

RESEARCH ARTICLE

Burrowing crabs and physical factors hasten marsh recovery at panne edges

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Abstract

Salt marsh loss is projected to increase as sea-level rise accelerates with global climate change. Salt marsh loss occurs along both 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, but remains poorly understood. We conducted a two-year field investigation in a central California estuary to identify key factors associated with panne contraction or expansion. Our study explored how an abundant burrowing crab, shown to have strong negative effects on marsh biomass near creek edges, affects panne dynamics. We also explored which physical panne attributes best predicted their dynamics. To our knowledge, ours is the first study of panne dynamics in a California marsh, despite how ubiquitous pannes are as a feature of marshes in the region and how often extensive marsh dieback occurs via panne expansion. 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 detected near creek edges in a previous study, 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.

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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 [1, 2]. 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 [3]. The degradation of salt marsh habitat is of great concern, especially in the face of accelerating sea-level rise [1, 4]. Since the 1800s, it is estimated that 25–90% of salt marsh habitats have been lost [5, 6]. 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) [7, 8]. From the perspective of coastal managers and practitioners, studies that identify drivers of marsh loss and recovery are critical for maintaining existing wetland habitat and informing restoration design. Yet, few studies have explored both physical and biological drivers of interior marsh loss, and rarely have researchers compared, during the same time period, marsh evolution across the marsh plain, from creek edges to the marsh interior. Our study is the first to explore the relative importance of physical and biological factors in driving panne dynamics in a California marsh, while also comparing how an ecosystem engineer affects marsh plants along creek versus panne edges.

Loss of vegetation can occur along tidal channel or creek bank edges (hereafter creek edges) and in the marsh interior [9]. Along creek edges, wave erosion can undercut the marsh scarp and lead to erosional events where large sections of marsh are lost [2, 10]. Insufficient sediment supply [11, 12], low belowground marsh biomass [13], and algal wrack deposition [14] further hasten creek edge retreat. Features that reduce wave fetch and intensity of wave or boat wake action such as oyster reefs can slow salt marsh erosion [15]. Similarly, benthic diatoms secrete extracellular polymeric substances that both enhance sediment accretion and cohesion and reduce erosion [16, 17]. Marsh aboveground vegetation builds elevation capital [18] by slowing water flow and facilitating surface sediment deposition, while belowground plant roots and rhizomes stabilize sediments, prevent erosion and contribute to building marsh elevation [19].

In the marsh interior, unvegetated patches can form, expand and coalesce leading to massive marsh dieback [20, 21]. 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 [19, 22, 23]. Such deterioration of the marsh facilitates further erosion and increased inundation triggering marsh dieback [19, 24]. These poorly drained mud depressions, devoid of vegetation are called salt pannes. Salt pannes (hereafter ‘pannes’) are also referred to as salt pans [20, 25], tidal flats, saline supratidal mudflats, salterns [26], pools [27, 28], tidal ponds [29], or pond holes [10] (S1 Table). While many distinguish pannes from ponds and consider them to be two separate features of the marsh landscape [29, 30], 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 are poorly understood and likely vary across systems [20]. Pannes are thought to be formed by biogeomorphological processes [31] or physical stressors such as topographic depressions [32], tidal litter, waterlogging, or snow [33].

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 US National Estuarine Research Reserves found that marsh cover is

better predicted by elevation (and thus affected by sea-level rise) than crab or burrow abundance, though there are likely to be interacting effects between the two [34]. For example, in New England marshes, crab (*Sesarma reticulatum*) abundance has increased due to sea-level rise [35] and overfishing of predators [36]. This has led to runaway herbivory in the low marsh and changes to edaphic conditions induced by sea-level rise allowing crabs to move into previously inaccessible marsh, due to decreases in substrate hardness [37]. Environmental conditions can also intensify herbivory by crabs; for example, during and after periods of drought, grazing by *S. reticulatum* hinders marsh recovery along the border of die-off areas [38]. Burrowing fronts of *S. reticulatum* caused overgrazed creekheads which increased the drainage density and area of creeksheds and creek elongation, transforming the geomorphology of the marsh [39]. 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 [31]. A study across three sites in two separate Southern California estuaries found that crab (*Pachygrapsus crassipes* and *Uca crenulata*) effects differed across sites and marsh plant species and when detected were positive [40]. 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.

