

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

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

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26 **Abstract**

27 Salt marsh habitats in estuaries play important roles in species compositions and
28 macrobenthos abundances. Here, the macrobenthic communities and environmental
29 conditions in two habitats, which are dominated by the invasive species *Spartina*
30 *alterniflora* (SA) and native species *Suaeda glauca* (SG), in the Yellow River Delta
31 were studied to assess habitat function. The seasonal data showed that the species
32 diversity and abundance of macrobenthos in the SA habitat were much higher than
33 those in the SG habitat. The functional groups in the former showed significant
34 seasonal changes and shifted from polychaeta (68%) in spring to mollusca (97%) in
35 autumn, but in the latter, it was dominated by crustacea (63-86%), mollusca (1-25%)
36 and polychaeta (9-13%), and only mollusca exhibited obvious seasonal changes. The
37 sediments in the SA habitat contained richer organic matter contents and exhibited
38 higher Chl-*a* concentrations than those in the SG habitat, although the grain sizes
39 were coarser in the SA habitat. At the seasonal scale, macrobenthos in the SA habitat
40 displayed significant negative correlations with salinity and organic matter. The
41 results indicated that the macrobenthos functional groups in the SA habitat were
42 simpler and more sensitive to environmental changes than those in the SG habitat.
43 The vegetation structures may give rise to the differences in macrobenthos
44 distributions in both habitats, which need to be further observed and explored.

45

46 **Keywords:** Salt marsh, macrobenthos distribution, environmental variables,

47 Chlorophyll *a*

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51 **1. Introduction**

52 Estuarine wetlands are among the most important ecosystems due to their
53 invaluable ecological functions and unique location advantages (Dai et al., 2013; Chi
54 et al., 2018). These wetlands exert an enormous influence on matter cycling and
55 energy flow between rivers and oceans (Sheaves et al., 2015; Yang et al., 2019).
56 Strong land-sea interactions result in distinct sediment accretion and rapid vegetation
57 succession (Chen et al., 2005), which brings about spatially complex heterogeneity in
58 estuarine areas (Kong et al., 2015) and determines the spatial distributions of plant
59 communities (Zhao et al., 2009). The community features of halophytes in different
60 estuarine wetlands play important roles in benthic ecosystems (Vinagre et al., 2008;
61 Du et al., 2012). Higher organic matter contents are present in sediments that are
62 vegetated with plants than in uncovered sediments (Danovaro and Gambi, 2002; Cui
63 et al., 2011) which, therefore, impact macrobenthos communities (Wiegert et al., 1981;
64 Snelgrove and Butman, 1994; Cutajar et al., 2012). Salt marsh habitats provide dead
65 plant tissues and support highly productive benthic microalgal communities to
66 accelerate macrobenthos growth as food sources (Miller et al., 1996; Ward et al., 1997;
67 Middelburg et al., 2000; Takai et al., 2002; Yoshino et al., 2006). Furthermore, salt
68 marsh plants reduce water velocity and increase sedimentation, which can facilitate
69 fine particle accretion from the water column to surface sediment, which may
70 indirectly alter macrobenthos distributions (Brusati and Grosholz, 2007; Quan et al.,
71 2016).

72 As one of the fastest-growing deltas in the world (Liu et al., 2018; Liu et al.,
73 2019), the Yellow River Delta (YRD) in China is an important, valuable coastal
74 ecosystem with enormous biological resources (Wang et al., 2009) and forms unique
75 habitats for rare and endangered bird species (Kong et al., 2015). The evolution of the

76 YRD is influenced by changes in river discharges and suspended sediment loads (Cui
77 et al., 2011; Liu et al., 2019). The water flow and sedimentation from the Yellow
78 River (YR) have formed an important base for the extension and development of the
79 YRD and its wetland landscape (Li et al., 2009a; Liu et al., 2019). Cordgrass (SA) and
80 seepweed (SG) are two dominant salt marsh species in the YRD (Han et al., 2012).
81 SA, an invasive species that was firstly recorded in 2007 in the YRD (He et al., 2009),
82 has negative effects on intertidal ecosystems, for example, by replacing the original
83 salt marsh (Li et al., 2009b) and reducing the distribution area of native species (Li et
84 al., 2018). However, Cui et al. (2011) found that SA plants promoted crab biomass
85 and abundance in the YRD, which were similar to the results of studies conducted on
86 the California coast, USA (Levin et al., 1998) and Changjiang estuary, China (Gao et
87 al., 2014), where SA had positive effects on macrobenthic species compositions and
88 food supplies. In contrast, SG, as the main native species in the YRD, is a key habitat
89 that provides a food source for macrobenthos and water birds (Li et al., 2011; Li et al.,
90 2016; Li et al., 2018). However, the SG habitat area is decreasing owing to land
91 reclamation for agriculture and the intensification of marine aquaculture (Fang et al.,
92 2005; Zhang and Wang, 2008).

