Comparison of macrobenthic communities between the invasive *Spartina alterniflora* and native *Suaeda glauca* habitats in the Yellow River Delta

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**Abstract** Salt marsh habitats in estuaries play important roles in species compositions and macrobenthos abundances. Here, the macrobenthic communities and environmental conditions in two habitats, which are dominated by the invasive species *Spartina alterniflora* (SA) and native species *Suaeda glauca* (SG), in the Yellow River Delta (YRD) were studied to assess habitat function in four months of one year. The species diversity and abundance of macrobenthos in the SA habitat were much higher than those in the SG habitat. The taxonomic groups in the former showed significant changes over time and shifted from polychaeta (68%) in spring to mollusca (97%) in autumn, but in the latter, it was dominated by crustacea (63 ~ 86%), mollusca (1 ~ 25%) and polychaeta (9 ~ 13%), and only mollusca exhibited obvious month changes. The sediments in the SA habitat contained richer organic matter contents and exhibited higher Chl-a concentrations than those in the SG habitat, although the grain sizes were coarser in the SA habitat. Macrobenthos in the SA habitat displayed significant negative correlations with salinity and organic matter in four months. The results indicated that the taxonomic groups of macrobenthos in the SA habitat were simpler and more sensitive to environmental changes than those in the SG habitat. The effects of invasive SA on macrobenthos need to be further observed and explored, if it continues to expand in the YRD.

**Keywords** Salt marsh · Macrobenthos distribution · Environmental variables · Chlorophyll a

**Introduction**

Estuarine wetlands are among the most important ecosystems due to their valuable ecological functions and unique location advantages (Dai et al., 2013; Chi et al., 2018). For example, many national protected waterbirds overwinter and breed in the YRD, China, such as *Ciconia boyciana, Grus japonensis* and *Larus saundersi* (Yu et al., 2021). These wetlands exert an enormous influence on matter cycling and energy flow between rivers and oceans (Sheaves et al., 2015; Yang et al., 2019). Strong land-sea interactions result in distinct sediment accretion and rapid vegetation succession (Chen et al., 2005), which brings about...
spatially complex heterogeneity in estuarine areas (Kong et al., 2015) and determines the spatial distributions of plant communities (Zhao et al., 2009). The community features of halophytes in different estuarine wetlands play important roles in benthic ecosystems (Vinagre et al., 2008; Du et al., 2012). Higher organic matter contents are present in sediments that are vegetated with plants than in bare sediments (Danovaro and Gambi, 2002; Cui et al., 2011) which, therefore, impact macrobenthos communities (Wieger et al., 1981; Snellgrove and Butman, 1994; Cutajar et al., 2012). Salt marsh habitats provide dead plant tissues and support highly productive benthic microalgal communities that accelerate macrobenthos growth as food sources (Miller et al., 1996; Ward et al., 1997; Middelburg et al., 2000; Takai et al., 2002; Yoshino et al., 2006). Furthermore, salt marsh plants reduce water velocity and increase sedimentation, which can facilitate fine particle accretion from the water column to surface sediment, that may indirectly alter macrobenthos distributions (Brusati and Grosholz, 2007; Quan et al., 2016).

As one of the fastest-growing deltas in the world (Liu et al., 2018, 2019), YRD is an important valuable coastal ecosystem with enormous biological resources (Wang et al., 2009) and forms unique habitats for rare and endangered bird species (Kong et al., 2015). The evolution of the YRD is influenced by changes in river discharges and suspended sediment loads (Cui et al., 2011; Liu et al., 2019). The water flow and sedimentation from YR have formed an important base for the extension and development of the YRD and its wetland landscape (Li et al., 2009a; Liu et al., 2019). Cordgrass (SA) and seepweed (SG) are two dominant salt marsh species in the YRD (Han et al., 2012). SA, an invasive species that was first recorded in 2007 in the YRD (He et al., 2009), has negative effects on intertidal ecosystems, for example, by replacing the original salt marsh (Li et al., 2009b) and reducing the area occupied by native species (Li et al., 2018). However, Cui et al. (2011) found that SA plants promoted crab biomass and abundance in the YRD, which were similar to the results of studies conducted on the California coast, USA (Levin et al., 1998) and Changjiang estuary, China (Gao et al., 2014), where SA had positive effects on macrobenthic species compositions and food supplies. In contrast, SG, as the main native species in the YRD, is a key habitat that provides a food source for macrobenthos and water birds (Li et al., 2011, 2016, 2018). However, the SG habitat area is decreasing owing to land reclamation for agriculture and the intensification of marine aquaculture (Fang et al., 2005; Zhang and Wang, 2008).

