

Local and regional variation in effects of burrowing crabs on plant community structure

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Abstract. Burrowing animals can profoundly influence the structure of surrounding communities, as well as the performance of individual species. Changes in the community structure of burrowing animals or plants together with changing abiotic parameters could shift the influence of burrowers on surrounding habitats. For example, prior studies in salt marshes suggest that fiddler crabs stimulate cordgrass production, but leaf-grazing crabs suppress cordgrass production. Unfortunately, testing this prediction and others are impeded because few studies have examined crab impacts on the plant community and across multiple sites, multiple years, or both. This challenges our ability to predict how burrowing animals will influence plant community structure, and when and where these impacts will occur. We manipulated the densities of the dominant burrowing crabs in plant assemblages dominated by Pacific cordgrass (*Spartina foliosa*) and perennial pickleweed (*Sarcocornia pacifica*) at three sites in southern California for three years (2016, 2017, 2018). Crab impacts on plant community structure differed among each of our three sites. In contrast to our predictions, (1) leaf-grazing crabs (*Pachygrapsus crassipes*) had positive effects on cordgrass cover at one site and no effect on cordgrass production at a nearby site in the same marsh and (2) fiddler crabs (*Uca crenulata*) did not stimulate cordgrass production at another marsh. Because crabs affected traits of cordgrass, but not pickleweed, in the direction consistent with changes in cordgrass cover, we propose that marsh-specific crab effects on community structure were largely mediated through changes in cordgrass, as opposed to pickleweed. Importantly, crabs facilitated cordgrass during marsh-wide cordgrass loss, suggesting that crabs may mitigate environmental stress for this ecologically important plant. Because cordgrass abundance can be a critical measure of marsh functioning and is often a restoration target, we suggest that managing cordgrass populations would benefit from additional information about crab populations and their impacts among years, and among and within marshes.

Key words: burrowing animals; cordgrass; crabs; plant–animal interactions; salt marsh; spatial scales; temporal scales.

INTRODUCTION

Burrowing animals, such as earthworms, crabs, prairie dogs, ground squirrels, ghost shrimps, and rodents, are often considered to be ecosystem engineers given their influence on plant communities (Whicker and Detling 1988, Laundre 1993, Mulder and Keall 2001, Wilby et al. 2001, Davidson and Lightfoot 2008, Castorani et al. 2014, Craven et al. 2017). These animals can alter the total abundance of plant species (e.g., reducing vegetation cover), and their impacts on plants can vary both in size and direction. More subtle effects, such as the

direct and indirect effects on individual plant species, can influence plant community structure and are less understood. This is surprising given that such plant-specific effects may frequently influence ecosystem functioning (Fields et al. 1999, Eisenhauer et al. 2009, Andriuzzi et al. 2016). Few studies have tested these burrower effects across multiple sites, multiple years, or both, which challenges our ability to predict how burrowing animals will influence plant community structure, and when and where these impacts will occur.

Changes in the plant community by burrowing animals can affect important ecosystem functions, such as carbon and nutrient cycling (Vanni 2002, Andriuzzi et al. 2016), plant succession (Fields et al. 1999), and plant productivity (Eisenhauer et al. 2009). In temperate grasslands, earthworms can alter belowground competition and aboveground production of plants, which can

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benefit specific functional groups, and in turn, alter nutrient and carbon cycling (Eisenhauer et al. 2009, Andriuzzi et al. 2016). Similarly, in desert grasslands, prairie dogs and kangaroo rats can increase landscape heterogeneity by differentially altering plant community structure via their mound building, soil disturbance, nutrient input, and foraging (Davidson and Lightfoot 2008). In coastal salt marshes, burrowing crabs can influence plant communities by modifying plant zonation (Costa et al. 2003, Alberti et al. 2008), plant production (Bertness 1985, Bortolus and Iribarne 1999), plant colonization (Alberti et al. 2010), nutrient cycling (Smith et al. 2009, Holdredge et al. 2010, Fanjul et al. 2011), and erosion (Escapa et al. 2007, 2015, Alberti et al. 2015). Together, these studies suggest that burrowing animals may commonly impact ecosystem function by altering plant community structure.

Although the impact of burrowing animals on the composition of plant communities is known for some systems, the effect of burrowers on mixed plant assemblages is poorly known for other well-studied ecosystems, like salt marshes. For example, although a meta-analysis revealed that herbivorous burrowing crabs have overall negative effects on plants (e.g., reduced survival, density, biomass, and cover; He and Silliman 2016), it is unclear from these data what effect burrowing animals have on plant composition because (1) focusing on vegetation cover as a response variable could miss plant-specific effects, especially opposing responses of different plant species, and (2) most of the studies used in this analysis were conducted in mono-species stands (but see Alberti et al. 2007, He et al. 2015). In contrast, a broad survey of salt marshes across the United States found a weak relationship between crab burrow density and overall vegetation cover (i.e., percent unvegetated; Wasson et al. 2019), suggesting that environmental factors may outweigh the role of burrowing crabs. Although vegetation cover is an important parameter for marsh management, particularly in the face of recent marsh loss, marsh function is not simply a matter of vegetation cover: species identity matters. Interestingly, while the effects of burrowing crabs on salt marsh plant cover have been well studied, their impact on plant community structure has attracted little attention.

Burrowing crabs may commonly influence plant composition via two pathways. First, crabs could alter abiotic parameters that favor certain plant species (Smith et al. 2009, Fanjul et al. 2011, Natálio et al. 2017), thereby shifting interspecific interactions between plants. Second, crabs may preferentially graze plant species (Pennings et al. 1998, 2001, Ho and Pennings 2013). Such impacts should be most important in transition zones in salt marshes where dominant marsh plant species overlap in areas that often contain burrowing crabs (Zedler 1982, Costa et al. 2003, Alberti et al. 2008). These transition zones provide refugia for native and endangered species (e.g., Ridgway's Rail; Rosencranz et al. 2019), and increase local plant species richness

(Traut 2005). Unfortunately, these zones are more sensitive to sea-level rise due to restrictions on salt marsh transgression (Thorne et al. 2018, Rosencranz et al. 2019).

Similar to potential species specificity in how plants across ecosystems respond to burrowing animals, there is some evidence that these responses may be related to the ability of the animal to directly graze vegetation. For example, excluding folivorous prairie dogs increased vegetation cover (primarily by increasing the abundance of grasses), but excluding granivorous kangaroo rats had no effect (Davidson and Lightfoot 2008). Likewise, herbivorous crabs (*Sesarma reticulatum*) reduced cordgrass biomass in mesocosm studies (Szura et al. 2017), but detritivorous fiddler crabs (*Uca* spp.) stimulated cordgrass production at intermediate elevations (i.e., the tall zone of *Spartina alterniflora*, Bertness 1985). Consistent with these results, the meta-analysis by He and Silliman (2016) found that herbivorous crabs negatively affected marsh plants, but that omnivores generally had no effect on marsh plants. Together, these observations suggest that the size and direction of burrowing animal effects may depend upon the ability of the consumers to graze marsh plants directly. In salt marshes in particular, studies of different crab assemblages are needed to better understand this potential driver of spatiotemporal variability in crab effects.

