Long-term study reveals top-down effect of crabs on a California salt marsh

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Abstract. Consumers can structure plant communities and may function as keystone species or ecosystem engineers. In salt marshes, the prevailing paradigm has shifted in recent decades from nearly complete focus on bottom-up processes to inclusion of top-down effects. Although the number of studies investigating top-down control continues to climb, few experiments span multiple years, so temporal variability in or long-term impacts of consumers have not been well characterized. In addition, while top-down control has been found to be common in Western and Eastern Atlantic and Western Pacific salt marshes, our study is one of the first to experimentally consider top-down control of salt marsh plants in the Eastern Pacific. We conducted a five-year field experiment along eroding creekbank edges of a California salt marsh in which we manipulated densities of the shore crab, Pachygrapsus crassipes, and tracked marsh responses over time. Our results demonstrate that, through both consumption and engineering activities, this superabundant crab is regulating marsh vegetation and soil structure. Experimentally reducing crab abundance enhanced vegetation biomass and sediment bulk density. Moreover, root biomass and bulk density—factors known to increase marsh resilience to erosion and sea-level rise—decreased linearly with increasing burrow density. Our long-term study uniquely revealed that burrows can persist for years after crab abundances are reduced and that plant responses from grazer exclusions gradually strengthen over time, likely due to the relatively slow growth of woody perennial foundational plants. Since shore crabs are abundant throughout the marsh in most major estuaries within the range of the species (from Baja California, Mexico to Oregon, USA), we hypothesize that this species is exerting significant, yet underappreciated top-down control and modifying the sediment properties of many West Coast salt marshes.

Key words: consumer control; ecosystem engineer; plant–animal interactions; salt marsh; shore crab; top-down effects.

INTRODUCTION

Animals have been shown to have strong effects structuring many plant communities including grasslands, rain forests, kelp forests, and tidal marshes (Estes 1998, Terborgh et al. 2001, Silliman and Bertness 2002, Davidson et al. 2012). Animals can exert control over vegetated
communities directly by consuming plants or indirectly through trophic cascades or engineering of landscapes. For instance, elephants destroy trees, thereby maintaining savannas (Haynes 2012), sea otters maintain kelp forest ecosystems by consuming kelp-grazing urchins (Estes 1998), and burrowing worms can prevent seagrasses from establishing on mudflats (Hughes et al. 2000). Despite widespread acknowledgment that communities are structured by a combination of top-down and bottom-up effects (Gruner et al. 2008), most studies continue to emphasize abiotic drivers of landscape-scale ecosystem functioning, particularly in coastal wetlands (Odum 1988, Watson et al. 2016, Elschot et al. 2017, Raposa et al. 2017) where there remains a paucity of studies focused on top-down relative to bottom-up processes (He and Silliman 2016).

Consumers that also function as ecosystem engineers can have particularly strong effects and have the potential to transform the biotic structure and ecosystem function of the landscapes in which they occur. By modifying the physical state of abiotic and biotic resources, ecosystem engineers change the structure and function of the surrounding environment (Jones et al. 1994, 1997). For example, dam construction by beavers (Castor canadensis) creates wetland habitat (Pollock et al. 1998, Wright et al. 2002), burrowing by crabs (Sesarma reticulatum) improves soil quality (Moore 2019) and increases drainage (Crotty et al. 2020), decomposition, and erosion (Bertness 1985, Vu et al. 2017), and trampling by livestock enhances sediment carbon stock through increased soil compaction and anoxia (Elschot et al. 2015).

These ecosystem engineers, as well as all others that occur at intermediate and higher trophic levels, also function as consumers, and these two roles can simultaneously influence ecosystem functions and key processes. For example, targeted grazing by beavers can change the landscape by altering the patterns of succession (Barnes and Dibble 1988, Wright et al. 2002), consumer fronts of herbivorous crabs can cause widespread salt marsh die-off when stimulated by increased sea-level rise (Crotty et al. 2020), and grazing by livestock can have indirect positive (Elschot et al. 2015) and direct negative effects (Cahoon et al. 2012) on carbon sequestration. Cases such as these demonstrate that a single species can take on both functional roles as an ecosystem engineer and consumer. Yet, most investigations of top-down control consider one of these roles in isolation and have only evaluated the relative importance of each role over one or a few growing seasons. Dual roles should be looked at in concert and over sufficient timescales to track both immediate and delayed vegetative and community-level responses and evaluate how the effects of an engineer and consumer impact ecosystem functioning over time.

In salt marsh systems, there has been increasing recognition that marsh dynamics are driven in part by strong consumer effects (Silliman and Ziemann 2001, Alberti et al. 2015, He et al. 2015). On the east coast of the United States, both snails and crabs regulate marsh plant growth and, when left unchecked by predators or stimulated by drought, can form fronts that devastate marshes (Silliman and Bertness 2002, Silliman et al. 2005, He et al. 2017). Similarly, in China and Argentina, burrowing crabs affect plant diversity, production, and ranges across the intertidal zone (Bortolus and Iribarne 1999, Bortolus et al. 2002, He et al. 2015). In North America, the majority of marsh studies to date have been short-term experiments (1–2 yr) on grass-dominated (e.g., Spartina spp.) systems (Smith and Tyrrell 2012, Moore 2019). On the west coast of the United States, there have been many studies on bottom-up processes in tidal marshes (Thorne et al. 2014, 2018, Janousek et al. 2017, Osland et al. 2019) and comparatively few on consumer effects (Boyer and Fong 2005, Armitage and Fong 2006, Wasson et al. 2021). The role of consumers in woody perennial marsh systems, like those found along the Pacific Northwest Coast of the United States, Europe, Australia, South Africa, and South Asia (Kadereit et al. 2007), is likely to operate at considerably longer timescales than herbaceous grass-dominated systems, thus providing a novel perspective on consumer effects.

The modes of grazer control of salt marsh growth have varied from direct consumption of live plant tissue (Angelini et al. 2018) to grazer facilitation of microbial infection in plant wounds (Silliman and Newell 2003). Bioturbation has also been suggested as a major driver of top-down control of marsh plants (Daleo et al. 2007, Derksen-Hooijberg et al. 2019), especially in crabs, but that has been difficult to tease apart.
In addition, few marsh studies have examined the vegetative response rate associated with consumptive and engineering activities, both of which may take time to manifest, and as most marsh studies have been less than two years in duration (He and Silliman 2016), detecting delayed plant- and community-level responses is unlikely.

In a central California marsh, we focused our study on one key consumer and bioturbating ecosystem engineer, the shore crab *Pachygrapsus crassipes* Randall, which has been documented to be highly abundant in woody perennial marshes along the west coast of North America (Morgan et al. 2006). In our estuarine salt marsh system, Elkhorn Slough, *P. crassipes* is the numerically dominant crab species, followed by the less common and smaller grapsid crab, *Hemigrapsus oregonensis*, and invasive green crab, *Carcinus maenas*; both are rarely observed or trapped in our focal marshes and are almost exclusively subtidal. Generally considered an omnivorous crab because it feeds opportunistically on algae, diatoms (Armitage and Fong 2006), mud snails (Sousa 1993, Wasson et al. 2020), and detritus (Quammen 1980), feeding assays conducted in this study are the first to directly test whether *P. crassipes* also consumes vascular marsh plants, including the spatially dominant woody perennial, *Salicornia pacifica*. We observed crabs grazing plant roots in both the field and the laboratory and patterns of sparser marsh cover in areas with high crab and crab burrow densities. To test the hypothesis that crabs are significantly suppressing marsh plant communities and to begin unraveling the relative importance of this species’ consumptive versus sediment engineering effects, we conducted a crab removal experiment in Elkhorn Slough marsh areas immediately adjacent to creek banks, tracking responses to crab reduction for five years to detect potentially slow infilling of burrows, and delayed responses by the woody perennial marsh plants.

The goals of our study were to (1) experimentally manipulate crab abundance to evaluate effects along vulnerable marsh-bank edges, (2) assess whether effects of crab reductions strengthened, weakened, or plateaued over time, and (3) test in the laboratory whether crabs consume belowground root material when simultaneously offered algae. We had two experimental plot types: experimentally reduced and unmanipulated (ambient) crab densities. We expected reduced crab densities to result in the immediate disappearance of consumptive effects, with aboveground succulent tissue responding quickest and a lagged response in woody tissue. Similarly, we expected burrows to fill with fewer crabs resulting in a delayed positive response in belowground biomass and bulk density associated with crab reduction treatments. We expected that reducing crab densities would result in a related increase in epiphytic and benthic algal cover, as crabs are known consumers of benthic macroalgae and diatoms (Armitage and Fong 2006). With the assumption that burrows would fill, and marsh plant production would be higher in crab reduction compared to ambient treatments, we also expected salt marsh vertical accretion, measured using feldspar marker horizons, to be higher. In replicating the experimental treatments across gradients in initial crab densities, we were able to leverage naturally occurring spatial variability in crab density to holistically evaluate this species’ impacts in the system over time. The persistence of burrows throughout the study period allowed us to use correlation to explore the long-lasting effects of bioturbation while the experimental reduction of crabs allowed us to explore the effect of crabs present at the time of our experimental sampling. Thus, our long-term study allowed us to disentangle the present effect of crab herbivory from the legacy effect of burrowing on marsh biomass, percent cover, bulk density, and accretion.

