Herbivory drives zonation of stress-tolerant marsh plants

Qiang He,[1] Andrew H. Altieri,[2] and Baoshan Cui[1,3]

[1]*School of Environment, State Key Laboratory of Water Environment Simulation, Beijing Normal University, Beijing 100875 China*
[2]*Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancon, Republic of Panama*

Abstract. Ecological studies of plant distributions along environmental gradients, such as plant zonation in salt marshes, have primarily focused on abiotic stress and plant interactions (competition and facilitation). A decades-old paradigm is that the stressful and benign boundaries of salt marsh plants are determined by abiotic stress and competition, respectively. Although consumers have long been recognized as mediating algal and sessile animal zonation in the rocky intertidal, their role in generating plant zonation in salt marshes remains largely unexplored. We examined the zonation of two annual succulents, *Salicornia europaea* and *Suaeda salsa*, along an elevation gradient in a northern Chinese salt marsh, with and without manipulating the common herbivorous crab *Helice tientsinensis*. *Salicornia* occupies waterlogged, low-salinity habitats, whereas *Suaeda* dominates non-waterlogged, hypersaline habitats at higher elevations. We first conducted a pot experiment crossing salinity, waterlogging, and competition, followed by a field experiment with removal of competitors, and found that neither waterlogging nor salinity stress explained the absence of either species from the other's zone, while *Suaeda* competitively excluded *Salicornia* from the upper non-waterlogged zone. We then conducted field and lab herbivory experiments, which showed that *Helice* preferentially grazed *Suaeda* at waterlogged low elevations and that *Helice* grazing on *Suaeda* increased with waterlogging. These results reveal that while competition plays a role in the zonation by excluding *Salicornia* from the upper *Suaeda* zone, crab grazing limits the success of *Suaeda* in the lower *Salicornia* zone. These findings challenge the idea that plant interactions and abiotic stress are sufficient to explain marsh zonation in all cases, and highlight an overlooked role of consumers, a role potentially general across diverse intertidal ecosystems. Future models of plant distributions should consider how consumer pressure interacts with plant interactions and abiotic stress across environmental gradients.

Key words: coastal wetlands; competition; consumer control; crab grazing; distribution patterns; plant interactions; Salicornia europaea; *salinity and waterlogging; salt marsh;* Suaeda salsa; *Yellow River Delta National Nature Reserve, China.*

Introduction

Understanding the determinants of species distributions is essential to advancing ecology as a predictive science (Agrawal et al. 2007). Species distributions are mediated by multiple factors, including abiotic stress and competition (Agrawal et al. 2007). The relative importance of these factors depends on environmental settings and species traits (Pennings and Callaway 1992, McGill et al. 2006). Interspecific competition has long been deemed the primary biotic driver of plant distributions (Goldberg and Barton 1992). It has been increasingly recognized, however, that competition switches to facilitation with stress, and that facilitation expands species distributions in stressful habitats (Bertness and Callaway 1994, Callaway 2007). Facilitation does not occur for every species, and can be more beneficial to stress-intolerant species than to stress tolerators (Liancourt et al. 2005). Although consumers

have been shown to mediate distributions in many cases, such as in rocky intertidal and coral reef ecosystems (Menge and Branch 2001, Hughes et al. 2007), their importance in other habitats is less well understood.

Salt marshes are an ideal habitat for studying the determinants of plant species distributions, because they are characterized by conspicuous patterns of plant zonation across steep abiotic gradients (Adam 1990). Marsh zonation has been studied throughout the history of ecology (Ganong 1903, Miller and Egler 1950, Pennings et al. 2005), yielding many fundamental theories for the discipline (Sousa and Mitchell 1999). Ecologists currently recognize that both abiotic stress, such as waterlogging and salinity, and plant competition contribute to marsh zonation (Pennings et al. 2005, Engels and Jensen 2010). Classic studies suggest that the stressful boundaries of marsh plants are determined by abiotic stress and facilitation, and their benign boundaries by competition with plants in more benign habitats (Bertness and Ellison 1987, Bertness 1991; hereafter the marsh zonation paradigm). These studies have often examined species that differ in their stress tolerance (Crain et al. 2004). Although recent studies suggest that

the relative importance of abiotic stress and competition may vary geographically and that in extreme situations either abiotic stress or competition alone generates zonation (Costa et al. 2003, Fariña et al. 2009, He et al. 2009), the general mechanisms of zonation depicted in this paradigm are suggested to be universal to salt marshes (Pennings et al. 2005).

In contrast to abiotic stress and plant interactions, the impact of herbivory on salt marsh zonation has not been generally recognized. The impacts of consumers in salt marshes, nevertheless, have been increasingly documented. Early studies on geese (Jefferies et al. 1979, Smith and Odum 1981, Rowcliffe et al. 1998, Van Der Wal et al. 2000, Kuijper and Bakker 2005), mammals (Ranwell 1961, Bakker and Ruyter 1981, Bakker 1985, Jensen 1985, Furbish and Albano 1994, Levin et al. 2002), insects (Olmstead et al. 1997), and parasitic plants (Callaway and Pennings 1998, Pennings and Callaway 2002) have shown that consumers affect the performance and community composition of salt marsh plants. Recent studies revealed that small herbivores, such as snails and crabs, can exert strong top-down control in salt marshes (Bertness and Silliman 2008, Alberti et al. 2010, 2012), and that herbivory can limit marsh seaward boundaries (Paramor and Hughes 2004, Alberti et al. 2010, 2012). Despite the accumulating evidence of top-down control of marsh plants, including observations that suggest a role for herbivory in marsh zonation (van Wijnen et al. 1997, Costa et al. 2003), experimental tests of whether herbivory mediates marsh zonation (especially zonation of two species) are lacking (but see Callaway and Pennings [1998] for parasitic plants and zonation).

