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Abstract: In shallow lakes, floating-leaved plants can produce dense lakebeds that dramatically alter freshwater ecosystems and impact macrobenthic communities. Shorebirds are morphologically diverse and utilize different foraging strategies; they can partition food resources to achieve coexistence due to differences in food availability. In this study, we defined shorebird foraging guilds using a principal component analysis and explained differences in shorebird composition in terms of food availability by comparing macrobenthic and shorebird communities in Euryale ferox artificial planting areas, Trapa spp. natural growth areas, and control areas. The Mantel test and a Spearman analysis were used to correlate macrobenthic taxa with shorebird foraging guilds. We recorded four different macrobenthic taxa in the three study areas, including insects, gastropods, oligochaetes, and bivalves. Fifteen species belonging to three shorebird families were recorded across the three study areas. Our results suggest that floating-leaved plants are an important cause of differences in macrobenthic communities, and epifaunal macrobenthos (insects and gastropods) and infaunal macrobenthos (oligochaetes and bivalves) take on different patterns of diversity composition in different habitats. The macrobenthic and shorebird communities were potentially coherent. Different shorebird foraging guilds were limited by food availability and thus correlated differently with different macrobenthos. Therefore, differences in macrobenthic communities relative to floating-leaved plants can affect shorebird assemblages by affecting the availability of food resources.

Keywords: floating-leaved plants; macrobenthos; shorebirds; food availability; Shengjin Lake

1. Introduction

Waterbird assemblages coexist through various interactions determined by factors such as resources (e.g., food) [1]. Habitat quality, the availability of food resources, interspecific relationships, and anthropogenic disturbances all influence the food and energy requirements of waterbirds and ultimately their population fitness and ability to survive [2]. Food resources, as the energy and nutritional basis for the formation and maintenance of the waterbird community structure, influence the guild structure, ecological niches, and interspecific relationships of communities and are key to habitat quality [3]. Shorebirds are small- to medium-sized wading birds that are primary macrobenthic predators [4]. Shorebird distribution is strongly linked to the availability of their prey, which mainly consists of macrobenthos, especially during wintering and migratory stopovers [5]. However, aquatic plants are the most critical factor influencing the macrobenthos community [6]. Therefore, the effects of aquatic plants on macrobenthos indirectly affect shorebird assemblages.

In shallow lakes, aquatic plants play an important role in maintaining macrobenthic diversity [7]. Many aquatic plants directly change the spatial structures of lake ecosystems and increase spatial heterogeneity, not only providing macrobenthos with habitats and living, feeding, and breeding sites but also shelter from predators [7,8]. Macrobenthos



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Copyright: © 2022 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). in areas with aquatic plants show higher abundance, biomass, and species richness than those in areas characterized by bare sediments [9]. Post-apoptotic floating-leaved plants, which make water bodies more nutrient-rich, release organic matter directly into water bodies during senescence [10]. After the degradation of floating-leaved plants, large amounts of organic matter and nutrients are transferred to the sediment [11], creating an organic environment suitable for the survival of macrobenthos by providing a food source [12]. Gastropods have a particular affinity for lakes containing high quantities of organic matter [13], and floating-leaved plants are common plants that are indicators of gastropod populations. The death and decay of plants results in high rates of detritus production, providing favorable conditions for coleopteran growth and abundance [14]. However, floating-leaved plants create greater shade and reduce the production of surface sediment algae on which many macrobenthic feeders may depend [15]. Dense floating-leaved plant cover results in hypoxia, which significantly decreases the abundance of oligochaetes in the macrobenthic community [16].

Macrobenthos are the main prey of shorebirds [17], the abundance of which is significantly and positively correlated with the number of available macrobenthos [3,18–20]. The distribution of shorebirds also largely depends on macrobenthos, and the capacity to partition available resources varies according to shorebird morphological and behavioral diversity [21,22]. The morphological characteristics of shorebirds, such as the lengths of the tarsometatarsus and bill, influence food availability [23]. The tarsometatarsus length determines the depth of water in which shorebirds can roost [24]. Bills vary in length and shape, and the depth at which they are inserted into the water or sediment when foraging varies; thus, food available varies [25]. Moreover, shorebirds discover food through vision and touch, adopt continuous and intermittent movements to find food, and combine foraging mechanisms and movement patterns to form different types of foraging strategies [23]. There is evidence that different types of shorebird prey, such as surface-dwelling (epifauna) and substrate-inhabiting macrobenthos (infauna), have different functions [26]. This is because small short-billed species use a visual foraging strategy (superficial pecks), whereas long-billed birds favor tactile foraging (probing deep into the sediment) [27]. Phenotypic differences between species with similar ecological traits allow them to exploit different resources [28]. Shorebirds with morphologically distinct bills and different feeding techniques (superficial pecking or deep probing) exploit the various depths of sediment in the same mudflats in different ways, which mitigates interspecific competition between shorebird species for natural trophic resources [29].