**Methods**

**Study site**

Elkhorn Slough is an estuary located in Monterey Bay, California. Elkhorn Slough includes approximately 1000 ha of salt marsh habitat (Van Dyke and Wasson 2005, Brophy et al. 2019), the most extensive California marshes south of San Francisco Bay. Anthropogenic modification to tidal and freshwater flow (diking, construction of an artificial mouth, diverting freshwater inputs, etc.) has contributed to the widespread loss of salt marsh habitat (Van Dyke and Wasson 2005). Elevation-based estuary extent model (EBEEM) maps have estimated that Elkhorn Slough has lost 70% of its historical salt marsh habitat.
(Brophy et al. 2019). The majority of marsh loss in the estuary is through diking and interior marsh dieback. Long-term erosion monitoring has tracked horizontal marsh retreat and creek widening, from the 1930s to the early 2000s, mean creek width went from 2–2.5 to 9–17 m (Van Dyke and Wasson 2005). Highly impacted by the surrounding agricultural landscape (Fig. 1), Elkhorn Slough is considered a nutrient-loaded and eutrophic system (Hughes et al. 2011, Wasson et al. 2017). Excess nutrients in the system have led to the proliferation of algal mats which compromise the health of marsh plants through smothering along marsh banks, and act to accelerate marsh retreat and bank erosion (Wasson et al. 2017).

Elkhorn Slough salt marshes are dominated by the clonal perennial marsh halophyte, Salicornia pacifica, or pickleweed. One of the dominant consumers in the salt marsh is burrowing crab, Pachygrapsus crassipes, the lined shore crab (Fig. 2A). P. crassipes is omnivorous with a diet consisting mainly of algae, diatoms, detritus, and small invertebrates (Hiatt 1948, Ricketts et al. 1985). The life span of P. crassipes is estimated to be 3–4 yr with adult sizes ranging from 30 to 60 mm carapace width (Hiatt 1948). The channel and tidal creek bank faces are riddled with crab burrows. We conducted a long-term experiment near these marsh-bank edges, where crab densities in the system are highest (Wasson et al. 2019). Our study explores whether crab...
abundance and biomass and/or burrow density affect marsh plant biomass and cover, sediment bulk density, and accretion.

**Experimental design**

To test whether crabs had an effect on marsh vegetation and soil structure, we conducted the following experiment in five tidal creeks in Elk-horn Slough, extending from the lower to the upper reaches of the estuary (Fig. 1). At each tidal creek site (Figs. 1, 2B), there were five blocks; each block had two different treatments: (1) reduced crab densities (Fig. 2C, D), hereafter referred to as “Reduced Crab” (full fences where crab density was continually reduced using pit-fall traps) and (2) ambient crab densities (Fig. 2E), hereafter referred to as “Ambient Crab” (lifted fences where crabs were allowed to move in and/or out of the experimental plot area). We used a shovel to sever the root matrix of the marsh plants within our experimental plot area from those immediately outside of it (30 cm deep by 1 cm wide), which outlined the perimeter of each experimental plot. The wire-mesh fencing around the Reduced Crab plots extended into the substrate “10 cm to prevent crabs from burrowing into the experimental plot area. The fence wall of the Ambient Crab plots was lifted “5 cm from the marsh substrate to enable the crabs free access to move in and out of the plots. There were twenty-five replicates per treatment, five replicates per tidal creek site. Experimental plots (2 m × 1 m) were installed parallel to the bank edge, “50–150 cm from the edge. Nearness to the bank edge depended on bank stability. The fences were built using 19-gauge 1.3 cm × 123 cm × 30.5 cm galvanized hardware cloth (1.3 cm opening size) attached with staples to 1 m long wood posts. We acknowledge that as a lifted fence structure, our Ambient Crab treatment may not be entirely representative of an unfenced area. For the purposes of this study, we consider the Ambient Crab treatment to represent fenced marsh plots where we did not directly manipulate crab density, compared to Reduced Crab treatments where crabs were continually removed from the fenced plot area. (Note: These same lifted fences, plus adjacent unfenced controls, were used for a complementary investigation by our team to explore the effects of the Southern sea otter (Enhydra lutris) in Elkhorn Slough salt marshes conducted from 2013 to 2015.)

![Fig. 2. Different spatial scales of long-term salt marsh field experiment. (A) Native lined shore crab, Pachygrapsus crassipes in burrow. (B) Tidal creeks like the one pictured here were the sites of the field experiment. (C) Side view showing contrast in marsh production in Reduced Crab treatment (left) versus surrounding marsh. Top view showing visible differences between (D) Reduced Crab and (E) Ambient Crab treatments, the latter generally had sparser cover and more visible burrows.](image-url)
To maintain the Reduced Crab treatment, we continually trapped crabs, removing them from the experimental plot area using permanently uncapped pit-fall traps (i.e., tennis ball cans, 3.5 cm diameter and 20.5 cm depth with holes at the base for drainage) throughout the entire duration of the study. Pit-fall traps are a common trapping technique (Altieri et al. 2012, Wasson et al. 2019) that is especially appropriate for this particular species of crab (P. crassipes; Fig. 2A) which can be caught across all size classes using this technique. Pit-fall traps are also easy to install and maintain and do not require bait. Pit-fall traps were installed flush to the sediment substrate in the four corners of all experimental plots. We were unable to entirely remove or exclude crabs from the Reduced Crab treatments due to crabs moving into the plots during spring tides when water levels were at or near the top of the fence wall; in addition, small crabs (<13 mm) were able to move into the plots through the wire mesh or small gaps in fence corners. Pit-fall traps in Reduced Crab plots were left uncapped and emptied as needed, ranging from monthly (November–April) to bi-monthly (March–October). Pit-fall traps in Ambient Crab plots were installed to account for the potential effect of installing traps in the experimental plot area and remained capped except during our seasonal 24-hr crab trapping efforts.

Field data collection

Crab data.—During our 24-hr crab trapping efforts, Ambient Crab pit-fall traps were uncapped, and Reduced Crab pit-fall traps were emptied and reinstalled. Traps were checked following a 24-hr period, at which time all crabs were removed from traps, Ambient Crab pit-fall traps were capped and reinstalled. All trapped individuals were identified to species (P. crassipes was typically the only species present, occasionally (n < 20 individuals total over course of study) we caught Hemigrapsus oregonensis), sexed, and sized for all 50 experimental plots. Crabs caught in the Reduced Crab treatment were removed and placed outside of the experimental plot area; crabs caught in the Ambient Crab treatment were placed back into the experimental plot area after data were collected. We trapped during spring tidal cycles to allow sufficient time to visit all five tidal creeks in a single day, this was done haphazardly a total of eighteen times across five years; October 2013 to February 2018 (see results for exact months). In total, we trapped 7535 crabs over the course of our 5-yr study, 3903 of which were in our experimental plots.

Crab biomass was calculated using the relationship between carapace width and body mass generated from individuals collected and weighed. The best fit model was an exponential function of the form: Biomass = ae^(bx+c)—where biomass of an individual crab, measured in grams is a function of a, the scaling coefficient, 0.953, e (natural exponential function), b, the growth rate, 0.086, and c, carapace width (mm). The crab biomass assigned to each experimental plot (n = 50) was the sum total crab biomass for the individuals trapped within the plot area during the same month in which marsh sampling occurred (September 2014 and August 2015 and 2018). While we report crab counts (Appendix S1: Fig. S1), we used biomass for most analyses because this seems a better predictor of crab effect on vegetation (i.e., a few large crabs can have more of an effect than many small).

To track changes in burrow densities by treatment, burrow counts were measured in all experimental plots using a 0.25-cm² quadrat placed first at the back-center (landward edge) of the experimental plot area and then at the front-center (seaward edge) of the experimental plot area. Crab burrow data used in models were from data collected during the same month and years as our crab trapping data (September 2014 and August 2015 and 2018). We only counted burrows >1 cm and counts were broken down by size class with small burrows ranging from 1.0 to 2.9 cm and large burrows 3.0 cm and above. The total number of burrows did not change throughout the study period, but the number of large burrows increased through the widening of existing burrows allowing us to look at the effect of more large burrows over time. Large burrows were used for analyses because they were a stronger metric for measuring the effect of bioturbation on the marsh. To explore how crab burrowing affects marsh biomass, we used the average number of large burrows (3.0 cm + per 0.25 cm²) within each of the 100 × 50 cm surveyed areas of each experimental plot at each sampled year.
Crab biomass served as a potential proxy for consumptive effects and crab burrows a proxy for engineering effects. Consumptive effects are dependent on present crab activity in the experimental plots and are considered an immediate effect. Conversely, engineering effects due to the bioturbation of burrowing can persist and strengthen over time independent of present crab activity due to the longevity of burrows (legacy effects; Ryo et al. 2019).