Here, we examined the zonation of two annual succulents, *Suaeda salsa* (Linnaeus) Pallas (hereafter *Suaeda*) and *Salicornia europaea* L. (hereafter *Salicornia*; debates on *Salicornia* taxonomy exist, and all nomenclature here follows Anonymous [1979]), along an elevation gradient in a northern Chinese salt marsh. *Salicornia* and *Suaeda* exhibit striking zonation on the edge of tide pools in the high marsh, with *Salicornia* occupying the lower elevations and *Suaeda* dominating the higher elevations. Both species are obligate halophytes in the family of Amaranthaceae, and are known for their wide tolerances to salinity and waterlogging stresses (Ungar et al. 1979, He et al. 2009, 2012). The herbivorous crab *Helice tientsinensis* Rathbun (see Plate 1; Liu and He 2007; hereafter *Helice*) is abundant at the lower elevations, but its ecological relationship to these plant species has not been explored.

We first investigated whether the marsh zonation paradigm could explain the zonation of *Salicornia* and *Suaeda*. Using a pot experiment that crossed salinity, flooding, and competition treatments, we examined the hypotheses that competition or salinity limits *Salicornia* in the *Suaeda* zone and that competition or waterlogging limits *Suaeda* in the *Salicornia* zone. We then conducted a field experiment with competitor removal, to examine

the hypothesis that competition limits *Salicornia* in the *Suaeda* zone. Finally, we explored whether crab herbivory mediates the zonation by experimentally testing the hypotheses; (1) *Helice* grazing is more intense in the *Salicornia* than the *Suaeda* zone, (2) *Helice* preferentially grazes *Suaeda* rather than *Salicornia*, and (3) waterlogging in the *Salicornia* zone increases *Helice* grazing on *Suaeda*.

MATERIALS AND METHODS

Study site

Field work was conducted in a high marsh, located in the core zone of the Yellow River Delta National Nature Reserve (37°46′ N, 119°09′ E), northern China (see Fig. 1 in Cui et al. 2011). The climate is temperate monsoonal, with an average annual precipitation of 537.3 mm and an average annual temperature of 12.8°C (He et al. 2006). The tides are irregular semidiurnal, with an average tidal amplitude of 1.1–1.5 m (Hu and Cao 2003). The high marsh, flooded less than 20% of days per year, is often hypersaline, and is dominated by *Suaeda* (Cui et al. 2011), except for the edges of tide pools, which are dominated by a *Salicornia* band several meters wide. Tide pools are depressed, poorly drained areas in the high marsh that hold water <30 cm deep from high tides and precipitation, with salinities of 20–50 practical salinity units (PSU). Other plants that occur in the high marsh include *Tamarix chinensis* Loureiro, and *Phragmites australis* (Cav.) Trin. ex Steud.

Study species

Salicornia spp. are among the most salt-tolerant of plants in saline habitats (Ungar et al. 1979), and they are also tolerant of waterlogging (Cooper 1982), allowing them to occupy some of the lowest marsh zones (Paramor and Hughes 2004). Other factors influencing *Salicornia* success include competition and insect herbivory (Ellison 1987, Varty and Zedler 2008). At our study site, *Salicornia* occurs mostly at lower elevations on the edge of tide pools, and occasionally elsewhere in communities that are predominately *Suaeda*. *Salicornia* emerges in April and May, flourishes with heavy rains in late June/early July, then flowers in July and August, followed by seed dispersal in late fall.

Suaeda is widespread in the temperate salt marshes of East Asia. *Suaeda* is known for its wide tolerance to salt stress and waterlogging (He et al. 2009, 2012). In northern China, *Suaeda* is the only native plant species that spreads from low marshes through marsh terrestrial borders (Cui et al. 2011). At our study site, the phenology of *Suaeda* is similar to that of *Salicornia*, although *Suaeda* can flower until late September. *Suaeda* is competitively subordinate to perennial plants such as *Phragmites* and *Tamarix* (He et al. 2009, 2012). The relative competitive ability of *Suaeda* and *Salicornia* has not been examined previously.

Helice is a grapsoid crab distributed widely in East Asia, and is primarily herbivorous (Liu and He 2007,

Qin et al. 2010). At our study site, *Helice* is the only common crab, and it can be found from low marshes and mudflats to marsh terrestrial borders. *Helice* commonly occurs at densities of 10–30 individuals/m², with burrows having one to two surface openings (Zhou 1983).

Zonation survey

To document the zonation of *Salicornia* and *Suaeda*, we surveyed eight transects (8 m long) perpendicular to the zonation boundary on the edge of two tide pools (four transects per pool) in June 2013. The two tide pools were selected based on preliminary observations, and were representative of other pools at the study site. Eight 0.9×0.9 m quadrats were set every 1 m along each transect, four of which were located on the *Salicornia* side of the zonation boundary, and four on the *Suaeda* side. We estimated the percent cover of each species in each quadrat by dividing the quadrat into 100 9×9 cm cells and counting plant presence in each cell (Ewanchuk and Bertness 2004*a*). Crab abundance was estimated by counting the number of crab burrows in each quadrat. We collected soil cores and determined soil pore water salinity using the initial water content and the salinity of the water extracted from the soil cores (Pennings et al. 2005, He et al. 2009). The initial soil water content was determined by drying and reweighing the soil cores. To quantify waterlogging conditions, we used a water-level gauge and determined the relative elevation at five locations along each of six transects (three transects per tide pool): −4, −2, 0, 2, and 4 m from the zonation boundary (with 0 m being the boundary line). We did not survey eight transects or eight locations per transect due to logistical constraints. The elevation of the zonation boundary of the first transect was set to 0 cm. Salinity and waterlogging can fluctuate with time, but their relative differences between zones were consistent at our site (Cui et al. 2011). The effects of distance to the zonation boundary on crab abundance, salinity, and elevation were examined using ANOVAs followed by Tukey HSD multiple comparisons. Transect nested in tide pool was set as the blocking factor. Crab abundance and elevation data were sqrt($x + 1$)- and ($x + 10$)²-transformed, respectively, prior to ANOVAs. Analysis throughout this study was performed using R 3.04 (R Development Core Team 2013).