Shengjin Lake, where floating-leaved plants such as *Trapa bispinosa* flourish owing to eutrophication in early seine culture waters, provides an important wintering and stopover site for migratory waterbirds on the East Asian–Australasian flyway [30]. In 2018, the local government began to implement a variety of measures to restore vegetation in this wetland [31], and many areas were managed uniformly and planted with *Euryale ferox*. The return of large areas of floating-leaved plants to the sediment after dieback becomes a natural bait for macrobenthos, which enhances macrobenthic colonization and forms more diverse and abundant macrobenthic communities [32]. Differences among macrobenthic communities have the most direct impact on shorebird assemblages. Therefore, the natural resource conditions of Shengjin Lake provided a good opportunity to undertake this study.

Understanding the effects of macrobenthos relative to floating-leaved plants on wintering shorebird assemblages is crucial for the effective protection of wintering shorebirds at Shengjin Lake. In this study, we hypothesized that the effects of macrobenthos relative to floating-leaved plants on shorebird assemblages were based on food availability. We tested this hypothesis by analyzing the differences in the macrobenthic and shorebird communities in three areas (a *Euryale ferox* artificial planting area, a *Trapa* spp. natural growth area, and the control area) of Shengjin Lake and determining the correlations between the two communities. Specifically, (1) we compared the differences among macrobenthic communities in different areas and explored the effects of floating-leaved plants on these communities, and (2) we divided shorebirds into foraging guilds according to their foraging

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strategies and morphological characteristics, compared the differences among shorebird foraging guilds in different areas, analyzed the correlations between macrobenthos and shorebirds, and explored the responses of different shorebird foraging guilds to differences in food resource availability.

2. Materials and Methods

2.1. Study Area

Shengjin Lake (116°55′–117°15′ E, 30°15′–30°30′ N) is a river-connected lake located on the right bank of the middle and lower Yangtze River floodplain (Figure 1). The release of water from the sluice gate in autumn and the stepped decline in the water level result in a large number of mudflats and shallow waters, thus exposing the abundant large macrobenthos in the sediment and providing suitable foraging and roosting sites for shorebirds. Prior to 2016, a large area of Shengjin Lake (more than 75% of the lake surface) was used for aquaculture, and the excessive use of purse seine culture caused the degradation of aquatic plants, especially submerged plants, which mostly disappeared [33]. Floating-leaved plants are usually found in eutrophic conditions [34]. Serious eutrophication problems in a water body result in the presence of a large number of floating-leaved plants in some waters. We selected three types of study areas: a *Euryale ferox* artificial planting area (type H), a Trapa spp. natural growth area (type M), and a control area (type L). In the Euryale ferox artificial planting area, paddy fields had been converted into wetlands by planting *Euryale* ferox. The Trapa spp. natural growth area was mainly populated by a high coverage of *Trapa quadrispinosa,* and the control area had a lower coverage of fewer *Trapa* spp. plants. Floating leaves cover the water surface, and *Hydrophasianus chirurgus* often feed at the lake in summer. In winter, the lake begins to recede, tidal flats are exposed, and floating-leaved plants die and fall into the substrate. The wintering shorebirds arrived late, so the vegetation change did not influence the foraging habitat for shorebirds. Early- and late-settler macrobenthos lose their shelters and are exposed, providing abundant food for wintering shorebirds.



Figure 1. Study area at Shengjin Lake, China. Type H: the *Euryale ferox* artificial planting area, type M: the *Trapa* spp. natural growth area, type L: the control area.

2.2. Data Collection

The study areas were surveyed according to the topographic features of Shengjin Lake in Chizhou, Anhui, China. We conducted a total of 6 months of macrobenthic sampling and shorebird observation, removing survey locations that were unsuitable for shorebird foraging and retaining those that were suitable. All survey locations were covered with floating-leaved plants to varying degrees before plant wilting. By removing unsuitable survey locations (with deep water levels or hard substrates) and retaining those that provided suitable feeding habitat, 3–4 sites were selected in each study area, totaling 11 survey sites (Figure 1). The 11 survey sites were chosen in the shallow-watercovered soft mud substrate in a hydro-fluctuation belt with a depth of no more than 10 mm. Macrobenthos sampling was conducted during the waterbird wintering period from October 2021 to March 2022. Study sites were chosen based on the floating-leaved plant cover area, and three sample points were set up at each study site. A total of 198 macrobenthic samples were obtained. Four replicates were conducted around each sample point each month using a WHL15-HL-CN-type Peterson mud picker produced by Beijing HAIFUDA TECHNOLOGY CO., China (1/16 m²) [35]. The macrobenthos were identified to the class level in the laboratory by screening, sorting, and counting using 40-mesh sieves (0.45 mm). Monthly counts of shorebird numbers and species were conducted according to the extent of the pre-study sites, using GPS to locate boundary ranges and natural references as markers for accurate counts in the study area. The sampling locations were of similar size (about 0.5×0.5 km), and a total of 66 shorebird samples were obtained. Binoculars (Swarovski, 8.5×42 , Austria) and monocular telescopes (Swarovski, ATS 20-60 \times 85) were used to observe the number and species of shorebirds in the study area. Field surveys were conducted after sunrise in fine weather conditions and were terminated before sunset. Behavioral samples were collected daily from 7:00 to 17:00.