*Marsh biomass, cover, and accretion.*—In order to track marsh response to treatment effects through time, we sampled all experimental plots in years 1 (2014), 2 (2015), and 5 (2018); the latter was included to look at longer term effects of crab reduction. The experiment was maintained for the entire duration of the study period but we did not complete marsh surveys in years 3 (2016) and 4 (2017). Maintaining the experiment involved routinely cleaning fence walls (1–2 times per month), removing algal wrack following spring tides, and replacing fence walls when compromised due to rust or heavy oxidation. All experimental sampling was conducted in August–September. Using our sampling data, we were able to look closely at early years, when treatment effects were slow to emerge, long-term treatment effects, and interannual variation in crab-marsh dynamics. Sampling included measurements of percent cover of vegetation, crab burrow counts, and harvesting a single marsh core for above- and belowground biomass and bulk density measurements in each of the 50 experimental plots. To track sediment accretion across both treatments, feldspar marker horizons were placed in each experimental plot in July 2016 and sampled in August 2018. More detail on each of these measurements follows.

We collected vegetative cover data because it was a non-destructive method for assessing treatment effects, helped confirm our biomass data, and was our method for assessing algal cover. To collect percent cover data, we placed a 0.25-cm² gridded quadrat in the middle of the experimental plot area and dropped a metal rod at 20 intercepts. At each intercept, we recorded what the rod was touching. Marsh cover included either succulent or woody marsh plant tissue (*Salicornia pacifica*, *Jaumea carnosa*, *Frankenia salina*, or *Distichlis spicata*), only *S. pacifica*, the dominant marsh plant (Van Dyke and Wasson 2005), is reported below. We also recorded epiphytic algae cover (mainly, *Ulva* spp.) on woody tissue and substrate cover which included mud, benthic diatoms and benthic algae, or burrow. Due to the redundancy of including both burrow percent cover and burrow density data, we are not reporting burrow percent cover data. Benthic diatoms and other benthic algae were considered a single category because distinguishing between algal taxa in the field was challenging. To quantify each cover type as a percentage, we divided the number of intercepts per cover type from the total possible points, 20, and multiplied by 100.

We collected marsh cores to quantify differences in bulk density and marsh above- and belowground biomass in treatments over time. Cores were collected using a beveled 10 × 10 cm PVC coring device that was carefully placed into the marsh substrate without manipulating the overlying aboveground marsh vegetation. Marsh aboveground biomass included in the core itself was what we later sorted and weighed. Cores were then extracted from the coring device and stored in sealed pre-labeled plastic bags and immediately brought to UC Santa Cruz’s Long Marine Laboratory for post-processing. The desired core height was 10 cm, if shorter, the actual core height was recorded, and if longer, the core was cut so the top 10 cm of the core was processed, and the remaining material discarded. All aboveground biomass was cut flush with the sediment surface, rinsed, and sorted into succulent and woody tissue groups. The sediment core, free of aboveground tissue, was weighed for bulk density and later sieved to remove all sediment and collect all belowground biomass material. Bulk density is the weight of sediment per unit volume (g/cm³) and the volume of the sampled cores was 785.4 cm³, unless sampled core height was less than 10cm, in which case core volume was corrected to reflect the true core height. Succulent, woody, and belowground biomass material was individually wrapped in labeled foil and placed in a drying oven at 60°C for 24–48 h for aboveground material and 72–144 h for belowground material. After fully drying, samples were re-weighed for dry weight (g). This process was repeated at the end of the marsh growing season for all experimental plots (*n* = 50) in 2014, 2015, and 2018. Hereafter, aboveground biomass refers to the combined dry
weight (g) of both succulent and woody tissue collected from each of the experimental plots. Belowground biomass includes all the root material (live and dead) per core as dry weight (g).

To detect potential differences in sediment accretion by treatment, feldspar marker horizons (Cahoon et al. 1996) were placed in all experimental plots in July 2016. To apply the markers, we placed a 25 × 25 cm quadrat near the landward edge of each experimental plot and poured approximately 950 mL of feldspar powder evenly within the quadrat area. Feldspar marker horizons were placed off-center and outside the burrow count survey area (see “Crab Data”), and when possible, burrows were avoided entirely by placing the marker either to the left or right of the center back of the plot, otherwise burrows were evenly coated, not filled, with feldspar. In August 2018, one feldspar “brownie” was extracted, measured, and collected per experimental plot. Each “brownie” was extracted using a 2-cm PVC coring device and the height of the sediment above the feldspar layer was measured along four pre-marked points; the average of the four points was divided by two to get the annual accretion rate.

Laboratory feeding trials

The focus of these trials (Summer 2017) built upon previous trials in Summer 2015 that showed preference for pickleweed belowground tissues over aboveground; thus, the trials described below did not include aboveground marsh plants. In the field, we observed crabs “trimming” roots extending into their burrows and in high numbers under macroalgal mats, often grazing on deposited wrack. We also detected potential evidence of herbivory reflected in the marsh biomass data. To test whether crabs consume pickleweed roots when also offered common green alga (Ulva lactuca), we ran crab feeding trials in Summer 2017. Crabs were caught (n = 34) in close proximity to Site 5 (Appendix S1: Fig. S1). All individuals greater than 25 mm were kept for the trials, starved for 72 h, and placed in 16 oz. (0.47 L) glass mason jars with 10 mL of regularly replaced seawater at UC Santa Cruz’s Long Marine Laboratory. The trials began on 18 July 2017, ran for 72 h, and included the following independent trials; (i) 3 g wet weight of pickleweed roots (n = 13), (ii) 3 g wet weight of algae (n = 12), and (iii) 1.5 g wet weight of pickleweed roots and 1.5 g wet weight of algae (n = 9); each trial type was run with both a crab and without crab treatments. The pickleweed root material used in the trials only included live thin root hairs, not highly lignified taproots. Following the trials, crabs were removed, and all remaining root or algae material was extracted, placed in labeled pre-weighed foil, and left in a dehydrating oven for 48 h.

Statistical approach and analyses

Our first approach was to examine the effects of treatments (Reduced Crab vs Ambient Crab) on various response variables, including marsh biomass and cover, bulk density, and accretion. To test for treatment effects, we ran a repeated-measures MANOVA with marsh cover and above- and belowground biomass in years 1, 2, and 5 each as response variables. The repeated-measures MANOVA approach was used instead of individual ANOVAs because the same plots were sampled through time and were therefore not independent. The model effects were site, block nested within site, treatment, and treatment × site (Fig. 3; Appendix S1: Table S1). We used the same analytical approach to analyze bulk density data for years 2 and 5. We ran diagnostics to assess normality and homogeneity of variances, or homoscedasticity (Quinn and Keough 2002). Data were transformed to meet assumptions of normality and improve homoscedasticity. Belowground biomass was log-transformed to meet assumptions of normality; aboveground biomass and bulk density data were analyzed using raw values. Succulent and woody cover were also log-transformed to meet assumptions of normality. Epiphytic algae and benthic diatom/algae cover were often 0% within the surveyed plot area and was therefore log + 1-transformed to account for the right skew of the data. High spatial variability in ambient crab densities led us to a regression approach. Accretion rate was normally distributed and first analyzed using a two-way ANOVA to test for differences in accretion rates by treatment, site, block nested within site, and treatment × site.

As noted above and was confirmed by the experimental results, the Reduced Crab treatment did not entirely exclude crabs, which provided an opportunity to assess the effect of...
Fig. 3. Treatment differences in (A) above and (B) belowground marsh biomass, (C) bulk density, and (D) burrow density across years. Data are shown as means (±SEM, n = 25). Ambient Crab treatments are in blue; Reduced Crab treatments in red.
crabs as a continuous rather than categorical variable. To do this, we also conducted regression analyses using crab biomass (log + 1-transformed) or large crab burrow density (log + 1-transformed) as independent variables and marsh response (marsh biomass, cover, bulk density, or accretion) as dependent variables. Here, we were able to use a mixed model with an auto-regressive covariance structure to account for carry-over effects (over time) that account for the unequal time between sampling years (i.e., 2014–2015 vs. 2015–2018), using as the repeated subject the 50 experimental plots. The random effect in the model was block, nested within site. We included these random effects because variation across sites needed to be accounted for. Depending on the analysis, the fixed effects were either crab biomass or large burrows, year, and the interaction between year and crab biomass or burrows (Table 1). Interactions between fixed effects were removed if non-significant. This approach allowed us to separately examine crab biomass and crab burrows as potential drivers of marsh response. We also ran a regression analysis to assess whether accretion rates varied as a function of crab biomass or crab burrows using values from 2018, the year the brownies were collected and measured. All statistical analyses were performed in R software (R Development Core Team, 2016).