Macrobenthos are critical components of estuarine ecosystems (Heip et al., 1995; Herman et al., 1999) and are frequently used as indicators to evaluate the health status of ecosystems (Bilyard, 1987; Diaz et al., 2004; Zhou et al., 2009). Studies of macrobenthos in the YRD have mainly focused on macrobenthic biomass, dominant species (Wang et al., 2010), community structure features (Gu et al., 2013; Leng et al., 2013), biodiversity (Xia et al., 2009) and environmental impact evaluations (Dong and Li, 2012; Dong et al., 2012). SA invasion has aroused the concern of central and local governments in China. SA was included in the list of invasive species by State Environmental Protection Administration of China. An Implementation Plan of Spartina alterniflora Prevention and Control in Shandong Province was published in 2020. Until now, there have been no studies that have compared the community differences in macrobenthos between SA and SG salt marsh habitats and their relationships with environmental variables in the YRD. Hence, the present study aimed to compare taxonomic differences of macrobenthos between SA and SG habitats in the YRD. This research explored the role of invasive SA and native SG habitats on macrobenthos distribution in the YRD development.

Materials and methods

Site description, sample collection and analysis methods

The sampling sites were located in the YRD (37°26′–38°09′N, 118°33′–119°18′E) and are adjacent to the Bohai Sea, China (Fig. 1). The salinity range of the seawater near the YRD is 16–29 (Li, 2000), and the mean tidal height difference is approximately 1.0 m (Song et al., 2004). The annual average temperature and rainfall are 12.1 °C and 552 mm, respectively (Xu et al., 2020). Macrobenthos samples were collected and their species compositions, abundances and biomass were surveyed in the intertidal zone of the YRD during March (winter), May
(spring), August (summer) and November (autumn) in 2013. Three sampling transects were designed in the SA and SG habitats. The SA community was distributed in the northern part of the YRD, with an area of 0.6 ha (Fig. 1c). The SG community was located in the southern part of the YRD, with an area of 150 ha (Fig. 1d).

The distance between transects was 80 and 400 m, and the distance between samples within each transect was 10 and 200 m in SA and SG habitats, respectively (Fig. 1c and d). In total, there were 19 and 15 sampling sites in the SA and SG habitats, respectively. Three random samples were collected at each location, with a 50×50 cm quadrat plot at each site for quantitative analysis, and the sampling depth was approximately 30 cm. The total numbers of collected macrobenthos samples were 57 and 45 in SA and SG each sampling month, respectively. Sediments were washed through a 500 μm mesh sieve to collect macrobenthos, and all samples were immersed in 95% ethanol until laboratory identification. The specimens were sorted using a dissecting microscope (30× magnification), and the number of each species was counted as the abundance. All macrobenthos
of each species were weighed using a 0.01 g precision electric balance as the biomass in each sample. Finally, the macrobenthos species numbers were counted.

Environmental variables, including seawater temperature and salinity, total nitrogen (TN), total organic carbon (TOC) and grain sizes of the sediments, were measured. Chlorophyll a (Chl-a) concentrations in the sediments were also measured. Three seawater samples were collected in the nearest seawater from the SA and SG habitats during the sampling times because macrobenthos were collected in the low tide period. Seawater temperature and salinity were measured using a YSI 30 portable metre (YSI, USA). The sediments used for grain size, TOC, TN and Chl-a concentration analysis were collected with a plastic sampler with a 3 cm diameter and 5 cm height. Three random sediment samples were collected at each site. The grain sizes of the sediment samples were analysed using a Mastersizer 2000 Laser Particle Sizer (Malvern, UK). TOC and TN were measured using an elemental analyser (Flash EA1112 Thermo Scientific, Italy). The Chl-a concentrations in the sediments were measured by a fluorometer (Shimadzu, Japan) after extraction with 15 ml of 90% and refrigeration in the dark for 24 h (Wang, 1986).

Data analyses

The dominant species were determined according to the important value index (IVi) (Masson and Greig, 1983), where:

\[
IV_i = \left( \frac{n_i}{N} \right) \times f_i
\]

\( n_i \): each macrobenthos species abundance,
\( N \): total species abundance,
and \( f_i \): the proportion of each macrobenthos species occurring in all quadrats.