2.3. Statistical Analysis

2.3.1. Macrobenthic Community

According to their ecological characteristics, macrobenthos were assigned to epifaunal and infaunal life forms to examine the prey availability for different types of shorebirds [36]. Gastropods inhabiting the surface belong to epifauna. Insects that swim in water bodies also fall into this category. Oligochaetes and bivalves living on substrates are infaunal macrobenthos. The density of macrobenthos was the sum of the densities converted from the densities sampled by the Peterson mud picker (ind./m²). The densities of epifaunal and infaunal life-forms were obtained by summing the densities of the corresponding macrobenthic species. The data passed the Shapiro–Wilk test, showing that the variables were not normally distributed (p < 0.05), and the Kruskal–Wallis test was used to test the differences in the macrobenthic communities between the different study areas.

The Bray–Curtis similarity resemblance matrix was used for a hierarchical clustering analysis, and ordination axes were generated using non-metric multidimensional scaling (NMDS) to continuously demonstrate similar relationships in species composition among samples, thus better expressing the community response to more continuous abiotic environmental gradients [37] and representing differences among communities. Finally, an analysis of similarities (ANOSIM) was used to determine significant differences between the groups.

2.3.2. Characteristics of Shorebird Communities and Structure of Foraging Guilds

The shorebird data of the three study area types were collated, and the density was calculated [38,39]. The diversity index (H') and Pielou's evenness index (J') were calculated [40].

The Shannon–Wiener diversity index (H') was used as an indicator of species diversity and was calculated as follows:

$$H' = -\sum p_i ln p_i \tag{1}$$

where p_i is the ratio of the number of species *i* to the total number of species. Pielou's evenness index (*J*') was calculated as follows:

$$J' = H'/H_{max} \tag{2}$$

where *Hmax* is the maximum species diversity value.

According to differences in foraging behavior, sensory mechanisms, and locomotion styles, the shorebirds were classified as three types of foraging strategists [23]: (i) Pausetravel: all plovers belong to this category, and birds move between alternating stationary periods and short runs and capture prey by pecking; (ii) Visual continuous: birds rely on visual and superficial techniques to capture prey inhabiting the surface and peck at the surface or probe in the substrate while walking steadily; (iii) Tactile continuous: Calidris *alpina* is classified under this type of strategy. It has tactile sensory cells in its bill that allow it to detect prey living in the substrate. In practice, Tringa totanus has been observed sweeping through water, relying on tactile mechanisms to find food, and thus this species is also classified as tactile continuous [35]. According to the dataset of the life history and ecological characteristics of Chinese birds [41], we classified the tarsometatarsus and bill lengths of shorebirds into long and short classes by a K-Means analysis, and the diets of shorebirds were classified into insectivorous and omnivorous (insectivorous and carnivorous or other) classes (Table A1). Each shorebird species was assessed using nine variables for the variable type, and those that met the variable requirements were assigned a value of 1, while the remainder were assigned a value of 0 [42]. The scores for each species were then analyzed using a principal component analysis, and the principal components with eigenvalues ≥ 1 were intercepted for dimensionality reduction. Among the principal components, the variable with an absolute value ≥ 0.6 was selected as the significant variable for each principal component [43]. The significant variables of each principal component were selected as significant variables. The data of the nine variables of each bird species were substituted into each principal component. A systematic cluster analysis was performed to obtain a dendrogram of the principal component scores of each shorebird species. Then, the affiliation of the shorebird foraging guild for each species was determined. The data passed the Shapiro–Wilk test, which showed that the variables were not normally distributed (p < 0.05), and the Kruskal–Wallis test was used to determine the differences in shorebird foraging guilds between the study areas based on the results of the shorebird foraging guild classification.

2.3.3. Correlation of Macrobenthos with Shorebirds

Based on the matrix of differences between macrobenthos and shorebirds between communities obtained by calculating the Bray–Curtis dissimilarity index, the Mantel test was used to test the null hypothesis of no relationship between the two matrices and to determine the correlations between the macrobenthic and shorebird communities. It produced a measure of correlation between the two matrices (standardized Mantel R statistic) and a measure of significance (*p*-value) to indicate whether the two matrices were correlated, and the consistency of the two datasets was visualized using Procrustes analysis plots. The correlations between the densities of shorebird foraging guilds and macrobenthos were calculated to determine the relationship between the two [26], and according to the availability of food, explain the differences between the shorebird assemblages in the different study areas.

We used the Software Package for Social Statistics (IBM SPSS Statistics Version 25.0) and Origin 2021 to analyze the data and construct the graphs.