Table 1. Mixed model output. Reported are the parameter estimates and standard error, degrees of freedom, df, F ratio, and P-value for the fixed effect test.

| Parameter                                | Fixed effects | Estimate | SE  | df  | F    | P   |
|------------------------------------------|---------------|----------|-----|-----|------|-----|
| Total crab biomass (log+1)               | Crab biomass  | -2.413   | 0.749| 81.9| 10.362** | **  |
| Aboveground biomass (g)                  | Crab biomass  | 0.492    | 0.191| 57.0| 6.632 | *   |
| Belowground biomass (g)†                 | Crab biomass  | -0.217   | 0.083| 142.7| 6.808 | **  |
| Bulk density (g/cm³)‡                    | Crab biomass  | -0.105   | 0.038| 65.3 | 7.508 | **  |
| Succulent % cover†                       | Crab biomass  | -0.153   | 0.068| 118.4| 5.135 | *   |
| Woody % cover†                           | Crab biomass  | -0.001   | 0.017| 100.0| 0.210 | >0.05|
| Epiphytic algae % cover§                 | Crab biomass  | 0.342    | 0.073| 99.5 | 21.600*** | *** |
| Benthic diatom/algae % cover§            | Crab biomass  | -0.009   | 0.250| 79.7 | 0.125 | >0.05|
| Average no. large burrows (log+1)        | Crab burrows  | -1.502   | 1.131| 113.4| 1.764 | >0.05|
| Aboveground biomass (g)                  | Crab burrows  | 0.536    | 0.226| 135.5| 5.615 | *   |
| Belowground biomass (g)‡                 | Crab burrows  | -0.334   | 0.118| 138.2| 7.973 | **  |
| Bulk density (g/cm³)‡                    | Crab burrows  | -0.053   | 0.022| 131.8| 6.086 | *   |
| Succulent % cover‡                       | Crab burrows  | -0.108   | 0.097| 106.8| 1.227 | >0.05|
| Woody % cover‡                           | Crab burrows  | -0.005   | 0.020| 135.6| 0.059 | >0.05|
| Epiphytic algae % cover§                 | Crab burrows  | 0.014    | 0.009| 136.3| 2.414 | >0.05|
| Benthic diatom/algae % cover§            | Crab burrows  | 0.042    | 0.415| 104.2| 0.010 | >0.05|
| Benthic diatom/algae % cover§            | Crab burrows  | 0.365    | 0.086| 137.0| 16.246*** | *** |

Notes: The table includes mixed models with year and (Top) crab biomass and (Bottom) crab burrows. If the interaction between crab biomass and year or crab burrows and year was non-significant, it was excluded from the model.
* P < 0.05, ** P < 0.01, *** P < 0.001.
† Log-transformed.
‡ Log +1-transformed data.
§ Data that include years 2 (2015) and 5 (2018) only.
If no interaction was detected, we used another approach to assess whether there was a pattern to the crab effect over time by examining the trend of the slopes of each response variable. We expected lag effects associated with perennial marsh plant growth patterns and burrow infilling to change the per capita crab effect monotonically over time, meaning we expected the effect of each additional crab (n + 1) to have a greater negative effect than crab, n. This approach allowed us to determine whether there was a trend in crab effect and look at its pattern, if changing. For each relationship, we looked at if and in what direction the slope changed over time. Looking at the trend, we assessed whether the per capita crab effect becomes more negative, positive, or remains constant through time. With only two time points for accretion and bulk density, we were unable to assess the progression of effects using this approach. We were able to look at the progression of the slopes for our main response variables, marsh above- and belowground biomass. Lastly, to test for post-trial differences between treatments (with crab) and controls (without crabs) in our laboratory feeding trials, we ran Welch's two-sample t-test which accounts for different variance structures, for each trial (i)–(iii).

**RESULTS**

**Crab abundance by treatment**

Periodic crab trapping allowed us to verify that our Reduced Crab treatments were effective in maintaining densities below ambient levels throughout the course of the experiment (Appendix S1: Fig. S1A, B). The crab trapping data were analyzed by grouping all blocks across all sites together by treatment and looking at mean crab biomass (Appendix S1: Fig. S1A) and mean number of individuals trapped by treatment or CPUE (Appendix S1: Fig. S1B). Fewer crabs were trapped in Reduced Crab plots. When comparing CPUE, irrespective of trapping date, Reduced Crab plots had 65% fewer crabs trapped than Ambient Crab plots. Crab biomass in Reduced Crab plots was 71% lower than that of Ambient Crab plots and the mean carapace width of trapped individuals across all trapping efforts was 21.0 and 26.5 mm for Reduced and Ambient Crab plots, respectively. The largest difference in CPUE and biomass between Reduced and Ambient Crab plots was observed in September 2014 (Appendix S1: Fig. S2). During this month, 70 total crabs were trapped in the Reduced Crab treatments, while 337 crabs were trapped in the Ambient Crab treatment. Crab densities were kept consistently below ambient densities in the Reduced Crab treatments beginning in September 2014, one year after the experiment first began in September 2013. It is for this reason that we focus the rest of our analyses on the 2014–2018 study period.

Overall, burrow density was not affected by treatments. Instead, burrows persisted throughout the experiment in all plots despite reductions in crab densities in the Reduced Crab relative to Ambient Crab treatments (Fig. 3D). However, we did track a steady increase in large burrows (Appendix S1: Fig. S1C) concurrent with a decrease in small burrows across years irrespective of treatment. From 2014 to 2018, the average number of large burrows in the 0.5-m² area sampled in Reduced Crab plots increased from 1.9 to 7.9 and 3.4 to 10.2 in Ambient Crab plots (Appendix S1: Fig. S1C). For large burrow density (log + 1-transformed), there was an effect of year ($F_{2,39} = 38.48, P < 0.0001$), but no effect of treatment ($F_{1,40} = 1.088, P = 0.303$), site ($F_{4,40} = 0.817, P = 0.522$), or the treatment × site interaction ($F_{4,40} = 0.862, P = 0.495$). Similarly, for small burrow density (log+1-transformed), there was an effect of year ($F_{2,39} = 43.50, P < 0.0001$) but not of treatment ($F_{1,40} = 2.088, P = 0.100$), site ($F_{4,40} = 2.088, P = 0.100$), or the treatment × site interaction ($F_{4,40} = 1.051, P = 0.393$).

**Effects of crab reduction on marsh biomass, cover, and accretion**

Treatment effects varied by response variables. The full report of model effects between and within subjects for biomass and bulk density can be found in Appendix S1: Table S1. For aboveground biomass, there was a treatment effect, with higher (44% to 56%) aboveground biomass in Reduced versus Ambient Crab treatments ($F_{1,19} = 2.067, P < 0.0001$), a year effect ($F_{2,18} = 0.512, P = 0.024$), a marginally significant site effect ($F_{4,19} = 0.60, P = 0.053$), and no year × treatment or year × site interaction (Fig. 3A). Sites 2, 4, and 5 had relatively higher aboveground biomass than sites 1 and 3, and aboveground biomass varied across years, irrespective
of treatment or site. For belowground biomass, there was a marginally significant effect of treatment ($F_{1,19} = 0.228$, $P = 0.051$) (Fig. 3B) and an effect of site ($F_{4,19} = 4.73$, $P < 0.0001$) and a year × site (Pillai’s trace; $F_{8,36} = 0.66$, $P = 0.035$) interaction. Sites 2 and 4 had higher and less variable belowground biomass across years, whereas Sites 1, 3, and 5 had relatively lower and more variable belowground biomass across years. For bulk density, there was no effect of treatment (see Appendix S1: Table S1), but there was a year effect ($F_{1,12} = 2.209$, $P < 0.0001$) with higher bulk density in 2015 than 2018 (Fig. 3C).

Overall marsh vegetation cover was higher in Reduced Crab treatments where crab densities were maintained below ambient levels (Appendix S1: Fig. S4). Other model effects, mainly site and year, accounted for a significant amount of the variation in cover. The full report of model effects between and within subjects for each cover type can be found in Appendix S1: Table S1. For succulent cover, there was a treatment ($F_{1,19} = 0.755$, $P = 0.0012$) and year effect ($F_{2,18} = 54.29$, $P < 0.0001$) and year × treatment ($F_{2,18} = 0.60$, $P = 0.101$) interaction. While treatment effects on succulent cover persisted throughout the study, the degree to which treatments differed from one another varied by year (Appendix S1: Fig. S4A). For woody cover, there was a treatment ($F_{1,20} = 0.270$, $P = 0.0258$) and site effect ($F_{4,20} = 4.72$, $P < 0.0001$) and year × treatment ($F_{2,19} = 1.15$, $P = 0.001$) and year × site (Pillai’s trace; $F_{8,40} = 2.19$, $P = 0.005$) interactions (Appendix S1: Fig. S4B). The year × treatment interaction is due to the lag in response to our experimental treatments, as treatment differences in woody cover did not emerge until after 2014 (Appendix S1: Fig. S4B). The year × site interaction is driven by patterns of woody cover increasing over time at some sites (i.e., Site 1) and decreasing (i.e., Sites 3 and 4) or remaining unchanged (i.e., Sites 2 and 5) in others. For epiphytic algal cover, there was an effect of treatment ($F_{1,20} = 0.932$, $P = 0.0003$), site ($F_{4,20} = 4.72$, $P < 0.0001$), year ($F_{2,19} = 2.54$, $P < 0.0001$), and a year × site interaction ($F_{8,40} = 2.95$, $P = 0.011$) (Appendix S1: Fig. S4C). Treatment effects did not emerge before our 2014 surveys, after which epiphytic cover generally increased across all sites (with the exception of Site 2 that increased after 2015). From 2015 to 2018, Sites 1, 2, and 5 showed an increase in epiphytic cover, whereas Sites 3 and 4 showed a decrease. The site, year, and year × site effects highlight the spatial and temporal patterns of epiphytic cover. For benthic algal cover, there was no effect of treatment or related interactions (Appendix S1: Table S1), but there was an effect of site ($F_{4,20} = 2.38$, $P < 0.0001$), year ($F_{2,19} = 4.50$, $P < 0.0001$), and year × site ($F_{8,40} = 5.63$, $P < 0.0001$) (Appendix S1: Fig. S4D). Benthic algal cover was generally higher in 2018 than 2014 or 2015 (Appendix S1: Fig. S4D) and varied across sites within and across years (i.e., in 2014, cover was highest at Site 2 and lowest Site 1, while in 2018, cover was highest at Site 5 and lowest at Site 4).

