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Loss and recovery of coastal foundation species: salt marsh and seagrass dynamics in a central California estuary

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LOSS AND RECOVERY OF COASTAL FOUNDATION SPECIES: SALT MARSH AND SEAGRASS DYNAMICS IN A CENTRAL CALIFORNIA ESTUARY

A dissertation submitted in partial satisfaction
of the requirements for the degree of

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in

ECOLOGY AND EVOLUTIONARY BIOLOGY

by

Kathryn M. Beheshti

March 2021

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Abstract

Loss and recovery of coastal foundation species: salt marsh and seagrass dynamics in a central California estuary

Kathryn M. Beheshti

In many systems there has been extensive loss of foundation species and associated ecosystem services over the past century, as human alterations have increased. This is particularly true in temperate estuaries, where the main foundation species—salt marsh, seagrasses and oysters, have been in a state of decline. As restoration and conservation efforts increase, there is a critical need to better understand factors that affect the recovery of estuarine foundation species, as well as to characterize the consequences of such recovery. My dissertation research examines drivers and consequences of loss and recovery in two foundation species in Elkhorn Slough, a highly impacted estuary in Central California.

In Chapters 1 and 2, I explore the role of a prolific crab species as both a consumer and ecosystem engineer in marsh ecosystems. I focus on vulnerable marsh edges prone to marsh loss; tidal creek bank edges (Ch. 1) and salt pannes. (Ch. 2). In Chapter 1, I show that crab grazing and the engineering of extensive burrow networks has a negative effect on marsh biomass, and this combined effect compromises the ability of the marsh to stabilize sediments, prevent erosion, and accrete and track sea level rise. In Chapter 2, I show that the rate of marsh recovery and panne contraction is driven by both physical and biological drivers. In Chapter 3, I conducted two small-scale experimental seagrass restorations and tracked structural and functional recovery. I detected astonishingly rapid expansion of restored plots and a related increase in associated ecosystem services such as biodiversity and improvement of water quality. Unlike other foundation species (corals, mangroves, redwood forests), seagrasses are fast-growing and I have demonstrated the rapidity of restoration success and a trajectory of multifunctional recovery.

My work highlights how estuary management can be improved by investigations grounded in experimental field ecology, because they increase our understanding of the spatial variability of top-down effects and how they affect ecosystem function. In highly impacted estuaries like Elkhorn Slough, testing restoration strategies and their broad-scale outcomes are also critical for informing adaptive management and conservation efforts through time.

This body of work is dedicated to:

My grandma, Dawn Sillesen who was the biggest supporter of doing what you love and whose "waste not want not" mentality permeated into everything she did, from traveling to over 90 countries to teaching her grandchildren the importance of being a life-long learner.

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Beheshti, K.M., S. Williams, K.E. Boyer, C. Endris, A. Clemons, T. Grimes, K. Wasson and B.B. Hughes. Rapid enhancement of multiple ecosystem services following the restoration of a coastal foundation species.

Introduction

Foundation species define ecosystems by providing habitat and refuge from biotic and abiotic stressors (Dayton 1972). Typically abundant and found near the base of ecosystems, foundation species play a crucial role in facilitating key ecosystem processes (i.e. nutrient cycling) and are themselves heavily influenced by environmental conditions. My research focuses on two coastal foundation species found in temperate estuaries—the salt marsh dominant of California estuaries (*Salicornia pacifica*) and a widespread native seagrass (*Zostera marina*). Through this work I explore how both physical and biological factors influence foundation species in Elkhorn Slough, a highly impacted estuary located in Central California that has retained only 30% of its historical salt marsh habitat (Brophy et al. 2019) and 60% of its historical seagrass extent.

Accelerated human population growth along the world's coasts has amplified the impact of human activities on coastal foundation species, triggering widespread degradation or loss of associated ecosystem services and functions (Ellison et al. 2005, Waycott et al. 2009, Barbier et al. 2011). Local impacts include pollution associated with agricultural and urban development (Wasson et al. 2017, Coverdale et al. 2013) and overfishing (Altieri et al. 2012) and global impacts include acidifying ocean conditions (Bellwood et al. 2004), sea level rise (Thorne et al. 2018) and rising sea surface temperatures (Zimmerman et al. 2015). Restoration has been the primary approach to combat these losses and facilitate the recovery of foundation species and the ecosystems they support (Ellison 2019). One common approach to facilitate the recovery of foundation species is to improve environmental conditions that inhibit their successful establishment and expansion, such as restoring the natural hydrology or sediment dynamics or improving water quality (i.e. "build it and they will come" approach). An alternative approach to restoration is to directly seed or plant foundation species—such efforts have yielded variable success and many argue that restoring fast-growing foundation species (i.e. salt marshes, seagrasses) is an effective way to hasten ecological recovery (Yando et al. 2019).

As foundation species are functionally lost from many systems, it is vital to identify site-specific and context dependent physical and biological drivers of loss or recovery (Nomann and Pennings 1997, Chamberlain et al. 2014). The distribution of salt marsh and seagrass is largely limited by physical factors—salt marsh occurs within a narrow tidal elevation range, limited by tolerance for inundation and salinity (Odum 1988) and seagrass occurs within a narrow depth range limited by light availability at depth and desiccation in the shallow intertidal (Short et al. 2007). Yet, within these narrow zones, biological factors such as herbivory and bioturbation can also have a strong effect on the abundance of these foundation species. For example, in one US east coast marsh, primary production of foundation species *Spartina alterniflora* was influenced by the engineering activities of crab, *Uca* spp. improving soil conditions in the low marsh (Bertness 1985) while in the high marsh of another east coast marsh, production was unaffected by crabs and was driven, rather, by salinity (Nomann and Pennings 1997). The disappearance of seagrass beds from Virginia's coastal lagoons was linked to seed recruitment limitation, not degraded environmental conditions, as was initially thought (Orth et al. 2020), while in San Francisco Bay, some restoration has failed due to poor environmental conditions attributed to an anomalous rain year (Boyer et al. 2018). Such spatiotemporal variability within and across systems highlights the importance of understanding site-specific drivers of loss and recovery of coastal foundation species.

In Chapter 1, I investigated marsh response to an abundant burrowing crab (*Pachygrapsus crassipes*) along tidal creek edges over five years (2013-2018). Tidal creek edges are prone to marsh loss through marsh dieback and erosive processes. Through this work, I characterized crab effects along these vulnerable bank edges in a perennial marsh system across multiple years where plant response is typically slower than more heavily studied grass-dominated marsh systems. I show that through both consumption and engineering activities, crabs play a strong role in regulating marsh vegetation and soil structure. By sampling broadly across space and time, I was able to track relationships across years, some of which remained unchanged while others strengthened. While this work revealed that crab effects on marsh structure and functioning is primarily negative, it also underscores the value of investigations on marsh trophic and non-trophic interactions that span multiple years. To better understand salt marsh habitat dynamics it is important to conduct experiments that incorporate or address spatial and/or temporal variability.

Motivated in part by the strong crab effects detected in Chapter 1, in Chapter 2 I investigated the role of crabs in the marsh interior where the formation and expansion of salt pannes contributes to the majority of marsh loss in the system. I also explored which panne attributes best predicted their dynamics. During a period of severe drought and an overlapping warm water event (2012-2016), extensive marsh dieback was observed in the marsh interior. This widespread marsh loss was of concern to regional stakeholders and prior to this study, panne dynamics were poorly understood in the system. During this two-year study (2016-2018), I tracked marsh recovery through panne contraction. Here I show that the rate of panne contraction was positively associated with crab burrows, panne depth and elevation (combined in a principal component analysis), and sediment accretion, and negatively associated with panne size and distance to nearest panne. The results from Chapters 1 and 2 suggest that crab effects on marsh dynamics in Elkhorn Slough are context dependent and likely influenced by differences in physical factors driving dynamics along tidal creek versus panne edges.

Seagrasses are in global decline (Waycott et al. 2009) and majority of restoration efforts have failed (van Katwijk et al. 2016). In Chapter 3, I conducted two small-scale experimental seagrass restoration projects and tracked restoration success relative to healthy, persistent reference beds, and in comparison to unrestored, unvegetated areas. Within the first three years, post-restoration, restored seagrass rapidly expanded (~8500%) and resembled reference beds both in structure (i.e. shoot density and biomass) and function (i.e. water quality, macrofaunal species density and abundance). To assess the cumulative functional performance of vegetated (restored and reference) and unvegetated habitats, I developed a multifunctionality index that revealed restored habitats as intermediate between unvegetated (lowest performing) and reference (highest performing) habitats. I expect restored habitats to edge towards reference levels as plots continue to expand. The rapidity with which functioning was enhanced in Elkhorn Slough through the successful restoration of seagrass, illustrates the potential for successful ecological restoration of a fast-growing foundation species.

Taken together, these chapters highlight the potential for recovery of estuarine foundation species. Both physical and biological factors affect the resilience of coastal vegetation, and the strength and direction of effects can vary across small distances within the estuary. Likewise, the ecological consequences of recovery, in terms of ecosystem services and functions, can be evident even in small patches short distances away from unvegetated habitat. Understanding the causes and consequences of recovery of coastal vegetation will allow us to better conserve and restore these foundation species and their estuarine ecosystems.

Chapter 1

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

ABSTRACT

Consumers can structure plant communities, and may function as keystone species or ecosystem engineers, with disproportionately strong effects on ecosystems. 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, causing temporal variability in or long-term impacts of consumer effects to remain poorly resolved. In addition, while top-down control has been found to be common in Western 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 bank edges of a California salt marsh in which we manipulated densities of the superabundant shore crab, *Pachygrapsus crassipes*, and tracked marsh responses over time. Our results demonstrate that, through both consumption and engineering activities, this crab is powerfully regulating marsh vegetation and soil structure. Experimentally reducing crab abundance significantly enhanced vegetation biomass and sediment bulk density. Moreover, with decreasing burrow density, root biomass and bulk density, factors known to increase marsh resilience to erosion and sea level rise, increased linearly. 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 marshes. We also found that more crabs were caught in warmer years, indicating that global warming may increase crab activity and exacerbate negative crab effects in the future. Since these crabs are widespread and abundant throughout the low marsh of most major estuaries within the range of the species (from Oregon, U.S. to Baja California, Mexico), we hypothesize that this species is exerting significant, yet underappreciated top-down control and modifying the sediment properties of many West Coast salt marshes.

Keywords: plant-animal interactions, salt marsh, ecosystem engineer, consumer control, top-down effects, shore crab

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, Altieri 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 and thereby maintain savannas (Haynes 2012), sea otters facilitate kelp forests by consuming kelp-grazing urchins (Estes 1998), and burrowing worms can prevent seagrasses from establishing on mudflats (Hughes et al. 2000). Despite widespread acknowledgement that communities are structured by a combination of top-down and bottom-up effects (Gruner at 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 is a paucity of studies focused on top-down relative to bottom-up processes (He and Silliman 2016).

Consumers that are ecosystem engineers can have particularly strong effects and have the potential to transform the biotic structure and ecosystem functions 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 et al. 1986, Wright et al. 2002), consumer fronts of herbivorous crab *S. reticulatum* can cause widespread salt marsh die-off when released from predation pressure (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 Zieman 2001, He et al. 2015, Alberti et al. 2015). On the east coast of the US, 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 (He et al. 2015, Bortolous et al. 2002). In North America the majority of marsh studies to date have been short-term experiments (1-2 years) on grass-dominated (e.g., *Spartina* spp.) systems (Smith and Tyrrell 2012, Moore 2019). On the west coast of the US, there have been multiple studies on bottom-up processes in tidal marshes (Thorne et al. 2014, 2018, Janousek et al. 2017, Osland et al. 2019) and still only a few on consumer effects (Boyer and Fong 2005, Armitage and Fong 2006). The role of consumers in woody perennial marsh systems, like those found along the Pacific Northwest Coast of the US, Europe, South Africa and South Asia, (Kadereit et al. 2007), are likely operating at considerably longer timescales than 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), 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 this common crab 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 lab 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 verses sediment engineering effects, we conducted a crab removal experiment near creek banks in Elkhorn Slough, 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: a) experimentally manipulate crab abundance to evaluate effects along vulnerable marsh-bank edges, b) assess whether effects of crab reductions strengthened, weakened or plateaued over time, c) characterize seasonal crab-marsh dynamics and d) test in the lab whether crabs eat 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 use the spatial variability in crab density to 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 1,000 hectares of salt marsh habitat (Van Dyke & 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 & 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 2-2.5m to 9-17m (Van Dyke & Wasson 2005). Highly impacted by the surrounding agricultural landscape (Fig. S1), 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. 1A). *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 years with adult sizes ranging from 30-60mm carapace width (Hiatt 1948). The channel and tidal creek bank faces are riddled with crab burrows. We conducted a long-term experiment along these marsh-bank edges, where crab densities in the system are highest (Wasson et al. 2019). Our study explores whether crab biomass and/or burrow density affects marsh biomass and cover, bulk density, and accretion.

Experimental design

To test whether crabs had an effect on marsh, we conducted the following experiment in five tidal creeks in Elkhorn Slough, extending from the lower to the upper reaches of the estuary (Fig. 1B, Fig. S1). At each tidal creek site, there were five blocks, each block had two different treatments: (i) reduced crab densities (Fig. 1C-D), hereafter referred to as 'Reduced Crab' (full cages where crab density was continually reduced using pit-fall traps) and (ii) ambient crab densities (Fig. 1E), hereafter referred to as 'Ambient Crab' (lifted cages 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 1cm wide), which outlined the perimeter of each experimental plot. The wire-mesh caging around the Reduced Crab plots extended into the substrate ~10 cm to prevent crabs from burrowing into the experimental plot area. The cage 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 x 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 cages were built using 19-gauge 1.3 cm x 123 cm x 30.5 cm galvanized hardware cloth attached with staples to 1m-long wood posts. (Note: these same lifted cages, plus adjacent uncaged controls, were used for a complementary investigation by our team (Hughes et al. in prep) to explore the effects of the Southern sea otter (*Enhydra lutris*) in Elkhorn Slough salt marshes conducted from 2013-2015.)

To maintain the Reduced Crab treatment, we continually trapped crabs, removing them from the experimental plot area using permanently un-capped 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*) 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 cage wall, in addition, small crabs (>10 mm) were able to move into the plots through the wire mesh or small gaps in cage 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 down to species (*P. crassipes* was typically the only species present, occasionally (n<20 individuals) we caught *Hemigrapsus oregonensis*), sexed and sized for all 50 experimental plots. Crabs caught in 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 was collected. We trapped haphazardly a total of eighteen times across five years; October 2013 to February 2018 (see results for exact months). In total, we trapped 7,535 crabs over the course of our 5-year study, 3,903 of which were in our experimental plots. Total number of crabs caught, or crab counts, and crab biomass were both measured (Fig. S2) but crab biomass was used for analyses because it was a more appropriate metric for exploring marsh effects, while Catch per Unit Effort (CPUE) (Fig. S3) was used to explore crab activity patterns.

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 = a(e^{b*c})—where biomass of an individual crab, measured in grams is a function of *a,* the scaling coefficient, 0.9532433, *e* (natural exponential function), *b,* the growth rate, 0.0857416 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, August 2015 and 2018). Similarly, crab burrow data used in models were from data collected during the same month and years (September 2014, August 2015 and 2018). 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).

Environmental correlates of crab abundance

To examine patterns between environmental conditions and temporal trends of crab activity (using crab CPUE as a proxy), we used the National Estuarine Research Reserve System's Centralized Data Management Office, CDMO database to generate multiple time series for air temperature (°C), precipitation (mm) and Photosynthetically Active Radiation ($\mu m/m^2$), or PAR. These abiotic variables were chosen based on field observations that showed patterns linking crab activity and the aforementioned variables over the course of the five-year study period. Temporal trends were assessed by qualitatively comparing crab CPUE to abiotic variables. Meteorological data was extracted from the Caspian Weather Station (Station Code "ELKCWMET", https://cdmo.baruch.sc.edu/dges/) and was collected every 15-minutes. In order to best characterize the abiotic conditions centered around each of the trapping dates, abiotic variables were averaged across the 72hrs of each trapping date, for example, a trapping date of 10/15/2013, CDMO data was averaged from 10/14-10/16/2013.

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 were unable to complete marsh surveys in years 3 (2016) and 4 (2017) due to time constraints related to a restoration project that began in Fall 2016 and the follow-up study for the restoration in Fall 2017. Maintaining the experiment involved routinely cleaning cage walls (1-2 times per month), removing algal wrack following spring tides, and replacing cage 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 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 cm^2 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, stratified by canopy, sub-canopy and substrate. Marsh canopy included either succulent or woody marsh plant tissue (*Salicornia pacifica, Jaumea carnosa, Frankenia salina,* or *Distichlis spicata*), only *S. pacifica*, the dominant marsh plant, is reported below. Sub-canopy included woody tissue or woody tissue with epiphytic algae (mainly, Ulva spp.) and substrate included mud, benthic diatoms and benthic algae, or burrow. Benthic diatoms and benthic algae were considered a single category because distinguishing between algal and diatom growth 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. If we were to add all of the marsh canopy and sub-canopy percent cover values, we would get total canopy cover with a range of 0-100%. For an individual plot, sub-canopy cover could not be higher than canopy cover because the former depends on the latter. If we add all the substrate percent cover values, they always add up to 100%.

To track changes in burrow densities by treatment, burrow counts were measured in all experimental plots using a 0.25 cm^2 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. We only counted burrows >1cm and counts were broken down by size class with small burrows ranging from 1.0-2.9 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 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+) within each of the 100 x 50 cm surveyed areas of each experimental plot at each sampled year. The average number of large burrows was log+1-transformed.

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 x 10cm PVC coring device that was carefully placed into the marsh substrate without manipulating the overlying aboveground marsh vegetation. 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/cm^3) and the volume of the sampled cores was 785.4cm^3, 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 hrs for aboveground material and 72-144 hrs for belowground material. After fully drying, samples were re-weighed for dryweight (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 dryweight of both succulent and woody tissue collected from each of the experimental plots (dryweight, g). Belowground biomass includes all the root material (live and dead) per core, this data was lognormal transformed (dryweight, 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 x 25 cm quadrat in the center back (landward edge) of each experimental plot and poured approximately 950 mL of feldspar powder evenly within the quadrat area. 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 4 pre-marked points, the average of the four points was divided by two to get the annual accretion rate.

Laboratory feeding trials

After detecting potential evidence of herbivory reflected in the marsh biomass data, and making field observations of crabs "trimming" roots extending into their burrows and in high numbers under macroalgal mats, often grazing on deposited wrack, we ran crab feeding trials, in July 2017, to test whether this crab consumes pickleweed plant roots when also offered common green alga (*Ulva lactuca*). The focus of these trials built upon previous trials in Summer 2015 that showed preference for pickleweed belowground tissues over aboveground (Hughes et al. in prep), thus the 2017 trials did not include aboveground marsh plants. Crabs were caught (n=34) in close proximity to Site 5 (Fig. S1). All individuals greater than 25 mm were kept for the trials, starved for 72 hours and placed in 16 oz. glass mason jars with 10 mL of regularly replaced seawater at UC Santa Cruz's Long Marine Laboratory. The trials began on July 18, 2017, ran for 72 hrs, and included the following independent trials; (i) 3 g of pickleweed roots (n=13), (ii) 3 g of algae (n=12) and (iii) 1.5 g of pickleweed roots and 1.5 g of algae (n=9); each trial type was run with both a crab and without a crab treatments. 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 hrs. To test for post-trial differences between treatments (with crab) and controls (without crabs) we ran Welch's two-sample t-test which accounts for different variance structures, for each trial (i)-(iii).

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. 2, 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 homoskedasticity (Quinn and Keough 2002). Data was transformed to normalize and improve homoskedasticity. Belowground biomass was log-transformed to meet assumptions of normality, aboveground biomass and bulk density data was analyzed using raw values. Succulent and woody cover were also log-transformed to meet assumptions of normality. Epiphytic algae, benthic diatom/algae and burrow cover was 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 one-way ANOVA to test for differences in accretion rates by treatment.

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 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 Core Team, 2016).

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 the per capita crab effect to change 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 if 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.

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 (Fig. S2A-B). The crab trapping data was analyzed by grouping all blocks across all sites together by treatment and looking at mean crab biomass (Fig. S2A) and mean number of individuals trapped by treatment or CPUE (Fig. S2B). Fewer crabs were trapped in Reduced Crab plots. When comparing CPUE, irrespective of trapping date, Reduced Crab plots had 16.3% fewer crabs trapped than Ambient Crab plots. Crab biomass in Reduced Crab plots was 54.6% lower than that of Ambient Crab plots and the mean carapace width of trapped individuals across all trapping efforts was 19.8 and 26.3mm 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. 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. Prior to September 2014, there were, on average, 6% fewer crabs in Reduced Crab plots relative to Ambient Crab plots. From September 2014-August 2018, Reduced Crab plots had on average 36% fewer crabs than Ambient Crab plots (Fig. S3).

Environmental correlates of crab abundance

Crab trapping also revealed seasonal patterns in crabs trapped in the marsh with CPUE being lowest during the winter months and highest during spring and summer months. The lowest observed CPUE coincided with periods of high rainfall (Fig. S4A), low air temperature (Fig. S4B) and low levels of PAR (Fig. S4C). While CPUE was similar across treatments during winter months, it was far higher in Ambient Crab than Reduced Crab treatments in all other months (Fig. S3). Comparing the same month across multiple sampling years, we found that crab CPUE was higher in years with warmer temperatures, higher PAR and low rainfall (Table S2).

Effects of crab reduction on marsh biomass, cover and accretion

Treatment effects varied by response variables. For aboveground biomass, there was a significant treatment effect, with higher aboveground biomass in Reduced versus Ambient Crab treatments ($F_{1,19}$=2.067, p<0.0001), a significant year effect ($F_{2,18}$=0.512, p=0.024), and no treatment*year interaction (Fig. 2A). Belowground biomass, in contrast, was insensitive to crab treatment ($F_{1,19}$=0.228, p=0.051) and year ($F_{2,18}$=0.111, p=0.389) (Fig. 2B). For bulk density, there was no effect of treatment ($F_{1,17}$=0.162, p=0.116), but there was a significant year effect ($F_{1,17}$=2.209, p<0.0001) (Fig. 2C). The full report of model effects between and within subjects for biomass and bulk density can be found in the Supplemental Information (Table S1). There was no effect of treatment on burrow density, when considering both small and large burrows together (Fig. 2D). Lastly, there was no effect of treatment on accretion rates, though accretion rates were higher on average in Reduced Crab (6.03 mm) versus Ambient Crab (5.81 mm) treatments (Fig. S5A).

For percent cover, significant treatment effects were observed for canopy and sub-canopy cover of succulent ($F_{1,19}$=0.755, p=0.0012), woody pickleweed ($F_{1,20}$=0.270, p=0.0258), and epiphytic algal cover ($F_{1,20}$=0.932, p=0.0003). Overall marsh cover was higher in Reduced Crab treatments where crab densities were maintained below ambient levels (Fig. S6). 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 the Supplemental Information (Table S1).

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. 2D). In addition, the number of large burrows increased steadily across years irrespective of treatment (Fig. S2C). From 2014 to 2018, the average number of large burrows in the 0.5 m^2 area sampled in Reduced Crab plots increased from 1.9 to 7.9 and 3.4 to 10.2 in Ambient Crab plots. In contrast, the number of small burrows increased from 2014 to 2015 and then decreased in 2018 across both treatments. Burrow percent cover data did not discriminate by crab burrow size, therefore there was no significant treatment effect ($F_{1,20}$=0.160, p=0.089). Burrow percent cover (0.25m^2 survey area) did have a significant year effect ($F_{2,19}$=1.467, p=0.0002) and therefore matches trends observed from burrow count data collected separately from cover data (Fig. 2D).

Crab effects on marsh biomass, cover and accretion

The number of crab burrows (large only) had a significant negative effect on belowground biomass and bulk density and no effect on aboveground biomass during our study period (Fig. 3), although, as we discuss below, the progression of the crab burrow effect on aboveground biomass is trending negative. Year had a significant negative effect on above- (Fig. S7A)and belowground biomass (Fig. S7B) and bulk density (g/cm^3) (Fig. S7C). Crab burrows had a significant negative effect on woody percent cover and no effect of burrows or year was detected for succulent cover (Fig. S8). Crab burrows did not have an effect on epiphytic cover, but year did have a significant positive effect (Fig. S8E). There was a significant negative effect of crab burrows and a positive effect of year on benthic diatom/algae cover (Fig. 4A). Lastly, crab burrows had no effect on accretion (Fig. S5D). The full model for each response variable is reported in Table 1.

We 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 significant negative effect on above and belowground biomass and bulk density (g/cm^3) (Fig. 3, Table 1). In addition, year had a significant positive effect on aboveground biomass (Fig. S9A), no effect on belowground biomass (Fig. S9B) and a significant negative effect on bulk density (Fig. S9C). Crab biomass had a significant 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 (Fig. S8). There was no effect of crab biomass on epiphytic or benthic algae/diatom cover but there was a year effect (Fig. S8). Crab biomass and year had a significant positive effect on burrow cover and there was a marginally significant effect of the interaction between crab biomass and year on burrow cover, this was driven by 2018 where crab biomass in Reduced Crab treatments was slightly higher compared to previous years (Table 1). Lastly, crab biomass had no effect on accretion (Fig. S5C). The full model for each response variable is reported in Table 1.

Over time, the effects of crab burrows (Fig. S7) and crab biomass (Fig. S9) on aboveground biomass became more negative. There was a similar pattern for the effect of crab biomass on belowground biomass (Fig. S9B). There was no trend over time for the effect of crab burrows on belowground biomass (Fig. S7B). 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 (Fig. S8).

Laboratory feeding trials

There was a significant negative difference in post-trial biomass (dryweight, g) when comparing treatments (with crabs) to controls (without crabs)—the latter having higher post-trial biomass than the former. In pickleweed root only trials, there was significantly less pickleweed root biomass in treatments than controls (Welch's Two Sample t-test; $t(20.5)=5.55$, $p<0.0001$). In algae only trials, there was significantly less algal biomass in treatments than controls (Welch's Two Sample t-test; $t(13.05)=6.098$, $p<0.0001$). Lastly, treatments had significantly less biomass than controls in trials with both pickleweed roots and algae offered simultaneously (Fig. 5, 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

In running this study for five years, we have revealed that crabs affect salt marsh structure and functioning and that those effects are primarily negative, at least at small scales, as demonstrated by the results of our experimental reduction of crabs. In those treatments, marsh performance across many attributes increased over time, relative to controls. In addition, through the manipulations, 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. We also showed that crabs are more active during warmer years. The negative consumptive and engineering effects on marsh structure and function was most consequential during the marsh growing season where crab activity is also at its peak. The combined effects of demonstrated crab related impacts, increased impacts in warmer years and climate related warming, is likely to accelerate degradation of marsh 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 & 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. In addition, we did not detect any relationship between burrow counts and crab biomass. Important to this argument, this means 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 has large implications for the stability and resilience of vulnerable marsh-bank edges. Belowground biomass is responsible for stabilizing sediment (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 prep*) 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. 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 effects 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 (Hughes et al. in prep) and will eat root tissue even when also offered algae (this study). Preference for roots over succulent tissue could be related to refuge from predators (Vu and Pennings 2018), palatability, or access (Bortolus and Iribarne 1999) as crabs are frequently observed in burrows "trimming" roots extending into the burrows and were not observed grazing aboveground plant structures throughout the study period (*K. Beheshti personal observation*), although, such aboveground foraging has been noted in Southern California marshes (Boyer and Fong 2005). 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). In these systems, the impact of crab herbivory is mitigated by many factors, such as predation risk associated with preferred foraging behaviors (Vu and Pennings 2018) and enhanced marsh production associated with elevated nutrient levels (Daleo et al.

2015). Such factors shown to dampen consumer effects in cordgrass-dominated systems do not apply to Elkhorn Slough where strong crab effects were detected despite being a eutrophic system (Hughes et al. 2011), burrows have been shown to persist, offering consumers long-term access to preferred belowground root tissue, and predation risk was negligible due to our caging design.

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 modelling 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) 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 (Fig. S9A). 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 significant 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 significant 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 each year we are able to isolate the crab effect and determine whether the crab effect weakened, strengthened or did not change over time (Fig. S7, S9). 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 was 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. Therefore, we suggest future studies on marsh trophic and non-trophic interactions span multiple years.

Lastly, this long-term study allowed us to detect seasonality and inter-annual variation in crab-marsh dynamics. By sampling multiple times per year, we were able to detect differences in crab activity across and within seasons and years. Crab activity has been shown to decrease with declining temperatures (Hiatt 1948) and we observed this pattern in our study. During cold and rainy winter months, crab activity, measured as CPUE, was relatively lower (Fig. S4). This seasonal pattern also coincides with periods of low marsh production (Boyer et al. 2001). Crabs trapped after winter include large individuals that were likely hunkering down in burrows leading to few crabs caught in pit-fall traps. Therefore, studies that span a single season in a particularly cold year would likely underestimate crab abundance and related crab-marsh dynamics. Consistent patterns also emerge as we compare crab activity in the same month across multiple years, we observed the highest crab activity in years with relatively higher air temperatures and PAR and lower rainfall (Table S2). Sampling multiple seasons across multiple years allowed us to explore how environmental conditions may affect crab activity levels within seasons, and given our strong experimental results showing the effect of crab activity on marsh biomass, we could infer that warmer climatic conditions may increase crab activity and exacerbate negative crab effects in the future. In many 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 crab populations in check, thus enhancing resilience to global warming and sea level rise.

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. 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-value cells are shaded using conditional formatting where darker colors indicate more significant (p<0.05) relationships and no shading indicates non-significant (p>0.05) relationships.

	Crab Data		**Model Output**				
	Total Crab Biomass (Log+1)	**Fixed Effects**	*Estimate*	*Standard Error*	*DF*	*F-ratio*	*p-value*
response variables	Aboveground Biomass (Succulent & Woody, g)	Crab Biomass	-2.413	0.749	81.9	10.362	0.0018
		Year	0.492	0.191	57.0	6.632	0.0126
	Belowground Biomass (Root, g)*	Crab Biomass	-0.217	0.083	142.7	6.808	0.0100
		Year	-0.020	0.017	98.5	1.347	0.2487
	Bulk Density (g/cm3) +	Crab Biomass	-0.105	0.038	65.3	7.508	0.0079
		Year	-0.053	0.011	40.5	25.340	<0.0001
	Succulent % Cover*	Crab Biomass	-0.153	0.068	118.4	5.135	0.0253
		Year	-0.001	0.017	100.0	0.210	0.6474
	Woody % Cover*	Crab Biomass	-0.026	0.034	137.9	0.592	0.4430
		Year	-0.001	0.007	99.6	0.005	0.9453
	Epiphytic Algae % Cover^	Crab Biomass	-0.176	0.299	118.1	0.348	0.5561
		Year	0.342	0.073	99.5	21.600	<0.0001
	Benthic Diatom/Algae % Cover^	Crab Biomass	-0.009	0.250	79.7	0.125	0.7251
		Year	0.353	0.068	67.6	27.100	<0.0001
	Burrow % Cover^	Crab Biomass	0.563	0.256	130.8	4.835	0.0296
		Year	0.173	0.054	60.3	10.286	0.0021
		Crab Biomass * Year	0.270	0.135	95.2	3.989	0.0487

	Average # of Large Burrows (Log+1)	**Fixed Effects**	*Estimate*	*Standard Error*	*DF*	*F-ratio*	*p-value*
response variables	Aboveground Biomass (Succulent & Woody, g)	Crab Burrows	-1.502	1.131	113.4	1.764	0.1867
		Year	0.536	0.226	135.5	5.615	0.0192
	Belowground Biomass (Root, g)*	Crab Burrows	-0.334	0.118	138.2	7.973	0.0054
		Year	0.053	0.022	131.8	6.086	0.0149
	Bulk Density (g/cm3) +	Crab Burrows	-0.118	0.045	75.7	6.734	0.0114
		Year	-0.047	0.011	65.5	16.959	0.0001
	Succulent % Cover*	Crab Burrows	-0.108	0.097	106.8	1.227	0.2705
		Year	-0.005	0.020	135.6	0.059	0.8090
	Woody % Cover*	Crab Burrows	-0.121	0.046	112.7	6.980	0.0094
		Year	0.014	0.009	136.3	2.414	0.1226
	Epiphytic Algae % Cover^	Crab Burrows	0.042	0.415	104.2	0.010	0.9199
		Year	0.365	0.086	137.0	16.246	<0.0001
	Benthic Diatom/Algae % Cover^	Crab Burrows	-0.948	0.326	75.9	8.453	0.0048
		Year	0.452	0.074	88.3	37.478	<0.0001

Figure 1. 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.

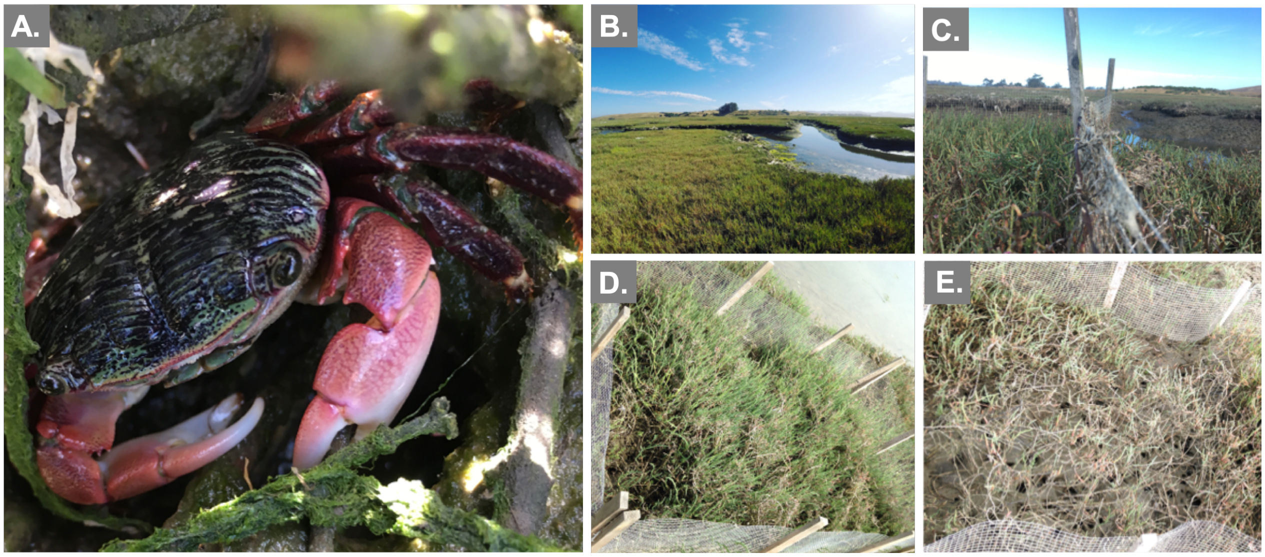


Figure 2. Treatment differences in **a)** above and **b)** belowground marsh biomass, **c)** bulk density, and **d)** burrows across years. Data are shown as means (± SEM, *n*=25). Ambient Crab treatments are in blue, Reduced Crab treatments in red.