When the IVi value was not less than 0.2, the species were the dominant species.

The Shannon–Wiener index (H') was calculated based on the taxonomic compositions of macrobenthos and their species numbers (Shannon and Weaver, 1949), where:

\[
H' = - \sum_{i=1}^{S} P_i \times \log_2 P_i
\]

\( S \): number of macrobenthos species, and \( P_i \): the proportion of each macrobenthos species in the total macrobenthos abundance.

Macrobenthic species number, abundance, H', biomass, the environmental parameters and Chl-a concentration differences in each habitat in four months were analyzed according to one-way ANOVA and post hoc test using the SPSS 11.5 (Statistical Product and Service Solutions) software. Macrobenthic species number, abundance, H', biomass, the environmental parameters and Chl-a concentration differences between both habitats in each month were analyzed according to independent-samples (two-sample/group) T Test using the SPSS 11.5. Correlation analyses between macrobenthos abundance, H', biomass, and the environmental parameters, Chl-a concentration in each habitat were analyzed according to a two-tailed test using the SPSS 11.5 software. Data were presented as means (± SE), and a significant level of 5% was used in all analyses.

Results

Environmental parameters and Chl-a concentrations

The seawater temperatures significantly varied among months in SA (\( F = 25,452.490; \ p < 0.001 \)). The lowest (3.20 ± 0.01 °C) and highest (29.63 ± 0.02 °C) values were recorded in March and August, respectively (Fig. 2a). The seawater salinities exhibited significant changes in SA in four months (\( F = 95.311; \ p < 0.001 \)). The lowest value (23.48 ± 0.02) occurred in August, and the highest value (30.47 ± 1.15) occurred in November (Fig. 2b). The TN levels in the sediments were not significantly different in SA among months (\( F = 1.313; \ p = 0.280 \)). The TOC in the sediments did not exhibit significant changes in SA among months (\( F = 0.682; \ p = 0.567 \)). The grain sizes of the sediments were significantly different across months in SA (\( F = 3.598; \ p = 0.014 \)). The highest (47.48 ± 9.38 μm) and lowest (41.04 ± 15.95 μm) values were recorded in May and March, respectively (Fig. 2e). The Chl-a concentrations of the sediments were significantly different across months in SA (\( F = 3.041; \ p = 0.030 \)), with the highest value (1.25 ± 0.66 μg/g) in March and lowest value (0.75 ± 0.44 μg/g) in November (Fig. 2f).
The seawater temperatures significantly varied among months in SG ($F=1491.141; p<0.001$). The lowest ($3.6\pm0.00$ °C) and highest ($35.2\pm0.74$ °C) values were recorded in March and August, respectively (Fig. 2a). The seawater salinities displayed significant month changes in SG ($F=36.084; p<0.001$). The lowest value ($13.49\pm2.58$) occurred in August, and the highest value ($26.62\pm1.94$) occurred in November (Fig. 2b). The TN levels in the sediments significantly differed for each month in SG ($F=201.300; p<0.001$). The TOC values in the sediments were significantly different across months in SG ($F=83.038; p<0.01$). The lowest value ($0.14\pm0.03\%$) was recorded in August, and the highest ($0.32\pm0.05\%$) was recorded in November in SG (Fig. 2d). The grain sizes of the sediments were significantly different among months in SG ($F=20.031; p<0.001$). The TN was significantly higher in SA than SG in May ($t=3.250; p=0.003$), August ($t=3.200; p=0.003$), and November ($t=5.838; p<0.001$). Temperature and salinity values did not show significant differences between the two habitats in each sampling month, although the temperatures in SG were higher than those in SA (Fig. 2a), and the salinities in SG were lower than those in SA (Fig. 2b). The TOC was significantly higher in SA than SG in May ($t=3.200; p=0.003$) and August ($t=5.217; p<0.001$), and it was significantly lower in SA than SG in November ($t=2.302; p=0.030$) (Fig. 2c). The grain sizes were significantly different among months in SG except August (March: $t=3.703; p<0.001$; May: $t=5.838; p<0.001$; August: $t=1.360$; November: $t=2.302; p=0.030$) (Fig. 2d).
Table 1 Macrobenthic species identified in both sampling habitats of the YRD