Species- or assemblage-specific impacts of crabs could be important because crab communities often vary between habitat types within marshes, among marshes (Raposa et al. 2018, Wasson et al. 2019), and among years (Coverdale et al. 2013, Bertness et al. 2014b, Vu and Pennings 2018). A recent survey of 15 salt marshes across the United States indicated that burrow density, a proxy for crab density, (1) peaks around mean high water, (2) decreases with distance from tidal creeks, and (3) differs dramatically among marshes (Wasson et al. 2019). We hypothesize that this variability in crab distribution and abundance affects marsh vegetation. For example, massive die-offs of the dominant vegetation (*S. alterniflora*) in New England marshes (Bertness et al. 2014a) co-occurred with shifts in the crab community (Holdredge et al. 2009, Coverdale et al. 2013, Raposa et al. 2018).

The magnitude and direction of burrower effects on plant communities can vary with space and time; however, we lack an understanding of the mechanisms contributing to spatial and temporal variation in important animal-plant interactions for the broader system (Whitford and Kay 1999, Hastings et al. 2007, Coggan et al. 2018). For example, although burrowing crabs in salt marshes can modify important ecosystem functions, few studies have used manipulative experiments to test these effects across multiple sites, multiple years, and multiple species (but see Nomann and Pennings 1998, Bortolus et al. 2004, Holdredge et al. 2009). Because manipulative experiments hold other factors that could impact plants constant, we can more directly test for the variability of crab effects in time and space.

Here, we conducted a multi-site, multi-year, field manipulation to examine burrowing crab impacts on plant communities in transition zones of southern California salt marshes. We focused on the effects of crabs in salt marsh plant communities dominated by two plants, Pacific cordgrass (*Spartina foliosa*) and perennial pickleweed (*Sarcocornia pacifica*). We used this model system to explore the mechanisms underlying crab effects on plant communities by monitoring plant traits and sediment biogeochemistry. Because previous studies suggested that fiddler crabs can increase cordgrass production (Bertness 1985) and omnivores (e.g., *Pachygrapsus crassipes*) tend to have no effect on salt marsh plants (He and Silliman 2016), we predicted that (1) crabs would increase cordgrass cover at the site where fiddler crabs dominated the community (San Dieguito Lagoon) and (2) crabs would have no effect on cordgrass cover at the site where omnivorous crabs dominated the community (Kendall-Frost Marsh).

METHODS

Study sites and species

We conducted experiments at two marshes: Kendall-Frost Marsh (San Diego, California) and San Dieguito Lagoon (Del Mar, California). We deployed cages at two sites at Kendall-Frost Marsh (KF1 and KF2, 32°47'41.0" N, 117°13'46.4" W and 32°47'38.9" N, 117°13'41.4" W, respectively) and at one site at San Dieguito Lagoon (SDL, 32°58'47.0" N, 117°14'43.6" W). At both marshes, high and low elevations are dominated by pickleweed (*Sarcocornia pacifica*) and cordgrass (*Spartina foliosa*), respectively, and intermediate elevations are primarily a mixture of these two species. Subordinate plants were more common at Kendall-Frost Marsh, and included *Jaumea carnosa*, *Salicornia bigelovii*, *Batis maritima*, and *Triglochin maritima*. Subordinate plants may be less common at San Dieguito Lagoon because it is an active restoration site, where only *S. foliosa* and *S. pacifica* were transplanted in 2009 and 2011.

To compare the crab community in these marshes, we monitored crab sightings, burrow density, and burrow diameter. The two dominant burrowing crabs at these sites are *Pachygrapsus crassipes* (lined shore crab) and *Uca crenulata* (Mexican fiddler crab). The densities of these co-occurring crabs vary greatly between and within marshes in southern California (Zedler 1982, DeRivera 2003, Wasson et al. 2019). Rocky shore populations of *P. crassipes* graze macroalgae (Aquilino et al. 2012), and salt marsh populations consume macroalgae, horn snails (*Cerithidea californica*), detritus, conspecifics, and small invertebrates (Willason 1981, Zedler 1982, Sousa 1993, Boyer and Fong 2005). However, no studies have specifically measured herbivory on plants by salt marsh populations of *P. crassipes*. *Uca crenulata* are primarily deposit feeders (Hoffman et al. 1984). The burrowing

crab, *Hemigrapsus oregonensis* (yellow shore crab), also occurs in these marshes at much lower densities. Over the 3 yr working at these sites, *H. oregonensis* made up less than 1% of crab sightings (J. Walker, *personal observation*).

Experimental manipulation

To study the impact of crabs on the plant community, we manipulated burrowing crab access to plots at all three sites with cages from May 2016 to October 2018. We selected plots within the transition zone that contained burrows and mixture of cordgrass and pickleweed. Because most areas within the transition zone contained burrows, our plots are generally representative of transition zones. At KF1, plots were 2–3 m from the creek bank edge. At both KF2 and SDL, plots were adjacent to the main channel and ~30 and ~10 m from the water edge at mean lower low water (MLLW), respectively. Our manipulations included three levels of crab density (ambient, high, removal; $n = 5$). We started the experiment in 2016 with only ambient and removal plots. High crab density plots were added in year two (2017). Thus, the ambient and high crab density plots were in place for three and two growing seasons, respectively. Square plots were manipulated by installing plastic-mesh cages (mesh opening = 0.6 cm; $0.7 \times 0.7 \times 0.6$ m, length \times width \times height). Crab migration was minimized by inserting cages 30 cm into the substrate, and by attaching aluminum flashing to the top of cages (aluminum flashing did not change the height of the cage). Rhizomes were severed at all plot borders to prevent nutrient and resource exchange with outside plants. All plots were at least 1 m apart, and all cages remained in the field until October 2018.

Cage controls were created by cutting one large window (15×10 cm, height \times width) along the marsh surface into each side of the cage. Cage controls allowed for a test of the impact of caging structure, while allowing for migration of crabs into and out of cages. Cage control replication changed through time, from two in 2016 to five in 2017 and 2018. Control replication changed through time because we were initially limited on person hours to monitor additional replicates. Unmanipulated controls were marked with corner stakes (0.7×0.7 m plots) to monitor natural marsh habitat. All unmanipulated controls were established in 2017 ($n = 5$).

Two pitfall traps (empty tennis ball canisters, diameter = 7 cm, height = 20 cm) were installed at opposite diagonal corners of all cages. Holes were drilled at the bottom of the traps to allow for water drainage and ease of removal and replacement. These traps were consistent with those used in previous studies (Holdredge et al. 2009, Angelini et al. 2018, Wasson et al. 2019). Traps remained throughout the experiment and were replaced each year. For removal cages, we removed crabs from pitfall traps and from the plot substrate when they were visible outside of burrows. Closed pitfall traps were

installed in all other plots to standardize disturbance across treatments. Existing burrows in removal cages were filled with mud once from outside the cage at the start of the experiment (April/May 2016). After this time, burrows in removal cages were squeezed shut. We used burrow density as a proxy for crab abundance (sensu Martinetto et al. 2016, Angelini et al. 2018, Wasson et al. 2019).