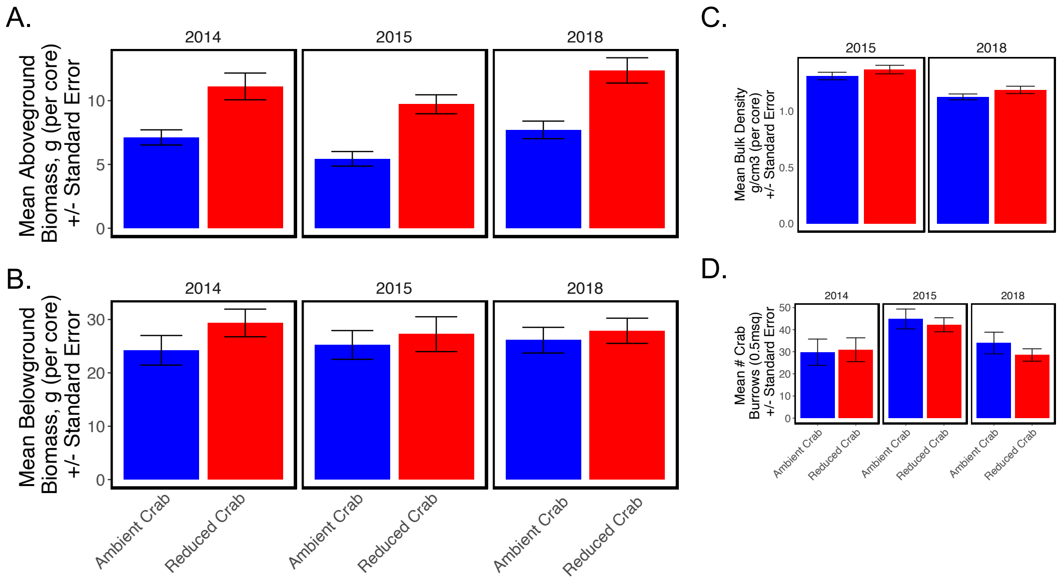


Figure 3. Effects of **a)** crab burrows and **b)** crab biomass on mash aboveground biomass (triangles) and belowground biomass (circles) and effects of **c)** crab burrows and **d)** crab biomass on bulk density. The plotted data **(a-c)** is from year 5 (2018) only. The reported p-values correspond 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) is the mean number of large burrows surveyed per experimental plot (0.5m^2). Crab biomass (log+1 transformed) is the total crab biomass per experimental plot (2 m^2) calculated using crab trapping data. Raw data was analyzed and plotted for aboveground biomass and bulk density and belowground biomass is log transformed. Plotted regressions include 95% C.I. The relationship for marsh above- and belowground and bulk density across all years can be found in **Supplemental Figure 7,9.**

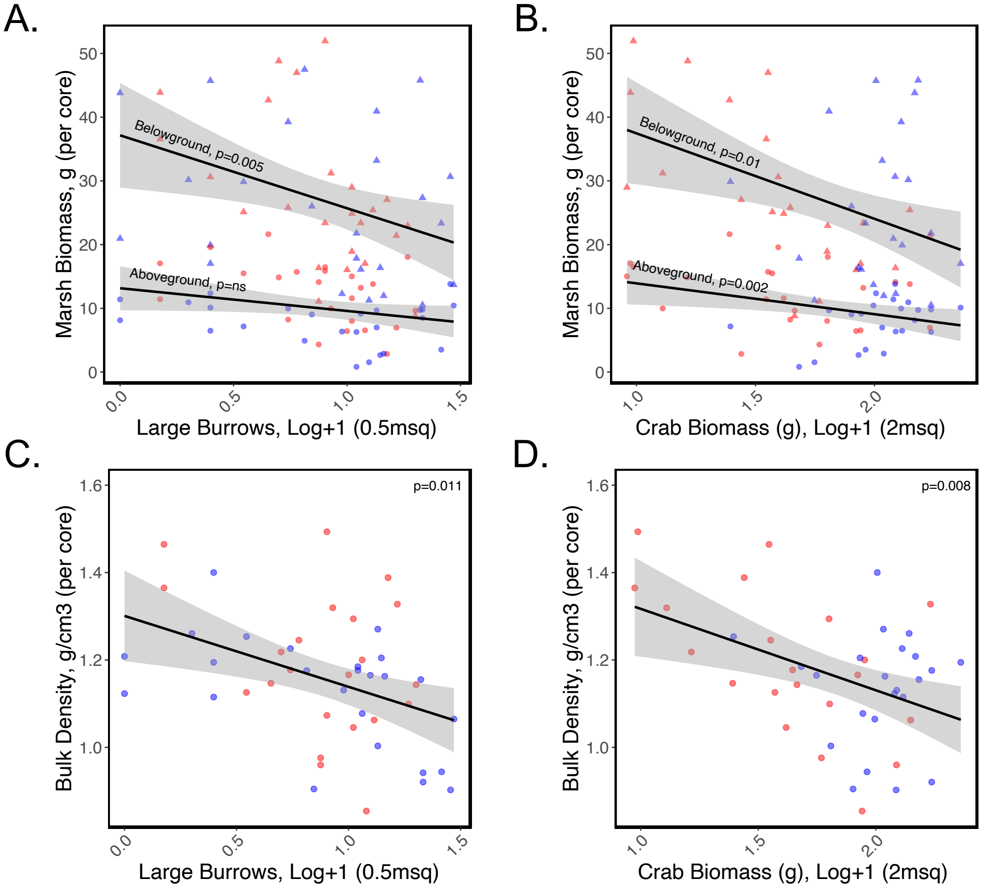


Figure 4. Effects of **a)** crab burrows and **b)** crab biomass on % cover of benthic algae/diatom cover. The plotted data is from year 5 (2018) only. The reported p-values correspond to the main effect variable (crab biomass or crab burrows) from the mixed model, which includes all years. Percent cover is log+1 transformed and represents the 0.25 m^2 area surveyed in each experimental plot. Plotted regressions include 95% C.I. Ambient Crab treatments are in blue, Reduced Crab treatments in red. The relationship for each response variable across all years can be found in **Supplemental Figure 8**.

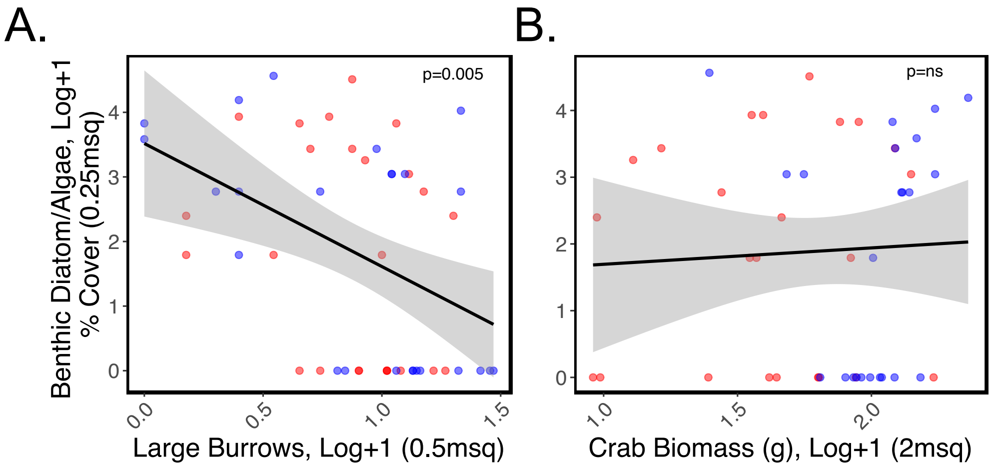
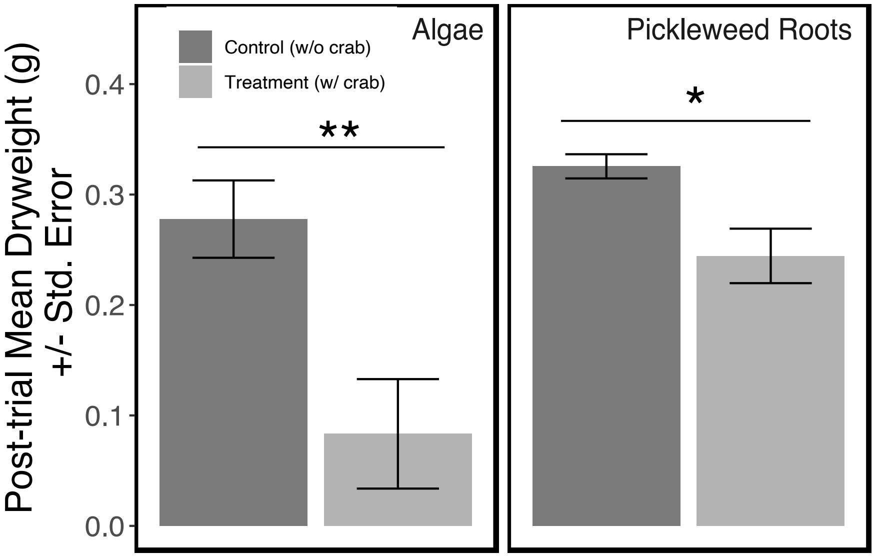


Figure 5. Crab feeding trials (Summer 2017), showing post-trial results comparing controls (dark grey bars) where crabs were absent and treatments (light grey bars) where crabs were present. The plotted data is the mean post-trial dryweight (g) of offered green alga, *Ulva lactuca*, and marsh (*S. pacifica*) belowground root material (± SEM, *n*=9). Significant ($p<0.05$) differences between treatment and control groups are indicated by asterisk ($p<0.0001$, "***").



Chapter 2

Physical and biological factors influence panne dynamics in a California estuary

Abstract

Salt marsh loss is projected to increase as sea level rise accelerates with global climate change. Salt marsh loss occurs both along lateral creek and channel edges and in the marsh interior, when pannes expand and coalesce. Often, edge loss is attributed to erosive processes whereas dieback in the marsh interior is linked to excessive inundation or deposition of wrack. We conducted a two-year field experiment (2016-2018) in a Central California estuary, where, immediately preceding our study, marsh dieback at creek edges and panne expansion occurred during a period of severe drought and an overlapping warm water event. Our study explored how an abundant burrowing crab, shown to have strong negative effects on marsh biomass along marsh-bank edges, affects panne dynamics. We also explored what panne attributes best predicted their dynamics. Overall, we found that pannes contracted during the study period, but with variable rates of marsh recovery across pannes. Our model incorporating both physical and biological factors explained 86% of the variation in panne contraction. The model revealed a positive effect of crab activity, sediment accretion, and a composite of depth and elevation on panne contraction, and a negative effect of panne size and distance to nearest panne. The positive crab effects detected in pannes contrast with negative effects we had earlier detected at creek edges, highlighting the context-dependence of top-down and bioturbation effects in

marshes. As global change continues and the magnitude and frequency of disturbances increases, understanding the dynamics of marsh loss in the marsh interior as well as creek banks will be critical for the management of these coastal habitats.

Introduction

Salt marshes are dynamic systems and generally resilient to perturbations, yet their ability to respond to the multitude of stressors they face has been compromised (Kirwan and Megonigal 2013, Fagherazzi et al. 2013). This is largely due to the many human alterations (diversion of freshwater, depleted sediment supply, reclamation, pollution, eutrophication, barriers to marsh migration) that salt marshes have endured over the last two centuries (Kirwan and Megonigal 2013). The degradation of salt marsh habitat is of great concern, especially in the face of accelerating sea level rise (Gedan et al. 2009, Kirwan and Megonigal 2013). Since the 1800s, it is estimated that 25-90% of salt marsh habitats have been lost (Bromberg and Bertness 2005, Mcleod et al. 2011, Gardner et al. 2015). Further loss of salt marsh habitat would come at a great cost as these systems are some of the most productive coastal habitats in the world and they support many high-valued ecosystem services (carbon sink, storm buffer, nursery habitat) (Zedler 2004, Barbier et al. 2011).

Loss of vegetation can occur along channel or tidal creek bank edges (hereafter bank edges) and in the marsh interior (Ganju et al. 2017). Along bank edges, wave erosion can undercut the marsh scarp and lead to erosional events where large sections of marsh are lost (Redfield 1972, Fagherazzi et al. 2013). Insufficient sediment supply (Fagherazzi et al. 2012, Ganju 2019), low belowground marsh biomass (Kirwan and Murray 2007), and algal wrack deposition (Wasson et al. 2017) further hasten bank edge erosion. Features that reduce wave fetch and intensity of wave or boat wake action such as oyster reefs can slow salt marsh erosion (Herbert et al. 2018). Similarly, benthic diatoms secrete extracellular polymeric substances (EPS) that both enhance sediment accretion and cohesion and reduce erosion (Tolhurst et al. 2006, Garwood et al. 2015). Marsh aboveground vegetation builds elevation capital (Cahoon and Guntenspergen 2010) by slowing water flow and facilitating surface sediment deposition, while belowground plant roots and rhizomes stabilize sediments, prevent erosion and contribute to the marsh substrate (Cahoon et al. 2019).

In the marsh interior, unvegetated patches can form, expand and coalesce leading to massive marsh dieback (Yap et al. 1917, Fagherazzi and Wilberg 2009). The genesis of these unvegetated patches can take multiple forms. Degraded marsh is less effective at accreting and building organic matter in the soil which can cause the marsh to lose elevation to a level outside of the growth range of marsh plants (Nyman et al. 1993, Cahoon et al. 2019, Janousek et al. 2019). Such deterioration of the marsh facilitates further erosion and increased inundation triggering marsh dieback (Day et al. 2011, Cahoon et al. 2019). These poorly drained mud depressions, devoid of vegetation are called salt pannes. Salt pannes (hereafter ‘pannes’) are also referred to as salt pans (Yap et al. 1917, Pethick 1974), tidal flats, saline supratidal mudflats, salterns (Hoffman and Dowes 1997), pools (Wilson et al. 2010, Schepers et al. 2016), tidal ponds (Koop-Jakobsen and Gutbrod 2019), or pond holes (Redfield 1972) (Table S1). While many distinguish pannes from ponds and consider them to be two separate features of the marsh landscape (Millette et al. 2010, Koop-Jakobsen and Gutbrod 2019), the latter retaining water and rarely draining and the former only inundated on the highest tides, in our study, we classify them collectively as 'pannes'. Yap and colleagues first characterized the general morphology and dynamics of pannes in 1917, but noted that the factors that facilitate the original formation of pannes is poorly understood and likely varies across systems (Yap et al. 1917). Pannes are thought to be formed by biogeomorphological processes (Escapa et al. 2015) or physical stressors such as topographic depressions (Linhoss and Underwood 2016), tidal litter, waterlogging, or snow (Goudie 2013).

One potential driver of salt marsh dynamics at both bank edges and interior pannes is herbivory and bioturbation by crabs. Ubiquitous to most salt marsh systems, crabs have been shown to have strong yet variable effects on salt marsh structure and function. An observational study across fifteen National Estuarine Research Reserves (NERRs) found that sea-level rise is the greatest threat to marsh loss, not crabs, though there are likely to be interacting effects between the two (Wasson et al. 2019). For example, in New England marshes, crab (*Sesarma reticulatum*) abundance has increased due to sea-level rise (Raposa et al. 2018) and overfishing of predators (Altieri et al. 2012). This has led to runaway herbivory by crabs in the low marsh and with sea level rise induced changes to edaphic conditions crabs have moved into previously inaccessible marsh (Crotty et al. 2017). Eighty-six percent of existing marsh is projected to be lost due to the synergistic interaction between crab activity (burrowing and overgrazing) and moderate sea level rise (Crotty et al. 2017). Further investigation identified *S. reticulatum* in the Southeastern US Atlantic as a keystone species due to its cascading effects on marsh community structure, geomorphology, and function (Crotty et al. 2020). In Argentina, the engineering of burrows by crabs (*Neohelice granulata*) facilitates the formation of salt pannes by lowering marsh elevation causing depressed patches to pool leading to marsh dieback and panne formation (Escapa et al. 2015). In a Central California estuary, crab (*Pachygrapsus crassipes*) engineering and consumptive effects were shown to be negatively associated with marsh above- and belowground biomass along tidal creeks (Beheshti et al. in review), while another study across three separate Southern California estuaries found that crab (*P. crassipes* and *Uca crenulata*) effects differed across sites and marsh plant species and when effects were detected they were positive (Walker et al. 2020). Thus crab effects on marsh health likely vary temporally and spatially (across and within systems) and should be directly tested across a gradient of physical factors over time to gain a more complete understanding of potential effects to marsh health. Our study aims to identify the role of crabs in the marsh interior of a Central California estuary where such plant-animal interactions have yet to be studied, despite widespread interior loss and strong negative crab effects detected along tidal creek edges in the system.

Elkhorn Slough is an estuary located in Monterey Bay, California where salt marsh loss has been documented at bank edges and the marsh interior (Van Dyke & Wasson

2005), resulting in net loss of 70% of its historical salt marsh habitat (Brophy et al. 2019), a major concern for regional stakeholders (Wasson et al. 2015). Majority of marsh loss in Elkhorn Slough occurs in the marsh interior through the formation and expansion of salt pannes (Van Dyke & Wasson 2005). Bank edge loss is affected by increased tidal velocities resulting from an artificial harbor mouth (Caffrey et al. 2002) and eutrophication (Wasson et al. 2017). Bank edges are riddled with crab burrows, constructed and maintained by native grapsid shore crab, *P. crassipes*. *P. crassipes* is an omnivorous crab that burrows and is found at its highest densities along bank edges and low marsh elevations (Wasson et al. 2019). Through both consumptive and engineering effects, *P. crassipes* has been shown to have strong negative effects on marsh plant biomass along bank edges (Beheshti et al. in review) and to increase bank edge erosion rates (Hughes et al. in prep). The majority of interior marsh loss in the system is through the formation and expansion of pannes. Pannes were observed expanding during a period of severe drought (2012-2016) (Lund et al. 2018) and high water levels related to the warm water event known as "the Blob" (2013-2015) (Peterson et al. 2015). Panne dynamics remain poorly understood in the system and the majority of investigations thus far have focused exclusively on physical factors with little attention paid to the role of crabs, although crab burrows are prominent along panne edges.

Our study investigates panne dynamics in Elkhorn Slough salt marshes, and elucidates the role of crabs vs. other factors in driving marsh loss or recovery in the marsh interior. First, to explore the role of crabs, at different densities, on panne dynamics, we conducted a two-year field experiment where we attempted to manipulate crab densities across twenty pannes and evaluate panne response. We failed to successfully manipulate crab densities and instead utilized the experimental plots as replicates or sub-samples to characterize the twenty pannes. We tracked the trajectory of pannes over the course of the study period by carefully monitoring the marsh-panne boundary where there is an abrupt transition from vegetated to unvegetated habitat. Second, we explored how crab abundance and burrow density differed along tidal creek bank versus panne edges using experimental data collected from studies conducted concurrently (2016-2018) at both areas of potential marsh loss. Given that we observed widespread panne expansion in the years leading up to the study, tracking whether pannes continued to expand and coalesce was a priority of the study. Thus, the major emphasis of our investigation was to better understand which panne attributes (elevation, panne depth and size, distance to nearest panne, microphytobenthos, crab activity, and sediment dynamics) best predict panne expansion (marsh dieback) or contraction (marsh recovery). Our investigation will help inform the management of this estuary, as the first analysis of drivers of panne dynamics in a system that has experienced extensive interior marsh loss through panne expansion. Moreover, our study illustrates how integration of field data and modeling can elucidate the relative importance of multiple factors in driving marsh loss or gain, an approach applicable to any marsh system.

Methods

Overview

We investigated dynamics at 20 pannes. Our study design involved experimental treatments manipulating crab densities replicated at each panne (Figure S1). Since treatments were unsuccessful in affecting crab densities (see Supplemental Information), for later modeling of factors affecting panne dynamics, we used panne as replicate, averaging across treatment plots.

Study site

This study was conducted in Elkhorn Slough, an estuary located in Monterey Bay, California. Tides in the estuary are semidiurnal; tidal range has increased since the opening of the harbor mouth in the 1930s to a mean diurnal range of 1.7 m with a spring tidal range of 2.5 m and a neap tidal range of 0.9 m (Caffrey and Broenkow 2002). The climate is mediteranean with winter temperatures averaging 11.1°C and summer temperatures averaging 15.4°C (Caffrey 2002). The dominant marsh plant is *Salicornia pacifica* or pickleweed and the dominant grazer and bioturbator is *Pachygrapsus crassipes* or the lined shore crab.

Panne selection

We selected 20 pannes to study in a ~3 km stretch of salt marsh along the northwest side of Elkhorn Slough (Figure 1). Panne elevation was near Mean High Water (see details on elevations below) and the vegetation surrounding these pannes consisted almost entirely of the marsh dominant in this system, *Salicornia pacifica*. We used geospatial analyses to select relatively similar pannes as follows (Figure S2). Each panne had to 1) have been relatively stable in size from 2004 - 2012 as assessed in aerial imagery (chosen because we had access to high resolution imagery for these years), 2) be within 35 m from the nearest tidal creek bank edge, 3) have a minimum 1 m buffer from the nearest panne, 4) have a diameter greater than 1.5 m, and 5) have either no secondary creek or if a secondary creek was present the width had to be less than 1 m. The chosen pannes that met the criteria described above had an average panne perimeter distance of 11.6 m (mean diameter = 3.7 m, standard deviation = 2.1 m) and the minimum and maximum panne perimeter distance was 8.16 m (diameter = 1.7 m) and 16.2 m (diameter = 5.1 m), respectively. Average distance to the nearest tidal creek bank edge was 12.5 m (standard deviation = 8.5 m), the minimum and maximum distance was 2.13 and 34 m. Distance to nearest panne averaged 3.8 m (standard deviation = 2.3 m), the minimum and maximum distance was 1.18 and 11.4 m. The average secondary creek or ‘microchannel’ (Wilson et al. 2014) width was 0.51 m (standard deviation = 0.28 m) and the maximum was 0.93 m, three pannes had no secondary creek. One of the pannes was discarded from the analyses because it was adjacent to a large seagrass meadow, resulting in extensive year-round wrack accumulation (n=19).

Crab Experiment

Our original study design had one replicate of four treatments associated with each panne. The goal of the field experiment was to manipulate crab densities by means of cage design and either crab removals or additions (see Supplementary Information).

These manipulations were ineffective at significantly altering burrow or crab numbers, and as a result we treated the 4 experimental plots in each panne as replicates or sub-samples for each panne (n=19). We derived variables measured at the plot level by taking the average across replicate samples per panne (e.g. burrow density was estimated as the average number of burrows of four replicate samples per panne). All other variables were taken at the panne scale (e.g. elevation, panne size and depth).

Field data collection and indices

We collected data on movement of the vegetation edge, crabs, sediment dynamics and percent cover of succulent tissue and benthic algae within each of the four experimental plots in each of the 19 pannes.

Tracking panne expansion and contraction

To assess whether pannes expanded or contracted over the study period, we installed five permanent transect line markers within each of the plots. Zip ties were used to mark the longitudinal start and end of each transect to ensure we were surveying the same points over time. During surveys, each of the transect lines was resurveyed and the last rooted vegetation along each transect line was recorded. Surveys were conducted annually from 2016 to 2018 (Figure S3). To quantify whether a panne was contracting or expanding we calculated the average “marsh-panne boundary” difference per panne between 2018 and 2016. A positive value meant marsh colonization and panne contraction and a negative value meant marsh dieback and panne expansion.

Crab Activity

To monitor crab density across treatments we conducted 24 hr crab trapping efforts annually (August 2016, March 2017, August 2018) and visually assessed crab presence or absence and approximate abundance seasonally. We monitored crab burrow densities annually to track any changes in burrow densities over time by counting all burrows over 1.0 cm in the each plot (1.5 x 0.5 m), though burrows only occurred in the marsh zone of the plots (1.25 x 0.5 m). The 'Crab Activity Index' represents the mean number of burrows per panne (including both small, 1.0 cm - 2.9 cm, and large, 3.0 cm+ burrows) in 2018 and 'Change in burrow density' represents the relative change in burrow densities over the study period, both were included in the initial model. Previous work in Elkhorn Slough showed that the relationship between marsh biomass and crab engineering effects, measured as burrow density, are not the same as crab consumptive effects, measured as crab abundance (Beheshti et al. in review). Additionally, crab consumptive effects can be measured as either crab count, CPUE, or biomass. We included each of these measures of crab activity in the initial model (Table S2).

Sediment Dynamics

To assess sediment dynamics in the panne and marsh of each experimental plot, we installed galvanized conduit rods (3.048 m-long with a 1.905 cm diameter) in the panne and marsh zone of all seventy-six plots (n=152); per panne there were four rods in the pannes and four rods in the marsh. Rods were installed using a ladder and post driver until we reached hard ground, this typically occurred around 2.75 m, leaving around 30 cm of rod exposed (Video S1). More of the rod exposed over time indicated erosion and less of the rod exposed over time, accretion. The change in rod exposed was calculated using the following equation: $\Delta_{rod} = (Rod_{2016} - Rod_{2018})$. The 'Panne Sediment Dynamics Index' and 'Marsh Sediment Dynamics Index' represent the mean change (from 2016 to 2018) in panne and marsh rod exposed, respectively. Both were included in the initial model (Table S2).

Percent cover of succulent tissue and benthic algae

To determine the potential role of aboveground productivity on panne dynamics, we evaluated the change in new succulent growth over the study period (2016-2018), hereafter termed the 'Marsh Productivity Index'. 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). We were interested in the relative changes to succulent growth as a proxy for marsh productivity; a relative increase in succulent cover would indicate potential marsh recovery (Table S2). To assess percent cover of succulent tissue, we placed a 50 x 50 cm gridded quadrat in the middle of the marsh portion of each plot and dropped a metal rod at 20 intercepts. The number of succulent cover intercepts was divided by the total possible points (20) and multiplied by 100 to get succulent tissue percent cover. This was done in 2016, 2017 and 2018 at each of the four replicate plots per panne.

To determine the potential role of benthic algae, a catch-all category that included diatom biofilms and macroalgae (*Ulva* sp., *Vaucheria* sp., etc.), on panne dynamics, we evaluated the relative change in benthic algae over the study period (2016-2018). We assessed benthic algae cover, hereafter termed the 'Biofilm Index', using the same methods described above. The secretion of EPS has been shown to improve sediment cohesion and accretion in wetland sediments (Tolhurst et al. 2006). We were interested in the relative changes (2016-2018) to the Biofilm Index and the possible relationship between the Biofilm Index and panne contraction or expansion (Table S2). This was done in 2016, 2017 and 2018 at each of the four replicate plots per panne.

Geomorphological data collection and indices

We used geospatial analyses to characterize potential factors that might affect marsh dynamics at each of the 19 pannes.

Indices for panne depth, elevation, size, and distance to nearest panne

Using a LiDAR Digital Elevation Model (2018), we extracted the elevations for all nineteen pannes that were used in analyses. To calculate panne depth, we used ArcGIS v. 10.7 and 2018 NAIP 4-band orthoimagery (upgraded to 15 cm resolution) to create polygons of each panne (Figure S4). We applied a 1m buffer to the polygons and used the panne/buffer mask to extract cell values from the 2018 LIDAR (1 m resolution) using the Spatial Analyst Zonal Statistics as Table tool. Depending on size, between 12 to 37 cells per panne were used to compute the minimum, maximum, range, and mean elevation values (NAVD88 meters) of each panne (n=19). LIDAR elevations were corroborated by real-time kinematic positioning (RTK) at five experimental plots. We did not detect a significant positive elevation bias due to vegetation (Buffington et al. 2016). Panne depth is measured as the elevation difference between a single elevation point in the middle of the panne (panne elevation) and the surrounding marsh (non-vegetated vertical accuracy between 8-10 cm).

Pannes are typically circular in shape, but can be irregular. The ‘Panne Size Index’ represents the panne perimeter distance. The perimeter of each panne (at the last rooted vegetation) was carefully traced using a transect tape. Using the same transect tape we measured the shortest possible distance to the nearest panne (‘Distance to Nearest Panne’), the width of any branching microchannel in the panne (‘Microchannel width’), and the shortest distance to the nearest tidal creek (‘Distance to bank edge’) (Table S2). Our hypotheses for each of the aforementioned parameters and indices are outlined in Table 1 and Table S2.

Comparison of crab and burrow densities along panne and tidal creek bank edges

To compare crab and burrow densities in panne vs. bank edges, we summarized data at the block level for panne (n=19) and tidal creek bank (n=25) edges (Beheshti et al. in review). Crab abundance data from both experiments was compared by calculating the average crab Catch Per Unit Effort (CPUE), with effort being a single sampling unit or pit-fall trap. For the panne study, Crab CPUE was averaged across 8 pit-fall traps and for the tidal creek bank study, crab CPUE was averaged across 4 pit-fall traps. For the panne study, burrow densities were averaged across 4 replicate plots, and for the tidal creek bank edge study, burrow densities were averaged across 2 replicate plots. Burrow densities for both panne and tidal creek plots were expressed as density per m^2. Data used to compare crab effects across both studies were collected in August 2018.

Statistical analyses

We examined the role of a suite of physical and biological factors (Table S2) in explaining the rate of marsh recovery or dieback along panne edges. To do this, we summarized the data at the level of panne (n=19), using the four plots in each block (panne and surrounding marsh) as subsamples. We then used a stepwise regression to determine which model effects were predictive of panne contraction or expansion. Final model selection was based on Akaike Information Criterion (AIC). We tested for spatial differences in crab CPUE and burrow densities by running two separate one-way ANOVAs with two levels (Tidal Creek Bank Edge and Panne Edge) of factor “Project”.

Results

Characterization of panne trajectory and indices

Overall we found that pannes contracted during the study period. The movement of the vegetation boundary towards the panne center averaged 16.30 ± 7.83 cm/year (minimum = 6.22 cm, maximum = 33.79 cm). Recovery appeared to consist entirely of clonal expansion by existing *Salicornia pacifica* growing around the panne edge. We did not observe plants colonizing the panne area via seed and was instead exclusively rhizomatic growth.

Model results identifying correlates of panne recovery rate

In our initial multiple regression model we checked the Variance Inflation Factor (VIF) and observed high (>10) VIF scores for elevation and depth, which was inappropriate for the model. After looking at the covariance structure between panne depth and elevation, we found that the two were highly inversely correlated (Figure S4; lower elevation associated with deeper pannes and higher elevation associated with shallower pannes). Therefore, we developed a Principle Component variable, hereafter PC1(Depth and Elevation) to include in the stepwise regression. Higher values of PC1 represent higher elevation and shallower pannes and lower values of PC1 represent lower elevation and deeper pannes.

The stepwise regression identified the best predictive model out of the initial 14 parameters measured (Table S1). The final model included 5 model effects: Panne Size Index, PC1 (Depth and Elevation), Distance to Nearest Panne, Sediment Dynamics Index, and Crab Activity Index (Table 2). All model effects in the final model were significant and had VIF scores less than 2.0. For definitions of the aforementioned indices see Methods and Table 1.

The overall fit of the model was high, with ~86% of the variation in the response (absolute movement of marsh-panne boundary (cm) from 2016-2018) explained by the model (R^2=0.857, $F_{5,13}$=15.664, p<0.0001). Panne size had a significant negative effect on panne contraction (Slope = -1.169), the larger the panne, the lower observed panne contraction. PC1 (Depth and Elevation) had a highly significant positive effect on panne contraction (Slope = 4.559), with higher elevation and shallower pannes contracting more than low elevation deep pannes. Nearness between focal pannes and adjacent pannes had a highly significant negative effect on panne contraction (Slope= -3.289), with larger distances between pannes correlated to less contraction. Crab burrowing activity had a significant positive effect on panne contraction (Slope= 0.315), as burrow density increased, so did panne contraction. Sediment dynamics had a significant positive effect on panne contraction (Slope=1.788); pannes that accreted contracted more than pannes that showed no change over the study period or eroded (Table 2, Figure 3).

Comparison between crabs at bank edge vs. pannes

Crab CPUE was significantly greater along bank edges relative to panne edges (ANOVA; $F_{1,42}$=30.53, p<0.0001) (Figure 3A). Additionally, burrow density was significantly greater along bank edges relative to panne edges, with approximately 4x as many burrows observed along bank edges (ANOVA; $F_{1,42}$=25.15, p<0.0001) (Figure 3B).

Discussion

Multiple local factors drive interior marsh dynamics

Recently, Zhu and colleagues called pannes the "unrecognized Achilles' heel of marsh resilience to sea level rise" (Zhu et al. 2020). Much marsh degradation results from panne formation and expansion, but the mechanisms behind panne dynamics are not broadly understood. Some seminal studies have characterized key drivers (Redfield 1972, Wilson et al. 2009, 2010, 2014, Goudie 2013). Our investigation complements this earlier work, and provides the first study of panne dynamics in California marshes, which are dominated by a perennial succulent, different from many of the other study systems.

Salt panne dynamics are strongly controlled by drainage (Yap et al. 1917, Redfield 1972, Goudie 2013). In Plum Island Estuary, salt marsh has kept pace with sea level rise while panne area has increased and drainage density decreased, suggesting that drainage is a stronger driver of panne dynamics than sea level rise (Wilson et al. 2014). Over a two-year period, an experimentally drained panne did not change in depth but marginal revegetation did occur on exposed mud with the alleviation of waterlogging stress (i.e. anoxia, sulfide toxicity, hypersalinity) (Wilson et al. 2014). In our study we saw similar patterns. In the most supported model, PC1 (Depth and Elevation) was positively associated with panne contraction, with marsh recovering relatively quicker at shallower high elevation pannes than deeper low elevation pannes (Figure 4, Figure S5). Deeper pannes pool and retain water after tidal inundation more than shallow pannes. Previous work has shown that panne formation may be driven by depth and inundation time (Millette et al. 2010). Elkhorn Slough was experiencing system-wide marsh recovery during our study period, and in the marsh interior, our study suggests that the potential for marsh recovery is greatest at shallower, high elevation pannes where drainage is likely higher. This is likely due to similar mechanisms as those observed in Plum Island Estuary, where waterlogging stress observed in deeper pannes inhibited marsh recovery into the panne area.

Panne size has also been shown to be critically important in predicting the trajectory of marsh recovery. Smaller pannes are prone to infilling and marsh formation while larger pannes experience wave-induced erosion and bed shear stress which causes pannes to deepen and expand (Mariotti and Fagherazzi 2013) into 'compound pan[nes]' (Yap et al. 1917). Our results complement previous work by showing greater rates of panne contraction for smaller versus larger pannes (Figure 4).

Panne density has been shown to be negatively correlated to creek density (Goudie 2013), further supporting the hypothesis that poor drainage (fewer creeks) promotes panne formation and persistence. Our results differ from those of Goudie (2013) and indicated that marsh recovery was greatest when pannes were near to one another (Figure 4). While we expected regions with high densities of pannes to signal poor marsh health, our data suggests that recovery is more rapid in regions where pannes are closer to one another suggesting that there may be inter-panne effects at play (i.e. sediment exchange, improved drainage from panne to panne, etc).

Sediment dynamics in the pannes themselves is also of great importance and affected by panne elevation (Day et al. 2011, Cahoon et al. 2019), depth (Wilson et al. 2014), size (Schepers et al. 2016), and crab burrows (this study). The results of our study also showed that panne accretion was positively correlated with panne contraction, indicating that accretion improves soil conditions by possibly both raising the panne to an elevation within the growth range of marsh plants and alleviating stressors associated with waterlogging (Figure 4). The pannes where soil was lost showed the lowest rates of marsh recovery. Our results mirror previous work by showing an association between accretion and marsh recovery (Wilson et al. 2014). We suspect that accretion and drainage are both necessary for marsh colonization into pannes, as it is likely that an erosional panne that is well drained will only deepen and ultimately reach a tidal elevation outside of the growth range of marsh plants (Shumway 1995, Goudie 2013, Wilson et al. 2014, Cahoon et al. 2019).

While crab burrows have been shown to have positive effects on marsh productivity, mainly by oxygenating anoxic sediments (Bertness 1985) or increasing nutrient uptake (Holdredge 2010), crab burrows have also been found to increase erosion and creek formation (Escapa et al. 2008, Vu et al. 2017) and elongation (Crotty et al. 2020). In Argentina marshes, crab burrows facilitate the formation of pannes through loss of elevation (see Fig. 9 in Escapa et al. 2015). In our study, we observed crab burrows having a positive effect on panne contraction (Figure 4). In Elkhorn Slough, it is likely that the positive effect of burrows is due to increased drainage (Crotty et al.

2020) and reduced waterlogging stress (Alldred et al. 2020), which outweighs any possible negative effects.