3. Results

3.1. Macrobenthic Communities

3.1.1. Characteristics of Macrobenthic Communities

The results of the Kruskal–Wallis test showed that insects differed significantly between the *Euryale ferox* artificial planting area (type H) and the *Trapa* spp. natural growth area (type M); gastropods and epifaunal macrobenthos differed significantly between type H and type M, and between type H and the control area (type L); oligochaetes and infaunal macrobenthos differed significantly between the three study areas; and bivalves differed significantly between type H, and between type M and type L (Table 1).

Table 1. Density $(ind./m^2)$ of four taxa of different macrobenthos and two life-forms in three study areas.

			Macrobenthos D	ensity (ind./m ²)		
Study Area	Insects	Gastropods	Oligochaeta	Bivalvia	Epifauna	Infauna
Type H (<i>n</i> = 18)	43.56 ± 10.73 $^{\rm a}$	$22.67\pm2.45~^{a}$	$15.33\pm2.16^{\text{ b}}$	$2.22\pm0.39^{\text{ b}}$	66.22 ± 4.82 $^{\rm a}$	$17.56\pm2.22^{\text{ b}}$
Type M (<i>n</i> = 24)	8.89 ± 1.37 ^b	$7.22\pm1.42^{\text{ b}}$	$32.28\pm2.10~^{a}$	6.00 ± 1.54 $^{\rm a}$	16.11 ± 1.13 ^b	$38.28\pm2.31~^{a}$
Type L (<i>n</i> = 24)	11.11 ± 1.96 ^{ab}	$3.72\pm0.92^{\text{ b}}$	$4.67\pm1.21~^{\rm c}$	$0.61\pm0.21~^{\rm b}$	$14.83\pm1.73~^{\rm b}$	$5.28\pm0.89\ ^{\rm c}$

The table shows means \pm SEs. Different letters in the same column indicate significant differences (p < 0.05), and the same letter indicates insignificant differences (p > 0.05).

3.1.2. Similarity of Macrobenthic Communities

The cluster analysis results (Figure 2) showed that the macrobenthic communities at all the survey locations were divided into three different groups. Type H, type M, and type L were each in separate groups. In other words, the macrobenthic communities in the *Euryale ferox* artificial planting area, the *Trapa* spp. natural growth area, and the control area could be clearly distinguished. The results of the NMDS ranking analysis (Figure 3a) also explained the similar relationships between the samples extremely well and supported the results of the cluster analysis, which divided the macrobenthic communities in all survey locations into three groups. The results of the ANOSIM analysis showed that intra-group differences were smaller than inter-group differences (Figure 3b).



Figure 2. Dendrogram for the hierarchical clustering of macrobenthic communities at different survey sites. H1–H3, M1–M4, and l1–l4 indicate the survey locations in the *Euryale ferox* artificial planting area (type H), the *Trapa* spp. natural growth area (type M), and the control area (type L), respectively.



Figure 3. NMDS plot of macrobenthic density at the different survey locations (stress = 0.042). H1–H3, M1–M4, and I1–I4 indicate the survey locations in the *Euryale ferox* artificial planting area (type H), the *Trapa* spp. natural growth area (type M), and the control area (type L), respectively (**a**). ANOSIM analysis results of R > 0 and p < 0.01 denote that the differences between groups were significantly greater than those within groups (**b**).

3.2. Shorebird Communities

3.2.1. Characteristics of Shorebird Communities

A total of 15 shorebird species were recorded (Table 2), and *Recurvirostra avosetta*, *Vanellus vanellus*, and *Tringa erythropus* accounted for a large proportion of the shorebirds recorded in each study area (74.3% of the total shorebirds). The species number and density of shorebirds were significantly different between the *Euryale ferox* artificial planting area (type H) and control area (type L), being the highest in type H and the lowest in type L. In terms of the shorebird diversity and evenness index, type H was significantly different from the other two areas; however, there was no significant difference between type M and type L. The highest diversity and evenness index was observed in type H, followed by type M, and the lowest was observed in type L (Table 3).

Table 2. The foraging guild to which each species belongs and the density proportion of shorebird species in the different study areas.

Common Nomo	Scientific Name	Formaing Cuild	Proportion of Shorebird Density (%)			
Common Name			Туре Н	Type M	Type L	
Pied Avocet	Recurvirostra avosetta	G6	18.80	11.22	10.89	
Northern Lapwing	Vanellus vanellus	G5	19.52	21.91	25.34	
Grey-headed Lapwing	Vanellus cinereus	G5	1.29	0.47	2.35	
Grey Plover	Pluvialis squatarola	G5	0.35	0.33	0.00	
Little Ringed Plover	Charadrius dubius	G3	1.79	0.17	0.00	
Kentish Plover	Charadrius alexandrinus	G5	1.67	0.17	0.00	
Pintail Snipe	Gallinago stenura	G3	1.22	0.49	0.00	
Common Snipe	Gallinago gallinago	G3	1.69	0.33	0.00	
Eurasian Curlew	Numenius arquata	G4	0.27	0.16	0.00	
Spotted Redshank	Tringa erythropus	G2	42.97	25.45	52.75	
Common Greenshank	Tringa nebularia	G2	1.85	0.99	1.81	
Green Sandpiper	Tringa ochropus	G3	0.72	0.00	0.00	
Common Sandpiper	Actitis hypoleucos	G3	0.70	0.00	0.00	
Dunlin	Calidris alpina	G1	5.75	36.16	0.00	
Common Redshank	Tringa totanus	G1	1.42	2.16	6.86	

