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Ecosphere

COASTAL AND MARINE ECOLOGY

Predicting burrowing crab impacts on salt marsh plants

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Abstract. Burrowing animals profoundly influence plant communities, and changes in the burrower and plant communities together with changing abiotic parameters can shift the influence of burrowers on plants. However, we lack an ability to predict when, where, and how burrowers will influence vegetation. To begin to understand how naturally, varying environmental conditions influence the impacts of burrowers, we need to examine how burrower impacts on marsh plants differ across sites differing in environmental conditions. We manipulated crab presence for multiple years and measured the responses of the dominant plants, Pacific cordgrass (*Spartina foliosa*) and perennial pickleweed (*Sarcocornia pacifica*), at three sites in northern California and two sites in southern California. Southern California (Point Conception, CA, to the U.S.–Mexico border) experiences higher air and water temperatures, lower precipitation, and higher porewater salinity levels. Combining data from these field studies with laboratory studies allowed us to generate predictions about burrowing crab effects in salt marshes. Our models included (1) an estimate of grazing pressure on marsh plants by the dominant burrowing crab (*Pachygrapsus crassipes*) and (2) several soil biogeochemical measurements. Crab effects varied from strongly positive to strongly negative and depended upon estimated crab grazing pressure and edaphic conditions (salinity, ammonium, and nitrate). Relative to crabs at other sites, crabs enhanced cordgrass at sites with intermediate levels of ammonium and extreme salinities. The dependence of crab effects on edaphic conditions suggests that projected interannual variability in temperature, precipitation, and nutrients could lead to more temporally variable impacts of crabs on cordgrass. Understanding the environmental controls on these interactions will help promote cordgrass productivity and stabilize salt marsh ecosystems.

Key words: burrowing crabs; comparative-experimental approach; cordgrass; environmental conditions; plant–animal interactions; salt marsh.

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Introduction

Burrowing animals, such as earthworms, crabs, prairie dogs, ghost shrimps, and rodents, can profoundly influence the structure and function of plant communities (Fields et al. 1999, Vanni 2002, Eisenhauer et al. 2009, Castorani et al. 2014, Andriuzzi et al. 2016). These impacts can vary both in size and direction, and 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). This variation is influenced by the plant and animal communities (Davidson and Lightfoot 2008, Eisenhauer et al. 2009, Baker et al.

2013) and abiotic factors (Crain and Bertness 2006, Crain 2008, Daleo and Iribarne 2009). However, we do not know how naturally, varying environmental conditions can influence the impacts of burrowers. Additionally, we lack an ability to predict when, where, and how burrowers will influence vegetation, because previous manipulative studies were rarely replicated in time, space, or both (but see Nomann and Pennings 1998, Bortolus et al. 2004, Holdredge et al. 2009). In order to begin to understand how burrower effects may change with varying environmental conditions, we examined animal impacts on plants across multiple years and sites in two distinct regions differing in environmental conditions (southern and northern California).

Coastal ecosystems, like salt marshes, vary in several key environmental factors that could influence the interactions between animals and plants (Harley et al. 2006, Kordas et al. 2011, Crotty et al. 2020). Spatiotemporal variation in such factors can influence marsh vegetation by altering rates of herbivory, plant growth, and nutrient cycling (Bertness and Ewanchuk 2002, Pennings and Silliman 2005). For example, consumer feeding rates may depend on air and water temperatures (Post and Pedersen 2008, O'Connor et al. 2009). Precipitation patterns (Snyder and Sloan 2005, Cayan et al. 2008, Largier et al. 2010) can alter the outcomes of plant–herbivore interactions via altered salinity (Kimmer 2002, Silliman et al. 2005, Long and Porturas 2014, Chang et al. 2018). For example, salt marsh burrowing crabs more strongly reduce marsh vegetation cover during droughts (Angelini et al. 2018). Variability in nutrients, for example due to the fluctuations in precipitation events (Caffrey et al. 2007, Aguilera and Melack 2018, Fong et al. 2020), can create variability in plant nutritional quality (Price 1991, Cronin and Hay 1996a, b) and plant responses to animals (Stout et al. 1998, Zhu et al. 2016).

Our understanding of how environmental conditions alter the outcomes of species interactions would benefit from manipulative experiments replicated in space and time (Menge and Sutherland 1987, Borer et al. 2014a, Duffy et al. 2015). Two recent studies used this rigorous approach to compare the impact of resources and herbivory on vegetation. In grasslands, a manipulative experiment across 40 sites and six continents found that nutrient additions reduced plant diversity, but herbivores rescued diversity in these areas (Borer et al. 2014b). In seagrass beds, a manipulative experiment across 20 degrees of latitude found that resource availability influenced plant defenses (Hernán et al. 2020). The significant replication of these experiments across sites provided a robust assessment of the roles of resources and herbivory on plants. Unfortunately, because few studies were replicated in space and time (Hastings et al. 2007), we lack an understanding of the impact of burrowing animals on vegetation and how this changes with environment.

Understanding how burrower impacts will change with environmental conditions is particularly important in salt marshes. Given their shallow depths, low relief shorelines, inputs from oceans, watersheds, and surrounding land, estuaries are among the first ecosystems to experience effects of climate change (IPCC 2007). Additionally, dominant and ecologically important salt marsh plants have recently experienced die-off (Alber et al. 2008, Marsh et al. 2016, Pettengill et al. 2018). These losses threaten several ecosystem functions (including carbon sequestration, shoreline erosion protection, water filtration, and habitat provisioning; Thorne et al. 2015, Kerr et al. 2016). In some marshes, such losses have been positively correlated with drought and were hypothesized to be related to increased interaction strengths with snails and burrowing crabs (Silliman et al. 2005, Angelini et al. 2018). However, burrowers have also been found to mitigate cordgrass loss during a marsh-wide cordgrass decline (Walker et al. 2020), suggesting that crabs could also facilitate cordgrass (Bertness 1985). The capacity of crabs to modify marsh loss may critically influence marsh functioning.

Here, we use data from field and laboratory experiments to examine how burrowing crab effects in salt marshes differ across environmental conditions. We manipulated burrowing crab density (*Pachygrapsus crassipes*) at three sites in northern California and combined these results with a previous manipulation at two sites in southern California, which experience higher air and water temperatures, lower precipitation, and higher porewater salinity levels. We also conducted multiple-choice feeding assays to

compare grazing pressure by the dominant salt marsh crab in California, *P. crassipes*. We predict crab effects using crab community and soil condition metrics.

