

Impact of habitat heterogeneity on the biodiversity and density of the zooplankton community in shallow wetlands (Upo wetlands, South Korea)

by

Jong-Yun Choi^{1,*}, Kwang-Seuk Jeong²,
Seong-Ki Kim², Gea-Jae Joo²

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Abstract

Macrophytes play a major role in the structuring of aquatic environments, and create diverse microhabitats. Therefore, these plants represent an important factor regulating the zooplankton biomass, taxonomic composition, and distribution in freshwater ecosystems. In the current study, we examined the effects of the structural heterogeneity provided by various macrophytes. We identified four habitat types in this study: (1) open water (without macrophytes), (2) the helophyte zone, (3) the pleustophyte zone, and (4) the mixed vegetation zone (containing pleustophytes, nymphaeids, and elodeids). We tested the hypothesis that complex habitat structures support large zooplankton assemblages. Specifically, we collected zooplankton samples from a total of 119 sampling points in the Upo Wetlands, South Korea, during the spring and autumn of 2009. The largest zooplankton assemblage was found in the mixed macrophyte zone, followed by the helophyte and pleustophyte zones. The pleustophyte zone supported larger zooplankton assemblages during autumn compared to spring. Differences in zooplankton assemblages were considered to be strongly related to seasonal variation in the development and growth of pleustophytes. However, two-way ANOVA revealed that seasons had no significant influence on the zooplankton density and diversity. Instead, different habitat types substantially determined zooplankton characteristics. In conclusion, we demonstrated that wetland areas with high macrophyte species diversity contribute toward higher zooplankton diversity.

¹*National Institute of Ecology, Seocheon-gun
Maseo-myeon Geumgang-ro 1210,
Chungcheongnam-do,
Republic of Korea*

²*Department of Biological Sciences, Pusan
National University, Busan 609-735,
Republic of Korea*

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* Corresponding author: jyc311@naver.com

Introduction

Habitat heterogeneity may provide more niches and diverse ways of exploiting the environmental resources (Bazzaz 1975). Habitats with high structural heterogeneity provide refuges from predators, suitable spawning and foraging substrates, thus supporting a greater diversity of animals (Declerck et al. 2005; Vieira et al. 2007). Empirical studies have demonstrated that habitat heterogeneity in woods and stands of trees (Ganzhorn et al. 1997; Southwell et al. 1999), grass (Dennis et al. 1998), coral reefs (Roberts & Ormond 1987; Jones & Syms 1998), and landscapes (Hanowski et al. 1997) create habitat space for various wildlife. The habitat heterogeneity of freshwater ecosystems is primarily determined by the physical structure and composition of macrophytes. Thus, these aquatic plants are expected to have a major impact on the distribution and interaction of various animal groups (Thomaz et al. 2008).

Freshwater macrophytes create a heterogeneous microhabitat in the water, providing a suitable food supply for animals, as well as a refuge from predators (Lauridsen & Lodge 1996; Lauridsen et al. 1996). Thus, macrophyte habitats are able to support a large abundance of animals, such as zooplankton, macroinvertebrates, and small fish. Of the various aquatic animal groups, it has been demonstrated that the zooplankton community effectively utilizes macrophyte habitats (Kuczynska-Kippen & Nagenast 2006; Burks et al. 2002). Previous studies have shown that zooplankton are strongly affected by the density (Snickars et al. 2004), life forms (Warfe & Barmuta 2004), and structural heterogeneity of macrophytes in vegetated beds (Meerhoff et al. 2006; Thomaz et al. 2008). For example, submerged macrophytes generally increase the physical complexity of aquatic environments, and hence provide a suitable habitat for the zooplankton community. However, free-floating or floating-leaved macrophytes have also been reported to fulfil important structuring functions in wetland systems (Meerhoff et al. 2003). Therefore, it may be hypothesized that mixed structures of various macrophyte species support more zooplankton.

The importance of habitat heterogeneity to zooplankton has been central to limnological research. Zooplankton is located at the intermediate level in the food web, between phytoplankton and fish, and plays a key role in regulating the food web dynamics (Wetzel 1983). Unfortunately, the distribution of the zooplankton community has not been comprehensively evaluated in relation to different types or combinations of macrophytes. This study aimed to understand the influence of habitat heterogeneity

on the zooplankton community in a wetland system. We predicted that greater macrophyte species diversity would enhance the abundance and species diversity of the zooplankton community.

