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Invasive Smooth Cordgrass (*Spartina alterniflora*) Eradication and Native Crab Recovery

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Case Study

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Abstract

Invasive smooth cordgrass (*Spartina alterniflora* Loisel) eradication is important for the health of many coastal ecosystems. An integrated regime of continuous submergence after clear mowing, with three interval levels between mowing and submergence (5, 10, and 15 d) and three submergence depths (20, 30, and 50 cm), was implemented in cofferdams enclosing invader populations along a Chinese coast. In July of the following year, after the roots of mowed *S. alterniflora* had been submerged for 12 mo, some ramets grew under the regime with an interval of 15 d and the regime with a submergence depth of 20 cm, but no ramets occurred under the regimes with submergence depths of 30 or 50 cm and intervals of 5 or 10 d. Four crab species were documented: *Helice tridens tientsinensis* Rathbun, *Sesarma dehaani* H. Milne-Edwards, *Ocypode stimpsoni* Ortmann, and *Chiromantes haematocheir* de Haan. Biomass and abundance values of crab species in the cofferdams were similar to those in the mudflats but different from those in *S. alterniflora* populations. Thus, the treatment of submergence after mowing, which was implemented in the cofferdams, can control *S. alterniflora* and provide a mudflat-like habitat that promotes crab recovery if this treatment uses the proper combination of submergence depth and interval between mowing and submergence.

Introduction

It is imperative to effectively control invasive plants. An integrated regime for invasive plant control is a treatment in which one control method is followed by another. An increasing number of recent studies have shown that an integrated regime has higher control efficacy than a single method (Hammond 2001; Hedge et al. 2003; Patten 2002, 2003; Roberts and Pullin 2007; Shaw et al. 2016; Strong and Ayres 2016; Wang et al. 2006). For example, some studies have found that mowing followed by application of glyphosate can inhibit the growth and infestation of invasive species of the genus *Spartina* (cordgrass), more than when either method is used alone (Hedge et al. 2003; Patten 2002, 2003; Wang et al. 2006).

The high control efficacy of an integrated regime is believed to occur because such regimes incorporate dual treatments (Hammond 2001; Hedge et al. 2003; Shaw et al. 2016; Wang et al. 2006). However, while many studies have indicated the importance of different types of methods on the control efficacy of an integrated regime, the effects of the intensity of an integrated regime and the interval between the applied methods have been mostly ignored and are still unclear.

The intensity of a control regime is the energy released per unit area and time (Chapin et al. 2002). For example, fire intensity can be defined as the temperature that invaders experience, which may determine their probability of surviving the fire (Chapin et al. 2002). Thus, the intensity of an integrated regime could influence the control efficacy. The stress tolerance and resilience of a plant varies at different life-history stages and can be altered by disturbances (Gao et al. 2009; Tang et al. 2009), implying that the interval between the methods used in an integrated regime may influence the regime's control efficacy. Therefore, for an integrated regime to effectively control invaders, the appropriate combination of interval and intensity should be used.

Invasive species of the genus *Spartina* have invaded many marshes, from the Udale Gulf (57.61°N) in northern England to Amazon estuaries (near the Equator), and have changed the

Management Implications

An integrated regime for invasive plant control is a treatment in which one control method is followed by another, such as herbicide spraying after mowing. While an increasing number of studies have shown that such a regime has higher control efficacy than a single method, few of them have demonstrated whether control efficacy is influenced by the combination of the intensity of integrated regime and the interval between methods. Moreover, few studies have described how to apply ecological engineering to provide the necessary conditions for the implementation of an integrated regime. In this study, the integrated regime was continuous submergence after clear mowing, the interval of the regime was the time between mowing and submergence, and the intensity was submergence depth. The results illustrate that the proper combination of intensity and interval enables this regime to eradicate invaders and subsequently provide a habitat similar to bare soil, which promotes the recovery of some native consumers. Additionally, the results indicate that improper combinations limit control efficacy. Here, the cofferdams enclosing the populations of invasive smooth cordgrass (*Spartina alterniflora* Loisel) are built to retain water. The height of the cofferdam can be slightly more than 30 cm, which is the depth of the continuous submergence after clear mowing, and the *S. alterniflora* population enclosed in the cofferdam needs to be mowed within 10 d. Species of the genus *Spartina* that invade wetlands may be controlled in this way.

vegetation patterns and the structure of the trophic functional groups in these invaded marshes (Morgan and Sytsma 2013; Nieva et al. 2003; Strong and Ayres 2016; Wang et al. 2006). Alien *Spartina* competitively excludes the native plants on nearly every coast in China (Gao et al. 2009; Wang et al. 2006). Because these invaders have a higher root density than natives, such as *Phragmites australis* (Cav.) Trin and species in the Cyperaceae, crabs in the invaded populations are usually smaller in size, and consequently, the depth, length, diameter, branch number, and degree of sinuosity of their burrows are also lower (Wang et al. 2010).

