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Impact of removing laver (*Porphyra*) farming racks on the distribution, diversity and foraging behavior of waterbirds in coastal wetlands in eastern China

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Introduction: The coastal wetlands in eastern China are important feeding and resting sites for migratory waterbirds. Intertidal aquaculture in this region has various effects on waterbird communities, yet research on the impact of coastal restoration on waterbird communities remains limited.

Methods: To explore the impacts of coastal restoration in the Lianyungang coastal wetland, an important staging area for migratory birds along the East Asian-Australasian Flyway (EAAF), we conducted comparative studies on changes in waterbird community structure, behavior composition, and intertidal food resources before and after the removal of laver racks during autumn months from 2020 to 2023.

Results: The results were as follows: (1) A total of 11544 birds belonging to 37 species were recorded in the study area, including 8 globally threatened or near-threatened species. (2) Following restoration, species richness, abundance, Shannon-Wiener diversity index, and Margalef richness index of waterbirds were significantly higher compared to pre-restoration levels. Notably, the numbers of ducks, plovers, and sandpipers increased significantly, while gull numbers decreased significantly, likely due to habitat structure loss. (3) The proportion of foraging behaviors of 4 common waterbird species increased significantly after restoration, while the percentage of resting behavior significantly decreased. (4) No significant differences in macrobenthos species richness, abundance, biomass or α -diversity indices were detected post-restoration, but the macrobenthos in laver racks area (lower tidal zone) were significantly more abundant than those in the non-racks area (middle tidal zone).

Discussion: The laver farming racks not only occupied intertidal zones with abundant food resources but also limited the ability of some waterbird species to

fly and evade predators, while the removal of these racks could restore foraging habitat accessibility by removing physical barriers. Our study revealed the trends in changes in waterbird communities before and after the removal of laver racks, providing practical insight and references for coastal restoration.

KEYWORDS

East Asian-Australasian Flyway (EAAF), ecological restoration, laver cultivation, migratory waterbirds, intertidal zone

1 Introduction

Coastal wetlands in eastern China are important feeding and resting sites for waterbirds along the East Asian-Australasia Flyway (EAAF), and they are crucial for the recovery of migratory waterbird communities and the conservation of endangered species (Studds et al., 2017). In recent years, the decrease in the area of intertidal mudflats due to reclamation and biological invasions has caused a sharp decline in the number of waterbirds relying on these habitats for migration (Ma et al., 2014; Qu et al., 2023). At the same time, aquaculture in the intertidal zone also impacts waterbird communities. Caldow et al. (2003) suggested that Mytilus edulis cultivation in the intertidal zone can increase food resources, thus enhancing the abundance of waterbirds in the cultivation areas. In contrast, Jennings et al. (2021) found that Ardea alba had fewer feeding opportunities in shellfish aquaculture areas than in natural wetlands. However, these studies have primarily focused on shellfish aquaculture in intertidal sediments and have overlooked the impact of intertidal algae farming on waterbird communities. Globally, seaweed farming has been shown to alter intertidal macrobenthic communities (Bhowmik et al., 2025), but impacts on avian assemblages remain understudied.

Laver (*Porphyra*) is one of the most commonly consumed edible seaweeds in China, with a long history of cultivation (Li, 2012), and its farming method is distinctly different from animal aquatic products. Semi-floating raft cultivation is the main method to farm laver in the intertidal zone. These semi-floating rafts (hereafter referred to as laver racks) can float on the water surface during high tide, and when the tide recedes, the rafts are supported by short pillars, remaining stable on the mudflat (General Administration of Quality Supervision, Inspection and Quarantine of the People's Republic of China, 2018). Fishermen typically fix net curtains with laver seedlings to the laver racks in the lower tidal zone in autumn, and remove the net curtains and harvest laver in Spring (Li and Zheng, 1992). However, lower tidal zone occupied by laver racks is also the primary foraging area for waterbirds (Zou et al., 2016), which could affect their use of the intertidal zone.