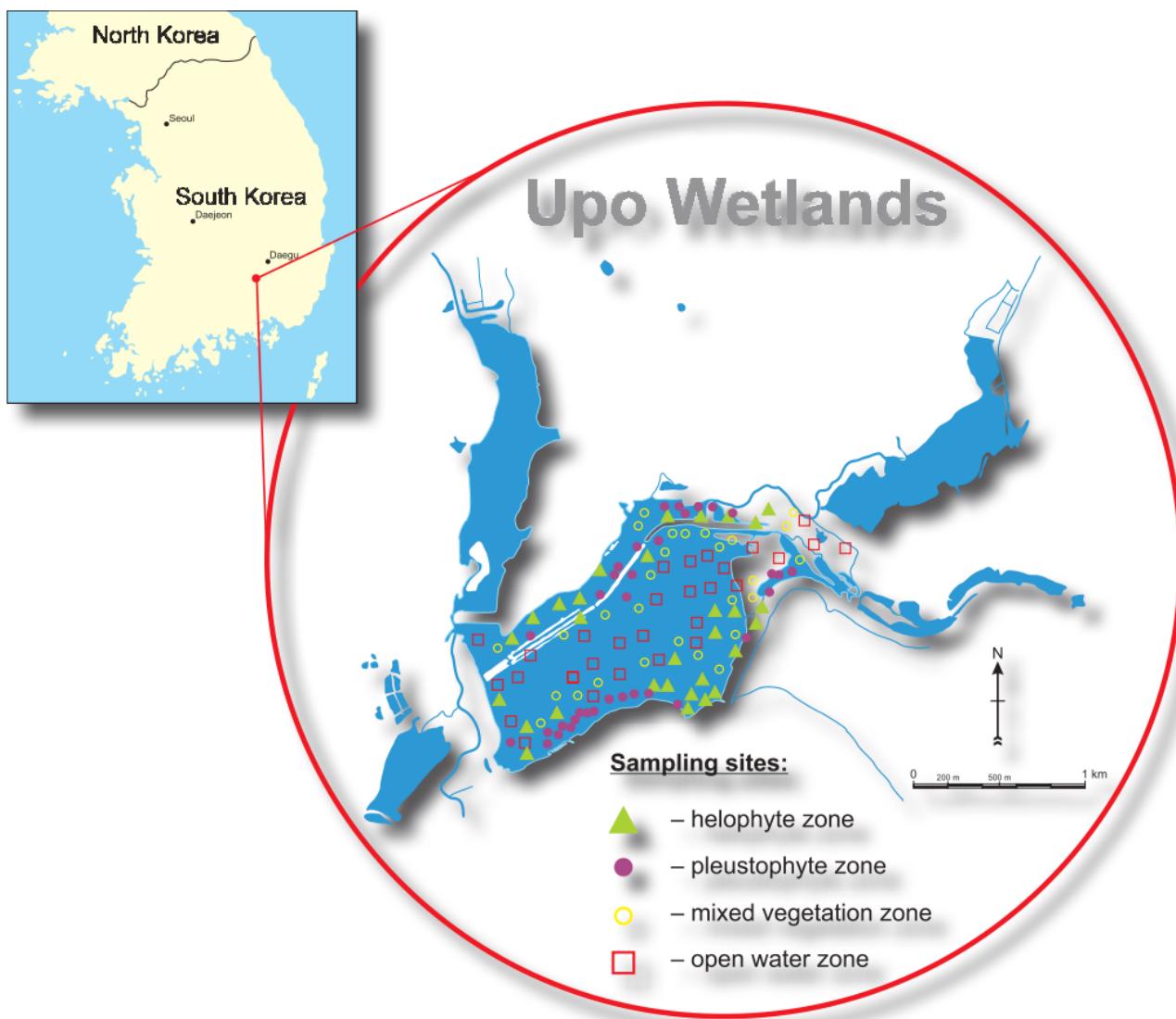
Materials and methods

Study site description

South Korea is located in Eastern Asia and has a temperate climate. The presence of four distinct seasons leads to the dynamic succession of the biological community in the Korean freshwater ecosystems. The annual average rainfall in South Korea is ca. 1,150 mm, with the freshwater ecosystems in this country being exposed to heavy rainfall during summer (ca. >60% of the annual rainfall occurs from June to early September; Jeong et al. 2007). Therefore, the summer season was excluded from this study, as it did not correspond with the study objectives. The study site (Upo Wetlands) is located in the southeastern part of South Korea and is the largest wetland floodplain along the Nakdong River. The total area of the study site is approximately 2.4 km², while the mean depth ranges from 1 m to 1.5 m. The study site is almost completely covered with macrophytes. We identified four different habitat types based on the heterogeneity of macrophyte composition: (1) the open water zone (without macrophytes), (2) the helophyte zone, (3) the pleustophyte zone, and (4) the mixed macrophyte zone (containing pleustophytes, nymphaeids, and elodeids). The sampling points were established by random number generation, with 119 sampling points being surveyed during the spring (May) and autumn (October) of 2009 (see Fig. 1 and Table 1). We have not observed changes in the habitat type between spring and autumn.

Environmental characteristics of water

Water temperature, dissolved oxygen, pH, conductivity, depth, and chlorophyll *a* were measured as environmental factors in the Upo Wetlands during the spring (May) and autumn (October) of 2009. We used a quadrat (0.5 m × 0.5 m in size) to obtain the water samples, macrophyte biomass and zooplankton specimens at each sampling point (n = 119) during spring and autumn. Table 1 provides a list of macrophyte species and the number of sampling points that correspond to the four identified habitat types. We used a dissolved oxygen (DO) meter (YSI DO meter; Model 58) to determine the water temperature and dissolved oxygen. The pH and

**Figure 1**

Map of the study site located in the southeastern part of South Korea

Table 1