There was no effect of treatment on burrow density, when considering both small and large burrows together (Fig. 3D; Appendix S1: Table S1), but there was an effect of site ($F_{4,19} = 0.90$, $P = 0.013$), year ($F_{2,18} = 1.44$, $P = 0.0003$), and year × site on this metric (Pillai’s trace; $F_{8,38} = 5.45$, $P = 0.0001$). Burrow density remained relatively unchanged over time at Site 1; however, at Sites 2, 3, 4, and 5, burrow density increased from 2014 to 2015 and decreased from 2015 to 2018, eventually decreasing to densities at or slightly above the 2014 densities (Fig. 3D). Lastly, there was no effect of treatment, site, or treatment × site on accretion rates, though accretion rates were slightly higher on average in Reduced Crab (6.03 mm) versus Ambient Crab (5.81 mm) treatments (for statistics, see Appendix S1: Fig. S3).

**Crab effects on marsh biomass, cover, and accretion**

Here, we report on our regression approach that utilized the natural variability in crab burrow density to determine relationships between burrows and marsh biomass, cover, and accretion. The number of crab burrows (large only) had a negative effect on belowground biomass and bulk density and no effect on aboveground biomass during our study period (Fig. 4), although, as we discuss below, the progression of the crab burrow effect on aboveground biomass has trended increasingly negative over time. Year had a negative effect on above- (Appendix S1: Fig. S5A) and belowground biomass (Appendix S1: Fig. S5B) and bulk density (g/cm³) (Appendix S1: Fig. S5C). Crab burrows had
Fig. 4. Effects of (A) crab burrows and (B) crab biomass on marsh aboveground biomass (triangles) and belowground biomass (circles) and effects of (C) crab burrows and (D) crab biomass on bulk density (diamonds). The plotted data (A–C) are from year 5 (2018) only. The reported P values correspond to the main effect variable (crab biomass or crab burrows) from the mixed model, which includes all years. Ambient Crab treatments are in blue; Reduced Crab treatments in red. Burrow data (log + 1-transformed) are the mean number of large burrows surveyed per experimental plot (0.5 m²). Crab biomass (log + 1-transformed) is the total crab biomass per experimental plot (2 m²) calculated using crab trapping data. Raw data were analyzed and plotted for aboveground biomass, and bulk density and belowground biomass are log-transformed. Plotted regressions include 95% CI. The relationship for marsh above- and belowground and bulk density across all years can be found in Appendix S1: Figs. S5, S7.
a negative effect on woody percent cover, and no effect of burrows or year was detected for succulent cover (Appendix S1: Fig. S6). Crab burrows did not have an effect on epiphytic cover, but year did have a positive effect (Appendix S1: Fig. S6E). There was a negative effect of crab burrows and a positive effect of year on benthic diatom/algae cover (Fig. 5A). The full model for each response variable outlined above is reported in Table 1. Lastly, crab burrows had no effect on accretion (Appendix S1: Fig. S3D).

Here, we report on our regression approach that utilized the natural variability in ambient and experimentally reduced crab treatments that produced a gradient of the continuous variable, crab biomass. Crab biomass had a negative effect on above and belowground biomass and bulk density (g/cm³) (Fig. 4, Table 1). In addition, year had a positive effect on aboveground biomass (Appendix S1: Fig. S7A), no effect on belowground biomass (Appendix S1: Fig. S7B), and a negative effect on bulk density (Appendix S1: Fig. S7C). Crab biomass had a negative effect on succulent percent cover and no effect on woody percent cover; no year effect or interaction between crab biomass and year was detected for succulent or woody cover (Appendix S1: Fig. S6). There was no effect of crab biomass on epiphytic or benthic algae/diatom cover but there was a year effect (Appendix S1: Fig. S6). The full model for each response variable outlined above is reported in Table 1. Lastly, crab biomass had no effect on accretion (Appendix S1: Fig. S3C).

Over time, the effects of crab burrows (Appendix S1: Fig. S5) and crab biomass (Appendix S1: Fig. S7) on aboveground biomass became more negative. There was a similar pattern for the effect of crab biomass on belowground biomass (Appendix S1: Fig. S7B). There was no trend over time for the effect of crab burrows on belowground biomass (Appendix S1: Fig. S5B). By contrast to the effects of crab biomass on aboveground biomass, there was no temporal trend on percent cover of succulent and woody pickleweed, epiphytic algae, or benthic algae/diatoms (Appendix S1: Fig. S6).

Fig. 5. Effects of (A) crab burrows and (B) crab biomass on percent cover of benthic algae/diatom cover. The plotted data are from year 5 (2018) only. The reported P values correspond to the main effect variable (crab biomass or crab burrows) from the mixed model, which includes all years. Percent cover is log + 1-transformed and represents the 0.25-m² area surveyed in each experimental plot. Plotted regressions include 95% CI Ambient Crab treatments are in blue; Reduced Crab treatments in red. The relationship for each response variable across all years can be found in Appendix S1: Fig. S6.
Laboratory feeding trials

There were differences in post-trial biomass (dry weight, g) when comparing treatments (with crabs) to controls (without crabs)—the latter having higher post-trial biomass than the former (Fig. 6). Here, we report the mean and standard deviation as well as the statistical differences in post-trial dry weights of treatments ("T") and controls ("C") for each of the three trials. In trial (i) with pickleweed root only, there was less pickleweed root biomass in treatments ($M_T = 0.21$, $SD_T = 0.07$) than controls ($M_C = 0.34$, $SD_C = 0.05$), indicating crab consumption of roots (Fig. 6, Welch’s two-sample $t$-test; $t(20.5) = 5.55$, $P < 0.0001$). In trial (ii) with algae only, there was less algal biomass in treatments ($M_T = 0.12$, $SD_T = 0.11$) than controls ($M_C = 0.33$, $SD_C = 0.03$), indicating crab consumption of algae (Fig. 6, Welch’s two-sample $t$-test; $t(13.05) = 6.098$, $P < 0.0001$). Lastly, in trial (iii) with both algae and pickleweed offered simultaneously, treatments had less biomass than controls for both pickleweed roots ($M_T = 0.24$, $SD_T = 0.07$, and $M_C = 0.32$, $SD_C = 0.03$) and algae ($M_T = 0.08$, $SD_T = 0.15$, and $M_C = 0.28$, $SD_C = 0.10$), indicating that crabs consume pickleweed roots as well as algae when both are offered (Fig. 6, Welch’s two-sample $t$-test; pickleweed roots, $t(11.03) = 3.00$, $P = 0.012$; algae $t(14.40) = 3.20$, $P = 0.006$).

Discussion

Over the course of this five-year experimental investigation, we demonstrate that crabs affect salt marsh structure and function near the edges of tidal creeks and that those effects are primarily negative, at least at small scales. In crab reduction treatments, marsh performance assessed by various metrics increased over time, relative to controls. In addition, through our experimental manipulation of crab abundance coupled with the spatial variability in ambient crab levels, we produced a gradient of crab burrow density and crab biomass and identified the likely dual role of crabs as consumers and ecosystem engineers. This allowed us to link consumption and engineering activities to decreases in above- and belowground biomass, bulk density, and benthic algae/diatom cover. The demonstrated crab-related impacts to marsh vegetation and soil structure near tidal creek banks are likely to accelerate degradation of this Eastern Pacific salt marsh’s resilience to erosion and sea-level rise.

Crabs as ecosystem engineers in marsh systems

Crab burrows have been shown to have variable effects on primary producers, sediment structure, and creek morphology. In Atlantic marsh systems, the effect of burrowing by fiddler...
(Uca spp.) and purple marsh (Sesarma reticulatum) crabs on cordgrass biomass has been shown to vary by sediment type (Holdredge et al. 2010), marsh zone (Bertness 1985), inundation time (Crotty et al. 2020), and predation pressure (Vu and Pennings 2018). Our study in a Pacific coast marsh system complements the few prior studies conducted along the west coast region that show similar negative effects of crabs (P. crassipes) on benthic algae/diatom (Armitage and Fong 2006) and pickleweed (Boyer and Fong 2005) cover, though ours is the first to untangle the mechanisms behind these trophic and non-trophic interactions. Our finding that crab burrows had a significant negative effect on pickleweed belowground biomass and bulk density contributes to the growing number of studies that collectively show how crab engineering affects the structure and function of marsh systems (Wasson et al. 2019).