Does the marsh zonation paradigm explain the zonation of Salicornia and Suaeda?

To examine whether salinity, waterlogging, and competition interact to determine the zonation of *Salicornia* and *Suaeda*, we conducted a pot experiment at our field station, ~13 km from the field site. The experiment fully crossed three levels of salinity (30, 60, 90 PSU), two levels of waterlogging (waterlogged and non-waterlogged), and three levels of competition (*Salicornia*-only, *Suaeda*-only, and both species). Each treatment combination was replicated six times ($n = 108$

total replicates). In early June 2013, we excavated 150 soil blocks (15 cm diameter, 20 cm depth) containing mixtures of *Salicornia* and *Suaeda* seedlings from the high marsh, and transplanted each into a 2.5-L plastic pot. After a two-week acclimatization period, during which the plants were watered with fresh water, 108 pots (with plants showing no significant transplant shock) were randomly assigned to experimental treatments (extra pots were discarded). We thinned seedlings to 30 plants/pot for *Salicornia*-only treatments, 60 plants/pot for *Suaeda*-only treatments, and 30 *Salicornia* and 60 *Suaeda* plants/pot for their mixture treatments. These treatments were achieved by thinning a small proportion of their total, and *Salicornia* and *Suaeda* densities were within their natural ranges. For waterlogged treatments, pots were fully submerged in standing water, while for non-waterlogged treatments, standing water was ~15 cm below the soil surface. These waterlogging treatments simulated field conditions: the *Salicornia* zone was typically water-saturated, while the *Suaeda* zone had a water table >10–20 cm below the soil surface (although the land-surface elevation in the *Suaeda* zone was <10 cm higher than in the *Salicornia* zone). Salinity treatments were applied by adjusting the salinity of the standing water. Salinities were increased gradually to avoid shock, and experimental levels of salinities were reached after 10 d. We monitored and adjusted the salinities every 1–2 d by adding fresh water or sea salt. All of the pots were placed under plastic roofs. Eight weeks later, plant density in each pot was counted, and aboveground biomass was harvested, sorted by species, oven-dried at 60°C for 48 h, and weighed.

We used generalized linear models (GLM) to examine the effects of salinity, waterlogging, and competition on the performance of each species. The GLMs were analyzed using quasi-Poisson distribution with log link (to account for overdispersion) for density and gamma distribution with inverse link for biomass. The biomass data were ($x + 0.01$)-transformed to avoid zero values. The effects were tested by comparing the resulting deviances to Wald χ^2 test statistics (Type II sum of squares) using the car package (Fox and Weisberg 2011) in R. Post hoc tests of significant interactions were conducted using the testInteractions function in the R phia package (De Rosario-Martinez 2013).

To examine interactions between *Salicornia* and *Suaeda* under field conditions and to test whether competition limits *Salicornia* in the *Suaeda* zone, we further utilized vegetation patches that contained both *Salicornia* and *Suaeda* in the high marsh and conducted a competitor removal experiment. In late May 2013, we established 18 plots with similar densities of *Salicornia* and *Suaeda* and even distribution of both species. The plots were 0.5×0.5 m and spaced >2 m apart. Six of these plots were randomly assigned to each of three treatments: *Suaeda* removal, *Salicornia* removal, and control. Removal treatments were applied by gently uprooting all plants of a given species, while the control

plots were left un-manipulated. Since the plants were small (~5–8 cm), disturbances caused by uprooting were negligible. We repeated removals every two weeks as necessary. In early September, the density of each species in each plot was quantified, and aboveground biomass was harvested, sorted by species, oven-dried, and weighed. To examine the effect of competitor removal on each species, the density data were compared between neighbor control and removal treatments using one-way ANOVAs, and the biomass data were compared using Kruskal–Wallis tests.

Does crab herbivory vary between the Salicornia and Suaeda zones?

To examine whether crab grazing is more intense in the *Salicornia* than the *Suaeda* zone, we conducted a field herbivory experiment, in which *Salicornia* and *Suaeda* were transplanted reciprocally into each other's zone. In mid-June 2013, we established 0.5×0.5 m plots (with 2–5 m intervals) in each of the two zones, 2–3 m away from the zonation boundary. Soil blocks (10 cm diameter, 10 cm depth) with either dense *Salicornia* or *Suaeda* plants were haphazardly transplanted into each plot. Following a one-week acclimatization period, during which all of the transplants were watered with fresh water twice and temporarily covered with crab exclusion cages, each transplant was thinned to a similar density (mean ± SD: 85 ± 6 individuals per block for *Salicornia* and 88 ± 6 individuals per block for *Suaeda*). Six replicate plots were assigned to each of 16 treatment combinations in a fully factorial design with 2 species × 2 neighbor × 2 crab × 2 zone treatments ($n = 96$ total plots). We included the neighbor treatments to test whether neighbors affect crab herbivory on transplanted *Salicornia* and *Suaeda* through associational defenses, in which plants derive protection by neighbors from consumer grazing (Bertness and Callaway 1994). Neighbor removal treatments were conducted by uprooting plants within the plots. Crab exclusion cages (30 cm high) were constructed of galvanized hardware mesh (7-mm mesh size), inserted flush with the soil surface, and held by a PVC pipe. Transplants in crab exclusion treatments were also covered belowground with cages of similar design (but shorter, 10 cm high). We did not include cage controls, as our previous experiments with cages of the same design showed no difference between uncaged and caged control treatments (Q. He, *unpublished data*). The number of plants surviving in each plot was examined every 2–3 d, and quantified after 9 d, when a substantial number of plants in any treatment were eaten. We used survival as the response variable, as (1) no new emergence was observed, and (2) crabs often ate the entire aboveground part of *Salicornia* and *Suaeda*, both of which were small seedlings early in the growing season. We examined the effects of crab exclusion, neighbor removal, and zone on the survival of *Salicornia* and *Suaeda* using GLMs (quasi-binomial distribution with logit link) and post hoc analysis.

