Consumer control and abiotic stresses constrain coastal saltmarsh restoration

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Highlights

- China's largest coastal saltmarsh plantation project was initiated in the Liaohe Estuary.
- The restoration effect of planted *Suaeda salsa* was better in low restored site than that in high restored site.
- The death of planted *Suaeda salsa* is primarily driven by herbivory, followed by abiotic stresses in high restored site, whereas plant death is only driven by herbivore in low restored site.
- Consumer control should be considered to enhance the success of coastal restoration.

Abstract

Die-off of coastal wetlands has been reported worldwide. Planting habitat-forming species is an important strategy to reverse the decline of coastal wetlands. However, how abiotic environmental stresses and consumers the establishment of the planted vegetation species is unclear. We reported a large-scale restoration project in the Liaohe estuary, China, where the native pioneer plant *Suaeda salsa* was planted. We evaluated the performance of the planted *S. salsa*, and examined the relationships between the establishment of *S. salsa* and abiotic and biotic factors. Results showed that the performance (density, coverage and survival rate) of planted *S. salsa* was higher in the low elevation marsh than that in the high elevation marsh. *S. salsa* dieback was primarily driven by crab herbivory, followed by abiotic stresses (low soil moisture and high salinity) in the high marsh, whereas dieback was only driven by crab herbivory in the low marsh. Herbivory strength in the high marsh was significantly higher than that in the low marsh. Moreover, Soil moisture content and flooding frequency were strongly and positively correlated with plant performance. However, soil porewater salinity, density and biomass of crabs, and herbivory strength was strongly and negatively correlated with plant performance. Our findings challenge the bottom-up paradigm used as the foundation for coastal restoration, and highlight the overlooked role of consumers. Therefore, protection measures against consumers pressure, especially in physically harsh conditions, should be considered to enhance the success of coastal wetland restoration.

Keywords: Liaohe Estuary; *Suaeda salsa*; Coastal restoration; Bottom-up paradigm; Top-down control; Herbivory

1. Introduction

Coastal saltmarshes are one of the most productive ecosystems on earth and provide valuable ecological and economic services to humans, such as food production, water purification, carbon sequestration, coastal protection and recreation (Costanza et al., 1997; Deegan et al., 2012). In recent decades, however, coastal saltmarshes have suffered extensive loss, degradation and fragmentation due to anthropogenic activities and climate change (Lotze et al., 2006; He et al., 2019; Murray et al., 2019). Coastal restoration has been implemented in several countries to stop and reverse the degradation of coastal saltmarshes, and to enhance ecosystem persistence and functioning (Temmerman et al., 2013; Liu et al., 2016; Bayraktarov et al., 2016).

Planting habitat-forming species is one of the adopted techniques to accelerate the recovery of saltmarshes, to facilitate ecological succession, to increase sediment accretion and biodiversity, and to enhance ecosystem services (Silliman et al, 2015; Zedler, 2003; Morgan & Short, 2002; Benayas et al., 2009; Curado et al., 2014). However, saltmarshes restoration using plantation is complex since target species and limiting factors vary from place to place (see Table 1). Moreover coastal saltmarshes are characterized by harsh environmental stresses for plant survival, establishment and growth, such as wind, waves, flooding and soil salinity (Castillo et al., 2000; Silliman et al, 2015; Hu et al., 2015). Biotic factors, like plant competition, consumer control and facilitation, are also critical to plant recovery after disturbance (Armitage et al., 2006; He & Silliman, 2016; Derksen-Hooijberg et al., 2018). Because of these stresses, the success of saltmarsh restoration projects is not always granted, and restoration attempts often result in failure (Wolters et al, 2005). Consequently, a better understanding of the main factors limiting the success of vegetation planting is essential for salt marsh restoration projects.

Clearly, favorable abiotic environmental conditions and biotic interactions are essential for the successful establishment and persistence of salt marsh plants (Lambers et al., 2008; Friess et al., 2012). Most research on saltmarsh plantation has focused on abiotic environmental factors affecting successful plant recruitment (Table 1). Handa

& Jefferies (2000) and O'Brien and Zedler (2006) suggested that fertilizer has a strong, positive influence on vegetation establishment. Sloey et al. (2015) indicated that a larger vegetation expansion occurred in transplant sites characterized by a short duration of flooding. Burchett et al., (1999), Dawe et al., (2000) and Castillo et al., (2008) suggested that substrate elevation was a major influence on the successful establishment and subsequent dynamics of recreated marsh communities. Zhang et al., (2020) indicated that water level was the most critical environmental factor limiting *Scirpus mariqueter* performance, followed by salinity.

However, the success of saltmarsh plantation also depends on biotic factors and species interactions. Armitage et al., (2006) found that *Salicornia virginica* was shorter when planted with *Juncus carnosa* than that when planted alone, due to competition between the two species. In a two-year field study, Beck and Gustafson, (2012) found that locally collected *Spartina alterniflora* from adjacent saltmarshes had higher plant performance than plants from non-local sources. In addition, propagule types also affect the plantation success. Sloey et al., (2015) revealed that transplanted adults outperformed rhizomes. Similarly, Zhang et al., (2020) proposed that planting with corm shoots outperformed plantlets and seedlings.

Table 1 Coastal saltmarsh restoration projects/experiments using planting and the factors limiting the establishment of plants. Bold fonts indicate biotic factors.

Site	Species	Factors	Reference
Sydney, Australia	*Sarcocornia Quinqueflora* (Bunge ex Ung.-Sternb) A. J. Scott, *Suaeda australis* (R. Br.) Moq., *Wilsonia Backhousei* Hook. f. *Lampranthus tegens* (F. Muell.) N. E. Br., and *Halosarcia Pergranulata* (J. Black) Paul G. Wilson	elevation, soil characteristics (water content, salinity, pH and organic content)	Burchett et al., 1999
Campbell River estuary, Canada	*Carex lyngbyei* Hornem., *Juncus balticus* Willd., *Potentilla pacifica* Howell, *Deschampsia caespitosa* (L.) P. Beauv., *and Eleocharis palustris* (L.) Roem.	elevation	Dawe et al., 2000