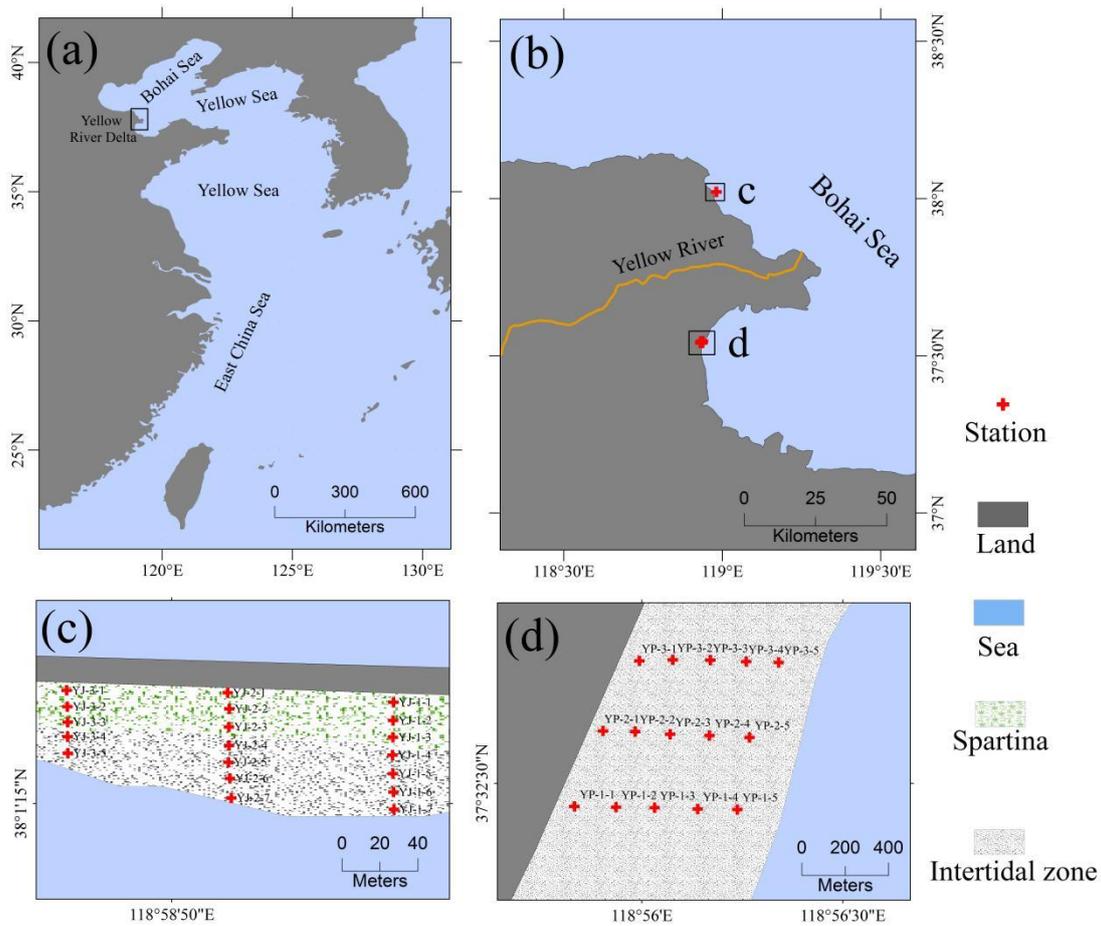
93 Macrobenthos are critical components of estuarine ecosystems (Heip et al., 1995;
94 Herman et al., 1999) and are frequently used as indicators to evaluate the health status
95 of ecosystems (Bilyard, 1987; Diaz et al., 2004; Zhou et al., 2009). Studies of
96 macrobenthos in the YRD have mainly focused on macrobenthic biomass, dominant
97 species (Wang et al., 2010), community structural features (Gu et al., 2013; Leng et al.,
98 2013), biodiversity (Xia et al., 2009) and environmental impact evaluations (Dong
99 and Li, 2012; Dong et al., 2012). Until now, there have been few studies that have
100 compared the seasonal community differences in macrobenthos between SA and SG

101 salt marsh habitats and their relationships with environmental variables in the YRD.
102 To better understand the differences in macrobenthic functional groups between the
103 SA and SG habitats, the seasonal changes of macrobenthos in their species
104 compositions, abundances and biomass were surveyed in the SA and SG habitats
105 along the intertidal zones of the YRD. Environmental variables, including seawater
106 temperature and salinity, total nitrogen (TN), total organic carbon (TOC) and
107 sediment grain sizes, were measured. Chlorophyll *a* (Chl-*a*) concentrations in the
108 sediments were also measured. This study aimed to compare the ecological function
109 on biodiversity between the invasive SA and native SG habitats in the YRD using
110 macrobenthos as indicators. The results lead to hypotheses concerning the factors that
111 determine whether the impacts of the invasive SA habitat on macrofauna are
112 beneficial or detrimental in comparison with the native SG habitat.

113 **2. Materials and methods**

114 ***2.1. Site description, sample collection and analysis methods***

115 The sampling sites are located in the YRD ($37^{\circ} 26' -38^{\circ} 09' N$, $118^{\circ} 33'$
116 $-119^{\circ} 18' E$) and are adjacent the Bohai Sea, China (Fig. 1). The salinity range of
117 the seawater near the YRD is 16~29 (Li, 2000), and the mean tidal height difference is
118 approximate 1.0 m (Song et al., 2004). The annual average temperature is 12.1°C, and
119 the annual average rainfall is 552 mm (Xu et al., 2020). Macrobenthos samples were
120 collected in the intertidal zone of the YRD during March (winter), May (spring),
121 August (summer) and November (autumn) in 2013. Three sampling transects were
122 designed in the *S. alterniflora* (SA) and *S. glauca* (SG) habitats. The *S. alterniflora*
123 community was distributed in the northern part of the YRD, with an area of 0.6 ha
124 (Fig. 1c). The *S. glauca* community was located in the southern part of the YRD, with
125 an area of 150 ha (Fig. 1d). In total, there were 19 and 15 sampling sites in the SA and



126

127 **Fig. 1.** Study areas (a: Bohai Sea, Yellow Sea and East China Sea in China; and b: YRD) and
 128 sampling sites in the *S. alterniflora* (SA, c) and *S. glauca* (SG, d) habitats.

129 SG habitats, respectively. Three replicate samples were collected at each location,
 130 with a 50 cm × 50 cm quadrat plot at each site for quantitative analysis, and the
 131 sampling depth was approximate 30 cm. Sediments were washed through a 500 μm
 132 mesh sieve to collect macrobenthos, and all samples were immersed in 95% ethanol
 133 until laboratory identification. The specimens were sorted using a dissecting
 134 microscope (30×), and the number of each species was counted as the abundance. All
 135 macrobenthos of each species were weighed using a 0.01 g precision electric balance
 136 as the biomass. Finally, the macrobenthos species numbers were counted.

137 Seawater samples were collected near the intertidal zone in three replicates
 138 during the sampling times. Seawater temperature and salinity were measured using a

139 YSI 30 portable metre (YSI, USA). The sediments used for grain size, TOC, TN and
140 Chl-*a* concentration analysis were collected with a plastic sampler with a 3 cm
141 diameter and 5 cm height. Three replicate samples were collected at each site. The
142 grain sizes of the sediment samples were analysed using a Mastersizer 2000 Laser
143 Particle Sizer (Malvern, UK). TOC and TN were measured using an elemental
144 analyser (Flash EA1112 Thermo Scientific, Italy). The Chl-*a* concentrations in the
145 sediments were measured by a fluorometer (Shimadzu, Japan) after extraction with
146 15 ml of 90% and refrigeration in the dark for 24 h (Wang, 1986).

147 **2.2. Data analyses**

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

$$150 \quad IV_i = \left(\frac{n_i}{N} \right) \times f_i$$

151 n_i : each macrobenthos species abundance,

152 N : total species abundance,

153 and f_i : the proportion of each macrobenthos species occurring in all quadrats.