Do crabs preferentially graze Suaeda rather than Salicornia?

To examine whether *Helice* prefered grazing *Suaeda* over *Salicornia*, we conducted a lab feeding trial in mid-July 2013, generally following Pennings et al. (2001). Ten *Helice* (carapace width 27–30 mm) were captured and brought into the laboratory, and each was placed into a bucket ($30 \times 23 \times 10$ cm; width × length × height) covered with plastic mesh to avoid crab escape (1-cm mesh size). Each bucket held a thin layer of seawater (~0.3 cm) at the bottom to reduce desiccation. Fresh *Suaeda* and *Salicornia* plants (no flowering stems were observed at this time) were collected in the field, transported back to the laboratory on ice, and cut into 2–3 cm pieces. Five grams of each plant were tied with fishing line to two opposite sides of each bucket. The crabs were allowed to feed over three natural day/night cycles. We also set three replicate control buckets that had the same treatment but no crabs. Both *Salicornia* and *Suaeda* plants were available for consumption over the course of the experiment. After 72 h, *Salicornia* and *Suaeda* materials in each bucket were collected, oven-dried, and weighed. The amount of plant material consumed by *Helice* was calculated by subtracting the dry mass of plant remains in the crab addition treatments from the average of the control treatments. We also calculated the plant material consumed by *Helice* as a percentage of the average of the control treatments. *Helice* feeding preferences were examined using paired *t* tests (two-sided).

Does crab grazing on Suaeda increase with waterlogging?

To examine whether increased crab herbivory on *Suaeda* in the *Salicornia* zone is mediated by waterlogging, we conducted a common garden experiment that crossed waterlogging and crab addition treatments. In late May 2010, soil blocks (10 cm diameter, 10 cm depth) with *Suaeda* seedlings were excavated in the high marsh and transplanted into the common garden. Three soil blocks were planted triangularly in each of 24 tanks (0.9×0.9 m) filled with homogeneous salt marsh soils 30 cm deep. After two weeks of watering to reduce transplant shock, *Suaeda* plants in each soil block were thinned to 10 plants. We assigned six tanks to each of four treatments in a fully factorial design that crossed two waterlogging treatments (waterlogged, non-waterlogged) and two crab treatments (with crabs, without crabs). Waterlogging treatments were applied by flooding tanks with seawater collected from the field. Waterlogged tanks were flooded every other day, while non-waterlogged tanks were flooded once every week (see *Methods* in He et al. 2012). The soil in waterlogged treatments was always wet and water-saturated, and the soil in non-waterlogged treatments was dry and had salt accumulation on the surface, as occurred in the field. Four weeks after the waterlogging treatments were initiated, 16 *Helice* (carapace width 24–30 mm) were captured in the field and released into each tank. To
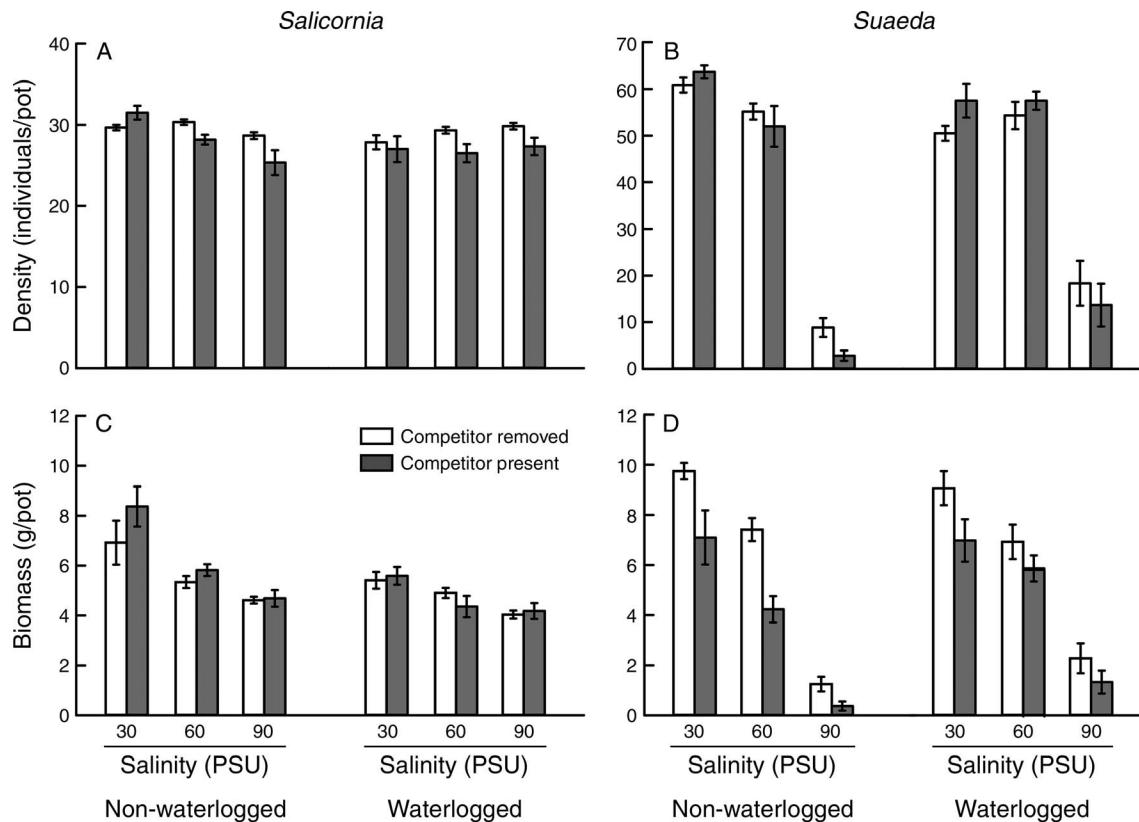
FIG. 1. Experiment testing the effects of salinity, waterlogging, and competition: (A, B) density and (C, D) biomass of *Salicorina europaea* and *Suaeda salsa* in each treatment. Experiments were conducted in 2.5-L pots. Data are means ± SE ($n = 6$ pots). The experiment had three levels of salinity (30, 60, and 90 practical salinity units; PSU), two levels of waterlogging (waterlogged and non-waterlogged), and three levels of competition (*Salicornia*-only, *Suaeda*-only, and both species). Test statistics are in Appendix B: Table B1.