Legacy effects of ecosystem engineers occur when the engineer is dead or absent, but the engineered landscape persists for an extended period of time (Hastings et al. 2007). The longevity of engineered landscapes has been studied in other systems. For example, beavers build and maintain dams for many years, after which the dam breaks down forming a beaver meadow which can persist for decades (Wright et al. 2003). Similarly, the legacy effect of cup-shaped borings by sea urchins in rocky reefs (Asgaard and Bromley 2008) and nest mounts of leaf-cutter ants in woodland savannas (Costa et al. 2018) persist in the near or total absence of engineering organisms. Our five-year study suggests that similar to the aforementioned examples, crab burrows outlast the presence of the engineers—that is the crabs. Experimentally reducing crab biomass in our Reduced Crab treatments did not affect burrows nor did we observe burrows filling in—as has been seen in other marsh systems. Elkhorn Slough has relatively low water quality sediment concentrations and surface accretion rates (Raposa et al. 2016) and this could have contributed to the lack of burrow infilling. In addition, we did not detect any relationship between burrow counts and crab biomass, meaning that as crab biomass decreased there was no detectable decrease in burrow count, which supports the idea that burrows persist beyond the period of burrowing.

The persistence of burrows may have large implications for the stability and resilience of vulnerable marsh-bank edges. Belowground biomass is responsible for stabilizing sediment on salt marsh banks (Silliman et al. 2012, Silliman et al. 2019); therefore, the effect of burrowing on both belowground biomass and bulk density may promote erosion (Escapa et al. 2008, Hughes et al. in preparation) and decrease carbon stores (Martinetto et al. 2016) by lowering marsh biomass and/or increasing decomposition rates (Vu et al. 2017). Similarly, the ability of marsh vegetation to track sea-level rise through subsurface expansion and marsh accretion (Cahoon et al. 2019) is likely degraded along marsh-bank edges due to the negative effect of burrows on belowground biomass and benthic algae/diatom cover; the latter of which includes sediment-binding biofilms that promote sediment trapping and accretion (Sullivan 1999). Due to crab suppression of marsh biomass and grazing of sediment-binding diatom films on the marsh surface, we hypothesized that crab reduction would increase surface sediment deposition. Our failure to detect such an effect suggests that effects of burrows on sediment properties may outweigh those of crab behavior, and since burrows did not fill in, sediment deposition patterns remained similar across treatments. In Elkhorn Slough, transects surveys running from tidal creeks to the upland revealed that P. crassipes is most abundant along the creek edges but present in 50% of quadrats surveyed (Wasson et al. 2019). Because P. crassipes has the broadest geographic range of any shore crab species, spanning eastern (Oregon to Baja California) and western (Korea and Japan) Pacific coasts (Hiatt 1948), these top-down effects on marsh structure near creek banks may be geographically broad. In addition, P. crassipes is believed to be undergoing a range expansion with recent observations as far north as British Columbia (Cassone and Boulding 2006). Hence, shore crab effects on marsh plant biomass may have broad and increasing spatial impacts on the stability of the marsh by degrading its ability to mitigate erosive forces and track sea-level rise.

**Effects of crab activity beyond engineering**

Crab activities other than physical burrowing have also been shown to have effects on primary
producers and sediment structure. Our study found that reducing crab biomass, a proxy for current crab activity, increases pickleweed above- and belowground biomass, and bulk density. By successfully reducing crab biomass levels in Reduced Crab treatments and observing no related reduction in burrow densities, we were able to, at least in part, uncouple the engineering effect of burrows from other crab effects, such as herbivory.

Crab herbivory, specifically root consumption, is a possible mechanism driving the observed negative effects of crab biomass on marsh production and soil structure. Feeding assays show that crabs prefer root tissue to aboveground succulent tissue (B. Hughes personal observation) and will eat root tissue even when also offered algae (this study). Thus, the negative effects of crabs observed in our pickleweed-dominated marsh system may be a consequence of direct herbivory, which took time to manifest and following detection, strengthened over time. This is likely due to delayed vegetative responses associated with woody perennial marsh plants. By contrast, in cordgrass-dominated marsh systems, crab herbivory can be detected immediately as a leading contributor of extensive marsh dieback (Holdredge et al. 2009, Angelini et al. 2018).

Although we did not examine how predators could mitigate top-down effects of crabs, it is likely given that common snail and crab grazers in east coast marsh systems are controlled in part by predation (Bertness et al. 2014, Vu and Penning 2018). In many marsh systems, trophic cascades can help support vegetation, and recovery of predator populations is thus essential for ecosystem resilience (Silliman et al. 2018). Salt marsh conservation on this coast may thus be supported through recovery of predators (e.g., raccoons, herons, sea otters) that help keep grazer populations in check, thus enhancing resilience to erosion and sea-level rise.

**A powerful analytical approach: combining correlations and experiments**

Our analytical approach was key to understanding how engineering effects of crabs differ from their consumptive effects. Initially, our plan was to use crab abundance as a categorical factor (i.e., investigate the main effects of each of the two treatments), as is typical for manipulative experiments. However, our manipulations did not produce a clear categorical response (such as crab presence vs. absence); rather, they produced a gradient of crab densities allowing us to account for variability in crab abundance by modeling the manipulation as a continuous variable. Spatial variation of ambient crab biomass and burrow density may be due to predation pressure (Holdredge et al. 2009) or the many factors associated with tidal elevation (Raposa et al. 2018) including inundation time (Crotty et al. 2020), sediment grain size (Holdredge et al. 2010), compressibility (Wasson et al. 2019), recruitment (Ribeiro et al. 2005), and creek order (Vu et al. 2017). Using this approach, we were able to detect significant negative effects of both crab biomass and burrows on primary production and soil structure. Had we only used crab abundance as a categorical variable, we would have failed to detect a crab effect on belowground biomass or bulk density. Other studies have used a similar approach to better understand emerging treatment effects. In a mesocosm experiment testing, the effects of ocean acidification and excess nutrients on seagrass, algal biomass, and associated grazers, linear and nonlinear relationships from regression models provided evidence of resilience and ecological thresholds, respectively (Hughes et al. 2018). A study in a southwestern Atlantic marsh testing the effects of crab burrows on root architecture showed cases where treatment effects were not significant, but upon evaluation using treatment as a continuous variable the analysis showed a negative relationship between crab burrows and complexity of root architecture (Daleo and Iribarne 2009). In South Carolina marshes, nutrient enrichment treatments increased carbon dioxide emissions relative to controls and using the sets of treatments as a continuous variable allowed researchers to explore the nuanced effects of belowground processes and carbon emissions (Wigand et al. 2015). In summary, many field experiments, while categorically designed (e.g., crab presence vs. absence), often actually produce a continuous response. The reality of the experimental manipulations should be reflected in the analyses conducted and in so doing will better reflect the study design and likely reveal effects otherwise obscured by designated treatments.
**Importance of long-term experimental studies**

Critical and yet rare, long-term studies lend themselves to more accurately characterizing species’ roles through space and time (Witman et al. 2015; Hughes et al. 2017). By carrying out this field experiment for five years, we were able to better understand the generality and progression of crab effects along vulnerable marsh-bank edges and account for temporal and spatial variability of such effects. In pickleweed marshes, succulent tissue is new growth that represents the present growing season and the woody tissue is older growth from years prior (Boyer et al. 2001); therefore, we expected a lag in the woody tissue response to experimental treatments and the per capita effect of crabs to increase over time due to this time delay. Over time, we observed an increase in the per capita effect of crabs on aboveground biomass (Appendix S1: Fig. S7A). We expected effects on succulent tissue to be immediate and the same across years and woody tissue to have a delayed effect that strengthened in later years. We found that the in-time effects represented by crab biomass had a negative effect on succulent cover and no effect on woody cover. The opposite pattern was observed for the over-time effects represented by crab burrows; burrows had no effect on succulent cover and a negative effect on woody cover.

Conducting a long-term field experiment allowed us to uncover delayed crab effects and detect strong effects. In our mixed model testing crab and year effects, year represents any potential contributing factors that explain variation in our response variables, independent of the crab effect. The direction of the crab effects remained across years, despite the significant year effect. By looking at the slope of each relationship for multiple years, we were able to isolate the crab effect and determine whether the crab effect weakened, strengthened, or did not change over time (Appendix S1: Figs. S5, S7). The negative crab effect on belowground biomass was relatively constant, whereas the negative crab effect on aboveground biomass strengthened over time. This is likely due to a directional, delayed effect of woody tissue which, as previously stated, is slow to respond. Other changes in crab effect were a consequence of interannual variation, such as the case for epiphytic algae and benthic algae/diatom cover. We would not have detected these changes in crab effects or the importance of year, had we only conducted the study for a single growing season. Sampling broadly across space and time allowed us to track consistent relationships across years, some of which remained unchanged while others strengthened. Long-term sampling also allowed us to detect marked seasonality in crab CPUE (Appendix S1: Fig. S2). Fewer crabs caught of any size in winter relative to summer or fall suggests that the intensity of crab impacts on the marsh likely vary by season. Therefore, we suggest future studies on marsh trophic and non-trophic interactions span multiple years.

