead to loosing of protozoa. Additionally, reservoirs' lacustrine conditions provide optimal
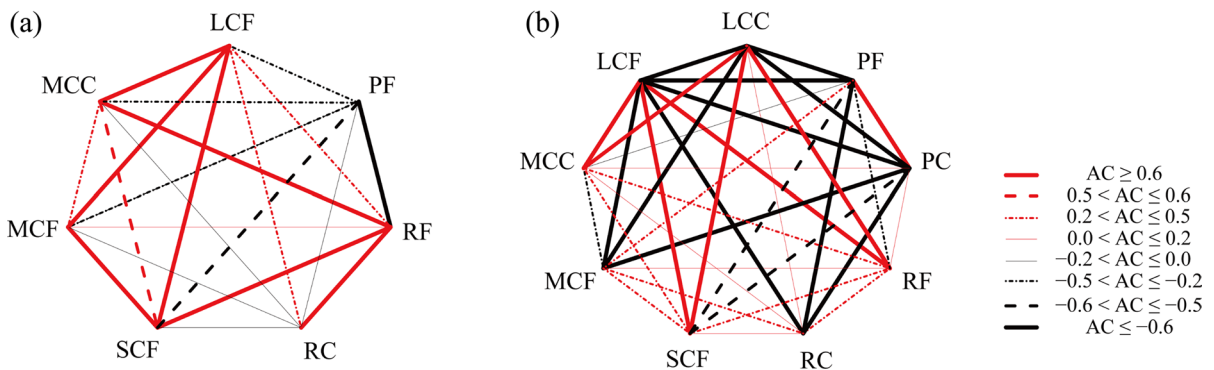

Fig. 9 Association coefficient (AC) between zooplankton functional groups in **a** spring and **b** autumn. Functional group abbreviations are defined in Fig. 4 caption

and constant circumstances for the reproduction and growth of zooplankton (Havel et al., 2009); therefore, zooplankton density and biomass were notably higher in reservoirs than in rivers (Fig. 4c, d).

From a ZFG structure perspective, the rivers (main stream and tributaries) showed similar characteristics in spring, which were different from those of the reservoirs (Fig. 5a). Environmental heterogeneity among different types of water bodies could lead to differentiation in ZFGs between rivers and reservoirs (Portinho et al., 2016). In autumn, the differences in ZFG structure between rivers and reservoirs were no longer significant (Fig. 5b). Presumably, the significant spatiotemporal dynamics of ZCS in the Yanhe River Basin were driven by environmental factors and biotic interactions (Louette & Meester, 2005).

Responses of zooplankton functional groups to environmental factors and biotic interactions

RDA showed that Turb, TN, NO_2-N, COD, pH, water depth, WT and Chl-*a* were the major environmental impact factors (Fig. 6), with turbidity having a negative effect on ZFGs basically in both seasons. High turbidity, caused by serious soil erosion, restricts the zooplankton abundance and distribution, as muddy aquatic environments are unsuitable for zooplankton (Sandlund, 1982; Marques et al., 2006). Meanwhile, there is an overall synchrony in biomass between zooplankton and phytoplankton (Li et al., 2019), high turbidity also reduces effective photosynthesis, negatively impacting phytoplankton growth (Houser et al., 2010), and indirectly affecting zooplankton growth through the food web (Ghadouani et al., 2010). In addition, lower pH also inhibits phytoplankton growth (Hussherr et al., 2016). In the present study, the pH values in autumn was significantly higher than in spring, but both showed weak alkalinity (Fig. 3), which was conducive to growth of phytoplankton. Thus, in spring, pH showed a positive relationship with ZFGs, while Chl-*a* became a main factor affecting ZFGs density in autumn.

In temperate regions, nutrients (nitrogen, phosphorus, etc.) and temperature are usually the primary environmental factors affecting zooplankton (Wen et al., 2011). In this study, nitrogen (TN and NO_2-N) and WT significantly influenced ZFGs structure, as supported by previous studies (such as Tornés et al., 2014; Xu et al., 2015; Li et al., 2019; Houliez et al.,

2021; etc.). Effects of water depth on ZFGs was mainly reflected in the reservoirs, where clear-water phases (Kim et al., 2005), lentic and deep water depth environment are more suitable for zooplankton survival (Yan et al., 2015; Ko et al., 2022). COD indirectly reflects organic pollution and high nutrients levels in water bodies. Generally, water with high COD and Chl-*a* concentrations tend to have a higher abundance of algae, bacteria, and debris (Wu et al., 2022), which creates favorable conditions for filter feeders. Environmental factors explained only a part of the variation in ZFGs structure (Fig. 6c, d), and the remaining unexplained part may be the contribution of biological interactions or unconsidered environmental variables.