reduce the likelihood of crabs escaping, each tank was surrounded by plastic netting on four sides (30 cm high). We checked the performance of crabs every other day in the first week, and the occasional dead or escaped crab was replaced. The performance of *Suaeda* in each tank was also examined. On day 13, when the majority of *Suaeda* in the waterlogged and crab addition treatments were consumed, the number of *Suaeda* surviving in each tank was counted, and aboveground biomass was harvested, oven-dried, and weighed. We examined the effects of crab addition and waterlogging on *Suaeda* survival and biomass using GLMs and post hoc analysis.

RESULTS

Zonation pattern

At the lower elevation below the zonation boundary, *Salicornia* had a mean cover of 40–60% (Appendix A: Fig. A1A). *Salicornia* occurred with a low cover in the *Suaeda* zone, but mainly within 3 m of the zonation boundary. In contrast, *Suaeda* was abundant at the higher elevation, having a mean cover of 50–70% (Appendix A: Fig. A1A). A few *Suaeda* were present

in the *Salicornia* zone, but *Suaeda* was completely absent >2 m below the zonation boundary.

Helice was most abundant in the *Salicornia* zone within 1–2 m of the zonation boundary (Appendix A: Fig. A1A). *Helice* density declined when it was measured further into either zone, and it did not differ between the two zones at distances >2 m from the boundary. Salinities were often higher in the *Suaeda* than the *Salicornia* zone (Appendix A: Fig. A1B). Elevation was also significantly higher in the *Suaeda* than the *Salicornia* zone (Appendix A: Fig. A1B), suggesting lower waterlogging stress in the *Suaeda* zone.

Does the marsh zonation paradigm explain the zonation of Salicornia and Suaeda?

In the pot experiment, *Salicornia* density (Fig. 1A) was significantly affected by the interactions between competition and salinity, and between waterlogging and salinity (significant at $P < 0.05$; detailed statistical results are provided in Appendix B: Table B1). In low-salinity treatments, the presence of *Suaeda* did not affect *Salicornia* density (post hoc analysis; 30 PSU: df = 1, 60, $\chi^2 = 0.21$, $P = 0.65$), while in higher-salinity treatments, it reduced *Salicornia* density (60 PSU: df = 1, 60, $\chi^2 =$
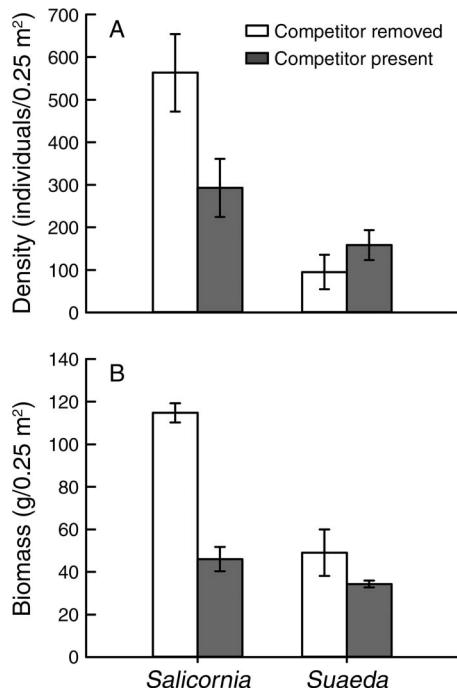
FIG. 2. Field experiment with competitor removal testing the effects of competition on the (A) density and (B) biomass of *Salicornia* and *Suaeda*. Data are means ± SE (*n* = 6 plots). The three competitor removal treatments are control, *Salicornia* removal, and *Suaeda* removal. See *Results: Does the marsh zonation paradigm explain the zonation of* Salicornia *and* Suaeda? for test statistics.