Salt marshes are structured by both physical and biological factors and their interactions, yet most investigations of panne dynamics have focused on geomorphology (Wilson et al. 2014, Goudie 2013, Li et al. 2020, but see Escapa et al. 2015). Our study is one of the first on the U.S. west coast to explore how physical (panne attributes and sediment dynamics) and biological (crab activity) factors affect marsh recovery and subsequent panne contraction. For example, the finding that depth was negatively and elevation and number of burrows were positively associated with panne contraction provides a potential mechanism through which drainage may have been improved and marsh recovery made possible.

Crab effects are context-dependent

Based on the results of this and previous studies, effects of crab *P. crassipes* on marsh dynamics in Elkhorn Slough are context-dependent, with different physical factors across the marsh landscape changing not only the strength but the direction of certain crab effects. Crab burrows were found to be negatively associated with marsh biomass along tidal creek bank edges (Beheshti et al. in review). In the current study we found that burrows are positively associated with marsh recovery and panne contraction. The positive association between burrows and panne contraction is likely linked to improved drainage and an indirect effect on soil improvement (i.e. oxygenation of anoxic sediments, less sulfide buildup) (Figure 4). The different direction of crab effects and spatial differences in abundance are likely due to different physical factors driving dynamics along tidal creek banks versus panne edges. For example, tidal creek bank edges are driven by erosive processes (Fagherazzi et al. 2013) and have different hydrodynamics and geomorphology compared to panne edges. This contrast highlights how complex and variable the geomorphology can be in salt marsh systems where pannes in close proximity (~2 to 34 meters) to bank edges can have entirely different relationships between the same physical and biological drivers.

Top-down effects on vegetation can be very strong (Bertness and Silliman 2008, Holdredge et al. 2009, Daleo et al. 2011), but such effects will always interact with physical factors and thus may vary in strength (snail grazing in marshes with drought (Silliman et al. 2005), pollinator and herbivore interactions with plants across environmental gradients (Maron et al. 2014), foraging behavior of coral reef fishes with distance from reef (Gil et al. 2017)). Crab effects on salt marshes have been shown to have such context-dependent variation when examined across different estuaries (He and Silliman 2016, Wasson et al. 2019, Walker et al. 2020). In a meta-analysis that included up to 42 studies assessing consumer effects of crabs on salt marsh plants, the average effect size (Hedges' g) for multiple response variables (e.g. above and belowground biomass, plant survival, density) was overwhelmingly negative (n=50) as opposed to positive (n=8) (see Fig. 4 in He and Silliman 2016), demonstrating that crab effects, though typically negative, are not uniform and are instead context dependent. In New England marshes, burrowing by crab *Uca pugnax* were shown to increase drainage and redox potential in the sediments of cordgrass marshes, promoting biomass production in soft sediment marsh environments (Bertness 1985). In another example showing positive effects of crabs on marsh vegetation, Holdredge et al. (2010) found that in sandy cordgrass marshes, crabs positively affected nutrient uptake by cordgrass. They also found that experimentally removing crabs caused above- and belowground biomass to drop by ~50% (Holdredge et al. 2010). These two studies show that the mechanisms driving positive crab effects differ for marshes with different physical characteristics (e.g. fine vs coarse sediment). In other studies, in Argentina marshes, the effects of burrowing by crab *Neohelice granulata* varied across the marsh landscape, promoting sediment trapping in the marsh interior (positive effect) and enhancing sediment transport on tidal creek edges (negative effect) (Escapa et al. 2008) and in a separate study, consumer pressure by crabs was shown to prevent marsh colonization of pannes (Daleo et al. 2011).

Regional and global drivers of marsh dynamics

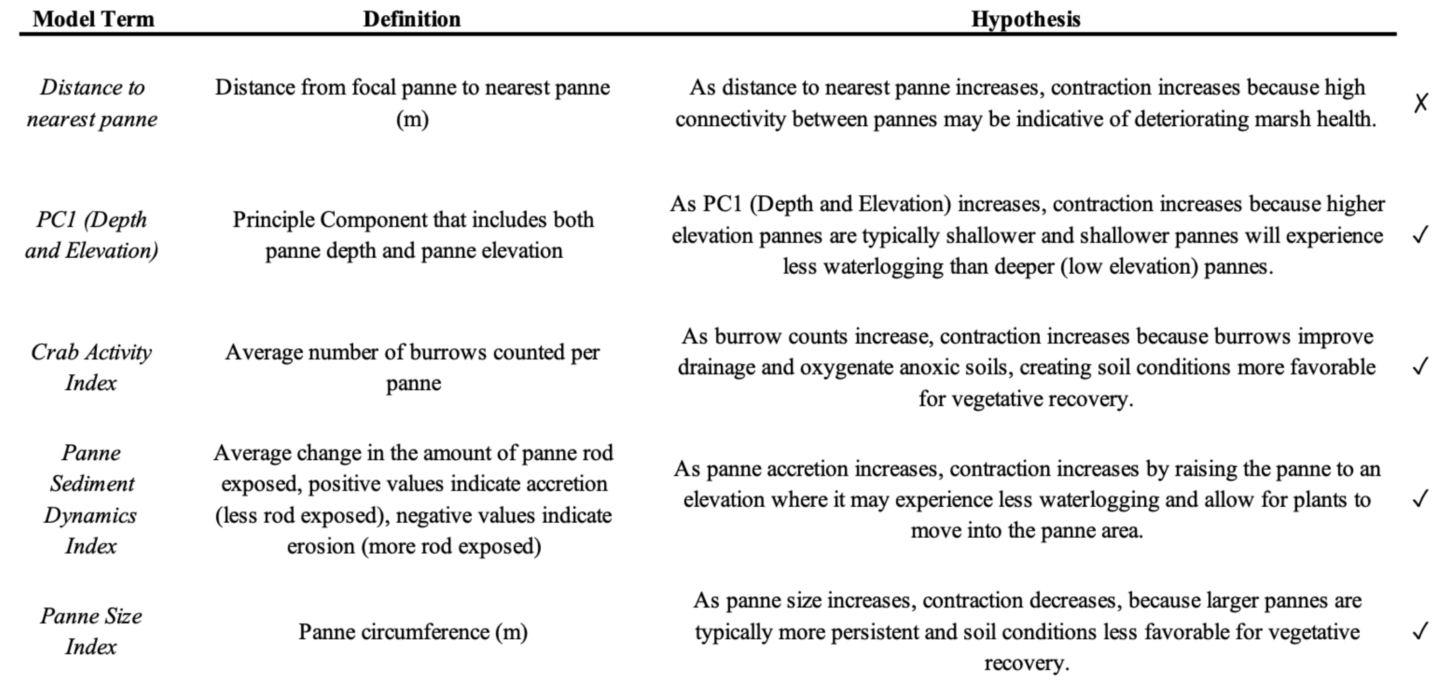
While local factors and attributes of the pannes themselves predict short-term panne dynamics, it is clear that regional and global drivers also can exert strong effects. Our study was conducted immediately following one of the worst droughts in California history (Lund et al. 2018) and a warm water event (Peterson et al. 2015) that coincided with a period of widespread marsh loss and panne expansion in Elkhorn Slough. Following these dry and warm periods was the second wettest season (2016-2017) in California since 1951, at 78.105 cm of rainfall (https://www.ncei.noaa.gov/).

That this anomalous rain year occurred during our study may suggest that precipitation plays an important role in facilitating the recovery of the marsh along these physically stressful panne edges. Although, we should note that the rate of recovery was steady through time and if precipitation had a large effect on marsh recovery we would have expected greater rates of panne contraction from 2016-2017 relative to 2017-2018. Further investigation is needed to understand how regional climatic and oceanographic events affect panne dynamics.

Our study showed how elevation, a proxy for relative sea level rise, can affect rates of panne contraction. We tracked relatively slower panne contraction at low elevations, suggesting that opportunities for marsh recovery are diminished with sea level rise. Some studies have indicated that sea level rise will increase the rate of panne formation, expansion, and coalescence, further contributing to marsh loss (Day et al. 2011, Zhu et al. 2020), while others suggest that poor drainage, insufficient accretion, and poor creek connectivity explain panne formation (Wilson et al. 2014). In our study we show that elevation, drainage, and inundation are inextricably linked and predictive of panne dynamics. Further, as sea level rise continues, channels may deepen and widen, increasing the tidal prism (Goudie 2013) and crabs may become more abundant as their fundamental niche widens (Raposa et al. 2018). This has already been demonstrated in New England marshes (Raposa et al. 2018, Crotty et al. 2020). The interaction between crab effects and sea level rise on panne dynamics needs further study. Our results indicate that crab burrowing along panne edges facilitates marsh recovery and panne contraction, likely by improving drainage and reducing waterlogging. Further study is needed to determine what the effect on pannes would be if crab densities were to increase to levels observed along tidal creek bank edges. We cannot assume effects to be negative, as was detected along tidal creek bank edges (Beheshti et al. in review), due to large differences in the local geomorphology between these two edge types. While it is possible that increased crab abundance along panne edges could trigger marsh dieback and panne expansion via elevation losses associated with depressed marsh production (Day et al. 2011), as was seen in Argentina marshes (Escapa et al. 2015), this needs to directly tested in a U.S. west coast marsh system. Further study is needed to explore how the factors identified in this study may change with projected sea level rise, one way to approach this would be to include pannes from a wider range of marsh elevations, as a better proxy for sea level rise (Figure S6).

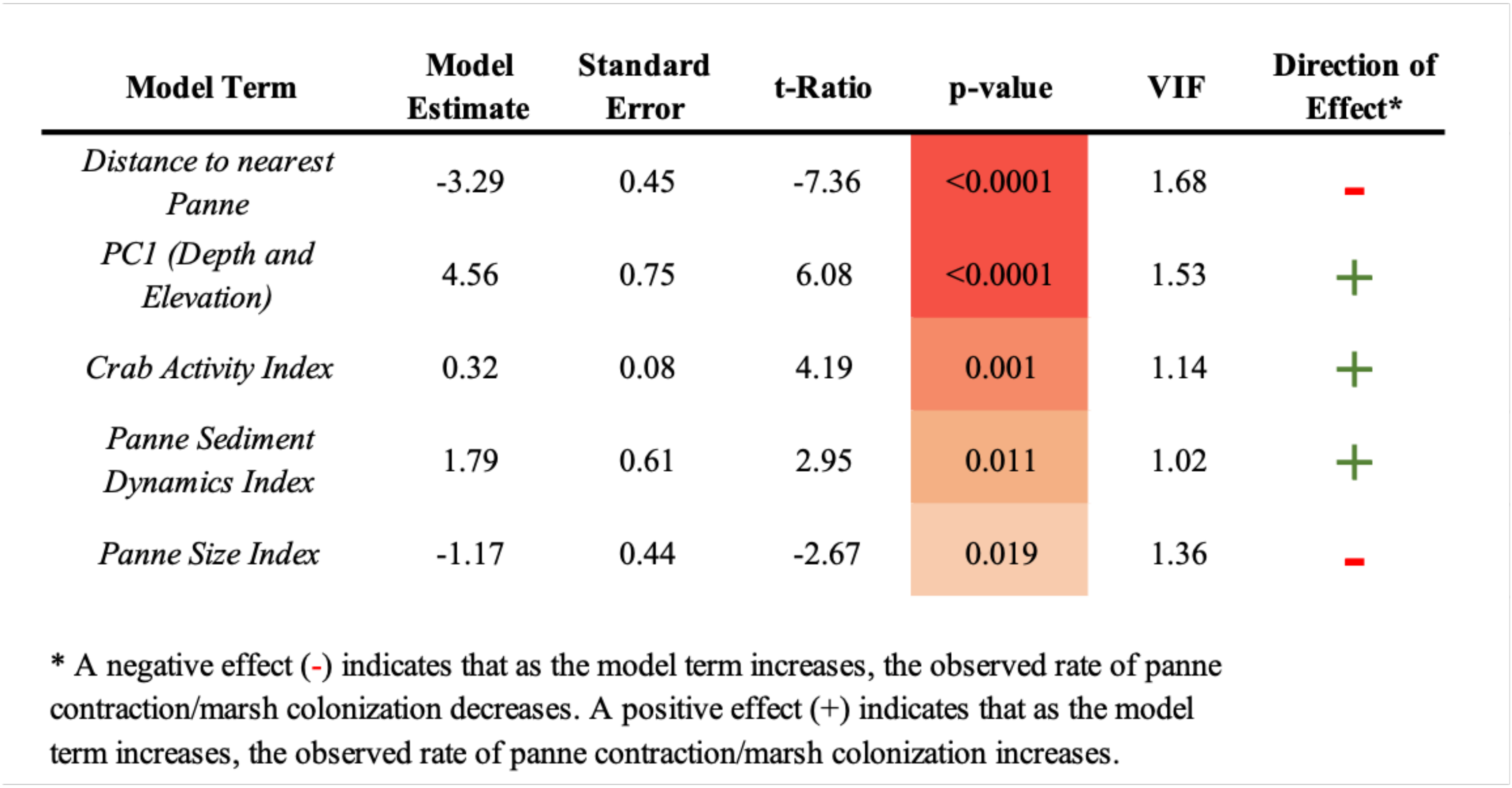
Our understanding of panne dynamics is improving, but more robust predictions are needed of how dynamics may shift with both short and long term disturbances associated with global change. Future work should track panne formation, expansion, coalescence, or contraction as sea-levels rise and anthropogenic stressors worsen (Millette et al. 2010, Ganju et al. 2017) and compare rates of interior marsh loss to historical rates to improve the management of these coastal habitats and inform marsh conservation strategies. Such studies are needed to better understand how extreme events, such as those that preceded and occurred during our study, affect marsh dynamics and resilience.

Table 1. Model terms, definitions and hypotheses about panne contraction. During our study, the entire estuary was undergoing a recovery period, hence the directionality of the language in the table describing how the model terms were hypothesized to affect panne contraction. These same terms could be used to explain panne expansion with the hypotheses reversed. "✓" indicate that our data support our hypothesis and "✗" indicates that our data did not support our hypothesis.



Model Term	Definition	Hypothesis	
Distance to nearest panne	Distance from focal panne to nearest panne (m)	As distance to nearest panne increases, contraction increases because high connectivity between pannes may be indicative of deteriorating marsh health.	✗
PC1 (Depth and Elevation)	Principle Component that includes both panne depth and panne elevation	As PC1 (Depth and Elevation) increases, contraction increases because higher elevation pannes are typically shallower and shallower pannes will experience less waterlogging than deeper (low elevation) pannes.	✓
Crab Activity Index	Average number of burrows counted per panne	As burrow counts increase, contraction increases because burrows improve drainage and oxygenate anoxic soils, creating soil conditions more favorable for vegetative recovery.	✓
Panne Sediment Dynamics Index	Average change in the amount of panne rod exposed, positive values indicate accretion (less rod exposed), negative values indicate erosion (more rod exposed)	As panne accretion increases, contraction increases by raising the panne to an elevation where it may experience less waterlogging and allow for plants to move into the panne area.	✓
Panne Size Index	Panne circumference (m)	As panne size increases, contraction decreases, because larger pannes are typically more persistent and soil conditions less favorable for vegetative recovery.	✓

Table 2. Multiple regression model output. Reported is the estimate, standard error, t-Ratio, p-value, and VIF for each model term. Also reported is the direction of the effect per term on panne contraction.



Model Term	Model Estimate	Standard Error	t-Ratio	p-value	VIF	Direction of Effect*
Distance to nearest Panne	-3.29	0.45	-7.36	<0.0001	1.68	-
PC1 (Depth and Elevation)	4.56	0.75	6.08	<0.0001	1.53	+
Crab Activity Index	0.32	0.08	4.19	0.001	1.14	+
Panne Sediment Dynamics Index	1.79	0.61	2.95	0.011	1.02	+
Panne Size Index	-1.17	0.44	-2.67	0.019	1.36	-

* A negative effect (-) indicates that as the model term increases, the observed rate of panne contraction/marsh colonization decreases. A positive effect (+) indicates that as the model term increases, the observed rate of panne contraction/marsh colonization increases.

Figure 1. A) Study map showing panne (yellow circles, labeled by panne ID) and bank edge (red circles, labeled by tidal creek bank edge site) studies. B-E) Examples of the panne study and variation in panne size, pooling, and drainage.

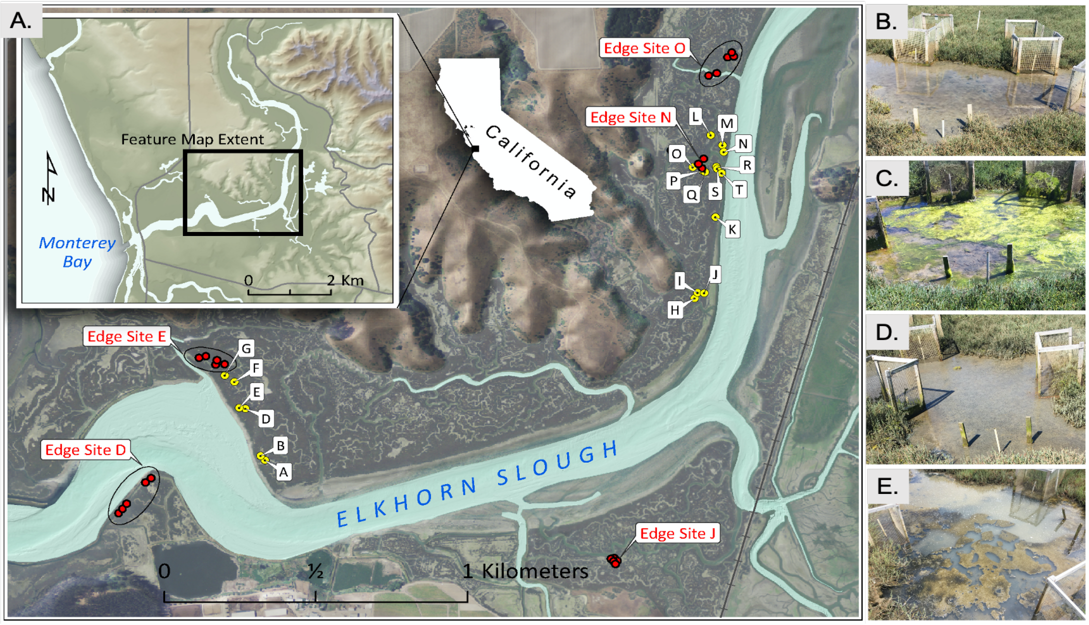


Figure 2. A) Crab CPUE along panne versus tidal creek bank edges. B) Burrow density (# per m^2) along panne versus tidal creek bank edges. Plotted is the Least Square Means Estimates ± Standard Error. Pink bars represent panne edges and blue bars represent tidal creek bank edges. Different letters denote significant differences ($\alpha = 0.05$) between panne and tidal creek bank edges.

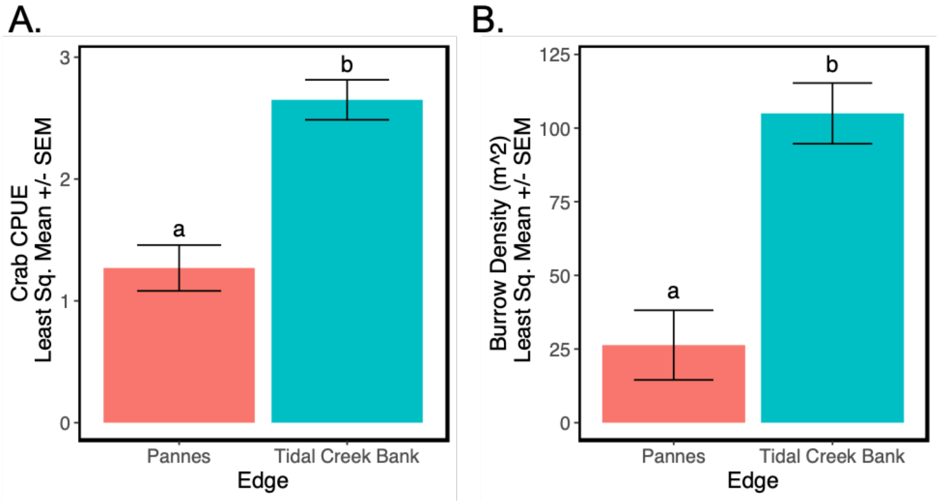


Figure 3. Partial leverage plots for all of the best-fit model effects. Plotted is the back-transformed data. Dotted red horizontal line represents the average marsh-pan boundary movement from 2016-2018 of 16.298 cm. Each partial leverage plot includes the 95% C.I. For a list of the parameters included in the plotted indices, see **Table 1**.

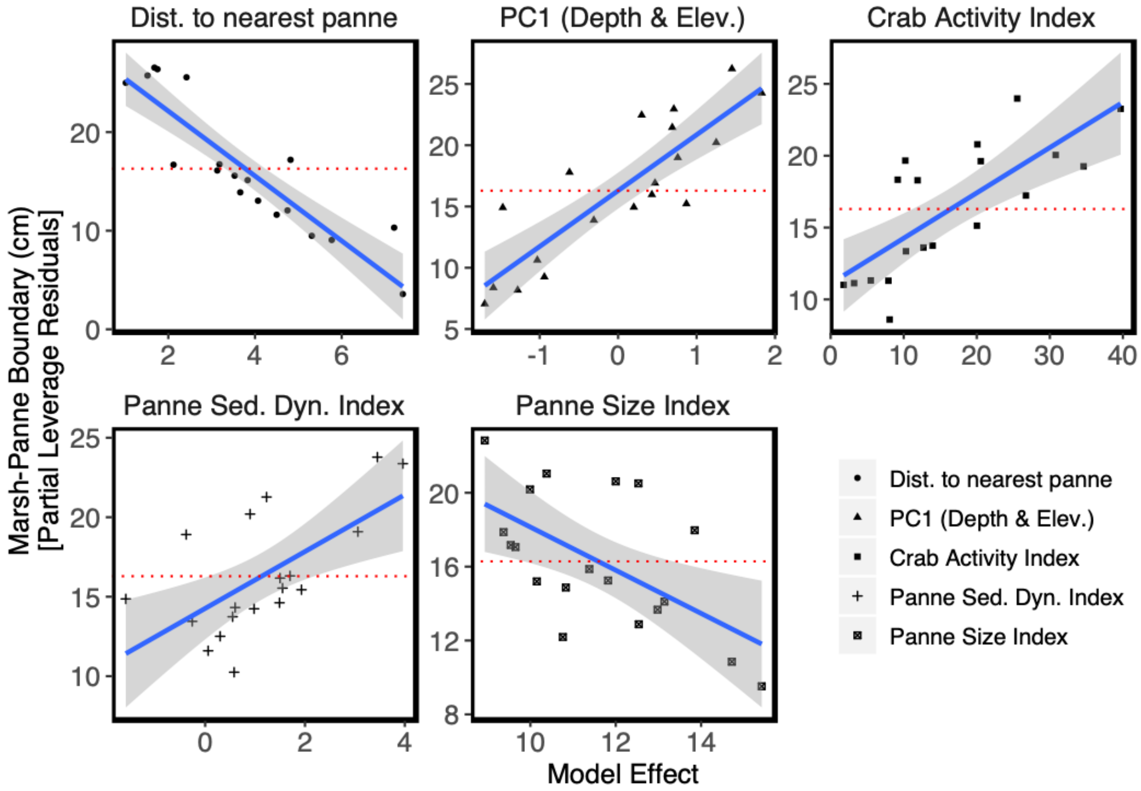
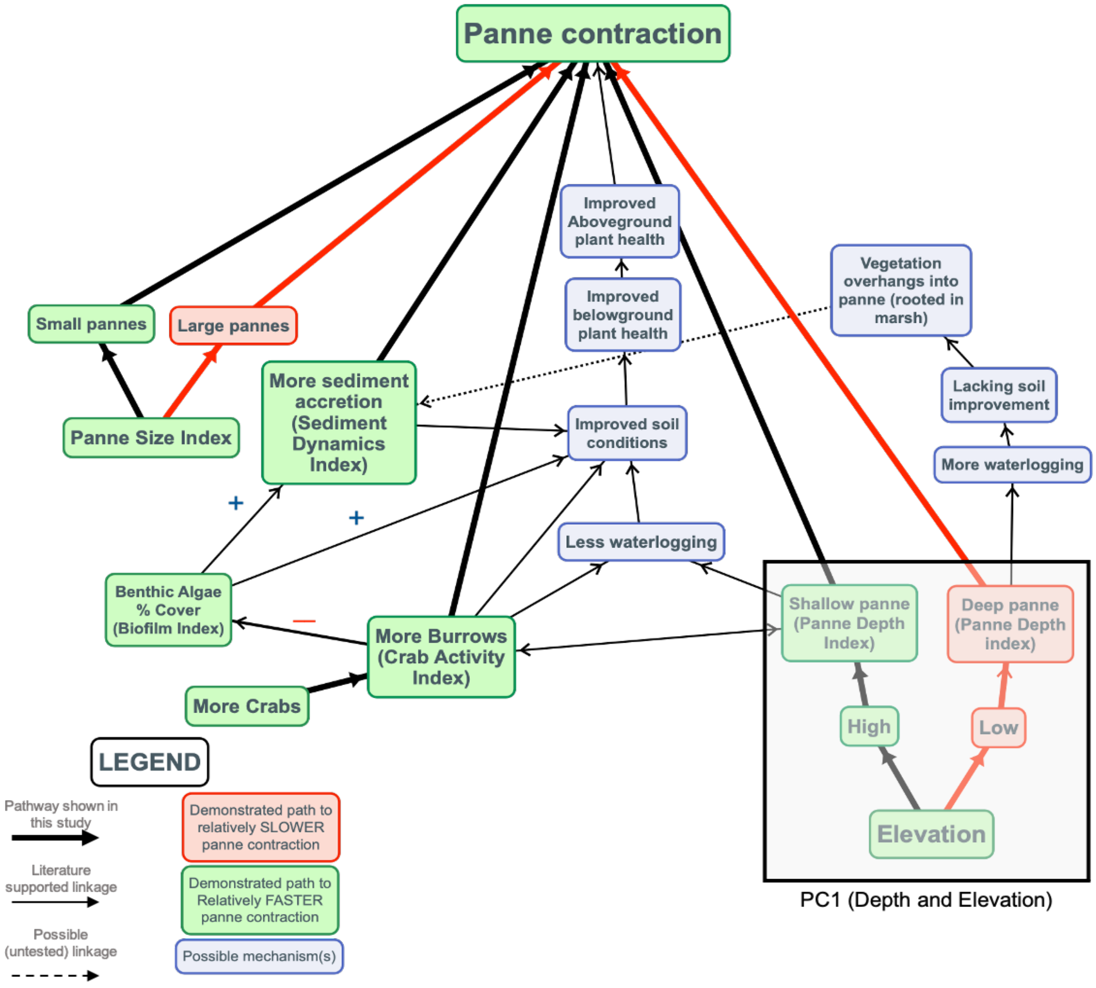


Figure 4. Conceptual model of panne contraction and possible mechanisms. Bolded arrows indicate relationships or main model terms that correlated to panne contraction and were shown in our study. Narrow or dotted arrows indicate pathways shown in the literature or untested, but likely pathways. Red arrows and cells indicate pathways to slower panne contraction and green cells indicate pathways to relatively rapid panne contraction. Blue cells indicate potential mechanisms.



Chapter 3

Rapid enhancement of multiple ecosystem services following the restoration of a coastal foundation species

Abstract

The global decline of marine foundation species (kelp forests, mangroves, salt marshes, and seagrasses) has led to the degradation of the coastal zone and threatens the loss of critical ecosystem services and functions. Restoration of marine foundation species to facilitate ecological recovery has had variable success, especially for seagrasses, where a majority of restoration efforts have failed. While most seagrass restorations track structural attributes over time, rarely do restorations assess the suite of ecological functions that may be affected by restoration. Here we report on the results of two small-scale experimental seagrass restoration projects in a central California estuary where we transplanted 117 0.25 m^2 plots (2,340 shoots) of the seagrass species *Zostera marina*. We quantified restoration success relative to healthy, persistent reference beds, and in comparison to unrestored, unvegetated areas. Within three years, our restored plots expanded ~8500%, from 29 m^2 to 2513 m^2. The restored beds rapidly came to resemble the reference beds in 1) seagrass structural attributes (canopy height, shoot density, biomass), 2) ecological functions (macrofaunal richness and abundance, epifaunal species richness, nursery function), and 3) biogeochemical functions (modulation of water quality, organic carbon storage). We also developed a multifunctionality index to assess cumulative functional performance, which revealed restored plots are intermediate between reference and unvegetated habitats, suggesting a rapid development of functions over a short time period. Our comprehensive study is one of few published studies to quantify how seagrass restoration can enhance both biological and biogeochemical functions. Our study serves as a model for quantifying ecosystem services associated with the restoration of a foundation species and demonstrates the potential for rapid functional recovery that can be achieved through targeted restoration of fast-growing foundation species under suitable conditions.

Keywords: eelgrass, ecosystem services, multifunctionality, small-scale restoration, carbon stocks, nursery habitat, species richness, community ecology, water quality, *Zostera marina*

Introduction

Restoration of coastal foundation species has become a conservation priority because many populations have undergone extensive declines (Ellison et al. 2005). As human populations continue to grow in coastal areas, the impact of human activities on the foundation species that define coastal marine environments has intensified (Barbier et al. 2011, Kirwan and Megonigal 2013, Osland 2019). Such impacts include local effects of runoff from agriculture (Wasson et al. 2017) and urban development (Coverdale et al. 2013), diversion of freshwater inputs (Kennish 2002), and overfishing (Altieri et al. 2012) leading to trophic downgrading (Estes et al. 2011, Kéfi et al. 2012). Global effects of ocean acidification on coral reefs (Bellwood et al. 2004), sea level rise drowning of tidal salt marshes (Thorne et al. 2018) and rising sea surface temperature effects on seagrass (Zimmerman et al. 2015) and kelp forests

(Muth et al. 2019, Rogers-Bennett and Catton 2019) are some prime examples of how humans are contributing to the loss of foundation species and the services they provide. To address these various stressors occurring at different spatial and temporal scales, researchers and managers are applying a diversity of restoration approaches. Intervention in the form of regulatory actions that limit harvest (Hughes et al. 2009b), implement water quality standards (Kennish 2002) or establish perimeters of protected habitat (e.g., Marine Protected Areas) has been shown to be effective in restoring environmental conditions conducive to the recovery of foundation species (Ling et al. 2009, Clements and Hay 2018, Geldmann et al. 2019). Transplanting foundation species (marsh plants, juvenile mangroves, oyster spat, corals, etc.) from areas where they are thriving to areas where they are scarce is a common restoration approach used to enhance foundation species coverage and the ecosystem services and functions they provide.

Often restoration fails to bring back all the functions and services associated with foundation species, or does so slowly (Zedler and Callaway 1999, Duarte et al. 2008, Bayraktarov et al. 2016). Restoration project goals need to be developed with consideration of the life history and demography of foundation species (Montero-Serra et al. 2018, Yando et al. 2019). For example, in regions where salt marshes (cordgrass) and mangroves co-occur, cordgrass is considered the preferred foundation species to transplant due to its fast growth, expansion, and recruitment, which expedites the restoration of ecosystem functioning (Yando et al. 2019). Generally, succession in wetland systems (e.g., salt marsh and seagrasses) is relatively rapid, making them ideal systems for understanding recovery through restoration and the ecological responses that affect a range of functions and services. Similarly, utilizing the rapid succession of fast-growing kelps (Dayton et al. 1992, Tegner et al. 1997), active restorations in the form of artificial reefs (Reed et al. 2006) and juvenile transplants (Carney et al. 2005, Layton et al. 2020) have been key in attempts to reverse widespread deforestation. In contrast, coral reef species are typically long-lived and slow-growing (Young et al. 2012, Ladd et al. 2018, 2019); consequently, returning reefs to pre-disturbance conditions can take decades (Jaap 2000, Victoria-Salazar et al. 2017). Thus, expectations for the rate of recovery of ecosystem services should be tailored to the growth rate of different foundation species and habitat types.

Seagrasses are a group of marine foundation species that are in accelerated global decline (Orth et al. 2006, Waycott et al. 2009, Short et al. 2011). As marine flowering plants, seagrasses are primarily limited by light availability, and most temperate seagrass species are restricted to the low intertidal or shallow subtidal zone (Zimmerman 1997). Light attenuation due to poor water quality triggered by increased sediment loading, eutrophication, contaminants, and other pollutants are frequently cited as the leading cause of seagrass loss (McGlathery et al. 2007, van der Heide et al 2007).

To combat the widespread loss of seagrass habitat, restoration efforts are on the rise (Cunha et al. 2012, van Katwijk et al. 2016). Approaches to seagrass restoration can be broadly categorized into intervention that is indirect, such as restoring environmental conditions conducive to seagrass recovery (e.g., improving water quality and clarity), and direct, such as transplanting and seeding. The majority (~63%) of direct seagrass restorations have failed, where failure was defined by both initial trial survival (presence/absence) and long-term trends of restored habitats (absent, declining, no change, or increasing) (Bayraktarov et al. 2016, Rezek et al. 2019). A meta-analysis of 1,786 restoration 'trials', defined as 1 or more shoots or seeds planted using the same technique at the same location and time of year, found that scale (i.e., the number of initial transplants or seeds), technique, proximity to donor beds, and the removal of threats or stressors to be critical factors in predicting the performance and persistence of seagrass restorations (van Katwijk et al. 2016). One might expect that seagrass, with its rhizomatic growth, high seed production, and potential for long-distance dispersal of seeds and reproductive shoot fragments (Kendrick et al. 2016), will expand rapidly following transplantation or seeding. Yet survival, let alone expansion, of restored beds is typically low, despite these advantageous life history traits.

As one of the world's most productive ecosystems, seagrasses support a suite of ecosystem functions linked to highly valued provisioning and regulating services (Duarte 2002, Duffy 2006). Yet it is largely unknown whether restoration of these foundation species is correlated to a related restoration of associated functions and services or how long it takes to achieve such functional recovery. For example, seagrass belowground biomass stabilizes sediment while aboveground biomass attenuates wave action; together these two functions provide the services of mitigating erosive forces and acting as a storm buffer. Additionally, organic particulate matter that is trapped within seagrass beds is stored in its oxygen-depleted sediments where decomposition is relatively slow, providing the service of carbon storage. Relatedly, during photosynthesis, seagrasses both transport O_2 to the rhizosphere building a barrier against phytotoxins (Frederiksen and Glud 2006) and absorb large quantities of CO_2, the latter of which has the potential to increase the pH and O_2 of seawater and serve as a buffer to acidifying oceanic conditions (Bergstrom et al. 2019). Seagrasses also provide structure that serves as nursery habitat for species of commercial importance—for example, along the U.S. West Coast, Dungeness crab (*Metacarcinus magister*) utilizes estuarine habitats, including seagrasses, during its early life stages and this particular fishery has an average annual value of over $100 million (Hughes et al. 2014). Given the tremendous value of seagrass ecosystems, restorations that assess both structural and functional attributes are required to evaluate whether restoration efforts can be defined as "successful". One such restoration was recently reported from a research group working in Virginia's coastal lagoons where seagrass had been absent for over 70 years due to seed recruitment limitation until a large-scale seeding effort (70+ million seeds) successfully restored seagrass to the region (Orth et al. 2020). Over the past two decades, restored habitats in the coastal lagoons continued to expand and resulted in the recovery of multiple ecosystem services and even a related restoration of commercially harvested bay scallops (Orth et al. 2020). Similar studies are needed, particularly for other regions of the country experiencing different environmental conditions and human-induced stressors. Our study was conducted in a nutrient-loaded estuary on the west coast of the U.S. from 2015 to 2018, and despite being comparably small in scale (<10,000 shoots or seeds; van Katwijk et al. 2016) and using a different technique (transplants), we observed, and set out to quantify, the rapid enhancement of multiple ecosystem functions and services from restored seagrass beds.