Many efforts have been made to control these invaders, and most studies have focused on improving the control efficacy of a single method (Evans 1986; Gao et al. 2009; Mateos-Naranjo et al. 2009; Patten 2002, 2003; Pritchard 1996; Ranwell and Downing 1960; Roberts and Pullin 2007; Strong and Ayres 2016). Some studies show that the tide has a substantial influence on the ecophysiology and population dynamics of invasive *Spartina* (Abbas et al. 2012; Nieva et al. 2003; Wang et al. 2006). In our previous studies, the regrowth of smooth cordgrass (*Spartina alterniflora* Loisel) after mowing decreased from the dike to the seaward side of Dongtan marsh, located on the Chinese coast. This is because tidal water limits the respiration of the mowed invader, and mowing therefore has greater control efficacy in low marsh than in high marsh (Gao et al. 2009; Tang et al. 2009, 2010, 2013). These findings imply that an integrated control regime of continuous submergence after clear mowing, with an appropriate interval and intensity, may work well for eradicating *S. alterniflora*.

The interval of continuous submergence after clear mowing is the time between mowing and submergence. The intensity of mowing is the energy consumed by people or machines during the removal of *S. alterniflora* ramets; therefore, it does not directly influence the regrowth of the invader. The submergence depth can represent the energy that is released by anaerobic respiration of mowed *S. alterniflora* in water and can substantially influence the regrowth of mowed *S. alterniflora* (Gao et al. 2014). Thus, the intensity of the regime is represented by submergence depth.

To apply the integrated control regime of continuous submergence after clear mowing and subsequently find a proper combination of intensity and interval, ecological engineering was conducted in Dongtan marsh. This engineering consisted of creating earth cofferdams. These cofferdams enclose the invasive populations and retain water. Thus, submergence can be performed after mowing.

Recovery of crab populations can be considered an objective of invasive *S. alterniflora* management. Crabs are omnivorous crustaceans that consume diverse foods, including fresh plant material, litter, and carrion (Bortolus and Iribarne 1999; Gittman and Keller 2013). Moreover, crab burrows can significantly modify microtopography; improve soil aeration, oxidation, and penetrability; increase soil carbon and nitrogen; and decrease soil bulk density (Wang et al. 2010). Thus, crab populations and, subsequently, the distributions of their burrows, are associated with the transfer of matter and energy flow in wetlands; as a result, they can significantly influence nutrient availability for plants, including invasive *S. alterniflora* and native species (Bortolus and Iribarne 1999; Gittman and Keller 2013; Wang et al. 2010). Therefore, if practices for the control of invasive *S. alterniflora* can simultaneously improve the recovery of crab populations, the recovery of the components, structures, and functions of invaded wetlands will also be improved.

We predict that a proper combination of intensity and interval exists and will enable the integrated regime of continuous submergence after clear mowing to substantially reduce *S. alterniflora* populations, while also providing mudflat-like habitat conducive to crab recovery. We also predict that the ecological engineering of cofferdams will provide the proper conditions required to implement the regime. If so, this study would offer a method for controlling invasive cordgrass and restoring habitat for native crabs.

Materials and Methods

Invader Control

The experiment was conducted in Dongtan marsh (31°25′11.57″N to 31°37′27.25″N, 121°51′13.41″E to 122°01′54.64″E), located on Chongming Island in the Yangtze River estuary, Shanghai, China (Figure 1). The sediment type in Dongtan marsh is clay. From the dike to the seaward side of Dongtan marsh, the ground is submerged by tidal water for ca. 6 h/tidal cycle to ca. 40 h/tidal cycle (Tang et al. 2013). In this wetland, the canopy height of the *S. alterniflora* population varies considerably and, depending on growing conditions, can be as high as 250 cm; moreover, *S. alterniflora* can produce large amounts of aboveground dry biomass, for example, 1,640 ± 176 (g m^{-2}) (Gao et al. 2009).