7.21, *P* = 0.007; 90 PSU: df = 1, 60, χ^2 = 10.12, *P* = 0.001). In non-waterlogged treatments, *Salicornia* density decreased with salinity (df = 2, 60, χ^2 = 15.17, *P* = 0.0005), while in waterlogged treatments it did not change with salinity (df = 2, 60, χ^2 = 1.55, *P* = 0.46). *Salicornia* biomass was significantly reduced by increased salinity and waterlogging, but was not affected by competition alone or its interactions with salinity and waterlogging (Appendix B: Table B1). These results suggest that in the *Suaeda* zone, where salinities are high and soils are non-waterlogged, competition and salinity limit the performance of *Salicornia*.

Suaeda density was significantly affected by the two-way interactions between salinity and competition, and between salinity and waterlogging (Fig. 1B; Appendix B: Table B1). In low-salinity treatments, the presence of *Salicornia* did not affect *Suaeda* density (post hoc analysis; 30 PSU: df = 1, 60, χ^2 = 1.13, *P* = 0.29; 60 PSU: df = 1, 60, χ^2 = 0.00, *P* = 0.99), while in high-salinity treatments, it decreased *Suaeda* density (90 PSU: df = 1, 60, χ^2 = 8.76, *P* = 0.003). *Suaeda* biomass was significantly affected by the interaction among salinity, waterlogging, and competition (Fig. 1D; Appendix B: Table B1). The presence of *Salicornia* decreased *Suaeda* biomass in non-waterlogged, high-salinity treatments (90 PSU: df = 1, 60, χ^2 = 9.83, *P* = 0.002), but had little effect in waterlogged conditions (*P* > 0.05 in all cases).

These results suggest that in the *Salicornia* zone, where salinities are low and soils are waterlogged, neither competition, salinity, nor waterlogging limits the performance of *Suaeda*.

In the field, the competitive effect of *Suaeda* on *Salicornia* was more substantial, reducing *Salicornia* density and biomass by ~50% (density: $F_{1,10}$ = 5.66, *P* = 0.0387; biomass: df = 1, χ^2 = 8.31, *P* = 0.0039; Fig. 2). In contrast, neither *Suaeda* density nor biomass was affected by *Salicornia* removal (density: $F_{1,10}$ = 1.38, *P* = 0.27; biomass: df = 1, χ^2 = 1.64, *P* = 0.20; Fig. 2).

Does crab herbivory vary between the Salicornia and Suaeda zones?

In the field herbivory experiment, *Salicornia* survival was significantly reduced by crab grazing in both zones, and was also affected by the two-way interaction between neighbor removal and zone (Fig. 3A; Appendix B: Table B2). However, the effect of crab exclusion on *Salicornia* survival did not differ significantly between the two zones (Fig. 3A; Appendix B: Table B2). *Suaeda* survival was significantly affected by the interactions between crab exclusion and zone (Fig. 3B; Appendix B: Table B2). *Suaeda* survival was reduced by crab grazing in the *Salicornia* zone (post hoc analysis; df = 1, 40, χ^2 =
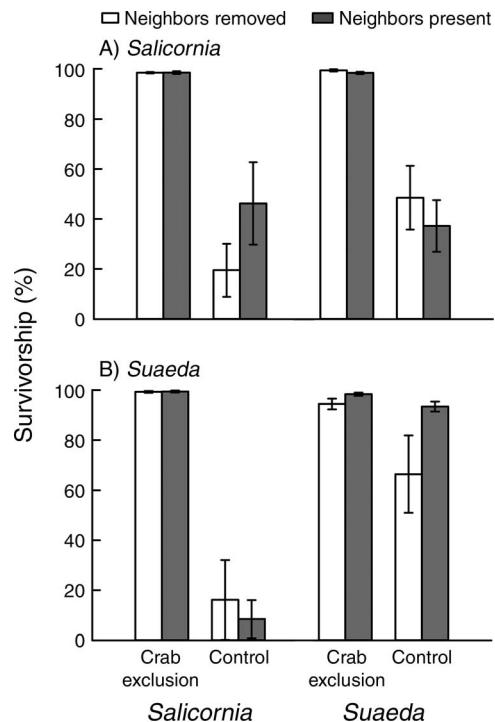

FIG. 3. Field herbivory experiment: (A) *Salicornia* and (B) *Suaeda* survivorship in each treatment. Data are means ± SE (*n* = 6 plots). The experiment had two levels of crab exclusion (exclusion and control), two levels of neighbor removal (removal and control), and two zones (*Salicornia* zone and *Suaeda* zone). See Appendix B: Table B2 for test statistics.

12.01, $P = 0.0005$), but not in its own zone (df = 1, 40, χ^2 = 2.52, $P = 0.11$).

Do crabs preferentially graze Suaeda rather than Salicornia?

In the lab feeding trial, *Helice* consumed significantly more *Suaeda* than *Salicornia*. The dry mass of *Suaeda* consumed by *Helice* was three times as high as that of *Salicornia* (mean ± SE: 0.51 ± 0.06 g vs. 0.17 ± 0.03 g; $t_9 = -7.40$, $P < 0.0001$). The percentage of *Suaeda* consumed by *Helice* was also higher than that of *Salicornia* (57.1% ± 6.2% vs. 35.8% ± 7.2%; $t_9 = -3.41$, $P = 0.008$).

Does crab grazing on Suaeda increase with waterlogging?

In the common garden experiment, *Suaeda* survival and biomass were both significantly affected by the interaction between crab herbivory and waterlogging (Fig. 4; Appendix B: Table B3). The negative effect of crab herbivory was stronger in waterlogged than in non-waterlogged treatments. Without crabs, waterlogging did not affect *Suaeda* survival (post hoc analysis; df = 1, 20, $\chi^2 = 1.56$, $P = 0.21$) or biomass (df = 1, 20, $\chi^2 = 1.45$, $P = 0.23$).

