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Human activities accelerated the degradation of saline seepweed red beaches by amplifying top-down and bottom-up forces

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Abstract.   Salt marshes dominated by saline seepweed (*Suaeda heteroptera*) provide important ecosystem services such as sequestering carbon (blue carbon), maintaining healthy fisheries, and protecting shorelines. These salt marshes also constitute stunning red beach landscapes, and the resulting tourism significantly contributes to the local economy. However, land use change and degradation have led to a substantial loss of the red beach area. It remains unclear how human activities influence the top-down and bottom-up forces that regulate the distribution and succession of these salt marshes and lead to the degradation of the red beaches. We examined how bottom-up forces influenced the germination, emergence, and colonization of saline seepweed with field measurements and a laboratory experiment. We also examined whether top-down forces affected the red beach distribution by conducting a field survey for crab burrows and density, laboratory feeding trials, and waterbird investigations. The higher sediment accretion rate induced by human activities limited the establishment of new red beaches. The construction of tourism facilities and the frequent presence of tourists reduced the density of waterbirds, which in turn increased the density of crabs, intensifying the top-down forces such as predators and herbivores that drive the degradation of the coastal red beaches. Our results show that sediment accretion and plant–herbivory changes induced by human activities were likely the two primary ecological processes leading to the degradation of the red beaches. Human activities significantly shaped the abundance and distribution of the red beaches by altering both top-down and bottom-up ecological processes. Our findings can help us better understand the dynamics of salt marshes and have implications for the management and restoration of coastal wetlands.

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Introduction

Salt marshes are important ecosystems that develop on wave-protected shorelines in temperate zones worldwide (Adam 1990). These intertidal ecosystems can sequester carbon (blue carbon), maintain healthy fisheries, and protect shorelines. The dynamics of salt marsh communities are impacted by both top-down (e.g., consumers) and bottom-up (e.g., physical factors) forces (Kaminsky et al. 2015, Rupprecht et al. 2015, Elschot et al. 2017). Understanding the responses of salt marshes to these biotic and abiotic factors is fundamental for assessing structural shifts in these coastal ecosystems (Prach and Walker 2011). A large body of literature has examined the dynamics of coastal salt marshes as a function of grazing pressure, drainage conditions, sedimentation accretion, and sea level rise (Leendertse et al. 1997, Spivak et al. 2007, He et al. 2015, He and Silliman 2016, Elschot et al. 2017). Human activities have constituted different types of disturbances to natural coastal wetland ecosystems, which can alter plant composition and distribution by influencing top-down and/or bottom-up mechanisms (Crain et al. 2008, Farina et al. 2016, He and Silliman 2016). Bottom-up and top-down effects can act together to exert strong control over community dynamics, while how human activities modify these interactive forces remains unclear.

Red beach salt marshes, located in coastal intertidal areas, are dominated by saline seepweed *Suaeda heteroptera*. The seepweed plants show a red color shortly after germination, contributing to the appearance of beautiful red beach landscapes from May to December (Jia et al. 2015). *Suaeda* is widespread in the temperate salt marshes of East Asia (He et al. 2009, 2012) and is the only native plant that extends from low marshes to terrestrial borders in northern China (Cui et al. 2011). It is known for its high tolerance to salt stress and waterlogging and is competitively subordinate to perennial plants such as the native reed *Phragmites australis* (He et al. 2009, 2012). The typical successional stages of red beach areas mainly include the following three phases: (1) the newly formed bared mudflat without vascular plants, (2) the dominance of *S. heteroptera* in the elevated part of the intertidal zones, and (3) the prevalence of *P. australis* in the supratidal zone (Wan et al. 2001).

As typical landscapes in the Liao River Estuary Wetland (LREW), red beaches provide important ecological services. The LREW, the world's second largest reed swamp, is the southern feeding boundary for the wild red-crowned crane (*Grus japonensis*), the world's largest breeding site for Saunders' Gull (*Larus saundersi*), and an important stopover site for migrating waterbirds including 45 protected birds in the East Asian–Australasian Flyway (Yang and Chen 1995, Tian et al. 2017). It became a national nature reserve of China in 1998 and a Ramsar site in 2005 (http://ramsar.org). *Suaeda* constitutes stunning red beach landscapes and has significantly contributed to the local economy. In recent years, the most important local economic driver has switched from petroleum production to red beach ecotourism. For example, the total number of tourists visiting this reserve and its National Red Beach Scenic Corridor during the National Day Golden Week (1–7 October) in 2016 was ~0.32 million. The total annual tourism revenue in 2016 increased by 15.5%. The local government has developed red beach ecotourism into a strategic pillar industry of the economy. The local government is investing 0.3 billion RMB to restore 20,000 ha of red beach and other natural marine ecosystems during the five-year period from 2016 to 2020 (i.e., the "13th Five-Year Plan" of China).

The total red beach area in the LREW lost 11,372 ha from 1988 to 2005 and 685 ha from 2005 to 2014, and the remaining area in 2014 was only 3166 ha (Tian et al. 2017). Land use change such as urbanization and the development of agriculture and aquaculture and the construction of roads and ports for crude oil transportation and tourism have led to the substantial shrinkage and fragmentation of the natural wetlands (Tian et al. 2017). Meanwhile, the degradation of salt marshes has also led to a substantial loss of the red beach area in the LREW (Tai et al. 2009, Wang et al. 2010). The degradation rate of red beaches to bare mudflat or *P. australis* communities has been dramatic (Fig. 1). It remains unclear how human activities influence the top-down and bottom-up forces that regulate the

Fig. 1. Photo gallery for red beach changes at the Yuanyang ditch within the Liao River Estuary Wetland from 2013 to 2017. All photographs were taken at the same place in late July or early August.

distribution and succession of these salt marshes and lead to the degradation of the red beaches.

There was once fundamental disagreement over whether bottom-up (e.g., nutrient availability or sediment elevation change) or top-down (e.g., predators or trophic cascade effects) forces predominate in controlling the abundance and distribution of plant populations and communities (Hunter and Price 1992, Strong 1992, Flores and Paula 2002, Silliman et al. 2013, He and Silliman 2016). In the early stage, most ecologists believed that climate and other physical factors, referred to as bottom-up forces, ultimately controlled the distribution of coastal vegetation (Odum and Odum 1953, Teal 1962, Tansley 1993). In 1960, Hairston et al. proposed an alternative view that consumers, top-down forces, play a major role in determining key features of plant-generated ecosystems. Some other studies also revealed that grazers could control plant growth and species composition in a variety of ecosystems such as salt marshes, rocky shores, coral reefs, and tropical forests (Paine 1980, Smith 1983, Hay 1984). This top-down vs. bottom-up debate generated tremendous interest in the field and served as an impetus for ecologists to search and test for examples of grazer control and physical factors of plant communities. It is later recognized that both top-down (e.g., predators) and bottom-up (e.g., nutrient availability) driving forces can act in concert with communities after decades of intense debate (Daleo et al. 2015, Vidal and Murphy 2018). Disentangling the relative contributions of top-down and bottom-up forces can help explain the abundance and patterns of plants. In general, the relative importance of these two types of mechanisms may be scale-dependent and vary by spatial or temporal scale (Strong 1992, Gratton and Denno 2003, Meserve et al. 2003, Hunt and Mckinnell 2006). However, few studies have examined the relative impacts of top-down and bottom-up forces and how they interacted with each other (Crain et al. 2008, Farina et al. 2016). Whether these two types of driving factors counteract or have additive or synergistic effects on ecosystems is poorly understood.

With the rapid growth and spread of the human population, human activities have introduced new types of disturbances into natural coastal wetland ecosystems, which can greatly shape plant composition in both top-down and bottom-up manners (Farina et al. 2016). A large body of studies have shown that multiple human impacts such as warming, eutrophication, and sea level rise in marine ecosystems can interact synergistically and exacerbate negative impacts

mainly through bottom-up processes (Crain et al. 2008), while some other studies have revealed an overwhelming role of top-down human impacts rather than bottom-up, eutrophication impacts or their interactions in salt marsh and seagrass ecosystems (Heck et al. 2000, Baden et al. 2010, Silliman et al. 2013, He and Silliman 2016). Bottom-up and top-down forces can exert strong control over community dynamics separately or synergistically, while how human activity modifies those forces remains unclear.