Species names of aquatic macrophytes and dry weight along with the number of samples collected in spring and autumn in the four identified habitat types

Habitat types	Species of aquatic macrophytes	Sampling point	Dry weight (g dw m ⁻²)	
			Spring	Autumn
Helophytes zones	<i>Phragmites communis</i> (TRIN.)	32	22.7±6.7	29.7±5.7
	<i>Paspalum distichum</i> var. <i>indutum</i> Shinners		12.3±5.4	16.4±9.4
Pleustophytes zones	<i>Spirodela polyrhiza</i> (L.)	27	12.6±6.4	21.4±8.7
	<i>Salvinia natans</i> (L.) ALL		8.2±2.4	14.8±4.4
Mixed plants zones	<i>Spirodela polyrhiza</i> (L.)	30	15.8±7.1	28.7±6.1
	<i>Salvinia natans</i> (L.)		6.7±4.7	21.8±9.8
	<i>Ceratophyllum demersum</i> (L.)		23.4±9.4	35.7±11.7
	<i>Potamogeton crispus</i> (L.)	30	25.7±6.8	36.7±8.7
	<i>Najas graminea</i> (L.)		13.4±5.4	21.7±6.9
Open water zones	-	30	-	-

conductivity were recorded using a pH meter (Orion pH Meter; Model 250A) and a conductivity meter (Fisher Conductivity Meter; model 152), respectively. The depth was measured for each quadrat in each sampling point. For the determination of chlorophyll *a* concentration, additional water samples were transported to the laboratory and filtered through a mixed cellulose ester (MCE) membrane filter (Advantech; Model No. A045A047A; pore size, 0.45 µm). Then, the filtrates were used to determine chlorophyll *a* concentration using a spectrophotometer (UV-visible spectrophotometer; model UV-2550), following the method of Wetzel and Likens (2000).

Macrophyte biomass and zooplankton

We collected macrophyte specimens from each quadrat. Entire macrophyte plants were removed from the quadrats, and sorted by species. The macrophyte samples were immediately transferred to the laboratory and dried for 48 hours at 60°C. The weight of each macrophyte species was measured and recorded as the dry weight of species in each quadrat (g dw m⁻²).

We obtained a 10 l water sample using a 12 l column water sampler from the quadrat at each sampling point to collect zooplankton. The 10 l water sample was filtered through a plankton net (68 µm mesh) and the filtered samples were preserved in formaldehyde (final concentration, ca. 5%). The zooplankton in the collected samples were identified and counted using a microscope (ZEIZZ, Model Axioskop 40; x200 magnification). Species identification was completed based on Mizuno and Takahashi (1999).

