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Temperate urban wetland plankton community stability driven by environmental variables, biodiversity, and resource use efficiency: A case of Hulanhe Wetland

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In this study, we explored the driving factors behind plankton community structure. Due to the rapid development of cities, the occupation and development of wetland resources have increased lately, making the urban wetland ecosystems unstable and degrading the ecological functions gradually. Understanding the driving factors behind plankton community structure has certain theoretical and guiding significance for the protection, sustainable development, and ecological restoration of aquatic biodiversity in urban wetland ecosystems. We set up 12 sampling points in the Hulanhe Wetland, with the continuous monitoring of plankton from April to August and October 2021. The eco-environmental factors, plankton community structure, biodiversity index, resource use efficiency (RUE), and Bray–Curtis community turnover value were analyzed. A total of 209 species of 91 genera, 42 families, 11 classes, 22 orders of phytoplankton, and 90 species of four classes of zooplankton were identified. The community structure was mainly composed of Bacillariophyta, Chlorophyta, Cyanophyta, Protozoa, and Rotifera. To explore the correlation between phytoplankton and zooplankton, a correlation study was performed. We found a stable feeding preference between phytoplankton and zooplankton. The key influencing factors were identified by ordinary least squares regression, and the main driving factors of plankton community structure were discussed. The results showed that the stability of the Increased biodiversity and resource utilization efficiency have led to more stable plankton communities. This stability pattern is also strongly affected by water temperature, pH and total nitrogen in the external environment. This study will be helpful in the restoration of damaged wetlands, which would be beneficial for the protection of urban wetland ecosystems.

KEYWORDS

Hulanhe Wetland, plankton, grazing, community stability, resource use efficiency, diversity indicators

1. Introduction

Plankton is an important part of the aquatic ecosystem (MacArthur, 1955; Liu et al., 2021). It has a short life cycle and responds quickly to anthropogenic effects and natural changes. They are also considered good biological indicators for assessing wetland ecological health (Seilheimer et al., 2009; Easson and Lopez, 2019; Jonkers et al., 2019; Liu et al., 2021). Therefore, studying the plankton community structure is beneficial for wetland ecological environmental protection.

Community stability refers to the ability of a community to maintain its original structural and functional state, resist disturbance, or return to its original state after disturbance (Holling, 1973; Boucot, 1985; Sennhauser, 1991). It is an important manifestation of ecosystem function (Tilman, 1999; Pennekamp et al., 2018). Community structure is affected by the combined effects of biotic and abiotic factors, such as resource use efficiency (RUE) (Tian et al., 2017), biodiversity (Zhang H. et al., 2016), and water environmental factors (Schaum et al., 2016; Tian et al., 2016; Amorim and Moura, 2021). In the same natural aquatic ecosystem, different habitats often cause differences in plankton community structure partly due to different nutrient concentrations (Zheng et al., 2020). The application of RUE can eliminate community differences caused by different nutrient concentrations; therefore, it is widely used in the study of plankton community structure. Anthropogenic disturbance can destroy ecosystem function and brings challenges to ecological restoration. The correlation between RUE and community stability depends on the degree of disturbance to the ecosystem. In other words, with the aggravation of human disturbance, such as water pollution and fishery, RUE will decrease with the decrease in plankton species abundance (Norberg et al., 2001; Filstrup et al., 2014). In recent years, the correlation between plankton diversity and community stability has become one of the ecological hotspots in conservation biology. Communities with more species or complex interspecies associations are more stable than single-species communities (Mougi, 2022). Communities with high biodiversity have less competition among species, which makes the community more stable and the ecological function guarantee insure higher (MacArthur, 1955; Elton, 2020). In addition, prior studies have shown that total phosphorus (TP), total nitrogen (TN), water temperature (WT), and dissolved oxygen (DO) have also been confirmed to relate to plankton community stability (Tian et al., 2016; He et al., 2021).

Global climate changes and anthropogenic activities lead to a rapid decrease in urban wetland areas and threaten the habitat integrity and stability of the urban wetland ecosystems (Matchett and Fleskes, 2017; Zhang et al., 2020). The overall ecological condition of urban wetlands has shown a declining pattern over the years (Hui et al., 2011). The Hulanhe Wetland Reserve is located on the north bank of Songhua River, Heilongjiang Province. It is the largest natural urban wetland in China (Xing, 2016). The community structure of diverse animals (Gao et al., 2015), diverse plants (Cheng, 2013), hydrozoan (Liu, 2012), and phytoplankton in the Hulanhe Wetland and surrounding waters has received much attention (Hui et al., 2011; Lu et al., 2014; Jia et al., 2021). To date, most research on the water ecology of the Hulanhe Wetland has mainly focused on the effects of plankton, plant community composition, abundance changes, and environmental factors (Hui et al., 2011; Lu et al., 2014;

Jia et al., 2021). However, the research on the stability of plankton community is still insufficient.

Our study focused on the Hulanhe Wetland Reserve and the Hulan River, a tributary of the Songhua River that flows through the wetland, in 2021. We aimed to describe the plankton community structures and the correlations between them in the Hulanhe Wetland, to screen and identify the main factors driving plankton community structure, and to provide a theoretical basis for the protection of wetland biodiversity in the Hulanhe Estuary for the restoration of the damaged wetland ecosystems. Therefore, we put forward the following hypotheses: (1) there was a specific corresponding tendency to a predatory relationship between phytoplankton and zooplankton in the Hulanhe Wetland and (2) the stability of the plankton community in the Hulanhe Wetland is driven and regulated by both biotic and abiotic factors. The validation of these hypotheses would provide a theoretical basis for the water environment management of the Hulanhe Wetland from the perspective of plankton stability, which is beneficial for local water quality management and makes specific contributions to the further research and development of the restoration of other damaged wetland ecosystems.

2. Materials and methods

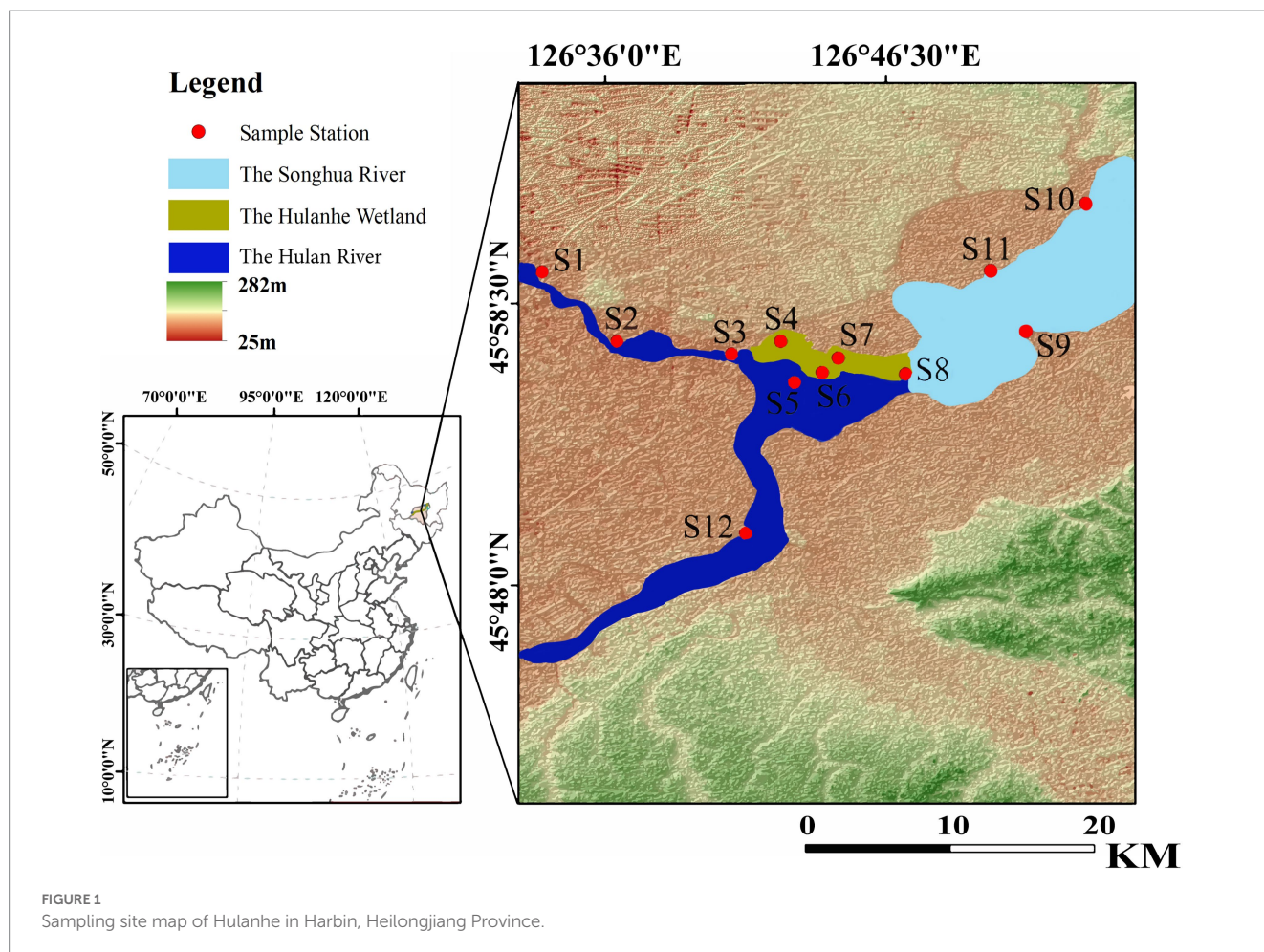
2.1. Research area, sampling point layout, and sampling time

The Hulan River, a tributary of the Songhua River, is located in the central part of Heilongjiang Province, between N 45°09′–46°10′, E 126°76′–127°31′. The reserve extends in the east–west belt along the north bank of the Songhua River. The length of the reserve is 63.5 km from east to west, 21.3 km from north to south, and 179.5 km in circumference. According to the habitat characteristics of the Hulanhe Wetland, it is divided into 12 sampling points: water inlet areas (S1, S2, S3, and S12), water outlet areas (S9, S10, and S11), wetland protection areas (S4, S5, S6, S7, and S8), an area affected by agriculture (S2), and an area affected by fisheries (S10) (Figure 1). In this study, phytoplankton and zooplankton specimens were collected in spring (April, May), summer (June, July, August), and autumn (October) in 2021, and the physicochemical indicators of the water body were analyzed. The longitude and latitude data of the sampling points were collected *via* GPS, and ArcGIS 10.2 (ESRI, Redlands, CA, United States) was used to draw the sampling points map.