Most investigations of panne dynamics and of crab effects have occurred on the US East Coast, thus studies are needed elsewhere, both to seek generality across systems and to inform local management. We examined panne dynamics in Elkhorn Slough, an estuary located in Monterey Bay, California, where salt marsh loss has been documented at creek edges and the marsh interior [41], resulting in net loss of 70% of its historical salt marsh habitat [42], a major concern for regional stakeholders [43]. The majority of marsh loss in Elkhorn Slough occurs in the marsh interior through the formation and expansion of pannes [41]. Creek edge loss is affected by increased tidal velocities resulting from an artificial harbor mouth [44] and eutrophication [14]. Creek edges are riddled with crab burrows, constructed and maintained by native grapsid shore crab, *P. crassipes*. *P. crassipes* is an omnivorous crab that is found at its highest densities along creek edges and low marsh elevations [34, 45]. Through both consumptive and engineering effects, *P. crassipes* has been shown to have strong negative effects on marsh plant biomass along creek edges, compromising the ability of the marsh to track sea-level rise and mitigate erosive forces [45]. Pannes were observed expanding during a period of severe drought (2012–2016) [46] and high water levels related to the warm water event known as “the Blob” (2013–2015) [47]. Panne dynamics remain poorly understood in the system and the majority of investigations [20, 24, 25, 27–29] 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 on panne dynamics, we conducted a two-year field experiment where we attempted to manipulate crab densities across nineteen pannes and evaluate panne response. We also explored how crab abundance and burrow density differed along creek versus panne edges using experimental data collected from studies conducted concurrently (2016–2018) at both areas of potential marsh loss. We failed to successfully manipulate crab densities and instead utilized the experimental plots as sub-samples to characterize the nineteen 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. Elkhorn Slough experienced system-wide interior marsh loss in the years leading up to 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 physical and biological factors in driving marsh loss or gain, an approach applicable to any marsh system.

Methods

Overview

We investigated dynamics at 19 pannes. Our study design initially involved experimental treatments manipulating crab densities replicated at each panne (S1 Fig). We installed three fenced enclosures per panne to prevent crab movement in or out of the experimental enclosures and either regularly removed or added crabs into the enclosures to simulate different crab densities; a fourth unfenced control plot per panne was also included in the design. Subsequent crab trapping revealed that intended treatments were unsuccessful; there were no significant differences in crab numbers or burrow density among treatments and high natural variation in crab and burrow densities across pannes (see Supplemental Information). Therefore, instead of examining differences among experimental treatments, we focused our analysis on examining differences among the 19 pannes. We used a multivariate modeling approach to examine relationships between potential physical and biological factors and panne contraction or expansion. For modeling of factors affecting panne dynamics, we used panne as replicate, averaging across treatment plots. Lastly, we compared the results from this study to results from concurrent work [45], to examine the role of crabs along creek [45] versus panne edges (this study).

Study site

This study was conducted in Elkhorn Slough, an estuary located in Monterey Bay, California. Tides in the estuary are semidiurnal with a mean diurnal range of 1.7 m, a spring tidal range of 2.5 m and a neap tidal range of 0.9 m [48]. The Mediterranean climate has temperatures averaging 11.1°C in the winter and 15.4°C in the summer [49]. The 18-yr average rainfall for the study system is 39.0 cm/year (S2 Fig). During our study period (2016–2018), there was an average of 49.4 cm/year, with totals of 52.5 cm in 2016, 68.7 cm in 2017, and 27.0 cm in 2018 (S2 Fig). 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 19 pannes to study in a ~3 km stretch of salt marsh along the northwest side of Elkhorn Slough (Fig 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, *S. pacifica*. Since our original focus was to conduct an experiment examining crab effects, we used criteria to select pannes that were physically similar to each other, to decrease variation in panne dynamics from other factors. We used geospatial analyses to select relatively similar pannes as follows (S3 Fig). 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 creek edge, 3) have a minimum 1 m buffer from the nearest panne, 4) have a diameter greater than 1.5 m,