Here, we examined how top-down and bottom-up forces amplified by human activities accelerated the degradation of the red beach landscapes in the LREW. We aimed at answering the following questions: (1) What are the main drivers of the degradation of red beaches? (2) What are the relative contributions of these drivers? and (3) Are top-down and bottom-up controls amplified by human activities? We hypothesize that the increase in sediment accretion rate and grazer population induced by human activities controlled the establishment, succession, and degradation of saline seepweed red beaches. We first examined how sediment surface elevation, a bottom-up force, influenced the germination, emergence, and colonization of saline seepweed with field measurements and a laboratory experiment. We then examined whether top-down forces (crab grazing and trophic cascade effects) controlled the abundance and distribution of seepweed by conducting a field survey for crab burrow and density, laboratory feeding trials, and waterbird investigations. Diagnosing the causes of the degradation of red beaches has implications for understanding the dynamics of these salt marshes and informing management practices and restoration efforts.

MATERIALS AND METHODS

Study area

Our study area is located in the southern LREW (Fig. 2) and has a monsoon climate (Xu et al. 2009). Annual mean air temperature is ~9.29°C, and there are 170 frost-free days per year. Mean annual precipitation is 616 mm, mostly falling between May and September. The 35-yr meteorological record (Data from China Meteorological Data Sharing Service System, http://data.cma.cn) shows that air temperature

increased by 0.02°C per year ($P < 0.05$, $R^2 = 0.16$) and annual precipitation did not significantly change from 1981 to 2016 ($P = 0.49$, $R^2 = 0.01$; Appendix S1: Fig. S1). The tides are irregular semidiurnal, with an average amplitude of 1.91–3.41 m.

The two dominant plant species in the wetland are *Phragmites australis* and *Suaeda heteroptera*. The vegetated wetlands in LREW can be divided into three categories: reed pond, coastal wetland, and island wetland (Fig. 2). Reed ponds are managed with obstructed waterways to prevent salt water intrusion, and the reed *Phragmites* is harvested in winter for paper production. Roads and dams constructed for oil industry and transportation separate reed ponds from coastal wetlands. The seepweed *Suaeda* is mainly distributed in coastal and island wetlands. Boardwalks have been constructed on red beaches in coastal wetlands for tourism (Fig. 2). The more recently formed island wetland is less influenced by anthropogenic disturbance than coastal wetlands.

We used satellite imagery from Landsat to quantify the changes of the red beach area. Images were acquired every two years from 2003 to 2017, with five images (2003, 2005, 2007, 2009, and 2011) from the Thematic Mapper on Landsat 5 and three images (2013, 2015, and 2017) from the Operational Land Imager on Landsat 8 (Appendix S1: Table S1). Each image consists of multiple spectral bands in visible, near-infrared, and thermal wavelengths. These images were shown in natural color with seepweed appearing in red (or pink) and reed in green and were used to illustrate changes in the spatial extent of seepweed and reed cover in our study area from 2003 to 2017 (Fig. 3). The island was still an inlet dominated by seepweed in 2003. With the rapid expansion of the inlet, the area of seepweed increased and reached its maximum extent in 2009. Starting in 2011, seepweed cover rapidly declined and was replaced by reed. By September 2017, the island was dominated by reed, and seepweed only accounted for a small fraction of the island's area and was mainly distributed in the southernmost portion and the east edge of the island. The rapid decrease in the red beach area during the recent seven years exceeded the normal succession of seepweed.

Rapid sedimentation has occurred in the estuary because of changes in land use and runoff.
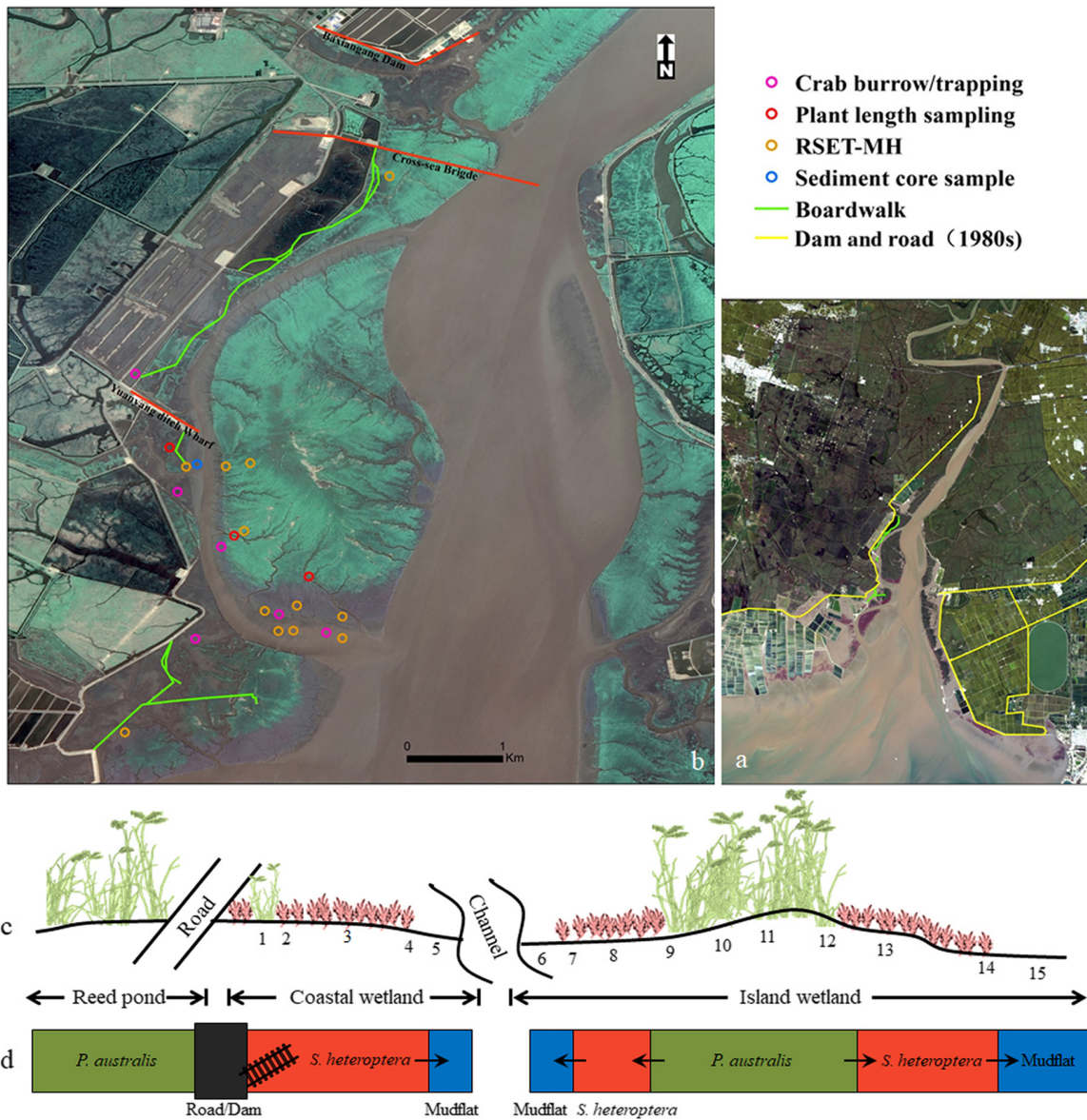
Fig. 2. (a) Location of the study area within the Liao River Estuary Wetland (LREW) in Panjin, Liaoning Province, China. The yellow line represents the dams constructed in the 1980s. (b) Sampling points in the lower LREW delta, where the green and red lines represent the boardwalks and other tourism facilities constructed on the red beach, respectively. The photograph in panel b was taken in July 2016. (c) Seepweed distribution along topographic gradients in shoreline habitats of the LREW. The vegetated wetland zones are partitioned into the following three zones: reed community, coastal wetland, and island wetland by roads and channels. The reed community is composed of reed ponds for paper industry. Red beaches are mainly distributed in coastal wetland and island wetland, both of which were exposed to the invasion of *Phragmites australis*. The red beach in the coastal wetland was exposed to higher pressure because of the tourism development and the extensive construction of boardwalks during recent years. The island wetland was relatively newly formed wetland and was under less anthropogenic disturbance compared to the coastal wetland. The numbers from 1 to 15 stand for the sites at which we measured the elevation. (d) The change trend or vegetation succession for reed, seepweed, and mudflat in three zones. The black rectangle represents the construction of roads or dams. The figure is not to scale.
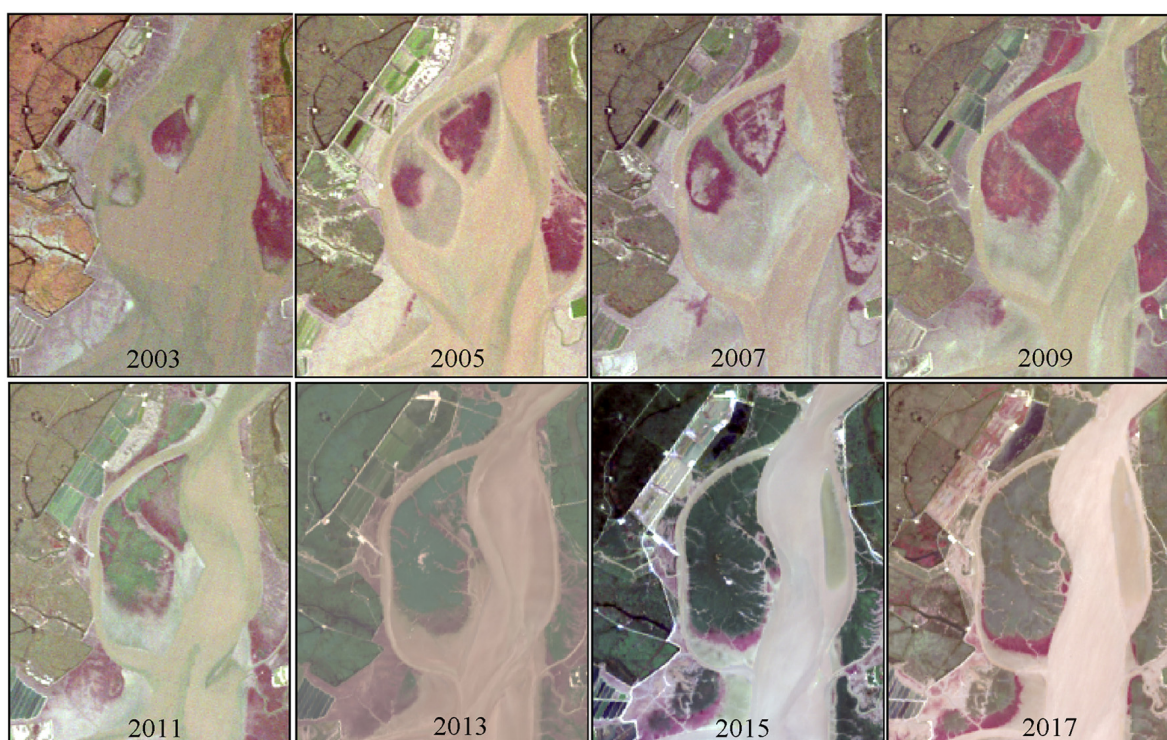
Fig. 3. Spatial distribution and temporal development of red beaches and the succession from seepweed to reed within the study area between 2003 and 2017. These Landsat images are shown in natural color with seepweed appearing in red (or pink) and reed in green.