DISCUSSION

Classic studies of salt marsh plant zonation emphasized the role of competition and abiotic stress. Our study, however, reveals that herbivory can also be an important driver of marsh zonation. The herbivorous crab *Helice* prefers and more strongly impacts *Suaeda*, thereby allowing the competitively subordinate *Salicornia* to occupy the waterlogged lower elevations, where top-down control by crabs is most intense. Our finding agrees with rocky intertidal studies, where the role of consumers in generating zonation along environmental gradients has long been recognized (reviewed in Menge and Branch [2001]).

The role of competition

Our results show that competition plays a role in the zonation of *Salicornia* and *Suaeda*, mainly by limiting *Salicornia* success in the upper *Suaeda* zone, consistent with the marsh zonation paradigm. The competitive dominance of *Suaeda* over *Salicornia* was evident in both the pot and field experiments (in the pot experiment, *Suaeda* competition reduced *Salicornia* density, but did not affect biomass), and was especially strong in the field experiment. Additionally, our results do not suggest that *Salicornia* can replace *Suaeda* in the high marsh. Although *Salicornia* competition limited *Suaeda* performance in the non-waterlogged, highest-salinity treatment in the pot experiment, it did not in the other two salinity treatments or in the field experiment (perhaps because pot salinity treatments are harsher than field conditions). In contrast, the absence of *Suaeda* from the *Salicornia* zone cannot be explained by *Salicornia* competition. First, the presence of *Salicornia*
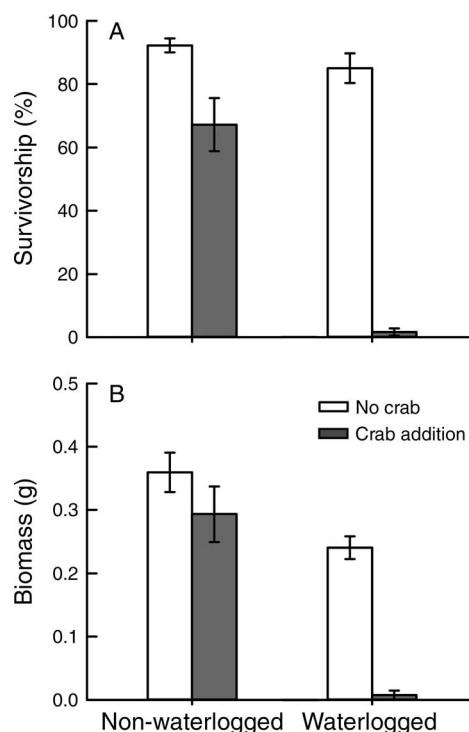

FIG. 4. Common garden experiment testing the effect of waterlogging on crab herbivory: (A) *Suaeda* survival and (B) *Suaeda* biomass in each treatment. Data are means ± SE (*n* = 6 plots). The experiment had two levels of crab addition (crab and no crab) and two levels of waterlogging (waterlogged and non-waterlogged). Test statistics are in Appendix B: Table B3.

had little effect on *Suaeda* in waterlogged conditions that mimic conditions at the lower elevations where *Salicornia* dominates. Second, as described, no competitive effect of *Salicornia* on *Suaeda* was observed in the field experiment.

Ineffective roles of abiotic stress

In contrast to competition, the role of abiotic stress as predicted by the marsh zonation paradigm was not evident in our study. Although waterlogging-induced anoxia has been previously found to limit the success of marsh dominants in forb pannes (Ewanchuk and Bertness 2004*a, b*), our results suggest that the absence of *Suaeda* from the waterlogged *Salicornia* zone is not mediated by waterlogging stress. First, waterlogging did not affect *Suaeda* performance. Second, *Suaeda* was more susceptible to salinity stress than waterlogging, but, paradoxically, salinity stress in its native zone has a more severe effect than waterlogging. The negative effect of increased salinity on *Suaeda* growth has also been previously documented (Song et al. 2011). In hypersaline habitats, *Suaeda* can still maintain abundant populations, likely through high seed production and vitality (Li et al. 2005, He et al. 2009). The wide tolerance of *Suaeda* to waterlogging has also been demonstrated experimentally in field conditions, and it is the only

PLATE 1. The herbivorous crab *Helice tientsinensis* and the two succulent plant species *Suaeda salsa* and *Salicornia europaea* at the study site. *S. salsa* plants have obvious leaf structures at the apex of their stems, in contrast to *S. europaea* plants with leaves undeveloped. Photo credit: Q. He.

native vascular plant that dominates the seaward borders of tidal marshes in northern China (He et al. 2009, Cui et al. 2011). Similarly, although salinity significantly reduced *Salicornia* biomass, the absence of *Salicornia* from the hypersaline *Suaeda* zone cannot be attributed to salinity stress, as (1) waterlogging, particularly at low salinities, as is typical of the *Salicornia* zone, had an effect on *Salicornia* comparable to high salinity, and (2) the salinity treatments had more detrimental effects on *Suaeda*, the dominant in this zone, than on *Salicornia*. A lack of abiotic stress effect on the lower limit of plants has also been observed in other salt marshes (Pennings and Callaway 1992, Costa et al. 2003, Fariña et al. 2009).