The goals of our study were to: 1) track the temporal trajectory of restored seagrass survival, expansion, and health and, 2) quantify a suite of ecosystem functions and determine if the restored seagrass ecosystem functionality rapidly reaches the levels of naturally existing beds. First, our investigation compared restored seagrass plots vs. naturally existing reference beds for seagrass areal expansion rates and indicators of health (productivity, canopy height, above and belowground biomass, etc.). Second, we quantified ecosystem functions including biodiversity, nursery habitat, modulation of water chemistry (pH, DO and water temperature), and organic carbon stocks and compared these functions individually and collectively using a multifunctionality index (Byrnes et al. 2014) across restored, reference, and adjacent unvegetated soft-bottom habitats. Our investigation thus serves as a model for investigating the restoration of foundation species, and the ecosystem functions they support.

Methods

Study site

Elkhorn Slough is an estuary located in Monterey Bay, California. Highly impacted by the surrounding agricultural land, Elkhorn Slough is classified as a nutrient-loaded system (Hughes et al. 2011, Wasson et al. 2017). The current distribution of *Zostera marina*, eelgrass, occurs in the lower reaches of the estuary (Figure 1), within the first 3 kilometers of the main channel, where residence time is only about one tidal cycle and conditions are moderately eutrophic (Hughes et al. 2011). In 1931, seagrass covered ~26 hectares (Appendix S1: Figure S1); thereafter, it began to decline. By the 1960s, seagrass habitat extent had plummeted to ~ 3 hectares. Beginning in the mid-1980s, coinciding with the local recovery of the southern sea otter (*Enhydra lutris*) population, seagrass in Elkhorn Slough began to recover to its current extent of ~15 hectares. Seagrass expansion in the estuary has been associated with the recovery of sea otters that have an indirect positive effect on seagrass health through a four-level trophic cascade (Hughes et al. 2013). Given their demonstrable impact on seagrass bed health and expansion in the system (Hughes et al. 2013), it is important to note that sea otters were highly abundant throughout our study area during the study (Tinker and Hatfield 2017, Hatfield et al. 2019).

Small-scale experimental restoration

We conducted two seagrass restoration projects, occurring in June 2015 and March 2016. In 2015, restoration plot locations were randomly generated using ArcGIS for Desktop v.10.2 with two qualifiers for suitable transplant sites: restoration plots had to be 1) at least 25 m from the nearest natural existing reference beds because these were areas not likely to revegetate naturally through vegetative growth and 2) within the tidal elevation range of 0 to -2 m relative to Mean Lower Low Water, because this is the observed distribution of eelgrass in the estuary (Figure 1). For ease of re-finding and monitoring plots and to limit the number of visible PVC posts in the main channel, each 2016 restoration plot was placed approximately 7 m away from 2015 plots, still meeting the same two criteria described above (Appendix S1: Figure S2).

To account for any physical or biological gradients within the study area we organized restoration plots to strata (A, B, C, D, and E), increasing in distance from the mouth of the estuary from strata A to E (Figure 1). The distance from strata A to E spanned approximately 3.1 kilometers and strata A, B and C had nearby natural existing reference beds, hereafter referred to as reference plots, strata D and E did not. Aerial imagery and historical accounts gave us a conservative estimate for when these reference plots were established—stratum A from 1931-1947 and strata B and C from 1996-2005 (Hughes et al. 2013). For the 2015 and 2016 restoration projects, there were 8 and 12 plots in stratum A, 10 and 13 plots in stratum B, 10 and 12 plots in stratum C, 13 and 16 plots in stratum D, and 10 and 13 plots in stratum E.

All source shoots for restoration (n=2,340) were harvested on SCUBA from a single donor bed, by far the largest seagrass bed in the estuary at 6.9 hectares (36.816115°, -121.766678°). Shoots were harvested over the entire extent of this bed (~500 x 110 meters) in an effort to increase genetic diversity and minimize disturbance that would otherwise result from concentrating harvest in a smaller area within the donor bed (Williams 2001, Hughes et al. 2009a). Rhizomes longer than 10 cm were trimmed to minimize breakage when transplanted and all shoots were trimmed to 20 cm above the most recent node to standardize starting biomass and lengths, as well as standardizing the epibiont community, essentially removing all epibionts that occur in the eelgrass canopy (Appendix S1: Figure S3). We assured that the 20 cm above the most recent node, but above the meristem included both sheath and blades. In 2015, 1020 shoots were transplanted into 51, 0.25 m^2 plots, while in 2016, 1320 shoots were transplanted into 66, 0.25 m^2 plots. Transplanted densities (20 shoots per 0.25 m^2) were chosen based on average shoot densities of reference plots. Shoots were transplanted using a common anchoring technique: a narrow trench was built in the sediment using a hand trowel and shoots were secured in the ground with 10-12" galvanized garden staples (Fonseca et al. 1996, van Katwijk et al. 2000).

Restoration survival and growth

To assess seagrass growth and survival, we counted the total number of vegetative and flowering shoots and recorded maximum canopy height within a quadrat placed in the initial plot area (0.25 m^2). To assess expansion of the restored plots, we measured the maximum distance between live shoots in the plots (plot length), then took a second measurement between live shoots in a perpendicular axis (plot width) and multiplied these to obtain an estimate of plot area. Each of these parameters was monitored using SCUBA surveys of the restoration and reference plots. Monitoring for the 2015 restoration project was conducted approximately 1, 3, 6, 9, 12, 16, 24, 30 and 40 months post-transplanting and monitoring for the 2016 restoration project was conducted approximately 1, 6, 18, and 30 months post-transplanting. Reference plots were monitored at a minimum once each summer from 2015-2018. To determine whether there were differences in vegetative shoot counts between restored and reference plots we ran an ANOVA with three levels (2015 and 2016 restoration plots and reference plots) of factor "habitat type". Multiple plots had zero flowering shoots; this was accounted for using a generalized regression analysis with a zero-inflated Poisson distribution and a maximum likelihood estimation method with "habitat type" as the explanatory variable. All data was analyzed in either JMP Pro 15 or R and all plots were generated using R version 3.5.3.

For a more detailed assessment of seagrass growth and health, in August 2018 (~ 40 and 30 months post-restoration for 2015 and 2016, respectively) we collected shoots and rhizomes (ramets) from restored and reference plots and evaluated them in the laboratory. First, we thoroughly searched and cleared all invertebrates from harvested shoots and rhizomes for later processing. Next, we carefully removed epiphytes off of the blades and placed them in a dehydrating oven for dry weight. More details are provided in Appendix S1. For each shoot, now clean of epiphytes, we cut the rhizome at the most recent node—separating the blades from the rhizome. To compare rhizome biomass in restored and reference plots, we cut each rhizome to a standardized length of 7 cm, wrapped in a labeled foil, and placed in a dehydrating oven for 72 hrs to estimate dry weight (g). We cut rhizomes to 7 cm to ensure we were processing live tissue (attempting to collect more than 7 cm of rhizome in the field often results in rhizomes breaking) and because at this length the rhizome is approximately the same age as the shoot. Each shoot was wrapped in a labeled foil and placed in a dehydrating oven for 72 hrs. Dried shoots, rhizomes, and epiphytes were weighed and recorded. We analyzed data using an ANOVA with three levels (2015 and 2016 restoration plots and reference plots) of factor "habitat type" and five levels (A, B, C, D, E) of factor "strata" to compare the mean biomass of shoots, rhizomes, and epiphytes of collected ramets; strata were removed as a factor when non-significant ($p<0.05$).

Seagrass time series

To quantify how much new seagrass habitat in Elkhorn Slough was due to restoration plot expansion versus natural seagrass filling in and expanding, a time series was developed using geospatial data on seagrass extent. Restored seagrass area was calculated by summing the plot area data collected in the field from all restoration plots (2015 and 2016) in August 2018. The total extent of seagrass habitat was calculated using ArcGIS Desktop v.10.5 that incorporated aerial imagery from Google Earth Pro and included both restored and natural seagrass. The Google Earth imagery included a time period prior to restoration (between March 2015 and April 2016), and a time period after restoration (between February and November 2018). To get the clearest images of seagrass possible, we used multiple images from within each period that represented slightly different spatial resolutions and tidal conditions. New or expanded seagrass habitat was calculated by subtracting the total estimated seagrass area post-restoration from pre-restoration. To calculate the percent of new seagrass habitat attributed to our restoration, we used the following equation; $y = [e_r/\Delta e_t)]*100$—where Δe_t is the change in total seagrass extent (restored and natural) from pre- to post-restoration and e_r is the total extent restored and subsequent expansion.

Measuring ecological functions

In order to assess the performance of various ecosystem functions across habitat types, we collected data on macrofaunal species richness and abundance, seagrass epifauna community assemblage and biomass, water quality parameters (temperature, pH, and dissolved oxygen), and sediment organic carbon stocks. Because we were interested in differences across habitats, without the potential influence of spatial differences, only functional attributes within strata A, B, and C were used in the analyses since these were the strata containing both habitat types; one exception to this was our assessment of seagrass epifauna community assemblages where we pooled all restored plots (strata A-E) and compared them to all reference plots (strata A-C). In order to provide an assessment of the functionality of vegetated vs non vegetated habitat we included marked unvegetated soft-bottom habitats, hereafter referred to as unvegetated plots, at the same depth and approximately 7 m away from each of the 2015 plots (Appendix S1: Figure S2). Unvegetated plots were monitored concurrently with restored and reference plots.

Biodiversity of macrofauna

To quantify biodiversity of mobile macrofauna we deployed a baited shrimp pot, hereafter referred to as a trap array, in each habitat type (unvegetated, restoration, and reference plots). More details are provided in Appendix S1. For each trapping effort, 3-4 trap arrays were deployed in restored (2015 and 2016), reference, and unvegetated plots in strata A, B, and C. Soak times averaged 24 hours and bait was replaced every other day. We trapped a total of 21 days in summer 2016, 36 days in summer 2017, and 4 days in summer 2018. For strata A, B, and C, across all trapping years, the sample size by habitat was as follows: n=30, 25, and 25 for 2015 restoration plots; n=41, 30, and 31 for 2016 restoration plots; n=57, 34, and 37 for reference plots; and n=43, 34, and 32 for unvegetated plots. Data collection on all trapped individuals was organized by trap type (minnow trap or shrimp pot) and included species identification to the lowest taxonomic level and size. All trapped individuals were released to the location where they were initially found. When data were later analyzed, trap type was not included as a factor as data were pooled from both trap types. We assessed both species density (number of species trapped per plot) and species richness (total number of species supported per habitat). Species density, while important, does not factor in the identity of the trapped species per sampling unit (in this case, 24 hr trapping efforts across 61 days). For example, a habitat that repeatedly traps species A and species B across multiple trap days would have a species density of 2, and a habitat that traps species A and species B one day and species C and D another day would also have a species density of 2 because, per effort, two species were trapped. Both overall species richness and species density provide important information about the potential for diversity to affect community structure and function. Species richness, as estimated by species accumulation curves provides a direct assessment of the number of species that occur in a habitat, which by itself is important for conservation and management and which may also provide information about habitat complexity and the potential for functional redundancy. Species density provides important information about the interaction (particularly competition) that may regulate species in a system. In addition, differences between species density and richness will direct attention to differences in species evenness, distributions, and patterns of spatial covariance.

In order to visually compare similarities in community composition for two consecutive trapping years (summer 2016 and summer 2017), we generated a cluster diagram using a Bray-Curtis similarity matrix using PRIMER statistical software. The endpoints for the Bray-Curtis similarity matrix included habitats; 2015 restoration, 2016 restoration, reference and unvegetated plots, and monitoring years; 2016 and 2017. To visually assess how many species each habitat may support, we generated a species accumulation curve. To compare relative species richness across habitats, the curves were truncated to the lowest number of observations made, 80, so as to allow assessment of richness at the same level of sampling effort. We also compared species density as a function of habitat type. Here we used the mean number of species trapped per trapping effort as the response variable in a generalized regression using a zero-inflated Gamma distribution with a lasso estimation method, to account for the large number of zeros in the dataset. Model selection was by Akaike Information Criterion (AIC) comparisons. Fish and invertebrate CPUE data were analyzed separately. To look at all pairwise comparisons, we used Tukey's HSD. Count data are typically non-normal, thus to analyze catch per unit effort (CPUE), total counts per habitat per 24-hr period, a generalized regression was used with a zero-inflated Poisson distribution (model effect, “Habitat”; response variable; “Abundance”).

Biodiversity of seagrass epifauna

To test for differences in the epifaunal community assemblage in restored versus reference plots, we harvested ramets from both habitats in September 2016. Collected ramets were later processed at San Francisco State’s Estuary & Ocean Science Center in Tiburon, CA. In the lab, all invertebrates were first removed from the shoots themselves using repeated freshwater dips and by hand-picking from the mesh bag the shoots were temporarily stored in. All epifauna were identified, sorted to the lowest taxonomic level possible (usually species) and counted. These data were visualized using non-metric multidimensional scaling (nMDS).

In August 2018, we harvested ramets to compare epifaunal biomass of the species *Phyllaplysia taylori,* a marine gastropod and the marine isopod, *Pentidotea resecata*. Both are known to be important in controlling epiphytic growth on seagrass (Hughes et al. 2013, Lewis and Boyer 2014). A single ramet from each restoration plot (n=71) and five representative ramets from each reference plot (strata A, B, and C; n=15) were harvested and later processed at University of California, Santa Cruz’s Coastal Science Campus Laboratory. Multiple ramets had zero grazers; this was accounted for in a generalized regression model using a zero-inflated Poisson distribution with a maximum likelihood estimation method. Post-hoc Tukey’s HSD Test (α=0.05) was used to determine differences in grazer counts between ramets from restored and reference plots. Because grazer biomass data did not meet the assumptions of any distributions available in the generalized approach, we used resampling with replacement (# of bootstrap samples = 1,000) to create distributions of means allowing comparison of habitats.

Supporting commercially important species

We conducted additional analyses on those macrofaunal species known to be caught as part of commercial fisheries (Hughes et al. 2014). Commercially important species included two crab species, *Cancer productus, M. magister* and fish species, *Sebastes* spp., and the general category of flatfish (order, Pleuronectiformes) which included, *Parophrys vetulus* and *Paralichthys californicus*. To determine if restored seagrass had similar abundances of juveniles of these species (i.e., had similar nursery habitat characteristics), we compared the CPUE of juvenile individuals and excluded any trapped individuals larger than the maximum juvenile size class as reported in the literature (Table 1). The dataset had many zeros, therefore the dataset was analyzed using a generalized regression with a zero-inflated gamma distribution and all pairwise comparisons were made using Tukey's HSD.

Dynamics of key water quality variables

To monitor certain water quality attributes (pH, Dissolved Oxygen (DO, mg/L) and water temperature (°C), three Yellow Springs Instruments (YAppendix S1: Figure S) data sondes were deployed in each habitat type within a single stratum at a time. We only had access to three sondes and therefore concentrated our sampling efforts on

2015 restored plots (to compare unvegetated and reference plots). The 2015 restored plots were chosen over 2016 plots because of their larger size. YAppendix S1: Figure Ssondes were secured to milk crates, positioned level and ~30 cm above the seafloor. Sondes were installed using "L"-shaped rebar, PVC, and an anchor to further secure the sonde its intended location. Deployment period ranged from 3-7 days with data collecting every 15 minutes. All sondes were calibrated using standard solutions at the Elkhorn Slough National Estuarine Research Reserve (ESNERR).

After deployment, each sonde went through a post-calibration process to ensure that the sonde readings did not drift from the initial calibration pre-deployment. The data was uploaded at ESNERR immediately following each deployment. Data were excluded from the analysis when the sonde was exposed at low tide and no longer submerged. Data was only used if a deployment was complete, meaning data was available for all three habitat types within strata (8 total complete deployments; 2 in stratum A, 3 in stratum B, and 3 in stratum C). Outliers were removed from the dataset if outside of the range of values recorded by more than two standard deviations, from a nearby long-term water quality monitoring station during the same period using the same instrumentation (ELKVMWQ station). Analyzed data included pH data within the range of 7.5-8.5, salinity greater than 25 PSU, and dissolved oxygen 2.58-12.82 mg/L equivalent to percent saturation of 30-155% (96% of data fell within these ranges).

In order to compare the distributions of each water quality parameter across habitats, we used the empirical cumulative distribution function to plot the data (Wickham 2016; R package ggplot2, stat_ecdf visualization tool). To compare the distributions we conducted a nonparametric test, the Kolmogorov-Smirnov test, to conduct a pairwise comparison of the cumulative frequency distribution of restored and unvegetated plots against the reference plot distribution. The Kolmogorov-Smirnov test (KS test) output includes a test statistic, D, the maximum difference between two cumulative distributions and a p-value indicating the probability that the two distributions are from different populations of values.

To further compare each water quality parameter across habitats and strata we used a mixed model approach and modeled the covariance structure using compound symmetry, which allows the variance to vary across time points. In the model the repeated random variable was "Time of Day" and the subject was an identifier that coded for the replicate that was repeated. The terms modeled using this approach were: Habitat + Strata + Time of Day + Habitat*Strata*Time of Day. Model term reduction/selection was by AIC assessment; reduced model outputs are reported in Table 3.

Low dissolved oxygen (DO, mg/L) and pH, as well as high water temperatures can be harmful in a non-continuous way, often presenting as a threshold (Zimmerman et al. 2015, Jeppesen et al. 2018). We examined the potential importance of this by determining the 10th percentile of observations relative to the harmful side of a particular threshold. This metric allows assessment of the value that divides the worst 10 % from the remaining 90% of observations for a particular variable, which can provide insight into the commonness of poor conditions.

Organic Carbon Stocks

To quantify and compare total organic matter (TOM) and organic carbon (OC) in the sediment of all three habitat types, approximately 20 cm of sediment was core sampled using open-barrel PVC pipes (30 cm length, 5.08 cm diameter) at representative locations for each habitat. Compaction was not common and when it did occur, it was limited (< 1.5 cm). Two to three sediment cores were collected from each habitat in late 2018 (reference, n=9; restoration, n=8; unvegetated, n=7), across strata A, B, and C. We focused our analyses on the top 10 cm of the 24 sediment cores (core depth—Maximum = 25 cm; Mean = 10.7 cm; Median = 10 cm). Once cores were extracted they were capped and taken to the laboratory where they were extruded into 2 cm sections (intervals), weighed for wet weight then dried at 60°C for 24 hrs. Bulk density (g/cm^3) of each interval was calculated as the ratio of dry weight to volume of the interval (i.e. 40.54 cm^3 for a 2 cm interval). Each interval was rinsed of salts, dried, and cone and quartered (Lewis and McConchie 1994) and a 10 g (± 0.1000 g) subsample was randomly selected for TOM analyses. TOM subsamples were acid-rinsed to remove inorganic carbonates. Inorganic carbonate-free sediments were subsampled again using cone and quartering methods (1.3 ± 0.1000g) and placed in crucibles to burn in the muffle furnace (550°C for 3 hrs) for loss-on-ignition, LOI (Davies 1974). The difference, converted to % loss, pre- and post-combustion is the % TOM. To convert % TOM to % organic carbon (OC), we used a power model ($y=0.22x^{1.1}$) derived using regional core data (Ward 2020). Carbon storage was calculated by multiplying % OC and the bulk density of each interval, reported as kg OC m^{-3}. We used an ANOVA to determine differences in organic carbon stocks across habitats. More details are provided in Appendix S1.

Multifunctionality index

In addition to examining the above functions separately, we examined them jointly to assess multifunctionality of the habitats, which is a way to assess the synthetic qualities of the examined habitats. We used one of the most commonly used methods for quantifying multifunctionality — the averaging approach (Byrnes et al. 2014). In addition we used an approach that converted all functions from raw values with an implicit floor of the possible range in values equal to zero to standardized values with a range equal to the range in values observed. Because the ranges in values often had extreme values we truncated the range to the 95th and 5th quantiles for each function, herein this range is referred to as a function scope. This approach accomplishes two goals. First, not using the scope of the data assumes values all the way to zero are possible, which is true for certain biological data but is impossible for physical factors (i.e. pH or DO). Using raw values biases the range of function values available for biological vs physical data. Truncating the range using percentiles accomplishes the goal of diminishing the effect of extreme values in an unbiased way (same percent of values are truncated for all functions). In order to calculate the scores for all functions where high values were considered better than low values all measurements were subtracted from the 5th quantile value and divided by the scope (the difference between 95th and 5th quantiles), yielding values ranging from ~1 (best) to ~0 (worst). For functions where low values were considered better than high (i.e. water temperature), the measured value was subtracted from the 95th percentile and divided by the function scope, yielding values ranging from ~ 1 (best) to ~0 (worst). Higher relative water temperature is considered to be a negative contribution to functional performance because, while the thermal tolerance for *Z. marina* is rather wide (10-25°C, Zimmerman et al. 2015), organisms that utilize the habitat may have greater sensitivity to high temperatures. For example, when exposed to water temperatures above 22°C, mortality rate of juvenile *M. magister* has been shown to increase (Sulkin et al. 1996) and a lab study found that increased temperatures (>12°C) produced the greatest deformities in *Ophiodon elongatus* hatchlings (Cook et al. 2005). Therefore, any buffering of higher relative water temperature by seagrasses is of interest because this could ameliorate conditions that would otherwise be classified as biologically stressful. Restoration plot data from the 2015 and 2016 projects were pooled into a single category "Restoration plot". To look for habitat differences in multifunctionality performance, we used re-sampling with replacement (# of bootstrap samples = 1,000). The bootstrap mean of one habitat was considered significantly different from another habitat if the mean fell outside of the 95% CI.

Results

Restoration survival and growth

Our August 2018 monitoring data showed that of 117 transplanted plots from both 2015 and 2016 restorations, 71 remained (~61%). Plot mortality, measured as the percentage of plots remaining where 1 or more shoots were present in the initial plot area, varied by restoration. The 2016 restoration had lower initial (1-3 months post-transplanting) plot mortality (32.4%, Figure 2A) than 2015 (52.9%, Figure 2A) and 2016 plots expanded much faster than 2015 plots (Figure 2B). Plot mortality remained relatively unchanged for both restorations following our September surveys in 2015 and 2016 (Figure 2A). In August 2018 we decided to visit all 2015 and 2016 restoration plots regardless of their previous status (present vs. absent) and found that seven of the 2015 plots, previously considered dead/absent had seagrass within the initial transplant area, indicating that the rhizomes remained intact and sprouted new vegetative tissue between December 2015 (when the plots were last monitored and marked as “absent”) and August 2018 (Figure 2A).

Our restored seagrass plots expanded rapidly and contributed to the seagrass expansion rate in this small estuary. A quarter hectare of new seagrass habitat resulted from the 2015 and 2016 restorations by year 2018. Initially, the combined area of our plots of newly transplanted seagrass totaled 12.75 m^2 (2015) and 16.5 m^2 (2016); by 2018 these had expanded to 1446 m^2 (Mean=39.1 m^2) and 1068 m^2 (Mean=19.1 m^2), respectively (Figure 2B). Between 2014 (14.04 hectares) and 2016 (14.13 hectares), seagrass habitat expanded 0.09 hectares (= 900 m^2) in the entire estuary. Of that new habitat, ~9% (0.008 hectares) can be attributed to our restoration. Between 2016 and

2018, seagrass expanded 1.49 hectares, reaching 15.62 hectares—our restored plots made up 17% or 0.251 hectares of seagrass habitat added during this 2-year period.

Within 2-3 years, in August 2018, structural attributes in restored plots were similar to reference plots which were higher in reference relative to restored plots, as further described below. Here we report the mean and standard deviation for the measured structural attributes as well as the median to further characterize the spread of the data. Shoot counts in reference plots were generally less variable than the restoration plots (Figure 2B) and mean shoot count in restored plots was not significantly different from reference plots (ANOVA; df=2,105, F=0.742, p=0.479). Mean shoot count was 30.3 (Median=36; Std Dev=22.1) and 34.9 (Median=40; Std Dev=22.8), and mean canopy height was 155 cm and 138 cm for 2015 and 2016 plots, respectively (Figure 2C, Appendix S1: Figure S4A). Mean shoot count in reference plots was 37.2 (Median=38; Std Dev=8.41) and mean canopy height 125 cm. There was a significant effect of habitat type (reference vs. restored) on flowering shoot counts (df=2,2, χ^2=14.72, p=0.0006). Flowering shoot counts in reference plots were significantly higher than 2015 (Tukey HSD; t=3.81, p=0.0007) and 2016 restored plots (Tukey HSD; t=2.38, p=0.049), with no significant differences detected between restored plots (Appendix S1: Figure S4B). Mean flowering shoot count was 1.81 (Median=1; Std Dev=2.21) and 2.93 (Median=3; Std Dev=2.85) for 2015 and 2016 plots, respectively. Mean flowering shoot count in reference plots was 5.0 (Median=4; Std Dev=3.95). There was no significant difference in mean biomass of shoots (Appendix S1: Figure S5A; ANOVA, df=2,85, F=0.186, p=0.831), rhizomes (df=2,4, F=0.529, p=0.591) or epiphytes (df=2,4, F=0.751, p=0.0.475) when comparing ramets harvested from reference and 2015 or 2016 restoration plots. There was a significant effect of strata on both rhizome (df=2,4, F=2.989, p=0.023) and epiphyte (d=2,4, F=4.65, p<0.0001) biomass, with a general increase in biomass moving from strata A to E (Appendix S1: Figure S5B).

Biodiversity of macrofauna

Macrofaunal communities of the restored plots changed over time. The cluster diagram revealed that by Summer 2017, restored plots (2015 and 2016) clustered with reference plots, whereas the year prior the restored plots clustered with unvegetated plots (Figure 3A). Similar community overlap was observed for seagrass epifauna, described below (Figure 3B). Species richness, quantified by a species accumulation curve (Appendix S1: Figure S6) shows that at 80 observations (minimum number of observations for 2015 restoration plots), restoration plots are more species rich than reference or unvegetated plots, with unvegetated plots being the least species rich. Species accumulation curves showed close overlap for fish between vegetated habitats (restored 2015 & 2016 and reference plots) and greatest differences between vegetated and unvegetated plots (Figure 4A). In contrast, invertebrate species accumulation curves showed similarity among all habitats (Figure 4B). These two results suggest that the overall difference between vegetated and unvegetated habitats is driven by fish.

Fish species density (number of species per sample) was not significantly different between reference and 2015 (t=2.19, p=0.1268) or 2016 restored plots (t=2.10, p=0.1543). However, fish species density (Figure 4C) was significantly lower in unvegetated plots vs. restored (2015 Restoration; t=4.39, p<0.0001, 2016 Restoration; t=4.55, p<0.0001) and reference plots (t=3.24, p=0.0068). Invertebrate species density was not significantly different between reference and restored plots (2015 and 2016), nor was there a significant difference between unvegetated and restored plots (2015 and 2016). Invertebrate species density (Figure 4D) was significantly lower in unvegetated plots than reference plots (t=2.99, p=0.0154). Fish CPUE was not significantly different when comparing restored and unvegetated plots or restored and reference plots, but there was a significant difference in CPUE between unvegetated and reference plots (Figure 4E, t=2.7544, p=0.0306). Invertebrate CPUE did not vary as a function of habitat (Figure 4F). A photo catalogue of the diversity of species trapped over the course of our study are presented in the Supplement (Appendix S1: Figure S7).

Biodiversity of seagrass epifauna

The nMDS plot showed overlap in the community assemblage of seagrass epifauna between ramets from restored and reference plots. Additionally, there was greater variation in community composition in restored plots relative to reference plots in 2016 (Figure 3B). In 2018, we examined a subset of species (*P. resecata* and *P. taylori*) known to be important grazers in temperate seagrass systems. For both species using a generalized regression with a zero-inflated Poisson distribution, we detected a significant effect of habitat on grazer counts (*P. resecata*; χ^2=14.69, p=0.0006; *P. taylori*; χ^2=17.13, p=0.0002). We found that restored plots (2015 Restoration, t=3.86, p=0.0008; 2016 Restoration, t=3.68, p=0.0013) had significantly more *P. resecata* (per ramet) than reference plots (Appendix S1: Figure S8A) and no significant difference in the number of *P. resecata* between restored plots. We also found that restored plots (2015 restoration, t=3.94, p=0.0006; 2016 restoration, t=2.46, p=0.043) had significantly more *P. taylori* than reference plots (Appendix S1: Figure S8A) and there were significantly more *P. taylori* in 2015 restoration plots than 2016 restoration plots (t=2.67, p=0.026). Biomass of *P. resecata* did not vary among restored plots, but the resampled means for *P. resecata* biomass in restored plots fell outside of and was greater than the 95% CI of the mean in reference plots (2015 restoration, resampled mean=0.0267, confidence interval for distribution of resampled mean=(0.0132, 0.0404)); 2016 restoration, resampled mean=0.0280, confidence interval for distribution of resampled mean=(0.0182, 0.0394)); reference, resampled mean=0.0048, confidence interval for distribution of resampled mean=(0.00045, 0.0105)); Appendix S1: Figure S8B). Biomass of *P. taylori* did not vary by habitat (Appendix S1: Figure S8B).

Supporting commercially important species

Generally, more individuals were trapped in reference plots compared to restored plots and in restored plots compared to unvegetated plots (Table 1). Few differences were observed between restored (2015 vs. 2016) plots (Table 1). There are notable exceptions to this—for example, 2016 restored plots and unvegetated plots trapped ~

3x as many *M. magister* as reference and 2015 restored plots and 2016 restored plots trapped ~2x as many *Sebastes* spp. as reference and 2015 restored plots, with the fewest number trapped in unvegetated plots (n=2; Table 1). Overall, the majority (79-100%) of individuals trapped across species, were considered juveniles and the total number of juveniles and adults trapped by habitat are reported in Table 1.

Considering the combined CPUE of all trapped species of commercial value (*M. magister, C. productus,* Sebastes sp., *R. antennarium, C. gracilis,* and Pleuronectiformes), we did not detect a difference among habitats (Figure 5A). Nursery function of commercially valuable species varied slightly by habitat, with differing patterns across species. Juvenile red rock crab (*C. productus*) CPUE was not significantly different when comparing restored and reference plots (Figure 5B). Juvenile red rock crab CPUE was not significantly different when comparing restored (2015 and 2016) and unvegetated plots, but CPUE was significantly greater in reference plots relative to unvegetated plots (t=3.28, p=0.006; Figure 5B). Juvenile Dungeness crab (*M. magister)* CPUE was highest in unvegetated plots but did not vary significantly as a function of habitat (Figure 5C). Juvenile rockfish (*Sebastes* sp) CPUE varied by habitat type (Figure 5D). The 2016 restored plots had significantly higher rockfish CPUE than reference (t=3.31, p=0.0053) and unvegetated plots (t=3.87, p=0.0007) and no significant difference from 2015 restored plots. There was no significant difference in juvenile rockfish CPUE among 2015 restored, reference, or unvegetated plots and juvenile flatfish were trapped in low numbers across habitats (Table 1).

Dynamics of key water quality variables

Generally, DO and pH were higher and water temperature lower in restored and reference plots compared to unvegetated plots. The water quality conditions observed in restored and reference plots were more similar than restored and unvegetated plots—this pattern was not captured in the mixed model where means were compared but was clearly shown by plotting the cumulative distribution function curves and verified using Kolmogorov-Smirnov tests (Table 2). Cumulative distribution function (CDF) curves for seagrass (restored and reference) show overlap and partial overlap, whereas there is clear separation in the CDF curves of seagrass versus unvegetated plots (Figure 6). The CDF curves show that DO (Figure 6A) is generally higher in seagrass than in unvegetated plots, pH (Figure 6B) is generally higher (less acidic) in seagrass than in unvegetated plots and water temperature (Figure 6C) is generally lower in seagrass than unvegetated plots. The Kolmogorov–Smirnov test showed that, for each of the parameters (temperature, DO, pH), test statistic D was greatest when comparing seagrass (restored and reference) to unvegetated plots and smallest when comparing restored and reference plots (Table 2).

Overall, the mixed model results showed that there was a significant effect of habitat type and/or strata and time of day for each of the water quality parameters analyzed (Table 3). Here we report the results from the mixed model followed by the ANOVA on 10th (DO, pH) or 90th (water temperature) percentiles (Appendix S1: Figure S9, S10).

For water temperature, there was a significant effect of strata and time of day, as well as a significant interaction between Time of Day and Strata (Strata, df=2,21.2, f=6.44, p=0.006; Time of Day, df=23,166.7, f=8.35, p<0.0001; Time of Day * Strata, df=46,215.4, f=5.912, p<0.0001). Water temperature was lower in reference plots than restored and unvegetated plots (Appendix S1: Figure 9A) and increased with distance from the estuary mouth (i.e. upstream). However, the 90th percentile of temperature (Appendix S1: Figure S10) did not differ across habitat types (ANOVA, df=2,21, F=0.163, p=0.851).

For DO there was a significant effect of habitat type, strata, and time of day, as well as a habitat by strata interaction (Habitat, df=2,29.1, f=5.37, p=0.01; Strata, df=2,29, f=9.097, p=0.0009; Time of Day, df=23,148.4, f=36.037, p<0.0001; Habitat*Strata, df=4,29.1, f=7.724, p=0.0002). Reference plots had significantly higher DO than restored and unvegetated plots and restored and unvegetated plots were not statistically different from one another (Appendix S1: Figure S9B, Tukey's HSD; reference & restored; t=2.68, p=0.031, reference & unvegetated; t=2.99, p=0.015, restored & unvegetated; t=0.31, p=0.948). However, there was no significant difference in the 10th percentile of DO (Appendix S1: Figure S10) across habitat types (ANOVA, df=2,21, F=0.122, p=0.886).

For pH there was a significant effect of habitat and time of day (Habitat, df=2, 38.1, f=5.074, p=0.011; Time of Day, df=23,177.1, f=15.855, p<0.0001). There was no significant difference in pH between reference and restored plots. Reference plots had significantly higher pH than unvegetated plots, but no significant differences were detected between unvegetated and restored plots (Appendix S1: Figure S9C, Tukey's HSD; reference & unvegetated; t=3.09, p=0.013, restored and reference plots; t=1.14, p=0.501, restored and unvegetated; t=2.02, p=0.128). There was no significant difference in the 10th percentile of pH (ANOVA, df=2,21, F=1.191, p=0.324) across habitat types (Appendix S1: Figure S10).

Organic Carbon Stocks

Organic carbon stock did not vary as a function of habitat (Figure 6D). Although there was no significant difference in OC across habitats, we detected significant differences in OC across strata (ANOVA; Habitat, df=2,2, f=0.416, p=0.661; Strata, df=2,2, f=1658.65, p<0.0001) with increases in OC with increased distance from the mouth (i.e. stratum A had the lowest OC values and stratum C the highest; see Appendix S1: Figure S11).

Multifunctionality Index

Multifunctionality was significantly higher in reference plots (resampled mean=0.498, confidence interval for distribution of resampled mean=(0.487,0.509)) relative to restored plots (resampled mean=0.449, confidence interval for distribution of resampled mean=(0.439, 0.459)) and in restored plots relative to unvegetated plots (resampled mean=0.389, confidence interval for distribution of resampled mean=(0.381, 0.398)) (Figure 7A; Appendix S1: Figure S12). The breakdown of which functions contributed substantially versus minimally to the significant overall differences in functional performance is shown in Figure 7B, with higher values indicating higher functional value. For example, the functional contribution of species abundance was far greater in reference plots relative to restored or unvegetated plots, whereas the functional contribution of pH was greatest in restored and reference plots and lowest in unvegetated plots, and no habitat differences were found in organic carbon storage (Appendix S1: Figure S12). The 95th and 5th quantiles used to standardize the data were as follows: 10.21 and 5.9 mg/L for dissolved oxygen, 8.18 and 7.78 for pH, 17.89 and 12.08°C for water temperature, and 19.34 and 4.85 kg/m^3 for OC.