Data analysis

We used one-way ANOVA ($\alpha = 0.05$) in the statistical package SPSS for Windows (version 14) to compare the zooplankton density and environmental factors in each habitat type. Differences in zooplankton density in relation to the season and habitat type were analyzed statistically by two-way ANOVA. Tukey's test was used in additional post-hoc comparison analysis to determine whether the differences were statistically significant.

Species diversity of zooplankton (H') was calculated according to the following equation (Shannon & Weaver 1963):

$$H' = - \sum P_i \log_2 P_i \quad P_i = \frac{N_i}{N}$$

where N_i is the number of individual organisms of the species, and N is the total number of individuals. The species diversity was analyzed using the rarefaction in the SPADE program (Chao & Shen 2010).

Results and discussion

During the study period, similar macrophyte species composition was observed during spring and autumn, but plant dry weight differed according to season (Table 1). A total of 6 macrophyte species were found at the study site. The helophyte and pleustophyte zones contained two species of macrophyte each, while the mixed vegetation zone contained a total of five macrophyte species. The dry weight of macrophytes was higher in autumn compared to spring, because of a different growth pattern changing with the seasons. The highest macrophyte dry weight was obtained for *Potamogeton crispus*, followed by *Ceratophyllum demersum*, and *Phragmites communis*.

Table 2 presents various environmental factors (i.e. depth, water temperature, dissolved oxygen, pH, conductivity and chlorophyll *a*) in relation to different macrophyte zones (i.e. zooplankton habitat types) at the study site. Most of the monitored environmental factors were similar in all four habitat types. The largest difference was observed for DO concentration (one-way ANOVA, $p < 0.05$), with relatively higher concentrations being obtained in the open water zone compared to the three other zones. Dissolved oxygen tends to be low when macrophytes are present on the water surface, because of different permeation rates (van der Valk 2006). Therefore, we expected that the zooplankton community might be affected by the structural heterogeneity of the four habitat types.

The collected zooplankton was represented by a total of 43 species, including 27 species of Rotifers and 16 species of Cladocerans and Copepods in the Upo Wetlands (Table 3). The mixed macrophyte zone supported the largest number of zooplankton species (spring – 25 species; autumn – 26 species), followed by the helophyte zone (spring – 16 species; autumn – 15 species) and the pleustophyte zone (spring – 10 species; autumn – 20 species). On the other hand, the lowest number of zooplankton species was documented in the open water zone (spring – 6 species; autumn – 5 species). Zooplankton density was statistically different among the four habitat types (one-way ANOVA, $p < 0.05$, $n=119$, Fig. 2). The highest zooplankton density was found in the mixed vegetation zone, followed by the helophyte zone and the pleustophyte zone. However, the zooplankton



Table 2

Environmental parameters measured during the spring and autumn of 2009 in the four identified habitat types

H – helophyte zone; P – pleustophyte zone; M – mixed vegetation zone (pleustophytes, nymphaeids, and elodeids); O – open water zone;

Mean \pm SE; ANOVA results (*statistically significant)

Seasons	Environmental parameters	H	P	M	O	Habitat types (p)
Spring	Depth (m)	0.3 \pm 0.1	0.5 \pm 0.2	0.7 \pm 0.2	0.5 \pm 0.4	0.846
	Water temperature (°C)	17.5 \pm 4.8	18.4 \pm 5.6	18.9 \pm 3.7	17.8 \pm 4.1	0.734
	Dissolved oxygen (%)	42.7 \pm 12.8	21.5 \pm 11.8	23.4 \pm 12.1	53.8 \pm 21.7	0.037*
	pH	7.5 \pm 0.7	7.6 \pm 0.8	7.6 \pm 0.9	8.1 \pm 0.4	0.627
	Conductivity (μ S cm $^{-1}$)	322.8 \pm 112	312.4 \pm 105	285.7 \pm 95	312.4 \pm 131	0.728
	Chlorophyll a (μ g l $^{-1}$)	25.8 \pm 12.6	28.4 \pm 13.5	27.6 \pm 17.2	16.7 \pm 6.2	0.157
Autumn	Depth (m)	0.4 \pm 0.2	0.6 \pm 0.2	0.6 \pm 0.2	0.5 \pm 0.2	0.748
	Water temperature (°C)	22.5 \pm 4.8	24.4 \pm 5.6	25.1 \pm 2.1	23.2 \pm 3.5	0.648
	Dissolved oxygen (%)	17.2 \pm 0.8	18.2 \pm 5.4	17.8 \pm 4.6	34.2 \pm 11.2	0.031*
	pH	7.5 \pm 0.7	7.6 \pm 0.8	7.6 \pm 0.9	8.1 \pm 0.4	0.681
	Conductivity (μ S cm $^{-1}$)	312.8 \pm 112	308.7 \pm 56	304.8 \pm 85	311.2 \pm 147	0.816
	Chlorophyll a (μ g l $^{-1}$)	36.3 \pm 14.7	32.8 \pm 21.7	33.1 \pm 14.1	22.7 \pm 9.7	0.213