| Taxa         | Species                  | SA | SG |
|--------------|--------------------------|----|----|
| Crustacea    | Cirolana japonensis     | ✓  | ✓  |
|              | Corophium sinensis      | ✓  | ✓  |
|              | Diastyris tricincta     | ✓  | ✓  |
|              | Gammarus sp.            | ✓  | ✓  |
|              | Helice (H.) tientsinensis | ✓  | ✓  |
|              | Helice (H.) tridenssheni | ✓  |   |
|              | Hemigrapsus penicillatus | ✓  |   |
|              | Hemigrapsus sanguineus  | ✓  |   |
|              | Hyale sp.               | ✓  |   |
|              | Macrophthalmus (Mareotis) japonicus | ✓  | ✓  |
|              | Melita palmata          | ✓  |   |
|              | Neomysis auatschensis   | ✓  |   |
|              | Orchestia sp.           | ✓  |   |
|              | Trachypheanae curvostris| ✓  |   |
| Mollusca     | Bullacta exarata        | ✓  |   |
|              | Cerithidea cingulata    | ✓  | ✓  |
|              | Crassostrea gigas       | ✓  |   |
|              | Dosinia corrugata       | ✓  |   |
|              | Glaucome primeana       | ✓  | ✓  |
|              | Mactra chinensis        | ✓  |   |
|              | Moerella iridescens     | ✓  | ✓  |
|              | Moerel larutila         | ✓  |   |
|              | Nitidotellina minuta    | ✓  |   |
|              | Potamocorbula laevis    | ✓  | ✓  |
|              | Trapezium liratum       | ✓  |   |
| Polychaeta   | Amphinome rostrata      | ✓  |   |
|              | Capitelle capitata      | ✓  |   |
|              | Chaetozone setosa       | ✓  |   |
|              | Cirratulus chrysoderma  | ✓  |   |
|              | Diopara bilobata        | ✓  |   |
|              | Diopatra chilensis      | ✓  |   |
|              | Eunoe longa             | ✓  |   |
|              | Glyceria chirori        | ✓  |   |
|              | Glycinde gurjanovae     | ✓  | ✓  |
|              | Goniada japonica        | ✓  |   |
|              | Goniada maculata        | ✓  |   |
|              | Haploproscoplos elongatus | ✓  | ✓  |
|              | Heteromastus filiforms  | ✓  | ✓  |
|              | Lambrineris heteropoda  | ✓  |   |
|              | Lambrineris latrellii   | ✓  |   |
|              | Lambrineris tetraura    | ✓  |   |
|              | Nematine sp.            | ✓  |   |
|              | Paraprionospio pinnata  | ✓  |   |
|              | Perinereis aibuhitensis | ✓  | ✓  |

Table 1 (continued)

| Taxa         | Species                  | SA | SG |
|--------------|--------------------------|----|----|
|              | Perinereis nunlia        | ✓  |   |
|              | Pseudopolydora kempi     | ✓  |   |
|              | Typosyllis armillaris    | ✓  |   |

Totals 39 18

$p = 0.178$; November: $t = 5.439$; $p < 0.001$) (Fig. 2c). Chl-a concentrations were significantly higher in SA than SG across months except May (March: $t = 4.184$; $p < 0.001$; May: $t = 1.141$; $p = 0.256$; August: $t = 4.598$; $p < 0.001$; November: $t = 9.165$; $p < 0.001$) (Fig. 2f).

Macrobenthos

Along the sampling sites in the YRD, 47 macrobenthic taxa were identified, including 22 polychaeta, 14 crustacea and 11 mollusca (Table 1). A total of 39 macrobenthic taxa were identified in SA (Table 1).

The highest species number (33) was observed in May in SA, and the lowest species number (11) was observed in August (Fig. 3a, Table 2). The macrobenthic abundances significantly varied among months in SA ($F = 7.205$; $p < 0.001$). The abundances in August were higher than those in May and were higher than those in March and November in SA (Fig. 3b, Table 2). The $H'$ values are shown in Fig. 3c and Table 2. The dominant species that were recorded at each site per month are shown in Table 3. In SA, Cerithidea cingulata was the only dominant species in August and accounted for 88% of the total abundance, which was greater than for the other species in May and accounted for 58% of the total abundance (Table 3). Moerella iridescens was the dominant species in all months at each site except for August in SA (Table 3). The macrobenthic biomass amounts were significantly different across months in SA ($F = 8.235$; $p < 0.001$). In SA, the taxonomic groups of macrobenthos showed significant month changes, and the abundances shifted from polychaeta (68%) in spring to mollusca (97%) in autumn (Fig. 4A). The crustacean abundances accounted for the lowest proportion in all sampling months and accounted for only 2 ~ 4% (Fig. 4A). In SA, the mollusca biomass accounted for...
the greatest proportion in all months (Fig. 4B) and accounted for 61–97% of the total (Fig. 4B).