We used a sediment core sample and the ^{210}Pb-based dating technique to estimate the sediment accretion rate. ^{210}Pb has been widely used to study environmental changes during the last 100 yr through dating of undisturbed sediment cores (Sanchez-Cabeza and Ruiz-Fernández 2012). One sediment core sample with the depth of 100 cm was collected from the bare beach at the Yuanyang ditch in July 2016 (Fig. 2), and the sample was collected by the sediment core sword (Model number: C040903; manufacturer: Eijkelkamp, Giesbeek, The Netherlands) and was then sectioned into 5-cm subsamples. After drying, grinding, and sieving by 0.2-mm mesh, all sediment subsamples were weighed and sealed in plastic boxes (25 × 70 mm) for at least 120 d to achieve equilibrium between the mother and daughter radionuclides (^{226}Ra-^{222}Rn, ^{238}U-^{234}Th), and were then measured by the high-purity germanium γ spectrometer (GEM-MX7080P4, ORTEC, Oak Ridge, Tennessee, USA). We used the widely used constant rate of supply model

for the ^{210}Pb-based dating (Appleby and Oldfield 1978). The dated chronology was used to calculate the deposition rate of sediment based on interval ages and the core depth. The average sediment accretion rate showed an increasing trend over time, showing that the siltation level has been rising in the past 100 yr, particularly during the last five decades (Fig. 4). The accretion rates dramatically increased in 1968 and 1984 when the Shuangtaizi Dam and the Coastal Levee were built, respectively. Peak accretion rates also occurred in 2001, 2008, and 2012 in which the Baxiangang Dam, the Yuanyang ditch Wharf, and the Cross-sea Bridge were built, respectively. Hence, the substantial increase in the sediment accretion rate during the recent decades was likely mainly driven by human activities.

Elevation measurements

Elevation is a critical factor in determining the distribution and growth of salt marsh plants. We measured the elevation of both coastal and island
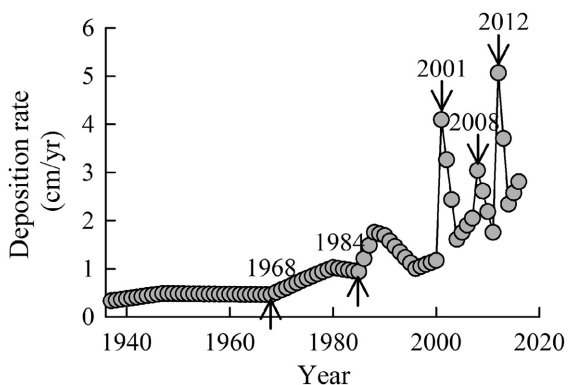
Fig. 4. Changes in the sediment accretion rate at the Yuanyang ditch within the Liao River Estuary Wetland from 1937 to 2016 based on the measurement of ^{210}Pb. The years above the curve stand for years in which dams, levees, or bridges were built: 1968, Shuangtaizi Dam; 1984, Coastal Levee; 2001, Baxiangang Dam; 2008, Yuanyang ditch Wharf; and 2012, Cross-sea Bridge. These constructions are all located within 5 km in the upriver of the sediment core sample point.

wetlands. To georeference each target habitat, target positions and elevations were measured. Elevation data were obtained with an RTK GPS system (Trimble Navigation R8, 2015) with a standard deviation <1 cm. Nine line transects (>50 m within habitat) were selected across the LREW, and each transect covered five habitats: reed community, reed–seepweed ecotone, seepweed community, seepweed–mudflat ecotone, and unvegetated mudflat. Three line transects were located in the coastal wetland, and the remaining six transects were located in the island wetlands. The average elevation for each habitat was calculated based on the measurements from the transects in coastal wetland (three transects) and island wetlands (six transects), respectively. The effects of habitat on the elevation were examined using ANOVA followed by Tukey's honestly significant difference (HSD) multiple comparisons. Data are presented as means ± standard error (SE).