All treatments were maintained every 2–3 weeks during the growing season of all years (April–October). During these visits, we repaired cages, removed crabs from removal cages, and added crabs to the ambient and high treatments as necessary. Crabs and burrows can disappear (e.g., crabs escape, burrows fill in, and/or crabs die), and without crab immigration into plots, overall crab numbers can go down. To adjust for this loss, crabs were added when burrow densities fell below the treatment's target number (i.e., when burrow density fell below the average burrow density in unmanipulated and cage controls [ambient plots] and when burrow density fell below 50% more than the burrow density in ambient plots [high plots]). During maintenance, we only added the dominant crab at each marsh; *U. crenulata* were added at SDL and *P. crassipes* was added at KF1 and KF2.

Crab community

The crab community was monitored throughout the experiment every 2–3 weeks during the growing season. We counted burrow number and recorded crab type when crabs were seen. Additionally, at three time points during the growing season (~April, July, and October), burrow diameter was measured across the opening of each burrow for 10 randomly selected burrows in each plot. We estimated burrow area per plot by multiplying the mean burrow density by the mean burrow area (calculating the area of a circle with burrow diameter) for each plot.

Plant cover and traits

During each growing season, we measured the percent cover of pickleweed and cordgrass and plant traits at three time points (~April, July, and October). We assessed the percent cover of the plant canopy nondestructively by placing a quadrat (0.5 × 0.5 m) on each plot and recording the uppermost species or substrate beneath 100 evenly spaced sampling nodes (4.5 cm apart). Percent cover was calculated by adding up the number of points containing each species/substrate and then dividing by 100. To help understand the factors contributing to changes in percent cover, we also measured species-specific plant traits. We haphazardly selected 10 cordgrass plants and measured plant height from the base of the plant (soil–plant interface) to the tip of the tallest leaf. We measured total cordgrass stem number by counting every stem within each cage, and we

recorded the number of flowering cordgrass stems. We also measured pickleweed canopy height: the distance from the soil–plant interface to the peak of the canopy.

In October 2018, we harvested all aboveground plant material to better understand crab effects on plant biomass. All plants were sorted by species per plot and frozen. Plants were thawed, dried at 60°C, and weighed. Then, we took a subsample of plots ($n = 15$; treatments: ambient, removal, and unmanipulated controls), and plants were homogenized by species per plot, subsampled, ground to a fine powder with a Wiley mill, placed into tin capsules, and measured for total carbon and nitrogen with a mass spectrometer (Stable Isotope Facility, University of California-Davis). The carbon to nitrogen ratio of each sample was calculated by dividing percent total carbon by percent total nitrogen.

Because burrowing crabs could impact belowground biomass (Szura et al. 2017), we also extracted sediment cores from the middle of each plot (~3,980 cm³). Cores were frozen until processed. Samples were thawed and sieved to extract plant roots. Roots were visually sorted without a microscope by species. Small-hair roots were classified as “unknown” due to our inability to efficiently differentiate between species and the volume of samples we needed to process. Following extraction and sorting, roots were dried at 60°C and weighed. Belowground biomass was then calculated for the entire plot (0.13 m³).

Biogeochemistry

To understand the abiotic parameters crabs modify, we analyzed porewater salinity, dissolved organic carbon (DOC), nitrate, and ammonium. Porewater was collected using 10 cm long, porous (0.15 μm) soil moisture samplers (Rhizophere Research Products, Wageningen, The Netherlands) inserted 10 cm into the soil at the start of the experiment. Porewater sippers were placed parallel to the mud surface to collect soil porewater at a constant depth. Porewater was sampled three times during the growing season (~April, July, and October) during low tide. Once collected, porewater was stored at –80°C until analyzed.

All soil water chemistry was analyzed using methods outlined in Lipson et al. (2012). Salinity was quantified with a refractometer. DOC, nitrate, and ammonium assays were all run with a spectrophotometer (SpectraMax 190; Molecular Devices, San Jose, California, USA). DOC was measured using an index of dissolved aromatic compounds and recording absorbance at 260 nm (A260) in UV-transparent microtiter. Nitrate was measured using a method involving vanadium III, Griess reagents with standards made from artificial seawater, and recording absorbance at 540 nm (Miranda et al. 2001). Ammonium was analyzed using a phenolate-hypochlorate chemical analysis with standards constituting artificial seawater and recording absorbance at 650 nm (U.S. EPA 1983).

Data analysis

We used generalized linear models (GLMs) when appropriate due to their ability to accommodate variance heterogeneity and non-normal distributions (Venables and Ripley 2002, Bolker et al. 2008). Goodness-of-fit statistics were calculated to determine the best distribution for each model. To evaluate the crab community, we tested for differences in burrow density and burrow diameter for each site and year. For both burrow density and burrow diameter, we ran GLMs with site and year as fixed terms. We used the mean burrow density and mean burrow diameter across the entire growing season (April–October) for each year.

Because (1) burrow density was only different between removal treatments and the other treatments (Appendix S1: Fig. S1), (2) burrow density varied largely within treatments (Appendix S1: Fig. S1), and (3) caging effects in salt marshes on plant growth are minimal/absent (McGuinness 1997, Lotze and Worm 2000, Holdredge et al. 2009, 2010, Angelini et al. 2018), we ignored treatment and tested for crab effects using burrow density as a continuous predictor variable in our models. For all response variables, we ran separate GLMs for each site (KF1, KF2, and SDL) with burrow density as a continuous predictor variable and year as a fixed term. Because of the heterogeneity of the habitat in salt marshes and because we wanted to explore the presence of between-year variation in crab effects, we treated plots across years as independent measurements. Such an approach is often adopted to document temporal patterns in the presence of heterogeneous communities (Murray et al. 2006). When necessary, post hoc tests were performed utilizing Tukey's HSD tests ($\alpha = 0.05$), and significant regression lines were reported if there was an interaction for each year at each site.

We analyzed plant metrics in the last sampling month in each year (either September or October). These months represent the end of the growing season for both cordgrass and pickleweed. We analyzed cordgrass and pickleweed cover separately in order to quantify crab effects on our two target plant species. For porewater characteristics, we analyzed the middle sampling month in each year (July). This month was selected to capture porewater changes occurring during the middle of the growing season and might, therefore, contribute to differences in plant metrics in October. Since C:N and biomass metrics were taken at the end of the experiment in one year (2018), we replaced year in our model with plant. Nonsignificant interactions for the GLMs are not presented in the results.

We also tested for crab effects with crab as a categorical variable grouping treatments by the presence and absence of crabs (crab [ambient crab density, high crab density, cage controls, and unmanipulated controls]; removal [removal]). This analysis was treated as a secondary analysis to the previous approach, and produced similar results. Therefore, we do not report this analysis in the results.

Statistical analyses were performed using R software vs. 3.6.0 (R Core Team 2019). GLM analyses were conducted using the lme4, nlme, and MASS packages for R. We tested significance of fixed effects with type III sums of squares using the Anova function in the car package.