2.2. Environmental data collection and sampling

2.2.1. Environmental variables

At each sampling site, surface water samples (0–0.5 m) were collected in triplicate for physicochemical analyses. The collection of water quality samples and plankton samples from the Hulanhe Wetland was carried out simultaneously. The WT, pH, conductivity (Cond.), DO, and turbidity (Tur) were measured with a multi-parameter water quality analyzer (YSI ProPlus, YSI, United States). TP, TN, chemical oxygen demand (COD_{Mn}), and biochemical oxygen demand (BOD₅) were the environmental factors analyzed in the laboratory within 24 h of sampling (GB 3838–2002).



2.2.2. Plankton sampling

Plankton samples and water samples were collected simultaneously in the Hulanhe Wetland. Phytoplankton (5L) and zooplankton (5L) samples were collected at 1 m depth from each sampling site. Phytoplankton samples were stored in acidified Lugol's solution, and zooplankton samples were stored in formaldehyde (4%). All samples were stored for 24 h before analysis and concentrated to 50 mL (Zhang and Hang, 1991).

Phytoplankton and protozoa were examined at $\times 400$ magnification ($\times 10$ eyepiece and $\times 40$ objective) using an Olympus microscope (Optec B302, Chongqing, China) with a 0.1 mL plankton counting chamber. Rotifera, cladocera, and copepods were examined at $\times 200$ magnification ($\times 10$ eyepiece and $\times 20$ objective) using an Olympus microscope with a 1 mL plankton counting chamber. Majority of the phytoplankton samples were identified at the species level, and their abundance was expressed as cells L^{-1} (Zhang and Hang, 1991).

Enumerating plankton cells, usually requires settling of samples in order to concentrate the cells (Claessens and Prast, 2007). Precipitation and concentration are carried out in a cylindrical funnel. Fix the funnel on a shelf and place it on a stable table. The water sample was poured into the funnel, and the plankton was naturally precipitated for 60 h. The supernatant was sucked with a siphon and the sample was concentrated to 50 mL (Zhang and Hang, 1991).

The publications 'Freshwater algae in China: systems, classification and ecology' (Hu and Wei, 2006), 'Freshwater Microorganisms and Benthic Animals Atlas' (Zhou and Chen, 2011), 'China Freshwater Rotifer' (Wang, 1961), the Rotifer World Catalog¹, International Commission on Zoological Nomenclature², and 'Chinese Fauna Freshwater Cladocera' (Board, 1979) were used to identify the plankton organisms.

2.3. Statistical analysis

The dominant species of plankton were determined based on the dominance value Y for each species, and plankton diversity was represented by the Shannon–Wiener (H') (Magnussen and Boyle, 1995), Margalef (H) (Margalef, 1969), Pielou evenness (J) (Pielou, 1966), and Simpson indices (D) (Simpson, 1949), as follows:

$$Y = \left(\frac{n_i}{N} \right) \times f_i$$

¹ <http://www.rotifera.hausdernatur.at/>

² <http://iczn.org/lan/rotifer>

Shannon–Wiener index:

$$H' = -\sum_{i=1}^s P_i \times \ln P_i$$

Margalef index:

$$H = (S - 1) / \ln N$$

Pielou evenness index:

$$J = H' / \ln S$$

Simpson index:

$$D = 1 - \sum_{i=1}^s P_i^2$$

where n_i and N are the number of individuals of species i and the total number of individuals of all species within a given area in the whole year, respectively; P_i is the relative proportion of species i , which is calculated by n_i / N ; S is the number of species within a given sample; and f_i is the occurrence frequency of species i , which is calculated by the ratio of the number of samples with species i to the total number of samples within the given area in the whole year. If the dominance value Y of a species was greater than 0.02, it was considered dominant.

2.4. Plankton RUE

In this experiment, the mass per unit volume was used to represent the biomass of plankton, and the calculation formula was: biomass = density × volume × abundance × 10⁻⁶. It is assumed that the density of plankton is 1 g/L, the volume unit is μm³, the abundance unit is cells/L, and the biomass unit is μg/L.

RUE represents the amount of standing stock biomass per unit resource. We evaluated the RUE of phytoplankton (RUE_{pp}) and zooplankton (RUE_{zp}) communities, which quantifies the ratio of realized to potential productivity. RUE_{pp} was calculated as phytoplankton biomass per unit TP (Davidson and Howarth, 2007; Filstrup et al., 2014). RUE_{zp} was calculated as zooplankton biomass per unit of phytoplankton biomass. As we were interested in calculating community biomass per unit resource directly available to each trophic level, RUE_{zp} was calculated in relation to phytoplankton biomass, whereas RUE_{pp} was calculated in relation to TP (Filstrup et al., 2014).

$$RUE_{pp} = \frac{BIO(Phyto)}{TP}$$

$$RUE_{zp} = \frac{BIO(Zoo)}{BIO(Phyto)}$$

Here, $BIO(Phyto)$ is phytoplankton biomass; $BIO(Zoo)$ is zooplankton biomass; and TP is total phosphorus.

Plankton community turnover was determined by Bray–Curtis dissimilarity index between the two samples; the smaller the community turnover, the stronger the community stability (Jeppesen et al., 2011; Filstrup et al., 2014). Bray–Curtis dissimilarity index was calculated as:

$$BC = \frac{\sum_{i=1}^n |y_{i1} - y_{i2}|}{\sum_{i=1}^n |y_{i1} + y_{i2}|}$$

Here, BC is the Bray–Curtis dissimilarity index between samples 1 and 2; y_{i1} and y_{i2} are the biomasses of plankton species i in the two samples, respectively; and n is the total number of plankton species in both the samples.

2.5. Data analysis

Analysis of variance (ANOVA) and *Post-hoc* test were conducted to evaluate differences in environmental data and was performed using SPSS 22.0 for Windows. Pearson correlation coefficient between community stability and RUE, biodiversity, and water environment factors were determined using SPSS 22.0 for Windows. Then, Origin 2022 was used for ordinary least squares regression analysis. The ‘vegan’, ‘ggpubr’, ‘ggplot2’, and ‘corrplot’ packages in R 4.0.3 were used for the difference tests and heat maps.

3. Results

3.1. Physicochemical characteristics of water samples

There were significant differences in WT (ANOVA, $p < 0.001$), pH (ANOVA, $p < 0.001$) and TN (ANOVA, $p < 0.001$) (Tables 1, 2). The variation range of WT was 8.10–27.80°C and an average of 18.07°C. The variation pattern of Tur, DO, and BOD₅ was to increase gradually with the change of season, with a variation range of 1.70–186.80 NTU (Tur), 4.47–14.11 mg/L (DO), and 0.05–10.04 mg/L (BOD₅). The mean values were 54.65 NTU (Tur), 9.96 mg/L (DO), and 5.53 mg/L (BOD₅). TN decreased gradually with the change of spring, summer, and autumn, with a variation range of 0.15–0.78 mg/L and an average of 0.46 mg/L. The pH, COD_{Mn}, TP, and Cond. values were the greatest in summer, followed by in spring, and the lowest in autumn, ranging from 6.47–9.06 (pH), 2.47–15.80 mg/L (COD_{Mn}), 0.03–1.03 mg/L (TP), and 160.90–1123.00 μS/cm (Cond.), with an average of 7.72 (pH), 6.46 mg/L (COD_{Mn}), 0.30 mg/L (TP), and 359.03 μS/cm (Cond.).

TABLE 1 Environmental characteristics of the Hulanhe Wetland.

Mental variables	Unit	Spring	Summer	Autumn	ANOVA		
					Eta-Squared	p-value	q-value
Tur.	NTU	49.90 ± 71.90	51.45 ± 94.25	53.30 ± 51.45	0.051	0.186	0.233
pH	-	7.94 ± 7.76	8.02 ± 7.89	6.64 ± 6.58	0.552	0.001**	0.001
WT	°C	16.30 ± 16.75	21.95 ± 21.65	9.05 ± 10.30	0.463	0.001**	0.001
DO	mg/L	9.37 ± 9.29	9.46 ± 12.44	12.21 ± 11.77	0.081	0.059	0.132
BOD ₅	mg/L	4.26 ± 5.05	5.17 ± 8.76	7.60 ± 7.19	0.068	0.096	0.144
TN	mg/L	0.51 ± 0.59	0.45 ± 0.42	0.42 ± 0.47	0.004	0.884	0.884
TP	mg/L	0.17 ± 0.26	0.30 ± 0.53	0.25 ± 0.42	0.179	0.001**	0.004
COD _{Mn}	mg/L	6.17 ± 6.20	6.45 ± 9.51	4.82 ± 7.61	0.021	0.502	0.565
Cond.	μS/cm	310.75 ± 597.90	323.85 ± 641.95	241.15 ± 380.65	0.075	0.073	0.132

** Represents $p < 0.01$ (extremely significant correlation).

TABLE 2 Post-hoc test of environmental characteristics in Hulanhe Wetland.

	Spring × Summer	Summer × Autumn	Spring × Autumn
WT	0.929	0.001**	0.001**
pH	0.382	0.001**	0.001**
TP	0.001**	0.211	0.451

** Represents $p < 0.01$ (extremely significant correlation).

3.2. Plankton community structure

3.2.1. Composition of plankton community

The species composition and dominant species of the plankton community in the Hulanhe Wetland are shown in Figures 2, 3 and Tables 3, 4. The identified phytoplankton in the Hulanhe Wetland belonged to eight phyla, 11 classes, 22 orders, 42 families, 91 genera, and 209 species. Among them, Bacillariophyta had the most number of species (74 species), followed by Chlorophycophyta (73 species), Cyanophyta (32 species), Euglenophyta (16 species), Pyrrophyta (6 species), Cryptophyta (4 species), Chrysophyta (3 species), and Xanthophyta (1 species), respectively.