With respect to biotic interactions, there was an overall positive association between different ZFGs in spring (Table 1; Fig. 9a), with significant niche overlap between filter feeding groups (Fig. 8a, b). This is because species/populations with the same adaptability to environmental conditions or responses to environmental stress often coexist (Freilich et al., 2018). Moreover, the predator groups such as MCC highly overlapped in niches with the filter feeder groups (Fig. 8a, b), suggesting that the predators and prey were close in space and time (Zhang et al., 2021). In autumn, only SCF and RF exhibited a high degree of overlap in the filter feeding groups (Fig. 8c, d), and the overall associated in the zooplankton community was negative (Table 1; Fig. 9b). Accordingly, in spring, competition among ZFGs was weak and tend to be positive association, which contributed to the overall positive succession of zooplankton community (Chai et al., 2016). In autumn, competition between ZFGs was intense, and vulnerable groups such as MCF and LCF were excluded, resulting in low zooplankton community stability in autumn (Chen et al., 2018).

In freshwater ecosystems, where resources are often limited, competition is most common among species/populations with similar diets (Dodson, 2003). In the present study, the reduction in average niche breadth may indicate a lower diversity of available resources in autumn (Peng et al., 2015). Some studies have pointed out that when food and other resources are scarce, small zooplankton, which have a lower food threshold, exhibit greater advantages under competition (Steiner & Roy, 2003). Compared with the RF and SCF groups, the MCF and LCF

groups are larger and thus inferior under competition. There are two possible outcomes of competition; one is that the inferior species are gradually expelled, and the other is that species coexist because of ecological niche differentiation (Dodson, 2003). PF had a high niche breadth in both seasons, but maintained a low degree of niche overlap and a negative association with other ZFGs (Figs. 7, 8, and 9). Hence, it can be inferred that the niche of PF has differentiated, leading to reduced competition with other filter-feeding ZFGs (Lindegren et al., 2020). Conversely, in autumn, the MCF group no longer significantly overlapped with other ZFGs but exhibited an increased overlap with the differentiated PF (Fig. 8c), indicating that the niche of the MCF group has undergone differentiation, allowing MCF to coexist with dominant groups. However, in reservoirs where competitors and predators were more abundant than those in the rivers, the MCF still cannot avoid being eliminated. Additionally, LCF did not demonstrate better resistance to intense competition, as its niche breadth significantly decreased from spring to autumn (Fig. 7) and almost eliminated entirely in the autumn.

Ecological significance of niche processes for zooplankton community succession

Niche processes have long been recognized as key determinants of community diversity and composition (Leibold & McPeek, 2006), but high spatial connectivity also could facilitate the homogenization of community composition through passive zooplankton dispersal and exchange (Heino et al., 2015). However, intense niche process and the ecological barrier function of reservoir can weaken the diffusion ability of organisms (Soininen et al., 2007).

Environmentally selected species are better suited to local conditions. Consequently, environmental conditions act as a species filter, so that similar biomes may develop in similar environments. Conversely, when similar biomes are observed under similar environmental conditions, niche processes may play a dominant role in community assembly (Coz et al., 2018). Such a mechanism explains the observed similarity of ZCS in rivers and difference between rivers and reservoirs in spring (Fig. 5; Fig. S1). After environmental selection has determined species composition, adverse habitat conditions and biotic interactions will further shape community structure (Dodson,

2003; Larned et al., 2010). In this process, species with similar ecological niches compete for resources, and the dominant species acquire more resources and persist. Therefore, niche differentiation is considered a key factor for the coexistence of ecologically and functionally similar organisms (Lindegren et al., 2020). This indicated that the survival of group MCF in rivers throughout the seasons can be attributed to its niche differentiation. Niche processes resulted in the expulsion and elimination of vulnerable groups, further enhancing the aggregation of advantageous groups (Lancaster, 2006). This process simplified the ZCS and led similarities of ZCS among different water bodies, ultimately reshaping the ZCS in the Yanhe River Basin.

Conclusions

The present study investigated zooplankton community structures in the main stream, tributaries, and reservoirs of the Yanhe River Basin in different seasons. Significant spatiotemporal heterogeneity in aquatic environment characteristic and zooplankton community structure was observed across the study area. Zooplankton community structure dynamics were mainly influenced by water environment factors such as turbidity, nitrogen (TN, NO_2^--N), chemical oxygen demand, pH, water depth, water temperature, and chlorophyll a. Positive community succession in spring was due to weak competition between functional groups, whereas a lack of community stability in autumn was attributed to intense competition and predation between functional groups. The niche processes driven by environmental factors and biotic interactions selected the dominant groups, while the disadvantaged groups were eliminated, and only groups with niche separation survived. Consequently, intense niche process played a potentially greater role in zooplankton community succession in the Yanhe River Basin. Our study deepens the understanding of zooplankton communities responses to environmental pressures, and offering valuable guidance for the conservation of water resources and aquatic environments.

comments and valuable suggestions on the manuscript particularly on statistical approaches.

Declarations

Conflict of interest The authors declare that there is no conflict of interest.

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