Literature review

Because we wanted to identify how frequently studies examined between-year and between-site variation in the interaction between burrowing crabs and salt marsh plants, we performed a literature review of manipulative experiments. Although we recognize that other factors (e.g., elevation and distance to the nearest creek) can determine crab distribution and abundance in salt marshes, we focused on manipulative experiments to examine the impact of crabs independent of other environmental variables. Because a previous meta-analysis found weaker effects of crabs in consumer manipulations than observational studies (He and Silliman 2016), studies in our review should represent conservative impacts of crabs on plants. Additionally, He and Silliman (2016) did not examine the frequency of multi-year or multi-site studies of crab impacts on marsh plants. We searched an internet database, Web of Knowledge, to collect peer-reviewed research with the criteria ["burrowing crab" AND "salt marsh"] OR ["crabs" AND "salt marsh" AND "herbivory"] and a forward search on "Bertness 1985". We used the preferred reporting practices outlined by PRISMA to structure our overall literature search (Moher et al. 2009). The initial search yielded 363 papers. Of these, 64 papers mentioned testing the effects of burrowing crabs on plants, and of those, 51 papers included manipulations of burrowing crabs in the field. We focused our search on manipulative field experiments because field manipulations allow scientists to control for more confounding variables influencing plants (e.g., distance to creek bank, elevation, density of vegetation; Wasson et al. 2019). Results from observational experiments may be different and are worthy of consideration (He and Silliman 2016), but these are outside the scope of this current study. For each study, we identified the number of sites (this could include multiple sites at a single marsh) and the number of years across which the primary response variable was measured. Studies were classified as "Multi-year" when they measured the response variable across multiple years. A description of the results can be found in Appendix S1, as well as Appendix S1: Tables S1, S2.

RESULTS

Crab community

We found marsh-specific differences and annual variation in crab burrow density and burrow diameter, and crab composition. Site and year interacted to influence burrow density (Fig. 1A; GLM [gamma], $\chi^2 = 24.12$,

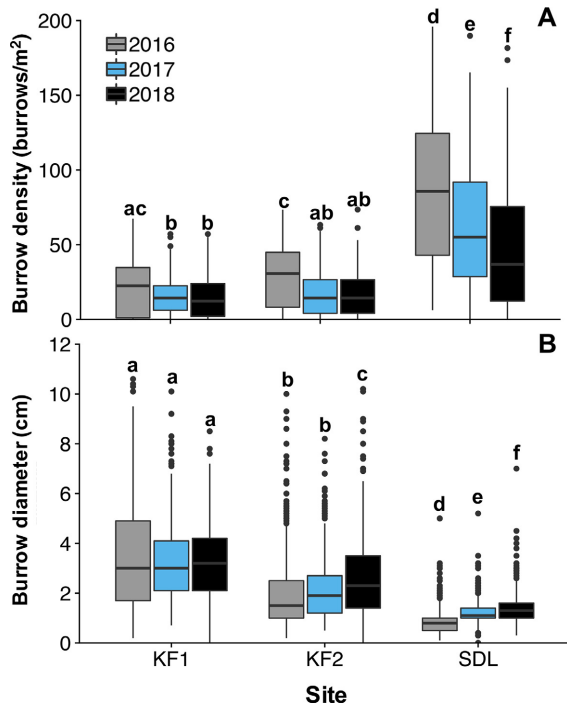


FIG. 1. (A) Crab burrow density and (B) crab burrow diameter averaged across the growing season (April–October) in 2016, 2017, and 2018 at KF1, KF2, and SDL. Lines inside boxes are median values, box limits are first and third quartiles, and whiskers represent non-outlier ranges. Points represent outliers ($>1.5\times$ and $<3\times$ the interquartile range beyond either end of the box). Letters represent significant interactions between site and year (Tukey HSD test; $\alpha = 0.05$).

$df = 4$, $P < 0.001$), with burrow density decreasing each year at SDL, but only decreasing between 2016 to 2017 at the other two sites (Fig. 1A; year: $\chi^2 = 104.70$, $df = 2$, $P < 0.001$). Across all three years, SDL had $\sim 3\times$ more burrows as KF1 and KF2 (mean \pm SE = 61 ± 2.0 , 17 ± 1 , and 20 ± 1 , respectively; site: $\chi^2 = 1,010.39$, $df = 2$, $P < 0.001$).

Similar to burrow density, site and year interacted to influence burrow diameter (Fig. 1B; GLM [gamma], $\chi^2 = 290.22$, $df = 4$, $P < 0.001$). This interaction was explained by an increase in burrow diameter over time at KF2 and SDL, but not KF1 (year: $\chi^2 = 86.04$, $df = 2$, $P < 0.001$). In general, burrow diameter differed among our sites with $KF1 > KF2 > SDL$ (Fig. 1B; 3.3 ± 0.1 cm, 2.3 ± 0.0 cm, 1.2 ± 0.0 cm, respectively; site: $\chi^2 = 3,036.72$, $df = 2$, $P < 0.001$).

Because burrow diameter differs between *P. crassipes* and *U. crenulata* due to differences in crab size, differences in burrow size among sites provided an indirect and non-destructive method to describe the crab composition at our sites. Importantly, burrow size distributions matched crab composition in the number of crab sightings and crabs caught in pitfall traps (e.g., smaller burrows were found in areas with more fiddler crabs;

Appendix S1: Table S3). Across all three years, we saw 90% more fiddler crabs (*U. crenulata*) in our plots at SDL than either KF1 or KF2. Additionally, total burrow area per plot was higher at KF1 (47.8 ± 4.08 cm²) than KF2 and SDL (28.9 ± 2.7 cm², 18.9 ± 1.37 cm², respectively). At SDL in 2018, we saw 2.5 \times more *P. crassipes* than the other two years. This was consistent with decreases in burrow density and increases in burrow diameter at this site during 2018.

Plant cover and traits

Cordgrass and pickleweed responses to burrowing crabs varied between marshes. Burrow density influenced cordgrass and pickleweed cover, but only at KF2 and SDL, and the direction of the crab effect was opposite at these two sites (Table 1, Fig. 2). Cordgrass cover increased with burrow density at KF2 (Fig. 2B), the site dominated by the omnivorous crab, *P. crassipes*, but decreased with burrow density at SDL (Fig. 2C), the site dominated by fiddler crabs, *U. crenulata*. Crab impacts on cordgrass were also associated with opposing impacts on pickleweed cover at KF2 and SDL (Fig. 2E and F, respectively). Across all three sites, cordgrass and pickleweed cover varied across years (Table 1, Fig. 2). Although burrow density never interacted with year to affect cordgrass or pickleweed cover, there were trends for crab effects at KF2 to be stronger in 2017 and 2018, and for crab effects at SDL to be stronger in 2016 and 2018.

Neither burrow density, nor the interaction of burrow density with year, impacted unvegetated cover at KF1 or SDL (Table 1, Fig. 2G and I, respectively). In contrast, burrow density interacted with year to influence unvegetated cover at KF2 (Table 1, Fig. 2H). At this site, burrow density increased unvegetated cover in 2017 and 2018, but not 2016. However, even in 2017 and 2018 at KF2, the percentage of the plot that was unvegetated remained $<5\%$.