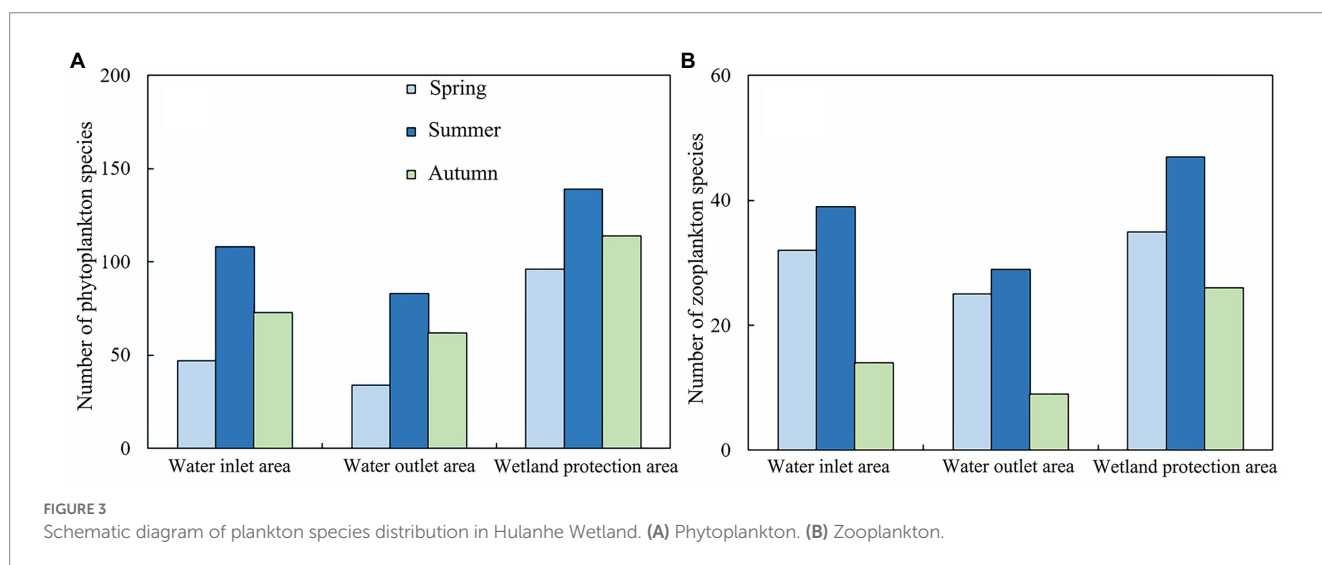
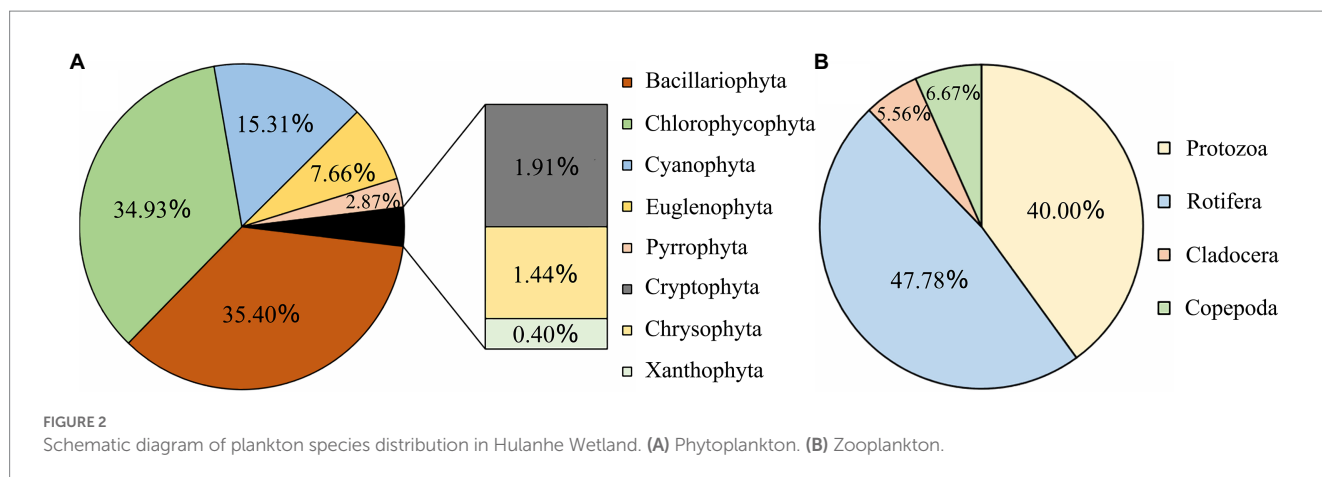
A total of four categories and 90 species of zooplankton were identified in the Hulanhe Wetland, including 43 species of rotifers, 36 species of protozoa, 5 species of copepods, and 6 species of cladocerans. There were 18 dominant species of zooplankton. The dominant species of zooplankton in spring and summer were mainly protozoa and rotifers. The dominant species in autumn were less, mainly copepods. Figure 3 shows the spatio-temporal distribution of plankton species in the Hulanhe Wetland. In terms of time distribution, the number of phytoplankton species was in the order of summer>autumn>spring and the number of zooplankton species was in the order of summer>spring>autumn.

There were 39 dominant species of phytoplankton, with a significant seasonal distribution. In spring, the dominant species were mainly Bacillariophyta and Cryptophyta, such as *Cyclotella meneghiniana* and *Chroomonas acuta*. The dominant species in summer were Chlorophyta, Cyanophyta, and Chrysophyta, among which *Ankistrodesmus angustus*, *Arthrospira platensis*, and *Dinobryon cylindricum* were the most dominant. Bacillariophyta and some cyanobacteria were the dominant species in autumn, and *Cyclotella meneghiniana* and *Chroomonas acuta* were the dominant species in

spring. The spatial distribution also had certain differences. The proportions of the dominant species (cyanobacteria) in the water outlet areas were higher than those in the water inlet areas, while the proportions of other categories were lower than those in the water inlet areas. The dominant species in the wetland protection area were evenly distributed and much higher than those in the water inlet and outlet areas. *Melosira granulata* had the highest dominance in the Hulanhe Wetland. There were eight dominant species of protozoa, among which *Strombidium viride* had the highest dominance in spring, while *Diffflugia acuminata* had absolute dominance in summer. There were seven dominant species of rotifers, *Polyarthra euryptera* in spring and *Polyarthra euryptera* and *Keratella valga* in summer. There were three dominant species of copepods. *Nauplius* was mainly dominant in summer, and the dominance of *Neutrodiaptomus incongruens* was the highest in autumn. Cladocera was the least dominant with only one species. From the perspective of spatial variation, the dominant species in the water inlet areas were mainly rotifers (such as *Anuiaopsis fissa* and *Polyarthra euryptera*), while that at the water outlet areas were protozoa (such as *Diffflugia acuminata*). The dominant species in the wetland reserve were generally higher than those in the water inlet and outlet areas. Rotifers, protozoa, copepods, and cladocera were mainly distributed, among which *Neutrodiaptomus incongruens* and *Polyarthra euryptera* had the highest dominance in the entire region.

3.2.2. Plankton abundance

The variation range of phytoplankton abundance in the three seasons in 2021 was $0.53\text{--}16.61 \times 10^6$ cells/L. The average abundance of phytoplankton in the time scale was in the order summer>autumn>spring, and the variation range was $0.99\text{--}16.61 \times 10^6$ cells/L (summer), $0.85\text{--}14.96 \times 10^6$ cells/L (autumn), and $0.53\text{--}13.55 \times 10^6$ cells/L (spring) (Figure 4A). The zooplankton



community structure also showed temporal distribution differences, and the community abundance was mainly dominated by protozoa and rotifers. The abundance of zooplankton in the three seasons in 2021 was in the range $0.15\text{--}8.60 \times 10^4$ cells/L, and the abundance of zooplankton species was in the order summer>autumn>spring, with a range of $0.20\text{--}8.60 \times 10^4$ cells/L (summer), $0.15\text{--}3.25 \times 10^4$ cells/L (autumn), and $0.20\text{--}4.08 \times 10^4$ cells/L (spring) (Figure 4C).

The variation in phytoplankton abundance on a spatial scale was in the order wetland protection area > water inlet area > water outlet area > agriculture-affected area > fisheries-affected area. The wetland protection area had the highest abundance, with a range of $0.53\text{--}15.75 \times 10^6$ cells/L; the abundance in the water inlet area was the second, with a range of $0.85\text{--}8.67 \times 10^6$ cells/L; the abundance of the water outlet area ranged from $1.92\text{--}9.43 \times 10^6$ cells/L; the abundance was the lowest in the agriculture-affected area and fisheries-affected area, with a variation range of $0.05\text{--}4.28 \times 10^6$ cells/L and $0.22\text{--}5.61 \times 10^6$ cells/L, respectively (Figure 4B). The overall spatial variation of zooplankton was in the order wetland protection area > water

inlet area > water outlet area > agriculture-affected area > fisheries-affected area. The wetland protection area had the highest abundance, with a range of $2.25\text{--}8.60 \times 10^4$ cells/L; the abundance in the water inlet area was second, with a range of $0.20\text{--}7.25 \times 10^4$ cells/L; the variation ranges were $0.20\text{--}2.25 \times 10^4$ cells/L, $0.35\text{--}3.00 \times 10^4$ cells/L, and $0.20\text{--}0.95 \times 10^4$ cells/L for water outlet area, agriculture-affected area, and fisheries-affected area, respectively (Figure 4D).

3.2.3. Correlation between phytoplankton and zooplankton

Predation and competition are the main driving forces for regulating the structure of plankton communities in freshwater ecosystems. Plankton can be classified into phytoplankton and zooplankton according to the trophic relationship (Bottom-up/Top-down effect) of the food web, and there is a long-term predation and predation relationship between them. In this study, the correlations between phytoplankton (eight phyla) and zooplankton (four categories) were analyzed by correlation heatmap (Figure 5). As shown in the diagram, rotifers showed a

TABLE 3 Dominant species of phytoplankton in Hulanhe Wetland.