	& Schult.		
Hudson Bay, Canada	*Puccinellia phryganodes* (Trin) Scribn. & Merr., and *Carex subspathacea* Wormskj	soil nutrient (total soil carbon, total soil nitrogen)	Handa & Jefferies, 2000
Pamlico River estuary, USA	*Spartina alterniflora* Loisel and *Juncus roemerianus* Scheele	elevation and tidal inundation	Craft et al., 2002
Tijuana Estuary, USA	*Salicornia virginica* C. Linnaeus, *Salicornia bigelovii* Torr., *Batis maritima* C. Linnaeus, *Frankenia salina* (Molina) I. M. Johnst., *Jaumea carnosa* (Less.) A. Gray, *Suaedaesteroa* Ferren & S. A. Whitmore, *Triglochin concinna* Burtt Davy, and *Limonium californicum* (Boiss.) A. Heller	elevation and **plant species richness**	Lindig-Cisneros & Zedler 2002
Tidal Linkage and Friendship Marsh, USA	*Jaumea carnosa* Gray, *Limonium californicum* Heller, *Batis maritima* L., and *Frankenia salina* (Molina) Johnston	soil hypersalinity, soil organic matter, tidal inundation, and sediment accretion	Zedler et al., 2003
Mugu Lagoon, California, USA	*Salicornia virginica* C. Linnaeus, *Distichlis spicata* (L.) Greene, *Jaumea carnosa* (Less.) Gray, and *Frankenia salina* (Molina) IM Johnston	**plant species richness**	Armitage et al., 2006
Tijuana Estuary, USA	*Jaumea carnosa* (Less.) Gray, *Limonium californicum* (Boiss.) Heller, *Batis maritima* L., turtleweed, *Frankenia salina* (Molina) I.M. Johnston, *Suaeda esteroa* Ferren & S. A. Whitmore, and *Spartina foliosa* Trin.	soil nutrient, presence or absence of tidal creeks, and **planting seedlings with varied spacing (10-cm apart and 90-cm apart)**	O'Brien and Zedler, 2006
Odiel Marshes, Spain	*Spartina maritima* (Curtis) Fernald	elevation, sediment accretion rate, sediment redox potential , sediment interstitial water conductivity, soil organic content	Castillo et al., 2008
Kiawah Island and Morgan Island, USA	*Spartina alterniflora* Loisel.	**the source of plant material (local or non-local population)**	Beck and Gustafson, 2012
Gulf of Mexico,	*Spartina alterniflora* Loisel.	Elevation, soil oxygen levels,	Silliman et al.,

USA and Baarland, the Netherlands		erosion stress and **plant configuration**	2015
Sacramento-San Joaquin Bay Delta, USA	*Schoenoplectus acutus* (Muhl. ex Bigelow) Á. Löve & D. Löve, *Schoenoplectus californicus (C. A. Mey.) Soják, and Typha latifolia* L.	elevation, tidal inundation, soil redox potential, soil bulk density, soil organic matter, **plant species** and **propagule types**	Sloey et al., 2015
Yangtze Estuary, China	*Scirpus mariqueter* Ts. Tang & F. T. Wang	**Planting density**, sedimentation processes, hydrological regimes	Hu et al., 2015; Chen et al., 2017
Sapelo Island, Georgia, USA	*Spartina alterniflora* Loisel.	**Mutualistic interactions,** nutrients and sulphide stress	Derksen-Hooijberg et al., 2018
Western Scheldt, the Netherlands	*Spartina anglica* C.E. Hubbard	sediment accretion, erosion and wave height	Poppema et al,m 2019
Yangtze Estuary, China	*Scirpus mariqueter* Ts. Tang & F. T. Wang	Water level, salinity, nitrogen addition and **propagule types**	Zhang et al., 2020

In recent years, the recognition that interactions among species regulate the composition of communities made coastal saltmarsh restoration and conservation projects more successful (Halpern et al., 2007; Gómez-Aparicio 2009; Hawkins et al., 2019; Renzi et al., 2019). Silliman et al., (2015) suggested that *Spartina alterniflora* planted with a clumped configuration has significantly higher plant performance than that planted with dispersed configuration. This study was performed in the Gulf of Mexico, USA and in Baarland, The Netherlands, where *S. alterniflora* is non invasive. Similarly, Derksen-Hooijberg et al., (2018) documented that mutualism between marsh-forming *S. alterniflora* and the mussel *Geukensia demissa* can increase cordgrass growth and clonal expansion. On the contrary herbivory, one of the most important species interactions, has rarely been examined in coastal restoration projects (He & Silliman, 2016; Freitas et al., 2016; Johnson et al., 2019; Williams et al., 2019). In Chesapeake Bay USA, Moore et al., (2010) found that the success rate of seedlings produced by transplanted seeds of *Vallisneria americana* (wild celery) can be very low because of the potential for herbivory. He et al., (2017b) also found that crab herbivory is an ecological constraint to saltmarsh recovery after extreme droughts.

In our study, we focused on *Suaeda salsa,* a native plant species that dominates the coastal saltmarshes of northern China. This foundation species is also an ecosystem engineer (Jia et al., 2015). From 1988 to 2014, more than 80% of *S. salsa* saltmarshes were lost in the Liaohe estuary due to human activities and extreme climate (Jia et al., 2015, Tian et al., 2017). To restore the *S. salsa* population, the local government launched a ~1,333 ha large-scale coastal saltmarshes restoration project based on planting (Panjin Bureau of Oceans and Fisheries, 2015). Along with the restoration project, we conducted a series of ecological surveys and field experiments to: 1) evaluate the performance of planted *Suaeda* at different elevations; 2) identify causes of *S. salsa* dieback; and 3) examine the relationships between plant performance and abiotic & biotic factors. We tested the following hypotheses: 1) the performance of planted *S. salsa* in restored sited would be significantly higher at low elevation than at high elevation; 2) constraints to the establishment of planted *S. salsa* strongly vary with the elevation of restored sites.

2. Materials and methods

2.1 Study area and restoration project

This study was conducted in the Liaohe Estuary Nature Reserve (120°30′-122°00′E,40°45′-41°10′N) in Liaoning Province, Northeast China (Fig. 1). The Liaohe Estuary has been listed as a national nature reserve in 1998 and a Ramsar wetland site in 2005 (Jia et al., 2015; Tian et al., 2017). It has a typical semi-humid temperate monsoon climate with distinctive seasons and a rainy summer. The average annual temperature is 8.4°C, the frost-free period is about 175 days per year and the average annual precipitation and evaporation are 623 mm and 1669 mm, respectively (Ye et al., 2015; Liu et al., 2018). The 62.9% of precipitation is received between May and September, and the evaporation can be more than ten times higher than precipitation in spring (Lang et al., 2012; Li et al., 2014). The study area experiences an irregular semidiurnal tide, with an average tidal range of 2.7 m (Zhu et al., 2010).