Similar to the lack of a crab burrow effect on plant cover at KF1 (Fig. 2A), burrow density did not impact plant aboveground biomass at KF1 (Fig. 3A, Appendix S2: Table S1). At this site, burrow density also did not interact with plant species to affect aboveground biomass. Although there was no main effect of burrow density on aboveground biomass or a burrow density \times plant species interaction at KF2 (Fig. 3B), there was a trend for burrow density at this site to decrease pickleweed and increase cordgrass biomass, a trend consistent with the increase in cordgrass percent cover by crabs at this site (Fig. 2B). Finally, burrow density and plant species interacted to influence aboveground biomass at SDL (Fig. 3C; Appendix S2: Table S1). Upon further inspection, this interaction was driven by a negative relationship between burrow density and aboveground biomass for cordgrass but not pickleweed. Crabs decreasing aboveground biomass for cordgrass was

TABLE 1. Output table of generalized linear models of plant community and plant trait metrics.

Site		Dependent variables											
		Cordgrass cover		Pickleweed cover		Unvegetated cover		Cordgrass plant height		Cordgrass stem density		Pickleweed canopy height	
Factors	df	χ^2	<i>P</i>	χ^2	<i>P</i>	χ^2	<i>P</i>	χ^2	<i>P</i>	χ^2	<i>P</i>	χ^2	<i>P</i>
KF1													
Burrow density	1	0.8537	0.3555	1.8218	0.1771	0.468	0.494	0.395	0.530	0.135	0.714	6.294	0.0121
Year	2	7.4402	0.0242	10.736	0.0047	16.025	<0.001	44.636	<0.001	86.616	<0.001	4.128	0.127
Year × Burrow	2	0.1255	0.9392	0.5870	0.7457	3.772	0.152	0.610	0.737	2.647	0.2688	6.144	0.0463
KF2													
Burrow density	1	7.271	0.0070	9.122	0.0025	0.717	0.397	1.475	0.225	0.761	0.383	2.698	0.1005
Year	2	31.037	<0.001	35.579	<0.001	47.853	<0.001	55.099	<0.001	18.084	<0.001	28.474	<0.001
Year × Burrow	2	1.557	0.459	1.554	0.460	9.084	0.0107	6.885	0.0320	5.179	0.0750	2.171	0.338
SDL													
Burrow density	1	10.689	0.0012	28.805	<0.001	0.0016	0.969	1.787	0.181	15.755	<0.001	0.00094	0.9756
Year	2	8.3485	0.0154	5.7296	0.057	5.092	0.0809	4.140	0.126	15.598	<0.001	1.966	0.3742
Year × Burrow	2	0.4664	0.792	0.9316	0.6276	1.766	0.414	0.325	0.850	0.375	0.829	0.267	0.875

Notes: Results of GLMs testing burrow density and year effects on plant cover and plant traits at the end of each growing season for KF1, KF2, and SDL. Gaussian distributions were used for cordgrass cover, pickleweed cover, unvegetated cover (SDL), cordgrass plant height, cordgrass stem density (KF1, SDL), and pickleweed canopy height. A gamma distribution was used for unvegetated cover (KF1, KF2) and cordgrass stem density (KF2).

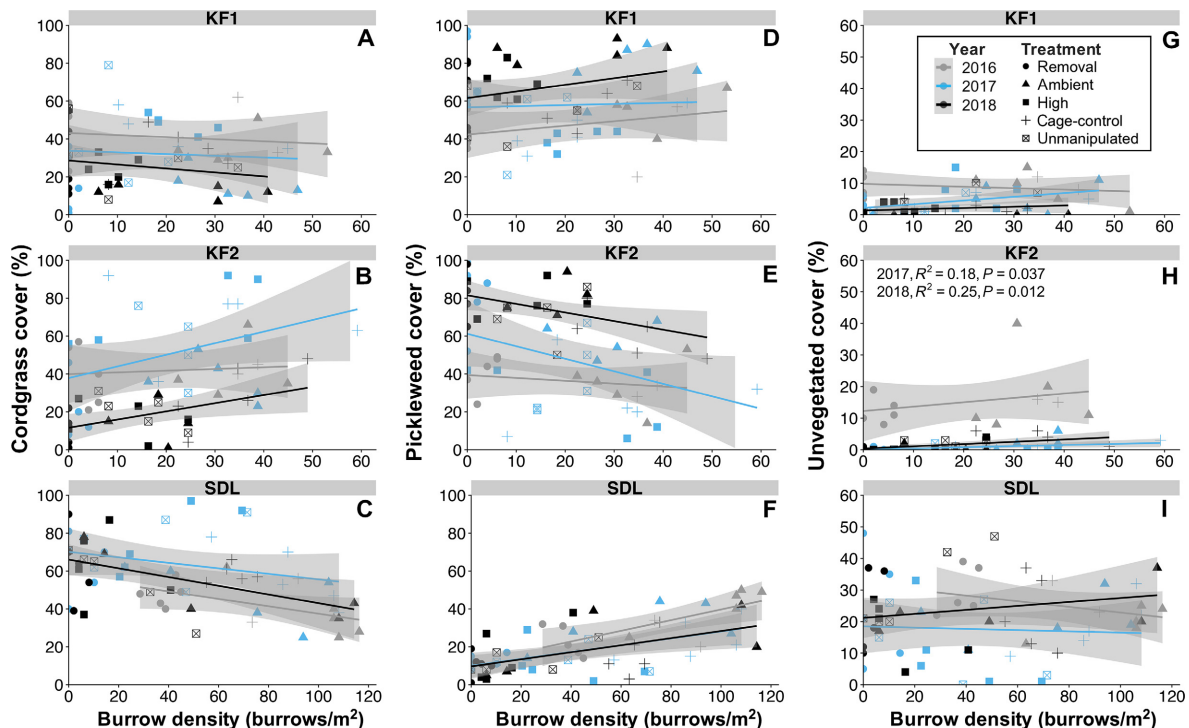


FIG. 2. (A–C) Cordgrass cover, (D–F) pickleweed cover, and (G–I) unvegetated cover vs. burrow density measured at the end of the growing season (September or October) in 2016, 2017, and 2018 at KF1, KF2, and SDL. Lines represent linear regressions for each site × year combination; R^2 is reported for significant interactions of burrow density and year.