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**Literature Cited**

Alberti, J., P. Daleo, E. Fanjul, M. Escapa, F. Botto, and O. Iribarne. 2015. Can a single species challenge paradigms of salt marsh functioning? Estuaries and Coasts 38:1178–1188.

Altieri, A. H., M. D. Bertness, T. C. Coverdale, N. C. Herrmann, and C. Angelini. 2012. A trophic cascade triggers collapse of a salt-marsh ecosystem with intensive recreational fishing. Ecology 93:1402–1410.

Angelini, C., S. G. van Montfrans, M. J. S. Hensel, Q. He, and B. R. Silliman. 2018. The importance of an underestimated grazer under climate change: how
crab density, consumer competition, and physical stress affect salt marsh resilience. Oecologia 187:205–217.

Armitage, A., and P. Fong. 2006. Predation and physical disturbance by crabs reduce the relative impacts of nutrients in a tidal mudflat. Marine Ecology Progress Series 313:205–213.

Asgaard, U., and R. G. Bromley. 2008. Echinometrid sea urchins, their trophic styles and corresponding bioerosion. Pages 279–304 in M. Wisshak, and L. Tapanila, editors. Current developments in bioerosion. Erlangen Earth Conference Series. Springer, Berlin and Heidelberg, Germany. https://doi.org/10.1007/978-3-540-77598-0_15.

Barnes, W. J., and E. Dibble. 1988. The effects of beaver in riverbank forest succession. Canadian Journal of Botany 66:40–44.

Bertness, M. D. 1985. Fiddler crab regulation of Spartina alterniﬂora production on a New England salt marsh. Ecology 66:1042–1055.

Bertness, M. D., C. P. Brisson, M. C. Bevil, and S. M. Crotty. 2014. Herbivory drives the spread of salt marsh die-off. PLOS ONE 9:e92916.

Bortolus, A., and O. Iribarne. 1999. Effects of the SW Atlantic burrowing crab Chasmagnathus granulata on a Spartina salt marsh. Marine Ecology Progress Series 178:79–88.

Bortolus, A., E. Schwindt, and O. Iribarne. 2002. Positive plant-animal interactions in the high marsh of an Argentinean coastal lagoon. Ecology 83:733–742.

Boyer, K. E., and P. Fong. 2005. Co-occurrence of habitat-modifying invertebrates: effects on structural and functional properties of a created salt marsh. Oecologia 143:619–628.

Boyer, K. E., P. Fong, R. R. Vance, and R. F. Ambrose. 2001. Salicornia virginica in a Southern California salt marsh: seasonal patterns and a nutrient-enrichment experiment. Wetlands 21:315–326.

Brophy, L. S., C. M. Greene, V. C. Hare, B. Holycross, A. Lanier, W. N. Heady, K. O’Connor, H. Imaki, T. Haddad, and R. Dana. 2019. Insights into estuary habitat loss in the western United States using a new method for mapping maximum extent of tidal wetlands. PLOS ONE 14:e0218558.

Cahoon, D. R., J. C. Lynch, and A. N. Powell. 1996. Marsh vertical accretion in a Southern California estuary, U.S.A. Estuarine, Coastal and Shelf Science 43:19–32.

Cahoon, D. R., J. C. Lynch, C. T. Roman, J. P. Schmit, and D. E. Skidds. 2019. Evaluating the relationship among wetland vertical development, elevation capital, sea-level rise, and tidal marsh sustainability. Estuaries and Coasts 42:1–15.

Cahoon, S. M. P., P. F. Sullivan, E. Post, and J. M. Welker. 2012. Large herbivores limit CO2 uptake and suppress carbon cycle responses to warming in West Greenland. Global Change Biology 18:469–479.

Cassone, B. J., and E. G. Boulding. 2006. Genetic structure and phylogeography of the lined shore crab, Pachygrapsus crassipes, along the northeastern and western Pacific coasts. Marine Biology 149:213–226.

Costa, A. N., E. M. Bruna, and H. L. Vasconcelos. 2018. Do an ecosystem engineer and environmental gradient act independently or in concert to shape juvenile plant communities? Tests with the leaf-cutter ant Atta laevigata in a Neotropical savanna. PeerJ 6: e5612.

Crotty, S. M., et al. 2020. Sea-level rise and the emergence of a keystone grazer alter the geomorphic evolution and ecology of southeast US salt marshes. Proceedings of the National Academy of Sciences 117:17891–17902.

Daleo, P., E. Fanjul, A. Mendez Casariego, B. R. Silliman, M. D. Bertness, and O. Iribarne. 2007. Ecosystem engineers activate mycorrhizal mutualism in salt marshes. Ecology Letters 10:902–908.

Daleo, P., and O. Iribarne. 2009. The burrowing crab Neohelice granulata affects the root strategies of the cordgrass Spartina densiﬂora in SW Atlantic salt marshes. Journal of Experimental Marine Biology and Ecology 373:66–71.

Davidson, A. D., J. K. Detling, and J. H. Brown. 2012. Ecological roles and conservation challenges of social, burrowing, herbivorous mammals in the world’s grasslands. Frontiers in Ecology and the Environment 10:477–486.

Derksen-Hooijberg, M., T. Van Der Heide, L. P. M. Lamers, A. Borst, A. J. P. Smolders, L. L. Govers, J. R. H. Hoogveld, and C. Angelini. 2019. Burrowing crabs weaken mutualism between foundation species. Ecosystems 22:767–780.

Elschot, K., J. P. Bakker, S. Temmerman, J. van de Koppel, and T. J. Bouma. 2015. Ecosystem engineering by large grazers enhances carbon stocks in a tidal salt marsh. Marine Ecology Progress Series 537:9–21.

Elschot, K., A. Vermeulen, W. Vandenbruwaene, J. P. Bakker, T. J. Bouma, J. Stahl, H. Castelijns, and S. Temmerman. 2017. Top-down vs. bottom-up control on vegetation composition in a tidal marsh depends on scale. PLOS ONE 12:e0169960.

Escapa, M., G. M. E. Perillo, and O. Iribarne. 2008. Sediment dynamics modulated by burrowing crab activities in contrasting SW Atlantic intertidal habitats. Estuarine, Coastal and Shelf Science 80:365–373.

Estes, J. A. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. Science 282:473–476.
Gruner, D. S., et al. 2008. A cross-system synthesis of consumer and nutrient resource control on producer biomass. Ecology Letters 11:740–755.

Hastings, A., J. E. Byers, J. A. Crooks, K. Cuddington, C. G. Jones, J. G. Lambrinos, T. S. Talley, and W. G. Wilson. 2007. Ecosystem engineering in space and time. Ecology Letters 10:153–164.

Haynes, G. 2012. Elephants (and extinct relatives) as earth-movers and ecosystem engineers. Geomorphology 158:99–107.

He, Q., A. H. Altieri, and B. Cui. 2015. Herbivory drives zonation of stress-tolerant marsh plants. Ecology 96:1318–1328.

He, Q., and B. R. Silliman. 2016. Consumer control as a common driver of coastal vegetation worldwide. Ecological Monographs 86:278–294.

He, Q., B. R. Silliman, Z. Liu, and B. Cui. 2017. Natural enemies govern ecosystem resilience in the face of extreme droughts. Ecology Letters 20:194–201.

Hiatt, R. W. 1948. The biology of the lined shore crab, Pachygrapsus crassipes Randall. Pacific Science 2:135–213.

Holdredge, C., M. D. Bertness, and A. H. Altieri. 2009. Role of crab herbivory in die-off of New England salt marshes. Conservation Biology 23:672–679.

Holdredge, C., M. Bertness, N. Herrmann, and K. Gedan. 2010. Fiddler crab control of cordgrass primary production in sandy sediments. Marine Ecology Progress Series 399:253–259.

Hughes, B. B., et al. 2017. Long-term studies contribute disproportionately to ecology and policy. BioScience 67:271–281.

Hughes, B., J. Haskins, K. Wasson, and E. Watson. 2011. Identifying factors that influence expression of eutrophication in a central California estuary. Marine Ecology Progress Series 439:31–43.

Hughes, B. B., S. C. Lummis, S. C. Anderson, and K. J. Kroeker. 2018. Unexpected resilience of a seagrass system exposed to global stressors. Global Change Biology 24:224–234.

Hughes, R. G., D. Lloyd, L. Ball, and D. Emson. 2000. The effects of the polychaete Nereis diversicolor on the distribution and transplanting success of Zostera noltii. Helgoland Marine Research 54:129–136.