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

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

$$158 \quad H' = - \sum_{i=1}^S P_i \times \log_2 P_i$$

159 S : number of macrobenthos species,

160 and P_i : the proportion of each macrobenthos species in the total macrobenthos
161 abundance.

162 The macrobenthic species numbers, abundances, H' values, biomass amounts,

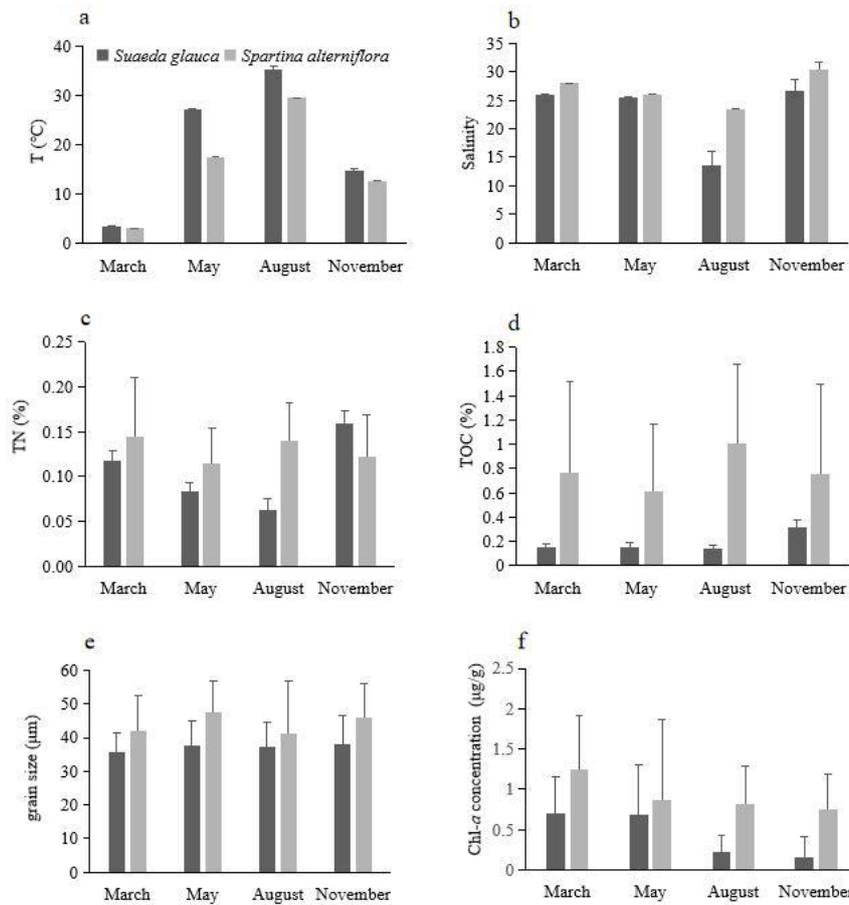
163 environmental parameters and Chl-*a* concentration differences in each habitat in four
164 seasons, between both habitats, and correlation analyses between macrobenthos
165 abundances, H' values, biomass amounts, and the environmental parameters, Chl-*a*
166 concentrations in each habitat were separately analysed according to one-way analysis
167 of variance (ANOVA) and post hoc tests, paired-sample T tests, and Pearson's
168 correlations in a 2-tailed test using Statistical Product and Service Solutions (SPSS)
169 11.5 software. The data are presented as the means (\pm SE), and a significance level of
170 5% was used in all analyses.

171 **3. Results**

172 ***3.1. Environmental parameters and Chl-a concentrations between the two habitats***

173 The seawater temperatures significantly varied among months in SA
174 ($F=25452.490$; $p<0.001$). The lowest ($3.20\pm 0.01^{\circ}\text{C}$) and highest ($29.63\pm 0.02^{\circ}\text{C}$)
175 values were recorded in March and August, respectively (Fig. 2a). The seawater
176 salinities exhibited significant seasonal changes in SA ($F=95.311$; $p<0.001$). The
177 lowest value (23.48 ± 0.02) occurred in August, and the highest value (30.47 ± 1.15)
178 occurred in November (Fig. 2b). The TN levels in the sediments were not
179 significantly different in SA seasonally ($F=1.313$; $p=0.280$). The highest TN occurred
180 in November ($0.15\pm 0.07\%$), and the lowest TN occurred in August ($0.11\pm 0.04\%$) in
181 SA (Fig. 2c). The TOC in the sediments did not exhibit significant seasonal changes in
182 SA ($F=0.682$; $p=0.567$). The lowest TOC value ($0.62\pm 0.55\%$) was recorded in May,
183 and the highest ($1.00\pm 0.65\%$) was recorded in August (Fig. 2d). The grain sizes of the
184 sediments were significantly different across seasons in SA ($F=3.598$; $p=0.014$). The
185 highest ($47.48\pm 9.38\ \mu\text{m}$) and lowest ($41.04\pm 15.95\ \mu\text{m}$) values were recorded in May
186 and March, respectively (Fig. 2e). In SA, the grain sizes of the sediments were
187 significantly different in their spatial distributions for each season (March: $F=19.751$;

188 $p < 0.001$, May: $F = 34.187$; $p < 0.001$, August: $F = 18.707$; $p < 0.001$, and November:
 189 $F = 26.906$; $p < 0.001$), which may be because sediment samples were collected in both
 190 *S. alterniflora* wetlands and bare mudflats. The Chl-*a* concentrations of the sediments
 191 were significantly different across seasons in SA ($F = 3.041$; $p = 0.030$), with the highest
 192 value ($1.25 \pm 0.66 \mu\text{g/g}$) in March and lowest value ($0.75 \pm 0.44 \mu\text{g/g}$) in November (Fig.
 193 2f).



194

195 **Fig. 2.** Environmental parameters and Chl-*a* concentrations of sediments at the two sampling sites
 196 in 2003 (a: temperature, b: salinity, c: TN, d: TOC, and e: grain size; f: Chl-*a* concentration,
 197 seawater temperature and salinity data in March were missing, so we referred to the data from Li
 198 (2000).).