Discussion

Successful seagrass restoration

Ecological restoration has been defined as "the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed" (SER 2004). A strategic approach to recovery is the ecological restoration of foundation species, which play a critical role in structuring communities and regulating key ecosystem processes (Ellison 2019). Seagrasses are a group of foundation species in accelerated decline (Waycott et al. 2009), and this has triggered an increase in restoration efforts globally (Short et al. 2011, van Katwijk et al. 2016). Seagrass restoration has proven challenging with a global success rate of ~37%, with success measured as an index that accounts for initial restoration survival and the longer-term, ≥ 23 months, trajectory (i.e. absent, decreasing, no change, increasing) of the restoration (van

Katwijk et al. 2016). Our small-scale restoration project had a success rate, calculated as the percentage of plots remaining 30-40 months post-transplanting, of 61%, far exceeding the global average for both small (22%) and large (42%) scale seagrass restorations (van Katwijk et al. 2016) and we observed rapid expansion of our restored plots in total area (~8500 %). Overall transplant survivorship and spread was remarkably high in our study, indicating that our restoration efforts were successful and on par with the well-documented outcomes of larger scale restorations (Evans and Short 2005, Leschen et al. 2010, McGlathery et al. 2012).

Our success in Elkhorn Slough is likely due to many factors related to the site itself and our restoration design. Despite high nitrate concentrations and the proliferation of macroalgal blooms (Wasson et al. 2017), the natural recovery of seagrass in Elkhorn Slough over the past thirty years (Appendix S1: Figure S1) is evidence of an overall improvement of environmental conditions conducive to seagrass growth and expansion. Elkhorn Slough is also the only estuary along the California coast with a large (100+) population of resident sea otters, *Enhydra lutris* (Tinker and Hatfield 2017). Sea otters have been shown to have strong top-down effects on the health of seagrass beds in Elkhorn Slough (Hughes et al. 2013). The return of this keystone predator to the system has been linked to natural seagrass recovery and may have contributed indirectly to our positive restoration outcomes by improving seagrass health and promoting natural expansion throughout the system. Additionally, seagrass restoration outcomes have been shown to improve when the distance between restored and natural seagrass habitats is <1 km and when donor beds are intact (van

Katwijk et al. 2016). Our transplanted sites were within 250 m of natural existing seagrass habitat (natural patch or large bed) and the donor bed from which we harvested is considered the most robust bed in the entire estuary. We also transplanted within a narrow depth range of 0 to -2 m MLLW. Within this tidal range, restoration plots were exposed infrequently at low tides and had sufficient light availability at high tide, nearly eliminating plot mortality linked to desiccation stress or high light attenuation. Lastly, our transplanting method of anchoring ramets (shoots with intact rhizomes) to the substrate has been shown to have higher rates of success than other transplanting methods (Park and Lee 2007, Bell et al. 2008, van Katwijk et al. 2016, Eriander et al. 2016). All of these factors associated with site suitability and restoration design likely contributed greatly to our restoration success. By contrast, attempts to restore seagrass in other degraded systems in the region have had minimal success. For example, in Morro Bay, CA 95% of eelgrass has been lost and efforts to restore have had variable success; this may be linked to the degraded state of natural meadows (Harenčár et al.2018), massive system-wide erosion and sediment re-suspension shifting tidal elevations throughout the estuary (Walter et al. 2020), or restoration design.

Our small-scale restoration provides lessons learned for future restorations elsewhere. While it is appealing to attempt restorations in systems where seagrass has entirely disappeared, the likelihood of success may be low if the same factors that led to the decline still apply. Prioritizing restoration in areas that are recovering or appear stable is better insurance towards a return to baseline conditions that resemble the historical landscape, as opposed to the traditional restoration approach of prioritizing degraded sites which may require repeated intervention (Rohr et al. 2018, Volis 2019). We concur with the findings of others that emphasize the need to address adverse conditions first or fully assess site suitability prior to transplanting or seeding (Fonseca et al. 1982, Bell et al. 2008, Thom et al. 2012; 2018).

Restoring multiple functions of foundation species

Foundation species provide ecosystem structure (Dayton 1972) and structure begets ecosystem function (Dobson et al. 1997, Bruno et al. 2003). For example, successful large scale seeding efforts in Chesapeake Bay led to the restoration of seagrass habitat and associated functions and services (i.e. decreasing turbidity levels, increasing carbon stocks, habitat provisioning) (Orth et al. 2020). Therefore, ecological restoration of declining foundation species, such as seagrasses (Short et al. 2011), not only supports recovery of the vegetation itself, but has the added benefit of enhancing biodiversity and ecosystem functions (Evans and Short 2005, Benayas et al. 2009, Angelini et al. 2015). The primary focus of seagrass restoration monitoring has been the foundation species itself (structural attributes) and to determine how site characteristics (van Katwijk et al. 2009, Thom et al. 2018) and methodology (transplantation or seeding techniques) (Park and Lee 2007, Bell et al. 2008, Eriander et al. 2016) affect survival. In select restoration studies, structural attributes and a few additional associated ecosystem functions (canopy friction and sediment movement; Fonseca and Fisher 1986, faunal communities; Leschen et al. 2010, carbon and nitrogen sequestration; McGlathery et al. 2012, Greiner et al. 2013, Reynolds et al.

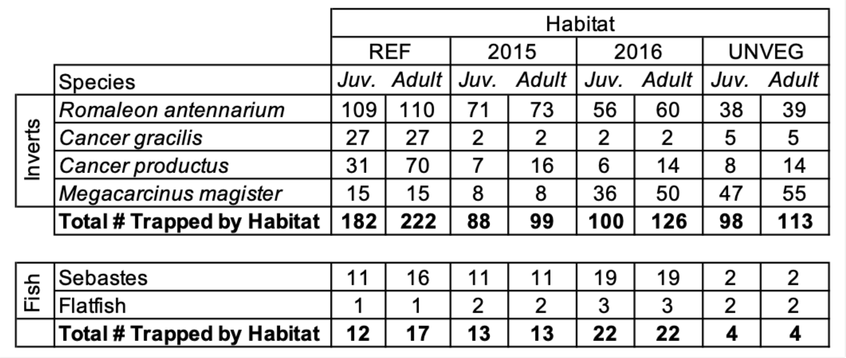
2016) have been assessed. Yet, few studies have simultaneously tracked multiple structural and functional attributes of biological and biogeochemical importance. Our study is the first comprehensive investigation of eelgrass restoration on the eastern Pacific Coast to track structural attributes and a suite of biological and biogeochemical ecosystem functions and to combine all functions into a multifunctionality index to compare overall performance in restored seagrass to nearby reference and unvegetated plots. We used the multifunctionality index to assess the overall functional performance of measured functions for each habitat. Our data visualization (Figure 7B) showed which functions drove differences (i.e. species diversity) versus which were more nuanced or subtle (i.e. DO, mg/L). In so doing, we gained a comprehensive understanding of how restoration can enhance ecosystem multifunctionality. This approach of fully characterizing the success of our ecological restoration was powerful and assuming sufficient funding is available, could be broadly applied to restorations of other foundation species. To infer functional recovery in other systems, we recommend similar focal studies be conducted to validate that certain functions are enhanced with restorations elsewhere.

As restoration plots expanded they quickly resembled reference plots (i.e. shoot densities, canopy height) and this likely contributed to the rapid colonization and higher relative species richness of critical mesograzers in 2016 (Healey and Hovel 2004, Hughes et al. 2013, Lefcheck et al. 2017). Interestingly, by 2018, mesograzers *P. resecata* and *P. taylori* were more abundant in restored plots and *P. resecata* biomass was greater in restored versus reference plots. This could be due to relatively fewer known predators (i.e. Cancridae crabs) of mesograzers found in restored plots compared to reference plots. Additionally, within 2-3 years, macrofaunal community composition and certain biological functions of restored plots recovered to levels at or nearing those observed in reference plots. We expected the nursery function to be greatest for reference plots and instead observed no overall difference in nursery function across habitats, suggesting that restoration did not enhance or degrade this function. The few habitat differences in nursery function that emerged may be due to a known preference for structured habitat (i.e. red rock crab), refugia, or edge effects of restored plots (i.e. rockfish). By plotting both species density and species accumulation curves, we were able to assess the expected number of species per plot type and the number of species supported per habitat, respectively. Discrepancies between species density and species accumulation curves can be due to differences in overall abundances or evenness. While restored and reference plots supported the highest fish species richness, fish CPUE in restored plots was in the middle—a similar pattern was observed for invertebrate species richness, indicating that fish CPUE and invertebrate richness in restored plots is moving towards levels observed in reference plots. This is further supported by the cluster diagram (Figure 3A), as years progressed and restored plots expanded, the similarity in macrofaunal community composition of restored plots shifted from unvegetated to reference plots. In summary, certain biological functions in restored plots are currently performing at or near levels observed in reference plots while others are higher than unvegetated plots and lower than reference plots. We expect such functions to edge towards reference plots over time as restored plots continue to expand. We would need to monitor for a longer period of time to provide further support that our results 2-3 years post restoration track the long-term trajectory of functional recovery.

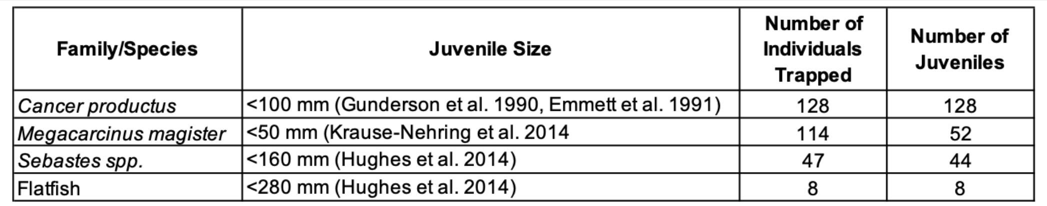
While biological functions were fast to emerge, biogeochemical functions either did not vary across habitats (i.e. organic carbon stocks, OC) or were more subtle and nuanced (i.e. DO, pH, water temperature) requiring multiple analytical approaches in order to truly characterize and compare habitats. Specifically, the CDF curves were more informative than the mixed model approach and percentile comparison, both of which failed to capture the habitat differences visible in the CDF curves. The K-S test further supports that the CDF curves of restored and reference plots were statistically more similar to one another than either were to unvegetated plots. Generally, water temperature was lower and pH and DO higher in restored and reference plots compared to unvegetated plots. Lastly, we expected restored and reference plots to have greater OC than unvegetated plots, and instead observed no detectable differences among habitats but a near doubling of OC with increased distance from mouth. This is likely due to a change in grain size moving upstream, from predominantly sandy to silty (Ward 2020).

The rapidity with which functioning was enhanced in Elkhorn Slough illustrates the potential for successful ecological restoration of a foundation species. Fast-growing foundation species such as seagrasses are able to restore ecosystem function faster than foundation species that take years to reach maturity, or than species for which old tissue plays a large role in engineering effects (Montero-Serra et al. 2018). For example, in semideciduous tropical forests, restored habitats can take up to 70 years to reach old growth forest levels of species richness (Suganuma and Durigan 2015). Similarly, in coral reef systems, coral transplants assist in the recovery of rugose structures and yet functional recovery is slow to follow due to slow growth of such reef-building coral species (Ladd et al. 2019). In addition to contrasts among species with different life histories, there are contrasts among functions—some, such as providing structured habitat for animals, may be achieved more rapidly than others, such as carbon storage. As more restoration projects include monitoring of multiple ecosystem functions as we have done here, conservation planners can form realistic expectations of the rate of recovery of different important ecosystem services across

Table 1. Total number of individuals broken down by both fish and invertebrate species trapped across habitat type. Bottom table indicates how many juvenile individuals were trapped in total by species or lowest taxonomic level.



		Habitat							
		REF		2015		2016		UNVEG	
	Species	*Juv.*	*Adult*	*Juv.*	*Adult*	*Juv.*	*Adult*	*Juv.*	*Adult*
Inverts	*Romaleon antennarium*	109	110	71	73	56	60	38	39
	Cancer gracilis	27	27	2	2	2	2	5	5
	Cancer productus	31	70	7	16	6	14	8	14
	Megacarcinus magister	15	15	8	8	36	50	47	55
	Total # Trapped by Habitat	**182**	**222**	**88**	**99**	**100**	**126**	**98**	**113**
Fish	Sebastes	11	16	11	11	19	19	2	2
	Flatfish	1	1	2	2	3	3	2	2
	Total # Trapped by Habitat	**12**	**17**	**13**	**13**	**22**	**22**	**4**	**4**

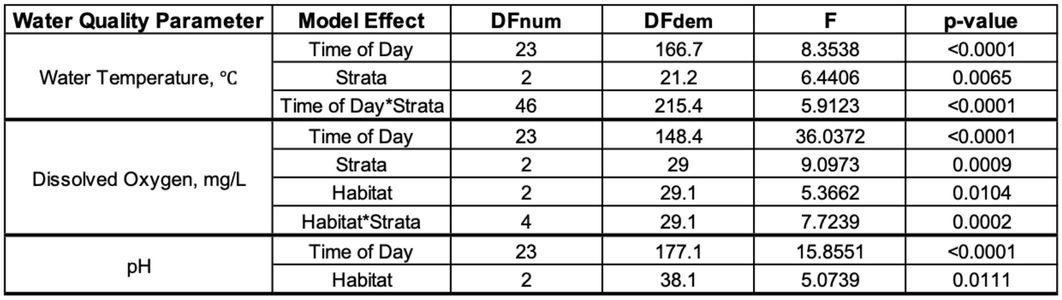


Family/Species	**Juvenile Size**	**Number of Individuals Trapped**	**Number of Juveniles**
Cancer productus	<100 mm (Gunderson et al. 1990, Emmett et al. 1991)	128	128
Megacarcinus magister	<50 mm (Krause-Nehring et al. 2014	114	52
Sebastes spp.	<160 mm (Hughes et al. 2014)	47	44
Flatfish	<280 mm (Hughes et al. 2014)	8	8

Table 2. Two-sample Kolmogorov-Sminrov test outputs comparing temperature, dissolved oxygen and pH between two habitats, reporting the test statistic, *D* and p-value for each habitat combination. Test statistic, *D*, is conditionally formatted with darker colors indicating greater values. 'REF' refers to reference plots (green), 'UNVEG' to unvegetated plots (brown), and 'RESTORE' to restoration plots (red).

		Temperature		**Dissolved Oxygen**		**pH**	
		D	p-value	D	p-value	D	p-value
🟩🟫	REF x UNVEG	0.14363	7.25E-13	0.15166	2.69E-14	0.35117	< 2.2e-16
🟩🟥	REF x RESTORE	0.073314	0.001888	0.070334	0.003288	0.10374	1.76E-06
🟥🟫	RESTORE x UNVEG	0.13417	3.56E-12	0.13494	2.60E-12	0.25698	< 2.2e-16

Table 3. Mixed model output for each water quality parameter. P-values from the reduced mixed model are reported in the column farthest to the right.



Water Quality Parameter	Model Effect	DFnum	DFdem	F	p-value
Water Temperature, ℃	Time of Day	23	166.7	8.3538	<0.0001
	Strata	2	21.2	6.4406	0.0065
	Time of Day*Strata	46	215.4	5.9123	<0.0001
Dissolved Oxygen, mg/L	Time of Day	23	148.4	36.0372	<0.0001
	Strata	2	29	9.0973	0.0009
	Habitat	2	29.1	5.3662	0.0104
	Habitat*Strata	4	29.1	7.7239	0.0002
pH	Time of Day	23	177.1	15.8551	<0.0001
	Habitat	2	38.1	5.0739	0.0111

Figure 1. Restoration Map. All sites were chosen randomly given a suite of parameters that needed to be met. All sites had to fall within a tidal elevation range that was pre-determined as potential seagrass habitat (-2 to 0 m MLLW). All plots had to be greater than 25 m from naturally occurring seagrass beds or patches. Yellow dots indicate the 2015 restoration plot locations; 2016 plots were approximately 7 m away from 2015 plots (not indicated on the map). The donor bed used to harvest shoots for both restorations was within Strata C (indicated with a red star).

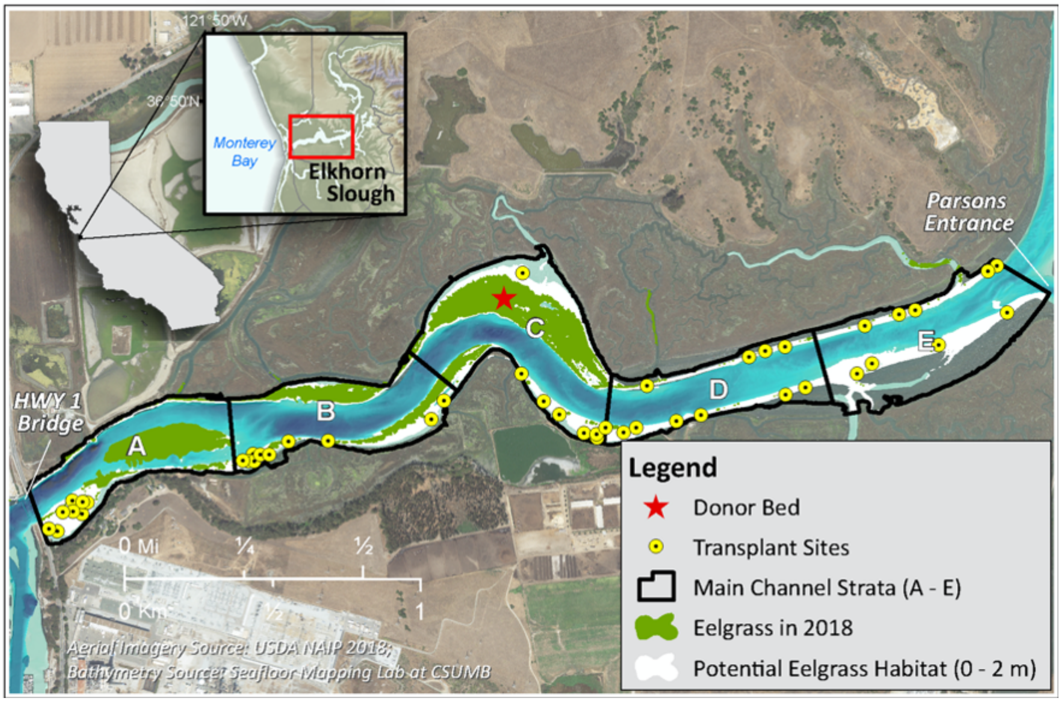


Figure 2. A) Percentage of surviving restoration plots, B) mean restoration plot area (m^2) ± SEM and C) mean shoot counts ($0.25m^2$) ± SEM in restored (2015 and 2016) and reference plots over time. 2015 restoration plots, "2015", in red, 2016 restoration plots, "2016", in blue and reference plots, "REF", in green.

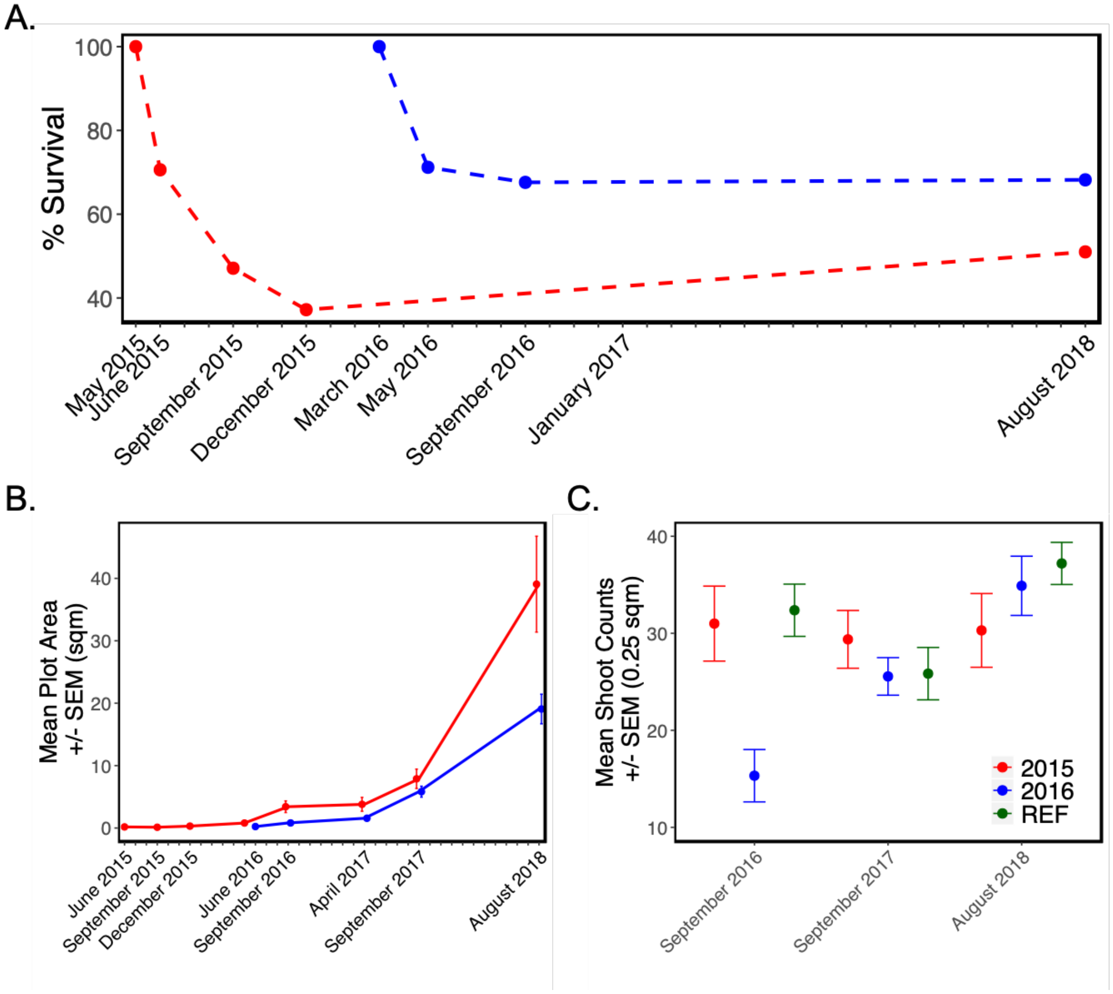


Figure 3. A) Cluster diagram (Bray-Curtis similarity matrix) for all counts of fish and invertebrate species caught in trapping years 2016 (circles) and 2017 (triangles). Communities from 2015 restoration plots are in red, 2016 restoration plots in blue, unvegetated plots in brown and reference plots in green. B) nMDS plot of seagrass epifauna community assemblage in restored and reference plots in the year 2016. Reference plots are plotted as green circles and restored plots as red triangles.

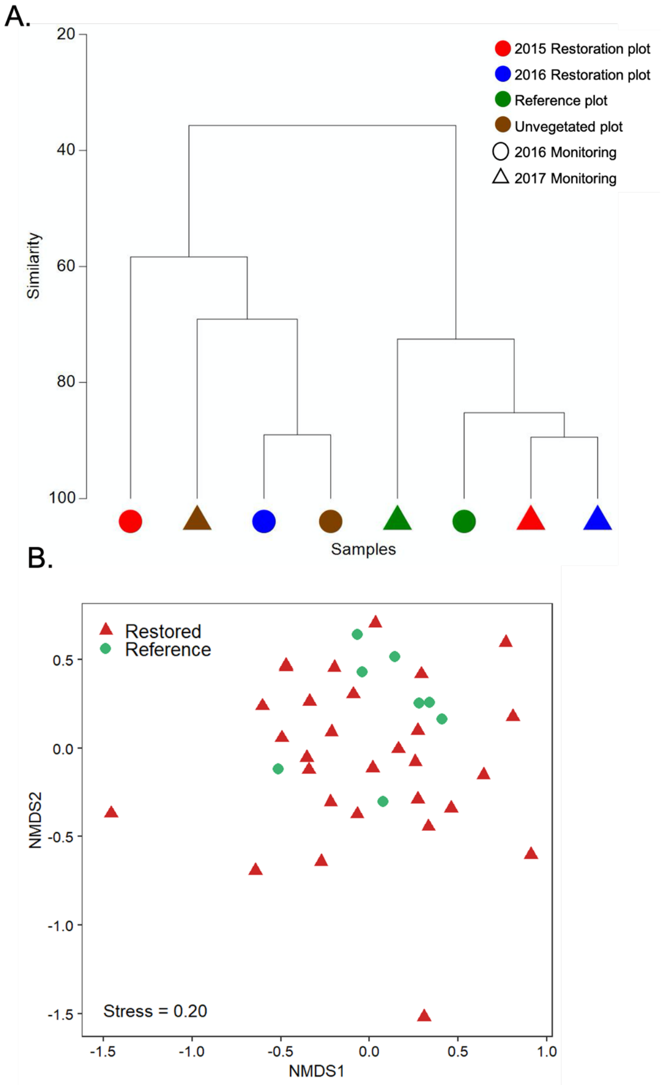


Figure 4. Macrofaunal Diversity Function *Top Panel,* Species accumulation curves for A) fishes and B) invertebrates. *Bottom Panel,* C) Fish and D) invertebrate species density, quantified as the number of species trapped across 61 trapping days, plotted as the Least Square Means Estimate ± SEM. E) Fish and F) Invertebrate CPUE, or the mean number of individuals trapped (all species) across 61 trapping days, plotted as the Least Square Means Estimate ± SEM. Different letters denote significant differences between habitats according to Tukey's HSD post-hoc tests. 2015 restoration plots are in red, 2016 restoration plots in blue, unvegetated plots in brown and reference plots in green (a-b).

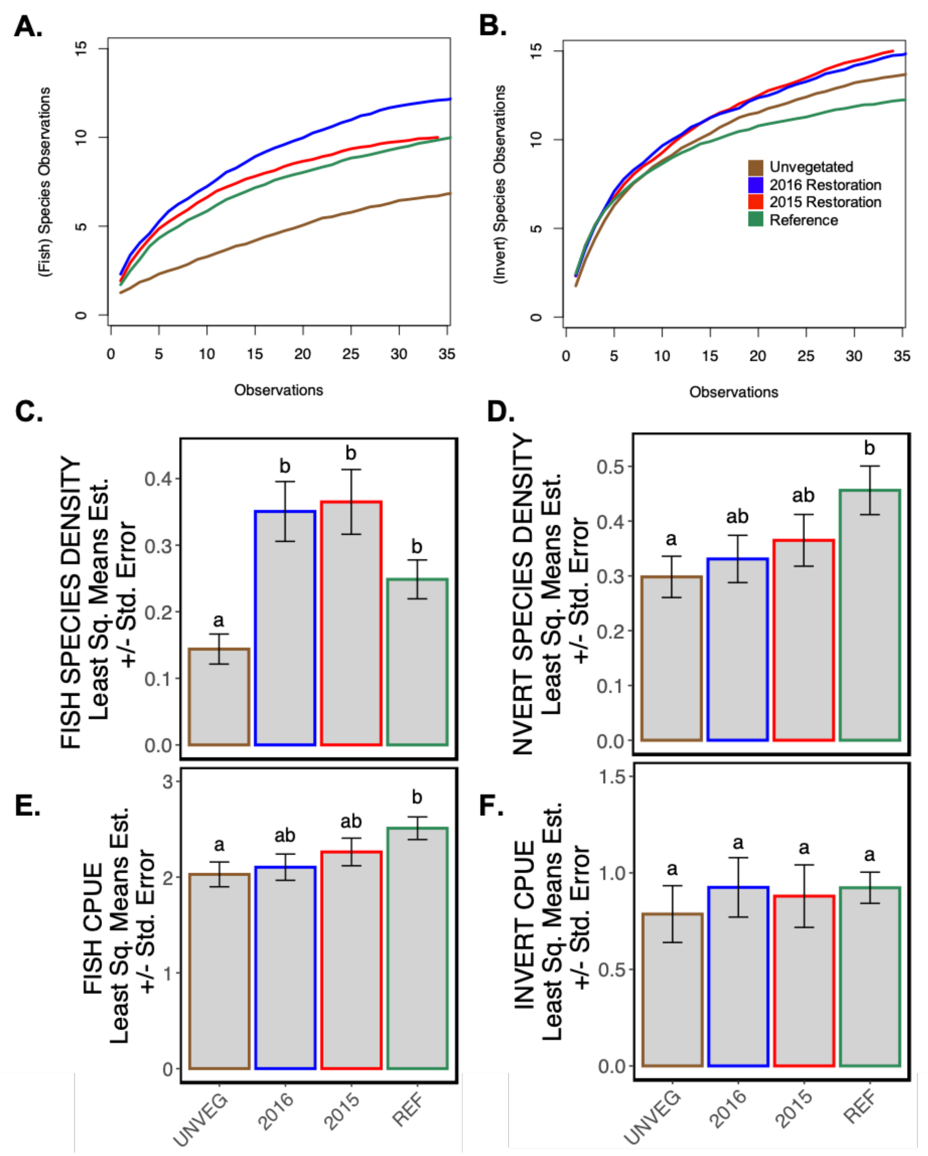


Figure 5. Nursery Function A) Nursery CPUE by habitat type (from left to right: 'UNVEG', '2015', '2016', and 'REF'), quantified as the combined CPUE of all species of commercial interest (*M. magister, C. productus,* Sebastes sp., *R. antennarium, C. gracilis,* and Pleuronectiformes). Species specific CPUE by habitat type is also presented for B) Red rock crabs (*C. productus*), C) Dungeness crabs (*M. magister*) and D) Rockfish (Sebastes sp). Plotted data is the CPUE Least Square Means Estimate ± SEM. Different letters denote significant differences between habitats according to Tukey's HSD post-hoc tests.

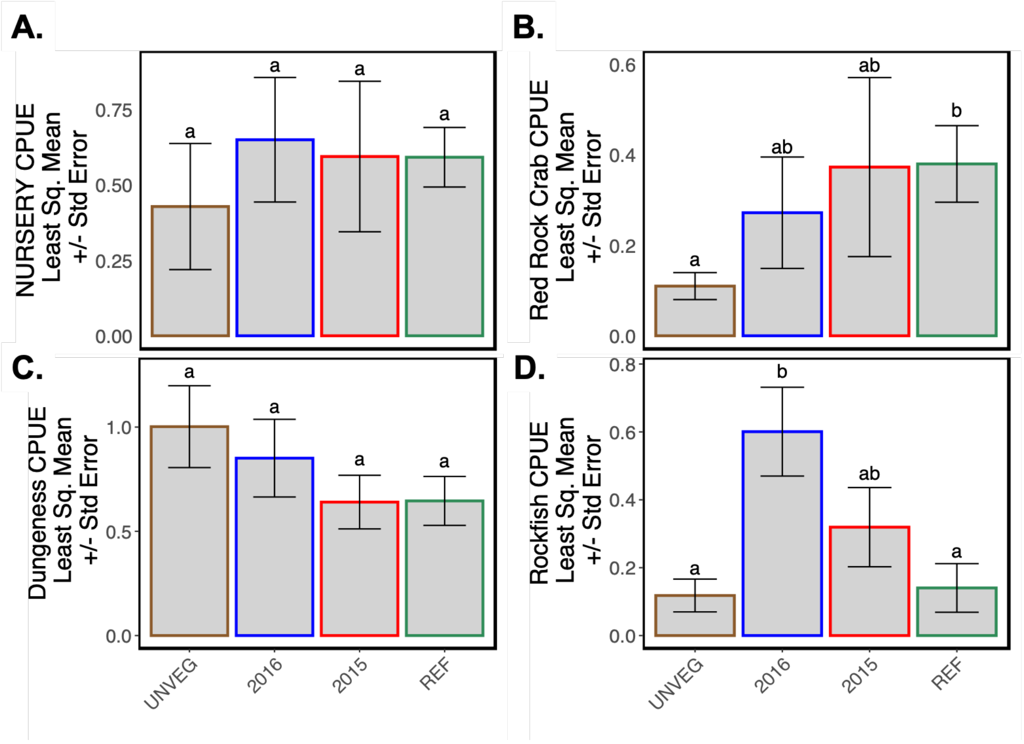


Figure 6. Biogeochemistry Functions Empirical cumulative distribution function curves for A) dissolved oxygen (mg/L), B) pH and C) temperature (degrees Celsius). D) Organic carbon, OC (kg/m^3) in unvegetated and seagrass (restored and reference) plots, plotted data is OC Least Square Means Estimate ± SEM.

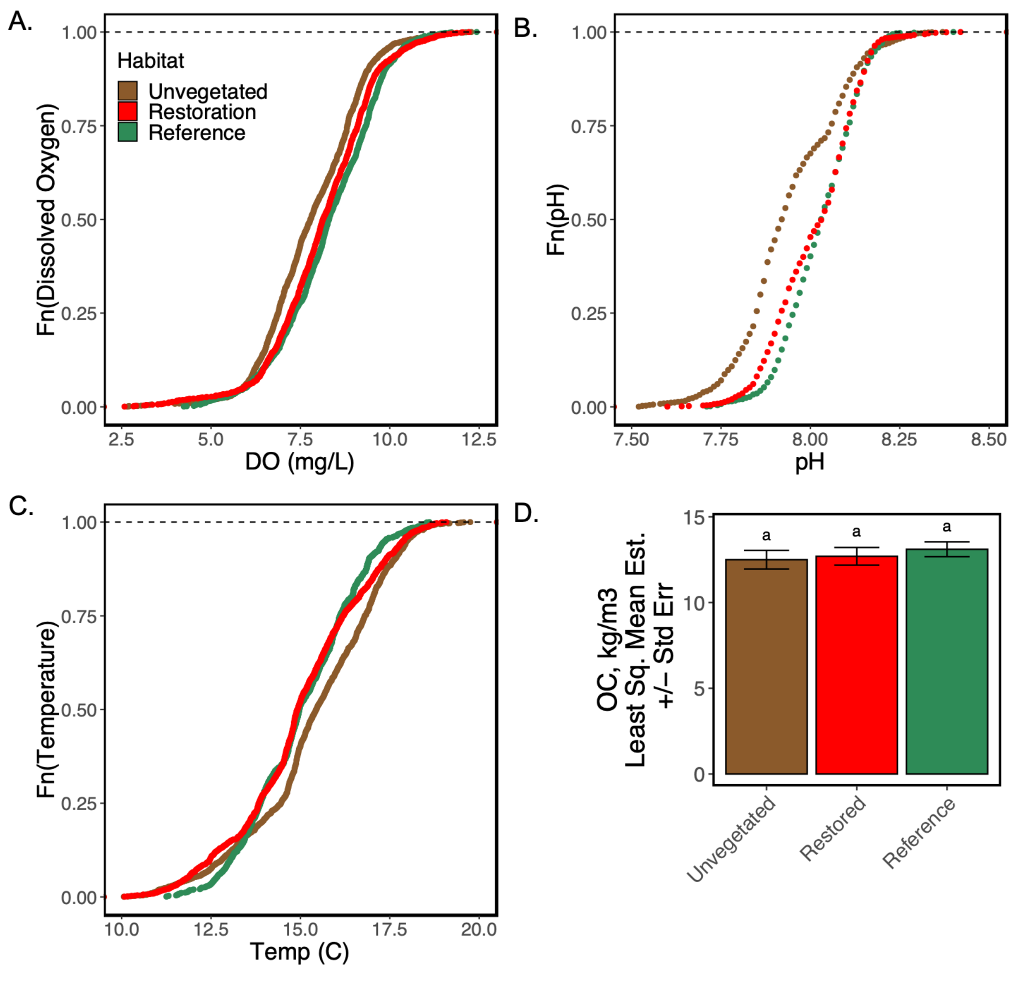
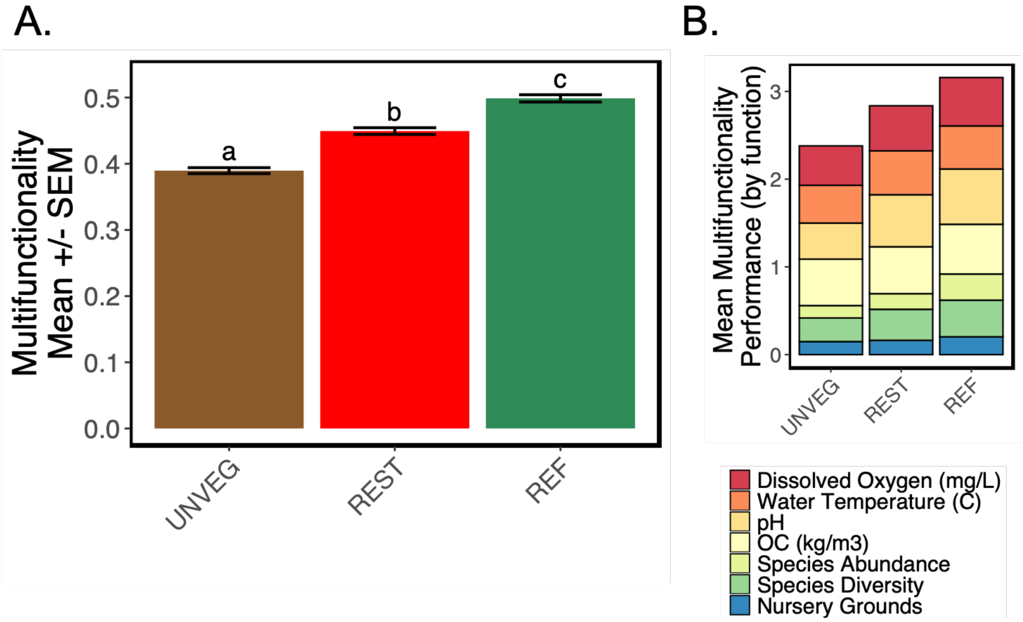


Figure 7. Multifunctionality A) Overall habitat performance plotted as the bootstrap means for each habitat (± SEM). Different letters denote significant differences between. Plotted data is the bootstrap means ± standard deviation (of the resampling distribution), which, according to the Central Limit Theorem, is approximately equal to the standard error of the raw data. **B)** Stacked bar graph of mean multifunctionality to further describe differences in performance across habitats, color-coded by ecosystem function to demonstrate the relative functional contribution of each of the seven functions in driving habitat differences.