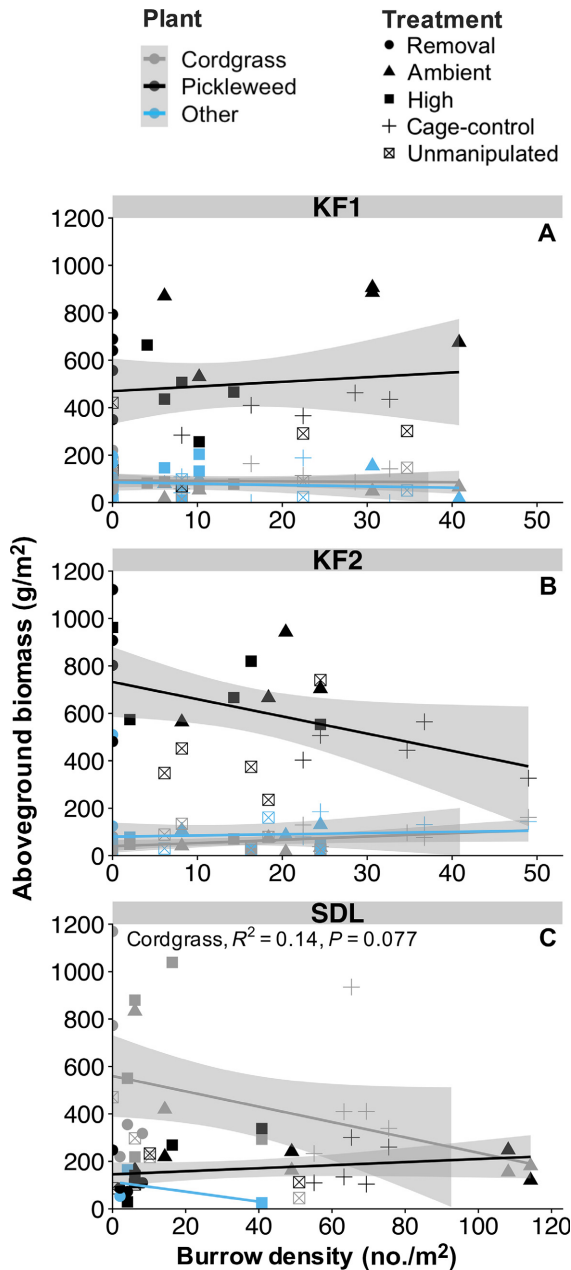


FIG. 3. Aboveground biomass (g/m²) vs. burrow density measured at the end of the growing season (September or October) in 2018 at (A) KF1, (B) KF2, and (C) SDL. Lines represent linear regressions for each site × plant combination; R^2 is reported for significant interactions of burrow density and plant.

consistent with the decrease in cordgrass percent cover by crabs at this site (Fig. 2C).

At the site level, the effects of crabs on cordgrass abundance were often in a direction consistent with crab effects on assemblage characteristics of cordgrass (e.g., increases in cordgrass cover were associated with

increases in cordgrass stem height and density). At KF1, crabs (mostly *P. crassipes* dominated) did not affect cordgrass cover (Table 1, Fig. 2A), aboveground biomass (Fig. 3A), plant height (Fig. 4A), or stem density (Fig. 4D). However, at KF2, where crabs (mostly *P. crassipes* dominated) increased cordgrass cover (Table 1, Fig. 2B) and tended to increase cordgrass aboveground biomass (Fig. 3B), burrow density interacted with year to influence cordgrass height (Fig. 4B) and stem density (Fig. 4E). Importantly, at KF2, burrow density sometimes increased cordgrass height (2017) and stem density (2018), which was consistent with positive effects of crabs on cordgrass at this site. At SDL where crabs (mostly *U. crenulata* dominated) decreased cordgrass cover and aboveground biomass (Figs. 2C, 3C), crabs did not affect cordgrass height (Fig. 4C), but did decrease cordgrass stem density (Fig. 4F). Crabs did not affect the number of flowering cordgrass stems at any of our sites (Appendix S2: Fig. S1).

Cordgrass traits differed between our marshes. For example, cordgrass plants were ~35% taller at SDL (84 ± 2 cm) than KF1 and KF2 (55 ± 1 cm and 56 ± 1 cm, respectively). Also, across all years and treatments, SDL had more flowering stems (28 ± 3) than KF1 and KF2 (2 ± 0.3 and 3 ± 0.4 , respectively; Appendix S2: Fig. S1). The final cordgrass stem densities after each growing season also suggested that KF1 and KF2 experienced a marsh-wide die-off of cordgrass between 2016 and 2017—losing 60% and 35% of cordgrass stems, respectively. However, we never observed die-off at SDL.

Unlike cordgrass traits that were often impacted by crabs in a direction consistent with the impacts on cordgrass abundance, crab impacts on pickleweed traits rarely were consistent with crab impacts on pickleweed abundance. At KF1, burrow density interacted with year to influence pickleweed canopy height, a pattern driven by a positive relationship between these variables in 2018, but not other years (Table 1, Fig. 4G). These results were inconsistent with the lack of an effect of crabs on pickleweed cover and aboveground biomass at this site (Figs. 2D, 3A). However, burrow density interacted with year to influence belowground biomass, where crabs had a positive effect on pickleweed root biomass (Appendix S2: Table S1, Fig. S2). This pattern occurred in 2018, which was consistent with patterns in pickleweed canopy height (Fig. 4G).

At KF2 and SDL, where crabs impacted pickleweed cover, we observed no main effects of burrow density or any interaction between burrow density and year to affect pickleweed canopy height (Table 1, Fig. 4H and I, respectively). Pickleweed canopy height only varied among years at KF2, where plants were taller in 2017 than the other two years (Table 1, Fig. 4H). Among sites, SDL and KF2 had the tallest canopy (48 ± 1 cm for both sites) and KF1 had the shortest canopy (43 ± 1 cm). When examining total belowground root biomass, KF1 and KF2 had higher total root biomass