Lianyungang is an important staging area for migratory shorebirds in the EAAF, 22 shorebird species in Lianyungang region spans more than 1% of the total population along the migratory route, which ranks highest among the >300 shorebird sites in East Asia (Chan et al., 2019), and the history of laver farming in this region has been more than 50 years (Shang et al., 2008). In recent years, the local government has recognized the ecological value of coastal wetlands, and in the spring of 2022, all laver farming racks in the coastal intertidal zone have been removed with the aim of restoring intertidal habitats for migratory waterbirds. Previous studies have shown that ecological restoration efforts in the intertidal zone often have a positive impact on waterbird communities. In the Chongming Dongtan wetlands in eastern China, restored wetlands with relatively high habitat heterogeneity support a relatively high abundance of waterbirds (Zou et al., 2016). In a study of coastal restoration in California, revealed that the abundances, behaviors, and assemblages of birds on restored reefs are similar to those on live reefs (Copertino et al., 2022). However, there are still few studies about the impact of ecological restoration in intertidal laver farming areas on waterbird communities.

Therefore, we conducted a study in the coastal intertidal zone of Lianyungang, Jiangsu Province, to explore the utilization of the intertidal waterfowl communities on the laver farming racks, and to investigate the impacts of the removal of these racks on waterbird communities, which aligned with UN Decade on Ecosystem Restoration targets for coastal habitat recovery. We hypothesized that laver rack removal would (1) increase waterbird diversity by restoring foraging habitat and (2) reduce predation risks by eliminating physical barriers.

2 Materials and methods

2.1 Study area

The study area was located in the mixed-sediment intertidal zone between the Wanghe Estuary (north side) and the Xingzhuanghe Estuary (south side) in the Lianyungang, Jiangsu Province (34.52-34.55°N, 119.11-119.13°E) (Figure 1a), which was affected by irregular semidiurnal tides and covers an area of about 4.5km² (about 3km in length from north to south and 1.5 km in width from east to west). Laver farming in this region typically began in September and continues until April of the following year.

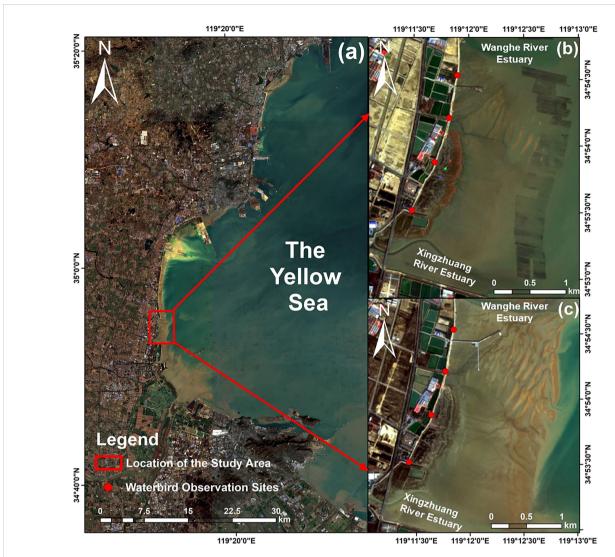


FIGURE 1
Overview of the study area. (a) shows the approximate location of the study area, (b) is the satellite remote sensing image of the study area before the removal of the laver farming racks on November 7, 2021, and (c) is the satellite remote sensing image of the study area after the removal of the laver farming racks on November 7, 2022.

We obtained Sentinel-2 satellite images (resolution 10m) of the study area during low tide periods, both before (November 7, 2021) and after (November 7, 2022) the removal of laver farming racks (https://browser.dataspace.copernicus.eu/). The study area was divided into three intertidal zones (upper intertidal zone: Having large number of shell fragments; middle intertidal zone: Bare flat; lower intertidal zone: Laver farming area) of roughly equal width, each approximately 500 meters wide. Before spring 2022, the laver farming racks occupied the lower tidal zone of the intertidal zone (Figure 1b), while the middle and upper tidal zones were mudflats, with disturbances mainly caused by laver farming and beachcombing activities of fishermen. After spring 2022, the laver racks were removed, and the entire intertidal zone became mudflat (Figure 1c), with disturbances primarily due to beachcombing activities of fishermen.