The experiment was conducted as a two-factor design ($n = 3$), with three interval levels between clear mowing and continuous submergence (5, 10, and 15 d) and three depth levels for continuous submergence (20, 30, and 50 cm), which represent the intensity of the integrated regime.

These treatments were randomly distributed among the 27 earthen cofferdams that enclosed *S. alterniflora* populations. The cross section of the cofferdam wall was in the shape of an

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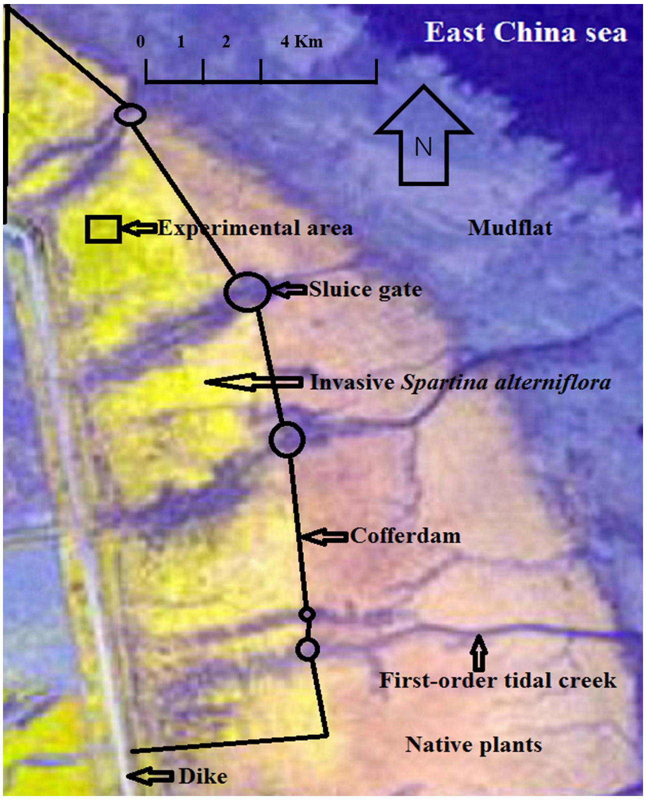

Figure 1. Diagram of the experimental area and the cofferdam construction locations in Dongtan marsh.

Figure 2. Experimental processes: A, cofferdams; B, experimental units; C, *Spartina alterniflora* eradication and gradual collapse of cofferdams.

isosceles trapezoid of 0.5 by 1.0 by 0.8 m (top length by bottom length by height), and the area of each cofferdam was 7.0 by 7.0 m (length by width) (Figures 2 and 3).

Spartina alterniflora ramets in the cofferdams were mowed using sickles, as close as possible to the ground, and then their roots were submerged. We mowed *S. alterniflora* in all cofferdams in early July, which we previously reported to be effective (Gao et al. 2009). Subsequently, we pumped reservoir water into the cofferdams for the continuous submergence treatment. The reservoirs include natural pools and puddles created when digging the mud to build the cofferdams. During the experiment, we monitored the water level every 2 wk and pumped water into the cofferdams when the water level dropped below the level required by the experimental design.

At the same time, 10 quadrats (7.0 by 7.0 m) were randomly established in the populations of *S. alterniflora* near the cofferdams. The populations within five quadrats were mowed once, and populations in the other five quadrats were not treated; thus, they served as a control (Figure 3).

We tried to eradicate *S. alterniflora* populations. Therefore, the ramet density of treated *S. alterniflora* was the best and most important index to estimate the efficacy of control. *Spartina alterniflora* is a perennial geophyte. Our previous studies showed that even though some populations of this plant suffered from high-frequency mowing treatments and could not sprout in the same year, they were able to grow the following year (Gao et al. 2009; Tang et al. 2009, 2010). Moreover, a study on the seasonal growth pattern of *S. alterniflora* showed that the ramet density of the plant did not significantly increase due to the onset of sexual reproduction (Gao et al. 2009). Thus, we determined that mowed *S. alterniflora* can be considered to be dead only if it has no ramets at the end of July in the following year. Therefore, we measured the ramet density of *S. alterniflora* in each treatment and the control on July 30 of the following year, when the roots of mowed *S. alterniflora* had been submerged for 12 mo.