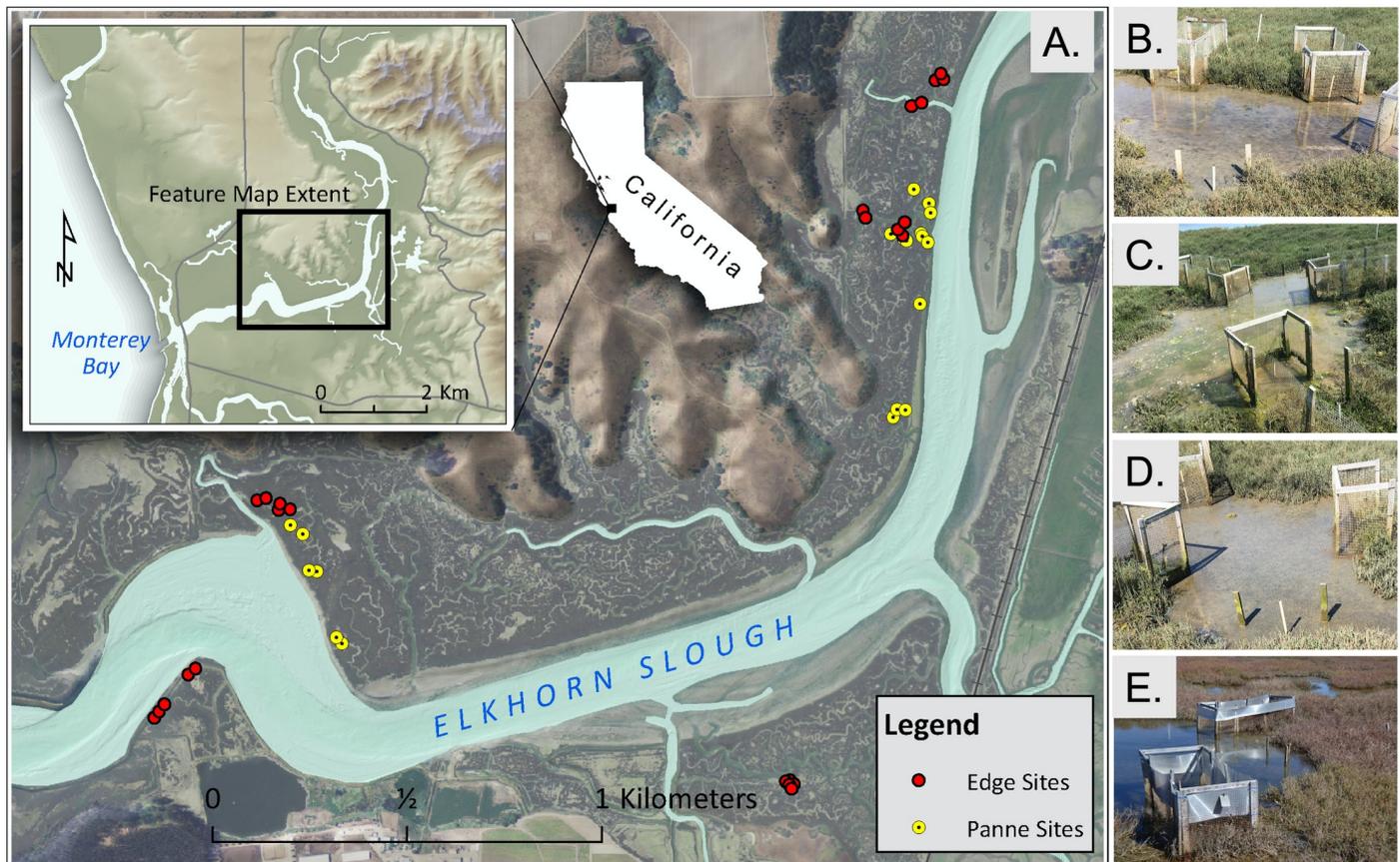


Fig 1. Study design from the landscape to plot scale. (A) Study map showing panne (yellow circles) and creek edge (red circles) studies courtesy of the U.S. Department of Agriculture, Farm Service Agency with topo-enhanced NAIP. Examples of the panne study and variation in panne size, pooling, and drainage, pre (B-D) and post (E) flashing installation (See [Supplementary Information](#)).

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and 5) have either no secondary creek or if a secondary creek was present the width had to be less than 1 m (hereafter ‘microchannel’). 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 creek 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 microchannel [50] width was 0.51 m (standard deviation = 0.28 m) and the maximum was 0.93 m, three of the pannes had no microchannel.

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 fence design by 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 sub-samples of each panne ($n = 19$). We derived variables measured at the plot level by taking the average across sub-samples per panne (e.g.

burrow density was estimated as the average number of burrows of four sub-samples per panne). Pannes are fairly variable, therefore characterizing each panne by averaging across four sub-samples was more accurate and robust than using a single sample (e.g. unfenced plots; see [Supplementary Information](#)), especially for these dynamic parameters. All other variables were taken at the panne scale (e.g. elevation, panne size and depth).

For the purposes of this study, we acquired a Scientific Collecting Permit from the California Department of Fish and Wildlife (SC 389; Project 8). This permit allowed us to install fenced enclosures into the marsh and regularly trap and release crabs. Since we were working exclusively with invertebrates (crabs) for this study, our work did not require review or approval by The Institutional Animal Care and Use Committee or IACUC. Additionally, no endangered or protected species were harmed during this study.

Field data collection and indices

To model potential correlates of panne contraction and/or expansion along the marsh-panne border, we examined the role of a suite of physical and biological factors ([S2 Table](#)) 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 as sub-samples. 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).

Tracking panne expansion and contraction. To assess whether pannes expanded or contracted over the study period and at what rate, we installed three (unfenced) to five (fenced) permanent transect line markers within each of the plots (See [Supplementary Information](#)). Zip ties or other permanent markers were used to mark the longitudinal start and end of each transect to ensure we were surveying the same points over time (See [Supplementary Information](#)). 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 ([S4 Fig](#)). To quantify contraction or expansion we calculated the average “marsh-panne boundary” difference per panne between 2016 and 2018. A positive value meant marsh colonization and panne contraction and a negative value meant marsh dieback and panne expansion. Our hypotheses for each of the parameters and indices outlined below can be found in [Tables 1](#) and [S2](#).

Crab activity. To monitor crab density across pannes we conducted 24 hr crab trapping efforts annually (August 2016, March 2017, August 2018) within each of four plots per panne and visually assessed crab presence or absence. We monitored crab burrow densities annually to track any changes over time by counting all burrows over 1.0 cm in 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 plot (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, is not the same as crab consumptive effects, measured as crab abundance [[45](#)]. Additionally, crab consumptive effects can be measured as either crab count, CPUE, or biomass [[45](#)]. We included each of these measures of crab activity in the initial model ([S2 Table](#)).

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 each of the four plots per panne. Rods were installed using a ladder and post driver until we reached hard ground or until the rod was exposed ~30 cm ([S1](#)

Table 1. Model terms, definitions, and hypotheses about panne contraction.

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.	✘
PC 1 (Depth and Elevation)	Principle Component that includes both panne depth and panne elevation	As PC1 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) and negative values indicate erosion (more rod exposed)	As panne accretion increases, contraction increases by raising pannes 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.	✓

During our study, the entire salt marsh in the 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 the statistical modeling results supported our hypothesis and “✘” indicates that the results did not support our hypothesis.