Additionally, the middle tidal zone within the laver farming racks was also included in our study due to the difficulty in defining

the exact boundaries of the former seaweed farming areas after the removal of the racks. Moreover, our field surveys revealed that the upper tidal zone of the study area was rarely used by waterbirds during low tide, so it was excluded from the study.

2.2 Waterbird survey

Our surveys were conducted during the peak period of the autumn migration, from September to November, over the years 2020 to 2023, with a frequency of at least once per month, due to the overlap between the laver farming period and the autumn migration period of waterbirds in the study area. We conducted 9 surveys before the removal of the laver farming racks and 7 surveys after their removal. For each month, the data from the survey date with the highest total species counts and abundance was retained to standardize sampling effort (Tavernia et al., 2021). We only used

data from 6 surveys before and after the removal for analysis. The remaining data were discarded because of higher human disturbance during those survey dates, which resulted in low numbers of waterbirds. All surveys were carried out by 3 experienced researchers on days with favorable weather conditions in the intertidal zone, and the specific survey dates and personnel details were provided in Appendix 1.

To avoid disturbing waterbirds and causing them to flee the study area, we set up four observation points along the coastline (the coordinates of the observation points were provided in Appendix 1), each approximately 500 meters apart, and used a point sampling method to survey waterbirds in the laver farming area (lower tidal zone) and the adjacent bare flat (middle tidal zone). To ensure data integrity and avoid duplicate records, the same group of researchers used monoculars and a long-focus DSLR camera (Canon 7D Mark II, SIGMA 150-600mm F5-6.3 DG OS HSM) to identify and record the species and numbers of birds present in the study area from one observation point to another during the lowest tide. Each survey lasted approximately 15 minutes before and after the lowest tide, when the waterline receded to the outer edge of the laver racks. To ensure data integrity and avoid redundancy, only individuals entering the study area were recorded, while those exiting the study area were excluded (Gan et al., 2009). For easily identifiable and less numerous flocks, direct counting was used to record their species and abundance. For harder-to-identify and more numerous flocks, photographs were taken first, followed by species identification and individual count.

To understand the impact of coastal restoration on the behavioral composition of waterbirds, we employed instantaneous scan sampling to record the behaviors of individual waterbirds in the study area, both before and after the removal of the laver farming racks during the waterbird surveys. We categorized the observed behaviors of waterbirds into three types (Zhou et al., 2010): (1) Foraging behavior, in which there were obvious activities such as feeding and swallowing, which were specifically manifested as waterbirds constantly searching for food with its beak or directly inserting its beak into the mud; (2) Resting behavior, in which birds stand on one foot, preened, tilted their heads to one side, and buried them under their wings; (3) Other behaviors, including vigilance, fighting, and flying (Zhou and Zhou et al., 2010).

2.3 Macrobenthos sampling

Macrobenthos is one of the primary food sources for waterbirds during migration, and their abundance may influence the composition and distribution of waterbird communities in the intertidal zone (Choi et al., 2019). Therefore, in the autumn from 2020 to 2023, we randomly collected macrobenthos from 16 quadrats (25 cm × 25 cm × 30 cm) in both the laver farming area (lower tidal zone) and the non-farming area (middle tidal zone) of the study region by using sampling frames, and these sampling were conducted quarterly (Bijleveld et al., 2012). This was done to investigate whether seaweed farming could affect waterbird communities by influencing food resources. The specific sampling

dates for each year were provided in Appendix 1. Additionally, our preliminary survey found that the species and abundance of macrobenthos collected in upper tide zone were very low, so this area was not included as a sampling zone.