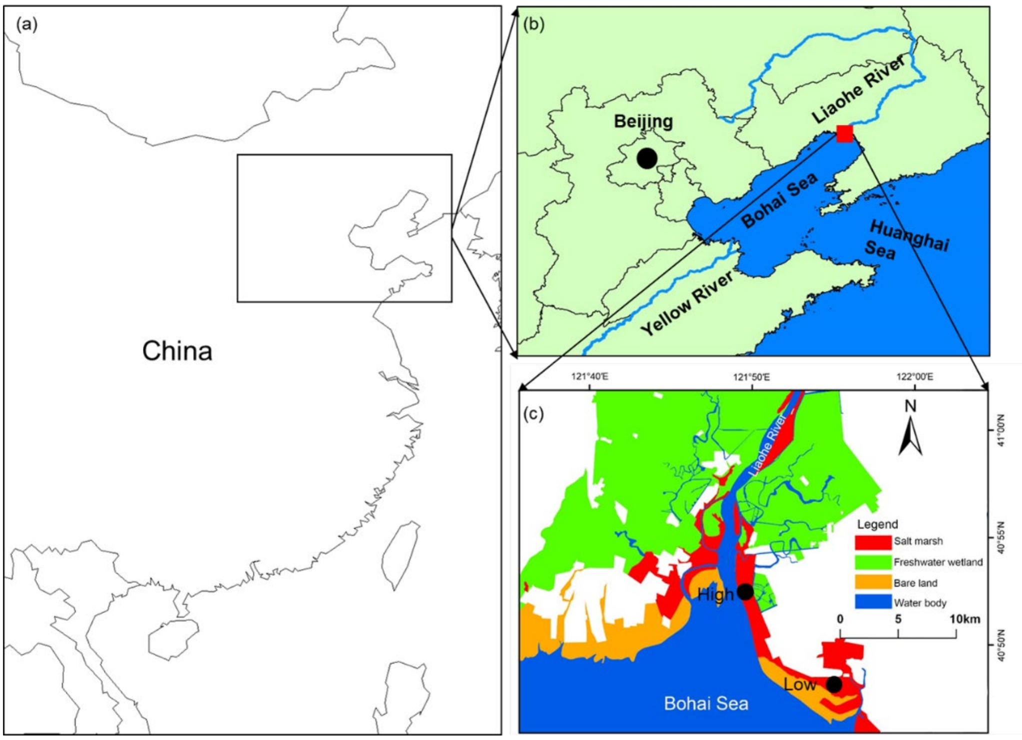

Fig. 1. Location of the Liaohe Estuary in China (a and b) and sampling sites in the Liaohe Estuary (c).

The two dominant vascular plant species in these saltmarshes are *Suaeda salsa* (an annual succulent plant dominant in both low and high marshes) and *Phragmites australis* (a perennial plant dominant in the high marshes and in reed ponds) (Jia et al., 2015). *Suaeda salsa* marshes (named Red Beach) are important for tourism and recreation, offer job opportunities, and drive economic development (Bardzinska-Bonenberg and Liu, 2019). *Suaeda salsa* community provides an important habitat for invertebrates and birds (e.g. the gull *Larus saundersi*), and is also very important for flood control, pollution control and shoreline protection (Jia et al., 2015). Unfortunately, the *S. salsa* population in the Liaohe Estuary experienced a dramatic reduction because of reclamation activities and extreme drought. The total marsh area decreased by 12,856 ha from 1988 to 2014, and the remaining area in 2014 was only 3166 ha, which accounted for less than 20% of the area in 1988 (Jia et al., 2015, Tian et al., 2017).

In recent years, the severity of saltmarsh degradation has motivated the local government to launch several restoration projects (Liu et al., 2016). In the early spring season (April-May) of 2015, a restoration project encompassing an area of ~1,333 ha was initiated by the Panjin Bureau of Oceans and Fisheries. The goals of the project included the restoration of the native plant population and improvement of shorebird habitats (Panjin Bureau of Oceans and Fisheries, 2015). The saltmarsh was created by dredging tidal creeks, smoothing sediment surfaces, and then planting *S salsa* seedlings. To keep the local microhabitat, cores with the original soil substrate and *Suaeda salsa* seedlings were carefully dug from the adjacent natural vegetated area (7-10cm diameter, 10 cm depth). On average, 30 healthy similar-sized seedlings were found in each soil core. Before burying the soil cores, holes with 10 cm depth (spaced ~30 cm) were made in the restoration area. Soil cores with seedlings were slowly pushed into the holes by hand, and the top of the buried cores were levelled to the surface of the marsh. The soil cores were planted during low tide (non-flooded conditions).

2.2 Measurements of plant growth

To study plant growth at different elevations, we selected two study zones (High marsh: 40° 51′ 48.74″ -40° 51′ 56.32″ N, 121° 50′ 02.90″ - 121° 50′ 22.89″ E and Low marsh: 40° 48′ 38.60″ -40° 48′ 42.50″ N, 121° 52′ 41.68″ -121° 52′ 59.61″ E, Fig. 1). The flooding frequency in the low marsh is higher than that in the high marsh (Table 2). Performance of *Suaeda salsa* in adjacent natural and restored marshes was surveyed at high and low elevations. At the end of the growing season in October 2015 and 2016, We randomly established ten 1m ×1m quadrats (~50m intervals) and recorded stem density and percent cover (visually estimated) of *Suaeda salsa*. At the end of the first growing season (October 2015), we also assessed the survival rate of the planted *Suaeda salsa* in two restored sites. Dead plants were inspected in situ to determine the cause of death (herbivory or abiotic stress). Plants grazed by crabs were assigned to the category death by herbivory stress, otherwise, by abiotic stresses (Fig. 2 e and f) (Feller et al., 1995; He et al., 2017). We also considered transplant stress as a possible abiotic cause of plant death, because it is difficult to separate transplant stress from other abiotic environmental stresses. Due to regulations, we were unable to harvest plant biomass. However, density and percent cover of *Suaeda salsa* are good indicators of plant performance (He et al., 2012 and 2017).

