



Variable Effects of Experimental Sea-level Rise Conditions and Invasive Species on California Cordgrass

Julie A. Gonzalez^{1,2} · Matthew C. Ferner² · Edwin D. Grosholz¹

Received: 3 January 2024 / Revised: 19 June 2024 / Accepted: 24 June 2024 / Published online: 8 July 2024
© The Author(s) 2024

Abstract

Sea-level rise (SLR) will produce unprecedented changes in tidal marsh systems that already cope with daily tidal fluctuation, disturbances from storms, and salinity changes from droughts and runoff events. Additionally, negative impacts from non-native invasive species may alter marsh plants' ability to respond to SLR stressors like increased inundation and salinity. Increasingly, tidal marsh communities must tolerate both changes in the physical environment from SLR and increased risk of invasion by non-native species. To assess the response of a threatened tidal marsh cordgrass (*Spartina foliosa*) to both stressors, we implemented a field experiment in San Francisco Bay, CA, USA, exposing cordgrass to a treatment that extended tidal inundation projected with SLR using a recently developed in situ method. At one of two field sites, we also enclosed the cordgrass with or without the invasive European green crab, *Carcinus maenas*. We found that cordgrass responded negatively to longer inundation, although these effects varied by site and year. In higher inundation treatments, cordgrass survival increased with increasing surface elevation of the plot. Cordgrass survival was lower in the presence of invasive green crabs relative to controls. We did not find interacting effects of responses to increased inundation and invasive species presence, which highlights the need to consider how latent or sequential effects of multiple stressors may affect ecosystems. This study demonstrates significant biological responses to invasive species presence and increased inundation. Evaluating relative effects and timing of multiple stressors, especially those induced by climate change and invasive species, will help us to manage threatened ecological communities in a changing world.

Keywords *Spartina foliosa* · Salt marsh · Multiple stressors · Estuarine · *Carcinus maenas* · Inundation

Introduction

Sea-level rise (SLR) is projected to produce unprecedented changes in tidal marshes, especially those that have experienced habitat degradation from land use change and other stressors (Dahl 1990). Tidal marshes already must cope with daily tidal fluctuations as well as stochastic disturbances from large storms and salinity changes from droughts and runoff events. SLR is projected to increase salinity and

inundation in estuaries (Cloern et al. 2011) and periods of hypoxia (Morris et al. 2002) likely increasing the edaphic stress experienced by estuarine communities. Increased inundation associated with SLR can negatively impact tidal marsh plant communities through increased levels of hydrogen sulfide or other toxins that directly impact rhizomes and roots (Cronk and Fennessy 2016) and limit biomass, growth, and nutrient uptake (Mendelssohn and Seneca 1980; Koch and Mendelssohn 1989). Tidal marsh plant distribution within estuaries is influenced by a combination of factors, including tolerance to inundation and salinity stress from tidal fluctuations (Bertness and Ellison 1987). These stressors determine the range limits of plant species along the marsh plain, reflecting their varying degrees of tolerance. Consequently, as marsh plants have differential responses to the rate and magnitude of SLR-driven increases in inundation, species distributions will likely undergo shifts over time.

In addition to abiotic factors, such as inundation and salinity, biotic interactions play a critical role in structuring

Communicated by R. Scott Warren

✉ Julie A. Gonzalez
gonzalez@sfsu.edu

¹ University of California, Davis, One Shields Ave, Davis, CA, USA

² San Francisco Bay National Estuarine Research Reserve and San Francisco State University, 3150 Paradise Drive, Tiburon, CA 94920, USA

tidal marsh communities. These interactions encompass competition, grazing, and facilitation, which can influence the distribution and abundance of plant species within marsh ecosystems (Bertness 1985; Bertness and Grosholz 1985; Bruno and Bertness 2001; Emery et al. 2001; Pennings et al. 2005; Alberti et al. 2007). Effects of multiple stressors, whether biotic or abiotic, can be additive, synergistic, or antagonistic. On the east coast of the USA, Crotty et al. (2017) found that SLR facilitated the expansion of native crabs (*Sesarma reticulatum*) into the high marsh. This expansion, coupled with increased inundation, led to synergistic negative impacts on a native habitat-forming smooth cordgrass, *Spartina alterniflora*, ultimately contributing to marsh die-off. Increased inundation resulted in sediment softening that facilitated burrowing and grazing by crabs which decreased both above and belowground cordgrass biomass. Using projections from models assessing SLR scenarios, they found that marshes previously impacted by die-off were projected to be more impacted by future SLR. Since crabs will readily move from areas with harder sediment to adjacent habitat with softer sediment to forage (Crotty et al. 2017), marsh die-offs may increase exponentially with SLR and without predation control of *S. reticulatum*. However, the effects of crabs on tidal marsh plants vary contextually, ranging from severe negative impacts, such as runaway herbivory (Holdredge et al. 2009; Bertness et al. 2014), to positive associations, such as sediment oxygenation, characterized by increased oxidation-reduction potential (redox), through bioturbation (Bertness 1985; Daleo et al. 2007). Furthermore, physical factors influenced by inundation, such as sediment hardness, may interact with other variables, such as tidal regime and species composition, leading to diverse outcomes across tidal marshes.