A total of 18 macrobenthic taxa were identified in SG (Table 1). The highest species number (10) was observed in May and August in SG, and the lowest species number (8) was observed in March (Fig. 3a, Table 2). The abundances significantly varied across months in SG ($F=11.120; p<0.001$). The abundance in August was higher than that in May and was higher than those in November and March in SG (Fig. 3b, Table 2). The $H'$ values were less than 1 in SG (Fig. 3c, Table 2). *Perinereis aibuhitensis* was the dominant species in all months in SG, greater than those of the other species in August and November, which separately accounted for 36.21% and 48.52% of the total abundance (Table 3). *M. iridescens* was the dominant species in all months except for May in SG (Table 3). The macrobenthos biomass amounts significantly differed among months in SG ($F=8.543; p<0.001$). In SG, the macrobenthos biomass was dominated by crustacea (63–86%), mollusca (1–25%) and polychaeta (9–13%) (Fig. 5B-b). In May, the mollusca biomass accounted for the lowest proportion (1%) in SG (Fig. 5B-b).

The species numbers of macrobenthos were higher in SA than in SG (Fig. 3a, Table 2). The macrobenthos abundances were significantly greater in SA than in SG among months (March: $t=3.539; p=0.001$; May: $t=4.144; p<0.001$; August: $t=5.636; p<0.001$; November: $t=3.321; p=0.003$) (Fig. 3b, Table 2). The biomass amounts ($t=0.640; p=0.568$) were significantly different between the two habitats in August ($t=5.865; p<0.001$) (Fig. 3d, Table 2). In both habitats, *M. iridescens* was the dominant species in all months except for August in SA and May in SG (Table 3).

**Fig. 3** Species numbers, abundances, $H'$ values and biomass of macrobenthos at the two sampling sites in 2003

**Discussion**

This study provides the first investigation of the differences in intertidal macrobenthos communities between the invasive SA and native SG habitats in the YRD, China. The taxonomic groups of macrobenthos...
in the SA habitat exhibited significant month changes and shifted from polychaeta (68%) in spring to mollusca (97%) in autumn; however, in the S. glauca habitat, the taxonomic macrobenthos groups were dominated by crustacea (63 ~ 86%), mollusca (1 ~ 25%) and polychaeta (9 ~ 13%), and only mollusca showed obvious month changes (Fig. 5). The SG habitat supported lower abundances (29 ~ 96 ind/m²) than the SA habitat (148 ~ 471 ind/m², Fig. 3b), and the latter values were higher than the macrobenthos abundances in the mudflats of the YRD (210 in spring and 108 ind/m² in autumn, Wang et al., 2010), but were lower than SA habitat in the Changjiang estuary, China (286 ~ 553 ind/m², Xu et al., 2006; 1599 ind/m², Quan et al., 2016).

Seasonal changes have key impacts on the macrobenthos distributions in salt marsh habitats (Tang and Kristensen, 2010). In our study, higher macrobenthos biomass amounts occurred in spring and summer (Fig. 3d), which were mainly due to more food sources from the leaves and stems of plants in the growing seasons (Zhou et al., 2009; Tang and Kristensen, 2010). The lower temperatures in autumn and winter could limit the growth and reproductive efficiency of macrobenthos (Grilo et al., 2011). Moreover, benthic microalgae in salt marsh habitats may promote macrobenthos growth as food sources (Takai et al., 2002; Yoshino et al., 2006, 2012). Our study also found that the Chl-a concentrations reached their highest values in March in both SA and SG (Fig. 3). Therefore, the macrobenthos biomass amounts reached their highest values in May through the