METHODS

Study sites and species

We studied crab impacts on salt marshes in five sites in two regions. In northern California, we conducted experiments at Bodega Bay (BOD; 38°19′06.28″ N 123°02′23.65″ W), Tomales Bay (TOM; 38°12′35.67″ N 122°55′38.01″ W), and Bolinas Lagoon (BOL; 37°55′13.57″ N 122°41′10.09″ W). In southern California (Point Conception, CA to the U.S.-Mexico border), we conducted experiments at two sites in Kendall-Frost Marsh Reserve (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). The regions were separated by ~900 km, and sites within a region were separated by 40–55 km and 0.16–25 km (northern and southern California, respectively). In both regions, high and low elevations of marshes are dominated by perennial pickleweed (*Sarcocornia pacifica*) and Pacific cordgrass (*Spartina foliosa*), respectively. These two species overlap in the transition zone of intermediate elevations at both regions. Subordinate plants were more common in southern marshes, but only represented a modest portion of the plant community (<5%) in the transition zone. Relative to southern marshes, northern marshes in California experience greater annual rainfall (86 ± 13 cm vs. 26 ± 3 cm; Menne et al. 2012, Data provided by the University of California, Davis, Bodega Marine Laboratory), and lower annual air temperatures (12° ± 0.0°C vs. 19° ± 0.1°C; National Data Buoy Center 1971, Menne et al. 2012) and water temperatures (12° ± 0.0°C vs. 19 ± 0.0°C; National Data Buoy Center 1971).

To compare the crab communities among sites, we monitored crab sightings, burrow density, and burrow diameter (Appendix S1). *Pachygrapsus crassipes* (lined shore crab) dominated burrowing crab abundance at all marshes. Salt marsh populations of *P. crassipes* consume macroalgae, horn snails, detritus, conspecifics, and small infaunal invertebrates (Willason 1981, Zedler 1982, Sousa 1993, Boyer and Fong 2005). Although *P. crassipes* will also graze above- and belowground

plant material (Boyer and Fong 2005, J. Walker *personal observation*), no publications have quantified grazing rates by *P. crassipes* on perennial pickleweed or cordgrass (but see Wasson et al. [2019] for *personal observation* regarding plant consumption in the laboratory). *Leptuca crenulata* (Mexican fiddler crab) ranges from Pt. Conception, California, to Tenacatita Bay in Jalisco, Mexico (Crane 1975), and was present at southern marshes but was completely absent in northern marshes. The invasive *Carcinus maenas* (European green crab) was rare in northern marshes during the study period (<5% of all crab sightings; Appendix S1: Table S1). Another burrowing crab, *Hemigrapsus oregonensis* (Yellow shore crab), represented <1% of crab sightings at both northern and southern marshes (J. Walker, *personal observation*).

Field manipulation

To study the impact of crabs on the plant community, we manipulated burrowing crab access to plots at both regions. Manipulations in southern marshes (KF1 and KF2) were conducted May 2016 to October 2018 (Walker et al. 2020). Manipulations in northern marshes were started on different dates (May 2017, April 2018, and June 2018 at BOL, BOD, and TOM; respectively) and were run through October 2019. Start dates varied because of the logistics of simultaneously running experiments in northern and southern California. We selected plots within the transition zone that contained burrows, cordgrass, and pickleweed. Burrow density in our plots was representative of most areas within the transition zone (J. Walker, *personal observation*). All plots were adjacent to the main channel and ~30, ~200, ~380, and ~260 m from the water edge at mean lower low water (MLLW; KF2, BOL, TOM, and BOD, respectively), except at KF1, where plots were 2–3 m from the creek bank edge.

To manipulate burrow density, we followed methods as detailed in Walker et al. (2020). Briefly, square plots (0.7 × 0.7 × 0.6 m, *l* × *w* × *h*) were fenced in with plastic-mesh cages (mesh opening = 0.6 cm). Crab migration was minimized by inserting cages 30 cm into the substrate and attaching aluminum flashing to the tops 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 one meter apart. Our experiments included five plot types: three crab densities (Ambient, High, Removal), Cage-controls, and Unmanipulated controls ($n = 5$). Cage-controls were created by cutting one large window (15×10 cm, height x 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. Unmanipulated controls were marked with corner stakes (0.7×0.7 m plots). Control replication changed through time because we were initially limited on person hours to monitor additional replicates (Appendix S1: Fig. S2, Walker et al. 2020). Two pitfall traps (empty tennis ball canisters: diameter = 7 cm, height = 20 cm) were installed at opposite, diagonal corners of all cages.

All treatments were maintained every 2–3 weeks during the growing season of all years (April to October) following methods in Walker et al. (2020). 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 decrease over time (e.g., crabs escape, burrows fill in, and/ or crabs die; J. Walker, *personal observation*) without crab immigration into plots. To adjust for this loss, *P. crassipes* were added when burrow densities fell below the treatment's target number (i.e., when burrow density in Ambient plots fell below the average burrow density in Unmanipulated and Cage-controls and when burrow density in High plots fell below 50% more than the burrow density in Ambient plots). Roughly one crab was added to high plots every two weeks and ambient plots every 1 to 2 months.

To assess the effect of burrowing crabs on the plant community, we counted burrow number and burrow diameter in all of our plots (Appendix S1). At three time points during each growing season (~April, July, and October), we measured the percent cover of pickleweed and cordgrass. To help understand the factors contributing to changes in percent cover, we also measured species-specific plant characteristics (cordgrass stem height, cordgrass stem density, and pickleweed canopy height). In October 2019, we harvested all aboveground plant material to better understand crab effects on plant biomass. At this time, we also extracted sediment cores

from the middle of each plot for quantifying belowground plant biomass (cores extracted from the surface to 27 cm deep; ~3980 cm^3). Finally, we collected and analyzed porewater salinity, dissolved organic carbon (DOC), nitrate, and ammonium three times during each growing season (~April, July, and October) to understand the ambient conditions between sites and the abiotic parameters crabs may modify.

The main focus of this paper is predicting crab effects on the ecologically important salt marsh plant, cordgrass. For a detailed description of the crab community for both southern and northern California, see Appendix S1. For a description of the crab impacts on plant cover and plant characteristics for both cordgrass and pickleweed and biogeochemistry, see Walker et al. 2020 and Appendix S2 (for southern California and northern California, respectively).

Estimating crab grazing pressure on plants

To estimate crab grazing pressure in the field, we multiplied per capita grazing rates of *P. crassipes* by the burrow density of this crab because *P. crassipes* is the dominant burrowing crab at all sites. Per capita grazing rates were determined by offering local plants to crabs (e.g., crabs from BOD were offered plants from BOD). Feeding assays were performed at UC Davis's Bodega Marine Laboratory (BML) for northern populations (Bodega, CA; average water temperature between June and July in 2018 from the BML shoreline buoy = 12° ± 2°C, mean ± SE) and San Diego State University's Coastal Marine Institute and Laboratory for southern populations (San Diego, CA; average water temperature between June and July in 2018 from San Diego Bay = 22° ± 2°C). Crabs were housed in single containers ($15 \times 14 \times 8$ cm; $l \times w \times h$) with window-screen mesh sides to allow for water exchange. All containers were placed in flow-through seawater tables. Prior to the start of the experiment, crabs were starved for 48 h. All assays were conducted between June and July in 2018 to minimize the effect of temporal variability on spatial comparisons.