Study Area	Shannon–Wiener Diversity Index	Pielou Evenness Index	Density (ind./ha)	Species Number
Type H (<i>n</i> = 18)	0.79 ± 0.11 $^{\rm a}$	0.64 ± 0.09 a	2.63 ± 0.70 $^{\rm a}$	$4.11\pm0.54~^{\rm a}$
Type M (<i>n</i> = 24)	0.26 ± 0.31 ^b	0.23 ± 0.29 ^b	$1.86\pm2.15~^{ m ab}$	$1.75\pm1.33~\mathrm{ab}$
Type L ($n = 24$)	$0.11\pm0.29~^{\mathrm{b}}$	0.07 ± 0.20 ^b	0.74 ± 0.96 ^b	0.79 ± 0.88 ^b

Table 3. Characteristics of shorebird communities in different study areas.

The table shows mean \pm SEs. Different letters in the same column indicate significant differences (p < 0.05), and the same letter indicates insignificant differences (p > 0.05).

3.2.2. Distribution of the Foraging Guilds of Shorebirds

The results of the principal component analysis based on nine variables (Table 4) showed that the eigenvalues of the first three principal components (PC1–PC3) were greater than 1, with a cumulative contribution of 88.45%; therefore, PC1, PC2, and PC3 were selected for the next analysis. The significant variables for PC1 were the pause–travel foraging strategy and diets. The significant variables for PC2 were the visual continuous foraging strategy and the lengths of the tarsometatarsus and bill. The significant variable for PC3 was the tactile continuous foraging strategy.

Table 4. Principle component analysis results based on nine variables.

X7 • 1 1	I	Principal Components	
Variables	PC1	PC2	PC3
Pause-travel	-0.808 *	0.509	-0.100
Visual continuous	0.541	-0.647 *	-0.469
Tactile continuous	0.370	0.217	0.832 *
Long bill	-0.540	-0.659 *	0.372
Short bill	0.540	0.659 *	-0.372
Long tarsometatarsus	-0.477	-0.753 *	-0.096
Short tarsometatarsus	0.477	0.753 *	0.096
Insectivorous birds	0.866 *	-0.432	0.101
Omnivorous birds	-0.866 *	0.432	-0.101
Explained variance (%)	40.248	34.437	13.769
Eigenvalue	3.622	3.099	1.239

An asterisk indicates significant variables in this component.

The systematic cluster analysis results (Figure 4) showed that all shorebirds could be divided into six foraging guilds. By combining the significant variables of the PC1–PC3 principal components and the morphological characteristics of shorebirds, the six shorebird foraging guilds were defined as: (i) G1, insectivorous birds with short bills using the tactile continuous foraging strategy, which includes two shorebird species, Calidris alpina and Tringa totanus; (ii) G2, insectivorous birds with long tarsometatarsi using the visual continuous foraging strategy, which includes two shorebird species, Tringa erythropus and Tringa nebularia; (iii) G3, insectivorous birds with short tarsometatarsi using the visual continuous foraging strategy, which includes five shorebird species, Charadrius dubius, Gallinago stenura, Gallinago gallinago, Tringa ochropus, and Actitis hypoleucos; (iv) G4, insectivorous birds with long bills using the visual continuous foraging strategy, which includes only one shorebird species, Numenius arquata; (v) G5, omnivorous birds with short bills using the pause-travel foraging strategy, which includes four shorebird species, Vanellus vanellus, Vanellus cinereus, Pluvialis squatarola, and Charadrius alexandrinus; and (vi) G6, omnivorous birds with long bills using the pause-travel foraging strategy, which includes only one shorebird species, Recurvirostra avosetta.



Dendrogram using Average Linkage (Within Groups)

Figure 4. Dendrogram using the average linkage (within groups) with the principal component scores of shorebirds. The shorebird name abbreviations are shown below. AVO: *Recurvirostra avosetta;* VAN: *Vanellus vanellus;* CIN: *Vanellus cinereus;* SQU: *Pluvialis squatarola;* DUB: *Charadrius dubius;* ALE: *Charadrius alexandrinus;* GAL: *Gallinago gallinago;* STE: *Gallinago stenura;* ARQ: *Numenius arquata;* ERY: *Tringa erythropus;* NEB: *Tringa nebularia;* OCH: *Tringa ochropus;* HYP: *Actitis hypoleucos;* ALP: *Calidris alpina;* TOT: *Tringa totanu.*

At the shorebird foraging guild level, shorebird densities differed significantly between the different study areas (Table 5). G1 differed significantly between the *Trapa* spp. natural growth area (type M) and the control area (type L); type M > type L. G2 and G3 differed significantly between the *Euryale ferox* artificial planting area (type H) and type L; type H > type L. G4, G5, and G6 did not differ significantly among the three types of study areas.