| Taxa            | Species                | SA Species number | Abundance (ind/m²) | 
|-----------------|------------------------|-------------------|-------------------| 
| Crustacea       | Helice (H.) tridenssheni | 20.54             | 5.94              | 
|                 | Macrophthalmus (Mareotis) japonicus | 11.70             | 8.91              | 
|                 | Neomysis auntschensis | 25.78             |                   | 
| Mollusca        | Bulcata exarata        | 12.81             | 18.81             | 
|                 | Cerithidea cingulata   | 58.27             | 87.99             | 12.84             | 
|                 | Moerella tridescens    | 25.48             | 9.83              | 11.26             | 17.53             | 11.98             | 9.90              | 
|                 | Potamocorbula laleaves |                   |                   |                   |                   |                   |                   |                   | 
| Polychaeta      | Glycinc gurjanovae     | 18.41             |                   |                   |                   |                   |                   |                   | 
|                 | Haplospanolos elongatus| 07.95             |                   | 11.71             |                   |                   |                   |                   | 
|                 | Heteromastus filiforms |                   |                   |                   |                   |                   |                   |                   | 
|                 | Lumbrineris lateriell  | 19.73             |                   | 13.73             |                   |                   |                   |                   | 
|                 | Lumbrineris tetraura   | 2.92              |                   |                   |                   |                   |                   |                   | 
|                 | Paraprionospio pinnata | 8.25              |                   | 11.94             |                   |                   |                   |                   | 
|                 | Perinereis aibuhitensis| 4.57              |                   | 8.11              |                   | 22.68             | 20.05             | 36.21             | 48.52             |
growth period after March and April. Dense above-ground canopies may reduce light availability and subsequent benthic microalgal development, which would thus inhibit macrobenthos grazers in summer in comparison with spring (Lana and Guiss, 1991). According to the study from Jiang (2021), SA fragments and detritus are the main food sources of macrobenthos, even exceeding the proportion of benthic microalgae in the YRD. SA occupied 91.39% of the intertidal zone area of current estuary in the YRD, with the area of 4063 ha in 2018, locating in seven regions, which reduced Suaeda salsa area by more than 50% (Ren et al., 2021). That demonstrated that food sources of macrobenthos may further change with the development of SA invasions. How temperature impacts predator–prey interactions and food sources in invasive and native salt marsh habitats should be considered in the future, because it is one
of factors influencing the macrobenthic communities via global climate change and in the late stage of SA invasion.

The taxonomic macrobenthos groups in the SA habitats were obviously different from those in the SG habitats in our study. That is, the mollusca biomass was the largest in SA in all sampling months (Fig. 5B), which indicated that SA plays an important role in creating dense bivalve mollusca populations as a result of dead leaves and stems on the ground (Ward et al., 1997; Brusati and Grosholz, 2006; Quan et al., 2016). In contrast, crustacean biomass accounted for the largest proportion in all months in SG (Fig. 5B), which was the first study in the SG habitats worldwide. *Macrophthalmus* (Mareotis) japonicus, *Perinereis aibuhitensis* and *P. laevis* were the dominant species at both sampling sites (Table 3), which is in accordance with other reports for the SA habitats (Cai and Tian, 2000; Wang et al., 2010; Leng et al., 2013; Gao et al., 2014) and *Suaeda japonica* habitats (Bon et al., 2011). *Helice* sp. was present and was not the dominant species in SA, while it was the dominant species in SG (Table 1 and 3), which disagreed with the results of Cui et al. (2011), who found that SA invasions enhanced the abundances of *Helice* sp.* Bullocka exarata* was the dominated species in August and November in SG and did not appear in SA (Table 1 and 3). Our study demonstrated that SG may support more suitable habitats for macrobenthos by providing food sources and comfortable environments in comparison with SA in the YRD. *B. exarata* was introduced to the YR estuary in 2001 (Leng et al., 2013), which indicated that this species adapted to SG conditions. *B. exarata* and *P. laevis* are superior feed for aquaculture in the YR estuary. Fishermen collected them in the intertidal zones in spring and summer, thus their densities changed more than those of other species (Leng et al., 2013).

Our results showed that the number of polychaeta species in SA was more than SG (Table 1). On the one hand, SA invasions may result in changes in biogeochemical cycles by increasing nutrients and decreasing oxygen in the sediments, which induces changes in macrobenthos from bigger to smaller species, especially increasing the biomass of polychaeta (Zhou et al., 2009). On the other hand, complexity of SA underground parts could negatively impact the food of macrobenthos and limit the growth of bigger species, finally leading to the taxonomic groups changing in the SA. How later stages of the SA invasion affect the local macrobenthos community should be explored in the future.