To standardize comparisons among marshes, we used undamaged, new tissues in all assays. Plant tissues were blotted dry and weighed at the start of the experiment. We offered each crab a choice of four plant tissues (cordgrass roots,

cordgrass leaves, pickleweed roots, and pickleweed leaves). Crabs were fed both leaves and roots due to their ability to access both above- and belowground material via burrowing. Tissue type was marked with negatively buoyant PVC clips. For all assays, no-crab replicates were paired with experimental replicates to control for autogenic changes in plants (Peterson and Renaud 1989). Experimental replicates ($n = 20$ crabs) and paired no-crab controls ran 1–3 d. All replicate pairs were checked once per day and removed if at least 33% of one plant tissue in the experimental replicate had been eaten (Pennings et al. 1998). At the end of the assays, plants were blotted dry and re-weighed. For each experimental replicate, we calculated consumption with the following equation $(H_i \times C_f / C_i) - H_f$, where H_i and H_f are the initial and final mass of the experimental replicate plants and C_f and C_i are the final and initial mass of the controls (no-crab replicates; Cronin and Hay 1996*a*).

We used Linear Mixed-Effect Models (LMEMs) to examine feeding preferences because of the lack of independence among tissues types within each replicate (Bates et al. 2015, Brauer and Curtin 2018, Schielzeth et al. 2020). For these analyses, the arcsine–square root transformation was applied to consumption rates (for all tissue-types) to normalize their distributions (Rhoades et al. 2018). We ran separate LMEMs for each site (KF1, KF2, BOL, TOM, and BOD) with tissue-type (cordgrass leaves, cordgrass roots, pickleweed leaves, and pickleweed roots) as a fixed term and replicate as a random term (to account for nonindependence). Next, we ran models to determine differences in consumption of plant species by grouping tissue-type by plant species (cordgrass or pickleweed). We ran LMEMs for each site with plant species as a fixed term and replicate as a random term. We calculated a ratio of cordgrass to pickleweed consumption as an estimate of site-specific feeding preference for these two plants. Lastly, we compared total consumption rates between northern and southern California by adding all consumption rates within a site. Total consumption rates between northern and southern California were compared with a two-tailed, two sample *t*-test after transformation. For a detailed description of these results see Appendix S3.

To estimate crab grazing pressure in the field, we multiplied the average total consumption values for both cordgrass and pickleweed from our feeding assays by the average number of *P. crassipes* burrows per year from our field manipulations (Appendix S1: Fig. S1). We found the mean number of burrows for all plots across all months for each year. *Leptuca crenulata* are detritivores and do not consume vascular plants; therefore, *L. crenulata* burrows were excluded from these calculations. To find only *P. crassipes* burrow density for southern California (there were no *L. crenulata* in northern California), we binned our burrow diameter data by burrow size—*L. crenulata* burrows ≤1.5 cm and *P. crassipes* >1.5 cm. Bins were chosen based on the average, largest burrow (burrows greater than the 97.5% confidence interval) from another southern site San Dieguito Lagoon (SDL, 32°58′47.0″ N, 117°14′43.6″ W) because SDL was dominated by *L. crenulata* (Walker et al. 2020). Binning by the average, largest burrow diameter at SDL ensured that we removed *L. crenulata* from the burrow count. Since we only measured 10 burrow diameters each sampling period, we calculated a ratio of the number of *P. crassipes* burrow diameters out of 10. This ratio was then multiplied by the average number of burrows for that sampling period. Because we estimated crab density with burrow density, we may have overestimated grazing pressure since burrow counts sometimes overestimate crab abundance (Martínez-Soto and Johnson 2020). However, this strategy is commonly employed to nondestructively estimate burrowing crab abundance. Additionally, we have no reason to suspect that the relationship between burrow density and crab density changes between marshes and regions. We also calculated a ratio of cordgrass to pickleweed consumption and adjusted the consumption values by multiplying the average number of *P. crassipes* burrows per year from our field manipulations. Both of these variables were used in the analysis below.

Although our estimates of grazing rates have some limitations, we believe they provide reasonable approximations of relative grazing rates between marshes for the following reasons. First, our laboratory measurements of grazing used local crabs from each site. Second, our grazing assays were conducted under relevant

environmental conditions (e.g., crabs from southern sites were assayed at a southern facility with seawater conditions representative of southern sites). This accounted for the major environmental conditions that could have influenced grazing rates (e.g., temperature).

Predictors of crab effects

Because crab effects vary in space and time (He and Silliman 2016, Wasson et al. 2019, Walker et al. 2020), we examined the influence of several factors on crab effects across all of our site-year combinations. To facilitate this analysis, we focused on crabs as a categorical variable, and we combined all treatments with crabs into a +Crab treatment (Ambient, High, Cage-controls, and Unmanipulated controls). Thus, we compared +Crab vs. –Crab treatments. We justify this grouping because (1) burrow density was only different among removal treatments and the other treatments (Appendix S1: Fig. S2) and (2) caging artifacts in salt marshes on plant growth are either weak or absent (McGuinness 1997, Lotze and Worm 2000, Holdredge et al. 2009, 2010, Angelini et al. 2018).

We used two analyses to predict crab effects on vegetation. First, we calculated log response ratios (LRR) to represent +Crab vs. –Crab effect sizes on cordgrass cover (Hedges et al. 1999, Lajeunesse 2011). Positive LRR values indicate that crabs enhanced cordgrass cover. We focused on cordgrass cover as our main response variable due to its important ecological role, numerous ecosystem services, and the significant variation of crab effects on cordgrass observed across sites and years (Walker et al. 2020). We compared LRR for each site-year combination by creating a forest plot and measuring how many site-year combinations deviated from zero.

Next, we performed a principal component analysis (PCA). We used seven variables and treated each treatment-site-year combination as an individual sample for a total of six samples per site (30 samples total). We treated each year as an independent sample to provide a more robust assessment of the factors driving crab effects. This approach was justified because of large within-site and between-year variation in predictors and crab effects (e.g., KF1 and KF2, Walker et al. 2020). The predictors we included in our models were measurements of the crab community (burrow density and diameter), biogeochemistry (salinity, nitrate, and ammonium), and crab grazing (cordgrass to pickleweed consumption and estimated grazing pressure).

We determined the average value of each variable for every treatment (+Crab and –Crab), site, and year combination. For crab metrics (burrow density and diameter) and biogeochemistry metrics (salinity, nitrate, and ammonium), we used the mean of all samples across all months for each year. For crab grazing, we used the two variables that were adjusted for burrow density (described in 'Estimating crab grazing pressure on plants')—the ratio of cordgrass to pickleweed consumption and the estimated grazing pressure of all plant material. All variables were tested for collinearity prior to the PCA. Burrow density was correlated with grazing pressure, and therefore, we removed burrow density from subsequent analyses. Principle components were retained if eigenvalues were >1.0 and 60% of the total variance was retained (Jackson 1993, Jolliffe and Cadima 2016, Banda and Kumarasamy 2020).