Wetland rod surface elevation tables

Understanding changes in relative salt marsh elevation is important for interpreting changes in salt marsh vegetation communities and other estuarine ecosystem components. Salt marsh

erosion and accretion are also important parameters for measuring the response of formerly impounded marshes to restoration of tidal influence and will be particularly critical if the rate of sea level rise accelerates as predicted. Rod surface elevation table-maker horizon (RSET-MH) is a nondestructive method to measure small changes in elevation (i.e., millimeter-to-centimeter scale) in intertidal wetlands over an extended period of time. It is a well-established method for studying coastal wetland change (Cahoon et al. 2002, Webb et al. 2013). The measurements are useful for studying coastal wetland dynamics, spatial patterns, and the delicate interplay among surface elevation change (SEC), vertical accretion (VA), and shallow subsidence rate (SS). SEC was determined by calculating the difference between site visit and baseline pin heights and then calculating the mean of all measurements. Vertical accretion measurements were carried out using the maker horizon methodology. Three measurements were taken from each of three MHs which comprise the first established VA plot set. Shallow subsidence is defined as VA minus SEC relative to a fixed vertical reference point (i.e., the rod depth), or the amount of SEC that does not result from the addition/subtraction of material at the land surface.

We installed RSET-MH systems at 12 locations in the LREW from June 2016 to monitor SEC, VA, and SS, following the RSET-MH methodology (Lynch et al. 2015). Three RSET-MH systems were set up for four habitats: coastal seepweed community, island mudflat, island seepweed community, and island reed community (Fig. 2). Surface elevation was measured in the beginning and end of the growing season (from May to November), and SEC was determined by calculating the difference between site visit and baseline pin heights and then averaging all measurements. Vertical accretion measurements were carried out using the maker horizon methodology. Three measurements were taken from each of three MHs which comprise the first established plot set. Shallow subsidence was then calculated based on the SEC and VA measurements. The effects of different habitats on SEC, VA, and SS were examined using ANOVAs followed by Tukey's HSD multiple comparisons. SEC of non-growing and growing seasons was also examined by using ANOVAs followed by

Tukey's HSD multiple comparisons to test the different patterns in the four habitats.

Seepweed length measurements

The above- and below-ground length of seepweed is related to the depth at which seeds are buried and can reflect the stress from sedimentation. Moreover, the ratio of below-ground length to above-ground length can be calculated to explain the effects of sediment immersion on the difference of distance zonation. We hypothesize that the sediment elevation has significant effects on seepweed growth. We thus performed a field experiment along the profile to test this hypothesis by using the increase in seepweed length to measure the seedling growth. Four habitats along the topographic gradients for coastal and inland wetlands were selected for growth measurement. We selected one seepweed habitat in the narrow red beach band (always <50 m) in the coastal area and three habitats on the island wetlands. Five and ten transects (>50 m apart for each other) were selected for the coastal and island wetlands, respectively. In each sample point, six seepweed seedlings were dug out to measure both above- and below-ground length in spring (5 May 2017), summer (7 July 2017), and autumn (23 August 2017). The below-ground length was the length below the sediment surface which contains taproot, hypocotyl, and the stem buried in the sediment. The effects of the distance to the zonation boundary on above- and below-ground length were examined for each season using ANOVA followed by Tukey's HSD multiple comparisons. The interactive effect of seasons and habitats on below-ground length, above-ground length, and below- to above-ground length ratio was examined using generalized linear models (GLMs). The correlation of the ratio with zonation distribution was evaluated for the island wetland to explain the effects of sediment immersion on the difference of distance zonation.

Seed germination and emergence experiment

Sediment burial was recognized as a major selective force in the evolution of seed germination, seedling emergence, seedling establishment, and survivorship of seedlings and adult plants. A greenhouse study was conducted to determine the impact of burial depth on seedling germination of

S. heteroptera. Seeds of *S. heteroptera* were collected from ~50 randomly selected individuals from the LREW in the fall of 2016. They were cleaned and dried at room temperature for one week and then stored at 5°C under dry, dark conditions. Seeds (~50 each) were then buried in sediment in plastic pots (20 cm in diameter, 15 cm in height) at depths of 1, 3, 5, 7, and 9 cm, respectively. There were six replicates for each depth treatment. During the entire experiment, the pots were watered with freshwater daily for three days in a row and with seawater only for the fourth day; air temperature was maintained at 22°C during the day and 15°C at night to simulate field temperatures. Drainage holes covered with nylon mesh at the bottom of the pots prevented loss of sediment and allowed drainage. Seedling germination was defined as the first appearance of seedling at the sediment surface, and the number of emerged seedlings was counted daily. No new seedlings emerged 40 d after the beginning of the experiment. We used GLMs to examine the effects of sediment immersion depth and growth period on the seedling emergence. The GLMs were analyzed using quasi-Poisson distribution with log link (to account for overdispersion) for density and gamma distribution with inverse link for emergence ratio. The emergence ratio was $(x + 0.01)$-transformed to avoid zero values. The effects were tested by comparing the resulting deviances to F test statistics (Type II sum of squares). Post hoc tests of significant interactions were also conducted. All statistical analyses were performed with SPSS software, version 17.0 (SPSS, Chicago, Illinois, USA).

Crab burrow and crab trapping

To understand the relationships between crabs and habitats, we assessed crab densities using both crab burrow counting and trapping experiments. *Helice tridens tientsinensis* Rathbun is a widely distributed grapsoid crab in the LREW and is the main grazer of seepweed (He et al. 2015). *Helice* is the dominant crab species in our study area, accounting for more than 95% of the crabs. It can be found from low marshes and mudflats to terrestrial borders. Estimating the number of intertidal burrowing crabs is challenging because of the nature of the substratum and behavior of crab. Thus, we estimated crab population density by both counting burrow openings and trapping crabs. *Helice* commonly burrows

with one to two surface openings. Burrow counts can provide quick density estimates (Warren 1990). Crab burrow sampling was done on transects from land to sea in seepweed habitats in coastal wetlands and three island wetland habitats (mudflat, seepweed community, and reed community). For the island wetlands, we randomly selected thirty 1-m² quadrats (1 × 1 m, $n = 10$/habitat, >50 m apart within habitat) in each habitat along the pre-labeled transects and counted the number of burrow openings larger than 1 cm. For the coastal wetland, three study sites were identified and eighteen quadrats (1 × 1 m, $n = 6$/habitat, >50 m apart within habitat) were randomly selected for each site because of the limited seepweed patches. Data were collected in spring, summer, and autumn 2017.

Besides crab burrows, we also measured crab density with crab trapping for mutual verification. We deployed pitfall traps (24 h per sample) on 5 May, 11 July, and 11 September 2017 following Li et al. (2014b). Crab trapping was done in the same habitats as the crab burrow counting. Five replicate traps were assigned to each of the three habitats in the island wetland and the one habitat in the coastal wetland, leading to a total of 20 traps (5 replications/habitat × 4 habitats). All traps were set >50 m apart to minimize damage to the red beach. Crab traps (16 cm diameter, 50 cm deep) were made of PVC pipe with galvanized hardware mesh (2 mm mesh size) at the bottom, and inserted flush with the sediment surface by digging the hole. Crabs collected in the traps during a 24-h period were scored for species and numbers. The effects of habitat on crab burrows and crab density were examined using ANOVAs followed by Tukey's HSD multiple comparisons. Moreover, the GLMs were analyzed using quasi-Poisson distribution with log link (to account for overdispersion) for habitats and seasons with inverse link for emergence ratio. The effects were tested by comparing the resulting deviances to F test statistics (Type II sum of squares). Post hoc tests of significant interactions were also conducted.