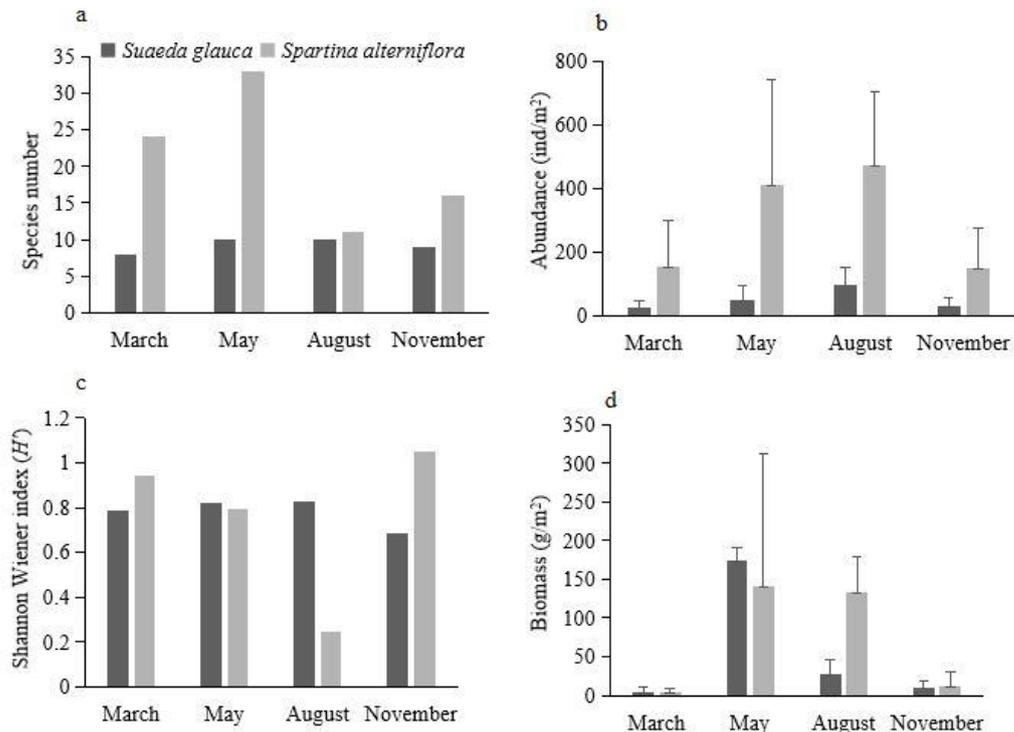
199 The seawater temperatures significantly varied among months in SG
 200 ($F = 1491.141$; $p < 0.001$). The lowest ($3.6 \pm 0.00^\circ\text{C}$) and highest ($35.2 \pm 0.74^\circ\text{C}$) values
 201 were recorded in March and August, respectively (Fig. 2a). The seawater salinities

202 displayed significant seasonal changes in SG ($F=36.084$; $p<0.001$). The lowest value
203 (13.49 ± 2.58) occurred in August, and the highest value (26.62 ± 1.94) occurred in
204 November (Fig. 2b). The TN levels in the sediments significantly differed across
205 seasons in SG ($F=201.300$; $p<0.001$). The highest TN was in November
206 ($1.16\pm 0.01\%$), and the lowest TN was in August ($0.06\pm 0.01\%$) (Fig. 2c). The TOC
207 values in the sediments were significantly different across seasons in SG ($F=83.038$;
208 $p<0.01$). The lowest value ($0.14\pm 0.03\%$) was recorded in August, and the highest
209 ($0.32\pm 0.05\%$) was recorded in November in SG (Fig. 2d). The grain sizes of the
210 sediments were significantly different among months in SG ($F=20.031$; $p<0.001$). The
211 lowest ($35.79\pm 5.51\ \mu\text{m}$) and highest ($37.45\pm 7.48\ \mu\text{m}$) values were recorded in March
212 and May, respectively (Fig. 2e). There were no significant differences in the spatial
213 distributions of each season (e.g., March: $F=1.965$; $p=0.153$, May: $F=2.918$; $p=0.065$,
214 August: $F=2.183$; $p=0.125$, November: $F=0.641$; $p=0.529$) in SG. The Chl-*a*
215 concentrations in the sediments were not significantly different in SG ($F=0.944$;
216 $p=0.420$), with the highest value ($0.71\pm 0.45\ \mu\text{g/g}$) in March and the lowest value
217 ($0.15\pm 0.25\ \mu\text{g/g}$) in November (Fig. 2f).

218 The TN ($t=1.023$; $p=0.381$), temperature ($t=-2.207$; $p=0.114$), and salinity
219 ($t=1.957$; $p=0.145$) values did not show significant differences between the two
220 habitats, although the temperatures in SG were higher than those in SA (Fig. 2a), and
221 the salinities in SG were lower than those in SA (Fig. 2b). The TOCs ($t=6.028$;
222 $p=0.009$), grain sizes ($t=5.295$; $p=0.013$) and Chl-*a* concentrations ($t=4.884$; $p=0.016$)
223 in the sediments were significantly higher in SA than in SG (Fig. 2d, e & f).

224 **3.2. The macrobenthos between two habitats**

225 Along the sampling sites in the YRD, 47 macrobenthic taxa were identified,
226 including 22 polychaeta, 14 crustacea and 11 mollusca (Table A1). A total of 39



227

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

230 macrobenthic taxa were identified in SA (Table A1). The lowest value (11) occurred

231 in August, and the highest value (33) occurred in May (Fig. 3a). The macrobenthic

232 abundances significantly varied among months in SA ($F=7.205$; $p<0.001$). The

233 abundances in August were higher than those in May and were higher than those in

234 March and November in SA (Fig. 3b). The highest (470.7 ± 234.6 ind/m²) and lowest

235 (148.0 ± 127.0 ind/m²) abundances were observed in August and November,

236 respectively (Fig. 3b). The H' values are shown in Fig. 3c. The highest H' value was

237 1.05 in November, and the others were less than 1 in SA (Fig. 3c). The lowest H'

238 value (0.24) was recorded in August in SA (Fig. 3c). The dominant species that were

239 recorded at each site per month are shown in Table A2. In SA, *Cerithidea cingulata*

240 was the only dominant species in August and accounted for 88% of the total

241 abundance, which was greater than for the other species in May and accounted for 58%

242 of the total abundance (Table A2). *Moerella iridescens* was the dominant species in all
243 months at each site except for August in SA (Table A2). The macrobenthic biomass
244 amounts were significantly different across seasons in SA ($F=8.235$; $p<0.001$). The
245 lowest value (4.72 ± 5.15 g/m²) was recorded in March, and the highest value
246 (141.6 ± 171.2 g/m²) was recorded in May (Fig. 3d). In SA, the functional groups of
247 macrobenthos showed significant seasonal changes, and the abundances shifted from
248 polychaeta (68%) in spring to mollusca (97%) in autumn (Fig. 4A). The crustacean
249 abundances accounted for the lowest proportion in all months and accounted for only
250 2~4% (Fig. 4A). In SA, the mollusca biomass accounted for the greatest proportion in
251 all months (Fig. 4B) and accounted for 61-97% of the total (Fig. 4B).