Conclusion

My work has focused on the dynamics of coastal foundation species. I have uncovered some of the key physical and biological drivers of marsh resilience, and characterized functions such as productivity and sediment accretion and stabilization by the salt marsh dominant in Elkhorn Slough, *Salicornia pacifica*. I have also successfully restored seagrass (*Zostera marina*) and detected rapid recovery of key ecological processes and functions in restored beds.

One theme that has emerged from this work is the dual importance of physical and biological drivers. Here I show that crab activity (consumption and engineering of burrows) had a strong negative effect on marsh plants along tidal creek edges (Chapter 1) and a positive effect on marsh plant recovery in the marsh interior, where I found that physical factors such as elevation and depth were also important in driving panne dynamics (Chapter 2). Restored seagrass plot survival (61%) exceeded the global average for similarly sized (22%) and large-scale (42%) projects (van Katwijk et al. 2016). These positive outcomes were likely due in part to the conservative depth zone in which we transplanted where there was sufficient light during high tide and little risk of desiccation during low tide (Chapter 3). Here I also detected strong spatial and temporal variation in initial plot survival and supported functions—time of year had an effect on initial transplant survival due to trade-offs between increased turbidity associated with winter storms and overcrowding by ephemeral macroalgal blooms, both of which varied in severity with increasing distance from the mouth.

Along tidal creek edges, I found that crabs are negatively associated with marsh plant biomass and bulk density, both of which are known to increase resilience of salt marshes to sea level rise and erosion (Chapter 1). Here I show that the dual role of crab *Pachygrapsus crassipes* as both consumer and ecosystem engineer has the potential to depress key ecological functions supported by foundation species *S. pacifica*. I expected burrows to fill in when crabs were experimentally reduced; instead, crab burrows persisted and tidal creek bank stability was compromised due in part, to these legacy effects (Hastings et al. 2007). These results stand out from previous studies conducted in US east coast marsh systems that have shown that without crab maintenance, burrows either fill in or collapse (Bertness and Miller 1984, McCraith et al. 2003). Our understanding of crab-marsh interactions has been driven largely by these well-studied US east coast marsh systems, yet studies have cautioned against extrapolating experimental results even within *Spartina* marshes (Nomann and Pennings 1997). Therefore, more investigations such as the ones presented here are needed in US west coast *Salicornia* marshes because the role of crabs in driving woody perennial marsh dynamics were also found to vary with changes in abiotic conditions (Chapters 1 vs 2).

Marsh recovery along panne edges was driven by both physical and biological drivers. Over the study period, marsh recovered through panne contraction. The opportunity to track this recovery was rather serendipitous, considering that Elkhorn Slough experienced massive marsh loss in the years immediately preceding this study. My findings complement earlier work conducted along US east coast marshes (Day et al. 2011, Wilson et al. 2014) and provides the first study of panne dynamics in a California marsh. Physical factors (depth, elevation, panne size, sediment accretion, distance to nearest panne) and biological factors (crab burrows) influenced the rate of panne contraction. Further study is needed to move beyond the correlations presented here by testing possible mechanisms linked to drainage, elevation, and crab activities. To best manage and conserve salt marsh habitats we must continue to improve our understanding of panne dynamics. As foundation species, salt marsh plants are capable of raising marsh elevation with rising sea level through subsurface expansion and surface accretion (Kirwan and Megonigal 2013), whereas salt pannes are particularly vulnerable to sea level rise as erosive features of the marsh landscape. Thus, the formation and expansion of pannes in the marsh interior represents the "unrecognized Achilles' heel of marsh resilience to sea level rise" (Zhu et al. 2020) and as such, the management and monitoring of pannes should be integrated into plans to support resilient marshes.

Another theme that linked all three of my chapters is the importance of spatial variability and context dependence in the dynamics of these foundation species. Habitat-modifying species (i.e. foundation species, ecosystem engineers) often co-occur and interact (Bruno and Bertness 2001) and the effects of such interspecific interactions are likely context dependent (Thompson 1998) as are the functions and services supported by these important species (Ellison 2019). In my work, I found effects of engineering crabs on marsh foundation species to be context dependent due to differences in hydrology and geomorphology between two salt marsh habitats—tidal creek (Chapter 1) and panne (Chapter 2) edges. I also found seagrass restoration outcomes to be heavily influenced by abiotic conditions that vary through space and time and impact the functional performance of restored and natural seagrass habitats (Chapter 3).

My work also highlights the value of both experimental (causative) and observational (correlative) approaches to ecology. Chapter 1 demonstrated the value of a well-designed long-term field experiment (5+ years) by capturing crab effects across years where environmental conditions varied. Crab effects were spatially explicit (i.e. tidal creek edges), but the direction and strength of effects persisted, demonstrating that the negative effect of crabs on marsh foundation species does not represent transient dynamics, a concern for short-term manipulative field experiments (Tilman 1989). The observational study in Chapter 2 improved our understanding of possible drivers responsible for the pattern of recovery we tracked over a two-year period. The results from Chapter 2 have laid the foundation for future studies which should be experimental and designed to test the mechanisms underlying short-term recovery in a system experiencing long-term trends of marsh loss.

A final theme that has emerged from my work is the potential for recovery of coastal foundation species and the ecosystem services they provide. All three of my chapters provided evidence for this capacity for recovery. In Chapter 1 I found that with fewer crabs, marsh biomass and resilience against erosion along tidal creeks was enhanced. In Chapter 2 I tracked rapid marsh recovery along panne edges following a period of high sea levels and in Chapter 3 I show that seagrass restoration can hasten the natural recovery of seagrass and associated functions.

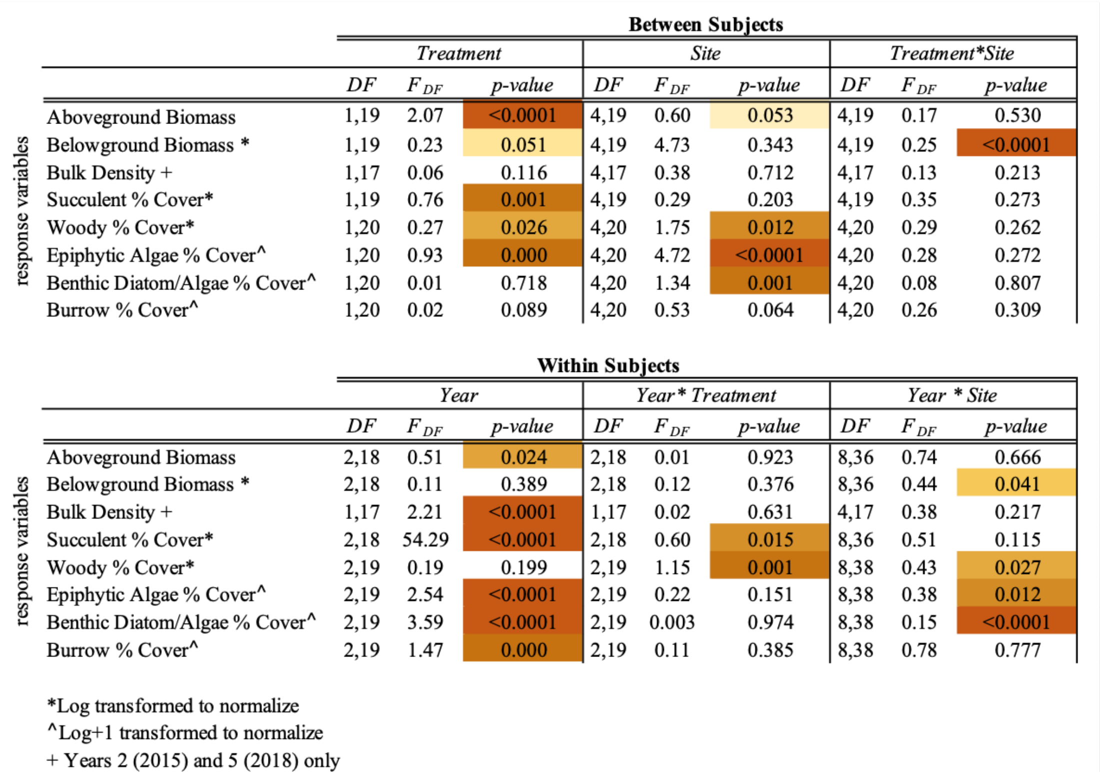
As part of California's 2020 Strategic Plan to build coastal resiliency to sea-level rise, erosion, and coastal storms, the California Ocean Protection Council has set a target of working with partner agencies to support projects that will continue the preservation of existing seagrass habitat while also creating an additional 1,000 acres by 2025 (Ocean Protection Council 2019). Despite these ambitious restoration goals, seagrass restoration success remains low at ~ 37% of transplanted plots surviving (van Katwijk et al. 2016). I conducted two small-scale experimental seagrass restorations in Elkhorn Slough where the cumulative success rate was ~61%. Restored plots expanded rapidly and quickly resembled the structural attributes of reference beds (i.e. shoot density, biomass) and appear to be on a trajectory of functional recovery (i.e. macrofaunal and seagrass epifaunal species density and abundance, modulation of water quality, organic carbon storage). Studies such as the one presented here will inform larger-scale projects that will help California reach its 2025 target of an additional 1,000 acres of seagrass habitat, it will also help inform our assessments of blue carbon mitigation banking and enhancement of biodiversity with restoration.

Despite the widespread loss of coastal foundation species, we are making strides in our understanding of loss and recovery dynamics. In this regard, my work has shown how dynamic salt marsh and seagrass systems are and that rapid recovery is possible. As we continue to gain insight into how these ecosystems are structured and how they respond to environmental change, regulators and policymakers are working hard in states such as California to prioritize the conservation and restoration of these critical habitats. I am hopeful that developing state-wide objectives and policies around the protection of salt marsh and seagrass habitats combined with our increased scientific understanding of the primary drivers that either build or degrade resilience, we will be able to adapt and manage these systems for generations.

Appendix S1
Supplementary Tables and Figures for Chapter 1

APPENDIX S1.

Table S1. Repeated Measures MANOVA Output. For each response variable, the table reports the degrees of freedom (DF), F-value, and p-value for all model effects. P-value cells are shaded using conditional formatting where darker colors indicate more significant relationships and no shading indicates non-significant (p>0.05) relationships.



Between Subjects

response variables	Treatment			Site			Treatment*Site		
	DF	*F_{DF}*	*p-value*	*DF*	*F_{DF}*	*p-value*	*DF*	*F_{DF}*	*p-value*
Aboveground Biomass	1,19	2.07	<0.0001	4,19	0.60	0.053	4,19	0.17	0.530
Belowground Biomass *	1,19	0.23	0.051	4,19	4.73	0.343	4,19	0.25	<0.0001
Bulk Density +	1,17	0.06	0.116	4,17	0.38	0.712	4,17	0.13	0.213
Succulent % Cover*	1,19	0.76	0.001	4,19	0.29	0.203	4,19	0.35	0.273
Woody % Cover*	1,20	0.27	0.026	4,20	1.75	0.012	4,20	0.29	0.262
Epiphytic Algae % Cover^	1,20	0.93	0.000	4,20	4.72	<0.0001	4,20	0.28	0.272
Benthic Diatom/Algae % Cover^	1,20	0.01	0.718	4,20	1.34	0.001	4,20	0.08	0.807
Burrow % Cover^	1,20	0.02	0.089	4,20	0.53	0.064	4,20	0.26	0.309

Within Subjects

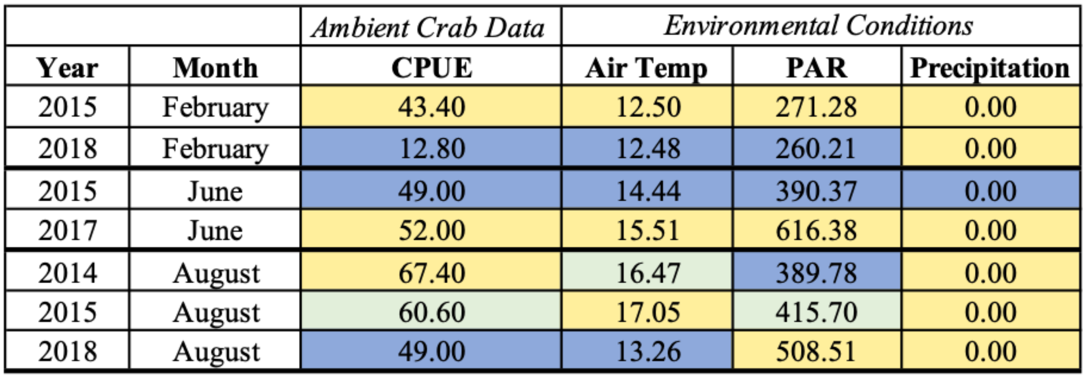
response variables	Year			Year* Treatment			Year * Site		
	DF	*F_{DF}*	*p-value*	*DF*	*F_{DF}*	*p-value*	*DF*	*F_{DF}*	*p-value*
Aboveground Biomass	2,18	0.51	0.024	2,18	0.01	0.923	8,36	0.74	0.666
Belowground Biomass *	2,18	0.11	0.389	2,18	0.12	0.376	8,36	0.44	0.041
Bulk Density +	1,17	2.21	<0.0001	1,17	0.02	0.631	4,17	0.38	0.217
Succulent % Cover*	2,18	54.29	<0.0001	2,18	0.60	0.015	8,36	0.51	0.115
Woody % Cover*	2,19	0.19	0.199	2,19	1.15	0.001	8,38	0.43	0.027
Epiphytic Algae % Cover^	2,19	2.54	<0.0001	2,19	0.22	0.151	8,38	0.38	0.012
Benthic Diatom/Algae % Cover^	2,19	3.59	<0.0001	2,19	0.003	0.974	8,38	0.15	<0.0001
Burrow % Cover^	2,19	1.47	0.000	2,19	0.11	0.385	8,38	0.78	0.777

*Log transformed to normalize

^Log+1 transformed to normalize

\+ Years 2 (2015) and 5 (2018) only

Table S2. Crab activity and environmental conditions. Months sampled multiple years were compared using crab data from the Ambient Crab treatment. Table includes crab activity (reported as CPUE) and environmental conditions. Table is color coded with cooler colors representing colder conditions and warmer colors representing warmer conditions.



		Ambient Crab Data	*Environmental Conditions*		
Year	**Month**	**CPUE**	**Air Temp**	**PAR**	**Precipitation**
2015	February	43.40	12.50	271.28	0.00
2018	February	12.80	12.48	260.21	0.00
2015	June	49.00	14.44	390.37	0.00
2017	June	52.00	15.51	616.38	0.00
2014	August	67.40	16.47	389.78	0.00
2015	August	60.60	17.05	415.70	0.00
2018	August	49.00	13.26	508.51	0.00

Figure S1. Map of Elkhorn Slough and Experimental Site Locations. Site map (top left) shows where the sites are relative to the mouth of the estuary and each other. Site 1 is nearest to the mouth and on the southern side of the main channel. Site 2 is on the northern side of the main channel and one of our higher elevation sites. Site 3 is on the southern side of the main channel within the Elkhorn Slough Reserve. Sites 4 and 5 are on the western side of the main channel and are the farthest distance from the mouth. Triangles indicate Ambient Crab treatments and squares indicate Reduced Crab treatments. Source: Google Earth.

Figure S2. Treatment differences in crab biomass, count and burrows across years. **A)** Mean crab biomass serves as a proxy for **B)** mean count (CPUE) trapping data. **C)** Large burrow counts by treatment and years. Ambient Crab treatment is in blue and Reduced Crab treatment in red. Significant differences between treatments, within year, are indicated by asterisk (p<0.0001, "***") and non-significant differences (p>0.05), "ns". Data are the mean values ± standard error of the mean.

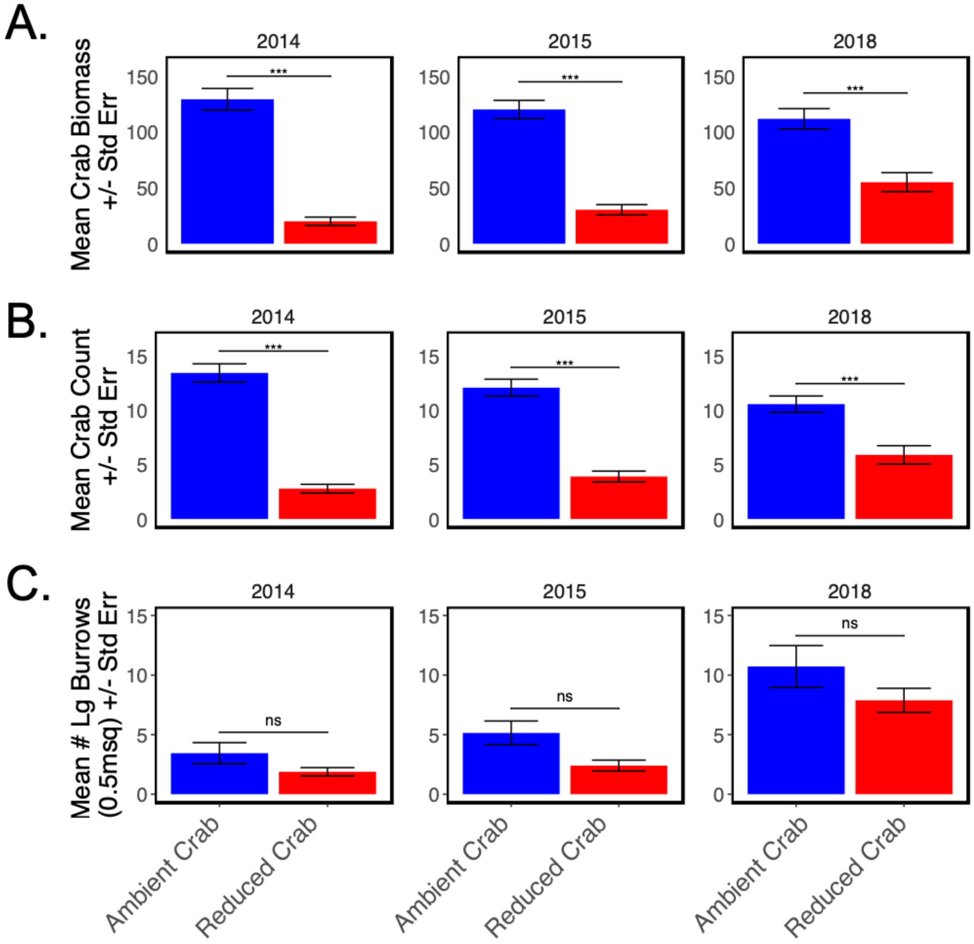


Figure S3. ***Pachygrapsus crassipes*** **time series based on semi-seasonal 24hr crab trapping across experimental sites grouped by treatment.** Fewer crabs were trapped on average in Reduced Crab treatments (red) relative to Ambient Crab treatments (blue) starting in September 2014 and extending through August 2018. ("+" indicates annual data collection efforts conducted in September 2014 and August of 2015 and 2018).

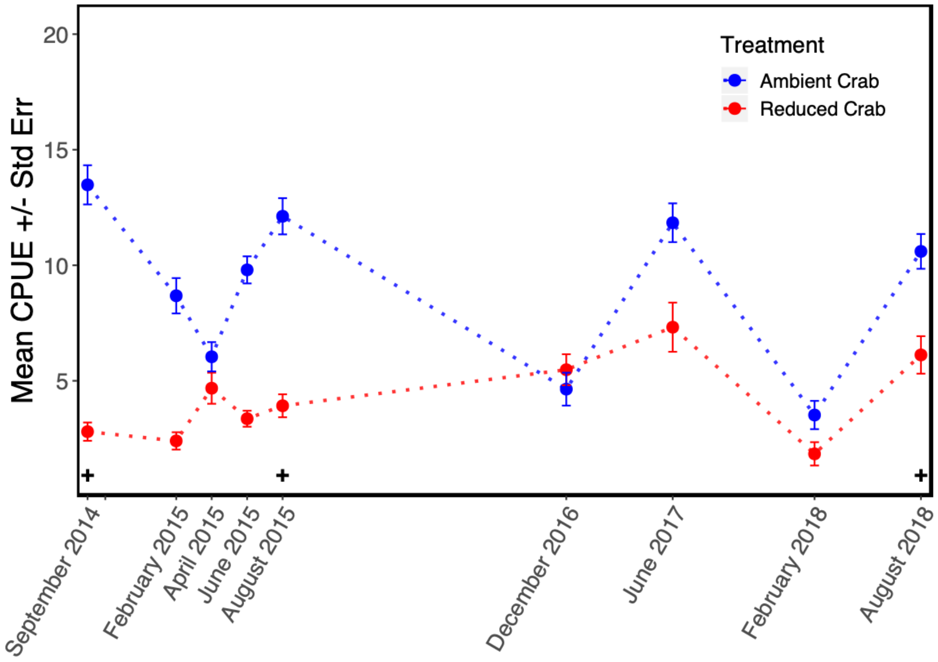


Figure S4. Seasonal pattern of crab activity tracks environmental conditions. Time series data from Ambient Crab treatments show clear seasonal declines in crab activity during late Fall-early Spring indicated by the light red bars showing periods with relatively lower mean number of individuals trapped. Periods of low crab activity, indicated by the relatively low mean number of crabs trapped in a 24-hour period (red-shaded bars) coincide with periods of **a)** high rainfall, **b)** low air temperature and **d)** low levels of light, indicated by lower levels of photosynthetically active radiation, PAR. The opposite is also observed, trapping efforts yielded higher crab numbers during periods of low rainfall and higher air temperatures and PAR.

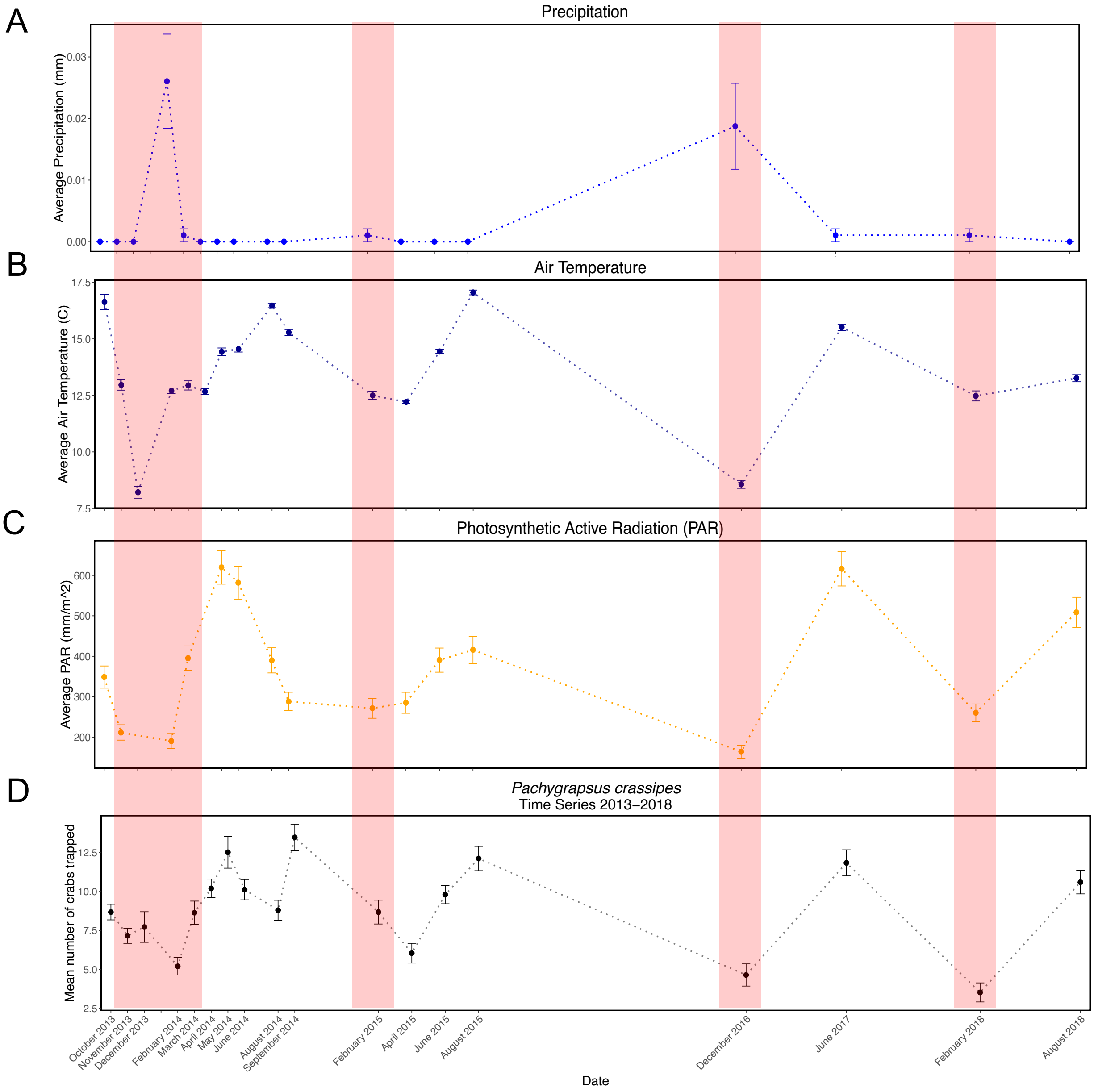


Figure S5. Sediment accretion by treatment and crab effects. A) Treatment had no effect on accretion rates (One-way ANOVA; $F_{1,48}$=0.0398, p=0.843). **B)** After "brownies" were extracted they left a nice ring in the marsh and a visible boundary in the excavated sample where the feldspar layer and the accreted sediment was visible (indicated by yellow dotted line). **C)** Crab biomass and **D)** burrows also had no significant effect on accretion. Ambient Crab treatments are blue, Reduced Crab treatments red. Plotted data is from 2018.

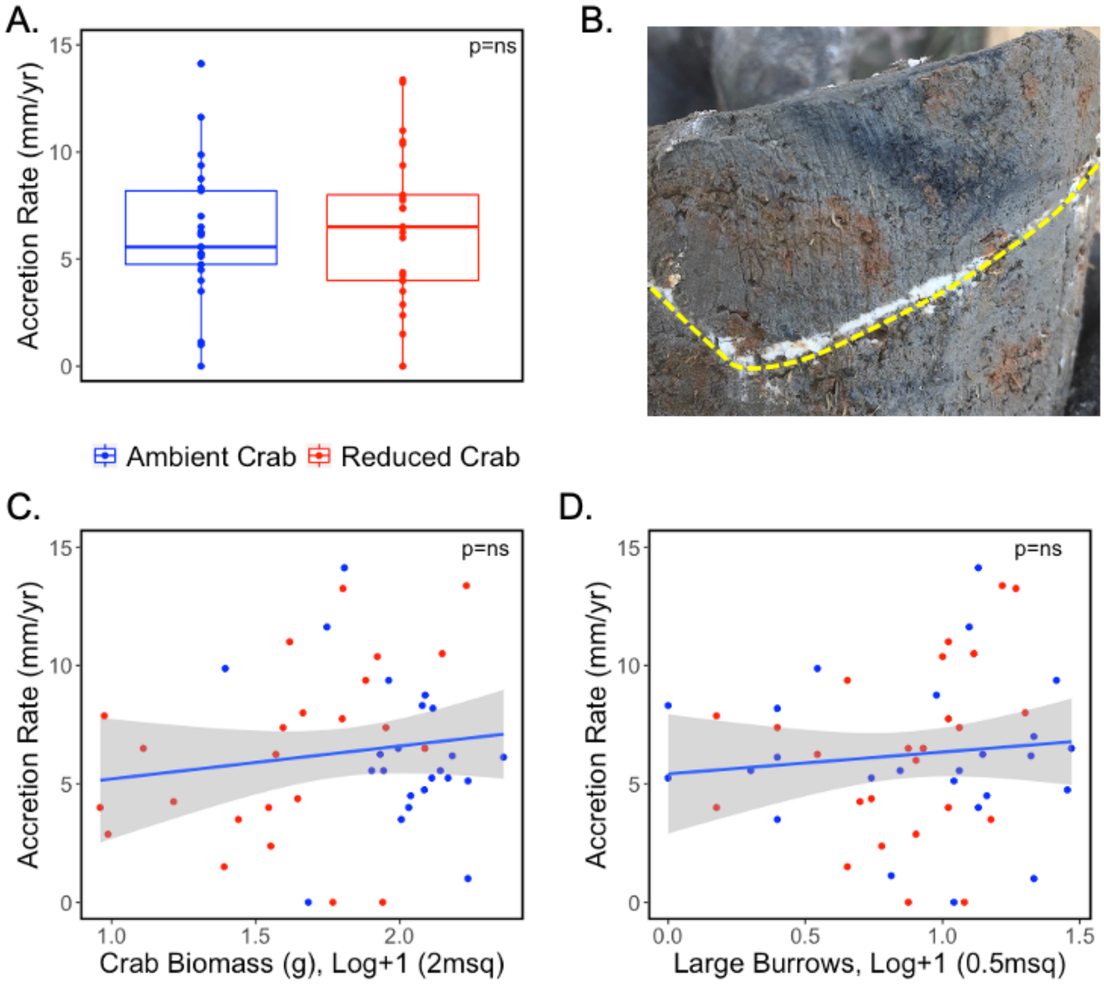


Figure S6. Percent cover by treatment across years. A) Benthic diatoms/algae percent cover, **B)** epiphytic algal cover, **C)** succulent percent cover and **D)** woody percent cover, by treatment and year. Benthic diatoms/algae and epiphytic algae are log+1 transformed and succulent and woody cover are log transformed. Ambient Crab treatments are blue, Reduced Crab treatments red. See **Supplemental Table 1** for statistics.

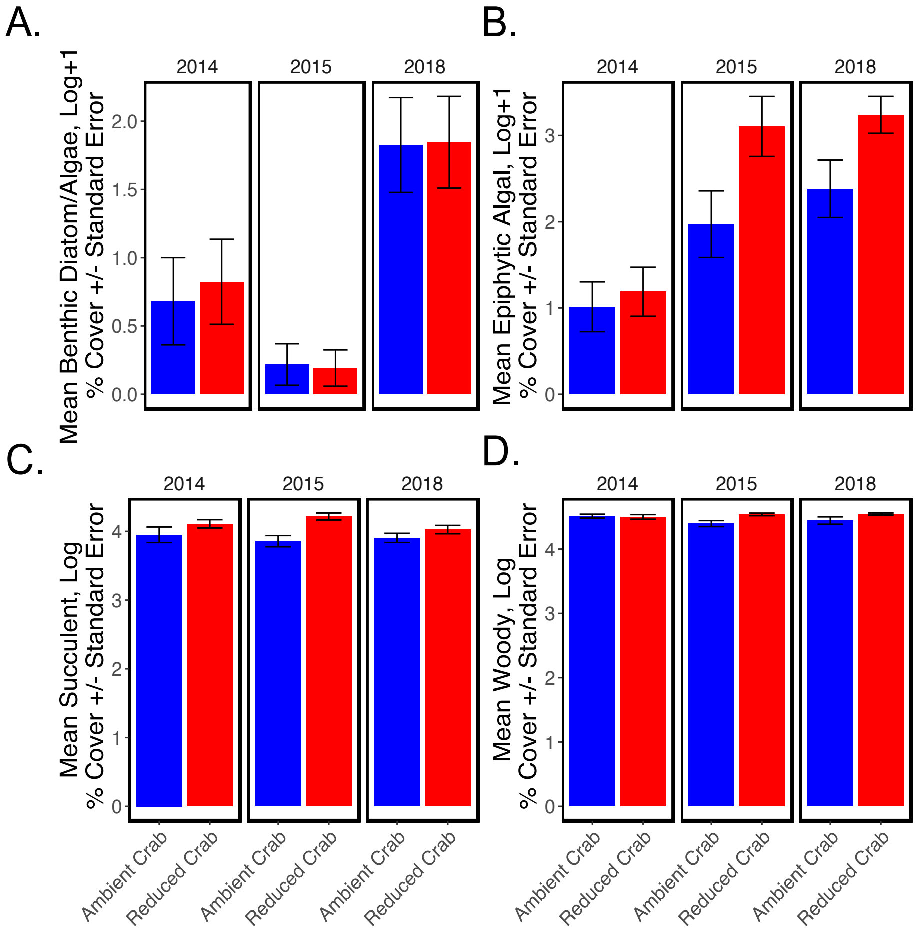


Figure S7. Crab burrow effect on marsh biomass over time with slope (*m*) reported. Regressions of **a)** aboveground biomass (g/core) and **b)** belowground biomass (g/core) in 2014, 2015 and 2018 as a function of large crab burrows. **C)** Bulk density (g/cm^3) in 2015 and 2018 (no data for 2014) as a function of large crab burrows. Plotted is the raw marsh biomass and bulk density data and the average number of large burrows per experimental plot by year is log+1 transformed. The slope of each regression is reported in the top-right corner of each panel. Ambient Crab treatments are blue, Reduced Crab treatments red. See **Table 1** for statistics.