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[Video](#)). More of the rod exposed over time indicated erosion or compaction and less of the rod exposed over time, accretion or expansion. 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 ([S2 Table](#)).

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 [51]. 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 ([S2 Table](#)). 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 ($n = 20$) 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. Here we present data comparing the absolute differences for each response variable between 2016 and 2018 only.

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. 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 ([S2 Table](#)). This was done in 2016, 2017 and 2018 at each of the four replicate plots per panne, we are presenting the absolute differences between 2016 and 2018 only.

Indices for panne depth, elevation, size, and distance to nearest panne. Using a LiDAR Digital Elevation Model (2018), we estimated 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 (S5 Fig). We applied a 1 m 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 pannes. We did not detect a significant positive elevation bias due to vegetation [52]. Panne depth was 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’) (S2 Table).

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

To compare crab and burrow densities in panne vs. creek edges, we summarized data at the block level for panne ($n = 19$) and creek ($n = 25$) edges [45]. 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. Crab CPUE was averaged across 8 pit-fall traps for the panne study and 4 pit-fall traps for the creek study. Burrow densities were averaged across 4 replicate plots for the panne study, across 2 replicate plots for the creek study. Burrow densities for both panne and creek plots were expressed as density per m^2 . Data used to compare crab effects across both studies were collected in August 2018. To compare crab CPUE and burrow densities between creeks and pannes, we took a non-parametric approach and used a Kruskal-Wallis Test (two levels of factor ‘Location’; Panne and Creek Edges).

Results

Tracking panne contraction and expansion

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 *S. pacifica* growing around the panne edge; we did not observe plants colonizing the panne area via seed.

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 (S6 Fig; lower elevation associated with deeper pannes and higher elevation associated with shallower pannes). Therefore, we developed a Principle Component variable combining these two variables, 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. None of the other variables showed significant covariance; they each had low VIF scores (<2).

The stepwise regression identified the best predictive model out of the initial 14 parameters included (S2 Table). 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 was negatively associated with panne contraction (Slope = -1.169), the larger the panne, the lower observed panne contraction. PC1 (Depth and Elevation) was positively associated with panne contraction (Slope = 4.559), with higher elevation and shallower pannes contracting more than low elevation deeper pannes. Nearness between focal pannes and adjacent pannes was negatively associated with panne contraction (Slope = -3.289), with larger distances between pannes correlated to less contraction. Crab burrowing activity was positively correlated with panne contraction (Slope = 0.315), as burrow density increased, so did panne contraction. Lastly, sediment dynamics was positively associated with panne contraction (Slope = 1.788); pannes that accreted contracted more than pannes that showed no change over the study period or eroded (Table 2 and Fig 2).

We developed a conceptual model of panne dynamics that applied previous findings from the literature and the significant drivers identified by the model in our study, as another way to visualize the complex processes that are likely driving panne dynamics (Fig 3).

Comparison between crabs at bank edge vs. pannes

Crab CPUE was significantly greater along creek edges relative to panne edges (Kruskal-Wallis; $H(1) = 19.02$, $p < 0.0001$) (Fig 4A). Additionally, burrow density was significantly greater along creek edges relative to panne edges, with approximately 4x as many burrows observed along creek edges (Kruskal-Wallis; $H(1) = 19.74$, $p < 0.0001$) (Fig 4B).

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” [53]. Much marsh degradation results from panne formation and expansion, but the mechanisms behind panne dynamics are not broadly understood. Some

Table 2. Multiple regression model output.

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	-

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 terms are ordered by their relative importance (absolute value of the t-Ratio). A negative (-) 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.