Crab feeding experiment

To examine how crabs consume seepweed tissue relative to reed leaves, we conducted a laboratory feeding experiment in July 2016. We hypothesized that *Helice* prefers seepweed to reed leaves. We conducted laboratory feeding trials in July 2016 to test this hypothesis. Crabs were collected from the field, housed individually in 800-mL laboratory aquaria, starved for 24 h, and then weighed. A total of 30 crabs (means ± SE: mean weight of 15.82 ± 0.38 g and mean carapace width of 2.59 ± 0.02 cm) were selected for the feeding experiment and randomly divided into three groups in separate plastic containers. Each container had ~5 mm of seawater at the bottom to reduce desiccation. The first 10 crabs were fed with 10 g of reed leaves, the second 10 crabs with 10 g of seepweed tissue, and the third 10 crabs with 5 g of reed leaves and 5 g of seepweed tissue. All crabs were fed plant tissue in separated containers, and there are 10 replications in each treatment. Three containers with the above plant treatments were simultaneously set up without crabs as control treatment for each group. All the leaves were collected locally within 24 h prior to the experiment. After the 72-h feeding experiment, all the remaining leaves in both feeding experiment and control treatment were collected, oven-dried, and weighed. The amount and percentage of plant material consumed by *Helice* were then calculated as the difference and ratio of dry weight leaves between feeding and control treatments, respectively. *Helice* feeding preferences were examined using paired t tests (two-sided).

Waterbird surveys

Crabs are important prey for shorebirds and gulls in coastal mudflats (Ellis et al. 2012). Previous research has found that *Helice* is a critical food source for waterbird populations, especially for the red-crowned crane (Li et al. 2014a). Thus, we conducted waterbird surveys in coastal and island wetland areas. We counted all waterbirds appearing in the target wetlands consisting of 57 ha of island wetland and 35 ha of coastal wetland and also recorded the category of each endangered species (IUCN 2017). Five monthly surveys were conducted from June to November in 2017 by observers using a pair of binoculars and telescope (Victory, Zeiss, Oberkochen, Germany). Surveys were conducted on foot or using vehicles between 07:00 and 16:00 hours during suitable weather conditions. The differences in species number and density of waterbirds between the coastal wetland and the island

wetland were also examined using paired *t* tests (two-tailed). Correlations between monthly waterbird density and crab density were examined for the coastal and island wetlands, respectively. The generalized linear model was used to test the significance of the regressions.

RESULTS

Bottom-up controls

The elevation range of the coastal (2.31 ± 0.05 m) and island (2.34 ± 0.04 m) wetlands was not significantly different (Fig. 5a). The elevation of different habitats, however, was significantly different (df = 4, F = 120.793, P < 0.001; Fig. 5b). The elevation varied in different habitats or ecotones in both coastal and island wetlands. The reed habitats were at higher elevation than the seepweed–mudflat ecotone and unvegetated mudflat (Fig. 5b). The reed–seepweed ecotone and seepweed habitat were at intermediate elevation compared with reed habitats and the seepweed–mudflat ecotone (Fig. 5b). The mudflat had the lowest elevation (2.02 ± 0.05 m) among all habitats (Fig. 5b).

The SEC was also different among habitats (df = 3, F = 4.947, P = 0.038; Fig. 6b). The seepweed community in the coastal wetland had a lower SEC rate than the island wetlands (Fig. 6b).

The surface elevation rate of the mudflat (96.4 ± 13.4 mm/yr) was not significantly different from that of the other two habitats in the island wetland. However, it should be noted that the patterns of the SEC exhibited large differences among the four habitats (Fig. 6c). The vegetated habitats accumulated more sediment in the growing season than in the non-growing season, while the unvegetated mudflat accumulated far more sediment in the non-growing season than in the growing season (92.2 ± 8.4 mm vs. 2.8 ± 11.2 mm; Fig. 6c). The VA rate exhibited the same pattern among habitats (df = 3, F = 6.415, P = 0.02; Fig. 6d). The seepweed community in the coastal wetland had lower VA than the other three habitats (Fig. 6d). Although the VA of the island wetland mudflat was the largest, there was no significant difference in VA between the reed and seepweed communities. There was no difference in subsidence among the four habitats (df = 3, F = 0.141, P = 0.933; Fig. 6e).

We found that there were significant differences in above-ground length of seepweed seedlings among the four habitats (df = 3, F = 4.050, P = 0.009; Fig. 7a); the landward seepweed on the island had the highest above-ground length and also had higher length than the seaward seepweed on the island. There were no differences in below-ground length among the four
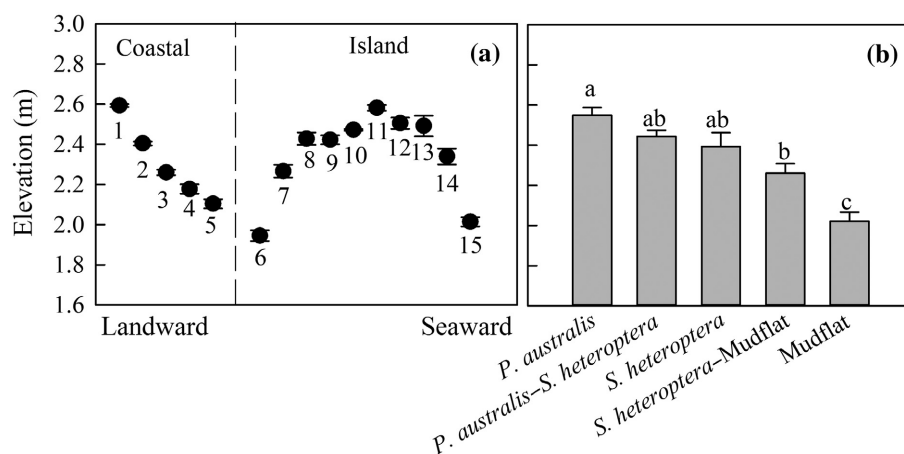

Fig. 5. Elevation along the estuary profile for both coastal and island wetlands of the Liao River Delta (left panel) and the elevation difference among five habitats (right panel). The numbers in the left panel stand for the elevation-measuring sites shown in Fig. 2c. The profile in the left panel is not to scale. The right panel represents the elevation difference between five habitats. Symbols in the figure are least-squares means (mean ± standard error, *n* = 9). The different letters above the bars represent the statistical differences among the habitats.
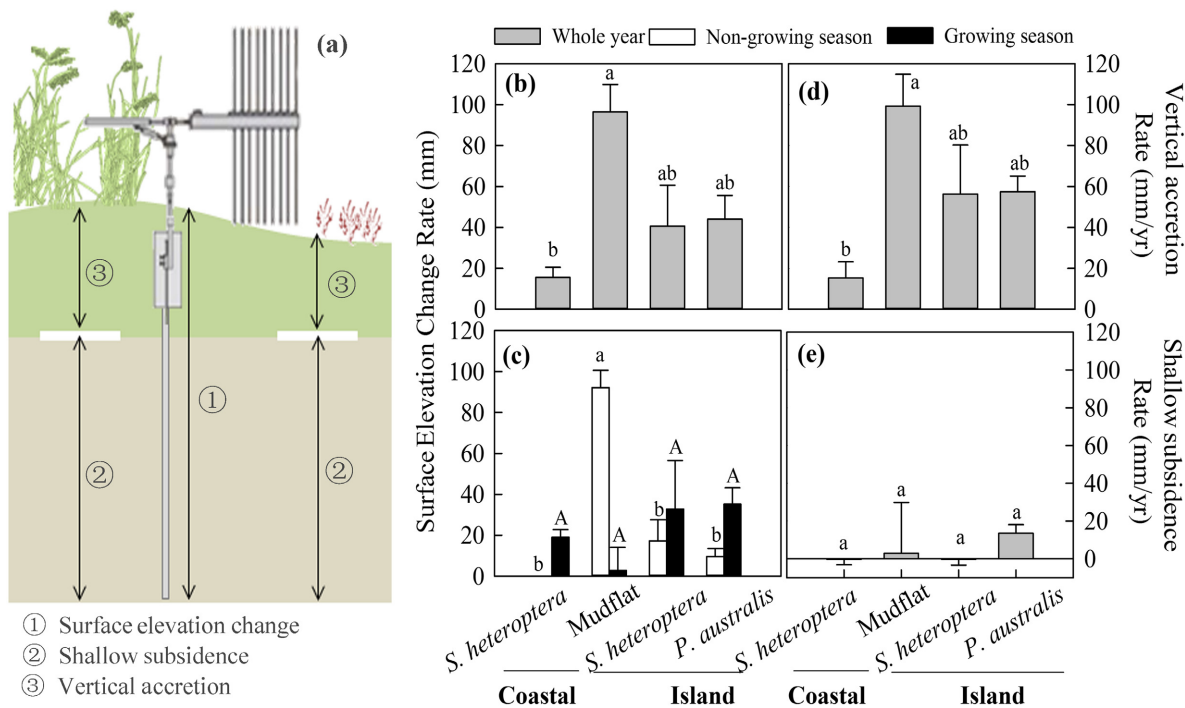
Fig. 6. The schematic and the results of the rod surface elevation table-maker horizon system (RSET-MH). (a) The RSET-MH installation monitors changes in soil surface elevation change (SEC), vertical accretion (VA), and shallow subsidence (SS) of four habitats in the coastal wetland (seepweed community) and island wetland (mudflat, seepweed, and reed community) in the Liao River Estuary Wetland (LREW); (b) all-year SEC; (c) non-growing and growing season SEC; (d) VA; and (e) SS. The different letters above the bars represent the statistical differences among the habitats.