		Dominant species	Season			Area		
			Spring	Summer	Autumn	Wetland	Water inlet	Water outlet
Phytoplankton	Bacillariophyta	<i>Cyclotella meneghiniana</i>	0.257	0.130	0.051	0.143	0.128	0.113
		<i>Melosira granulata</i>	0.195	–	0.421	0.476	–	–
		<i>Melosira varians</i>	0.165	–	0.101	0.101	–	0.165
		<i>Asterionella formosa</i>	0.121	–	–	0.096	–	–
		<i>Ulnaria ulna</i>	0.082	0.194	0.285	0.206	0.022	0.241
		<i>Nitzschia palea</i>	0.054	0.052	0.069	0.053	0.046	0.091
		<i>Navicula radiosa</i>	0.052	–	–	0.034	0.069	–
		<i>Aulacoseira pusilla</i>	0.048	0.079	0.057	0.056	0.072	0.062
		<i>Ulnaria acus</i>	0.037	–	–	0.037	–	–
				<i>Melosira granulata</i> var. <i>angustissima</i>	0.033	0.085	0.203	0.186
	Chlorophycophyta	<i>Ankistrodesmus falcatus</i>	–	0.158	–	0.158	–	–
		<i>Tetraëdron minimum</i>	–	0.084	–	0.084	–	–
		<i>Scenedesmus quadricauda</i>	–	0.082	0.069	–	0.076	–
		<i>Crucigenia tetrapedia</i>	–	0.026	–	–	–	0.026
		<i>Chlamydomonas globosa</i>	0.099	0.069	0.057	0.196	0.080	0.134
		<i>Ankistrodesmus angustus</i>	0.076	0.269	0.120	0.180	0.152	0.022
		<i>Scenedesmus dimorphus</i>	0.056	0.101	0.164	0.133	0.056	–
		<i>Schroederia setigera</i>	0.049	0.039	–	0.044	–	–
		<i>Chodatella quadriseta</i>	0.024	–	–	0.024	–	–
			Cyanophyta	<i>Arthrospira platensis</i>	–	0.389	0.068	0.319
<i>Anabaenopsis circularis</i>	–			0.156	0.032	0.156	–	–
<i>Merismopedia minima</i>	–			0.088	–	0.088	–	–
<i>Chroococcus minor</i>	–			0.069	–	–	–	0.069
<i>Anabaena azotica</i>	–			0.066	0.078	0.110	–	0.022
<i>Merismopedia convoluta</i>	–			0.054	–	0.054	–	–
<i>Oscillatoria chlorina</i>	0.082			0.146	0.027	0.098	–	–
<i>Anabaena circinalis</i>	0.042			0.156	–	0.099	–	–
<i>Pseudanabaena limnetica</i>	0.022			0.100	0.215	0.127	–	–
	Euglenophyta			<i>Strombomonas fluviatilis</i>	–	0.025	–	–
		<i>Trachelomonas planctonica</i>	0.040	0.071	0.038	0.119	0.047	–
		<i>Euglena geniculata</i>	0.036	–	–	–	0.036	–
		<i>Euglena viridis</i>	0.026	0.044	0.137	0.139	0.036	–
	Pyrrophyta	<i>Peridinium umbonatum</i>	–	0.094	–	–	0.094	–
		<i>Gymnodinium aeruginosum</i>	–	0.027	–	–	0.027	–
	Chrysophyta	<i>Dinobryon cylindricum</i>	0.123	0.251	0.196	0.215	0.132	–
	Cryptophyta	<i>Chroomonas acuta</i>	0.251	0.028	–	0.202	0.099	0.144
		<i>Cryptomonas erosa</i>	0.109	–	–	0.109	–	–
		<i>Cryptomonas ovata</i>	0.048	0.062	0.044	0.053	0.063	0.040

“–” means not involved; “Wetland” is wetland protection areas (S4–S8); “Water inlet” is water inlet areas (S1–S3, S12); “Water outlet” is water outlet areas (S9–S11).

significant correlation between Chlorophyta and Cryptophyta ($p < 0.01$); there was a significant correlation between Protozoa and Bacillariophyta ($p < 0.05$). However, compared with Chlorophyta, Cyanophyta was not significantly correlated with

zooplankton although it was the dominant phylum. It may be because Cyanophyta clusters often have gum sheaths and cyanobacterial toxins, resulting in discomfort and rarely preyed by zooplankton.

TABLE 4 Dominant species of zooplankton in Hulanhe Wetland.

		Dominant species	Season			Area		
			Spring	Summer	Autumn	Wetland	Water inlet	Water outlet
Zooplankton	Protozoa	<i>Centropixis aculeata</i>	–	0.136	–	0.132	–	0.094
		<i>Tintinnidium fluviatile</i>	–	0.036	–	0.032	–	–
		<i>Strombidium virid</i>	0.258	0.09	0.099	0.177	0.056	0.081
		<i>Diffugia urceolata</i>	0.097	0.025	–	0.097	–	0.025
		<i>Vorticella micostoma</i>	0.072	–	–	0.072	–	–
		<i>Arcella rotundata</i>	0.045	–	–	0.045	–	–
		<i>Diffugia acuminata</i>	0.031	0.454	–	0.025	–	0.246
		<i>Tintinnopsis wangi</i>	0.025	0.174	–	0.168	0.026	–
	Rotifera	<i>Lecane signifera</i>	–	–	–	–	–	–
		<i>Anuiaopsis fissa</i>	–	0.074	–	0.072	0.066	–
		<i>Polyarthra trigla</i>	–	0.053	–	0.049	0.027	–
		<i>Brachionus angularis</i>	–	0.039	–	0.039	0.021	–
		<i>Trichocerca cylindrica</i>	–	0.036	–	0.034	–	–
		<i>Polyarthra eurypetra</i>	0.073	0.335	–	0.213	0.054	–
		<i>Keratella valga</i>	0.046	0.086	–	0.066	–	0.023
	Copepoda	<i>Neurodiaptomus incongruens</i>	–	–	0.208	0.294	–	0.089
		<i>Nauplius</i>	–	0.132	–	0.126	0.047	–
	Cladocera	<i>Moina rectirostris</i>	–	–	0.032	0.028	0.024	–

“–” means not involved; “Wetland” is wetland protection areas (S4–S8); “Water inlet” is water inlet areas (S1–S3, S12); “Water outlet” is water outlet areas (S9–S11).

3.3. Factors affecting plankton community stability

3.3.1. Resource utilization and plankton community stability

As shown in Figures 6A,B the utilization rate of phytoplankton resources (RUE_{pp}) and zooplankton resources (RUE_{zp}) in the Hulanhe Wetland showed that they were much larger in summer than those in autumn and spring. As shown in Figures 6C,D, both RUE_{pp} and RUE_{zp} showed that they much larger in the wetland protected areas (S4–S8) than those in other regional samples, while RUE_{pp} and RUE_{zp} in the agriculture-affected area (S2) and fisheries-affected area (S10) were the lowest. The community turnover (BC) of the plankton community showed an opposite trend to the community stability. The larger the BC, the easier the community to produce species turnover (that is, the worse the community stability). The ordinary least squares regression curve between plankton community stability and RUE in Hulanhe Wetland is shown in Figure 6E. There was a significant correlation between stability and RUE ($p < 0.01$), indicating that plankton communities with high resource utilization often have higher stability.

3.3.2. Species diversity and plankton community stability

As shown in Figure 7, the Margalef diversity (H), Pielou evenness (J), Shannon-Wiener diversity (H'), and Simpson ecological dominance indices (D) of plankton in the Hulanhe

Wetland in three seasons were calculated. The variation ranges were 1.36–3.89 (H), 0.39–0.81 (J), 1.43–3.54 (H'), and 0.43–0.88 (D). The diversity of plankton communities was generally higher in summer than that in spring and autumn. The diversity of sampling sites (S4–S8) in wetland reserves was higher than that in other sites, and the areas affected by agriculture and fishery (S2, S10) were generally lower than other sites. The linear relationship between plankton community stability and species diversity is shown in Figure 8. BC had a significant positive correlation with H and J , and there was no significant linear relationship with H' and D . This shows that with the increase in species diversity and evenness, the community structure of plankton in the Hulanhe Wetland tended to be stable.

3.3.3. Environmental factors and plankton community stability

The ordinary least squares equation of the stability of the plankton community and environmental factors in the Hulanhe Wetland is shown in Figures 9, 10. There was a significant negative correlation between the stability of the phytoplankton community and WT and pH ($p < 0.01$), and there was a significant negative correlation between the stability of the zooplankton community and WT, pH, and TN ($p < 0.01$). There was no significant linear relationship between other environmental factors, indicating that only some water environmental factors can increase the stability of the plankton community.