252 A total of 18 macrobenthic taxa were identified in SG (Table A1). The highest
253 species number (10) was observed in May and August in SG, and the lowest species
254 number (8) was observed in March (Fig. 3a). The abundances significantly varied
255 across seasons in SG ($F=11.120$; $p<0.001$). The abundance in August was higher than
256 that in May and was higher than those in November and March in SG (Fig. 3b). In SG,
257 the highest (95.7 ± 54.9 ind/m²) and lowest (22.8 ± 24.4 ind/m²) abundances were
258 observed in August and March, respectively (Fig. 3b). The H' values were less than 1
259 in SG (Fig. 3c). *Perinereis aibuhitensis* was the dominant species in all months in SG,
260 greater than those of the other species in August and November, which separately
261 accounted for 36.21% and 48.52%, respectively, of the total abundance (Table A2). *M.*
262 *iridescens* was the dominant species in all months except for May in SG (Table A2).
263 The macrobenthos biomass amounts significantly differed among months in SG
264 ($F=8.543$; $p<0.001$), with the highest biomass in May (175 ± 15.9 g/m²) and the lowest
265 in March (3.61 ± 7.35 g/m²) (Fig. 3d). In SG, the macrobenthos biomass was
266 dominated by crustacea (63-86%), mollusca (1-25%) and polychaeta (9-13%) (Fig.

267 5B). In May, the mollusca biomass accounted for the lowest proportion (1%) in SG
 268 (Fig. 5B-b).

269 The macrobenthos abundances were significantly greater seasonally in SA than
 270 in SG (Fig. 3a, $t=1.687$; $p=0.047$). The species numbers ($t=2.421$; $p=0.094$), H' values
 271 ($t= -0.112$; $p=0.918$) and biomass amounts ($t=0.640$; $p=0.568$) were not significantly
 272 different seasonally between the two habitats. The species numbers of macrobenthos
 273 were higher in SA than in SG (Fig. 3a). The macrobenthic biomass was greater in SA
 274 than in SG in all sampling months except for May (Fig. 3c). In both habitats, *M.*
 275 *iridescens* was the dominant species in all months except for August in SA and May
 276 in SG (Table A2).

277 **3.3. Relationships between macrobenthos and environmental variables, Chl-a**
 278 **concentration**

279 The abundances, H' values and biomass amounts of macrobenthos were not
 280 significantly related to the environmental variables or Chl-a concentrations in SA
 281 (Table 1). The macrobenthos abundances in SG were significantly negatively related
 282 to seawater salinities (Table 1). The H' values of macrobenthos had significantly
 283 negative relationships with sediment TN and TOC in SG (Table 1).

284 Table 1 Relationships between macrobenthos parameters and environmental variables, Chl-a
 285 concentrations at the two sampling locations

	<i>S. alterniflora</i> habitat			<i>S. glauca</i> habitat		
	abundance	H'	biomass	abundance	H'	biomass
Temperature	0.872	-0.872	0.817	0.898	0.502	0.451
Salinity	-0.915	0.931	-0.845	-0.955**	-0.531	0.161
TOC	0.301	-0.753	0.132	-0.491	-0.967**	-0.307
TN	-0.165	-0.320	-0.320	-0.828	-0.953**	-0.432
Grain size	-0.088	0.576	0.085	0.216	-0.422	0.243
Chl-a	-0.143	0.269	-0.443	-0.350	0.518	0.478

286 ** Correlations are significant at the 0.05 level (two-tailed)

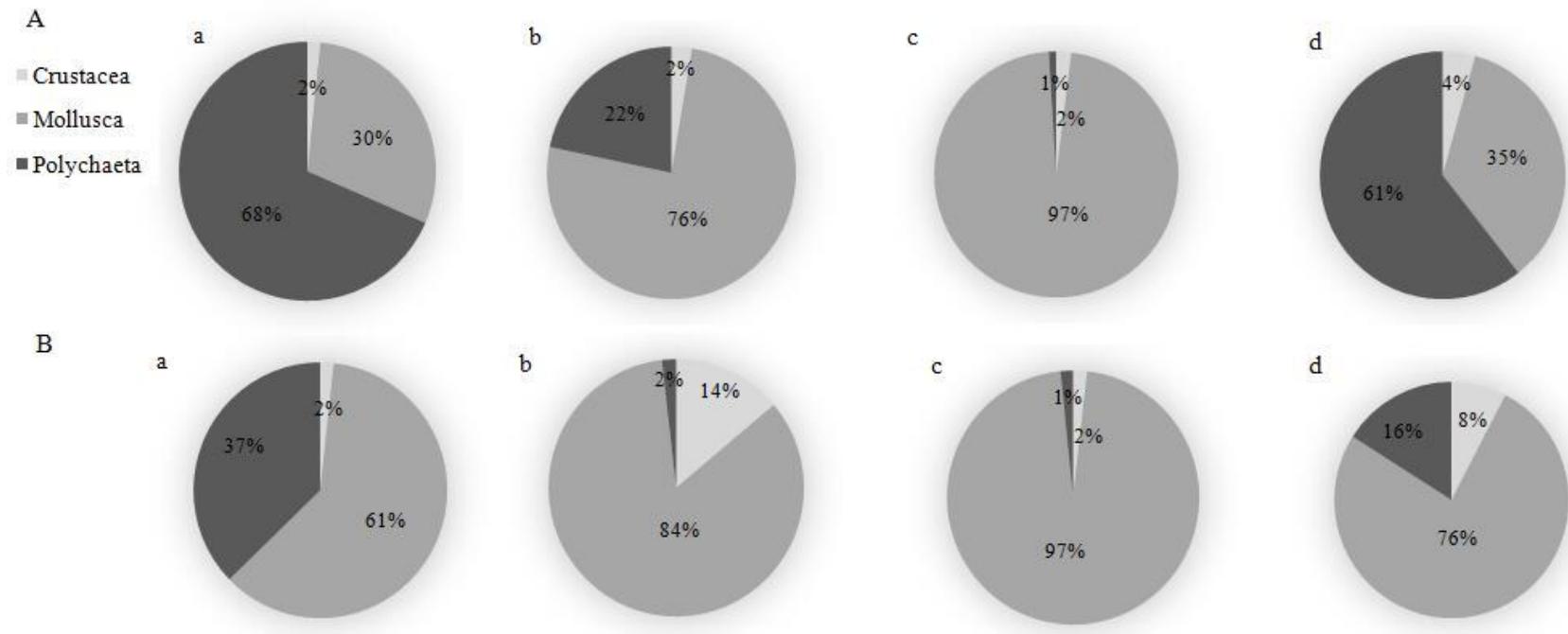


Fig. 4. Different macrobenthos taxa proportions of the abundances (A) and biomass (B) in the SA habitat (a: March, b: May, c: August, and d: November).