After identifying three principal components that accounted for 65% of the variation across all sites, we asked whether the effect of crabs on cordgrass cover (expressed as LRR) could be predicted by PC1, PC2, PC3, and the major factors of these principal components (i.e., those contributing >20%). We used the best fitting polynomial model to estimate and explore the relationships between LRR and variables because preliminary inspection showed unimodal relationships for variables. A linear mixed-effects regression model was used to test whether these main contributors could further aid in explaining the variation in the effect of crabs on cordgrass cover. We built a full model with six main contributors (burrow diameter, ammonium, salinity, nitrate, estimated grazing pressure, and cordgrass to pickleweed consumption). We did not include interaction terms in our full model due to our limited sample size. Quadratic terms were added into models based on the above data exploration. Site was included as a random factor in our models to separate the effect of site among variables. A subset of models was selected from backward and forward stepwise regression by removing variables based on AIC values. The best model was chosen based on a combination of the highest adjusted R^2 and AIC values.

Statistical analyses were performed using R software vs. 3.6.0 (R Core Team 2019). GLM and LMEM 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. PCAs were constructed using ggfortify and ggplot2, and LRRs were calculated using the metafor package.

Results

Although there was no overall effect of crabs on cordgrass, crabs influenced cordgrass (i.e., confidence intervals of LRR did not overlap zero) at 4 of the 13 site-year combinations (Fig. 1). At sites where crabs affected cordgrass, the effect of crabs across years was either in the same direction or neutral. For example, crabs at BOD tended to negatively impact cordgrass cover in all years measured, whereas at KF2, crabs enhanced cordgrass cover during all three years.
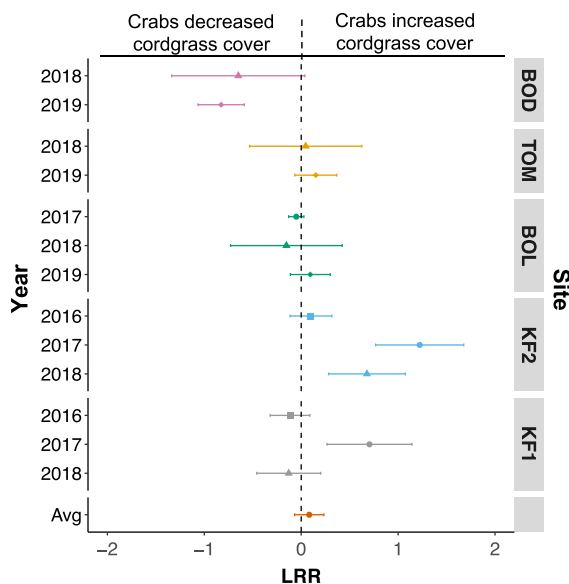

Fig. 1. Effect of crabs on cordgrass cover at each site-year combination. Log Response Ratios (LRR; + 95% confidence intervals) represent the directional effect of crabs on cordgrass cover. LRRs are arranged top to bottom by site, and chronologically by year within sites. Positive values indicate that crabs enhanced cordgrass cover. An average LRR for all site-year combinations is shown at the bottom. Symbols represent years, and colors represent sites.

PC1, accounting for 26% of the total variation across the five sites sampled, was negatively correlated with crab burrow diameter and cordgrass to pickleweed consumption (Fig. 2, Table 1). PC2, accounting for 21% of the total variation, was positively correlated with ammonium and negatively correlated with estimated grazing pressure and nitrate. PC3, accounting for 18% of the total variation, and salinity contributed 60% to PC3 (Fig. 2B).

PC1 was not associated with crab effects (Appendix S3: Fig. S3). PC2 and PC3 were associated with crab effects on cordgrass (Fig. 3). Of the six main contributors to PC1, PC2, PC3 (Table 1), only salinity had a functional relationship with LRR. Salinity had a best fitting polynomial model with a quadratic function, suggesting a threshold that represents a shift in the direction of crab effects. Salinity and LRR had a positive quadratic function, suggesting that crabs had a positive effect on cordgrass cover at sites with low and high salinity (vertex = 43 ppt; Fig. 3C). Ammonium was marginally related to LRR ($P = 0.105$; Fig. 3D). Crabs had no effect on cordgrass cover at low ammonium levels, enhanced cordgrass cover at intermediate levels, and negatively impacted cordgrass at high levels (Fig. 3).

The best fitting multivariate model (Appendix S3: Table S2) was generally similar to univariate regressions (Fig. 3). Crab effects on cordgrass were best explained by ammonium and salinity (Appendix S3: Table S2). Ammonium and salinity parameters were significant when site variation was accounted for in the model, suggesting that crab effects can be explained beyond site variation.

Discussion

Environmental conditions mediated crab impacts on plants. We found that two principle components explained variation in burrower impacts on cordgrass. Further, four environmental factors (ammonium, grazing pressure, nitrate, and salinity) contributed primarily to crab impacts. Crab effects contrasted between regions, in part because grazing pressure was higher in warmer, southern regions, and depended upon ambient soil conditions (i.e., salinity and ammonium). Crabs positively impacted cordgrass
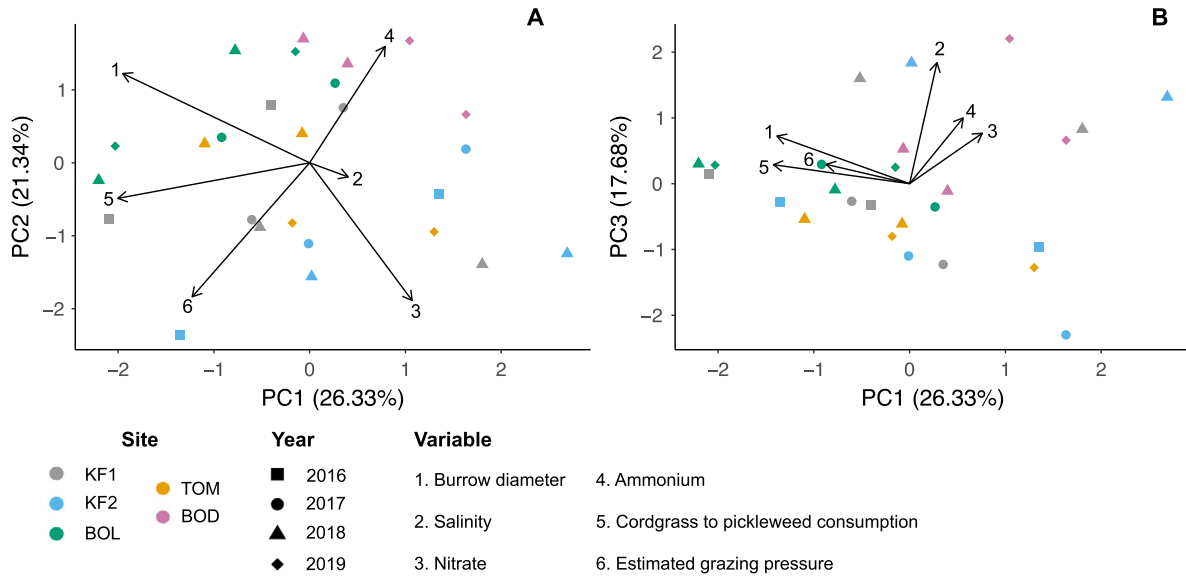
Fig. 2. Two-dimensional correlation-based principal component analysis (PCA) ordination of the treatment-year-site combinations, for a total of 6 samples per site (30 samples total), for (A) PC1 vs. PC2 and (B) PC1 vs PC3. PC1, PC2, and PC3 accounted for 65% of the total variation across the five sites sampled. Symbols represent years, and colors represent sites. Numbers represent variables: (1) Burrow diameter, (2) Salinity, (3) Nitrate, (4) Ammonium, (5) Cordgrass to pickleweed consumption, (6) Estimated grazing pressure.