First, the sediment samples collected from the laver racks area and the non-racks area were filtered through a 0.5 mm mesh sieve to obtain macrobenthos. Then these macrobenthos were stored in 95% ethanol, and taken back to the laboratory for identification, counting, and biomass measurement (biomass was expressed as gram ash free dry weight) (Rodrigues et al., 2006; Lyu et al., 2023). Finally, the total number and biomass of macrobenthos collected were divided by the total surface area of quadrats to calculate the density (ind/m²) and biomass (g/m²) per unit area for each region. Additionally, masses of *Balanus albicostatus* adhere to the pillars of the laver racks, but we failed to observe that waterbirds used them as food during our field surveys. Therefore, our sampling focused only on macrobenthic species in the sediment.

The tidal zone classification and macrobenthos sampling standards in intertidal zone followed the "Marine Monitoring Specifications, Part 7: Coastal Pollution Ecological Survey and Biological Monitoring" (General Administration of Quality Supervision, Inspection and Quarantine of the People's Republic of China, National Standardization Management Committee of China, 2008). The classification and nomenclature of macrobenthos followed the "Marine Biological Species List of China" (Liu, 2008). Fieldwork complied with Nanjing Forestry University's Animal Ethics Committee guidelines (Permit No. 2025002).

2.4 Data analysis

The Shannon-Wiener diversity index (H), Pielou evenness index (J), Margalef richness index (E), and Simpson dominance index (C) were employed to assess the α diversity of the waterbird and macrobenthic communities (Veríssimo et al., 2012). The formula for calculation is outlined below:

$$H' = -\sum_{i=1}^{s} (Pi \log_2 Pi)$$

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

$$E = (S - 1)/\log_2 N$$

$$C = 1 - \sum_{i=1}^{s} (Pi)^2$$

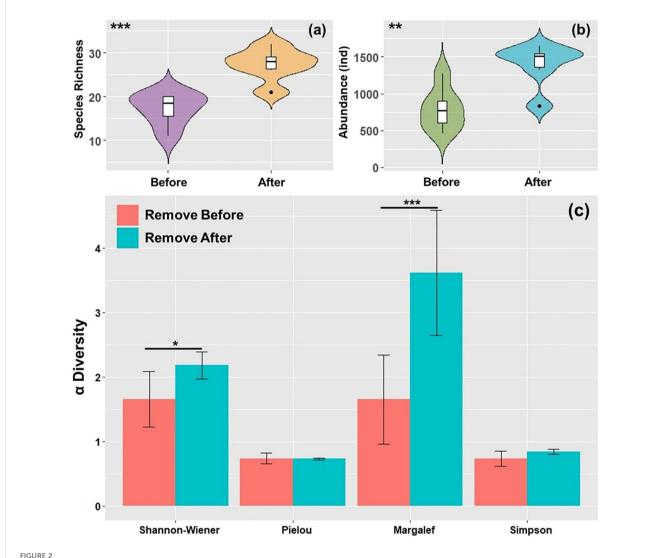
In these equations, "S" represents the total number of bird species; "Pi" denotes the proportion of individual birds belonging to species "i" out of all individual birds, and "N" indicates the overall count of individual birds within the study area.

We analyzed whether there were significant differences in the species richness, species composition, abundance, α diversity indices (H', J, E, C), and behavioral composition (foraging, resting, and others) of waterbird communities in the study area

before and after the removal of the laver farming racks by fitting generalized linear mixed model (GLMM). In the GLMM, species richness, abundance, and diversity indices were treated as response variables, "Remove" was included as fixed effect, while sampling month and year were treated as random effects. The residuals of species richness and abundance were assumed to follow a Poisson distribution, while the residuals of diversity indices were assumed to follow a gaussian distribution. Meanwhile, we examined the species number, density (ind/m²), biomass (g/m²), and α diversity of macrobenthic communities to determine whether there were significant differences between laver racks area (lower tidal zone) and non-racks area (middle tidal zone), as well as before and after the removal of the laver farming racks. We also used generalized

linear model (GLM) to analyze the changes in waterbirds abundance (response variable) with macrobenthos density (fixed effect) in the study area, and the residuals of waterbirds abundance were assumed to follow a Poisson distribution.