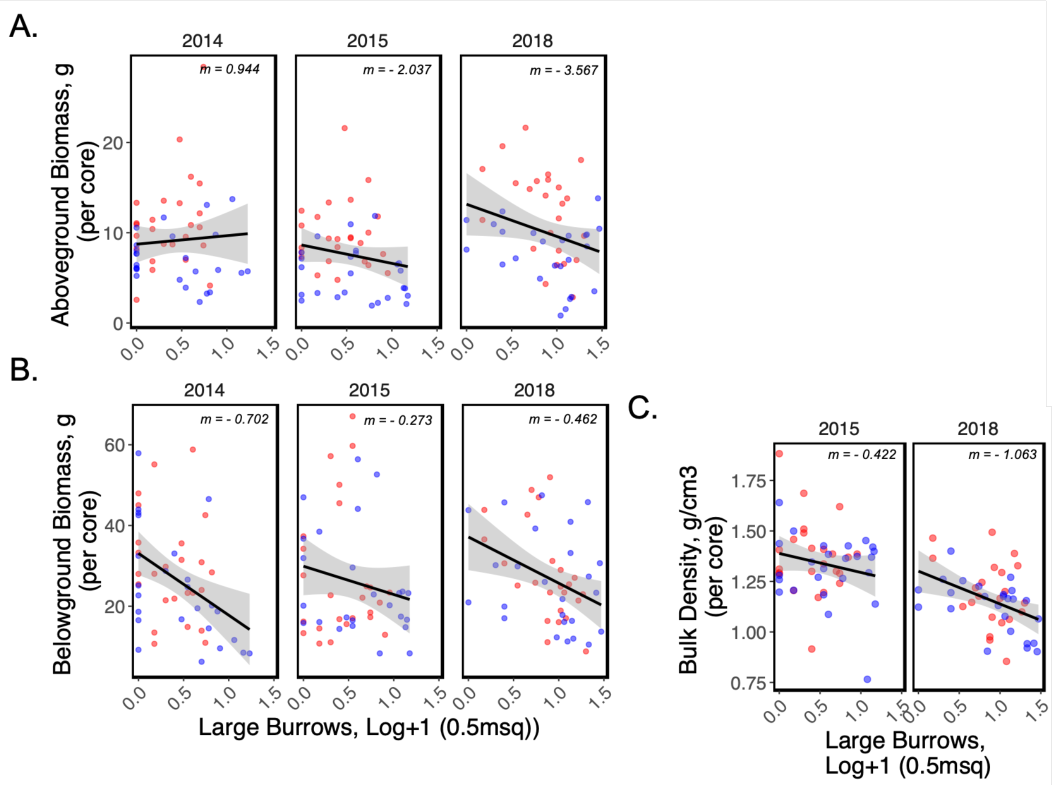


Figure S8. Crab effects on percent cover over time. Plotted relationships between crab burrows (*left*) and crab biomass (*right*) on **a-b)** succulent cover, **c-d)** woody cover, **e-f)** epiphytic cover, and **g-h)** benthic diatom/algae cover in 2014, 2015 and 2018. Succulent and woody percent cover data is log-transformed, and epiphytic algal cover and benthic diatom/algae cover is log+1 transformed. Ambient Crab treatments are blue, Reduced Crab treatments red. See **Table 1** for the p-values for each response variable.

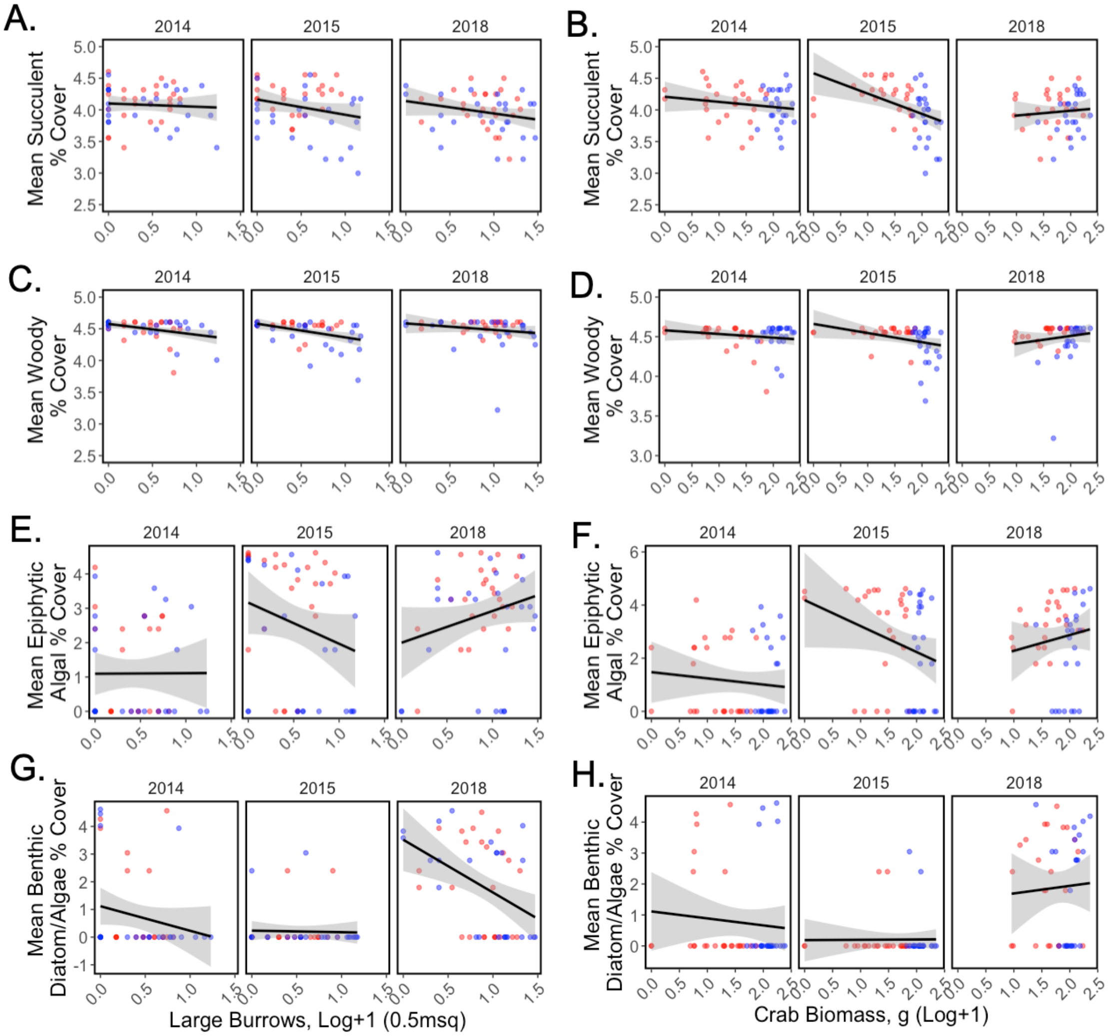
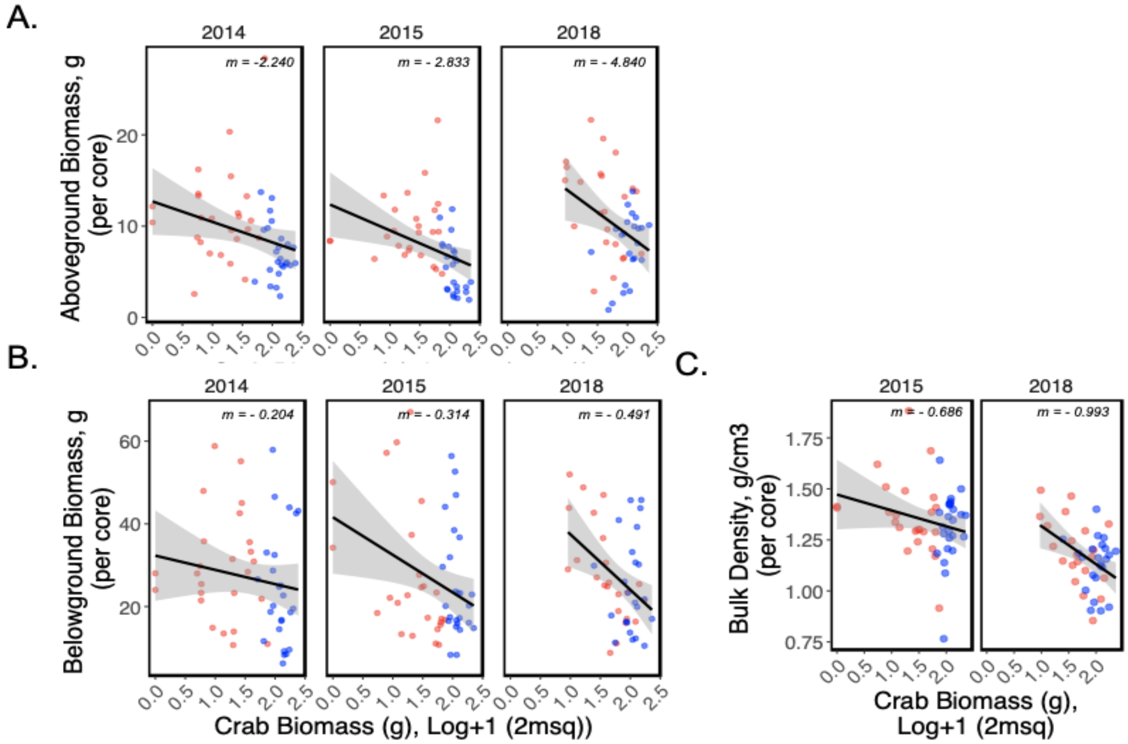


Figure S9. Crab biomass effect on marsh biomass over time with slope (*m*) reported. Regressions of **a)** aboveground biomass (g/core) and **b)** belowground biomass (g/core) in 2014, 2015 and 2018 as a function of crab biomass. **C)** Bulk density (g/cm^3) in 2015 and 2018 (no data for 2014) as a function of crab biomass. Plotted is the raw marsh biomass and bulk density data and the sum total crab biomass (g; log+1 transformed), per experimental plot in September 2014, August 2015, and August 2018. The slope of each regression is reported in the top-right corner of each panel. Ambient Crab treatments are blue, Reduced Crab treatments red. See **Table 1** for statistics.



Appendix S2
Supplementary Methods for Chapter 2

APPENDIX S2.1.

Crab experiment

To test whether crabs had an effect on salt panne dynamics and whether such effects varied by elevation, we conducted the following experiment from 2016-2018 at the 20 pannes. The key response variable we focused on was movement of the panne edge (transition from vegetated to unvegetated). Within each panne we applied four experimental treatments: (i) reduced crab densities (full cages where crab density was continually reduced using pit-fall traps), hereafter referred to as 'Reduced Crab', (ii) above ambient crab densities (full cages where crab density was kept above ambient densities through regular addition of individuals into the experimental plot area), hereafter referred to as 'Above Ambient Crab', (iii) ambient crab densities with cage (lifted cages where crabs were allowed to move in and/or out of the experimental plot area), hereafter referred to as 'Ambient Crab', and (iv) ambient crab densities without cage (experimental plot area marked by wooden posts), hereafter referred to as 'No Cage' (Figure S1). The roots were severed using a shovel (30 cm deep x 1 cm wide) in all plots in order to prevent exchange between our experimental plots and surrounding marsh. Each of the experimental plots was 1.5 x 0.5 m with ~0.25 x 0.5 m of plot inserted into the panne itself, and the remaining 1.25 x 0.5 m in the marsh (Figure S2A). The cages were built using 19-gauge 1.3 cm x 123 cm x 30.5 cm galvanized hardware cloth attached with staples to 1 m-long wood posts. The wire-mesh caging around the Above Ambient Crab and Reduced Crab plots extended into the substrate ~10 cm to prevent crabs from burrowing in or out of the experimental plot area. The cage 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. To keep crabs in the Above Ambient Crab plots, aluminum flashing was installed flush to the interior cage wall to prevent crabs from escaping by climbing up and out of the cage (crabs were unable to grip the flashing). To account for the potential confounding effects of the flashing, it was installed on all caged plots. To keep crabs from entering the Reduced Crab experimental plots, flashing was installed on the outside of the cage wall and flashing was installed on the inside of Ambient Crab plots to mimic the Above Ambient Crab plots. Cages were cleaned regularly (once per month from November-March, twice per month from April-October) to remove any algal wrack deposited on the cage walls or inside the plots during high tides.

To measure ambient crab densities and set Above Ambient Crab treatment levels, we conducted a 24 hr crab trapping effort at the start of the study in 2016 using the two pit-fall traps installed flush to the sediment surface in the back marsh-end of each of the 4eighty experimental plots in each panne. Pit-fall traps (i.e. tennis ball cans, 3.5 cm diameter and 20.5 cm depth with holes at the base for drainage) were installed in all experimental plots to account for the potential effect of installing traps in the experimental plot area and remained uncapped except during our 24 hr crab trapping efforts (August 2016, March 2017, August 2018). Above Ambient Crab densities was set at one standard deviation above the mean, or 8 crabs. To maintain the Reduced Crab treatment, we continually trapped crabs, removing them from the experimental plot area using permanently un-capped pit-fall traps throughout the entire duration of the study. Pit-fall traps in the Reduced Crab plots were emptied as needed, typically monthly.

Elevation data was extracted after the pannes were selected. Pannes were selected on several factors including approximate relative elevation, plant community, substrate firmness, the degree of consolidation of the sediment etc.) Using a LiDAR Digital Elevation Model (2018), we extracted the elevations for all nineteen pannes that were used in analyses. We set the low elevation cut-off at 1.45 m NAVD 88. This cut-off was chosen because it allowed for somewhat even replicates by elevation (low, n=10; high, n=9). We acknowledge that a more appropriate cut-off would have been ~1.53 m which is approximately the Mean High Water (MHW) elevation of Elkhorn Slough. Low elevation blocks ranged from 1.37 to 1.45 m NAVD 88 and high elevation blocks ranged from 1.48 to 1.61 m NAVD 88.

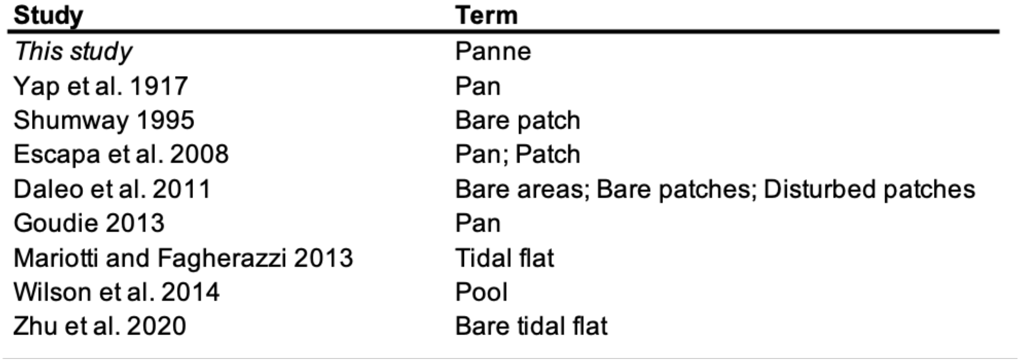
To test for treatment effects on panne contraction or expansion we first ran a mixed model with Block(Relative Elevation Category) as a Random Effect. After detecting no effect of Block(Relative Elevation Category) we removed it from the model and ran a two-way ANOVA with four levels (Above Ambient Crab, Ambient Crab, Reduced Crab, No Cage) of factor "Treatment" and two levels (High and Low) of factor "Relative Elevation Category". We then tested for differences in crab CPUE and burrow density by treatment and elevation using a full factorial ANOVA with four levels (Above Ambient Crab, Ambient Crab, Reduced Crab, No Cage) of factor "Treatment" and two levels (High and Low) of factor "Relative Elevation Category".

Overall, we failed to manipulate crab or burrow densities as initially designed (Figure 7A). We found no consistent reduction in burrows or crabs in the Reduced Crab treatments, and no significant increase in the Above Ambient treatments, relative to the Ambient and No Cage treatment. At our last sampling (August 2018), differences in crab CPUE by treatment were inconsistent with our study design, verifying that we were unable to manipulate crab densities as initially designed (ANOVA; $F_{3,72}=3.85$, $p=0.013$). According to Tukey's HSD post-hoc test, crab CPUE was not significantly different when comparing Ambient and Above Ambient Crab treatments and Above Ambient Crab was not significantly different from other treatments (Reduced Crab and No Cage). Additionally, we did not detect an effect of elevation ("Relative Elevation Category", high vs. low), or treatment*elevation and we failed to detect an effect of treatment, elevation, or treatment*elevation on panne contraction or expansion (Figure 7B).

Appendix S2
Supplementary Tables and Figures for Chapter 2

APPENDIX S2.2.

Table S1. Examples of the different terminology used to describe pannes in the literature. All of the terms listed in the table are collectively referred to as ‘pannes’ in our study.



Study	Term
This study	Panne
Yap et al. 1917	Pan
Shumway 1995	Bare patch
Escapa et al. 2008	Pan; Patch
Daleo et al. 2011	Bare areas; Bare patches; Disturbed patches
Goudie 2013	Pan
Mariotti and Fagherazzi 2013	Tidal flat
Wilson et al. 2014	Pool
Zhu et al. 2020	Bare tidal flat

Table S2. Full list of model terms and direction of significant effects. Non-significant terms were excluded from the final model and are denoted with “ns”. The directionality of effect for non-significant terms is the hypothesized directionality, the directionality of effect for significant terms is model-based. Some hypotheses (e.g. ‘Distance to nearest panne’) were the opposite of what we observed. *A negative effect (-) indicates that as the model term increases, the observed rate of panne contraction/marsh colonization decreases. A positive effect (+) indicates that as the model term increases, the observed rate of panne contraction/marsh colonization increases.

#		*Model Term*	Definition	Hypothesis	Model Estimate	Standard Error	t-Ratio	p-value	VIF	Direction of Effect*
1	geomorphology	*Panne Size Index*	Panne circumference (m)	smaller pannes = contraction, larger pannes = expansion/slow contraction	-1.34	0.38	-3.49	<0.0001	1.39	-
2		*PC1 (Depth and Elevation)*	Principle Component that includes both panne depth and panne elevation	shallower/higher elevation pannes = contraction, deeper/lower elevation pannes = expansion	-101.87	19.73	-5.16	0.000	1.89	+
3		*Distance to nearest panne*	Distance to nearest panne (m)	far pannes = contraction, near pannes = expansion	-3.07	0.38	-8.04	0.005	1.63	-
4	crab data	*Crab Activity Index*	Average number of burrows	more burrows = contraction, less burrows = expansion	0.31	0.07	4.24	<0.0001	1.44	+
5	sediment	*Panne Sediment Dynamics Index*	Difference in mean panne rod exposed per panne (+ = accretion, - = erosion)	accretion in pannes = contraction, erosion in pannes = erosion	2.27	0.53	4.28	0.001	1.04	+

Table S2. (continued):

#		*Model Term*	Definition	Hypothesis	Model Estimate	Standard Error	t-Ratio	p-value	VIF	Direction of Effect*
6	crab data	*Crab biomass*	See *Beheshti et al. in review* for calculation	low crab biomass = contraction, high crab biomass = expansion	–	–	–	ns	–	-
7		*Crab CPUE*	# of crabs per pit-fall trap	low crab CPUE = contraction, high crab CPUE = expansion	–	–	–	ns	–	-
8		*Crab Count*	Total number of crabs per panne	low crab count = contraction, high crab count = expansion	–	–	–	ns	–	-
9		*Change in burrow density*	Difference in burrow counts over time	more burrows = contraction, less burrows = expansion	–	–	–	ns	–	+
10	geomorphology	*Distance to bank edge*	Shortest distance to nearest tidal-creek bank edge (m)	close to bank edge = contraction, far from bank edge = expansion	–	–	–	ns	–	+
11		*Microchannel width*	Width of narrow channel branching out from panne (cm)	wide creek = contraction, narrow or no creek = expansion	–	–	–	ns	–	+
12	sediment	*Marsh Sediment Dynamics Index*	Difference in mean marsh rod exposed per panne (+ = accretion, - = erosion)	accretion in marsh = contraction, erosion in marsh = erosion	–	–	–	ns	–	+
13	cover	*Marsh Productivity Index*	Change in succulent pickleweed percent cover	more cover = contraction, less cover = expansion	–	–	–	ns	–	+
14		*Biofilm Index*	Change in benthic non-diatom algae and diatom percent cover	more biofilms = contraction, less biofilms = expansion/slow contraction	–	–	–	ns	–	+

Figure S1. A) Study design with treatments labeled at single block, B) Above Ambient Crab experimental plot with the flashing installed flush to the cage wall, C) *P. crassipes* crab in a burrow in one of our experimental plots and D) Close up view of the panne rod and the zip-tie marker for the transects that run from the panne-edge to marsh-edge of the plot (**See Figure S3**).

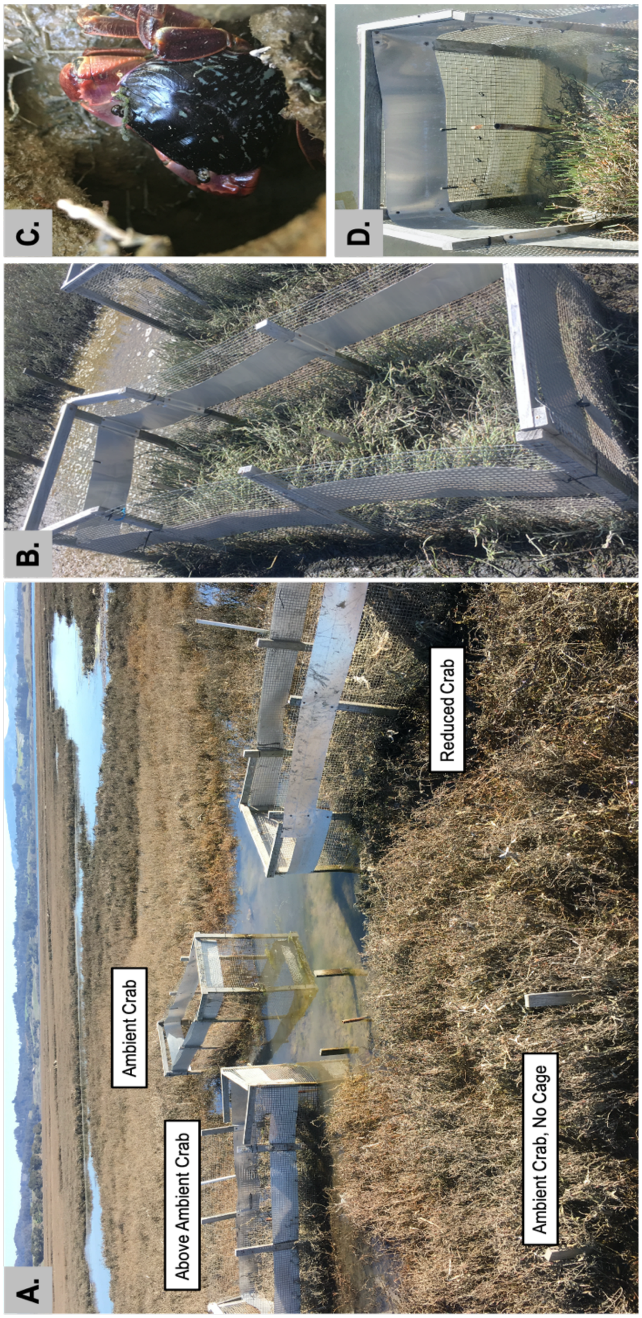


Figure S2. Heat map of salt marsh zones where there has been net gain (blue) or loss (red) of habitat from 2004-2012.

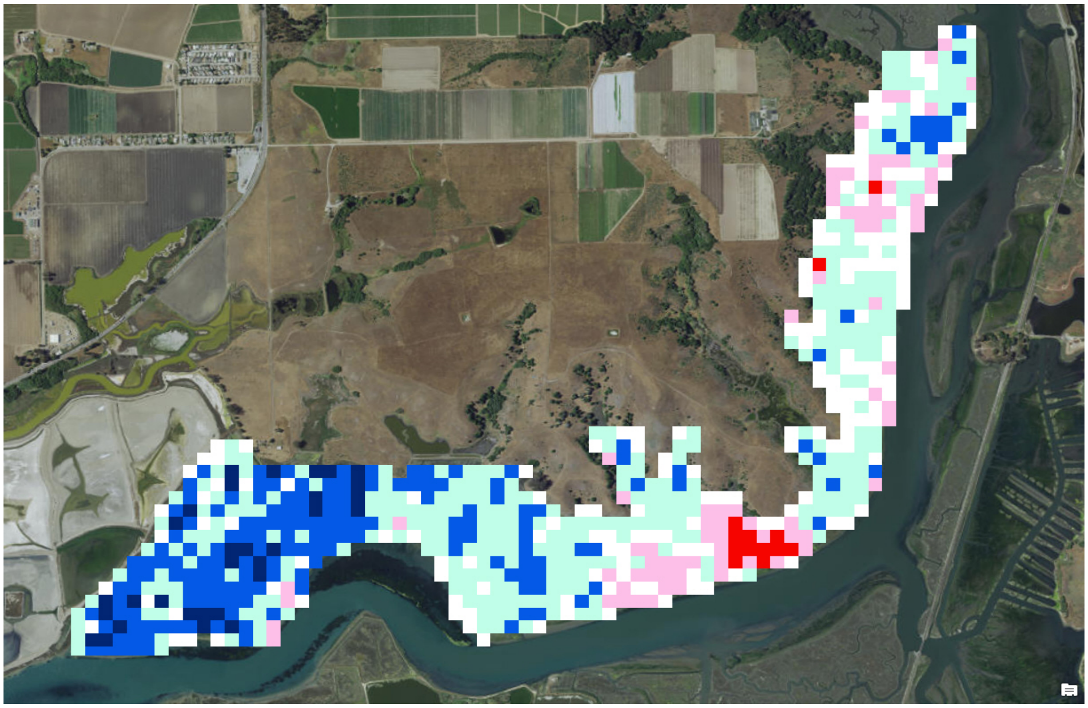
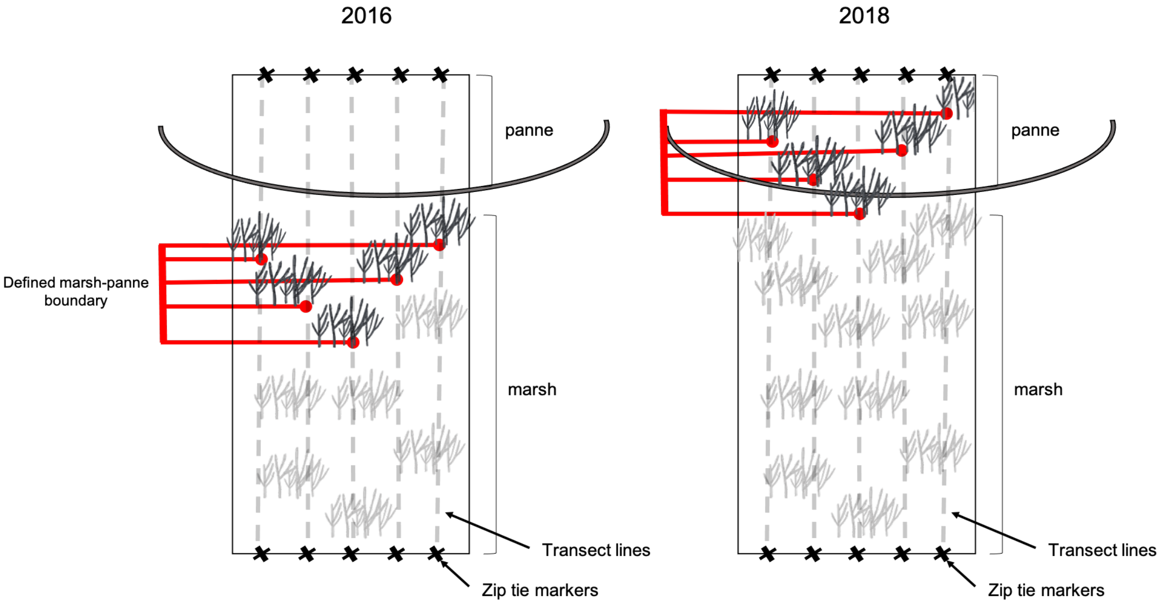


Figure S3. Schematic of how marsh-panne boundary was monitored over time in caged plots. Changes to the marsh-panne boundary over time indicate either marsh colonization and panne contraction (as pictured here) or marsh dieback and panne expansion.



Video S1. Installation of galvanized conduit rods into the panne and marsh area of each experimental plot across all twenty blocks, or pannes.

Link: https://youtu.be/nHdfJg4o-Bw

Figure S4. Example of panne polygons used to determine panne depth. A 1 m buffer circle (shown in yellow) was used to extract the 2018 DEM cells. Raw lidar points (shown in the image as green points) were not used since they were not particularly well-spaced. The DEM uses an interpolation between the points, and thus was reliable at representing the marsh-panne boundary and the pannes themselves.

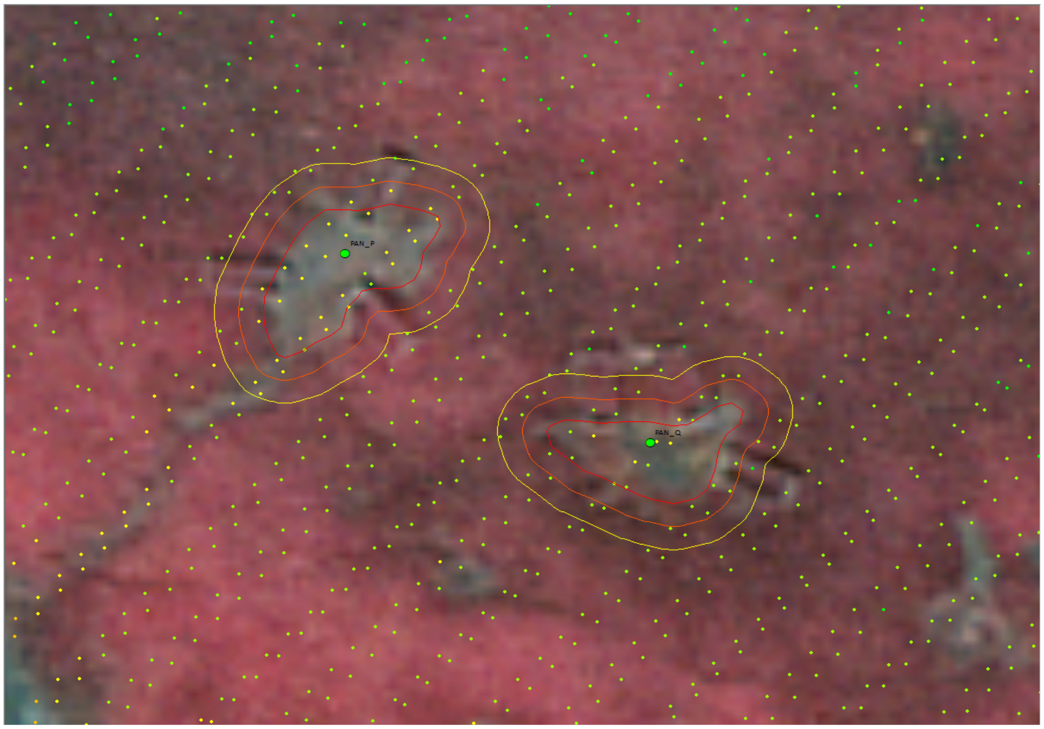


Figure S5. Relationship between elevation and panne depth that led to the development of a Principle Component (PC1 (Depth and Elevation)). Deep pannes are indicated by black circles and shallow pannes by blue triangles. Reported in the top left corner of the plot is the R^2 and plotted regressions include the 95% C.I.

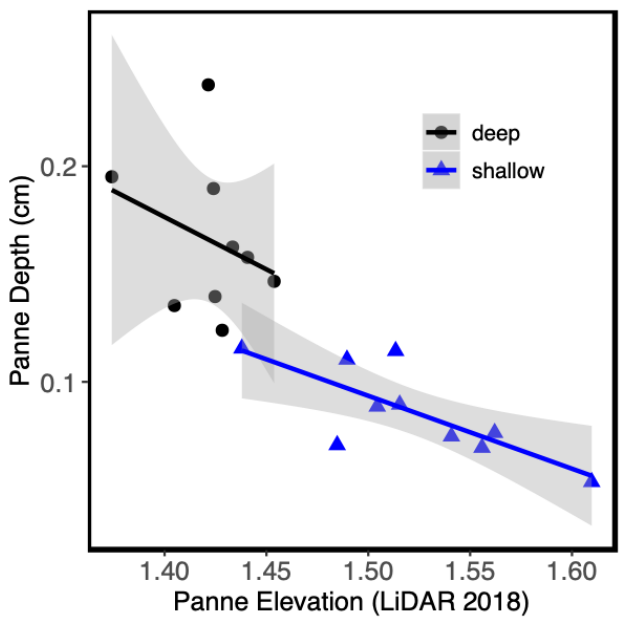


Figure S6. Elevation by panne size. As panne elevation increases, size decreases (R^2=0.15). Similar patterns were observed in Escapa et al. 2015 (See Fig. 3)--panne size (‘Patch diameter’; Escapa et al. 2015) decreased as elevation increased. The lower elevation edge for pickleweed in Elkhorn Slough is ~1.20 m NAVD 88 (*C. Endris, unpublished data*), our study did not extend lower than 1.37 m NAVD 88.

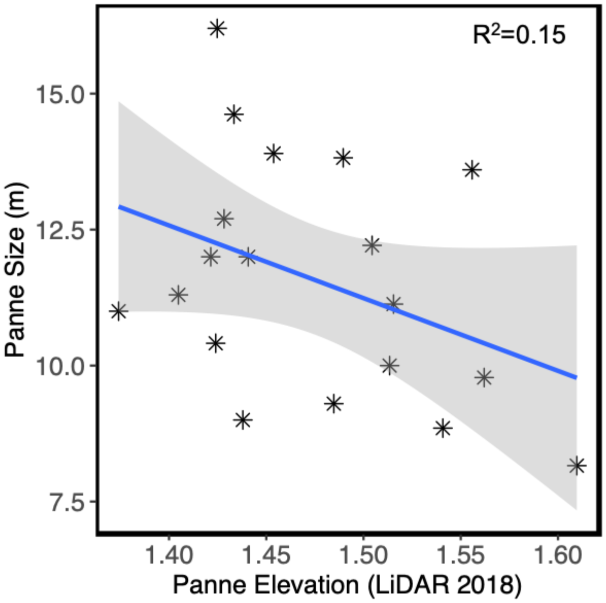
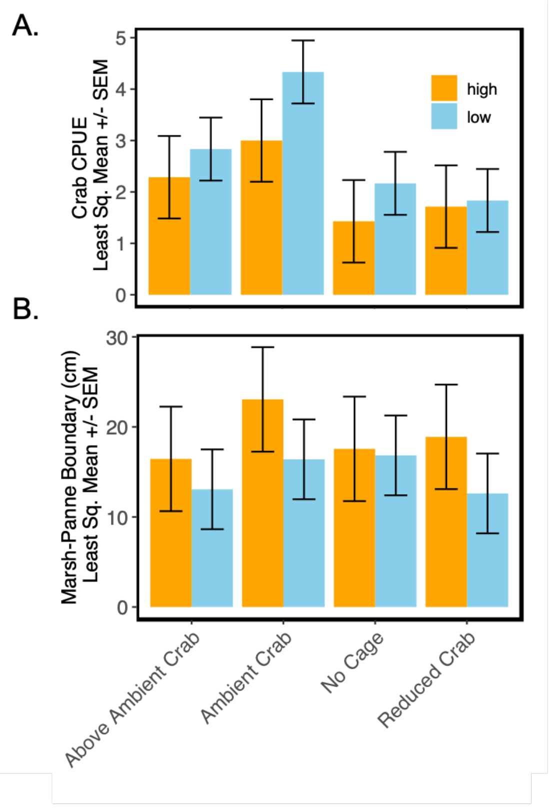


Figure S7. Experimental results showing A) crab CPUE and B) change in marsh-panne boundary (2016-2018) by treatment and elevation. High elevation blocks are plotted in orange and low elevation blocks in blue.



Appendix S3
Supplementary Methods for Chapter 3

APPENDIX S3.1.