habitats (df = 3, $F = 0.870$, $P = 0.459$; Fig. 7b). The below- to above-ground length ratios were different among the four habitats (df = 3, $F = 15.872$, $P < 0.001$). There were also significant interactions between seasons and habitats for below-ground length, above-ground length, and below- to above-ground length ratio (Appendix S1: Table S2). We also examined the effects of distance on the below- to above-ground length ratios for the seedlings of the island wetland. All comparisons (among all seasons) between geographic location and below- to above-ground length ratios exhibited moderate-to-strong correlations (Appendix S1: Fig. S2, all $P < 0.001$), indicating that the length ratio linearly increased with the decrease in the distance to the sea (Appendix S1: Fig. S2).

In the germination experiment, seed germination and seedling emergence were affected by sediment burial depth and time interactions

($P < 0.001$; see Appendix S1: Table S3). There was no *Suaeda heteroptera* emergence except in treatments with shallow sediment burial depth (1 and 3 cm; Fig. 8). During each cultivation period, sediment burial depths had large effects on seed germination (Fig. 8; Appendix S1: Table S3). The 1-cm burial led to higher emergence than the 3-cm burial treatment in all cultivation periods ($P < 0.01$ in all cases).

Top-down controls

Crab burrow density was significantly affected by habitat (df = 3, $F = 33.402$, $P < 0.001$), with the coastal seepweed community having higher crab burrow density than any other habitat in spring (Fig. 9a–c). The island mudflats had lower crab burrow density than the *Phragmites australis* habitats in summer and autumn. Moreover, there was no difference in burrow density between seepweed and reed communities in the island
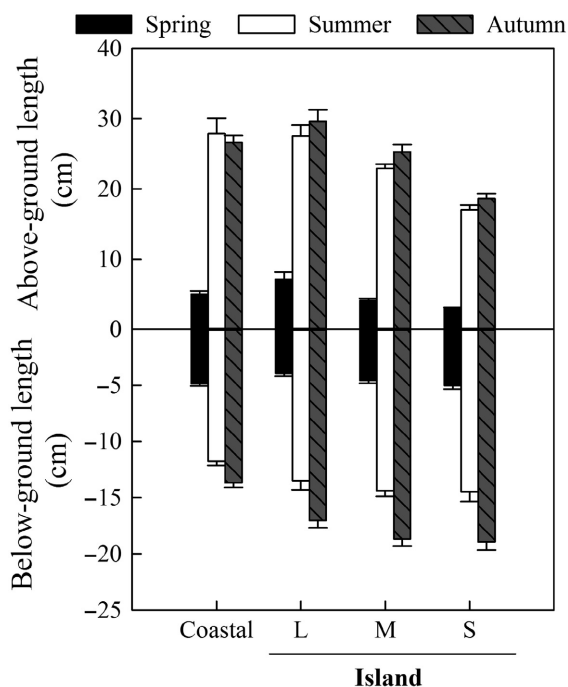
Fig. 7. Above- and below-ground length of seepweed along geographic locations for both coastal wetland and island wetland (L, landward seepweed; M, middle seepweed; S, seaward seepweed). The error bars stand for the standard error among sites.

Fig. 8. Experiment testing the effects of sediment burial depth and culture period on seed emergence. Data are presented as means ± standard error ($n = 6$ pots). The experiment consisted of five levels of sediment burial depth (1, 3, 5, 7, and 9 cm) and four levels of culture period (10, 20, 30, and 40 d). Test statistics are given in Appendix S1: Table S3.

wetlands. In the spring, the crab burrow density of *S. heteroptera* was higher in the coastal wetland than in the island wetland (df = 1, F = 346.774, $P < 0.001$), while the burrow density was lower in the unvegetated mudflat than in any vegetated habitats. In the summer, the coastal wetland had higher burrow density than the island wetland mudflats. However, the crab burrow density in *P. australis* and *S. heteroptera* community was higher than that in the unvegetated mudflat. This pattern was also observed in the autumn. Crab burrow density was affected by the two-way interactions between habitats and season (Appendix S1: Table S4).

Similarly, the coastal wetland had higher crab density than the island wetland, especially in the spring (Fig. 9d–f). In the summer and autumn, the crab density of the coastal seepweed was not different from that of the vegetated habitat on the island (seepweed and reed community) but higher than that of the mudflat habitats. However, crab density was not affected by the
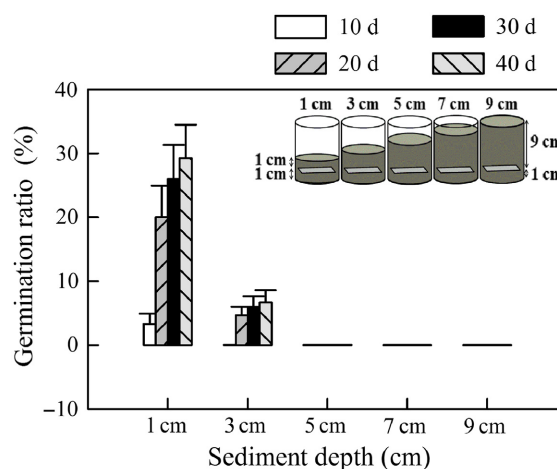
interactions between habitats and season (df = 6, F = 2.204, P = 0.059; Appendix S1: Table S4).

In the laboratory feeding trials, *Helice* consumed more *S. heteroptera* than *P. australis* (Fig. 10). The fresh weight of *S. heteroptera* consumed by *Helice* was 21 times higher than that of *P. australis* (means ± SE: 5.34 ± 0.45 g vs. 0.25 g ± 0.05 g; df = 17, t = 114.592, $P < 0.001$ in the mono-feeding treatment; 2.84 ± 0.22 g vs. 0.14 g ± 0.03 g; df = 16, t = 148.507, $P < 0.001$ in the mix-feeding treatment). The percentage of *S. heteroptera* consumed by *Helice* was higher than that of *P. australis* in the mono-feeding treatment (Fig. 10; means ± SE: 53.4% ± 4.47 g vs. 2.49% ± 0.50%; df = 17, t = 16.384, $P < 0.001$). The percentage of *S. heteroptera* consumed by *Helice* was also higher than that of *P. australis* in the mix-feeding treatment (means ± SE: 56.81% ± 4.39 g vs. 2.79% ± 0.63%; df = 16, t = 148.683, $P < 0.001$).