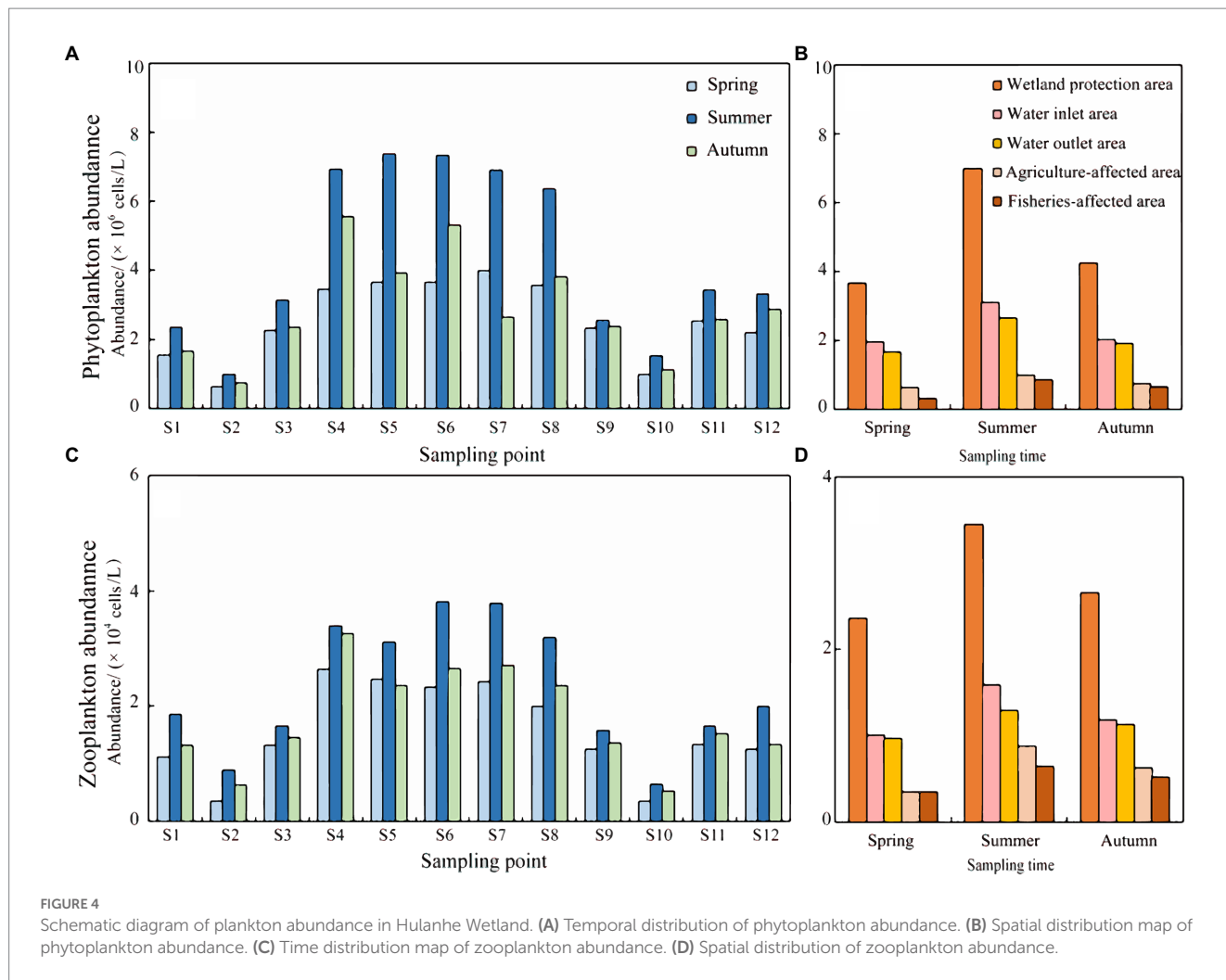


FIGURE 4 Schematic diagram of plankton abundance in Hulanhe Wetland. (A) Temporal distribution of phytoplankton abundance. (B) Spatial distribution map of phytoplankton abundance. (C) Time distribution map of zooplankton abundance. (D) Spatial distribution of zooplankton abundance.

4. Discussion

4.1. Plankton community structure

4.1.1. Spatio-temporal distribution characteristics of plankton community

During the study period, the plankton community structure in the Hulanhe Wetland showed some heterogeneity at the spatial and temporal scales (Tables 2, 3 and Figures 3, 4). The Hulanhe Wetland was affected by the temperate monsoon climate, and the physicochemical factors of the waterbody changed between seasons. In particular, the change in WT can directly affect the community composition and succession direction of phytoplankton in the Hulanhe Wetland. In spring and autumn, when the Hulanhe Wetland was just released or was about to enter the frozen period, the WT was low, and the dominant species of phytoplankton were mostly cold-tolerant Bacillariophyta, such as *Melosira varians*, *Cyclotella meneghiniana*. However, after entering summer, the WT and light intensity increased rapidly, and cyanobacteria and Chlorophycophyta that prefer warm water began to multiply and gradually occupy a dominant position (Zhu et al., 2022), such as *Arthrospira platensis*, *Anabaenopsis circularis*, and *Ankistrodesmus falcatus*. The results of this experiment are similar to the results of phytoplankton community characteristics and succession rules of Hui et al. (2011), Lu et al. (2014), and Jia et al. (2021)

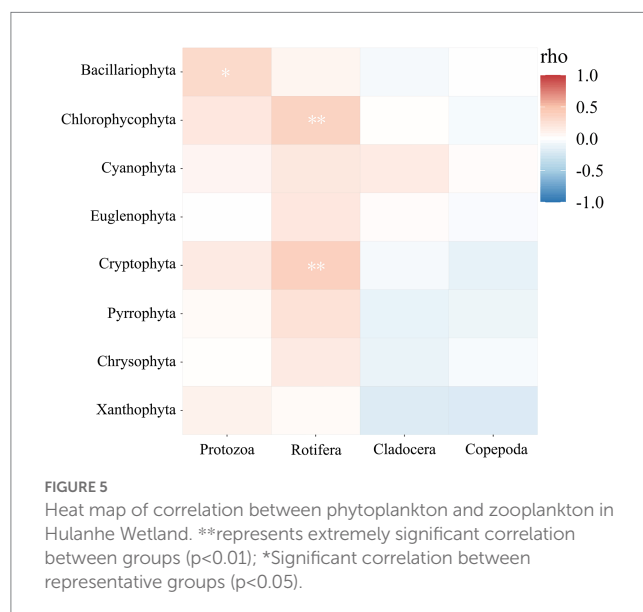
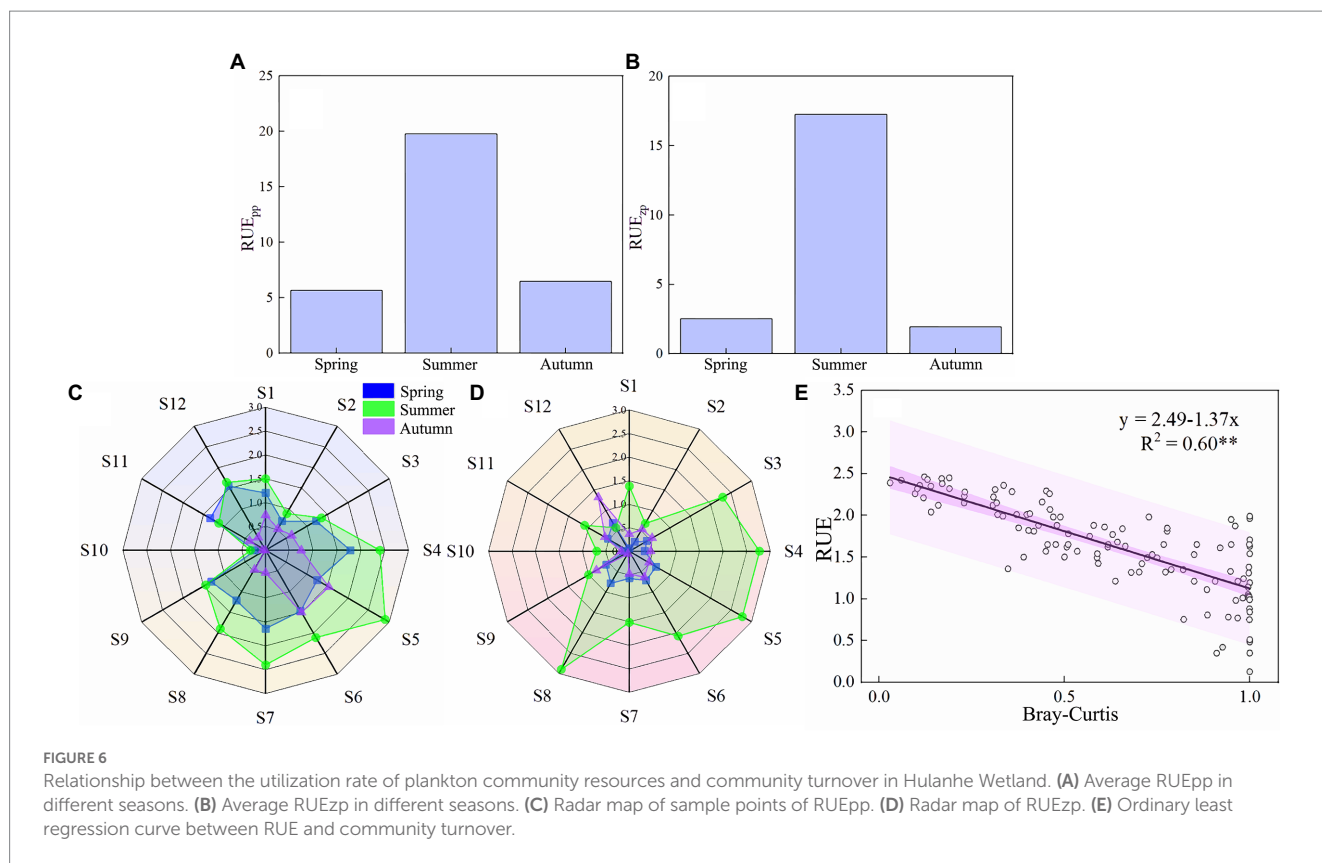


FIGURE 5 Heat map of correlation between phytoplankton and zooplankton in Hulanhe Wetland. **represents extremely significant correlation between groups ($p < 0.01$); *Significant correlation between representative groups ($p < 0.05$).

in 2013, 2018 and 2019, respectively. WT is an important environmental factor affecting the phytoplankton community, which further indicates that the composition and succession direction of phytoplankton