Because the densities of *S. alterniflora* in some treatments were zero, the probability distributions of the data were not normal, and the variances were heterogeneous. Thus, the differences in density among the ecologically engineered (i.e., integrated regime), the single-mowing treatment, and the control were tested using the Kruskal-Wallis nonparametric test, with a post hoc test. Friedman's two-way analysis, with a post hoc test, was used to test the effects of submergence depth and interval on plant density. To conduct the post hoc test, we used a SAS (SAS Institute, Cary, NC) macro implementation of a multiple-comparison test, based on significant Kruskal-Wallis results from the SAS NPAR1 WAY procedure (Elliott and Hynan 2011). A P-value lower than 0.05 was considered to be statistically significant.

Crab Distribution

When we tested control efficacy, we documented crab species and estimated their abundances and biomasses among three habitats: areas in the cofferdams, *S. alterniflora* populations, and mudflats. The crabs were sampled using pitfall traps. The traps were cylindrical plastic buckets (45-cm diameter, 50-cm depth) buried in the soil so that the upper part was level with the soil surface. Five holes (2-cm diameter) were drilled in the bottom of each bucket to allow tidal-water flow.

After the floodwaters in the cofferdams were drained away, a trap was set in each cofferdam. At the same time, 27 traps were set in *S. alterniflora* populations, and 27 traps were set in mudflats. The distance between adjacent traps was 7.0 m. Thus, there was a trap in each 49 m^2 (7.0 by 7.0 m) of the *S. alterniflora* population and mudflat. Preliminary tests showed that crabs were

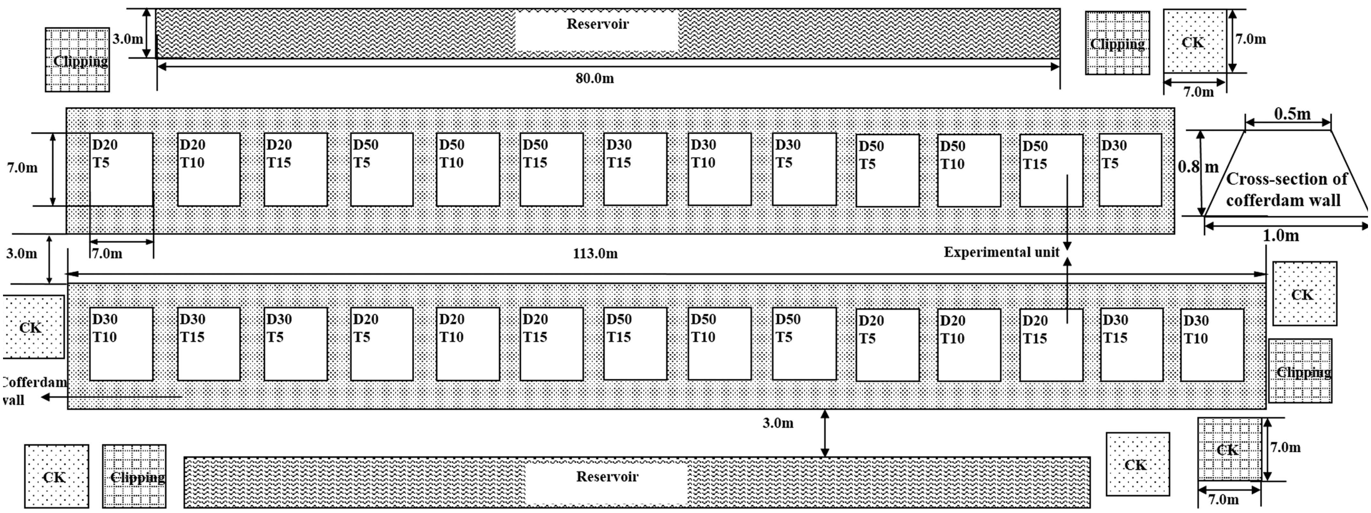

Figure 3. Schematic representation of the experimental layout in the study area. Submergence depths (D): D20, 20 cm; D30, 30 cm; D50, 50 cm. Interval between submergence and mowing (T): T5, 5 d; T10, 10 d; T15, 15 d. □, Experimental unit in cofferdam, ▧, reservoir created by digging the mud to build the cofferdams; ▦, earth dam; ⊞, mowing quadrats; ⊡, control quadrats.

unable to escape from the traps, and after 1 d, the crabs in the traps were collected.

The abundance and biomass of each captured crab species were measured. The biomass and abundance data could not be normalized by transformation. Therefore, Friedman's two-way analysis with a post hoc test was used to test the effects of habitat and crab species on biomass and abundance. Differences in biomass and abundance of each crab species among the cofferdams, invasive plant populations, and mudflats were tested using the Kruskal-Wallis nonparametric test, with a post hoc test. The post hoc test was the same as was used for analysis of invader control. A P-value lower than 0.05 was considered to be statistically significant.