Additionally, we classified the waterbird species observed into four groups (herons, ducks, plovers & sandpipers, and seagulls) based on morphological differences (Zhang et al., 2012). Moreover, we only analyzed the behavioral composition differences on the waterbird species that were all recorded in each monthly survey (Haematopus ostralegus, Charadrius alexandrinus, Calidris ruficollis, and Calidris alpina) due to the variations in species composition of waterbirds at different times during the autumn migration period. The Data analysis and graph production were



Changes in species number, abundance and α diversity of waterbird communities in the study area during the autumn migration season from 2020 to 2023. (a) and (b) are the changes in the species number and abundance of waterbird communities before and after the removal of the laver farming racks. (c) is the changes in the α diversity indices of waterbird communities before and after the removal of the laver farming racks. The significance of the differences is represented by "*", and *** for P< 0.001, ** for P< 0.01, and * for P< 0.05. The error bars are the mean \pm standard deviation (n = 6).

TABLE 1 Changes in species number and abundance of various waterbird groups in the study area before and after the removal of the laver farming racks.

Groups	Species Richness			Abundance		
	Before	After	P-Value	Before	After	P-Value
Herons	3	3	P = 0.83	12 ± 6.03	18.83 ± 11.41	P = 0.27
Ducks	0	2	P = 0.03	0	6.83 ± 5.64	P = 0.03
Plovers & Sandpipers	17	28	P< 0.001	503 ± 195.20	1174 ± 225.85	P< 0.001
Seagulls	4	4	P = 0.44	176.17 ± 31.56	33.5 ± 14.19	P< 0.001

The significance of the differences is represented by P Value. The abundance data are the mean \pm standard deviation (n = 6).

Herons mainly include species of the Ardeidae family, ducks mainly include species of the Anatidae family, plovers and sandpipers mainly include species of the Haematopodidae, Recurvirostridae, Charadriidae and Scolopacidae families, and seagulls mainly include species of the Laridae and Sternidae families.

Values in bold indicate significant differences (P<0.05).

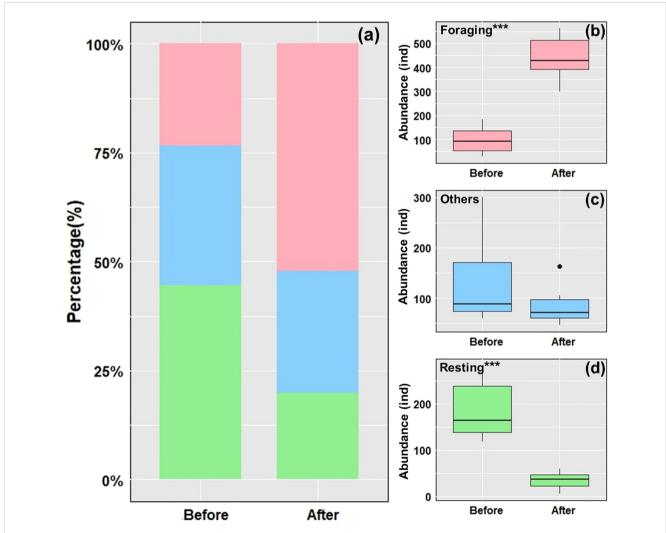


FIGURE 3
Behavioral proportions and changes of four species of shorebirds in the study area before and after the removal of laver farming racks. The significance of the differences is represented by "*", and *** for P< 0.001. The error bars are the mean \pm standard deviation (n = 6). Among them, (a) is the percentage of behavior composition of dominant species before and after the removal of laver racks, (b-d) are the T-testresults of different behaviors of dominant species before and after the removal of laver racks.

performed using the "dplyr", "ggplot2", "lme4" and "vegan" packages in R4.4.1 (Lai et al., 2019) and ArcGIS 10.8.

3 Results

3.1 Species composition and diversity of waterbirds

A total of 11544 birds belonging to 37 species, 8 families, and 3 orders were recorded in the four autumn migration seasons from 2020 to 2023. Among the total waterbird species recorded, 8 (21.6% of the total) are listed as threatened or 'near-threatened' species, including 2 (5.4%) that are listed as critically rare (EN), one species (2.7%) that is listed as vulnerable (VU), and five species (13.5%) that are listed as near threatened (NT) (Appendix 1).