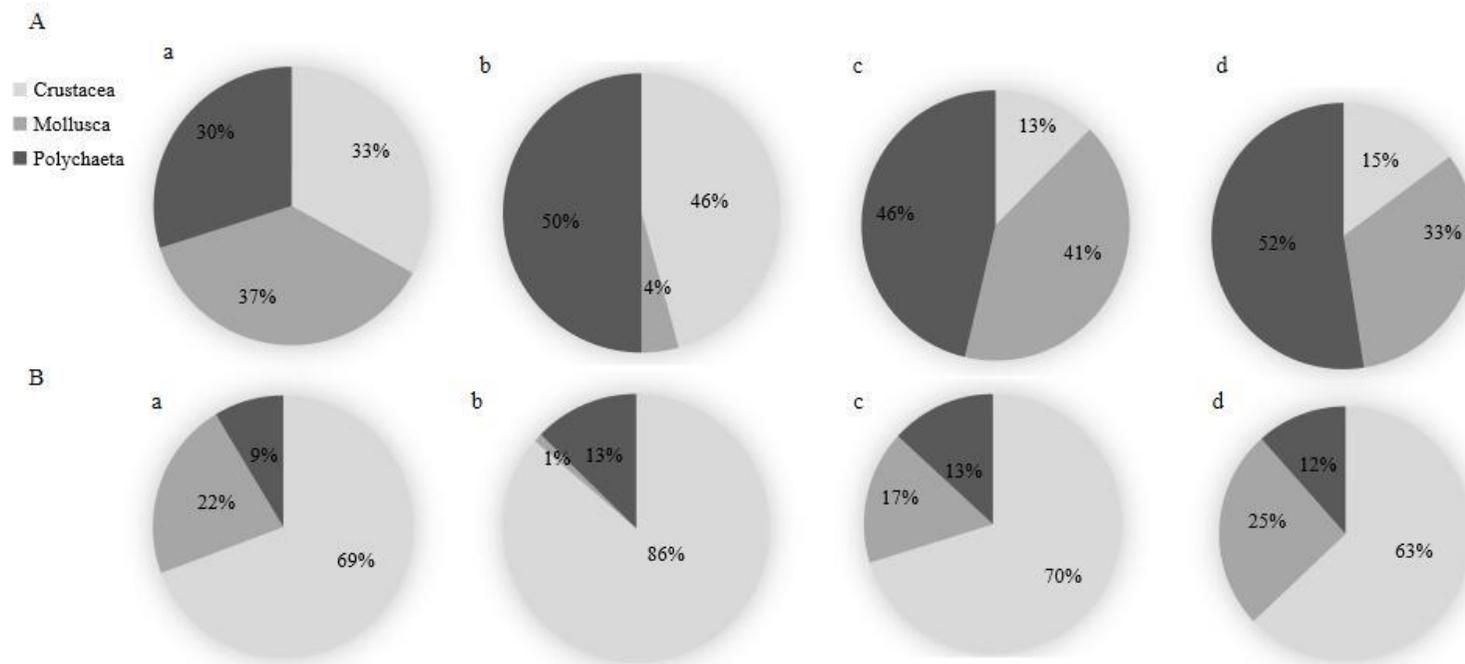


Fig. 5. Different macrobenthos taxa proportions of the abundances (A) and biomass (B) in the SG habitat (a: March, b: May, c: August, and d: November).

292 4. Discussion

293 This study provides the first comprehensive investigation of the differences in
294 intertidal macrobenthos communities between the invasive *S. alterniflora* and native *S.*
295 *glauca* habitats in the YRD, China. The functional macrobenthos groups in the *S.*
296 *alterniflora* habitat exhibited significant seasonal changes and shifted from polychaeta
297 (68%) in spring to mollusca (97%) in autumn; however, in the *S. glauca* habitat, the
298 functional macrobenthos groups were dominated by crustacea (63-86%), mollusca
299 (1-25%) and polychaeta (9-13%), and only mollusca showed obvious seasonal
300 changes (Fig. 5). The *S. glauca* habitat supported lower abundances (29~96 ind/m²)
301 than the *S. alterniflora* habitat (148~471 ind/m², Fig. 3b), and the latter values were
302 higher than the macrobenthos abundances in the mudflats of the YRD (210 ind/m² in
303 spring and 108 ind/m² in autumn, Wang et al., 2010), but were lower than *S.*
304 *alterniflora* habitat in the Changjiang estuary, China (286~553 ind/m², Xu et al., 2006;
305 1599 ind/m², Quan et al., 2016).

306 Seasonal changes have key impacts on the macrobenthos distributions in salt
307 marsh habitats (Tang and Kristensen, 2010). In our study, higher macrobenthos
308 biomass amounts occurred in spring and summer (Fig. 3d), which were mainly due to
309 more food sources from the leaves and stems of plants in the growing seasons (Zhou
310 et al., 2009; Tang and Kristensen, 2010). The lower autumn and winter temperatures
311 could limit the growth and reproductive efficiency of macrobenthos (Grilo et al.,
312 2011). Moreover, benthic microalgae in salt marsh habitats may promote
313 macrobenthos growth as food sources (Takai et al., 2002; Yoshino et al., 2006;
314 Yoshino et al., 2012). Our study also found that the Chl-*a* concentrations reached their
315 highest values in March in both SA and SG (Fig. 3). Therefore, the macrobenthos
316 biomass amounts reached their highest values in May through the growth period after

317 March and April. Dense aboveground canopies may reduce light availability and
318 subsequent benthic microalgal development, which would thus inhibit macrobenthos
319 grazers in summer in comparison with spring (Lana and Guiss, 1991).