Results and Discussion

Effects of Interval and Intensity

There was no significant difference in the density of *S. alterniflora* between the control and single-mowing treatment, and the density was ca. 307 ± 35 ramets m^{-2} (average ± SE); however, the density of *S. alterniflora* treated with submergence after mowing was much lower compared with densities in the control and the single-mowing treatment (Kruskal-Wallis nonparametric test, df = 2, $H = 22.09$, $P < 0.01$) (Figure 4).

Spartina alterniflora density declined when treated with submergence after mowing with a decrease in the interval between mowing and submergence (Friedman's two-way analysis, $\chi^2 = 25.91$, df = 2, $P < 0.01$); moreover, the density significantly declined with an increase in submergence depth (Friedman's two-way analysis, $\chi^2 = 35.22$, df = 2, $P < 0.01$) (Figure 5).

There were some ramets in the treatment with an interval of 15 d and in the treatment with a submergence depth of 20 cm (Figure 5). After evaluating different combinations of interval and intensity, we determined invasive *S. alterniflora* could be eradicated using the integrated regime with a submergence depth of 30 or 50 cm and an interval (time between mowing and submergence) of 5 or 10 d (Figure 5).

Abundance and Biomass of Crabs

Four species of crabs were captured: *Sesarma dehaani* H. Milne-Edwards (*Sesarma picta*), *Helice tridens tientsinensis* Rathbun, *Ocypode stimpsoni* Ortmann (*Uca arcuata*), and *Chiromantes haematocheir* de Haan (*Sesarma haematocheir*) (Figures 6 and 7).

There were significant differences among the biomass and the abundance of the four crab species (Table 1; Figures 6 and 7). The biomass and abundance of *H. tridens tientsinensis* was ca. 413.7 g 49 m^{-2} and ca. 55 individuals 49 m^{-2}, respectively, representing the highest biomass and abundance among the four crab species. Those of *C. haematocheir* were ca. 64.1 g 49 m^{-2} and ca. 6 individuals 49 m^{-2}, respectively; moreover, the biomass of *S. dehaani* was 51.5 g 49 m^{-2} and that of *O. stimpsoni* was 40.2 g 49 m^{-2}, and they had a similar abundance, which was ca. 5 individuals 49 m^{-2} (Figures 6 and 7).

The biomass and abundance of each species in *S. alterniflora* populations significantly differed from those in the mudflats and in the cofferdams, and there were no significant differences between the abundance and biomass of species found in the mudflats and the cofferdams (Table 2; Figures 6 and 7). The biomasses of *S. dehaani* and *C. haematocheir* in *S. alterniflora* populations were ca. 127% and 342% higher, respectively, than those in the mudflats or the cofferdams, and the abundances of these two crab species in *S. alterniflora* populations were ca. 192% and 390% higher, respectively; moreover, the biomasses of *H. tridens tientsinensis* and *O. stimpsoni* in *S. alterniflora* populations were ca. 67.3% and 70.7% lower, respectively, than those in the mudflats or the cofferdams, and

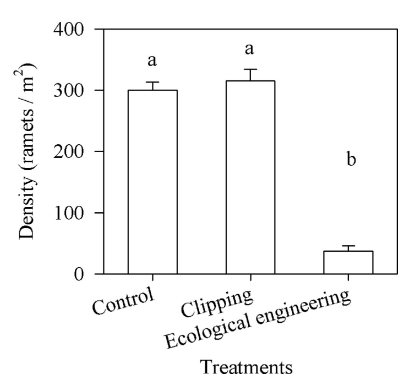

Figure 4. Effects of mowing and the integrated regime of continuous submergence after clear mowing (i.e., ecological engineering) on the density of *Spartina alterniflora*. Vertical bars indicate standard errors. The letters above the columns denote significant differences (Kruskal-Wallis nonparametric test, 5% significance level).

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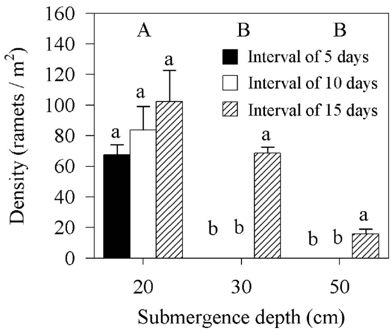

Figure 5. Effects of submergence depth and interval between mowing and submergence on the density of *Spartina alterniflora*. Vertical bars indicate standard errors of three replicates. Capital letters denote significant differences among submergence-depth groups; lowercase letters denote significant differences among interval groups (Friedman's two-way analysis for submergence depth and interval, 5% significance level).

the abundances of these two crab species in *S. alterniflora* populations were ca. 66% and 70.6% lower, respectively (Figures 6 and 7).