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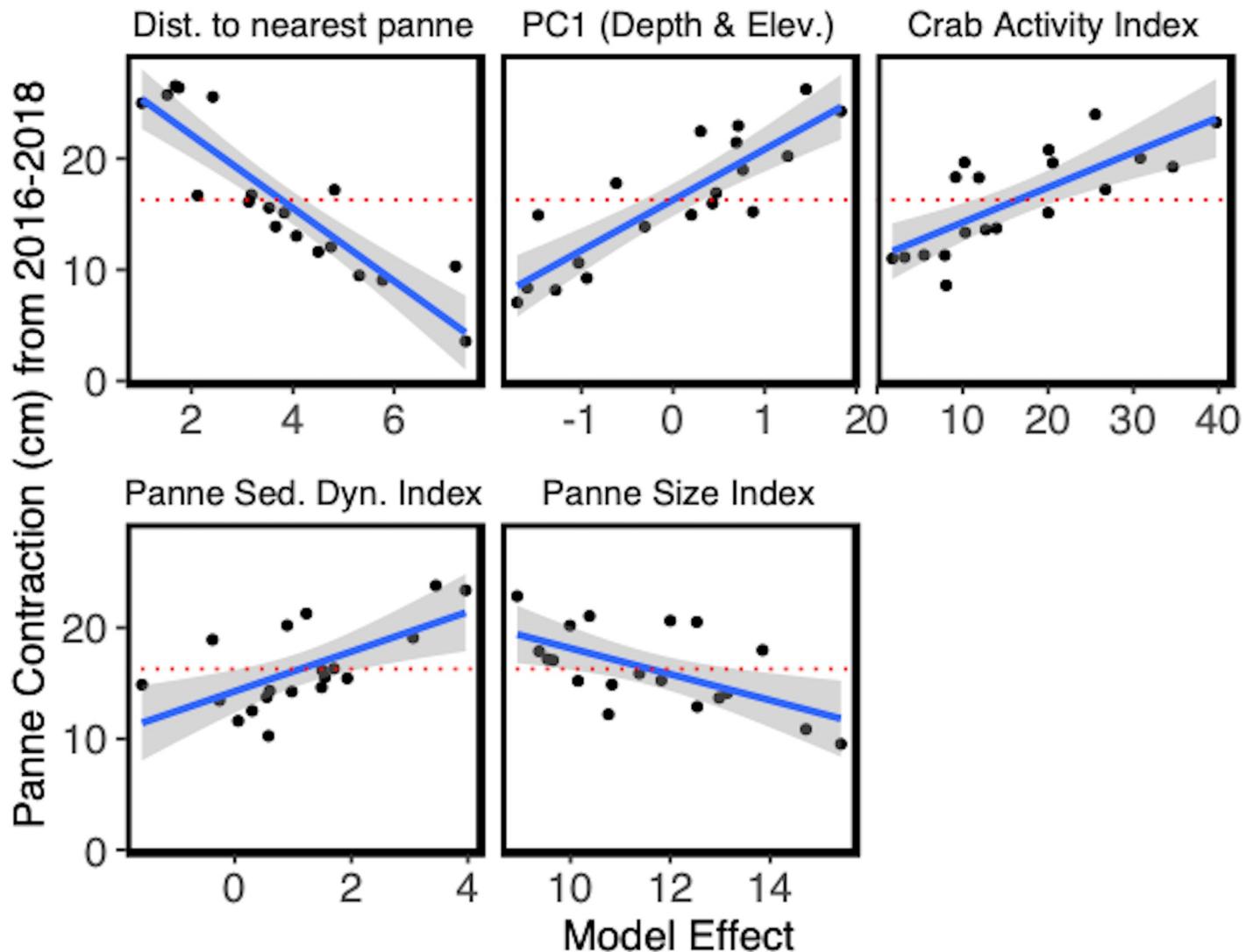


Fig 2. Partial leverage plots for all of the best-fit model effects. Plotted is the movement of marsh into the panne area (panne contraction along marsh-panne boundary) in cm. The dotted red horizontal line represents the average marsh-panne boundary movement from 2016–2018 of 16.298 cm. Each partial leverage plot includes the 95% C.I. For a list of the parameters included in the plotted indices, see [Table 1](#).

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seminal studies have characterized key drivers [10, 27, 33, 50, 54]. 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 (i.e. herbaceous grass-dominated marshes). Additionally, while there have been multiple studies demonstrating that salt marshes are structured by both physical and biological factors and their interactions [35, 55, 56], most investigations of panne dynamics have focused almost entirely on geomorphology [32, 49, 57; for exception see 30]. In exploring how physical (panne attributes and sediment dynamics) and biological (crab activity) factors affect marsh recovery along panne edges, our study provides a novel perspective on drivers of panne dynamics along the US west coast.

Salt panne dynamics are strongly controlled by drainage [10, 20, 33]. In Plum Island Estuary (Massachusetts, USA), salt marsh has kept pace with sea-level rise while panne area has