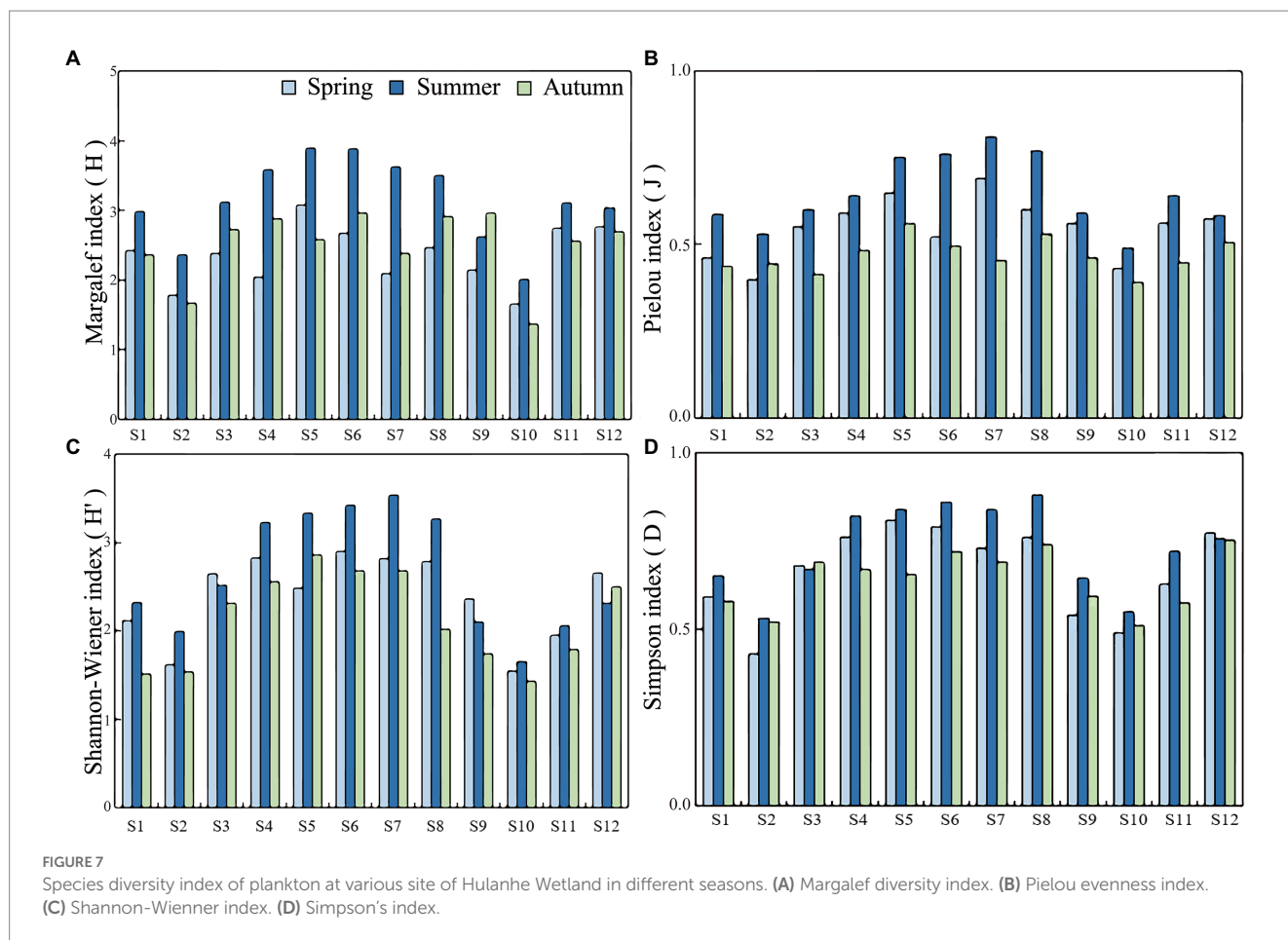
community in the Hulanhe Wetland were relatively stable in the past 10 years.

From the perspective of the zooplankton community structure, high similarity in species composition for three seasons in 2021 and the temporal variation was not obvious. The proportion of species and abundance of small zooplankton (protozoa, rotifers) was higher than that of large zooplankton (cladocerans, copepods). The community structure of zooplankton showed a trend of miniaturization, such as *Centorpyxis aculeata*, *Tintinnidium fluviatile*, and *Polyarthra trigla*, which was similar to the results of other wetland studies on the distribution of zooplankton (Chen et al., 2014; An et al., 2017; Wang et al., 2017). The reason may be that protozoa and rotifers have small size, short cycle, and rapid development (Arndt, 1993; Li et al., 2017). They can quickly adapt to changes in hydrological conditions and physicochemical environment in the water body; therefore, they often occupy a dominant position in wetland habitats. This result is consistent with the research results of Zhang et al. (2018) showing a trend of miniaturization of zooplankton community structure.

Anthropogenic activities and urban sewage are the reasons behind the nutrient content of the Hulan River being at a relatively high-level (Xing, 2016), and wetlands can restore the water quality of polluted rivers (Zheng et al., 2014). As the largest urban wetland in China, Hulanhe Wetland has achieved great results in ecological restoration in recent years. From the spatial scale analysis, phytoplankton and zooplankton species abundance changes are consistent. The species number and average abundance of plankton in the Hulanhe Wetland protection area were much larger than those in the Hulanhe Wetland water outlet and inlet areas, which may be because the wetland had the function of purifying water and depositing nutrients, and the slow

water flow rate in the wetland caused the deposition of nutrients (Kobayashi et al., 2014), which was also conducive to the growth and reproduction of plankton, such as *Cyclotella meneghiniana*, *Arthrospira platensis*, and *Tintinnidium fluviatile*. Compared with the area outside the wetland, the species number and abundance of plankton in the water inlet area were larger than those in the water outlet area. The richness and abundance of plankton in the water inlet area were higher than those in the water outlet area. Water outlet area through the wetland sediment filtration and biological filtration effect resulted in reduced nutrients (Aziz and Van Cappellen, 2021). The richness and abundance of plankton in the water outlet area decreased with the decrease in nutrients. Most of the plankton were *Anabaena circinalis*, *Ankistrodesmus angustus*, and *Polyarthra eurypetra*, indicating that the Hulanhe Wetland had a certain effect of nutrient salt deposition. This led to certain spatial differences in plankton communities.

The composition of the plankton community is a strong indicator of the water environment (Jagadeesan et al., 2019). As one of the key wetlands in Harbin, the Hulanhe Wetland has achieved great results in ecological restoration in recent years. During the investigation period, the dominant species of plankton communities in the Hulanhe Wetland in the three seasons were mainly pollution-indicator organism species of clean water and oligo-sewage bodies. Zooplankton, such as *Polyarthra eurypetra* (Chen et al., 2011), *Strombidium virid* (Ju et al., 2017), and *Diffugia acuminata* (Ju et al., 2017) were dominant. Phytoplankton, such as *Asterionella formosa* (Shan et al., 2022), *Dinobryon cylindricum* (Zhang and Li, 2016), *Ulmaria ulna* (Zhu et al., 2017), and *Navicula radiosa* (Zhang N. et al., 2016), which prefer clean water, also appeared as dominant communities, which are highly similar to the results of plankton



surveys in the Macquarie wetland (Chaparro et al., 2018), which is also a temperate area and has been ecologically restored. The results show that in recent years, with the restoration of the Hulanhe Wetland, the ecological function gradually improved, the water quality was cleaner, and the damage to water ecosystem health was reduced to a controllable range (Hui et al., 2011).

4.1.2. Correlation between phytoplankton and zooplankton

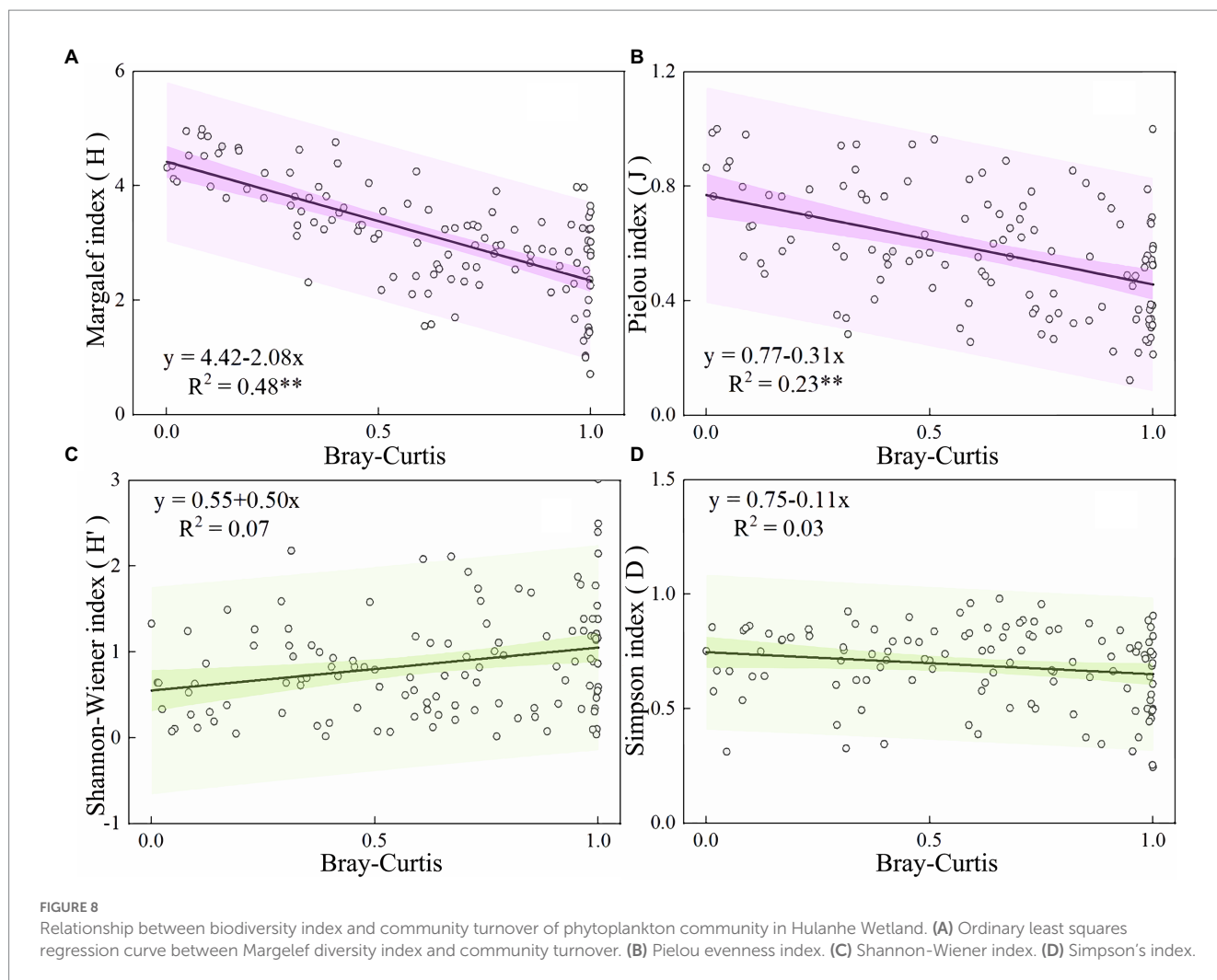
Phytoplankton and zooplankton are important components of the food web in aquatic ecosystems, and there is a very close competition between them and the relationship between predation and predation (Mcqueen et al., 1989). Some studies have confirmed that the predatory grazing behavior of zooplankton is the main reason for the change in the phytoplankton communities (Mcqueen et al., 1989; Vanni and Temte, 1990; Figure 5).