Seagrass time series

To quantify how much new seagrass habitat in Elkhorn Slough was due to restoration plot expansion versus reference beds filling in and expanding, a time series was developed using geospatial data on seagrass extent. Specific datasets were included (or excluded) for digitization based on the clarity of the water at each seagrass site. The good consistency in the outline of the seagrass beds within each dataset group improved our confidence in the delineations. It's possible, however, that deeper portions of the beds closer to the channel thalweg were under-represented in our delineations due to limited visibility. The data presented in the seagrass time series reported as Figure S1 was collected using similar aerial imagery extending as far back as 1931.

Tracking structural attributes and mesograzer abundance as a proxy for restoration survival and growth

In addition to measuring in situ canopy height, vegetative and flowering shoot density, we harvested shoots from both restored and reference plots for later lab processing of shoot, rhizome, and epiphyte biomass. We also collected data on the abundance and biomass of critical mesograzers, *Phyllaplysia taylori* and *Pentidotea resecata* from harvested shoots. While other invertebrate taxa were counted and recorded, we are only reporting on these two species because of their well-characterized role in promoting the health of seagrass beds and because they made up the majority of the mesograzer biomass across both restored and reference plots. Prior to measuring the structural attributes of harvested shoots, all invertebrates were cleared from the mesh bags the ramets were held in and from the shoots themselves. To process each ramet, we first used a 3.8 cm single edge razor blade to scrape epiphytic algae and diatom films off of the blades and wiped them on pre-weighed labeled cotton rounds before placing them in the dehydrating oven for 72 hrs. Dry weight (g) was measured by subtracting the weight of the clean, pre-weighed cotton round from the dried cotton round with sample. Once the shoots were free of epiphytes we measured shoot lengths. Five representative shoot lengths were measured from the tip of each blade to the base of the meristem at the first (most recent) node. After shoot lengths were recorded we used the razor blade to cut the shoot from the rhizome at the most recent note. We cut each rhizome to 7 cm in length and separately wrapped each shoot and rhizome (n=50) in labeled pre-weighed foil. We poked tiny holes to allow the moisture to escape and placed the samples in the dehydrating oven for 72 hrs for biomass in dry weight (g).

Biodiversity of macrofauna

To quantify biodiversity of mobile macrofauna, a baited shrimp pot and a mid-water minnow trap was deployed in each of the habitat types. To secure the trap arrays and prevent them from shifting from tidal currents, 2-4 plate weights (1.0-3.0 kg) were placed in the corners of the shrimp pots to prevent them from sliding along the seafloor and Danforth anchors were secured with line to the shrimp pots to further secure the trap arrays to their desired location. In the shrimp pots, bait (frozen anchovies or sardines) was placed in a tennis ball can with holes drilled in the base and top of the canister and depending on the size of the bait fish, held between 5-8 fish, travel-toothbrush holders with holes drilled on either side served as bait containers for minnow traps and held 1 frozen fish. Mid-water minnow traps were secured to the buoy line allowing enough slack to be suspended in the water column.

Organic carbon stocks

Sediment cores were collected from October 2018-February 2020. All cores were immediately stored in a refrigerator and processed within a week. First each core was sub-sampled into 2 cm intervals and placed in a beaker to measure wet weight. Each interval was rinsed with DI water and the sediment allowed to settle over 24 hours, after which we carefully poured off the surface water and decanted the remaining water so as to prevent sediment loss. Each interval was rinsed 2-3 times (2 times for sandy sediment and 3 times for more silty sediment). Following the last salt rinse, samples were dried and the dry weight (minus salts) was recorded. Each interval was cone and quartered (Lewis and McConchie 1994) into two 10g subsamples (± 0.1000g), one for TOM analyses and the other for grain size analysis (not reported). In order to remove inorganic carbonates from the TOM subsamples, 1.2 Molar HCl (15 minutes) was used to dissolve carbonates and DI water was added later and sat for over 4 hours or until the sediment settled. The diluted acid was decanted and DI water was again added, this process of diluting the acid was repeated four times. After the final DI rinse the sediment was dried and dry weight recorded. Acid washed sediment was then subsampled using cone and quartering methods (1.3 ± 0.1000g) and placed in crucibles to burn in the muffle furnace for loss-on-ignition, LOI (Davies 1974). The muffle furnace was set to 550°C and samples burned for 3 hours. After samples cooled, crucibles were re-weighed and the difference pre and post combustion (LOI) is the TOM that was lost. To translate TOM to organic carbon (OC), we used a power model ($y=0.22x^{1.1}$) derived using regional core data (Ward 2020). Carbon storage was calculated by multiplying % OC and the bulk density of each interval, reported as kg OC m^{-3}. We used an ANOVA to determine differences in organic carbon stocks across habitats.

References: Appendix S3

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Appendix S3
Supplementary Figures for Chapter 3

APPENDIX S3.2.

Figure S1. Seagrass Time Series from 1931 to 2018 showing seagrass aerial extent in Elkhorn Slough, CA starting at 26.01 hectares in 1931 to 15.62 in 2018. By the 1960s seagrass extent dropped as low as ~3 hectares. This data is based on aerial imagery data. See Appendix 1: Methods for details.

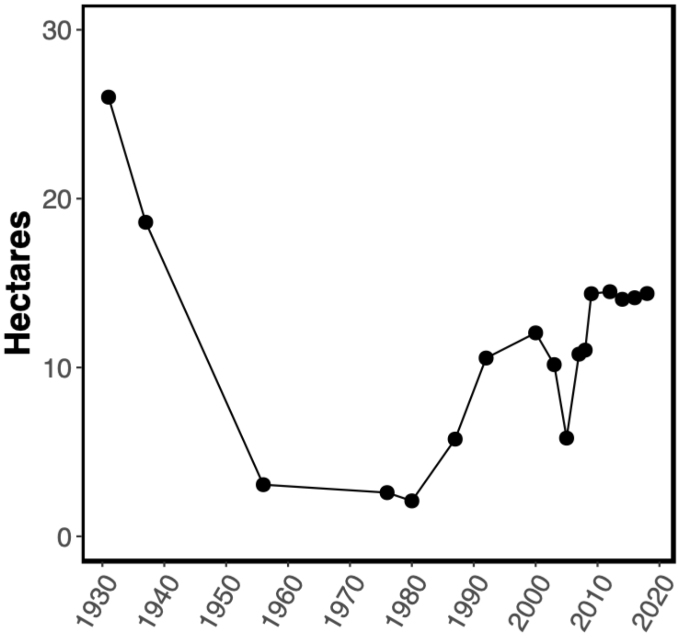


Figure S2. Schematic of restoration design (2015 and 2016). Restoration plots were ~7 m away and reference beds were at least 25 m from restored plots at the time of transplanting. Illustration by Kathryn Beheshti.

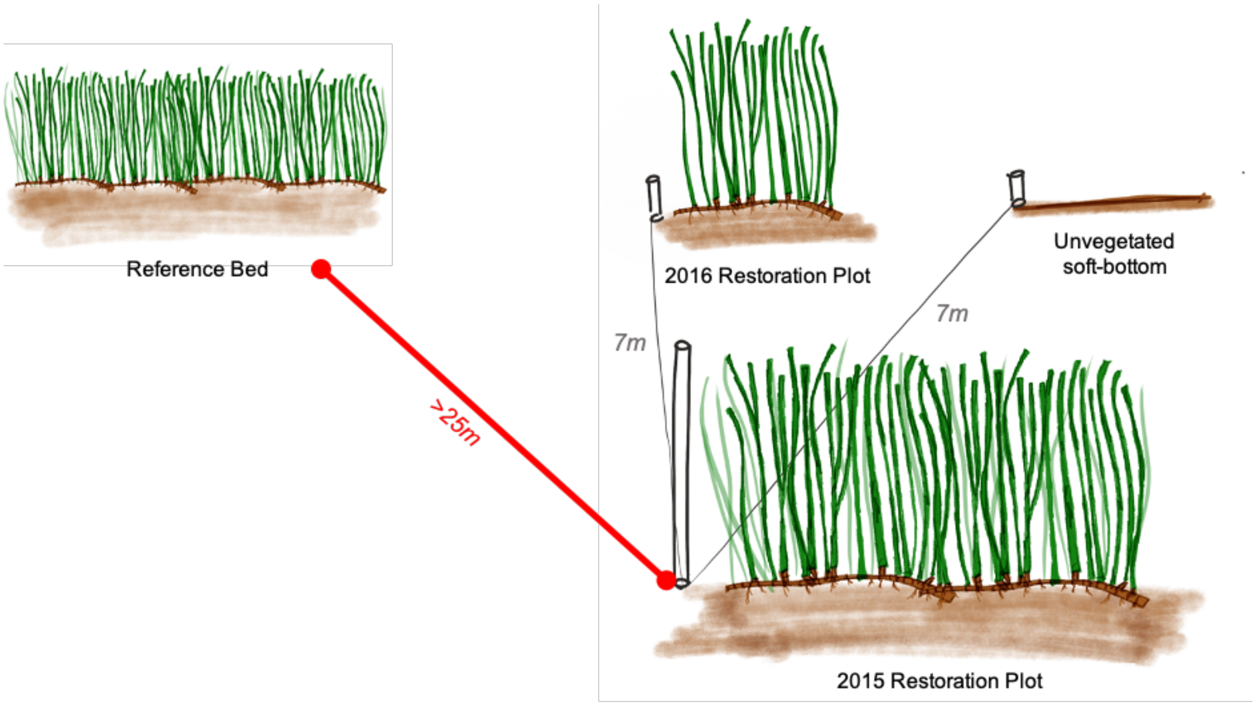


Figure S3. *Zostera marina* morphology and showing where shoots and rhizomes were trimmed for transplanting (shoot, 20 cm; rhizome, 10 cm) and later lab processing (rhizome, 7 cm). Illustration by Kathryn Beheshti.

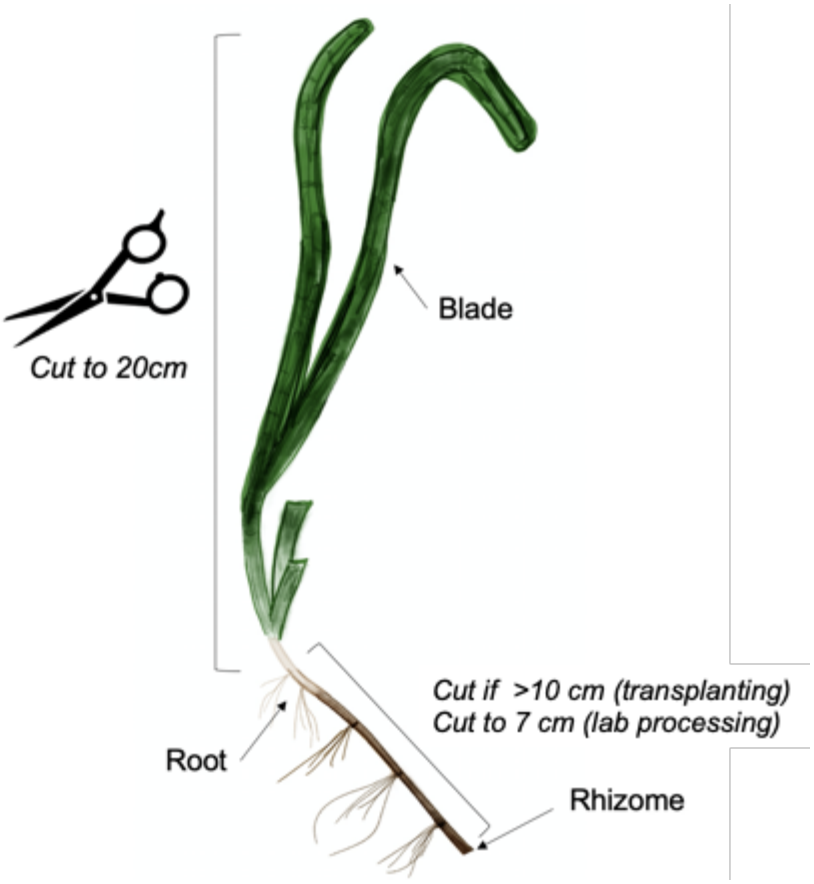


Figure S4. Structural attributes of restored (2015 and 2016) and reference plots from August 2018 monitoring. A) Canopy height (cm) and B) flowering shoot counts (per 0.25 cm^2) for August 2018 monitoring effort for 2015 and 2016 restoration plots and reference bed plots.

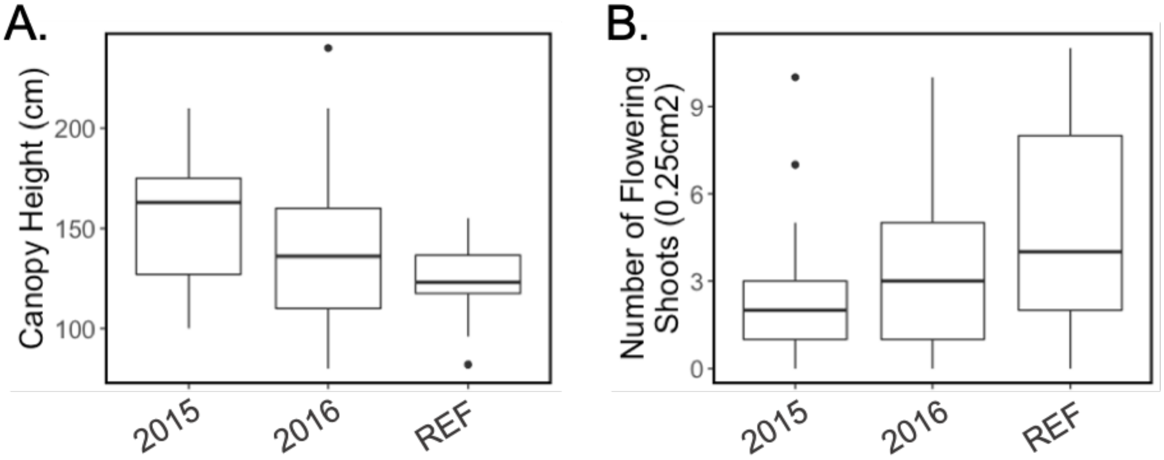


Figure S5. Shoot and rhizome mean biomass and epiphytic algae/diatom load by A) habitat type and B) strata. Plotted is the biomass data (least square mean estimate ± standard error) from August 2018, 2 and 3 years post-transplantation for the 2015 and 2016 restorations. ANOVA p-values are reported in the lower right (A) and upper left (B) hand corners. See Appendix 1: Methods for details.

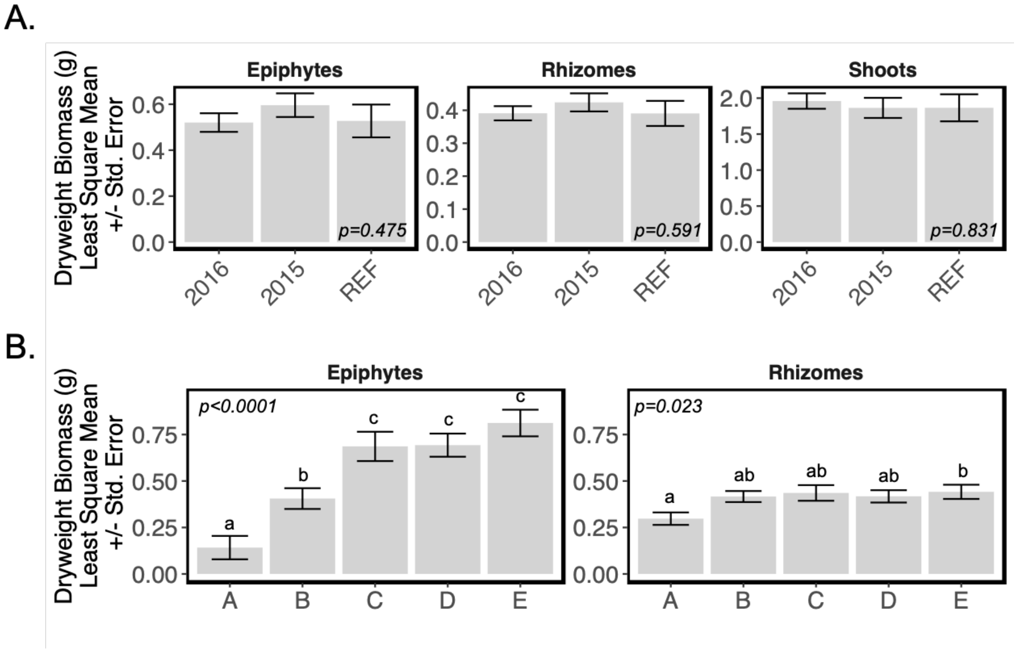


Figure S6. Species accumulation curve for all trapped species across all trapping years (2016, 2017, and 2018). The vertical dotted line represents where the lowest number of observations were, and therefore the comparison should be relative to the truncated value of 80 observations.

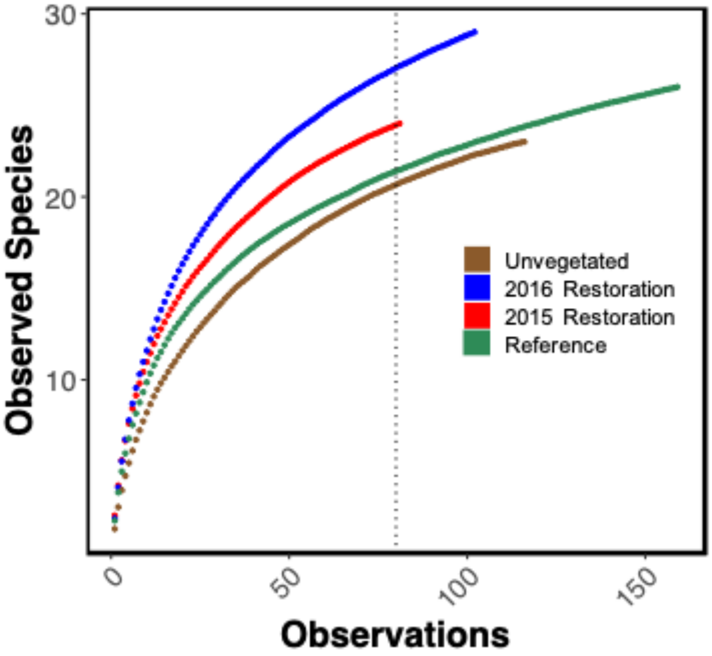


Figure S7. Most commonly trapped species of invertebrates (top) and fishes (bottom) organized by functional group. Photo credit: (1) Kat Beheshti, (2) Michael Langhans, (3) National Geographic, (4) Monterey Bay Aquarium.

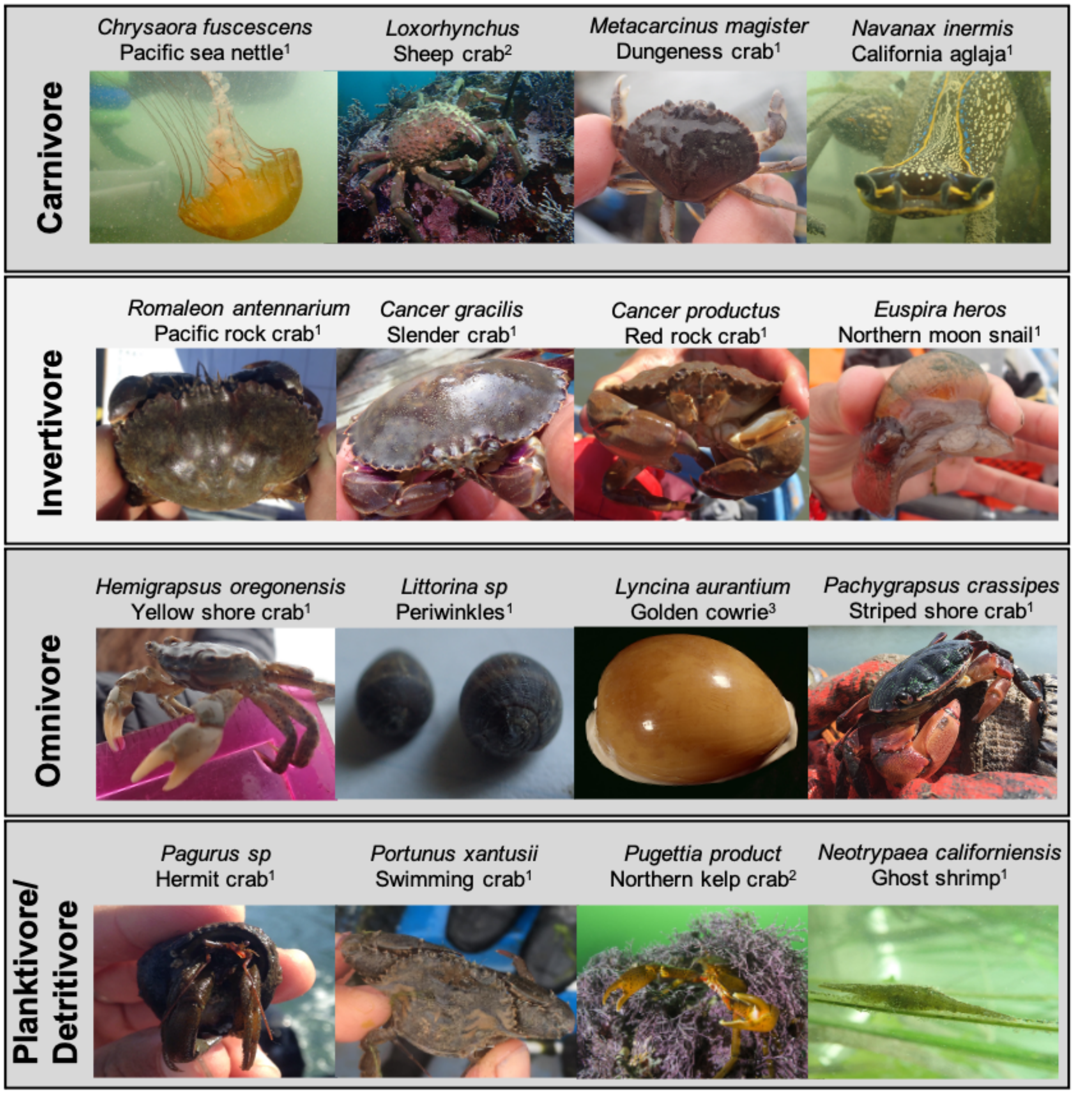


Figure S7 (continued):

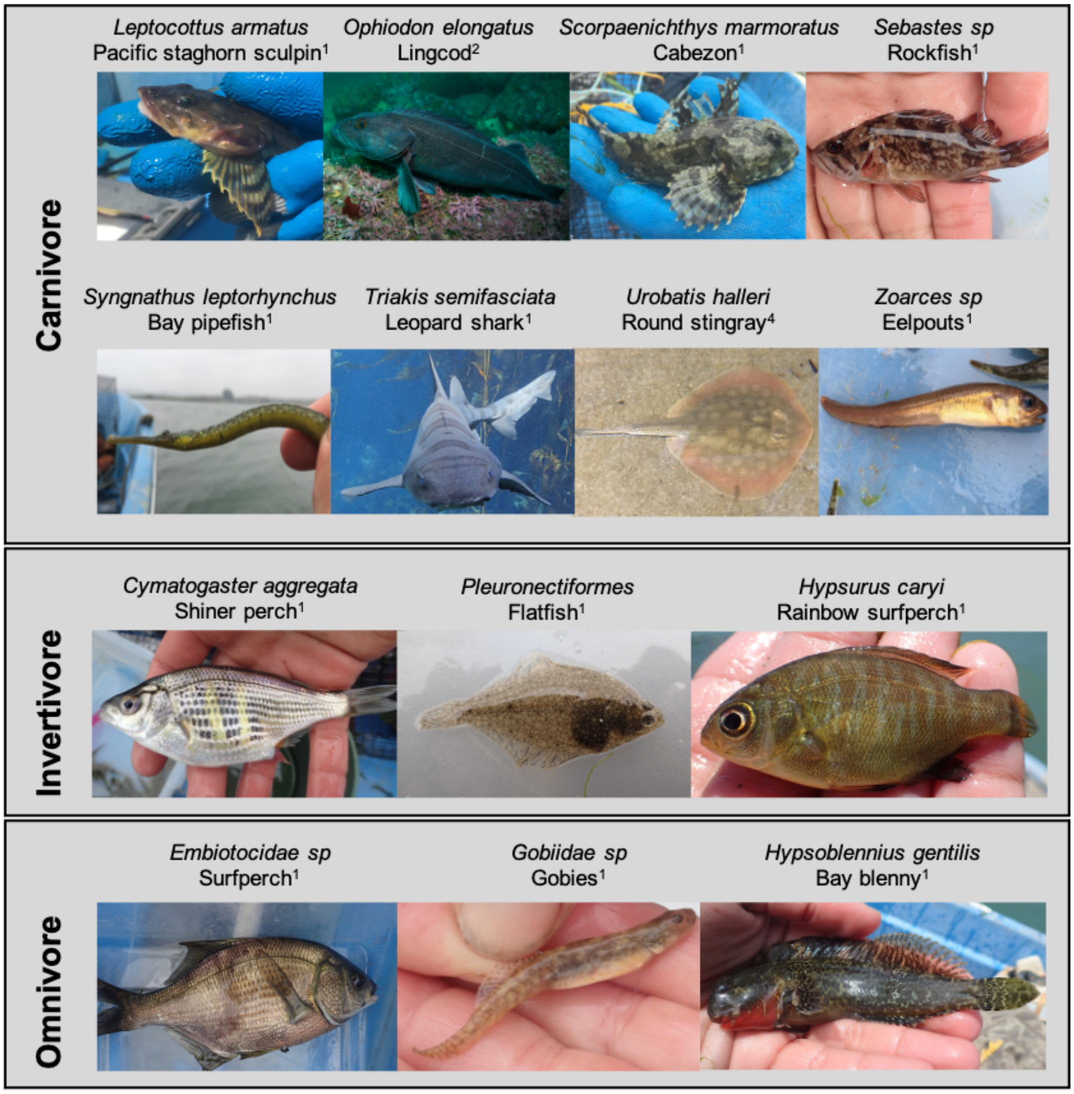


Figure S8. Least square means estimates for A) counts and B) resampling mean biomass (g, dry weight) of epifaunal grazers *Pentidotea resecata* and *Phyllaplysia taylori* by habitat type. The data presented is from the August 2018 monitoring effort. Different letters signify significant differences between habitat types (2015 restoration, 2016 restoration and reference plots). Count data is plotted as the least square means estimate ± standard error and biomass data as the bootstrap means (of resampling distribution) ± standard deviation (of the resampling distribution).

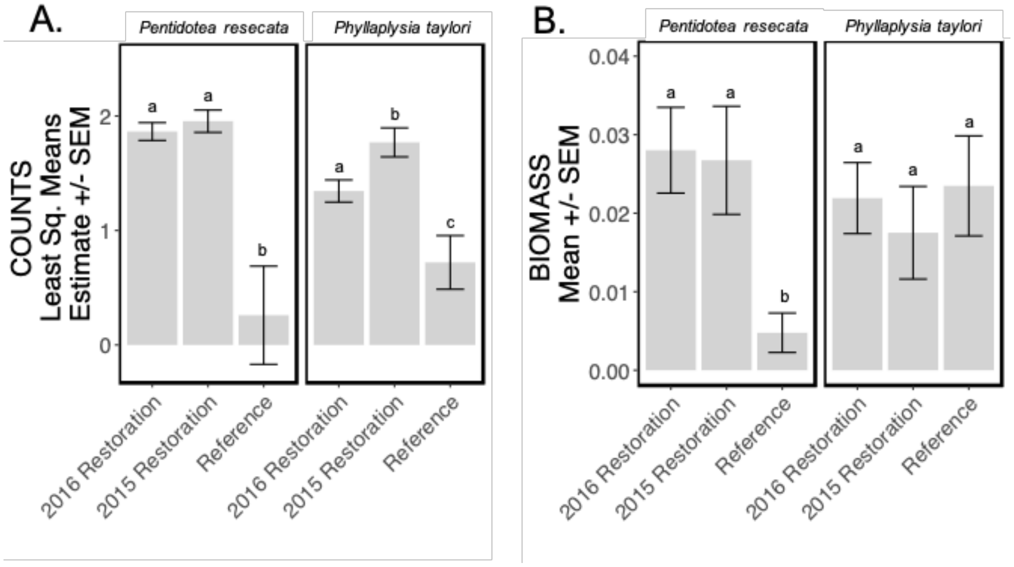


Figure S9. Mixed model output plotted as the least square means +/- standard error for A) water temperature (degrees Celsius), B) dissolved oxygen (mg/L) and C) pH, by habitat (brown=unvegetated, green=reference beds and red=restoration plots). Significant differences between habitat pairs are indicated by different letters.

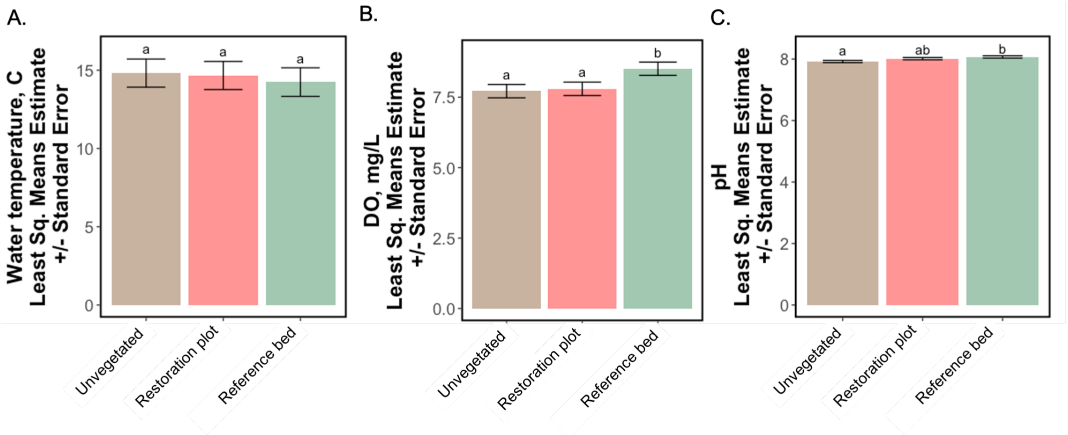


Figure S10. 10th percentile of dissolved oxygen and pH and 90th percentile of temperature data across all deployments. ANOVA p-values are reported in the lower right hand corner of the plots. Non-significant p-values imply there is no difference in the 90th percentile for water temperature or the 10th percentile for DO and pH when comparing habitat types across deployments.

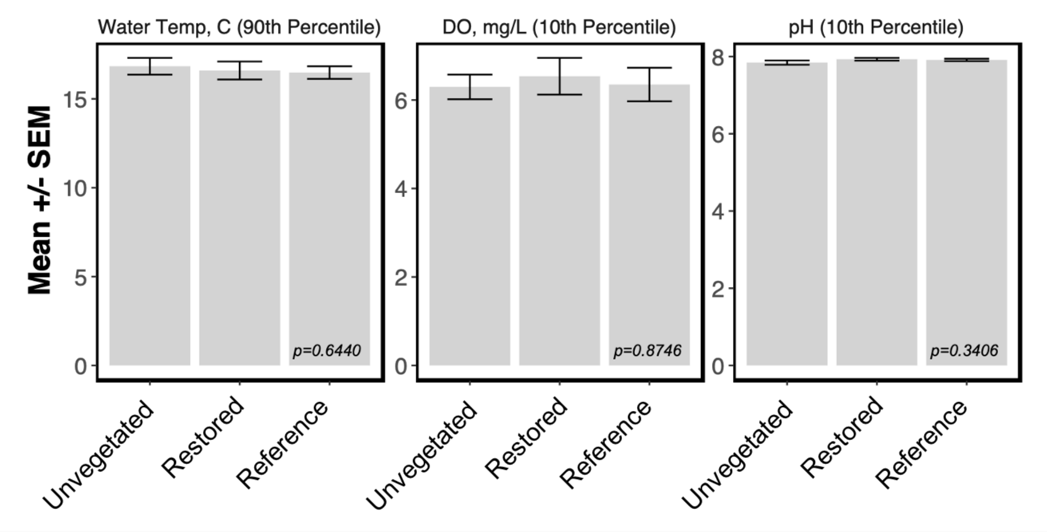


Figure S11. Organic carbon stocks (OC, kg/m^3) by habitat and strata, plotted as the Least Square Means Estimate ± SEM. Different letters denote significant differences between habitats according to Tukey's HSD post-hoc tests. Unvegetated plots are in brown, restored plots in red, and reference plots in green. Stratum A (nearest to mouth of estuary) is characteristically sandy while stratum C is silty.

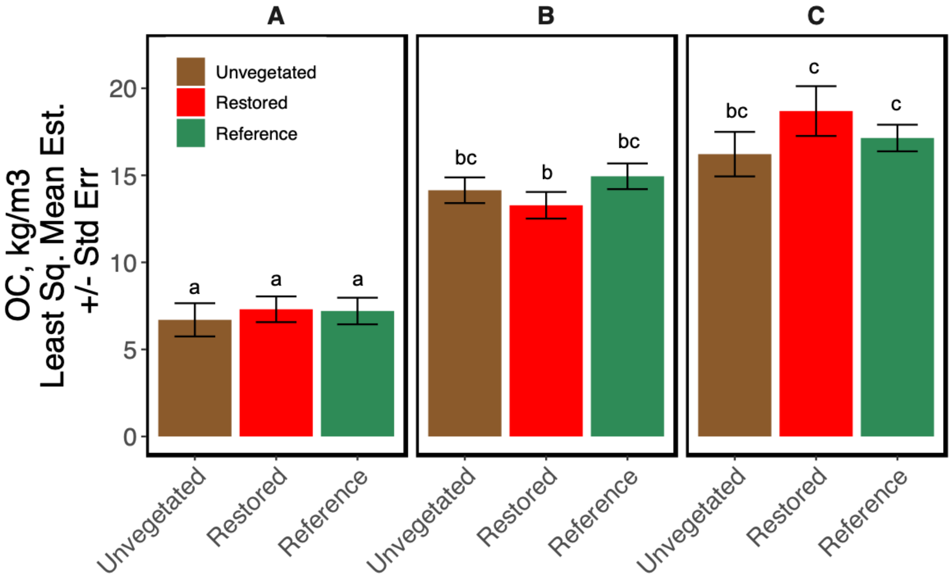
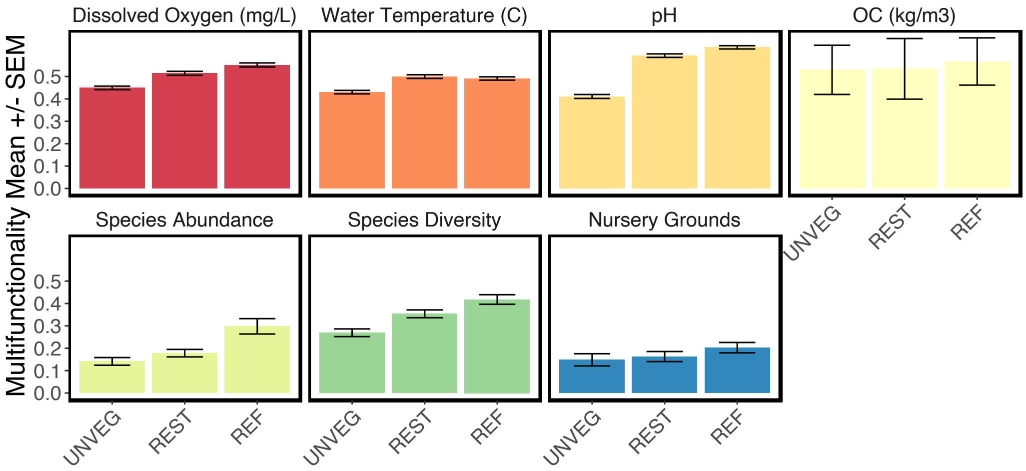


Figure S12. Average multifunctionality (± SEM) broken down by function. Top row is biogeochemical functions and the bottom row is biological functions. The y-axis is kept the same across functions to compare the relative contributions relative to the (best) 95th quantile (5th quantile for water temperature).



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