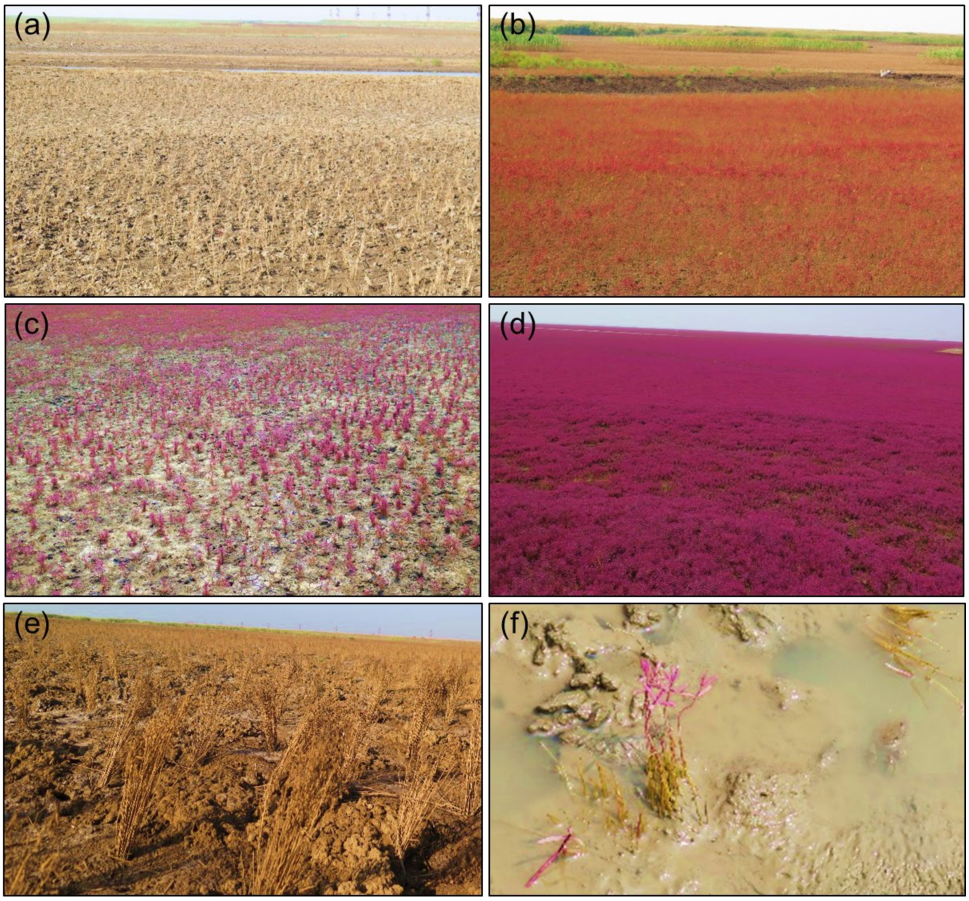

Fig. 2. Pictures of sample sites and *Suaeda salsa* dieback. Vegetation in (a) a restored site and (b) a natural reference site in the high marsh; Vegetation in (c) a restored site and (d) a natural reference site in the low marsh; vegetation dieback caused by (e) abiotic stress and (f) crab herbivory.

2.3 Measurements of abiotic factors

To quantify abiotic environmental parameters, a core of topsoil (5.05cm in diameter × 5cm in depth) was simultaneously collected at the center of each quadrat. The soil cores were weighted and dried at 60°C for 48 h and reweighed to determine soil moisture content and bulk density. Soil salinity and pH were measured after mixing dried soil with a known volume of deionized water (5:1 aqueous suspension, 1 min vibration) and letting the supernatant sit for 30 min (Cui et al., 2011; Pennings et al. 2005). Tidal flooding was measured daily using a water-level gauge from 23 August 2016 to 23 October 2016. Flooding frequency at each site was determined by dividing the number of days flooded by the total number of days observed. Soil organic matter and total nitrogen were not measured, since our previous studies in the estuary suggested these factors weakly related to variations in *Suaeda salsa* growth (Cui et al., 2011).

2.4 Measurements of biotic factors

A growing body of literature suggests that crabs play a crucial role in mediating the functions and dynamics of coastal ecosystems (e.g. Holdredge et al., 2009; Vu et al., 2017). In the coastal wetlands of northern China, the burrowing crab *Helice tientsinensis* is one of the most abundant herbivores. Crabs reduce the biomass of *S. salsa*, *Phragmites australis,* and *S. alterniflora*, and restrict the spatial distribution of these species (He et al., 2017b). To characterize crab communities, we counted the density of crab burrows in each 1 × 1 m quadrat in October 2015. We also estimated crab abundance by trapping crabs with pitfall traps (10 cm diameter and 20 cm depth) located near the quadrats (Fig. S1 a). Crabs collected in the traps every 24h from 9 July to 15 July 2016 were identified (species nd sex), counted, and weighed. To quantify grazing strength of crabs, we conducted a crab exclusion experiment in the spring (May) of 2016, when crabs have a strong impact on plant seedling (He et al., 2019). We transplanted 40 *Suaeda* clumps (20 replicates in high restored sites and 20 replicates in low restored sites) with soil blocks (10 cm diameter, 10 cm depth; containing > 30 seedlings) from an adjacent natural saltmarsh. At the beginning, all the transplants were covered with a grazing exclusion cage. During the first week, the surviving plant seedlings in each transplant were thinned to 10 individuals of similar size (3-6 cm high) for standardization (Fig. S1 b). Half of the crab exclusion cages in each site were removed. After a week, the number of surviving seedlings in each clump was counted (for details of the research design see *Methods* in He et al., 2019). We defined herbivory strength as the ratio between the number of plants that survived in a grazing treatment and the number of plants that survived in the grazing exclusion treatments.

2.5 Data analysis

The differences of plant density, plant cover, abiotic & biotic variables (except for flooding frequency and plant survival rate), cause of plant death and herbivory strength for different contrasts were tested based on one-way analysis of variance (ANOVA) with Tukey's post hoc multiple comparisons. We used *t*-tests to examine the difference in plant survival rate at two different elevation levels. The significance level was set at $p < 0.05$. To increase normality and homogeneity of variance, we used log10 (x+1) or square-root transformations when necessary. Spearman rank correlation analysis was performed to determine the correlation between plant performance and abiotic & biotic factors. All above analyses were carried out using the SPSS 22 software package (IBM, Armonk, New York, USA). We also used Redundancy discriminate analysis (RDA) to identify relationships between plant performance and abiotic & biotic factors (Leps and Smilauer, 2003). Prior to RDA, data were transformed as described above when necessary. RDA was performed using Canoco for window 4.5 (Ter Braak & Sˇ milauer, 2002).

3. Results

3.1 Evaluation of vegetation growth

Generally, the plant density and percent cover of *S. salsa* in the two restored sites were significantly lower than those in the corresponding adjacent natural marshes both in 2015 and 2016 ($p < 0.05$) (Fig. 3). However, the plant density and percent cover of planted *S. salsa* in the low restored marsh were significantly higher than those in the high restored marsh in 2015 and 2016 ($p < 0.05$). *Suaeda* plants were nearly completely eliminated in the high marsh at the end of the second growing season (Fig. 3). Therefore, we suggest that restoration by plantation was more successful at low elevation than at high elevation.