In this study, protozoa and diatoms showed a significant correlation. Protozoa are eukaryotic unicellular animals that belong to heterotrophic organisms and are preyed by large zooplankton (such as copepods and cladocerans) (Burns and Schallenberg, 2001; Turner et al., 2001). Protozoa constitute a complete food chain by preying on diatoms (Min et al., 2019). Many experiments have shown that (Liu and Dagg, 2003; Stelfox-Widdicombe et al., 2004; Kim et al., 2007; Hu et al., 2015) large zooplankton cannot directly ingest diatoms, probably because of the shell of diatoms or because diatoms release harmful substances (such as unsaturated aldehydes) when they reach a certain

high concentration to inhibit the growth and reproduction of large zooplankton. Therefore, large zooplankton will directly choose to feed on protozoa and then transfer the primary productivity of diatom sources upwards in the food chain, thus playing a role in the transmission of diatoms in the food chain.

During the study period, rotifers had a strong correlation with Chlorophycophyta, Euglenophyta, and cryptophytes. Rotifer is a small filter-feeding zooplankton. The efficiency of filtering phytoplankton is determined by the size of the phytoplankton. The palatable food range of most filter-feeding rotifers is between 1 and 15 μm (Zhang and Hang, 1991). Chlorophyta and some Cryptophyta (such as *Chroomonas acuta*), as the dominant species in the Hulanhe Wetland, have a fast reproduction rate and a palatable volume. They mostly exist in the filter-feeding range of Rotifers and are easy for rotifers to prey on. Some previous studies have shown that cryptophytes are often used as high-quality bait for zooplankton because of their cell wall digestibility, non-toxicity and suitable biochemical composition (Porter, 1973). Chlorophycophyta and cryptophytes can be successfully ingested by rotifers and can meet the corresponding nutritional needs; therefore, rotifers tend to prey on Chlorophyta and Cryptophyta (Wang et al., 2012). The predation of rotifers on green algae is also one of the reasons that affect the phytoplankton community structure, with Chlorophycophyta as the main dominant species (Yang, I., 2012).

Cyanophyta, Bacillariophyta, and Chlorophyta were the dominant species of phytoplankton in the Hulanhe Wetland, but there was no significant correlation between Cyanophyta and zooplankton. The



reason may be that zooplankton does not prefer ingesting cyanobacteria. Studies have shown that cyanobacteria do not have zooplankton palatability, and the lack of highly unsaturated fatty acids has a negative impact on the growth rate of zooplankton (Juliana et al., 2016); simultaneously, the life form of cyanobacteria is mostly gathered into filaments or surrounded by gelatinous sheaths, which are too large and not easy to be fed (Tan and Ransangan, 2017); some species of zooplankton may also be sensitive to toxins produced by cyanobacteria (De Silva and Jang, 2017).

In conclusion, we found that the abundance of phytoplankton in water was closely related to the growth and reproduction of zooplankton. Phytoplankton is an important food source for zooplankton. High-density phytoplankton ensures the supply of zooplankton food and promotes the reproduction and growth of zooplankton. However, the feeding of zooplankton on phytoplankton is also selective. Zooplankton is more inclined to be easily ingested and palatable than phytoplankton, such as Chlorophyta and Cryptophyta.

4.2. Driving factors of plankton stability

4.2.1. RUE

RUE can reflect the nutrient cycle and transfer process of the ecosystem (He et al., 2021). Communities with high abundance of

plankton often have higher RUE, and species in high-abundance communities have a high occupancy rate of trophic niches, increasing the overall RUE (Tian, 2017). In this study, the spatio-temporal differences in RUE and plankton abundance showed the same pattern (Figures 6A,B). The WT of the Hulanhe Wetland increased gradually with the increase of months, which was conducive to the growth and reproduction of plankton. Summer was the season with the most plankton species. At the same time, studies have shown that communities with diatoms, Chlorophycophyta, and protozoa as dominant species can use resources more efficiently (Tillmanns, 2006; Filstrup et al., 2014). Cyanobacteria, Chlorophycophyta, and Protozoa were the dominant phyla of plankton in the Hulanhe Wetland in summer. They have a wide ecological range and strong adaptability to the environment, which improves the RUE of plankton in summer; therefore, the RUE in summer was much greater than that in other seasons.

Some studies have found that the increase in biodiversity will increase RUE and community stability (Filstrup et al., 2014; Zhang et al., 2021), which is similar to the results of this study (Figure 6E). This study found that the gradually abundant plankton species community can use resources more effectively in the ecosystem, and the species community with high diversity has a large number of species and uniform distribution, which makes the community more stable. The abundance and diversity of plankton in the Hulanhe

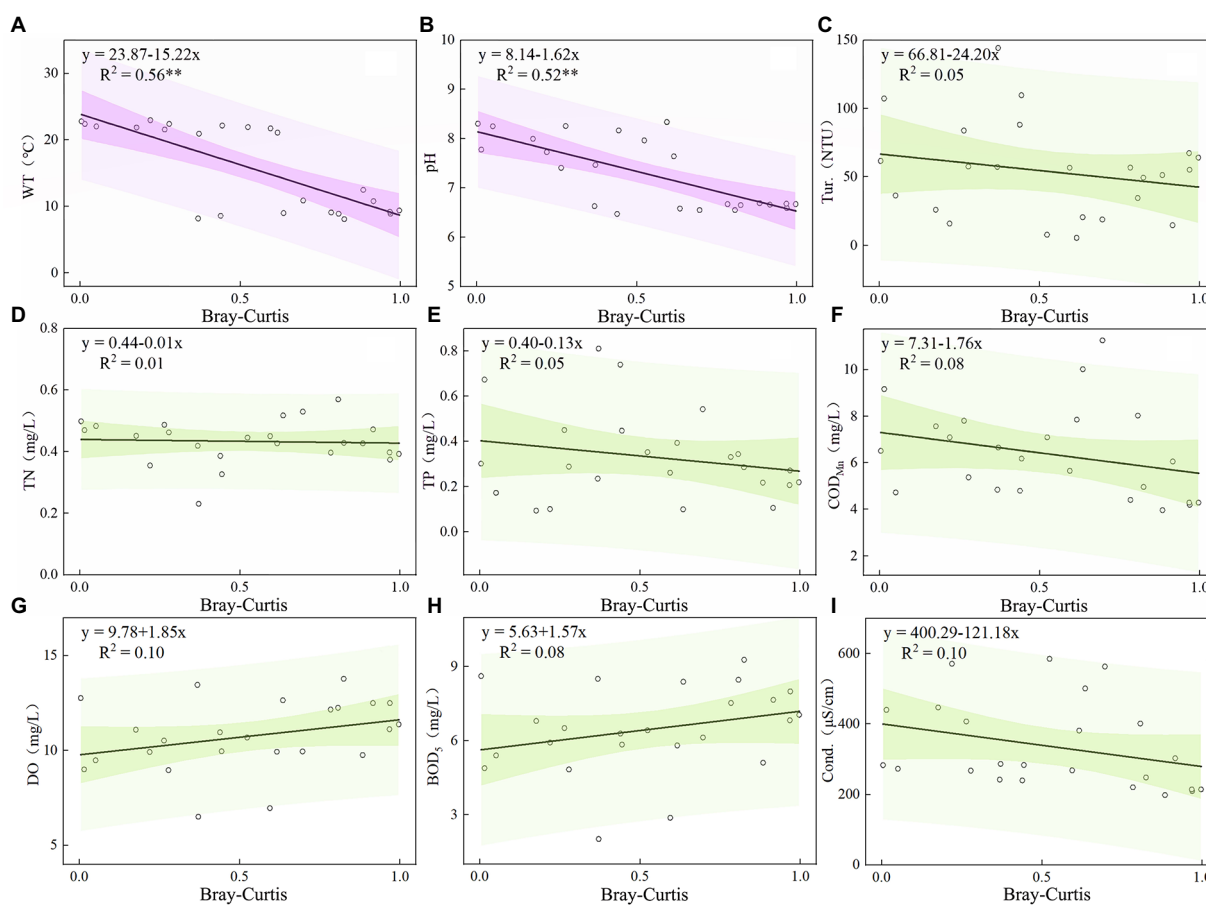


FIGURE 9

Relationship between Environmental Factors and Community Turnover of Phytoplankton Community in Hulanhe Wetland. (A) Water temperature and community turnover. (B) pH. (C) Turbidity. (D) Total nitrogen. (E) Total phosphorus. (F) Permanganate index. (G) Dissolved oxygen. (H) Bio-chemical oxygen demand. (I) Conductivity.

Wetland showed the same pattern (Figures 4, 7). The level of biodiversity increased with the increase in abundance, which enhanced the niche complementarity of plankton in the aquatic ecosystem to a certain extent. The ecological complementarity effect will cause overproduction (Hillebrand et al., 2008), which will promote the utilization efficiency of ecosystem resources.

High concentrations of nutrients are also one of the reasons for the correlation between RUE and the stability of plankton communities (Zhang et al., 2021). Higher concentrations of nutrients can promote the rapid growth and reproduction of plankton. The wetland ecosystem deposits nutrients and purifies water, which is one of the reasons for the high abundance of plankton in the Hulanhe Wetland protection area. Therefore, the RUE in the reserve was much higher than that in other areas (Figures 6C,D). In this study, the RUE in the agriculture-affected area (S2) and fisheries-affected area (S10) was the lowest of all samples (Figures 6C,D). The long-term effects of field herbicides on macrophytes may result in delayed, indirect responses to zooplankton and phytoplankton communities, and pollution may result in single species and a low abundance of plankton (Relyea, 2005). Due to the obvious agricultural disturbance, the RUE of the agriculture-affected area (S2) of the Hulan River inlet was low, indicating that anthropogenic disturbance destroyed the ecological function systems, resulting in low resource utilization (Wang et al.,

2019). S10 was an area greatly affected by the fishery. The disturbance caused by the fishing process inhibited the growth of plankton. At the same time, the fish school carries out a large number of downward effect control on plankton, resulting in low species number and abundance (Shen and Wang, 1991), which leads to a low RUE. Therefore, to maintain the stability and sustainability of the regional ecological security pattern, the regional ecological function system affected by anthropogenic disturbance needs further restoration.

4.2.2. Species diversity

Species diversity is an important measure of community stability. There is a certain coupling relationship between plankton species diversity and community stability (Tilman, 1999). Exploring the correlation between plankton diversity and community stability is of great significance for explaining plankton community structure and diversity. In aquatic ecosystems, the increase in plankton species diversity makes the community more stable (Ptacnik et al., 2007), which is the same as the results of this study (Figure 8A).