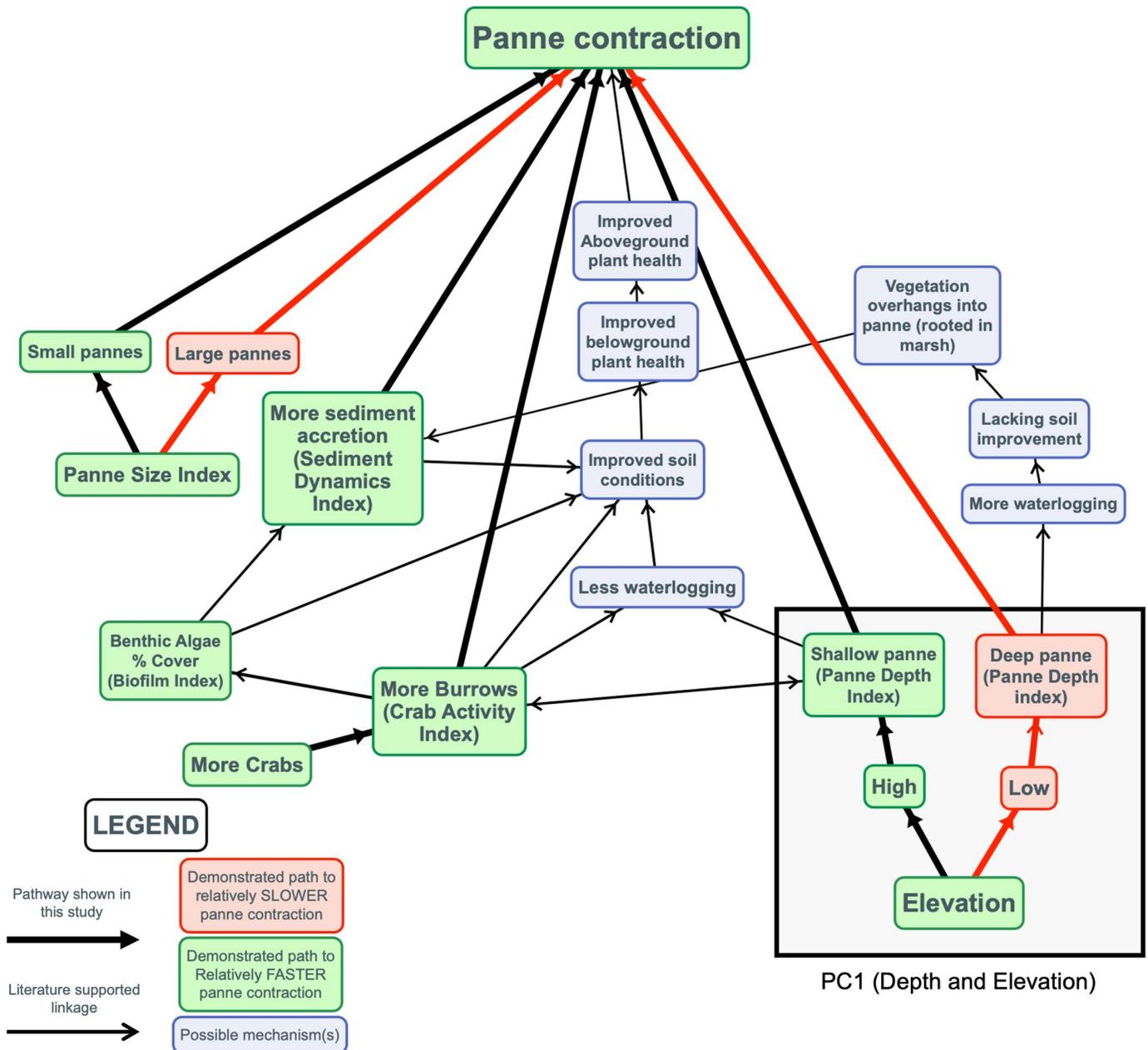


Fig 3. Conceptual model of panne contraction and possible mechanisms. Bolded arrows indicate relationships or main model terms that correlated to panne contraction and were shown in our study. Narrow arrows indicate pathways that were not demonstrated by our study but are likely to play a role based on marsh dynamics literature. 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.

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increased and drainage density decreased, suggesting that drainage is a stronger driver of panne dynamics than sea-level rise [50]. 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) [50]. 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