Table 1. Contributions of variables to PC1, PC2, and PC3. PC1 accounted for 26% of the total variation and was correlated with cordgrass to pickleweed consumption and burrow diameter.

Variable	Contribution (%)
PC1	
Cordgrass to pickleweed consumption	36
Burrow diameter	34
PC2	
Nitrate	32
Estimated grazing pressure	30
Ammonium	23
PC3	
Salinity	60

Notes: PC2 accounted for 21% of the total variation and was correlated with nitrate, estimated grazing pressure, and ammonium. PC3 accounted for 18% of the total variation and was correlated with salinity. Variables were only included if they contributed >20% to either PC1, PC2, or PC3.

at salinity extremes, but had no effect at intermediate salinities. The dependence of crab effects on edaphic conditions suggests that projected inter-annual variability in temperature, precipitation, and nutrients could lead to more temporally variable impacts of crabs on cordgrass.

Crabs positively impacted cordgrass at salinity extremes below ~40 ppt and above ~50 ppt, but had no effect at intermediate salinities. The positive impacts of crabs at lower salinities could be related to higher growth rates of cordgrass allowing plants the maximum capacity to respond to crabs, or higher activities of burrowing crabs (Crain et al. 2004, Pennings et al. 2005). The mechanism by which crabs positively influenced cordgrass at high salinities is less clear. Unlike other studies (Smith et al. 2009, Pestana et al. 2017), crabs did not influence salinity (this study and Walker et al. 2020). Therefore, other environmental factors may control crab–plant interactions at high salinities. For example, often high salinities due to high evapotranspiration are associated with higher levels of sulfide (Mendelssohn and Morris 2000).

Because soil salinity generally mediates the outcomes of plant-animal interactions, especially in salt marshes (Silliman et al. 2005, Long and Porturas 2014), increased interannual variation in precipitation patterns will likely modify how marsh plants interact with animals. For example, the resulting salinity changes driven by precipitation will mediate how cordgrass interacts with
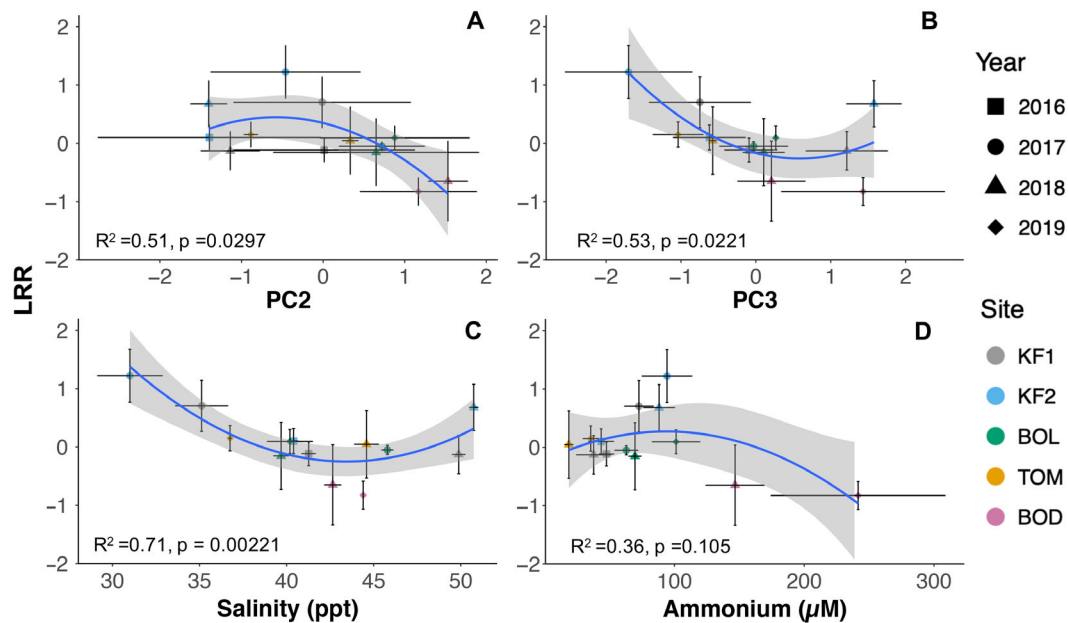
Fig. 3. Functional relationships between Log Response Ratios (LRR: the effect of crabs on cordgrass cover) and (A) PC2, (B) PC3, (C) salinity, and (D) ammonium. Lines represent quadratic models; R^2 reported for relationships. Symbols represent years, and colors represent sites.

snails, insects, and crabs. Increased grazing pressure from snails during dry years with reduced runoff and higher salinities may lead to runaway consumption and increased loss of salt marsh habitat (Silliman et al. 2005). Compensatory responses of cordgrass to scale insects were mediated by salinity (e.g., overcompensation was observed at salinity extremes and undercompensation was observed at intermediate salinities, Long and Porturas 2014). Finally, our current study suggests that salinity mediates interactions of cordgrass with crabs in a non-linear way. The diversity of interactions that salinity regulates combined with the foundational role played by cordgrass suggests that future changes in salinity will influence the structure and functioning of these important ecosystems in ways that may not be predictable from simple linear models.

Crabs tended to have no effect on cordgrass at low levels of ammonium (<~70 μM), positive impacts on cordgrass at intermediate levels of ammonium, and negative effects at high levels of ammonium (>92 μM). Stimulatory impacts of crabs on cordgrass may be impaired at low ammonium levels because nutrient-limited plants cannot respond to crabs. At high ammonium levels,

however, at least two mechanisms may explain the negative effect of crabs. First, positive plant responses may be countered by increased grazing on higher quality plants (Cronin and Hay 1996a, Silliman and Zieman 2001). Second, positive plant responses may be prevented if high ammonium levels stress plants. Such ammonium toxicity has been demonstrated for eelgrass at concentrations found in our study (van Katwijk et al. 1997).