Waterbird species and abundance might be closely related to the construction of roads and boardwalks (Fig. 11; Appendix S1: Table S5). The number of waterbird species on the island wetland (21) was five times higher than that of the coastal wetland (4; Appendix S1: Table S5). The density of waterbirds in the island wetland was
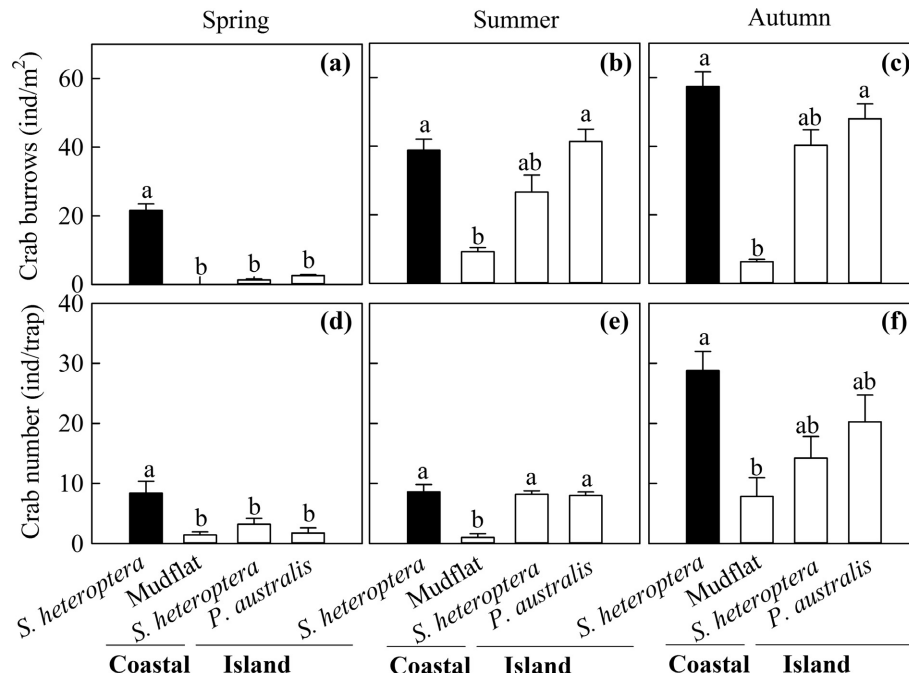
Fig. 9. Field observation with crab burrow count (a–c) and crab trap (d–f) testing the effects of habitat and seasons. The black bars represent the coastal areas, while the white bars represent the different habitats in the island wetland. Data are presented as means ± standard error.
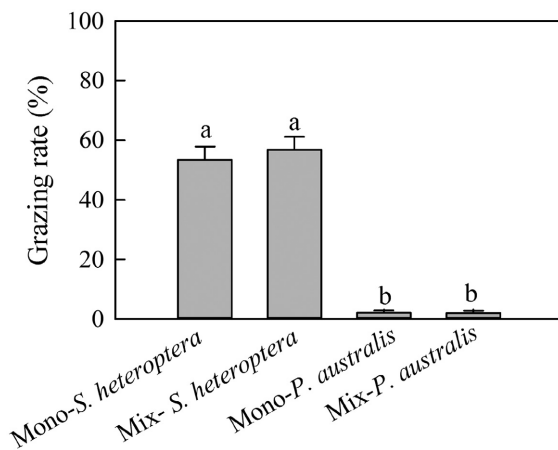

Fig. 10. Feeding trial with crab preference to *Suaeda heteroptera* over *Phragmites australis* in both mono- and mix-food source. Data are presented as means ± standard error ($n = 10$).

also significantly higher than that of the coastal wetland (5.37 ± 1.42 vs. 0.25 ± 0.09; df = 4, $t = 3.533$, $P = 0.024$; Fig. 11). The IUCN conservation priority endangered waterbird species
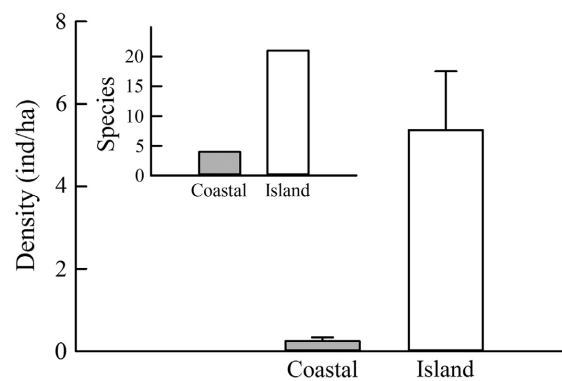

Fig. 11. Comparison of the number of species and density of waterbirds between the coastal wetland and the island wetland ($n = 5$).

such as *Ciconia boyciana*, *Grus japonensis*, and *Numenius madagascariensis* were only found on the island red beaches. Moreover, the number of vulnerable species *Larus saundersi* on the island wetland was larger than that on the coastal wetland (df = 4, $t = 3.445$, $P = 0.03$; Appendix S1: Table S5). A strong, negative relationship was

observed between crab density and waterbird density for the island wetland ($R^2 = 0.87$, $P < 0.05$; Appendix S1: Fig. S3), revealing that crab density decreased with the increase in waterbirds. There was no linear relationship for the coastal wetland likely due to low waterbird density ($R^2 = 0.66$, $P > 0.05$; Appendix S1: Fig. S3).

DISCUSSION

Some previous studies have shown that the red beach area experienced a dramatic loss in the 1990s and the early 2000s in the LREW mainly due to land use conversions (Jia et al. 2015, Tian et al. 2017). Our analysis based on the time series of Landsat imagery found that the red beach area also significantly decreased during the last seven years due to degradation. This loss of red beaches was mostly due to accelerated succession and replacement of seepweed by reed community, mainly occurring in high-marsh coastal wetland and in the high-elevation areas of the island wetland. Moreover, the expansion of red beach to unvegetated mudflat in lower elevation areas was restricted because the higher accumulation rate of mudflat sediment could lead to lower seed germination and seedling emergence rate, especially in the island wetland, and thereby limit the establishment of new red beaches. Based on our findings on the impacts of human activities (e.g., dam and port construction, tourism disturbances), we proposed a conceptual model (Fig. 12) illustrating the physical and biological drivers and their impacts on red beach succession/degradation. This model highlights how human activities influence top-down and bottom-up forces and accelerate the succession and degradation of red beaches. Our results suggest that both top-down and bottom-up controls affect the abundance, succession, and degradation of red beaches due to the additive effects with top-down and bottom-up controls acting in concert.

Sediment elevation plays an important role in the distribution of seepweed communities mainly by limiting seedling germination and emergence. The germination of seeds is related to the depth at which seeds are buried, and burial at shallow depths generally stimulates more germination and emergence and has stimulation to the morphological traits (Maun 1998). Excessive burial may prevent seedlings from emerging above the sediment surface and thus affect survival and seedling growth before it reaches the sediment surface, and the seeds are unable to germinate due to lack of oxygen, light, and temperature (Maun and Riach 1981, Zhang and Maun 1990). Our results revealed that deep sediment burial had large negative effects on seed germination and seedling emergence, and seeds could only geminate and emerge with sediment burial depth <5 cm. Matured seeds spread to the barren mudflats before December and are then covered by sediment till germination during the following April or May. The barren mudflat accumulated up to 10 cm of sediment during the non-growing season, which limited the germination and emergence of seedlings. A previous study suggested that seedling could emerge at a maximum of 10 cm depth in the Yellow River Delta mainly because of the increase in the length of hypocotyls and taproot (Sun et al. 2014). In addition, unlike our experiment based on one-time burial, this previous study used continual burial (burial of 1–5 mm/d) to simulate the sedimentation; the Yellow River also has a shorter ice period than the Liao River.