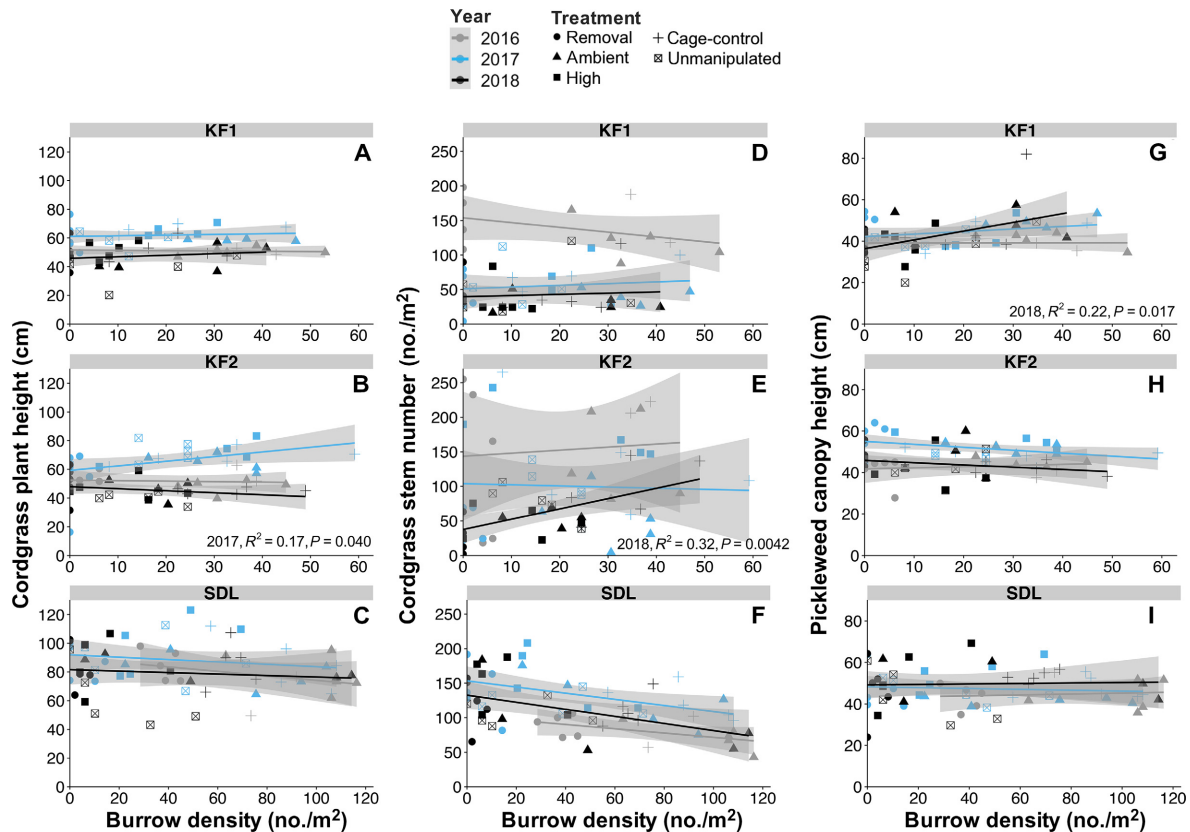


FIG. 4. (A–C) Cordgrass plant height, (D–F) cordgrass stem density, and (G–I) pickleweed canopy height vs. burrow density measured at the end of the growing season (September or October) in 2016, 2017, and 2018 at KF1, KF2, and SDL. Lines represent linear regressions for each site \times year combination; R^2 is reported for significant interactions of burrow density and year.

($1,204 \pm 187$ g and 997 ± 152 g, respectively) than SDL (262 ± 32 g; Appendix S2: Table S1, Fig. S2).

Burrow density did not affect C:N for plant tissues collected at the end of the experiment in 2018 (Appendix S2: Table S1, Fig. S3). Interestingly, C:N ratios were higher at SDL than the other two sites for both cordgrass (~40%) and pickleweed (~20%).

At all three sites, burrow density was highest in 2016 and was lower in the two subsequent years. This provided us the opportunity to use temporal patterns in burrow density (Fig. 1A) as a natural experiment to correlate with temporal patterns in cordgrass cover (Fig. 2A–C) at these sites. Although we observed significant effects of year on cordgrass cover (and pickleweed cover) at each site (Table 1), the only location where this was qualitatively similar to the temporal pattern of burrow density was KF1. At this site, cordgrass cover decreased through time as burrow density decreased. Interestingly, this pattern is consistent with positive impacts of crabs on cordgrass at the adjacent site (KF2). Although burrow density also decreased through time and there was a significant effect of year on cordgrass cover at the other two sites, cordgrass cover did not change directionally over time at these two sites.

Biogeochemistry

Because porewater sippers were left in situ through the entirety of the growing season for each year, we lost some samples. Here, we highlight main trends (for more comprehensive results, see Appendix S2). For all sites, there were no main effects of crabs on salinity, DOC, or nitrate (Appendix S2: Table S2). We did observe marsh-specific patterns in biogeochemistry metrics. For example, in 2016 and 2017, SDL had higher salinity (46 ± 1 ppt and 52 ± 1 ppt, respectively) than KF1 (40 ± 1 ppt and 39 ± 1 ppt) and KF2 (39 ± 1 ppt and 34 ± 3 ppt; Appendix S2: Fig. S4). However, this pattern switched in 2018 when SDL had the lowest salinity (44 ± 2 ppt) compared to KF1 (50 ± 1 ppt) and KF2 (51 ± 1 ppt). Regarding DOC, burrow density and year interacted to influence DOC at KF1 and KF2 (Appendix S2: Fig. S5A, B). At both sites, this interaction was explained by burrow density increasing DOC in 2018, and either having no effect (KF1) or by decreasing DOC (KF2 2017) in the other years.

Nitrate and ammonium varied annually at each site. In 2016, KF1 and KF2 had higher nitrate concentrations (1.7 ± 0.1 $\mu\text{mol/L}$ and 2.2 ± 0.2 $\mu\text{mol/L}$,

respectively) than SDL ($0.27 \pm 0.3 \mu\text{mol/L}$; Appendix S2; Fig. S6). At KF1, burrow density increased nitrate in 2017 but not in other years (Appendix S2; Table S2). All three sites had higher nitrate concentrations in 2018 than any of the other three years. At SDL, nitrate concentrations were $\sim 12\times$ higher in 2017 and 2018 than in 2016. Regardless of year, SDL had lower concentrations of ammonium ($8.69 \pm 2.3 \mu\text{mol/L}$) than KF1 ($62.6 \pm 8.85 \mu\text{mol/L}$) and KF2 ($66.5 \pm 9 \mu\text{mol/L}$; Appendix S2; Fig. S7). At KF2, crabs decreased ammonium levels (Appendix S2; Table S2), but there was no burrow density \times year interaction.

DISCUSSION

Burrowing crabs influenced plant communities in ways that were not predicted based on earlier studies. Fiddler crabs did not stimulate cordgrass, and leaf-grazing crabs (the omnivorous, *Pachygrapsus crassipes*) did not reduce cordgrass cover (and actually enhanced cordgrass at one site). Positive effects on cordgrass cover were associated with negative effects on pickleweed cover. These changes in cover were consistent with crab impacts on plant traits. At the site where *P. crassipes* increased cordgrass cover (KF2), crabs sometimes increased cordgrass height and stem density (2017 and 2018, respectively). Crabs at this site did not influence pickleweed canopy height. Because crabs affected cordgrass traits (e.g., height and stem density), but not pickleweed, in directions consistent with changes in cordgrass cover, we propose that marsh-specific crab effects on community structure were largely mediated through direct impacts on cordgrass and indirect impacts on pickleweed.

Experimental manipulations of burrow density resulted in significant effects at KF2, but did not affect cordgrass cover or traits at the site (KF1) that was in the same marsh and only ~ 160 m away. However, a natural gradient in burrow density at this site among years allowed us to further explore the effect of crabs on cordgrass. At KF1, cordgrass cover decreased with burrow density through time (Fig. 2 and Fig. 1, respectively). Interestingly, this pattern is consistent with positive impacts of crabs on cordgrass in this same marsh but at our adjacent site (KF2). This observation supports a more general positive impact of the crab assemblage on cordgrass throughout the transition zone at this marsh (Kendall-Frost Marsh).

Crab effects on plant composition sometimes occur independent of reductions in unvegetated cover. For example, crab-mediated reductions in cordgrass cover at SDL were not associated with a change in unvegetated cover (Fig. 2). This may be because burrowing crab effects on salt marsh vegetation as measured by unvegetated cover vary across large spatial scales. For example, a broad survey across multiple marshes throughout the United States found a significant relationship between

burrow density and unvegetated cover at only 4 of 15 marshes (Wasson et al. 2019). We found a similar amount of variation among our sites separated by <25 km (burrow density predicted unvegetated cover at only two of nine site-year combinations). This suggests that environmental differences within a single sub-habitat of salt marshes (i.e., transition zones between cordgrass and pickleweed) create spatial heterogeneity in crab effects on marsh vegetation.