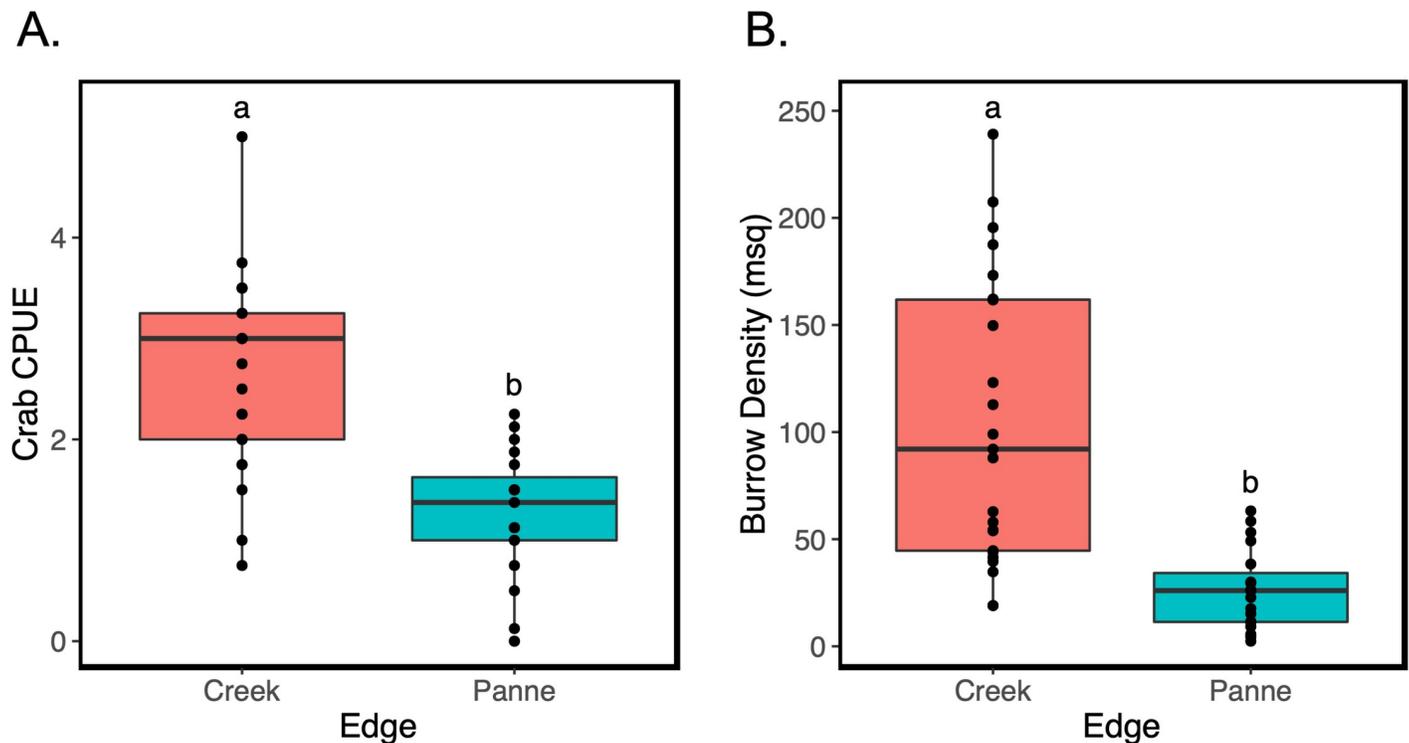


Fig 4. Comparison of crab CPUE and burrow density along panne versus creek edges. (A) Crab CPUE along panne versus creek edges. (B) Burrow density (# per m²) along panne versus creek edges. The data are plotted as points overlaid on top of boxplots. Pink points and boxplots represent panne edges and blue points and boxplots represent creek edges. Different letters denote significant differences ($\alpha = 0.05$) between panne and creek edges.

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high elevation pannes than deeper low elevation pannes (Figs 2 and 3 and S6). 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 [30]. 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 greater. This may be 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 resulting in marsh recovery while larger pannes experience wave-induced erosion and bed shear stress which causes pannes to deepen and expand [55] often coalescing into other pannes [20]. Our results complement previous work by showing greater rates of panne contraction for smaller versus larger pannes (Figs 2 and 3).

Panne density has been shown to be negatively correlated to creek density [33], further supporting the hypothesis that poor drainage (fewer creeks or microchannels) promotes panne formation and persistence. Our results differ from those of Goudie [33] and indicated that marsh recovery was greatest when pannes were near to one another (Figs 2 and 3). 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 are of great importance and affected by panne elevation [19, 24], depth [50], and size [28]. The results of our study also showed that local

increases in marsh elevation (due to panne accretion or soil expansion) was positively correlated with panne contraction. Conversely, the pannes with local marsh elevation loss at the marker rods showed the lowest rates of marsh recovery. Accretion can improve soil conditions by possibly both raising the panne to an elevation within the growth range of marsh plants and alleviating stressors associated with waterlogging (Fig 3). Our results mirror previous work by showing an association between accretion and marsh recovery [50]. We suspect that increased elevation and improved 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 below the growth range of marsh plants [19, 33, 50, 56].

While crab burrows have been shown to have positive effects on marsh productivity, mainly by oxygenating anoxic sediments [58] or increasing nutrient uptake [59], crab burrows have also been found to increase erosion and creek formation [60, 61] and elongation [62]. In Argentina marshes, crab burrows facilitate the formation of pannes through loss of elevation (see Fig 9 in [30]). In our study, we observed crab burrows having a positive effect on panne contraction (Fig 2). In Elkhorn Slough, it is likely that the positive effect of burrows is due to increased drainage [62] and reduced waterlogging stress [57], which outweighs any possible negative effects (Fig 3).

Crab effects are context-dependent

Top-down effects on vegetation can be very strong [63, 64], but such effects will always interact with physical factors and thus may vary in strength (i.e. snail grazing in marshes with drought [65], pollinator and herbivore interactions with plants across environmental gradients [66], foraging behavior of coral reef fishes with distance from reef [67]). Crab effects on salt marshes have been shown to have such context-dependent variation when examined across different estuaries [34, 40, 68]. 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) [68], 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 [58]. In another example showing positive effects of crabs on marsh vegetation, Holdredge and colleagues [59] 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% [59]. 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 creek edges (negative effect) [60] and in a separate study, consumer pressure by crabs was shown to prevent marsh colonization of pannes [64]. Crab effects can also vary by spatially and by scale. For example, research by Vu and colleagues [69] showed that *S. reticulatum* increases erosion at small scales, but increases drainage promoting marsh health at large scales. Building on this past work [45], our study in an Eastern Pacific salt marsh shows how interactions between similar crab behaviors (burrowing) and marsh plants can vary depending on the dominant stressor (erosion vs. poor drainage), which is often spatially explicit (creek edge vs. panne edge).

Based on the results of this and previous studies, effects of *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 creek edges [45]. 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) (Fig 3). The different direction of crab effects and spatial differences in abundance are likely due to different physical factors driving dynamics along creek versus panne edges. For example, creek dynamics are driven by erosive processes [2] 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 in our study) to creek edges can have entirely different relationships between the same physical and biological drivers.