320 The functional macrobenthos groups in our study in *S. alterniflora* habitats were
321 obviously different from those in *S. glauca* habitats. That is, the mollusca biomass
322 was the largest in SA in all sampling months (Fig. 5B), which indicated that *S.*
323 *alterniflora* plays an important role in dense bivalve mollusca populations as a result
324 of their ground dead leaves and stems (Ward et al., 1997; Brusati and Grosholz, 2006;
325 Quan et al., 2016). In contrast, crustacean biomass accounted for the largest
326 proportion in all months in SG (Fig. 6B), which was the first study in *S. glauca*
327 habitats. *Bullacta exarata*, *Macrophthalmus* (Mareotis) *japonicus*, *Perinereis*
328 *aibuhitensis* and *P. laevis* were the dominant species at both sampling sites (Table A2),
329 which is in accordance with other reports for *S. alterniflora* habitats (Cai and Tian,
330 2000; Wang et al., 2010; Leng et al., 2013; Gao et al., 2014) and *Suaeda japonica*
331 habitats (Bon et al., 2011). *Helice* sp. was present but was not the dominant species in
332 SA, while it was the dominant species in SG (Table A1 & A2), which disagreed with
333 the results of Cui et al. (2011), who found that *S. alterniflora* invasions enhanced the
334 abundances of *Helice* sp. *B. exarata* and *P. laevis* are superior feed for aquaculture in
335 the YR estuary. Fishermen collected them in the intertidal zones in spring and summer;
336 thus, their densities changed more than those of other species (Leng et al., 2013). *B.*
337 *exarata* was introduced to the YR estuary in 2001 (Leng et al., 2013), which indicated
338 that this species adapted to local conditions.

339 Sediment rugosity and hydrodynamics are two main driving factors that structure
340 macrobenthos communities (Yu et al., 2020). The aboveground biomass and litter
341 production of *S. alterniflora* and *S. glauca* plants can slow water currents and waves,

342 and thus decrease water velocities (Yang et al., 2012), which could promote fine
343 particle sedimentation from the water column to the surface sediments (Quan et al.,
344 2016) and have positive effects on mass loss and nutrient release (Yin et al., 2019). In
345 our study, the grain sizes of the sediments in SA were 41~47 μm , higher than those in
346 SG (36~37 μm) for all sampling months (Fig. 2e), which means that the sediments
347 consisted of clay in both sampling habitats, according to Folk et al. (1970). Such
348 amelioration of sediments may support crustacea survival (e.g., *Helice* (H.),
349 *tridenssheni*), which was the dominant species in SG. According to the literature (e.g.,
350 Neira et al., 2006; Brusati and Grosholz, 2007; Xie and Gao, 2013; Gao et al., 2014),
351 finer sediments were favourable for macrobenthos adaptation to intertidal habitats,
352 such as *C. cingulata*, *M. iridescens* and *M. japonicus* (Table A2). Furthermore,
353 detritivorous polychaetes are suitable for habitats with higher rugosity, such as SA,
354 because of their capacity to intercept the increased organic matter that is available in
355 the water (Yu et al., 2020). The higher water velocities that result from shorter plants
356 in SG habitats may promote the recruitment and growth of some crustaceans
357 compared with slower-velocity habitats such as SA due to the flow rate effects on the
358 delivery of planktonic larvae to the substrate (Leonard et al., 1998), which is in
359 agreement with the study by Graham and Sebens (1996), who found that the larvae of
360 barnacles were well mixed in the water column at higher flow rates.

361 The vegetation structures in salt marshes support important habitats for
362 macrobenthos by altering the organic content in sediments (Valiela et al., 1984; Sueiro
363 et al., 2011). Invasive marsh plants often outcompete native plants due to their higher
364 growth rates (Li et al., 2009b; Quan et al., 2016), which indicates that the higher
365 above- and belowground biomass of *S. alterniflora* gives rise to higher organic carbon
366 contents in the sediments and consequently fosters benthic food webs (Zhou et al.,

367 2009; Page et al., 2010; Wang et al., 2014). Many studies have implied that higher
368 organic matter contents in sediments are related to increased macrobenthos densities
369 (e.g., Sacco et al., 1994; Levin et al., 1996; Craft, 2000). For example, Levin et al.
370 (1998) found that there were significant positive associations between macrobenthos
371 abundances and TOC in the *Spartina* sp. habitats of the California coast, USA, where
372 the TOC in sediments was 2.4~25.9%. The range of surface organic carbon contents
373 of the sediments in the YRD was 0.06~0.40% (Yu, 2014). Our results showed that the
374 TOC of sediments in SA was 0.62~1.00% (Fig. 2d), which was in the middle range
375 for the *S. alterniflora* salt marshes on the coast of China (0.08~1.7%, Meng et al.,
376 2020), which indicated that *S. alterniflora* provided more organic carbon to sediments
377 as a result of its faster leaf growth, especially in flooding seasons (Levin, 1998),
378 although *S. alterniflora* was still in the early stage of its invasion in the YRD (Cui et
379 al., 2011).

380 In our study, the TN contents of sediments were 0.06~1.16% in SG (Fig. 2c),
381 which were lower than those of the *S. glauca* habitats on the coast of South Korea
382 (2.1%, Lee et al., 2016). According to the study by Cai et al. (2002), lower H' values
383 of macrobenthos (especially less than 1) indicated a serious pollution status. Normally,
384 macrobenthos that are tolerant to low dissolved oxygen concentrations can be thought
385 of as pollution indicator species (Pearson and Rosenberg, 1978). *Haploscoloplos*
386 *elongates* was present in SG (Table A1) and was also the dominant species in autumn
387 and winter in SA (Table A2), which can be viewed as a pollution indicator species
388 (Grizzle, 1984). There were higher TN levels in the sediments in SA (0.11~0.15%, Fig.
389 2c) than in the *S. alterniflora* marshes on the coast of North Carolina, USA (0.02~1.1%
390 within 21 years after restoration; Craft, 2000), which indirectly demonstrated that *S.*
391 *alterniflora* plants have high nitrogen contents (Gao et al., 2014; Meng et al., 2020),

392 although salt marshes are N limited owing to N regulating the development of
393 macrobenthos communities (e.g., Broome et al., 1975; Valiela and Teal, 1974). The N
394 contents of plant roots, stems and leaves were 0.41~1.43% in SA and 0.63~3.25% in
395 SG in the four seasons (our unpublished data) also indicated higher nitrogen sources
396 from salt marsh plants into sediments. The YR estuary was at risk of eutrophication
397 together with an increased marine aquaculture area (Liu et al., 2009). Dissolved
398 inorganic nitrogen pollution in the seawater was serious near the YR estuary (Zhang
399 et al., 2012), which could impact *S. alterniflora* and *S. glauca* growth (Meng et al.,
400 2020) and consequently alter macrobenthos diversity.