Table 5. Density (ind./ha) of shorebird foraging guilds in the different study areas.

		Dens	ity of Shorebird Fo	oraging Guilds (in	d./ha)	
Study Area	G1	G2	G3	G4	G5	G6
Type H (<i>n</i> = 3)	$0.189\pm0.031~^{\mathrm{ab}}$	1.179 ± 0.121 $^{\rm a}$	0.161 ± 0.031 $^{\rm a}$	0.007 ± 0.004 $^{\rm a}$	0.601 ± 0.425 $^{\rm a}$	$0.495 \pm 0.495~^{\rm a}$
Type M $(n = 4)$	0.712 ± 0.115 $^{\rm a}$	$0.492\pm0.074~^{\mathrm{ab}}$	0.018 ± 0.011 $^{\mathrm{ab}}$	$0.003 \pm 0.003 \ ^{\rm a}$	0.425 ± 0.175 $^{\rm a}$	0.209 ± 0.139 ^ a
Type L $(n = 4)$	$0.051 \pm 0.011 \ ^{\rm b}$	$0.403 \pm 0.100 \ ^{\rm b}$	0.000 ± 0.000 ^b	0.000 ± 0.000 $^{\rm a}$	0.205 ± 0.086 a	0.081 ± 0.081 a

The monthly mean shorebird species density at each survey location was used as a sample for the Kruskal–Wallis test. The table shows means \pm SEs. Different letters in the same column indicate significant differences (p < 0.05), and the same letter indicates insignificant differences (p > 0.05).

3.3. Correlation of Macrobenthos with Shorebirds

The Mantel test of the dissimilarity matrix based on the Bray–Curtis index between macrobenthos and shorebirds (r = 0.674, p < 0.01) indicated that shorebird communities were highly significantly correlated to macrobenthos communities. The results of the Procrustes analysis indicated a potential consistency in the density and composition of macrobenthos and shorebirds between the two paired sampling sites (Figure 5, M² = 0.585, p < 0.01).



Figure 5. Procrustes analysis of the correlation between macrobenthic and shorebird communities ($M^2 = 0.585$, p < 0.01, 999 permutations). H1–H3, M1–M4, and l1–l4 indicate the survey locations in the *Euryale ferox* artificial planting area (type H), the *Trapa* spp. natural growth area (type M), and the control area (type L), respectively.

The correlation analysis between the density of shorebirds and total macrobenthos was significantly positively correlated (Figure 6, r = 0.42, p < 0.01), and different shorebird foraging guilds had different correlations with different macrobenthic species and life-forms (Table 6).



Figure 6. Correlation between density of total macrobenthos and total shorebirds (r = 0.42, p < 0.01).

Table 6. The correlation coefficients (r) of shorebird guilds with four taxa and two life-forms of macrobenthos.

A 111	Correlation Coefficients of Shorebird Guilds (r)						
Guild	Insects	Gastropods	Oligochaeta	Bivalvia	Epifauna	Infauna	
G1	-0.255	0.336	0.980 **	0.858 **	0.178	0.973 **	
G2	0.682 *	0.891 **	0.273	0.397	0.911 **	0.291	
G3	0.597	0.870 **	0.369	0.504	0.788 **	0.368	
G4	0.451	0.260	0.214	0.270	0.414	0.214	
G5	0.141	0.164	0.370	0.318	0.349	0.360	
G6	0.232	0.137	0.016	0.153	0.158	0.042	

* indicates *p* < 0.05, ** indicates *p* < 0.01.

Guilds G4, G5, and G6 were positively but not significantly correlated with all macrobenthos (p > 0.05); guild G3 was highly significantly positively correlated with gastropods and epifaunal macrobenthos (p < 0.01), but not significantly correlated with insects, oligochaeta, bivalvia, or infaunal macrobenthos (p > 0.05); guild G2 was significantly positively correlated with insects (p < 0.05) and highly significantly correlated with gastropods and epifaunal macrobenthos (p < 0.01) but not significantly correlated with oligochaeta, bivalvia, or infaunal macrobenthos (p > 0.05); and guild G1 was highly significantly positively correlated with oligochaetes, bivalves, and infaunal macrobenthos (p < 0.01) but not significantly correlated with insects, gastropods, or epifaunal macrobenthos (p > 0.05).