Previous studies of contrasting ecosystems, prairies and salt marshes, suggest that the directional shifts in plant communities caused by burrowing animals may depend upon the ability of the consumers to graze plants directly. In these contrasting ecosystems, folivorous burrowing rodents and crabs reduced vegetation cover, particularly of grasses, but granivores or detritivores did not (Davidson and Lightfoot 2008, He and Silliman 2016, Szura et al. 2017). In contrast to this prediction, we found that crabs in the marsh dominated by the lined shore crab, *P. crassipes* (i.e., those that can graze marsh plants; Boyer and Fong 2005), only occasionally reduced vegetation (i.e., increased unvegetated cover, Fig. 2H) and enhanced, rather than reduced, cordgrass cover.

Our study suggests that *P. crassipes*-mediated increases in cordgrass cover are similar to the positive effect of fiddler crabs described by other studies (Bertness 1985, Smith et al. 2009). Although *P. crassipes* is generally considered more omnivorous than marsh herbivores like *Sesarma*, field and lab observations suggest that *P. crassipes* may more commonly graze marsh plants (Boyer and Fong 2005, Wasson et al. 2019, but see J. B. Walker E. D. Grosholz, and J. D. Long, *unpublished manuscript*). In contrast to other studies and our predictions, our study suggests that *U. crenulata* (fiddler crab) had a more negative effect on cordgrass. The mechanisms by which *U. crenulata* might exert a stronger negative impact on cordgrass relative to *P. crassipes* are unknown. However, because *P. crassipes* has higher per capita grazing rates on marsh plants, this effect does not appear directly related to grazing (J. B. Walker E. D. Grosholz, and J. D. Long, *unpublished manuscript*).

Crabs had little direct effects on pickleweed, and mostly influenced marshes via effects on cordgrass. Crab impacts on pickleweed traits rarely were consistent with crab impacts on pickleweed abundance. This pattern is similar in other systems, where burrowing animals in grasslands had stronger effects on grasses than other plants (Fields et al. 1999, Davidson and Lightfoot 2008). For example, kangaroo rats shifted plant community composition around their mounds from perennial grasses to forbs, shrubs, and succulents (Fields et al. 1999). Grasses may be more sensitive to burrowing animals given their tall stature, fast growth rates, and generally high palatability (Howe et al. 2002, Davidson and Lightfoot 2008, Smith et al. 2013).

Additionally, factors other than crab abundance or composition (e.g., plant traits, plant diversity, or sediment biogeochemistry) may drive marsh-specific impacts

of crabs. For example, compared to Kendall-Frost Marsh, cordgrass plants at San Dieguito Lagoon had lower root:shoot ratios (12, 15, 2; KF1, KF2, SDL, respectively; although these ratios should be interpreted with caution due to difficulties separating large amounts of fine roots by species). This lower root: shoot ratio at San Dieguito Lagoon may be a preexisting marsh characteristic that causes plants to be more susceptible to crabs, or may be driven by root destruction caused by the high density of crabs. Several observations support the claim that cordgrass at San Dieguito Lagoon allocates fewer resources to roots. Cordgrass at this marsh was 1.5× taller and contained 16× more flowering cordgrass stems than Kendall-Frost Marsh. Additionally, the biomass of unidentified roots was 11× lower at San Dieguito Lagoon, suggesting that our conclusion about resource allocation to shoots is conservative. Therefore, the lower root:shoot ratio of cordgrass at San Dieguito Lagoon may have made these plants more susceptible to negative impacts of burrowing crabs. Alternatively, crabs may be driving this lower root:shoot ratio by damaging or consuming roots. Previous studies have found that burrowing crabs can damage and deplete belowground root structures when maintaining their burrows (Wilson et al. 2012, Vu et al. 2017, Derksen-Hooijberg et al. 2018). Therefore, due to the high burrow density at San Dieguito Lagoon, plants may be unable to produce sufficient belowground biomass due to crab burrowing. This could also be cyclical, where plants in areas with lots of burrowers and/or grazers may also allocate less resources to develop belowground biomass (van Dam 2009, Bagchi and Ritchie 2010). This suggests that crab effects are extremely context-dependent and may be influenced by marsh-specific characteristics.

Of the sediment biogeochemistry properties we examined, ammonium differed most strongly between the two salt marshes suggesting it could have mediated the impact of crabs on plants. At San Dieguito Lagoon, ammonium concentrations were 10× lower than Kendall-Frost Marsh (Appendix S2: Fig. S7). Associated with this pattern, we observed 1.6× higher C:N ratios at San Dieguito Lagoon (Appendix S2: Fig. S3). A previous study found that crabs can reduce nitrogen availability (Derksen-Hooijberg et al. 2018). Together, these observations suggest that crabs may overwhelm cordgrass under nutrient limitation.

Although several properties of the plant community, crab community, and soil biogeochemistry may provide insight into spatial variation in the impacts of crabs, we are less certain about the environmental variables that drove temporal variation in crab impacts. Of the six studies that examined the effects of crabs in multiple years (Appendix S1: Table S1), most documented some sort of environmental difference among years (e.g., drought and rainfall [Angelini et al. 2018]; grazing pressure [Bortolus et al. 2004, Smith et al. 2012]) or found no difference in crab effect among years. We could not find any broad environmental variables that differed

among years at our sites, such as bay water temperature, ocean water temperature, or air temperature (J. Walker, *personal observation*).

Understanding the drivers of cordgrass production is pressing given the recent declines in the abundance of this foundation species. Over the past decade, there have been an increasing number of cordgrass die-off or die-back events (Alber et al. 2008, Marsh et al. 2016, Pettengill et al. 2018). This loss threatens critical ecosystem functions provided by cordgrass, such as carbon sequestration, shoreline erosion protection, water filtration, and habitat provisioning (Ward et al. 2003, Thorne et al. 2015, Kerr et al. 2016). Several studies highlight the central roles that consumers play in driving cordgrass loss (Bertness et al. 2014a, Escapa et al. 2015, Pettengill et al. 2018). Many studies have encouraged crab removals as a management strategy to prevent cordgrass loss, as well as strategies to protect predatory crabs in order to prevent die-offs via trophic cascades (Altieri et al. 2012, Bertness et al. 2014b, Vu and Pennings 2018). In our study, burrowing crabs mitigated cordgrass loss during a marsh-wide cordgrass decline (from 2016 to 2017 at Kendall-Frost Marsh). This facilitation of cordgrass suggests the possibility that marsh die-off could be mitigated by crabs. However, our results suggest that the impact of fiddler crabs and leaf-grazing crabs on cordgrass is not generalizable between regions (e.g., fiddler crabs in Atlantic marshes stimulated cordgrass but had negative effects in our study of Pacific marshes). The context-dependent nature of these interactions suggests more work is needed to predict the size and direction of burrowing crab impacts on salt marsh plants, and to better understand the spatial and temporal variation of crab impacts both within and between marshes. Overall, understanding the spatiotemporal dynamics of crab effects on cordgrass populations would develop a better predictive framework for when and where crabs may promote cordgrass productivity and stabilize salt marsh ecosystems.

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