In northern California, crab effects were neutral to negative, while in southern California, crab effects were neutral to positive. This regional pattern could have been driven by regional differences in crab behavior or abiotic factors. Estimated grazing pressure, a main contributor to crab impacts, was 4× higher in southern California marshes than northern California marshes (Appendix S3). Higher grazing rates in southern California may have stimulated cordgrass production via compensatory growth responses—a phenomenon previously described for southern populations of this cordgrass species (Long and Porturas 2014). In addition to regional differences in grazing pressure, regional patterns in temperature and precipitation may have influenced differences in crab effects. Southern marshes

experience harsher conditions because of higher temperatures and lower rainfalls via higher evapotranspiration. As a result, our finding that positive impacts of crabs were present only in southern marshes is consistent with the stress gradient hypothesis that predicts shifts toward positive interspecific interactions in harsh environments (Bertness and Callaway 1994, Bruno et al. 2003, Brooker et al. 2008). Further research is needed to fully understand the mechanism driving crab effects on plants.

In contrast to all other sites, crabs at BOD negatively impacted cordgrass, perhaps because plants at the northern limit of Pacific cordgrass (Ayres et al. 2003) are more stressed and/or restricted by a relatively short growing season and slow growth rates. Plant responses to crabs (e.g., compensatory growth, inducible defenses, nutrient uptake) may be impaired when plants are stressed or growing slowly. Three observations support the hypothesis that BOD plants were more stressed. First, unlike all the other sites, BOD cordgrass did not flower (Appendix S2: Fig. S4; Walker et al. 2020). Second, BOD cordgrass was ~20% shorter than the other sites. Third, ammonium levels at BOD were ~35× higher than the site with the lowest ammonium levels (TOM), perhaps because of a reduced ability of cordgrass to uptake ammonium and slow rates of growth (Bradley and Morris 1990, Alldred et al. 2017).

In addition to the environmental factors we considered, predators could have influenced burrowing crab–plant interactions. While we did not rigorously compare predator populations across our sites, we note that Tomales Bay (TOM) and BOD were the only sites where we observed the predatory, *Carcinus maenas* (European green crab) in our plots. At TOM, *C. maenas* comprised 20% of crab sitings, while only six crabs were sited at BOD and in only 2019 (Appendix S1: Table S1). Such differences in the predator community could have influenced burrower impacts on cordgrass. For example, *C. maenas* could have contributed to the neutral effect of burrowers on cordgrass at Tomales Bay by suppressing *P. crassipes* activity. Such an effect might be predicted by the numerous studies, demonstrating that green crab cues suppress feeding activity of grazers (Trussell et al. 2003, Kimbro et al. 2009). We are unaware of studies examining *P. crassipes* responses to predation risk by *C. maenas*.

Although *P. crassipes* strongly influenced cordgrass production in certain times and places (in both positive and negative directions), we did not find crab effects in 70% of our site-year combinations (Fig. 1). These results contrast with studies that consistently found that *Sesarma reticulatum* (purple marsh crab) suppresses cordgrass production in marshes of the northeastern United States (Holdredge et al. 2009, Coverdale et al. 2012, Bertness et al. 2014). Such negative impacts of *S. reticulatum* are beginning to occur in southeastern marshes of the United States (Crotty et al. 2020). These contrasting results could be explained by regional or species-specific impacts. Although crabs negatively impacted cordgrass at high ammonium and intermediate salinities (this study), it seems unlikely that the consistent negative impacts of *S. reticulatum* in eastern marshes results from differences in ammonium and salinity relative to western marshes. Rather, we hypothesize that *S. reticulatum* may exert stronger grazing pressure on cordgrass than does *P. crassipes*—thereby leading to *S. reticulatum's* more consistent and negative impacts.

Recently, salt marsh conservation has focused on determining the resiliency of these important ecosystems to climate change, especially sea-level rise (Morris et al. 2002, Mudd et al. 2010, Fitzgerald and Hughes 2019). Many marshes without sufficient sediment or without the space to migrate upward in tidal elevation are at risk of increased inundation with consequences for both burrowers and marsh plants. For example, at BOD where plants are already restricted by a relatively short growing season and slow growth rates, sea-level rise may exacerbate the negative effects of crabs on plants. Incorporating crab impacts and climate change into models of salt marsh functions will improve our understanding of resiliency and, ultimately, how these complex ecosystems will adapt to future change.

ACKNOWLEDGMENTS

LITERATURE CITED

Aguilera, R., and J. M. Melack. 2018. Relationships among nutrient and sediment fluxes, hydrological variability, fire, and land cover in coastal California catchments. Journal of Geophysical Research: Biogeosciences 123:2568–2589.

Alber, M., E. M. Swenson, S. C. Adamowicz, and I. A. Mendelssohn. 2008. Salt marsh dieback: an overview of recent events in the US. Estuarine, Coastal and Shelf Science 80:1–11.

Alldred, M., A. Liberti, and S. B. Baines. 2017. Impact of salinity and nutrients on salt marsh stability. Ecosphere 8:e02010.

Andriuzzi, W. S., O. Schmidt, L. Brussaard, J. H. Faber, and T. Bolger. 2016. Earthworm functional traits and interspecific interactions affect plant nitrogen acquisition and primary production. Applied Soil Ecology 104:148–156.

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.

Ayres, D. R., D. R. Strong, and P. Baye. 2003. *Spartina foliosa* (Poaceae) - a common species on the rode to rarity? Madroño 50:209–213.

Baker, B. W., D. J. Augustine, J. A. Sedgwick, and B. C. Lubow. 2013. Ecosystem engineering varies spatially: a test of the vegetation modification paradigm for prairie dogs. Ecography 36:230–239.

Banda, T. D., and M. Kumarasamy. 2020. Application of multivariate statistical analysis in the development of a surrogate water quality index (WQI) for South African watersheds. Water 12:1584.

Bates, D., M. Mächler, B. M. Bolker, and S. C. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

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.

Bertness, M. D., and R. M. Callaway. 1994. Positive interactions in communities. Trends in Ecology and Evolution 9:191–193.

Bertness, M. D., and P. J. Ewanchuk. 2002. Latitudinal and climate-driven variation in the strength and nature of biological interactions in New England salt marshes. Oecologia 132:392–401.

Borer, E. T., W. S. Harpole, P. B. Adler, E. M. Lind, J. L. Orrock, E. W. Seabloom, and M. D. Smith. 2014*a*. Finding generality in ecology: A model for globally distributed experiments. Methods in Ecology and Evolution 5:65–73.

Borer, E. T., et al. 2014*b*. Herbivores and nutrients control grassland plant diversity via light limitation. Nature 508:517–520.

Bortolus, A., P. Laterra, and O. Iribarne. 2004. Crab-mediated phenotypic changes in *Spartina densiflora* Brong. Estuarine, Coastal and Shelf Science 59:97–107.

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.

Bradley, P. M., and J. T. Morris. 1990. Influence of oxygen and sulfide concentration on nitrogen uptake kinetics in *Spartina alterniflora*. Ecology 71:282–287.

Brauer, M., and J. J. Curtin. 2018. Linear mixed-effects models and the analysis of nonindependent data: A unified framework to analyze categorical and continuous independent variables that vary within-subjects and/or within-items. Psychological Methods 23:389–411.