4. Discussion

The focus of our study was the effect of macrobenthos under the influence of floatingleaved plants, which affect the availability of shorebird food owing to differing environmental suitability, resulting in differences in shorebird assemblages. Therefore, whether more refined environmental conditions, such as physicochemical factors, support different faunal assemblages, such as macrobenthos and shorebirds, requires further investigation. Most shorebird studies focus on coastal wetlands, but there are few studies in shallow river-connected lakes. Coastal wetlands may have more abundant food resources and more species of shorebirds than shallow river-connected lakes. However, there are several references of food availability and the foraging behavior of shorebirds [4,5,18,19,23,26], which is the baseline for the study of shorebirds in shallow river-connected lakes. Our results showed that there were significant differences in the composition and abundance of macrobenthic and shorebird communities in the *Euryale ferox* artificial planting area, *Trapa* spp. natural growth area, and control area. Significant differences among the foraging guilds of shorebirds in different study areas were mainly due to differences in food resources, potential congruence between shorebirds and macrobenthos in the survey locations, and differences in macrobenthic life-forms, which affected food availability.

Macrobenthos in areas with aquatic plants were more abundant than those in areas characterized by bare sediments [9]. Our study also showed that areas with floating-leaved plants had a higher density of macrobenthos (Table 1). Correspondingly, shorebirds mainly feed on macrobenthos [17], and there is a clear positive correlation between their abundance and that of macrobenthos [3,18,19,44]. Shorebirds also showed a higher abundance in the floating-leaved plant area (Table 3), and their total density was significantly positively correlated with the total density of macrobenthos (Figure 6). In the early wintering stage, the shorebirds are migrating, and the total number rises. Without considering the turnover of macrobenthic reproduction, the abundance of macrobenthos may decline. In the later wintering stage, shorebirds gradually move northward. At this time, macrobenthos are less threatened by shorebird predation. Moreover, the air temperature rises, the breeding rate increases, and the abundance may grow. Therefore, their differences over time are not matched when temporal variability is considered. Thus, the linear fit was poor.

Aquatic plants can modify the environment and affect the spatial distribution of macrobenthos and the adaptation of various macrobenthic species to different habitats [45]. In our study, floating-leaved plants were key to influencing the composition of macrobenthic communities. The close relationship between macrobenthos as prey and shorebirds as predators is predictable [46]. The prey of shorebirds in different life-forms, such as surface-dwelling (epifauna) and substrate-inhabiting macrobenthos (infauna), have different functions in shorebirds [26], and prey availability is a key factor in determining the spatial distribution of shorebirds [47]. Therefore, aquatic plants that affect the composition and abundance of macrobenthos indirectly affect shorebird assemblages.

Studies have shown that large areas of floating-leaved plants can cause water hypoxia, which is not suitable for the survival of oligochaetes [16,48]. Our results show that oligochaetes and bivalves have higher densities in the *Trapa* spp. natural growth area (Table 1), which may be because Oligochaeta and Bivalvia belong to classes of grazing and filter-feeding collectors, respectively. Filter feeders are usually found in high-velocity

habitats, and their mouthparts have filtering structures to filter and feed on fine-grained organic matter in rivers. Compared with the *Trapa* spp. natural growth area, the *Euryale* ferox artificial planting area had wider leaves and a stronger shading effect, which is not conducive to the burrowing and habitation of macrobenthos living in the substrate. Further, the slowing of the water flow rate by stems and leaves is not conducive to bivalve filtration of organic matter. Coarse-grained organic matter is processed into fine-grained organic matter under the action of water flow, which is preferred by oligochaetes among the collectors of fine-grained organic matter [49]. Oligochaetes and bivalves are infaunal macrobenthos; therefore, the Trapa spp. natural growth area provides a favorable habitat for tactile continuous foragers, which mainly depend on a pressure sensory mechanism for prey detection [50]. The shorebird species of guild G1 typically adopt a tactile and continuous foraging strategy. In our study, the shorebirds of this foraging guild had a very significant positive correlation with oligochaetes and bivalves as well as a very significant positive correlation with infaunal macrobenthos (Table 6); therefore, the G1 shorebird densities in the Trapa spp. natural growth area were significantly higher than those in the other areas (Table 5).

Insects and gastropods had higher densities in the *Euryale ferox* artificial planting area (Table 1), and they belong to the epifaunal macrobenthos. The rich organic matter environment of the *Euryale ferox* artificial planting area provides suitable oviposition places for insects and is more popular with gastropods [14]. The shorebird density in guild G2 was significantly higher than that in the other areas (Table 5). This is because the shorebirds of G2 use the visual continuous foraging strategy. A shorter bill length is more suitable for feeding on epifaunal macrobenthos at the surface, and was significantly positively correlated with insects and extremely significantly positively correlated with gastropods and epifaunal macrobenthos. This is consistent with the findings of other studies [26,35]. The higher abundance of gastropods and insects created ideal foraging sites for the shorebirds of G2.