Importance of a Proper Combination of Intensity and Interval in Control Efficacy

Plants will allocate resources from remnants to buds or meristematic tissue for regrowth after defoliation (Briske and Richards 1995; Gao et al. 2014). *Spartina alterniflora* has developed rhizomes that store large amounts of oxygen and energy (Gao et al. 2014; Wang et al. 2006). These resources can be diverted to the buds or other aboveground parts for ramet regrowth after mowing (Briske and Richards 1995; Gao et al. 2014). Several days later, the resources in the rhizomes will be recovered due to anabolism and photosynthesis of the regrowing ramets (Briske and Richards 1995; Gao et al. 2014).

Thus, if the continuous submergence depth is too low, even if submergence occurs shortly after mowing, the regrowing ramets of *S. alterniflora* can grow out of the water using the stored resources in the rhizomes. On the other hand, if the interval between mowing and submergence is too long, even if the submergence depth is sufficient, the regrowing ramets can grow out of the water using the recovered resources (Gao et al. 2014; Tang et al. 2013). Once the ramets grow out of the water, they can provide oxygen and photosynthates that enable the whole clone to survive (Gao et al. 2014). This may be why there were some ramets when the treatment submergence depth was 20 cm and the treatment interval was 15 d. In contrast, when the submergence depth and the interval are appropriate, there may be too few resources left in the rhizome to support ramet growth out of the water; thus, the mowed *S. alterniflora* is asphyxiated (Gao et al. 2014).

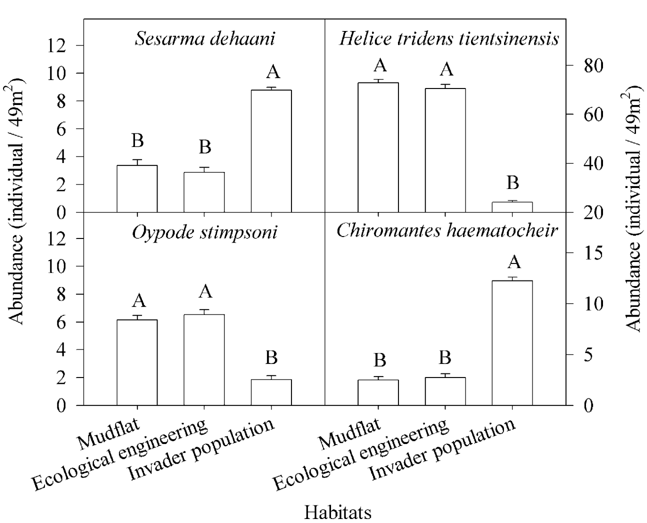

Figure 6. Differences in crab abundance among invader *Spartina alterniflora* populations, areas within the cofferdams (i.e., ecological engineering), and mudflats. The letters above the columns denote significant differences. Vertical bars indicate standard errors (Kruskal-Wallis nonparametric test, 5% significance level).

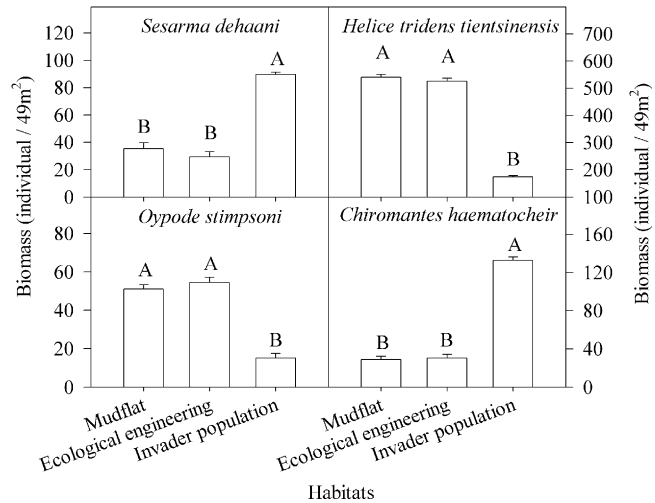

Figure 7. Differences in crab biomass among invader *Spartina alterniflora* populations, cofferdams (i.e., ecological engineering), and mudflats. The letters above the columns denote significant differences. Vertical bars indicate standard errors (Kruskal-Wallis nonparametric test, 5% significance level).