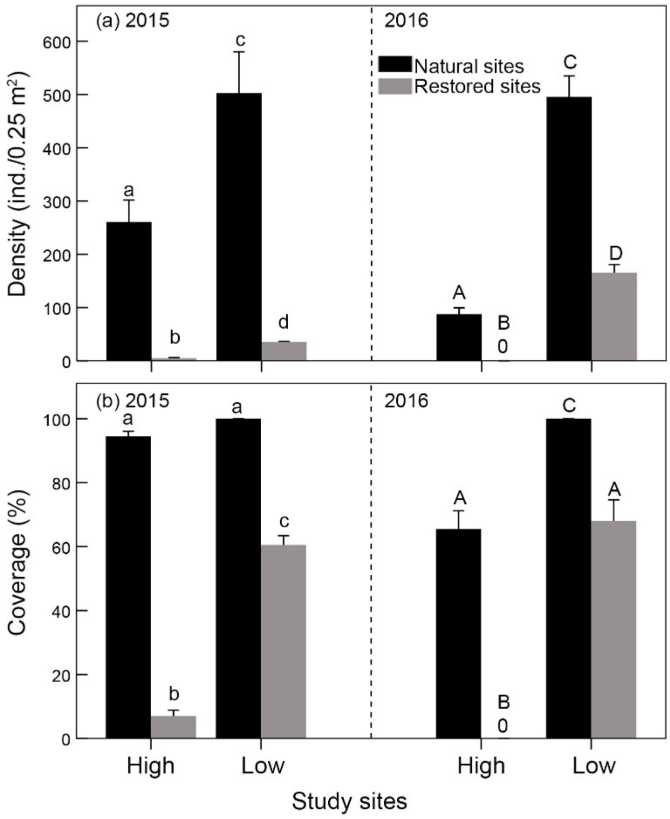

Fig. 3. Plant density (a) and coverage (b) at the end of the 2015 and 2016 growing seasons in different study sites. Data shown are means ± 1SE. The various letters above the bars indicate significant differences ($p < 0.05$).

At the end of the first growing season, the survivorship and cause of death of *Suaeda salsa* varied significantly with elevation. The survivorship of *S. salsa* at low elevation was significantly higher than that at high elevation ($p < 0.05$) (Fig. 4a). In the high restored marsh, *Suaeda* dieback in the restored area is primary caused by crab herbivory (51.0±4.0%), followed by abiotic stress (40.6±3.6%). In the low restored marsh, however, plant dieback is only caused by crab herbivory (40.1±2.1%) (Fig. 4b c). The mortality by herbivory was significantly higher in the high marsh ($p < 0.05$) (Fig. 4b).

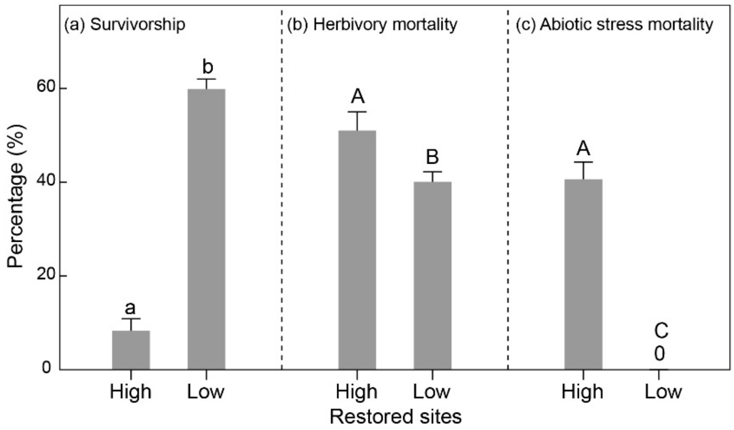

Fig. 4. Survival rate (a) and cause of vegetation dieback (b and c) in two restored sites in the high and low marsh. Data shown are means ± 1SE. The various letters above the bars indicate significant differences ($p < 0.05$).

3.2 Abiotic factors

Abiotic factors differed among marsh elevation levels (Table 2). However, there was no significant difference in soil characteristics between restored and natural marsh for the same elevation level (Table 2). Soil moisture was significantly lower, while soil salinity was significantly higher in the high marsh ($p < 0.05$) (Table 2). The flooding frequency in the high marsh was much lower than that in the low marsh. Soil pH was the lowest and bulk density was the greatest in the high natural marsh. Soil pH and bulk density did not significantly differ in the other sites.

Table 2 Abiotic and biotic parameters in different study sites.

Parameters	High natural site	High restored site	Low natural site	Low restored site
Abiotic factors				
Soil moisture (%)	19.40±0.80 ^{a}	19.85±0.72 ^{a}	23.75±0.46 ^{b}	24.14±0.69 ^{b}
Soil salinity (g/kg)	17.64±1.15 ^{a}	18.36±2.26 ^{a}	6.57±1.20 ^{b}	6.89±1.34 ^{b}
Soil pH	8.09±0.03 ^{a}	8.26±0.06 ^{ab}	8.55±0.04 ^{b}	8.47±0.10 ^{b}
Bulk density (g/cm^3)	1.47±0.05 ^{a}	1.32±0.01 ^{b}	1.38±0.02 ^{ab}	1.24±0.02 ^{b}
Flooding frequency (%)	-	17.74	-	72.26

Biotic factors				
Density of crab burrows (ind./m^2)	60.30±2.79 [a]	58.30±2.90 [a]	17.10±1.73 [b]	20.20±1.34 [b]
Crab number (ind./trap day)	40.10±2.09 [a]	48.20±1.21 [a]	23.00±2.76 [b]	24.90±2.33 [b]
Crab biomass (g/trap day)	462.65±24.66 [a]	475.39±21.22[a]	201.48±11.73 [b]	241.19±29.62 [b]

Data shown are means ± 1SE. The various letters indicate significant differences ($p < 0.05$).

3.3 Biotic factors

Density of crab burrows, crab number and cab biomass collected daily were significantly higher in the high elevation marshes than in the low elevation marshes ($p < 0.05$) (Table 2). However, there was no significant difference between the restored and natural marshes at the same elevation (Table 2). Crab species differed among the four study sites. Three crab species, *Helice tientsinensis*, *Macrophthalmus japonicusi*, and *Philyra pisum* were trapped in the low marsh, but only five and three individuals were trapped for the last two species. In the high marsh, only *Helice tientsinensis* was trapped. There were more *H. tientsinensis* males in the restored marshes, and more *H. tientsinensis* femaels in the natural marshes (Fig. 5).