Brooker, R. W., et al. 2008. Facilitation in plant communities: The past, the present, and the future. Journal of Ecology 96:18–34.

Bruno, J. F., J. J. Stachowicz, and M. D. Bertness. 2003. Inclusion of facilitation into ecological theory. Trends in Ecology and Evolution 18:119–125.

Caffrey, J. M., T. P. Chapin, H. W. Jannasch, and J. C. Haskins. 2007. High nutrient pulses, tidal mixing and biological response in a small California

estuary: variability in nutrient concentrations from decadal to hourly time scales. Estuarine, Coastal and Shelf Science 71:368–380.

Castorani, M. C. N., K. A. Hovel, S. L. Williams, and M. L. Baskett. 2014. Disturbance facilitates the coexistence of antagonistic ecosystem engineers in California estuaries. Ecology 95:2277–2288.

Cayan, D. R., E. P. Maurer, M. D. Dettinger, M. Tyree, and K. Hayhoe. 2008. Climate change scenarios for the California region. Climatic Change 87:21–42.

Chang, A. L., C. W. Brown, J. A. Crooks, and G. M. Ruiz. 2018. Dry and wet periods drive rapid shifts in community assembly in an estuarine ecosystem. Global Change Biology 24:e627–e642.

Coverdale, T. C., A. H. Altieri, and M. D. Bertness. 2012. Belowground herbivory increases vulnerability of New England salt marshes to die-off. Ecology 93:2085–2094.

Crain, C. M. 2008. Interactions between marsh plant species vary in direction and strength depending on environmental and consumer context. Journal of Ecology 96:166–173.

Crain, C. M., and M. D. Bertness. 2006. Ecosystem engineering across environmental gradients: implications for conservation and management. BioScience 56:211–218.

Crain, C. M., B. R. Silliman, S. L. Bertness, and M. D. Bertness. 2004. Physical and biotic drivers of plant distribution across estuarine salinity gradients. Ecology 85:2539–2549.

Crane, J. 1975. Fiddler crabs of the world. Ocypodidae: Genus Uca. Princeton University Press, Princeton, New Jersey, USA.

Cronin, G., and M. E. Hay. 1996a. Susceptibility to herbivores depends on recent history of both the plant and animal. Ecology 77:1531–1543.

Cronin, G., and M. E. Hay. 1996b. Within-plant variation in seaweed palatability and chemical defenses: optimal defense theory versus the growth-differentiation balance hypothesis. Oecologia 105:361–368.

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., and O. Iribarne. 2009. Beyond competition: the stress gradient hypothesis tested in plant-herbivore interactions. Ecology 90:2368–2374.

Davidson, A. D., and D. C. Lightfoot. 2008. Burrowing rodents increase landscape heterogeneity in a desert grassland. Journal of Arid Environments 72:1133–1145.

Duffy, J. E., et al. 2015. Biodiversity mediates top-down control in eelgrass ecosystems: A global comparative-experimental approach. Ecology Letters 18:696–705.

Eisenhauer, N., A. Milcu, N. Nitschke, A. C. W. Sabais, C. Scherber, and S. Scheu. 2009. Earthworm and belowground competition effects on plant productivity in a plant diversity gradient. Oecologia 161:291–301.

Fields, M. J., D. P. Coffin, and J. R. Gosz. 1999. Burrowing activities of kangaroo rats and patterns in plant species dominance at a shortgrass steppe-desert grassland ecotone. Journal of Vegetation Science 10:123–130.

Fitzgerald, D. M., and Z. Hughes. 2019. Marsh processes and their response to climate change and sea-level rise. Annual Review of Earth and Planetary Sciences 47:481–517.

Fong, C. R., R. L. Kennison, and P. Fong. 2020. Nutrient subsidies to southern California estuaries can be characterized as pulse-interpulse regimes that may be dampened with extreme eutrophy. Estuaries and Coasts 44:867–874.

Harley, C. D. G., A. R. Hughes, K. M. Hultgren, B. G. Miner, C. J. B. Sorte, C. S. Thornber, L. F. Rodriguez, L. Tomanek, and S. L. Williams. 2006. The impacts of climate change in coastal marine systems. Ecology Letters 9:228–241.

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.

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

Hedges, L. V., J. Gurevitch, and P. S. Curtis. 1999. The meta-analysis of response ratios in experimental ecology. Ecology 80:1150–1156.

Hernán, G., et al. 2020. Latitudinal variation in plant defence against herbivory in a marine foundation species does not follow a linear pattern: The importance of resource availability. Global Ecology and Biogeography 30:220–234.

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

IPCC. 2007. Climate Change 2007: Synthesis Report. Pages 104 in Core Writing Team, R. K. Pachauri, and A. Reisinger, editors. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva, Switzerland.

Jackson, D. A. 1993. Stopping rules in principal components analysis: A comparison of heuristical and statistical approaches. Ecology 74:2204–2214.

Jolliffe, I. T., and J. Cadima. 2016. Principal component analysis: A review and recent developments. Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences 374:20150202.

Kerr, D. W., I. B. Hogle, B. S. Ort, and W. J. Thornton. 2016. A review of 15 years of *Spartina* management in the San Francisco Estuary. Biological Invasions 18:2247–2266.

Kimbro, D. L., E. D. Grosholz, A. J. Baukus, N. J. Nesbitt, N. M. Travis, S. Attoe, and C. Coleman-Hulbert. 2009. Invasive species cause large-scale loss of native California oyster habitat by disrupting trophic cascades. Oecologia 160:563–575.

Kimmer, W. J. 2002. Physical, biological and management responses to variable freshwater flow into the San Francisco Estuary. Estuaries 25:1275–1290.

Kordas, R. L., C. D. G. Harley, and M. I. O'Connor. 2011. Community ecology in a warming world: The influence of temperature on interspecific interactions in marine systems. Journal of Experimental Marine Biology and Ecology 400:218–226.

Lajeunesse, M. J. 2011. On the meta-analysis of response ratios for studies with correlated and multi-group designs. Ecology 92:2049–2055.

Largier, J. L., B. S. Cheng, and K. D. Higgason, editors. 2010. Climate change impacts: Gulf of the Farallones and Cordell Bank National Marine Sanctuaries. *In* Report of a Joint Working Group of the Gulf of the Farallones and Cordell Bank National Marine Sanctuaries Advisory Councils. Marine Sanctuaries Conservation Series ONMS-11-04. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Office of National Marine Sanctuaries, Silver Spring, Maryland, USA, 121 pp.

Long, J. D., and L. D. Porturas. 2014. Herbivore impacts on marsh production depend upon a compensatory continuum mediated by salinity stress. PLoS One 9:e110419.

Lotze, H. K., and B. Worm. 2000. Variable and complementary effects of herbivores on different life stages of bloom-forming macroalgae. Marine Ecology Progress Series 200:167–175.