The results revealed that the species number (P< 0.001) and abundance (P< 0.01) of waterbirds communities in the study area were significantly greater than that before the removal of laver farming racks (Figures 1a, b). Meanwhile, for the α diversity, the results revealed that the Shannon-Wiener diversity index (P<0.05) and Margalef richness index (P<0.001) of the waterbird communities in the study area significantly increased after the removal of laver farming racks (Figure 2c).

With respect to waterbird community structure (Table 1), the results indicated that, after the laver farming racks were removed, the ducks, plovers & sandpipers (families Haematopodidae, Recurvirostridae, Charadriidae and Scolopacidae) showed an approximately increase in species richness and abundance, while the abundance of seagulls decreased significantly.

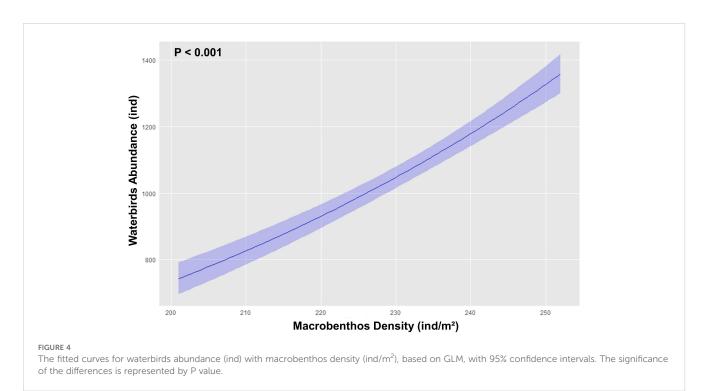
3.2 Differences in the behavior of waterbirds

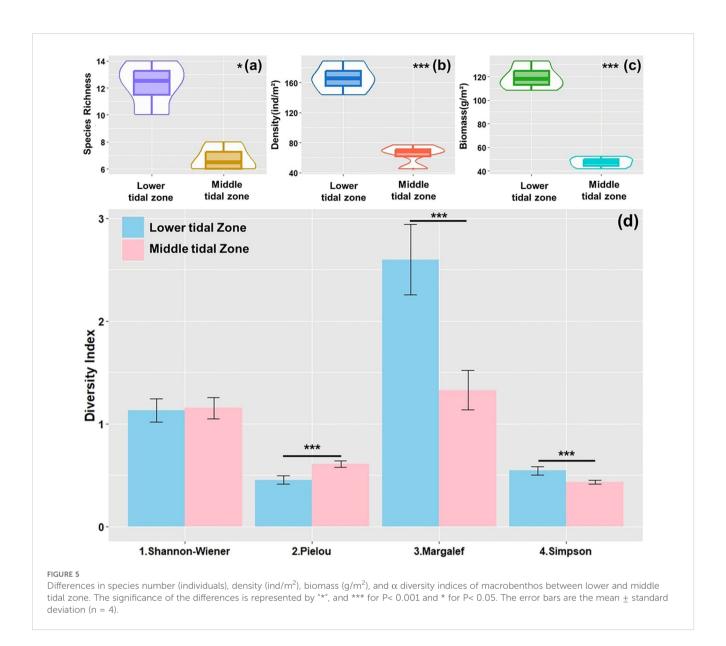
With respect to the behavior of the waterbirds, resting behaviors were the dominant behaviors of shorebirds before coastal restoration of the study area, followed by other behaviors and foraging behaviors. After the laver farming racks were removed, foraging behaviors were the main behavior, followed by other behaviors and resting behaviors (Figure 3a).

The results revealed that the percentage of foraging behaviors of dominant birds increased significantly after intertidal restoration (P<0.001) (Figure 3b), and the percentage of resting behaviors was significantly reduced after restoration (P<0.001) (Figure 3c). However, the proportions of the other behaviors of dominant species in different periods were not significantly different (Figure 3d).