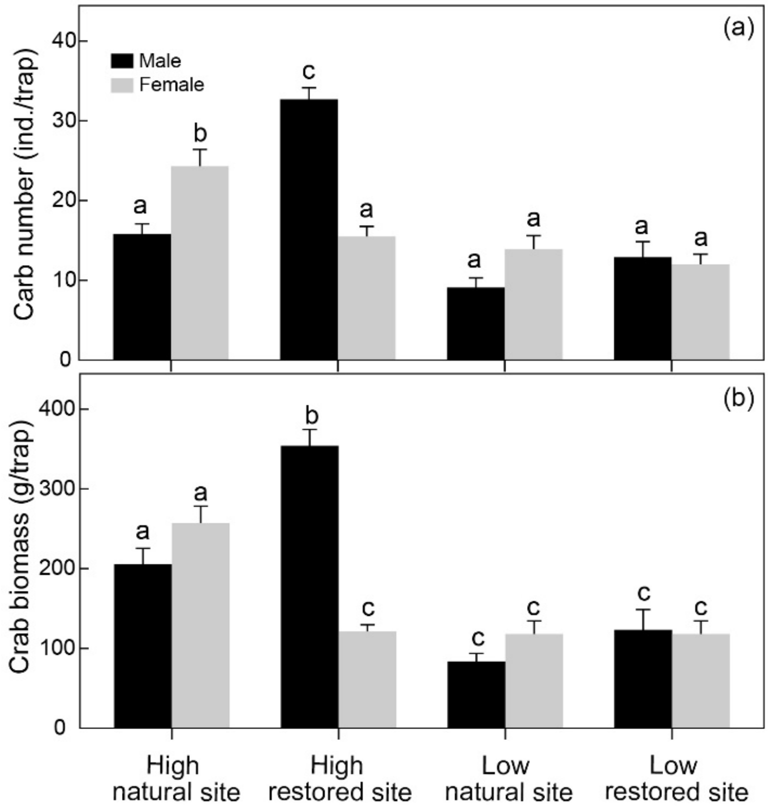

Fig. 5. Density (a) and biomass (b) of *Helice tientsinensis* females and males at the different study sites. Data shown are means ± 1SE. The various letters indicate significant differences ($p < 0.05$).

In the field herbivory experiment, *S. salsa* survival was significantly reduced by crab grazing at both elevations over a one-week period ($p < 0.05$). However, crab herbivory strength in the high restored site was significantly higher than that in the low restored site (Fig. 6).

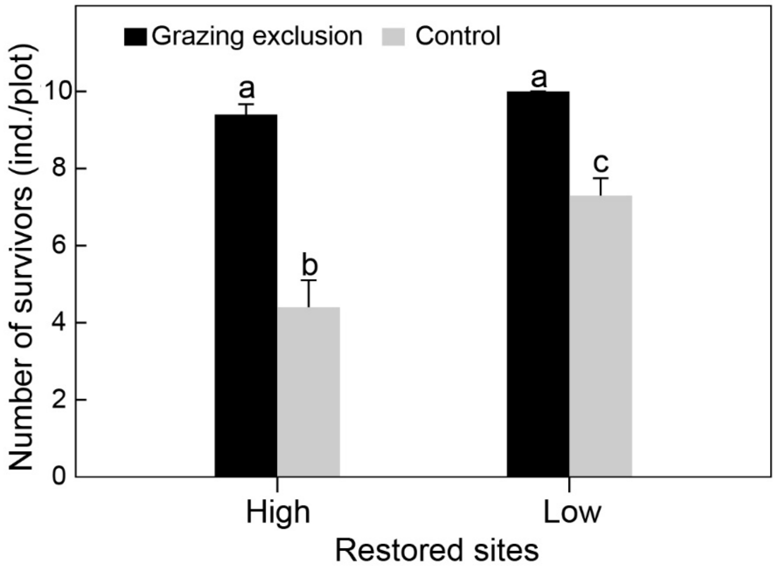

Fig. 6. Herbivory strength in different study sites. Data shown are means ± 1SE. The various letters above the bars indicate significant differences (p < 0.05).

3.4 Relationships between plant performance and abiotic & biotic factors

The abiotic and biotic factors were correlated with plant growth characteristics (Table 3). Soil moisture content and flooding frequency were strongly and positively correlated towith plant performance (density, coverage and survival rate) (p <0.01). However, soil porewater salinity, density of crab burrows, density and biomass of crabs, and herbivory strength was strongly and negatively correlated with plant performance (density, coverage and survival rate) (p <0.01). Soil pH was only strongly and positively correlated with plant coverage (p <0.05). Soil bulk density was only strongly and negatively correlated with plant coverage (p <0.01).

Table 3 Spearman rank correlations between plant performance and abiotic & biotic factors in restored sites.

	Soil moisture	Soil salinity	Soil pH	Bulk density	Flooding frequency	Density of burrows	Number of crabs	Biomass of crabs	Herbivory strength
Plant density	0.844**	-0.884**	0.427	-0.434	0.871**	-0.871**	-0.898**	-0.815**	-0.839**
Plant coverage	0.776**	-0.778**	0.536*	-0.568**	0.872**	-0.784**	-0.791**	-0.658**	-0.899**

Survival rate	0.812**	-0.908**	0.410	-0.413	0.869**	-0.889**	-0.902**	-0.861**	-0.807**

*, $P < 0.05$; **, $P < 0.01$

The RDA analysis was conducted to assess the relationships between plant performance and abiotic & biotic factors (Fig. 5). The first two axes of the RDA ordination explained 97.13% of the total variance for both high and low marsh restored sites (Table S1). All factors, except soil pH, were significantly correlated with the first axis of the ordination, and flooding frequency had the highest correlation coefficient (Table S1). The plant quadrats at high elevations were generally distributed on the right of the ordination chart and were characterized by high soil salinity and herbivory strength, but low soil moisture content and flooding frequency. In contrast, the plant quadrats at low elevations were generally distributed on the left of the ordination chart and were characterized by low soil salinity and herbivory strength, but high soil moisture content and flooding frequency (Fig 5).