Consumer effects: mechanisms and generality

We found that *Helice* grazing in the lower waterlogged zone plays a prominent role in establishing marsh zonation. *Helice* restricts the competitively dominant *Suaeda* to the herbivory refuge at higher elevations, and thereby allows the competitively subordinate *Salicornia* to persist at lower elevations. *Helice* grazing on *Suaeda* was substantially more intense in the *Salicornia* than the

Suaeda zone, likely due in part to the highest *Helice* densities in the *Salicornia* zone, especially on the edge (not the interior) of tide pools. The high marsh at our study site is infrequently flooded and dry. The edges of tide pools, where desiccation stress is low, are typically preferred habitats of *Helice*. Although *Helice* densities were not higher in the *Salicornia* zone overall, two additional findings explain why *Salicornia* persists over *Suaeda* in this low zone. First, *Helice* preferentially consumes *Suaeda* when both species are available. Grazing preferences have been reported in other marsh crabs, and have been shown to mediate interactions among salt marsh plants (Costa et al. 2003, Alberti et al. 2008). Second, waterlogging in the *Salicornia* zone increases crab grazing on *Suaeda*. Other herbivorous marsh crabs are also more active in waterlogged than in non-waterlogged conditions (Alberti et al. 2007). Considering that stresses for both *Helice* (desiccation) and *Suaeda* (salinity) are less severe in the *Salicornia* than the *Suaeda* zone, top-down control is predicted to be higher in the *Salicornia* zone (Menge and Sutherland 1987; see Moon and Stiling [2002], and Stiling and Moon [2005] for relevant studies in salt marshes). We did find that

Helice also grazed *Salicornia* (in both field and lab feeding trials), but this interaction is unlikely to contribute to the zonation pattern because grazing rates on *Salicornia* did not differ between zones. Given that *Helice* is most abundant in the *Salicornia* zone, *Salicornia* is probably its main food (*Helice* prefers *Suaeda* but rarely encounters it). Moreover, *Salicornia* was less grazed with than without neighbors in its own zone, probably due to group benefits that buffered transplanted *Salicornia* from grazing (Bertness and Callaway 1994).

Our study adds to the growing literature on the importance of consumers in salt marsh ecological functioning. Importantly, our study is one of the first that experimentally reveals the role of consumers in generating marsh zonation. Herbivory has been suggested to limit the lower boundaries of marsh vegetation in Atlantic salt marshes of North America (Alberti et al. 2010), South America (Altieri et al. 2012), and Europe (Paramor and Hughes 2004). Our study extends this role of herbivory to the zonation of two different plant species. Our finding agrees with Costa et al. (2003), who suggested a potential role of crab herbivory in marsh zonation but provided no experimental evidence. The present study and others (Costa et al. 2003, Alberti et al. 2010) together suggest that abiotic stress (such as waterlogging) and herbivory can be simultaneously more severe in lower marsh zones, so both have the potential to determine the lower distribution limit of plants. Plant species intolerant to abiotic stress in lower zones should be limited by abiotic stress, while those that are stress tolerators may be limited by consumers. Additionally, plant zonation patterns may differ between ungrazed marshes and those grazed by large mammals such as livestock (van Wijnen et al. 1997), further lending support to the role of consumers on marsh zonation.

The role of crab herbivory in generating marsh zonation as revealed in our study agrees with the suggestion that crab selective predation mediates mangrove zonation (Smith 1987, Lindquist and Carroll 2004), although Sousa and Mitchell (1999) found no role for crab predation in mediating mangrove zonation. Our finding also agrees with a number of rocky intertidal studies, which have found that herbivory or predation commonly (though not in all cases) regulate algal and sessile invertebrate zonation by determining lower distribution limits (reviewed in Menge and Branch [2001]). For example, herbivory sets the lower limits of marine algae (Lubchenco 1980, Harley 2003), and predation mediates the zonation of barnacles and mussels (Menge and Branch 2001). However, whether consumers commonly mediate zonation in salt marshes (as well as in mangroves) needs to be further investigated with studies from more sites. Studies that examine consumer impacts across various marsh plants with contrasting traits (e.g., tolerance to abiotic stress vs. herbivory) or phylogenies will be informative. Further-

more, because consumers are generally thought to have stronger impacts on algae than on angiosperms (Gruner et al. 2008), the role of herbivores may be less important in salt marshes than in the rocky intertidal. Future studies that explicitly compare rocky intertidal and salt marsh habitats are needed to improve understanding of the relative importance of consumers in these habitats.

Studying stress tolerators to rectify gaps in ecology

The novel mechanism of marsh zonation shown in our study may be most apparent in plants that are stress tolerators (defined within the context of each system). *Salicornia* is widely tolerant of salinity, which is the major abiotic stress in the *Suaeda* zone, while *Suaeda* is tolerant of waterlogging, which is the major abiotic stress in the *Salicornia* zone. As a result, abiotic stress played no detectable role in their zonation. Likely due to trade-offs between competitive ability and defense against consumers (Viola et al. 2010), the competitively superior *Suaeda* occupies the upper zone with lower grazing pressure and displaces *Salicornia*, which is less susceptible to consumer grazing, to the lower zone with higher grazing pressure. Thus, competition and herbivory operate as the determinants of their zonation. This is in contrast to the zonation of plants with distinct differences in stress tolerance, which is often mediated by competition and abiotic stress (Bertness 1991, Pennings et al. 2005, Engels and Jensen 2010). Our work highlights the importance of studying stress tolerators in rectifying gaps in ecological understanding (see also Doi and Kikuchi 2009).

In conclusion, our study suggests that the marsh zonation paradigm built upon studies that did not directly consider herbivores cannot fully explain the zonation of *Salicornia* and *Suaeda*, and that crab grazing, rather than abiotic stress or competition, limits *Suaeda* in the *Salicornia* zone. Consumers are likely to play a common role in mediating zonation across diverse intertidal ecosystems. Future models of plant distributions should consider not only how plant interactions and abiotic stress change across environmental gradients, but also how consumer pressure couples or decouples with plant interactions and abiotic stress across environmental gradients.

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A and B are available online: http://dx.doi.org/10.1890/14-0937.1.sm