401 Due to highly seasonal freshwater inputs, the salinity values exhibited broad
402 fluctuations in estuarine areas (Evin and Talley, 2000). In this study, the macrobenthos
403 abundances in SG were significantly negatively related to seawater salinities (Table 1).
404 This relationship was different from studies that reported that reduced salinity led to
405 decreased abundances and species richness in salt marsh habitats such as the Tijuana
406 Estuary, USA (Nordby and Zedler, 1991), California coast, USA (Levin et al., 1998),
407 Paranaguá Bay, Brazil (Lana et al., 1997) and St. Lucia estuary in South Africa (Pillay
408 and Perissinotto, 2008). Li et al. (2016) and Yang et al. (2019) also reported that
409 freshwater release reduced salinity, which thus altered macrobenthos densities and
410 diversities in the YR estuary. How seawater salinity impacts macrobenthos growth
411 and species distributions needs more research.

412 **5. Conclusions**

413 Understanding the ecosystem functions of salt marsh habitats is important for the
414 sustainable management of coastal zones. Our research determined that the
415 macrobenthos functional groups in the invasive *S. alterniflora* habitat were simpler
416 and more sensitive to environmental changes than those in the native *S. glauca* habitat,

417 although the former obviously supported higher benthic abundances and species
418 numbers in comparison with the latter in the YRD. The vegetation structures of *S.*
419 *alterniflora* and *S. glauca* habitats may result in differences in macrobenthos
420 distributions in both habitats, which has not been indicated using field data of
421 macrobenthos abundances and environmental factors. The long-term mechanisms by
422 which *S. alterniflora* and the *S. glauca* community structures impact macrobenthos
423 distributions need further study through more field investigations and transplanting
424 experiments for the sustainable management of salt marshes at different locations.

425 **Declarations**

426 **Conflict of interest** The authors declare that they have no conflict of interest.

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671 Appendix to: Comparison of macrobenthic communities between the *Spartina alterniflora* and *Suaeda glauca* habitats in the Yellow River Delta

672 3.2 Comparison of macrobenthos between *S. alterniflora* and *Suaeda glauca* habitats

673 Table A1 All macrobenthos species at both sampling sites.

674 Table A2 Dominant macrobenthos species at both sampling sites.

675 *Table A1 Macrobenthic species identified in the S. alterniflora and S. glauca habitats of the YRD*

Taxa	Species	SA	SG
Crustacea	<i>Cirolana japonensis</i>	✓	
	<i>Corophium sinensis</i>	✓	✓
	<i>Diastylis tricineta</i>	✓	
	<i>Gammarus</i> sp.		✓
	<i>Helice</i> (H.) <i>tientsinensis</i>		✓
	<i>Helice</i> (H.) <i>tridenssheni</i>	✓	✓
	<i>Hemigrapsus penicillatus</i>	✓	

	<i>Hemigrapsus sanguineus</i>	✓	
	<i>Hyale</i> sp.	✓	
	<i>Macrophthalmus</i> (Mareotis) <i>japonicus</i>	✓	✓
	<i>Melita palmata</i>	✓	
	<i>Neomysis auatschensis</i>		✓
	<i>Orchestia</i> sp.	✓	
	<i>Trachypenaeus curvirostris</i>		✓
Mollusca	<i>Bullacta exarata</i>		✓
	<i>Cerithidea cingulata</i>	✓	
	<i>Crassostrea gigas</i>	✓	
	<i>Dosinia corrugata</i>	✓	
	<i>Glaucanome primeana</i>	✓	✓
	<i>Mactra chinensis</i>	✓	

	<i>Moerella iridescens</i>	✓	✓
	<i>Moerel larutila</i>		✓
	<i>Nitidotellina minuta</i>		✓
	<i>Potamocorbula laevis</i>	✓	✓
	<i>Trapezium liratum</i>	✓	
Polychaeta	<i>Amphinome rostrata</i>	✓	
	<i>Capitelle capitata</i>	✓	
	<i>Chaetozone setosa</i>	✓	
	<i>Cirratulus chrysoderma</i>	✓	
	<i>Diopara bilobata</i>	✓	
	<i>Diopatra chiliensis</i>	✓	
	<i>Eteone longa</i>	✓	
	<i>Glycera chirori</i>	✓	

<i>Glycinde gurjanovae</i>	✓	✓
<i>Goniada japonica</i>	✓	
<i>Goniada maculata</i>	✓	
<i>Haploscoloplos elongatus</i>	✓	✓
<i>Heteromastus filiformis</i>	✓	✓
<i>Lumbrineris heteropoda</i>	✓	
<i>Lumbrineris latreilli</i>	✓	
<i>Lumbrineris tetraura</i>	✓	
<i>Nemertinea</i> sp.		✓
<i>Paraprionospio pinnata</i>	✓	
<i>Perinereis aibuhitensis</i>	✓	✓
<i>Perinereis nunlia</i>	✓	
<i>Pseudopolydora kemp</i>	✓	

	<i>Typosyllis armillaris</i>	√	
	<i>Totals</i>	39	18

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Table 2 Dominant macrobenthos species at both sampling sites and their percentages of the total abundance (%)

Taxa	Species	SA				SG			
		March	May	August	November	March	May	August	November
Crustacea	<i>Helice (H.) tridenssheni</i>						20.54		5.94
	<i>Macrophthalmus (Mareotis) japonicus</i>							11.70	8.91
	<i>Neomysis auatschensis</i>					25.78			
Mollusca	<i>Bullacta exarata</i>							12.81	18.81
	<i>Cerithidea cingulata</i>		58.27	87.99	12.84				
	<i>Moerella iridescens</i>	25.48	9.83		11.26	17.53		11.98	9.90
	<i>Potamocorbu lalaervis</i>								1.98
Polychaeta	<i>Glycinde gurjanovae</i>	18.41							
	<i>Haploscoloplos elongatus</i>	07.95			11.71				
	<i>Heteromastus filiformis</i>						23.79		
	<i>Lumbrineris latreilli</i>	19.73			13.73				

<i>Lumbrineris tetraura</i>	2.92					
<i>Paraprionospio pinnata</i>	8.25	11.94				
<i>Perinereis aibuhitensis</i>	4.57	8.11	22.68	20.05	36.21	48.52

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