3.3 Differences in macrobenthos

A total of 17 species of macrobenthos belonging to 5 classes and 15 families were recorded in the survey of the benthos (Appendix 1). The results of the GLM (Figure 4) showed that there is a significant positive correlation (P< 0.001) between the waterbirds abundance and the macrobenthos density in the study area. Meanwhile, the results revealed that the species number (P< 0.05), abundance (P< 0.001) and biomass (P< 0.001) of macrobenthos in lower tidal zone (laver racks area) were significantly greater than those in middle tidal zone (non-racks area) (Figures 5a-c). Meanwhile, for the α diversity (Figure 5d), the results revealed that both the Margalef richness index (P<0.001) and the Simpson dominance index (P<0.001) of





macrobenthos in lower tidal zone were higher than those in middle tidal zone. However, the Pielou evenness index (P< 0.001) showed the opposite trend, which may have been caused by the disproportionately high abundance of *Potamocorbula laevis* at the lower tidal zone area (Appendix 1). However, regardless of whether the lower tidal zone or the middle tidal zone, there were no significant differences in the species number, abundance, biomass, and α diversity indices of macrobenthos before and after the removal of laver farming racks.

4 Discussion

Our study suggested that the existence of laver farming racks not only occupied the intertidal regions with the higher food resources, but also limited the ability of some waterbirds to fly and evade dangerous in this region, while the removal of these racks could restore the ecological function of the intertidal zone to a certain extent.

The removal of artificial aquaculture facilities in the intertidal zone holds significant ecological importance for the restoration of waterbird communities. Our study found that the removal of laver racks significantly enhanced waterbird community diversity. Postremoval, the study area exhibited notable increases in species richness, individual abundance, the Shannon-Wiener, and the Margalef index compared to pre-removal conditions. Synchronous monitoring revealed that the species, density, and biomass of macrobenthos in the lower tidal zone were significantly higher than those in the middle tidal zone, with these indicators decreasing along the tidal gradient, a pattern consistent with previous findings (Copertino et al., 2022). Macrobenthos serving as the primary food resource for waterbirds, have significant impacts on waterbird communities through their abundance and spatial distribution in intertidal zones (Fonseca et al., 2017). The

spatial occupation of laver racks in lower tidal zone inhibits the development of waterbird communities by reducing the utilization rate of food resources, and the removal intervention effectively alleviated this constraint.

Furthermore, behavioral observation data indicated that, following the removal of the laver racks, foraging behavior among the four waterbird species significantly increased while resting behavior significantly decreased, which aligns with the ecological response pattern whereby the removal of artificial structures enhances foraging efficiency (Copertino et al., 2022). Notably, different waterbird groups exhibited varied responses to the removal of laver racks: species richness and abundance of ducks, plovers and sandpipers significantly increased, whereas the abundance of seagulls showed a declining trend. Field surveys revealed that seagulls tended to avoid unstructured habitats after the removal of the laver racks, relocating instead to streetlight facilities along roads adjacent to the study areas—a response similar to that reported by Burger et al (Burger, 2018), highlighting species-specific reactions to habitat changes.

The supply of food resources and changes in potential risks both influence the utilization of intertidal aquaculture areas by waterbird communities. Unlike seaweed farming, bivalve aquaculture conducted within intertidal sediments directly provides food for waterbirds, playing a crucial role in maintaining their populations (Basso et al., 2018; Cheng et al., 2022). However, artificial structures erected above intertidal sediments often exert significant negative effects on waterbird communities. For instance, in New Jersey, most waterbirds avoid intertidal areas with oyster farming racks (Burger, 2018); in southeastern coastal China, the installation of bird deterrent nets at razor clam aquaculture sites on intertidal mudflats by local fishers to prevent foraging has inadvertently led to a large number of unintentional waterbird deaths (Liang et al., 2024). This phenomenon is consistent with our study results: the laver racks in the lower tidal zone restrict waterbird flight, thereby reducing the ability of certain species (such as ducks, plovers, and sandpipers) to evade potential threats, which in turn hinders their utilization of the area to some extent.