Moreover, seaward seepweed had lower above-ground length and higher below- to above-ground length ratio, indicating that sediment burial limited the growth of seepweed. Previous studies also indicated that soil SEC may play an important role in the degradation of seepweed (Tai et al. 2009). Seepweed seedling might be damaged due to the prolonged un-inundation period as the tidal water can remove the salt shell excreted from the leaves surface (Tai et al. 2009). Increased salinity of new mudflat soils resulting from lack of flooding and strong evaporation is one of the important reasons for the disappearance of red beach (Tai et al. 2009, Wang et al. 2010). Understanding the response of seedling to burial is essential for assessing the distribution and composition of plants in different communities (Maun 1994, Sun et al. 2014). Sediment accretion rate in the LREW substantially increased during the last few decades mainly because of human activities. The higher sediment accretion rate likely led to the degradation of red beaches and limited the establishment of new red beaches.
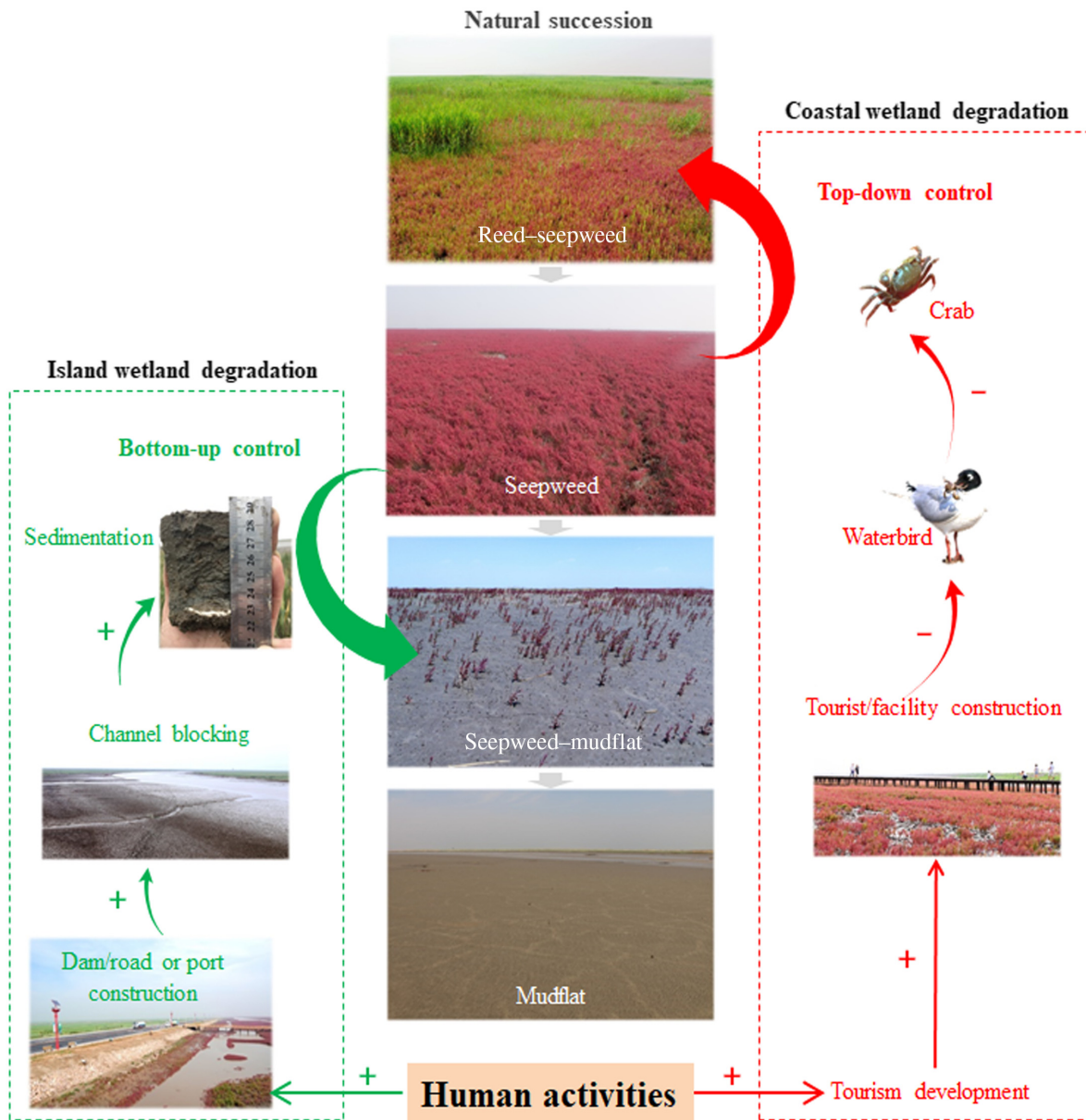
Fig. 12. Conceptual model of succession and degradation of red beaches in the Liao River Estuary Wetland based on the present research and assumptions.

Another type of driver limiting the distribution of salt marshes is top-down forces (e.g., herbivores). In contrast to sediment elevation effect in the island wetland, herbivory may have caused seepweed degradation in the coastal wetland (Fig. 12). Herbivore grazing was observed in both the laboratory feeding trials and field investigation, and crabs preferred seepweed over reed leaves in both mono- and mix-species treatments. The strong negative relationship between crab density and waterbird density in the island wetland was also found. These results suggested that consumer grazing may play an important role in controlling the emergence and growth of *Suaeda heteroptera* (He and Silliman 2016).

Crab grazing pressure was larger in the coastal area than that in the natural area (i.e., the island wetland), particularly in the period of seed germination and seedling emergence. Crab grazing could be an important factor that caused the significant degradation of seepweed in the coastal wetland. The higher density of crabs in this area was likely caused by the lower abundance of predators (i.e., waterbirds) in the coastal wetland area. Tourism is mainly concentrated on the salt marshes in the coastal area. The stunning red beach landscapes attract a large number of tourists annually. The construction of tourism facilities and the frequent presence of tourists likely led to the decrease in the abundance of waterbirds, which in turn increased the density of crabs. Previous studies conducted in salt marshes also showed top-down control by small invertebrate consumers including crabs, snails, and insects (Alberti et al. 2008, Daleo et al. 2009, Holdredge et al. 2009, He et al. 2015). Our results indicated that human activities (i.e., tourism) on the red beaches may indirectly cause the degradation of red beaches through cascade effects. Further control experiments focusing on the relationship among seepweed, crabs, and waterbirds should be implemented to confirm this finding in the future.

Sediment accretion and plant–herbivory changes, which might be induced by human activities, could be the two primary ecological processes leading to the degradation of the red beaches (Fig. 12). Anthropogenic forces can increase the intensity and frequency of these bottom-up and top-down forces through increasing sediment accretion rate, expelling predators, and influencing plant–herbivore interactions. Our study suggested that human activities indirectly amplified bottom-up (e.g., sediment elevation change) and top-down (e.g., grazing) controls. Island red beaches were mainly controlled by a bottom-up force (sedimentation), while coastal red beaches were mainly controlled by top-down forces (grazing and trophic cascade). Our study illustrated the coupled physical and biological responses of a coastal ecosystem to human activities. Our findings indicated that the red beach landscapes will likely be more vulnerable with the intensification of human activities.

Our study suggests how human activities induced the degradation of salt marsh red beaches by influencing both bottom-up and top-down forces. Conservation and restoration efforts of red beaches should consider the impacts of human activities. The emergence of seepweed seedling in the low marshes in the island wetland could be greatly enhanced if the sediment accretion rate could be slowed down by removing dams and thereby increasing runoff. Limiting and reducing tourism facility (e.g., boardwalks) and the presence of tourists are expected to increase the waterbird population, which in turn will reduce the crab density and thereby promote the growth of seepweed in the coastal area. Our findings have implications for the management and restoration of the salt marsh red beaches.

Conclusions

The red beach area in the LREW substantially decreased in recent several years due to degradation. The rapid degradation of the red beaches could be attributed to top-down and bottom-up forces amplified by human activities. The island red beach was mainly influenced by a bottom-up force (sedimentation), while the coastal red beach was mainly influenced by top-down forces (grazing and trophic cascade). Our results suggested that both bottom-up and top-down forces could exert strong control on the abundance and distribution of red beaches. Top-down and bottom-up forces could act in concert, and the effects could lead to rapid degradation of red beaches. Sediment accretion and grazing or trophic cascade effects were aggravated by human activities. Our findings have implications for the management and restoration of these salt marsh ecosystems.

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