Table 3

List of zooplankton species found in the four identified habitat types during the spring and autumn of 2009

Taxa	Spring				Autumn			
	H	P	M	O	H	P	M	O
Rotifers								
<i>Anuraeopsis fissa</i>	+	+				+	+	
<i>Brachionus angularis</i>	+		+		+	+	+	
<i>Brachionus quadridentatus</i>	+		+		+	+	+	
<i>Colurella obtusa</i>		+			+	+		
<i>Euchlanis dilatata</i>					+			
<i>Keratella valga</i>			+	+				+
<i>Lecane ludwigii</i>			+			+		
<i>Lepadella oblongata</i>	+	+	+			+	+	
<i>Monostyla bulla</i>	+		+					
<i>Monostyla closterocerca</i>							+	
<i>Monostyla hamata</i>		+				+	+	
<i>Monostyla pygmaea</i>	+	+	+		+	+	+	
<i>Monostyla furgata</i>			+					
<i>Mytilina ventralis</i>					+	+	+	
<i>Monomata grandis</i>	+							+
<i>Philodina roseola</i>		+						
<i>Platyias patulus</i>		+				+		+
<i>Ploesoma tetractis</i>								+
<i>Ploesoma truncatum</i>	+		+			+	+	
<i>Polyarthra remata</i>			+	+	+	+	+	
<i>Squatinella mutica</i>	+	+	+					
<i>Testudinella patina</i>			+				+	
<i>Trichocerca pusilla</i>			+		+	+		
<i>Trichocerca rutilus</i>			+					
<i>Trichocerca gracilis</i>	+		+					
<i>Trichotria pocillum</i>					+		+	
<i>Trichotria tetricus</i>								+
Cladocerans								
<i>Acropenae harpae</i>					+			
<i>Alonaguttata</i>			+			+	+	
<i>Campocercus rectirostris</i>								+
<i>Chydorus sphaericus</i>			+			+		
<i>Coronatella rectangula</i>	+	+	+	+	+	+	+	
<i>Diaphanosoma brachyurum</i>			+		+			
<i>Graptoleberis testudinaria</i>	+							+
<i>Illoctryptus spinifer</i>								
<i>Pleuxus denticulata</i>	+		+	+				
<i>Pleuxus laevis</i>								+
<i>Simocephalus exponitus</i>						+	+	
<i>Simocephalus vetulus</i>	+		+	+			+	
<i>Scapholeberis kingi</i>			+				+	
Copepods								
<i>Mesocyclops leuckarti</i>	+		+		+		+	+
<i>Thermocyclops crassus</i>	+		+		+		+	+
<i>Thermocyclops taihokuensis</i>		+	+	+	+			