Unlike the significant response observed in the waterbird communities, our study results indicated that the species richness, density, biomass, and α -diversity indices of the macrobenthic communities did not exhibit significant changes before and after the removal of the laver racks. This finding suggested that the dynamics changes observed in the waterbird communities following the removal were not driven by changes in food resources; rather, waterbird responses likely reflect habitat accessibility improvements rather than food resource shifts, as macrobenthos remained stable. Meanwhile, the potential variations in the macrobenthic communities can be closely associated with adjustments in habitat structure and food availability (Du et al., 2024; Yu et al., 2020). Bhowmik et al. proposed that nearshore aquaculture of Kappaphycus alvarezii significantly influences the availability of benthic resources and habitat structure by altering sedimentation patterns and organic matter content (Bhowmik et al., 2025). Our field survey also found a large number of raft-based laver farms in the coastal waters near the study area. In summary, although the removal of laver racks in the study area altered the local habitat structure, the continued presence of raft-based laver farming may have partially offset the potential effects on various ecological indices of the macrobenthic communities.

In our study, we only analyzed the behavioral changes of four waterbird species before and after the removal of the laver racks, and they all belong to the plovers and sandpipers group, which may not be enough to represent other waterbird groups. Since herons, ducks, and seagulls were not recorded in some of the monthly surveys, they were not included in our analysis. Although both spring and autumn are peak migration periods for waterbirds (Hua et al., 2015), we only analyzed data from the autumn migration period and did not include data from the spring migration period in the analysis. This was mainly because the laver cultivation cycle in Lianyungang did not cover the entire spring migration period, the laver cultivation in the study area usually ends around April of the following year (Shang et al., 2008). The lack of spring migration data and the relatively small scale of study area may limit the generalizability of the conclusions, as intertidal waterbird populations could be influenced by seasonal or interannual variations. For example, Harza et al. suggested that fluctuations in climate factors such as temperature and photoperiod across different seasons can affect the abundance and assemblages of migratory waterbirds (Hazra et al., 2012), and Amano et al. noted that interannual variations in waterbird species richness differ significantly among sites in different climatic zones (Amano et al., 2020). Furthermore, the study duration can also influence the results, as different waterbird species exhibit distinct migratory rhythms during the migration period (Chan et al., 2019). Therefore, monthly bird surveys during the migration season may not fully represent the waterbird abundance in the study area for that month. Future studies should focus on the differences in the response of different waterbird groups to intertidal aquaculture at different migration periods or study sites, as well as compare the impacts of different aquaculture types on waterbird communities. Meanwhile, restoration efforts should prioritize lower tidal zones where laver racks historically restricted waterbird access.

5 Conclusions

In summary, our study revealed the impact of the removal of laver farming racks in intertidal zone on the community structure, diversity, and behavioral composition of waterbird communities. The results showed that after the removal of laver racks, the species richness, abundance, and foraging behavior ratio of waterbirds in the study area significantly increased compared to before the removal. However, there were no significant differences in the species, abundance, biomass, and diversity indices of macrobenthos before and after the removal. The laver racks occupied the area with the higher food resources in intertidal zone and prevented some bird species from foraging in this area. Protecting Lianyungang's intertidal zones is critical for the

restoration of waterbird communities, especially for safeguarding 8 threatened species. Future coastal restoration projects should incorporate seasonal monitoring to assess spring migration impacts.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Ethics statement

The animal study was approved by Nanjing Forestry University Ethics Committee (Permit No. 2025003). The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

TC: Conceptualization, Methodology, Writing – original draft, Writing – review & editing. WH: Data curation, Investigation, Methodology, Software, Writing – original draft, Writing – review & editing. DW: Formal Analysis, Investigation, Writing – original draft, Writing – review & editing. CL: Conceptualization, Funding acquisition, Writing – original draft, Writing – review & editing.

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Conflict of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2025.1549717/full#supplementary-material

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