For the shorebirds of guilds G5 and G6, except for the shorebirds of G6, which have a longer bill length, the other shorebirds have shorter bill lengths [41], but they all use the pause–travel foraging strategy characterized by an alternation of very fast steps and abrupt stops to scan the surface of sediment and catch prey [27]. Pause–travel techniques increase the chances of successful predation attempts by shorebirds, even though it requires more time to scan the prey. The longer the time spent scanning prey, the higher the chance of catching it [51]. This strategy may be more suitable for foraging for macrobenthos in our study areas; not only does this strategy help shorebirds feed on macrobenthos inhabiting the surface, it may also help them find macrobenthos living in the substrates, so they are distributed in various areas and there is no significant difference in density (Table 5).

The shorebirds of guild G3 are insectivorous birds with short bills and tarsometatarsi. Except for *Charadrius dubius*, all these shorebirds employed the visual continuous foraging strategy. It is conceivable that they are significantly related to epifaunal macrobenthos (Table 6). Our results showed that they were significantly higher in the *Euryale ferox* artificial planting area than in the other areas (Table 5) because these species lack the tactile sensory cells in their bills that would enable them to detect prey living in the substrates through tactile hunting strategies similar to those of *Calidris alpina* [25]. Furthermore, they do not have long bills to probe deep into the rich infaunal macrobenthos in the *Trapa* spp. natural growth area. Therefore, they mainly gathered in the *Euryale ferox* artificial planting area

The single shorebird species of guild G4, *Numenius arquata*, is insectivorous, with a long bill and a long tarsometatarsus. Although it used a visual continuous foraging strategy, mainly feeding on macrobenthos inhabiting the surface, research has shown that longer-legged and longer-billed shorebirds are frequently observed hunting prey that occurs at deeper levels [52]. The long bill of *Numenius arquata* helps it to find prey buried in deeper substrates; thus, similar to the shorebirds of G5 and G6, the shorebirds of G4 were positively correlated but not significantly correlated with all the macrobenthos and

each of the two life-forms. They were also distributed in various areas, and there were no significant differences in density (Table 5).

The level of competition and predation risk can affect foraging and habitat use decisions [29,53]. However, in our study, the level of competition and predation risk had little effect. Due to the small shorebird densities, the competition impact was minimal. In our long-term field observation, we found few predators. In addition, the *Trapa* spp. natural growth areas were under the jurisdiction of the Anhui Shengjin Lake National Nature Reserve, and few people entered. From September to October, the *Euryale ferox* was artificially harvested before the coming of the wintering shorebirds. Our field observations showed almost no human disturbance in the *Euryale ferox* artificial planting areas after the harvest.

5. Conclusions

Food resources are the most important factors in the spatial distribution of wading birds, and macrobenthos play an important role in determining habitat utilization by shorebirds. The macrobenthic community, which is influenced by aquatic plants such as floatingleaved plants, had different effects on the shorebirds of each foraging guild. In short, the abundance and composition of the macrobenthic community due to floating-leaved plants affects the availability of food for shorebirds, thereby affecting the assemblages of shorebird communities. Therefore, for wetland waterbird protection, in addition to providing sufficient food resources through ecological restoration, the availability of food is also the key to maintaining waterbird communities.

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Appendix A

Table A1. Ecological characteristics for different species of shorebirds.

Common Name	Scientific Name	Foraging Strategy	Bill Length (mm)	Tarsometatarsus Length (mm)	Diet
Pied Avocet	Recurvirostra avosetta	pause-travel	80-90	79–88	omnivorous
Northern Lapwing	Vanellus vanellus	pause-travel	24-29	44–56	omnivorous
Grey-headed Lapwing	Vanellus cinereus	pause-travel	34–39	74-85	omnivorous
Grey Plover	Pluvialis squatarola	pause-travel	29-33	45-51	omnivorous
Little Ringed Plover	Charadrius dubius	pause-travel	11-14	22-26	insectivorous
Kentish Plover	Charadrius alexandrinus	pause-travel	13-19	25-30	omnivorous
Pintail Snipe	Gallinago stenura	visual continuous	53-71	30-39	insectivorous
Common Snipe	Gallinago gallinago	visual continuous	61-70	28-35	insectivorous
Eurasian Curlew	Numenius arquata	visual continuous	130-168	78-88	insectivorous
Spotted Redshank	Tringa erythropus	visual continuous	53–58	54-60	insectivorous

Common Name	Scientific Name	Foraging Strategy	Bill Length (mm)	Tarsometatarsus Length (mm)	Diet
Common Greenshank	Tringa nebularia	visual continuous	50-59	55-65	insectivorous
Green Sandpiper	Tringa ochropus	visual continuous	31–38	30-42	insectivorous
Common Sandpiper	Actitis hypoleucos	visual continuous	24-26	18–29	insectivorous
Dunlin	Calidris alpina	tactile continuous	31-41	21-27	insectivorous
Common Redshank	Tringa totanus	tactile continuous	38–46	45–51	insectivorous

Table A1. Cont.

Foraging strategy data came from actual observations. Diet, and bill and tarsometatarsus length data came from the dataset of the life history and ecological characteristics of Chinese birds, and omnivorous birds are birds that feed on both insects and other aquatic animals.

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