Previous studies have shown that invasive species of the genus *Spartina* can be efficiently controlled through an integrated regime of aboveground biomass removal followed by herbicide application (Hammond 2001; Hedge et al. 2003; Wang et al. 2006). The interval of the regime is the time between ramet removal and herbicide spraying. The intensity can be represented by the concentration of herbicide, as it reflects the energy that is released from the chemical reaction between the herbicide and the molecules in the plant cells. Some ecologists suggest that glyphosate should be applied at a concentration of 8.8 kg ha^{-1} when the new ramets of mowed *Spartina* reach heights of 30 to 45 cm; otherwise, this dual-treatment approach is time-consuming and expensive, with costs ranging from US\$1,700 to US\$3,700 ha^{-1} (Hammond 2001; Hedge et al. 2003). Both these findings and our results highlight the importance of using a proper combination of intensity and interval between treatment methods to maximize the control efficacy of an integrated regime.

Ecological Engineering

Ecological engineering can be used to create the required conditions for implementing an integrated regime (Bergen et al. 2001).

Table 1. Summary of Friedman's two-way analysis for the effect of habitat and crab species on the biomass and the abundance of captured crabs.

	Biomass			Abundance		
Source	df	χ^2	P	df	χ^2	P
Habitat	2	< 0.001	> 0.05	2	< 0.001	> 0.05
Species	3	131.01	< 0.001	3	146.46	< 0.001

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Table 2. Summary of Kruskal-Wallis nonparametric test on the difference in biomass and abundance of crab species among *Spartina alterniflora* populations, areas within the cofferdams (ecological engineering), and mudflats.

	Biomass				Abundance			
	Sesarma dehaani	*Helice tridens tientsinensis*	*Ocypode stimpsoni*	*Chiromantes haematocheir*	*Sesarma dehaani*	*Helice tridens tientsinensis*	*Ocypode stimpsoni*	*Chiromantes haematocheir*
df	2	2	2	2	2	2	2	2
H	54.07	54.38	53.63	53.77	49.75	49.59	53.41	53.91
P	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001

In this study, the cofferdams changed the topography and hydrology of the invaded regions in the Dongtan salt marsh, thereby creating a hypoxic environment for the mowed *S. alterniflora* (Gao et al. 2014). Thus, cofferdams should be built to enclose invasive *S. alterniflora* and retain water.

We recommend the use of this technique across large areas. The construction of cofferdams is a civil engineering project. The geotextile-encased sand-column method is recommended, because it is suitable for clay and sand sediment and is economical compared with other methods, such as the rear-anchored raking-pile solution (Yang et al. 2014). Geotextile columns are sunk into the sediment ca. 0.5 m, with a distance between the neighboring columns of ca. 15 m (Yang et al. 2014). Biodegradable, disposable, nonwoven cloth bags filled with clay are placed among the columns to complete the installation of the cofferdams.

To reduce costs, the height of the cofferdam should be as low as possible. According to our results, the height can be slightly more than 30 cm, which was an adequate depth for the continuous submergence treatment to function. Moreover, to facilitate water storage, the cofferdams should be constructed based on the distribution of tidal creeks along invaded coasts.

Wang et al. (2010) show that the tidal creeks of a coast can often be divided into three classes. First-order creeks, with a width of tens of meters, develop in high-tidal marshes and low-tidal mudflats and enter the subtidal zone (Figure 1). The width of second-order creeks is smaller but may be up to 10 m; these end at the outer margins of high-tidal flats. Third-order creeks, with a width of only approximately 1 m, are mainly distributed in the mudflats. The first-order tidal creeks are the main channels of tidal flow along coasts.

On the coastal section where experiments are conducted, some cofferdams should be built perpendicular to the first-order tidal creeks (Figure 1). These cofferdams should enclose the *S. alterniflora* populations that are closest to the sea. A sluice gate is needed at a first-order tidal creek to connect these cofferdams. Moreover, two cofferdams are needed to connect the dike and those cofferdams that are perpendicular to the first-order tidal creeks, and these two cofferdams should enclose the *S. alterniflora* populations that are located at the two ends of the coast (Figure 1). Thus, all invasive populations will be enclosed in the cofferdams.