Marsh, A., L. K. Blum, R. R. Christian, E. Ramsey, and A. Rangoonwala. 2016. Response and resilience of *Spartina alterniflora* to sudden dieback. Journal of Coastal Conservation 20:335–350.

Martínez-Soto, K. S., and D. S. Johnson. 2020. The density of the Atlantic marsh fiddler crab (*Minuca pugnax*, Smith, 1870) (Decapoda: Brachyura: Ocypodidae) in its expanded range in the Gulf of Maine, USA. Journal of Crustacean Biology 40:544–548.

McGuinness, K. A. 1997. Tests for artefacts in some methods used to study herbivory and predation in mangrove forests. Marine Ecology Progress Series 153:37–44.

Mendelssohn, I. A., and J. T. Morris. 2000. Ecophysiological controls on the productivity of *Spartina alterniflora* Loisel. Pages 59–80 *in* M. P. Weinstein, and D. A. Kreeger, editors. Concepts and controversies in tidal marsh ecology. Springer, Dordrecht, The Netherlands.

Menge, B. A., and J. P. Sutherland. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. American Naturalist 130:730–757.

Menne, M. J., et al. 2012. Global Historical Climatology Network - Daily (GHCN-Daily), Version 3. [indicate subset used]. NOAA National Climatic Data Center, Houston, Texas, USA. https://doi.org/10.7289/V5D21VHZ

Morris, J. T., P. V. Sundareshwar, C. T. Nietch, B. Kjerfve, and D. R. Cahoon. 2002. Responses of coastal wetlands to rising sea level. Ecology 83:2869–2877.

Mudd, S. M., A. D'Alpaos, and J. T. Morris. 2010. How does vegetation affect sedimentation on tidal marshes? Investigating particle capture and hydrodynamic controls on biologically mediated sedimentation. Journal of Geophysical Research: Earth Surface 115:1–14.

National Data Buoy Center. 1971. Meteorological and oceanographic data collected from the National Data Buoy Center Coastal-Marine Automated Network (C-MAN) and moored (weather) buoys. [Station 46254, 46013]. NOAA National Centers for Environmental Information. Dataset. https://www.ncei.noaa.gov/archive/accession/NDBC-CMANWx

Nomann, B. E., and S. C. Pennings. 1998. Fiddler crab-vegetation interactions in hypersaline habitats. Journal of Experimental Marine Biology and Ecology 225:53–68.

O'Connor, M. I., M. F. Piehler, D. M. Leech, A. Anton, and J. F. Bruno. 2009. Warming and resource availability shift food web structure and metabolism. PLoS Biology 7:3–8.

Pennings, S. C., T. H. Carefoot, E. L. Siska, M. E. Chase, and T. A. Page. 1998. Feeding preferences of a generalist salt-marsh crab: relative importance of multiple plant traits. Ecology 79:1968–1979.

Pennings, S. C., M. B. Grant, and M. D. Bertness. 2005. Plant zonation in low-latitude salt marshes: disentangling the roles of flooding, salinity and competition. Journal of Ecology 93:159–167.

Pennings, S. C., and B. R. Silliman. 2005. Linking biogeography and community ecology: latitudinal variation in plant–herbivore interaction strength. Ecology 86:2310–2319.

Pestana, D. F., N. Pülmanns, I. Nordhaus, K. Diele, and M. Zimmer. 2017. The influence of crab burrows on sediment salinity in a *Rhizophora*-dominated mangrove forest in North Brazil during the dry season. Hydrobiologia 803:295–305.

Peterson, C. H., and P. E. Renaud. 1989. Analysis of feeding preference experiments. Oecologia 80:82–86.

Pettengill, T. M., S. M. Crotty, C. Angelini, and M. D. Bertness. 2018. A natural history model of New England salt marsh die-off. Oecologia 186:621–632.

Post, E., and C. Pedersen. 2008. Opposing plant community responses to warming with and without herbivores. Proceedings of the National Academy of Sciences of the United States of America 105:12353–12358.

Price, P. W. 1991. The plant vigor hypothesis and herbivore attack. Oikos 62:244–251.

R Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Rhoades, O. K., R. J. Best, and J. J. Stachowicz. 2018. Assessing feeding preferences of a consumer guild: Partitioning variation among versus within species. American Naturalist 192:287–300.

Schielzeth, H., N. J. Dingemanse, S. Nakagawa, D. F. Westneat, H. Allegue, C. Teplitsky, D. Réale, N. A. Dochtermann, L. Z. Garamszegi, and Y. G. Araya-Ajoy. 2020. Robustness of linear mixed-effects models to violations of distributional assumptions. Methods in Ecology and Evolution 11:1141–1152.

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

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

Smith, N. F., C. Wilcox, and J. M. Lessmann. 2009. Fiddler crab burrowing affects growth and production of the white mangrove (Laguncularia racemosa) in a restored Florida coastal marsh. Marine Biology 156:2255–2266.

Snyder, M. A., and L. C. Sloan. 2005. Transient future climate over the Western United States using a regional climate model. Earth Interactions 9:1–20.

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.

Stout, M. J., R. A. Brovont, and S. S. Duffey. 1998. Effect of nitrogen availability on expression of constitutive and inducible chemical defenses in tomato, Lycopersicon esculentum. Journal of Chemical Ecology 24:945–963.

Thorne, K. M., K. J. Buffington, D. L. Elliott-Fisk, J. Y. Takekawa, K. M. Thorne, K. J. Buffington, J. Y. Takekawa, and D. L. Elliott-Fisk. 2015. Tidal marsh susceptibility to sea-level rise: importance of local-scale models. Journal of Fish and Wildlife Management 6:290–304.

Trussell, G. C., P. J. Ewanchuk, and M. D. Bertness. 2003. Trait-mediated effects in rocky intertidal food chains: Predator risk cues alter prey feeding rates. Ecology 84:629–640.

van Katwijk, M. M., L. H. T. Vergeer, G. H. W. Schmitz, and J. G. M. Roelofs. 1997. Ammonium toxicity in eelgrass Zostera marina. Marine Ecology Progress Series 157:159–173.

Vanni, M. J. 2002. Nutrient cycling by animals in freshwater ecosystems. Annual Review of Ecology and Systematics 33:341–370.

Walker, J. B., S. A. Rinehart, W. K. White, E. D. Grosholz, and J. D. Long. 2020. Local and regional variation in effects of burrowing crabs on plant community structure. Ecology 102:e03244.

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:e02813.

Willason, S. W. 1981. Factors influencing the distribution and coexistence of Pachygrapsus crassipes and Hemigrapsus oregonensis (Decapoda: Grapsidae) in a California salt marsh. Marine Biology 64:125–133.

Zedler, J. B. 1982. The ecology of southern California coastal salt marshes: a community profile. Biological Services Program: FWS/OBS-81/54.

Zhu, X., J. Wang, Q. Chen, G. Chen, Y. Huang, and Z. Yang. 2016. Costs and trade-offs of grazer-induced defenses in Scenedesmus under deficient resource. Scientific Reports 6:1–10.

Data Availability Statement

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3803/full