The spread of exotic Spartina has negative impacts on local birds communities (Gan et al., 2009) by ecosystem changes, such as predator–prey interactions and habitat alterations (Owens and Bennett, 2000; Clavero and Garcia-Berthou, 2005). Our study showed that mollusca were the main taxonomic groups in SA (Fig. 4). That is different from the studies of Stralberg et al. (2004) and Levin et al. (2006), who found that the dense roots and rhizomes and rapid deposition of sediments in Spartina-invaded areas limited bivalves colonization. It could be because SA was still in the early stage of its invasion in the YRD. Bivalves are the major food for shorebirds (Jing et al., 2007). Our results demonstrated that SA invasions may provide useable food for some birds in the YRD, although SA invasions have

| Table 4 Relationships between macrobenthos parameters and environmental variables, Chl-a concentrations at the two sampling locations |
|----------------------------------------|
|                                      | SA habitat | SG habitat |
| Abundance                             |            |            |
| H'                                    |            |            |
| Biomass                               |            |            |
| Temperature                           | 0.872      | 0.898      |
| Salinity                              | −0.915     | −0.955**   |
| TOC                                   | 0.301      | −0.491     |
| TN                                    | −0.165     | −0.828     |
| Grain size                            | −0.088     | 0.216      |
| Chl-a                                 | −0.143     | −0.350     |
|                                      |            |            |
| Chl-a concentrations                   |            |            |
| Abundance                              |            |            |
| H'                                    |            |            |
| Biomass                               |            |            |
| Temperature                           | 0.817      | 0.502      |
| Salinity                              | −0.845     | −0.531     |
| TOC                                   | 0.132      | −0.967**   |
| TN                                    | −0.320     | −0.953**   |
| Grain size                            | 0.085      | 0.243      |
| Chl-a                                 | −0.443     | 0.478      |

**Correlations are significant at the 0.05 level (two-tailed)**
reduced feeding habitats, therefore negatively impacting local bird communities in some places (e.g., on the Pacific coast of North America, Anttila et al., 1998; Chongming Dongtan coast of China, Gan et al., 2009). Crustacea are unusable for most shorebirds (Levin et al., 2006; Jing et al., 2007). That indicated that birds breeding success may be lower because the food resource are scarce in SG habitats.

Sediment rugosity and hydrodynamics are two main driving factors that structure macrobenthos communities (Yu et al., 2020). The aboveground biomass and litter production of SA and SG plants can slow water currents and waves, thus decreasing water velocities (Yang et al., 2012), which could promote fine particle sedimentation from the water column to the surface sediments (Quan et al., 2016) and have positive effects on mass loss and nutrient release (Yin et al., 2019). In our study, the grain sizes of the sediments in SA were 41–47 μm, higher than those in SG (36–37 μm) for all sampling months (Fig. 2e), which means that the sediments consisted of clay in both sampling habitats, according to Folk et al. (1970). Such amelioration of sediments may support crustacea survival (e.g., Helice (H.) tridenssheni), which was the dominant species in SG. According to the literature (e.g., Neira et al., 2006; Brusati and Grosholz, 2007; Xie and Gao, 2013; Gao et al., 2014), finer sediments were favourable for macrobenthos adaptation to intertidal habitats, such as C. cingulata, M. iridescens and M. japonicus (Table 3). Furthermore, detritivorous polychaetes are suitable for habitats with higher rugosity, such as SA, because of their capacity to intercept the increased organic matter that is available in the water (Yu et al., 2020). The higher water velocities that result from shorter plants in SG habitats may promote the recruitment and growth of some crustaceans compared with slower-velocity habitats such as SA due to the flow rate effects on the delivery of planktonic larvae to the substrate (Leonard et al., 1998), which is in agreement with the study by Graham and Sebens (1996), who found that the larvae of barnacles were well mixed in the water column at higher flow rates. That demonstrated the vegetation structure (e.g. shoot height and density) in salt marshes may be the main factor impacting macrobenthos groups in both habitats of the YRD, which should be well considered in the future.