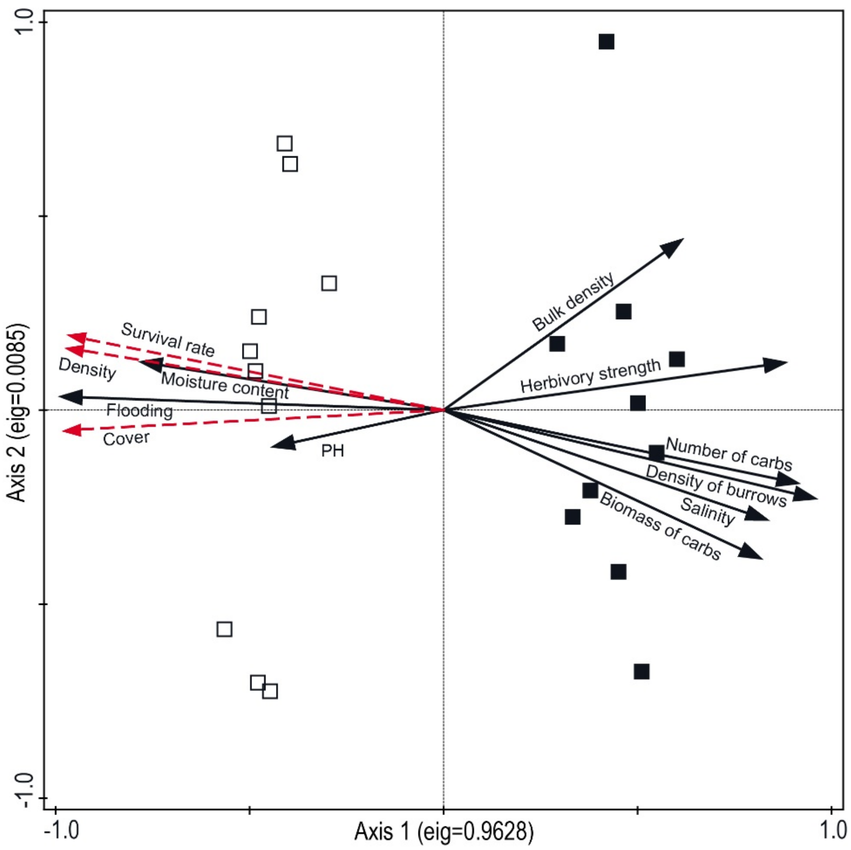

Figure 5. RDA biplots showing relationships between plant characteristics (plant coverage, density and survival rate) and abiotic & biotic factors. Red dashed arrows indicate plant characteristics and black solid arrows indicate abiotic & biotic factors. The length of each arrow represents the strength of the relationship between the environmental variable and the distribution of sampling plots. Dark open squares: samples in the low restored marsh; dark filled squares: samples in the high restored marsh.

4. Discussion

Identifying the main factors that limit success of planting is essential for the restoration of ecological processes and ecosystems functioning of coastal wetlands (Zedler and West, 2008; Castillo and Figueroa, 2009; Johnson et al., 2019). Success of artificial planting was strongly influenced by both biotic and abiotic factors. Therefore our results demonstrate that restoration success of *Suaeda* is also controlled by strong top-down factors and not only by bottom-up processes (abiotic factors). In the high restored sites, harsh environmental conditions and crab grazing almost killed all the transplanted seedlings after one growing season, whereas reduced grazing causes less than half of the transplanted seedlings death in the low restored site. These results suggest that the factors controlling restoration success of *S. salsa* change with elevation. To our knowledge, our study is the first that provides clear evidence that native consumers also control the outcomes of saltmarsh restoration through plantation, and provides insights into the spatial heterogeneity of abiotic and biotic factors.

4.1 Physical stresses as ecological constraints on restoration

Consistent with previous studies suggesting that abiotic environmental stresses limit the success of saltmarsh plantation (Handa & Jefferies, 2000; O'Brien and Zedler, 2006; Sloey et al., 2015; Zhang et al., 2020), our study found that soil moisture content and salinity stresses strongly suppress plant survival, especially in high elevation marshes. Our results suggest that soil salinity is higher, whereas soil moisture content is lower in the high marsh. Our study also determined that flooding was one of the primary physical stress. Wang et al. (2007) and He et al. (2009) also found similar results indicating that flooding frequency generally decreases with increasing elevation, and salinity reaches a conspicuous peak in the high marsh, where soil moisture content is low. Despite *S. salsa* is one of the most salt-tolerant halophytes (Song et al., 2008; Cui et al., 2008; He et al., 2017a), extremely high levels of salinity in the high marsh inhibited *Suaeda*'s recovery, thus preventing subsequent development. As a result, vegetation cover was absent in the high marsh at the end of the second growing season. The hypersaline conditions in the high marsh were also triggered by high evaporation rates and low rainfall intensity. Zhao (2015) showed that the 2015 drought in the Liaohe estuary, the second-worst on record, triggered a 70% reduction in rainfall in June and July.

Although physical characteristics of restored and natural marshes at the same elevation were no significantly different, except for bulk density, plant growth in restored sites was significantly lower than in the corresponding adjacent natural marshes. In addition to transplant stress, this difference can be attributed to the initial density of planted *S. salsa* in restored sites, which is not comparable to the vigorous natural population. The initial planting density in restored sites is about 270 ind./m^2, which is only about a quarter and an eighth of the density in the high and low marsh, respectively. Although some studies indicated that competition among plants decreases with a decrease in plant density (Armitage et al., 2006), positive interactions such as facilitation also decrease due to unnatural transplant density and the formation of vegetation clusters. O'Brien and Zedler (2006) and Silliman et al., (2015) suggested that planting seedlings in tight clusters improve transplant establishment, survival and growth. Hu et al., (2015) also found that planting with high density leads to a higher survival rate and shoot density than with low planting density. Therefore, natural populations with higher plant density and tighter spacing have stronger facilitative interactions than restored populations, such as provision of structural support, protection neighbors from wave and wind, reduction of microsite salinity, or sharing oxygen in the root layer (O'Brien and Zedler 2006 and Silliman et al., 2015).

4.2 Consumer control as an ecological constraint on restoration

In order to restor saltmarshes, many projects have used planting of propagules in the form of seeds, seedlings or stem cutting. Most studies suggest that the success of these restoration projects is primarily controlled by physical forces, such as salinity, flooding, and nutrients (Handa & Jefferies, 2000; O'Brien and Zedler, 2006; Zhang et al., 2020). The bottom-up paradigm has become the foundation for saltmarsh restoration. However, our study provided evidence that pressure from natural consumers also played an important roles in the success of coastal restoration. Many experiments on consumer exclusion and addition revealed that herbivores, such as insects, snails, crabs, geese, and livestock, could substantially and strongly limit the growth of saltmarsh grasses (Ranwell, 1961; Smith and Odum, 1981; Denno et al., 2002; Silliman et al. 2005; He et al., 2019), however, the effect herbivores on coastal restoration projects was never quantified. Our study is one of the first that reveals the role of consumers in a large-scale saltmarsh revegetation project, and adds to the growing literature on the importance of consumers control in coastal ecosystems.