According to our results, *S. alterniflora* ramets enclosed within a cofferdam need to be removed within 10 d. Then, water should be poured into the cofferdam, and the water level should be maintained until June of the following year. The sluice gates should be opened when the tidal level is higher than the water level in the cofferdams, and gates should be kept closed to retain water when the tidal level is low. During the submergence period, any leaks observed in the cofferdams should be repaired. Additionally, there may be higher regions in the microtopography of large areas. Thus, the submergence depth will be lower than 30 cm, and *S. alterniflora* may have some regrowing ramets that need to be removed.

After invasive *S. alterniflora* is eradicated, the ecological engineering provides a mudflat-like habitat for crabs. Thus, the biomasses and abundance of four crab species in the area of ecological engineering were similar to those in the mudflats. Notably, the performances of *S. dehaani* and *C. haematocheir* were greater in *S. alterniflora* sites than in the mudflats or ecologically engineered sites. The analysis of feeding preference proves that these two crab species consume invasive *S. alterniflora* more than twice as much as native plants such as *P. australis* and species in the Cyperaceae (Wang et al. 2010). Interestingly, some invasive plants such as *Impatiens glandulifera* Royle have a particular trait of pollen abundance; this invader can attract a higher visitor species richness, visitor abundance, and flower visitation than native plants (Lopezaraiza-Mikel et al. 2007). This implies that greater abundance of native animals in invader sites may simply be a result of decreased animal abundance in native plant sites rather than an absolute increase in their numbers. Thus, the reason for the greater abundance of those two crab species in *S. alterniflora* sites may just be that *S. alterniflora* offers a more suitable food source for the crabs, not that crab abundance increases after the invasion.

If so, the population sizes of *S. dehaani* and *C. haematocheir* would decrease over time, because *S. alterniflora* can have a negative impact on the crabs' development and reproduction (Wang et al. 2010). Moreover, the function of the two crab species will be limited. Because crabs burrow, they can entirely mix the surface and deeper layers of sediment over a period of 1 to 4 yr and accelerate litter decomposition (Gittman and Keller 2013; Silliman and Bortolus 2003; Wang et al. 2010). However, the size and the density of crab burrows in *S. alterniflora* sites, as mentioned in the "Introduction," are lower than those in native plant sites or mudflats (Wang et al. 2010). Thus, the crabs in *S. alterniflora* sites have a low effect on transfer of matter and energy. Consequently, the crabs have a limited ecosystem benefit in the entire marsh, because too many of them are in *S. alterniflora* sites.

After ecological engineering projects are implemented, natural processes take over, and the species composition is dominated by those that are best suited to respond to the conditions imposed upon the system (Bergen et al. 2001). In this study, when the invader is eradicated by the ecological engineering, that particular food source is eliminated, and the distributions of these crabs in the entire marsh will be recovered. Thus, the nutrients available to native vegetation and subsequently to other native species will be increased, prompting their recovery.

While the crab population distribution recovered, our cofferdams were gradually eroded by tides (Figure 2C). Similarly, if the cofferdams are constructed of biodegradable, disposable nonwoven cloth bags filled with clay, they will disappear over time. Cofferdams can also be constructed using encapsulated-air plastic, which can be easily collected. Managers have applied a similar ecological engineering effort in the Dafeng wetlands, Jiangsu province, China, to control *Spartina* populations and to prompt the recovery of native species and coastal topography, which was changed by invasive *S. alterniflora*.

Implications

Considerable resources have been invested in controlling invasive species of the genus *Spartina*, and management practices have evolved since the 1960s, from small-scale field trials to a large-scale integrated pest management programs (Evans 1986; Mateos-Naranjo et al. 2009; Patten 2002, 2003; Pritchard 1996; Ranwell and Downing 1960; Roberts and Pullin 2007; Strong and Ayres 2016). At present, the most effective *Spartina* control technique is a single-mowing event followed by glyphosate application (Hedge et al. 2003). The integrated regime of submergence after mowing applied in cofferdams can be expected to control invasive *S. alterniflora* in a single growing season and subsequently provide a habitat similar to bare soil that promotes the recovery of native crabs. More broadly, invasive species of the genus *Spartina* may be controlled using the integrated regime of submergence after mowing. These integrated regimes in which one control method is followed by another are efficient for controlling invasive plants when the regime includes the proper combination of intensity and interval between treatment methods; additionally, such an efficient regime subsequently provides habitat similar to bare soil, which promotes the recovery of some native consumers. Relevant ecological engineering can be conducted to create the conditions required for implementing an integrated regime.

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