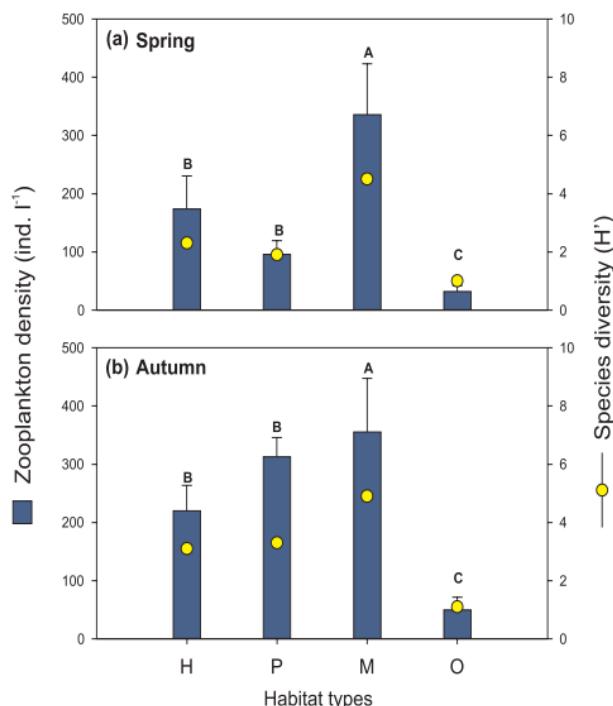


Figure 2

Zooplankton density and species diversity during spring and autumn for the four identified habitat types H – helophyte zone; P – pleustophyte zone; M – mixed vegetation zone (pleustophytes, nymphaeids, and elodeids); O – open water zone. The bars represent an average of 3 replicates (\pm SD). Letters above the bars indicate statistically different mean values.

density in the open water zone was on average two to five times lower compared to the three other habitat types (spring – on average 32 ind. l^{-1} ; autumn – on average 50 ind. l^{-1}). The pattern of species diversity was similar to that of the density.

Zooplankton density was greater in autumn compared to spring in all habitat types (Fig. 2). In particular, zooplankton density was three times higher in the pleustophyte zone during autumn compared to spring (on average 96 ind. l^{-1} and 313 ind. l^{-1} in spring and autumn, respectively). A larger number of pleustophyte species occurred in autumn. It produced a more complex habitat structure and attracted more zooplankton (Fennessy et al. 1994). Therefore, the larger zooplankton assemblages in autumn were considered to be strongly correlated with the development and growth of macrophytes.

Previous studies have suggested that the zooplankton community is more abundant in complexly structured macrophyte zones (Manatunge

et al. 2000; Warfe & Barmuta 2004). Helophytes tend to have a simple structure compared to other macrophyte types in the water; thus, this group is expected to support a lower density of zooplankton. In the current study, we observed that pleustophytes often occurred together with elodeids. Hence, the coexistence of these two different macrophyte types was expected to be advantageous to zooplankton diversity due to the increased complexity of the habitat structure. Elodeids and pleustophytes are known to support different types of zooplankton (Meerhoff et al. 2003; Moss et al. 1998). Thus, the highly complex habitat structure in the mixed macrophyte zone may explain the high density and diversity of zooplankton observed in this zone compared to the three other zones.

Statistically significant correlation between the zooplankton density with the habitat type supports this observation. Two-way ANOVA (Table 4) showed that there was no seasonality in the zooplankton density and diversity, but the habitat type had a strong effect. The interaction between the season and the habitat type was not significant, which implies that zooplankton density and diversity in wetland ecosystems was primarily affected by the macrophyte type.

Even though some studies have indicated a positive relationship between zooplankton and the presence of certain types of vegetation, our findings expand on the existing information about the correlation between the zooplankton community and the structural heterogeneity of macrophytes. Empirical studies show that elodeids have a complex structure in the water, but they are also more easily agitated by the wind and water currents compared to nymphaeids and pleustophytes (Vermaat et al. 2000). Therefore, elodeids are mainly used by pelagic zooplankton species such as daphnids (Schröder et al. 1995; Beklioglu & Moss 1996; Jeppesen et al. 1998). A few studies have reported that epiphytic zooplankton often inhabit stands of nymphaeids with high biomass (Moss et al. 1998). The surface macrophyte bed is relatively stable because of the fixed location (i.e. by roots) of nymphaeid species. Thus, nymphaeids are suitable for the attachment of epiphytic zooplankton species. We found that the pleustophyte habitat supports mainly epiphytic rotifer species rather than other zooplankton species. The surface macrophytes (e.g. nymphaeids and pleustophytes) and elodeids had different spatial structures and were used by different zooplankton species. The higher zooplankton diversity in mixed wetland habitats might attract different predators, consequently leading to an ecologically healthy food web.



Table 4

Two-way ANOVA results for the relationship between the season (spring and autumn) and the habitat and the zooplankton density

Factors	n	d.f.	F	P
Season	119	1	0.074	0.724
Habitat	119	1	7.906	0.008
Season × Habitat	238	1	0.000	0.895

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