Janousek, C. N., K. J. Buffington, G. R. Guntenspergen, K. M. Thorne, B. D. Dugger, and J. Y. Takewaka. 2017. Inundation, vegetation, and sediment effects on litter decomposition in Pacific coast tidal marshes. Ecosystems 20:1296–1310.

Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. Oikos 69:373–386.

Jones, C. G., J. H. Lawton, and M. Shachak. 1997. Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78:1946–1957.

Kadereit, G., P. Ball, S. Beer, L. Mucina, D. Sokoloff, P. Teege, A. E. Yaprak, and H. Freitag. 2007. A taxonomic nightmare comes true: phylogeny and biogeography of glassworts (Salicornia L., Chenopodiaceae). Taxon 56:1143–1170.

Martinetto, P., D. I. Montemayor, J. Alberti, C. S. B. Costa, and O. Iribarne. 2016. Crab bioturbation and herbivory may account for variability in carbon sequestration and stocks in South West Atlantic salt marshes. Frontiers in Marine Science 3:1–12.

Moore, A. 2019. What is the role of ecosystem engineers in New England salt marshes? A mesocosm study of the fiddler crab and the purple marsh crab. Wetlands 39:371–379.

Morgan, S., S. Spilseth, H. Page, A. Brooks, and E. Grosholz. 2006. Spatial and temporal movement of the lined shore crab Pachygrapsus crassipes in salt marshes and its utility as an indicator of habitat condition. Marine Ecology Progress Series 314:271–281.

Odum, W. E. 1988. Comparative ecology of tidal freshwater and salt marshes. Annual Review of Ecology and Systematics 19:147–176.

Osland, M. J., J. B. Grace, G. R. Guntenspergen, K. M. Thorne, J. A. Carr, and L. C. Feher. 2019. Climatic controls on the distribution of foundation plant species in coastal wetlands of the conterminous United States: knowledge gaps and emerging research needs. Estuaries and Coasts 42:1991–2003.

Pollock, M. M., R. J. Naiman, and T. A. Hanley. 1998. Plant species richness in riparian wetlands – a test of biodiversity theory. Ecology 79:94–105.

Quammen, M. L. 1980. The impact of predation by shorebirds. benthic feeding fish and a crab on the shallow living invertebrates in intertidal mud flats of two southern California lagoons. Dissertation. University of California, Irvine, California, USA.

Quinn, G., and M. Keough. 2002. Multivariate analysis of variance (MANOVA) and discriminant analysis. Pages 433–442 in Experimental design and data analysis for biologists. Cambridge University Press, New York, New York, USA.

R Development Core Team. 2016. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Raposa, K. B., et al. 2016. Assessing tidal marsh resilience to sea-level rise at broad geographic scales with multi-metric indices. Biological Conservation 204:263–275.

Raposa, K. B., R. A. McKinney, C. Wigand, J. W. Hollister, C. Lovall, K. Szura, J. A. Gurak Jr, J. McNamee, C. Raithel, and E. B. Watson. 2018. Top-down and bottom-up controls on southern New England salt marsh crab populations. PeerJ 6:e4876.
Raposa, K. B., R. L. J. Weber, M. C. Ekberg, and W. Ferguson. 2017. Vegetation dynamics in Rhode Island salt marshes during a period of accelerating sea level rise and extreme sea level events. Estuaries and Coasts 40:640–650.

Ribeiro, P. D., O. O. Iribarne, and P. Daleo. 2005. The relative importance of substratum characteristics and recruitment in determining the spatial distribution of the fiddler crab Uca uruguayensis Nobili. Journal of Experimental Marine Biology and Ecology 314:99–111.

Ricketts, E., J. Calvin, and J. W. Hedgpeth. 1985. Between pacific tides. Fifth edition. Stanford University Press, Stanford, California, USA.

Ryo, M., C. A. Aguilar-Trigueros, L. Pinek, L. A. H. Muller, and M. C. Riligg. 2019. Basic principles of temporal dynamics. Trends in Ecology & Evolution 34:723–733.

Silliman, B. R., et al. 2019. Field experiments and meta-analysis reveal wetland vegetation as a crucial element in the coastal protection paradigm. Current Biology 29:1800–1806.

Silliman, B. R., and M. D. Bertness. 2002. A trophic cascade regulates salt marsh primary production. Proceedings of the National Academy of Sciences 99:10500–10505.

Silliman, B. R., B. Hughes, L. Gaskin, J. Nifong, T. Tinker, J. Nifong, D. Johnson, A. Read, and R. Stepp. 2018. Are the ghosts of nature’s past haunting ecology today? Current Biology 28:532–537.

Silliman, B. R., and S. Y. Newell. 2003. Fungal farming in a snail. Proceedings of the National Academy of Sciences 100:15643–15648.

Silliman, B. R., J. van de Koppel, M. D. Bertness, L. E. Stanton, and I. A. Mendelsohn. 2005. Drought, snails, and large-scale die-off of Southern U.S. salt marshes. Science 310:1803–1806.

Silliman, B. R., J. van de Koppel, M. W. McCoy, J. Diller, G. N. Kasozi, K. Earl, F. N. Adams, and A. R. Zimmerman. 2012. Degradation and resilience in Louisiana salt marshes after the BP-Deepwater Horizon oil spill. Proceedings of the National Academy of Sciences 109:11234–11239.

Silliman, B. R., and J. C. Ziemann. 2001. Top-down control of Spartina alterniflora production by periwinkle grazing in a Virginia salt marsh. Ecology 82:2830–2845.

Smith, S. M., and M. C. Tyrrell. 2012. Effects of mud fiddler crabs (Uca pugnax) on the recruitment of halophyte seedlings in salt marsh dieback areas of Cape Cod (Massachusetts, USA). Ecological Research 27:233–237.

Sousa, W. P. 1993. Size-dependent predation on the salt-marsh snail Cerithidea californica Haldeman. Journal of Experimental Marine Biology and Ecology 166:19–37.

Sullivan, M. J. 1999. Applied diatom studies in estuaries and shallow coastal environments. Pages 334–351 in E. F. Stoermer, and J. P. Smol, editors. The diatoms: applications for the environmental and earth sciences. Cambridge University Press, Cambridge, UK. ISBN: 9780521509961.

Terborgh, J., et al. 2001. Ecological meltdown in predator-free forest fragments. Science 294:1923–1926.

Thorne, K., et al. 2018. U.S. Pacific coastal wetland resilience and vulnerability to sea-level rise. Science. Advances 4. eaa03270.

Thorne, K. M., D. L. Elliott-Fisk, G. D. Wylie, W. M. Perry, and J. Y. Takekawa. 2014. Importance of biogeomorphic and spatial properties in assessing a tidal salt marsh vulnerability to sea-level rise. Estuaries and Coasts 37:941–951.

Van Dyke, E., and K. Wasson. 2005. Historical ecology of a central California estuary: 150 years of habitat change. Estuaries 28:173–189.

Vu, H. D., and S. C. Pennings. 2018. Predators mediate above- vs. belowground herbivory in a salt marsh crab. Ecosphere 9:e02107.

Vu, H. D., K. Wieski, and S. C. Pennings. 2017. Ecosystem engineers drive creek formation in salt marshes. Ecology 98:162–174.

Wasson, K., et al. 2017. Eutrophication decreases salt marsh resilience through proliferation of algal mats. Biological Conservation 212:1–11.

Wasson, K., et al. 2019. Pattern and scale: evaluating generalities in crab distributions and marsh dynamics from small plots to a national scale. Ecology 100:02813.

Wasson, K., et al. 2020. Multiple factors contribute to the spatially variable and dramatic decline of an invasive snail in an estuary where it was long-established and phenomenally abundant. Biological Invasions 22:1181–1202.

Wasson, K., K. E. Tanner, A. Woofolk, S. McCain, and J. P. Suraci. 2021. Top-down and sideways: Herbivory and cross-ecosystem connectivity shape restoration success at the salt marsh-upland ecotone. PLOS ONE 16:e0247374.

Watson, E. B., K. Szura, C. Wigand, K. B. Raposa, K. Blount, and M. Cencer. 2016. Sea level rise, drought and the decline of Spartina patens in New England marshes. Biological Conservation 196:173–181.

Wigand, C., E. Davey, R. Johnson, K. Sundberg, J. Morris, P. Kenny, E. Smith, and M. Holt. 2015. Nutrient effects on belowground organic matter in a minerogenic salt marsh, North Inlet, SC. Estuaries and Coasts 38:1838–1853.
Witman, J. D., R. W. Lamb, and J. E. K. Byrnes. 2015. Towards an integration of scale and complexity in marine ecology. Ecological Monographs 85:475–504.

Wright, J. P., A. S. Flecker, and C. G. Jones. 2003. Local vs. landscape controls on plant species richness in beaver meadows. Ecology 84:3162–3173.

Wright, J. P., C. G. Jones, and A. S. Flecker. 2002. An ecosystem engineer, the beaver, increases species richness at the landscape scale. Oecologia 132:96–101.

**DATA AVAILABILITY STATEMENT**

Data are available at Dryad: https://doi.org/10.7291/D1H971

**SUPPORTING INFORMATION**

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3703/full