SA invasion promoted TOC storage compared with wetland covered by native plant species in the YRD (Zhang et al., 2021), therefore supported important habitats for macrobenthos (Valiela et al., 1984; Sueiro et al., 2011). Invasive marsh plants often out-compete native plants due to their higher growth rates (Li et al., 2009b; Quan et al., 2016), which indicates that the higher above and belowground biomass of SA gives rise to higher organic carbon contents in the sediments and consequently fosters benthic food webs (Zhou et al., 2009; Page et al., 2010; Wang et al., 2014). Many studies have implied that higher organic matter contents in sediments are related to increased macrobenthos densities (e.g., Sacco et al., 1994; Levin et al., 1996; Craft, 2000). For example, Levin et al. (1998) found that there were significant positive associations between macrobenthos abundances and TOC in the Spartina sp. habitats of the California coast, USA, where the TOC in sediments was 2.4–25.9%. The range of surface organic carbon contents of the sediments in the YRD was 0.06–0.40% (Yu, 2014). Our results showed that the TOC of sediments in SA was 0.62–1.00% (Fig. 2d), which was in the middle range for the SA salt marshes on the coast of China (0.08–1.7%, Meng et al., 2020), that indicated that S. alterniflora provided more organic carbon to sediments as a result of its faster leaf growth, especially in flooding seasons (Levin, 1998). Higher TOC content resulting from SA invasions could reduce abundance and biomass of macrobenthos (Chen et al., 2018), or lead to the community change by increasing the toxicity of sulfide (Chen et al., 2009). With the development of SA invasions, SA may replace native salt marshes such as SG habitats. The food sources of macrobenthos may change from several organic carbon sources to single organic carbon sources, which will have negative effects on ecosystem stability in the YRD.

In our study, the TN contents of sediments were 0.06–1.16% in SG (Fig. 2c), which were lower than those of the SG habitats on the coast of South Korea (2.1%, Lee et al., 2016). According to the study by Cai et al. (2002), lower H′ values of macrobenthos (especially less than 1) indicated a serious pollution status. Normally, macrobenthos that are tolerant to low dissolved oxygen concentrations can be thought of as pollution indicator species (Pearson and Rosenberg, 1978). Haploscoloplos elongates was present in SG (Table 4) and was also the dominant species in autumn and winter in SA (Table 3), which can
be viewed as a pollution indicator species (Grizzle, 1984). There were higher TN levels in the sediments in SA (0.11 ~ 0.15%, Fig. 2c) than in the SA marshes on the coast of North Carolina, USA (0.02 ~ 1.1% within 21 years after restoration; Craft, 2000), which indirectly demonstrated that SA plants have high nitrogen contents (Gao et al., 2014; Meng et al., 2020), although salt marshes are N limited owing to N regulating the development of macrobenthos communities (Valiela and Teal, 1974). The N contents of plant roots, stems and leaves were 0.41 ~ 1.43% in SA and 0.63 ~ 3.25% in SG (our unpublished data) also indicated higher nitrogen sources from salt marsh plants into sediments. The YR estuary was at the risk of eutrophication together with an increased marine aquaculture area (Liu et al., 2009). Dissolved inorganic nitrogen pollution in the seawater was serious near the YR estuary (Zhang et al., 2012), which could impact SA growth (Meng et al., 2020) and consequently alter macrobenthos diversity. In the late stage of SA invasions, less density of SA will reduce TN content of the sediments. Effects of TN on macrobenthos in the different stages of SA invasions should be concerned in the future, which can provide useful information for understanding ecosystem responses to biogeochemical processes resulted from salt marsh succession.

Due to highly seasonal freshwater inputs, the salinity values exhibited broad fluctuations in estuarine areas (Evin and Talley, 2000). In this study, the macrobenthos abundances in SG were significantly negatively related to seawater salinities (Table 4), which was different from reports that reduced salinity led to decreased abundances and species richness in salt marsh habitats such as the Tijuana Estuary, USA (Nordby and Zedler, 1991), California coast, USA (Levin et al., 1998), Paranaguá Bay, Brazil (Lana et al., 1997) and St. Lucia estuary in South Africa (Pillay and Perissinotto, 2008). Li et al. (2016) and Yang et al. (2019) also reported that freshwater release reduced salinity, which thus altered macrobenthos densities and diversities in the YR estuary. How seawater salinity impacts macrobenthos growth and species distributions in the YRD warrants further research.

Conclusions

Understanding the ecosystem functions of salt marsh habitats is important for the sustainable management of coastal zones. Our research determined that the taxonomic groups of macrobenthos in the invasive SA habitat were simpler and more sensitive to environmental changes than those in the native SG habitat, although the former obviously supported higher benthic abundances and species numbers in comparison with the latter in the YRD. The long-term mechanisms by which SA and the SG community, such as vegetation structure, impact macrobenthos distributions need further study through more field investigations and transplanting experiments for the sustainable management of salt marshes at different locations.

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Declarations

Conflict of interest

The authors declare that they have no conflict of interest.

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