In addition, our study further illustrated that consumer control varied significantly with elevation. One interesting result that occurred in the grazer exclusion experiment was that the herbivory strength of crabs was significantly higher in the high marsh with respect to the low marsh (Fig 4). Some previous studies indicated that the distribution of crabs and the relative strength of crabs herbivory is mediated by the abiotic environmental factors (Alberti et al. 2007; Wang et al., 2009; Alberti et al., 2010; He & Silliman, 2016). Our results showed that the number of herbivorous crab *Helice tientsinensis* decreases with increasing flooding frequency, while the number of the non-herbivorous crabs *Macrophthalmus japonicusi*, and *Philyra pisum* increases. These results are in agreement with the findings of He (2012) in the Yellow River Delta. Although some studies indicated that herbivorous crabs are more active with an increase in flooding (Alberti et al. 2007; He et al., 2015; Szura et al., 2017), our results suggest that total herbivory strength is higher in the high marsh, probably because the herbivorous crab *Helice tientsinensis* is more abundant in the high marsh of our study area (Fig. 5). A significant number of salt marsh species can survive grazing, likely due to higher plant density and the availability of other food sources for crabs (e.g. zoobenthos and detrital sediments). The shore crab *Helice tientsinensis* does forage on other food sources, like polychaetes and detrital sediments (Bang et al., 2019) and healty natural vegetation provides a better habitat for zoobenthos than bare land (Qiu et al., 2019). Therefore, the role of crab herbivory could be stronger in restored sites than in natural sites.

4.3 Implications for coastal restoration

In recent decades, ecological restoration has been increasingly elevated as an important strategy to reverse the degradation of coastal wetlands. In this regard, a better understanding of the role of biotic and abiotic factors and their interactions in limiting coastal restoration is important, and restoration activities may fail if these information is missing. Traditionally, restorers or managers of coastal ecosystems have considered the bottom-up paradigm as the foundation of coastal restoration (Handa & Jefferies, 2000; O'Brien and Zedler, 2006; Sloey et al., 2015). However, our study demonstrated that consumers control also plays a crucial role in the re-establishment of coastal foundation species (see also Alberti et al. 2007; He et al., 2019) Here we show that top-down control by crab grazing suppresses plant growth. Furthermore, the dominant abiotic and biotic stress varied with marsh elevation. Grazing by crabs suppresses plant survival in the high marsh more strongly than in the low marsh, likely because other food sources (e.g. zoobenthos, detrital sediments and algae) are less available when marsh elevation increases (Zedler 1980; Bang et al., 2019; Qiu et al., 2019). Thus, our work indicates that managers should consider top-down controls and the variation of grazing strength in different physical environments within a restoration project. Moore et al., (2010) suggested that using mesh exclosures to protect plants from herbivory is critical to restoration success of *Vallisneria americana* (wild celery) in the Chesapeake Bay, USA. Similar approaches are currently being used in the Liaohe Estuary. In order to protect *Suaeda salsa* from crab herbivory, managers have used cages to trap crabs (Fig. S2). The main findings of our study are consistent with previous studies in other ecosystems (e.g., Bourque and Fourqurean 2013; Ladd et al., 2018; Vaz et al., 2019).

5. Conclusion

In summary, we found that success of coastal restoration projects is not only controlled by abiotic environmental stresses, but also by the top-down effect of native consumers. The relative role of herbivors in controlling restoration depends on marsh elevation. Our study is among the first to emphasize the keystone role of native consumers in coastal restoration projects. These results provide important data for the correct planning of future salt marsh restorations.

Authors' contributions

Zezheng liu, Baoshan Cui, Jin Li, Xu Ma and Chengjie Xie conceived and designed the study. Zezheng Liu and Chengjie Xie did the field work. Zezheng Liu and Sergio Fagherazzi analyzed the data and wrote the draft. All authors significantly contributed to the final manuscript.

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Competing interests

The authors declare no competing interests.

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Supplementary Materials

Table S1 Summary of the RDA ordinations.

	Axis 1	Axis 2
Statistics		
Eigenvalue	0.9628	0.0085
Species–environment correlations	0.9879	0.7928
Cumulative % variance	96.28	97.13
Correlations		
Moisture content	-0.7683**	0.0981
Porewater salinity	0.8218**	-0.2237
pH	-0.4317	-0.0746
bulk density	0.6050*	0.3472
Flooding frequency	-0.9724**	0.0275
Density of burrows	0.9446**	-0.1805
Number of carbs	0.9003**	-0.1491
Biomass of carbs	0.8057**	-0.3026
Herbivory strength	0.8681**	0.0969

**, $P < 0.01$; *, $P < 0.05$.

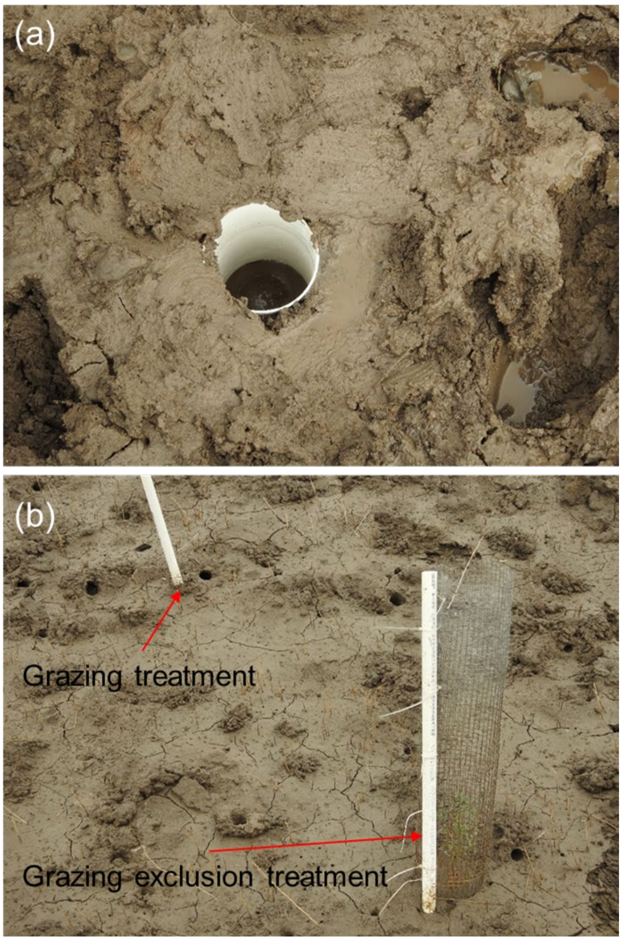

Fig. S1. Pitfall trap (a) and grazing exclusion experiment (b).

Fig. S2. Crab cages in the Liaohe river estuary.