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 [46] and a warm, high water event [47] that coincided with a period of 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 [70]. Precipitation may play an important role in facilitating the recovery of the marsh along these physically stressful panne edges in Mediterranean marshes prone to high salinities (S2 Fig). In San Francisco Bay, during one of California's historic droughts (2011–2015), vegetative cover in a restored, former industrial salt-evaporation pond, increased at a rate 10.4 times slower than preceding years (2009–2011) when the state was not in a drought and salinities were significantly lower [71]. In Tijuana River Estuary, heavy rains (1978–1980) flushed hypersaline soils resulting in a substantial (40%) increase in marsh plant biomass [72]. The intensity and frequency of rainfall is likely a factor in the rate of marsh recovery, especially following periods of severe drought; the marsh may respond differently to a few large winter storms (high intensity, low frequency) versus an extended wet season (low intensity, high frequency) [73]. 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. We also found that local increases in elevation at our marker rods correlated with panne recovery. Some studies have indicated that sea-level rise will increase the rate of panne formation, expansion, and coalescence, further contributing to marsh loss [24, 53], while others suggest that poor drainage, insufficient accretion, and poor creek connectivity explain panne formation [50]. 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 [33] and crabs may become more abundant as low marsh extent increases [35]. This has already been demonstrated in New England marshes [35, 62]. 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. As a reminder, our study was initially designed as a crab experiment and we specifically chose pannes that were relatively stable and did not vary greatly in geomorphology to reduce the possible confounding factors that may have impacted our ability to detect treatment effects. This makes our findings all that more

compelling considering that we were able to identify predictors of panne contraction across 19 pannes with slight physical differences. A recent study by Himmelstein and colleagues found that stable interior pannes ('ponds') in Chesapeake Bay had lower porewater sulfide and ammonium concentrations, greater shear strength, and higher surrounding plant biomass than unstable interior pannes, which were more prone to expanding and coalescing with nearby pannes [74]. We recommend future studies encompass the actual variation in panne characteristics seen across the estuary (including stable and unstable pannes) and expect patterns shown here to only strengthen with the inclusion of pannes of a wider range of sizes, shapes, elevations, and statuses. Relatedly, 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 (S7 Fig).

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 [9, 30, 74] 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 meteorological and oceanographic events, such as those that preceded and occurred during our study, affect marsh dynamics and resilience.

Supporting information

S1 Table. 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.

(PNG)

S2 Table. Full list of model terms. Non-significant terms were excluded from the final model and are denoted in italics. Terms that were significant and included in the final model are bolded. For each term we have included the definition and hypothesis about how that factor may influence panne dynamics. Terms are organized by category (crab data, geomorphology, sediment, and cover).

(PNG)

S1 Fig. Photos of study design. (A) Study design with treatments labeled at single block, (B) Above Ambient Crab experimental plot with the flashing installed flush to the fence 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 S4 Fig).

(PNG)

S2 Fig. Rainfall over the study period. Time series of monthly precipitation (cm) from 2000–2018. The grey points represent the water years leading up to the study (2000–2015) and the blue points represent our study period (2015–2018). The dotted red line represents the long-term average annual precipitation of 39 cm. Data are from the NOAA National Estuarine Research Reserve System (NERRS). System-wide Monitoring Program. Data accessed from the NOAA NERRS Centralized Data Management Office website: <http://www.nerrsdata.org/>; accessed 21 September 2021.

(PNG)

S3 Fig. Heat map of salt marsh zones. Areas where there has been net gain (blue) or loss (red) of habitat from 2004–2012. Areas of high gain or loss (dark colors) were not included in

this study. NAIP imagery, Courtesy of the U.S. Department of Agriculture, Farm Service Agency.

(PNG)

S4 Fig. Schematic of how marsh-panne boundary was monitored over time in fenced 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.

(PNG)

S5 Fig. 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. Courtesy of the U.S. Geological Survey.

(PNG)

S6 Fig. Relationship between elevation and panne depth. This inverse correlation 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.

(PNG)

S7 Fig. Elevation by panne size. As panne elevation increases, size decreases ($R^2 = 0.15$). Similar patterns were observed in Escapa et al. [31] (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.

(PNG)

S8 Fig. Experimental results. (A) crab CPUE, (B) burrow and (C) crab biomass data from 2018 plotted by treatment. To demonstrate that there was little evidence of caging effects on drivers related to sediment dynamics and/or crabs, we have shown the (D) panne ($F_{3,72} = 2.46$, $p = 0.07$) and (E) marsh ($F_{3,72} = 2.45$, $p = 0.07$) rod data.

(PNG)

S9 Fig. Treatment vs. elevation effects on marsh-panne boundary. There was no significant effect of treatment on marsh-panne boundary movement, or the rate of panne contraction ($F_{3,3} = 0.38$, $p = 0.77$). There was an elevation effect, with significantly greater rates of panne contraction for high versus low elevation pannes ($F_{1,1} = 4.77$, $p = 0.03$). Elevation data is collected at the panne level, treatment data is collected at the sub-sample level and averaged across all pannes. There was no treatment* elevation effect. Plotted is the least square mean \pm standard error. Treatment data (white bars) is plotted to the left of the dotted gray line and elevation data (gray bars) is plotted to the right of the dotted gray line.

(PNG)

S1 Video. Installation of galvanized conduit rods. Metal rods (9') were installed in the panne and marsh portion of each of the sub-samples at all nineteen pannes ($n = 152$). Rods were installed into the panne and marsh area of each experimental plot across all nineteen blocks, or pannes. Link: <https://youtu.be/nHdfjg4o-Bw>.

(MP4)

S1 Text. Crab experiment review. Methods and results are described in detail below. We designed a two-year field study to determine whether crabs affected salt panne dynamics and

whether such effects varied by elevation.
(DOCX)

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