In this study, with the increase in plankton community diversity, the community became more stable. It is speculated that the food chain and food web of communities with high diversity tend to be more complex, and there are more ways for energy flow within the

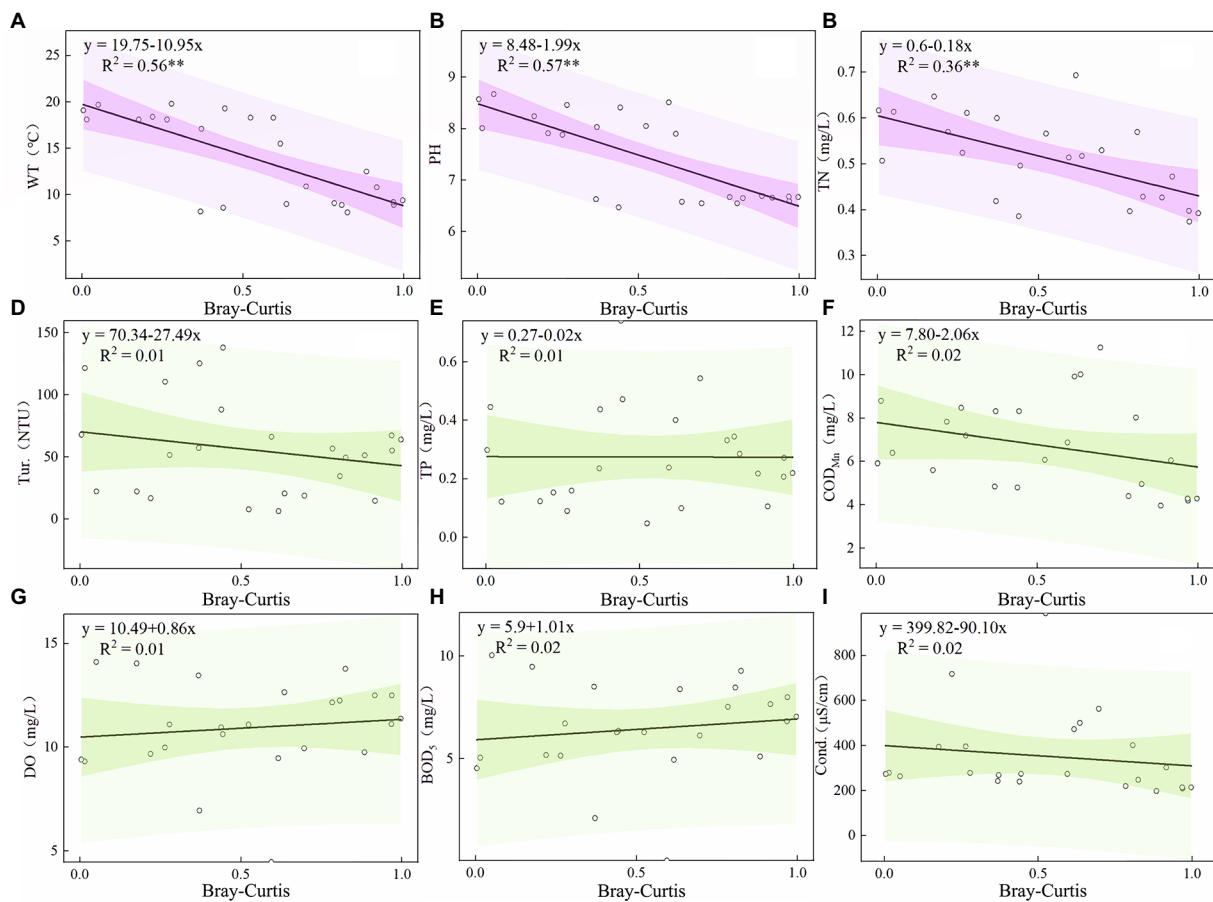


FIGURE 10

Relationship between Environmental Factors and Community Turnover of Zooplankton Community in Hulanhe Wetland. (A) Water temperature and community turnover. (B) pH. (C) Total nitrogen. (D) Turbidity. (E) Total phosphorus. (F) Permanganate index. (G) Dissolved oxygen. (H) Bio-chemical oxygen demand. (I) Conductivity.

community. If a certain way is blocked by interference, there may be other routes to compensate (Cao and Zhan, 2015). Therefore, a community with high diversity has less fluctuation among species, which makes the community more stable. A structurally stable plankton community has a strong feedback system, which can buffer environmental changes or fluctuations in the population from within the community and is less susceptible to external disturbances (MacArthur, 1955; Cao and Zhan, 2015).

The evenness index reflects the uniformity of the individual number distribution of each species. The higher the evenness, the more uniform the species distribution. This study showed high Pielou evenness, which implies high community stability (Figure 8B). Many studies have shown that the higher the species' evenness, the stronger the ecosystem function conversion, making the plankton community more stable (Wittebolle et al., 2009; Allan et al., 2011; Filstrup et al., 2014). The results of this study also reached the same conclusion. The community with high plankton evenness had a more uniform distribution of species resources, and the anti-interference ability of the community also increased, which is conducive for the better adaptation of the plankton community to the aquatic ecological environment (Tian, 2017; Zheng, 2019).

4.2.3. Environmental factors

Through ordinary least squares analysis, it was found that the physical and chemical environmental factors of the waterbody had a certain driving effect on the stability of the phytoplankton community, and the environmental factors affecting phytoplankton and zooplankton were similar. WT ($p < 0.01$, $p < 0.01$) and pH ($p < 0.01$, $p < 0.01$) were both the driving factors of phytoplankton and zooplankton community stability, while TN ($p < 0.01$) was only the driving factor of zooplankton community stability.

Plankton community stability will increase with the increase of WT (Figures 9A, 10A). WT can affect the metabolic intensity, growth and development, and reproduction cycle of plankton, and then affect its abundance and biomass changes and the distribution of community structure, and ultimately affect the material circulation and energy flow of the ecosystem. The average temperature of the Hulanhe Wetland in summer is 22.0°C, while cyanobacteria, Chlorophycophyta, and rotifers are more suitable for growing in warm water. The average temperature in spring and autumn is slightly lower than 16.3°C and 9.1°C, which is more suitable for the growth and reproduction of diatoms, Chrysophyta, and Protozoa, and is more dominant in the plankton community. In addition, the predation rate of zooplankton

is similar to the growth rate of zooplankton, which increases the grazing frequency and achieves rapid reproduction of zooplankton as the water temperature increases (Pulsifer and Laws, 2021). This further proves that the stability of plankton community will be more stable with the increase of WT.

pH is an important water environmental factor driving the stability of phytoplankton and zooplankton communities. The results showed that there was a significant negative correlation between pH and the turnover of zooplankton and phytoplankton communities (Figures 9B, 10B). Phytoplankton communities were more stable in alkaline water. The pH affects the absorption of nutrients by affecting the activity of some enzymes in plankton cells or transmembrane proton gradient. In the season with high WT, the dissolved CO₂ in water decreases, increasing the pH value, and the Hulanhe Wetland is weakly alkaline (7.51 ± 0.38), which promotes the growth and reproduction of plankton, thus affecting its community structure (Zhang et al., 2021). The alkaline environment is conducive to phytoplankton absorbing CO₂ for photosynthesis. In alkaline water, phytoplankton has high primary productivity, which ensures the food source of zooplankton. The abundance of zooplankton also increases, and the phytoplankton community gradually stabilizes (Jakobsen et al., 2015).

TN is an essential element for the synthesis and energy transfer of aquatic organisms and also an important nutrient source for zooplankton. The variation in TN concentration can affect the food source of zooplankton and the dynamic pattern of community (Shen et al., 2021). TN indirectly affects the composition of zooplankton by affecting the community structure of phytoplankton (Guo et al., 2017). At the same time, changes in the ratio of nitrogen to phosphorus in the water affects the competition between zooplankton with different growth characteristics and the change in population structure (Yang et al., 2021). During the study period, the average nitrogen-phosphorus ratio of the Hulanhe Wetland was 1.52 (N/P < 16:1), which was a nitrogen limitation. The average TN of the Hulanhe Wetland in spring, summer, and autumn was at a relatively high level (0.46 mg/L). High concentrations of TN made the zooplankton community more stable (Figure 10C). Bhavya et al. (2020) have shown that the total uptake of nitrogen by phytoplankton is in the range of 10.24–59.36% and 30.21–68.55%. Therefore, high concentration of TN promotes the reproduction of phytoplankton (Liu et al., 2022). Phytoplankton photosynthesis in water not only provides sufficient food for zooplankton but also creates an oxygen-rich environment for zooplankton, which makes zooplankton species more abundant and increases community stability.

Overall, the stability of the plankton community is a very complex problem. The stability of the plankton community is not only affected by the single factor of community structure characteristics but also has a certain correlation with RUE, biodiversity, and water environment factors.

For future studies, we suggest observing the effects of microorganisms on plankton (Pearce and Butler, 2002; Rana et al., 2021), the predation of plankton by fish (Villéger et al., 2019; Xia et al., 2020), and the variation in plankton stability under special conditions (e.g., heavy rain, freezing, and advection; Manna et al., 2019; Liu et al., 2021; Lu et al., 2022), which will help to improve our mechanistic understanding of the maintenance and stability of plankton community structure.

5. Conclusion

Specific predation relationship was observed between phytoplankton and zooplankton in the Hulanhe Wetland. Protozoa tend to prey on diatoms, rotifers prefer to ingest Chlorophycophyta and cryptophytes, but cyanobacteria are rarely preyed on by zooplankton because of their own cyanobacterial toxins and mismatched caliber. The stability of plankton community in the Hulanhe Wetland is controlled by biotic and abiotic factors. The stability of the plankton community had a significant linear relationship with the Margalef diversity index, Pielou evenness index, and RUE. The key factors affecting phytoplankton community stability in the Hulanhe Wetland were WT and pH, while zooplankton community stability was mainly driven by WT, pH, and TN.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

XL conceived the original concept. XL and YF developed experimental strategies and sampling design. TT carried out the collection of plankton samples and the determination of water physicochemical indicators under the guidance of XL. TT and HW carried out the counting and identification of plankton specimens and contributed in sampling collection, data analysis, and manuscript writing. TT, HW, and XN performed all data analysis and integration with help from XL and YF. TT prepared the manuscript with significant input from HW, XN, NZ, XL, YL, and YF. All authors contributed experimental assistance and intellectual input to this study.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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