However, the increasing prevalence of non-native species invasions poses a significant threat to coastal ecosystems, driven in part by heavy shipping traffic and human activities (Gallardo et al. 2016). Non-native invasive species have been shown to disrupt native plant populations and alter nutrient cycling dynamics (Garbary et al. 2014; Gallardo et al. 2016), thereby impacting the overall resilience of coastal habitats. Consequently, the introduction of species that become invasive may compromise the ability of marsh plants to respond to stressors associated with SLR, such as increased inundation and salinity. In order to persist, marsh vegetation and the organisms that utilize it will likely need to withstand or adapt to both physical changes from SLR and impacts from non-native invasive species.

In this study in San Francisco Bay, CA, USA, we experimentally increased inundation in situ in areas of tidal marsh cordgrass (*Spartina foliosa*) and additionally exposed these experimental areas to the non-native European green crab, *Carcinus maenas*, that is invasive in this region. Parker

and Boyer (2019) suggest that marshes in San Francisco Bay are projected to maintain pace with moderate sea-level rise (SLR) and moderate to high sediment supply by 2100. However, as SLR rates escalate, higher marsh areas may transition to low marsh or face loss due to infrastructure, shoreline armoring, and other impediments to marsh migration on the landward side (Parker and Boyer 2019). Our objective is to ascertain the thresholds of inundation, spanning from current levels to projected scenarios, at which the growth and survival of *S. foliosa* become constrained. Furthermore, we aim to investigate the extent to which non-native invasive crab impacts contribute to these limitations. We also aim to evaluate the physical mechanisms that determine these biological responses. We gathered physical and biological data to understand how tidal marsh cordgrass responds to these two stressors. We hypothesized that (1) in the presence of increased inundation, cordgrass growth and survival, and redox potential, would decline, porewater sulfide would increase, and porewater ammonium would increase due to lower redox potential inhibiting transformation to nitrate; (2) in the presence of invasive crabs, cordgrass growth and survival would decrease, and redox potential, and porewater ammonium from crab excrement (Montague 1980), would increase; and (3) invasive crabs and inundation would interact to negatively affect redox potential and cordgrass growth and survival, despite any positive effects on redox potential from crab bioturbation.

Methods

Study Site

China Camp State Park, a component site of the San Francisco Bay National Estuarine Research Reserve, is a centennial marsh complex, formed during the rapid expansion of marshes in the region in the late nineteenth century, with extensive meadows of California cordgrass (*Spartina foliosa*) and little anthropogenic impact in comparison to surrounding marshes. This native cordgrass is a foundational species in the low-elevation marshes of San Francisco Bay, providing habitat and nesting grounds for various species such as Ridgway's rail (*Rallus obsoletus*) and salt marsh harvest mouse (*Reithrodontomys raviventris*). Restoration initiatives targeting the native cordgrass are widespread throughout the Bay, in large part through the California State Coastal Conservancy's Invasive *Spartina* [*alterniflora*] Project. However, San Francisco Bay faces escalating invasion pressure, with invasions becoming more frequent (Seebens et al. 2017). Additionally, the rapid spread of hybrid cordgrass (*S. foliosa* × *Spartina alterniflora*, Ayres et al. 2003) poses a significant threat to native *S. foliosa* populations. Despite its relative tolerance to inundation,

S. foliosa is projected to persist at moderate rates of sea-level rise (SLR, ~6 mm/year), with higher rates leading to a substantial decline (Parker et al. 2011). The present study was conducted within native cordgrass meadows at the Bullhead Flat and Buckeye Point sites within China Camp State Park (Fig. 1). San Francisco Bay, characterized by mixed semidiurnal tides, is expected to experience sea-level rise of between 10 and 20 cm by 2050 (Vitousek et al. 2017). Tidal range is 1.80 m in the vicinity of China Camp State Park (Gallinas Creek, NOAA tide station 9,415,052, <http://tidesandcurrents.noaa.gov>). A projected increase of 20 cm in sea level is anticipated to nearly double the current inundation time at the current mean higher-high water (MHHW) at nearby sites (Janousek et al. 2016).

Green Crabs

In addition to SLR, another potential stressor for cordgrass is the non-native European green crab, *Carcinus maenas*, which was introduced to San Francisco Bay in the 1980s,

has spread along the west coast, USA (Cohen 1998), and is considered an invasive species in this region. In San Francisco Bay, green crabs are abundant mostly in low intertidal marsh areas, often co-occurring with cordgrass, and can negatively impact the establishment of newly planted native cordgrass in San Francisco Bay (Gonzalez et al. 2024). Green crabs consume a broad range of smaller invertebrates including native bivalves, native crabs, and surface-feeding amphipods (Grosholz et al. 2000; Neira et al. 2006) and can out-compete native crab species for food (Cohen 1998). Its foraging also leads to poor survivorship of tidal flat fauna by lowering sediment organic matter, redox potential, and chlorophyll *a* (Neira et al. 2006).

Experimental Design

Small-scale mesocosm experiments exploring impacts of increased inundation (Spalding and Hester 2007; Cherry et al. 2009) may not reflect natural conditions as well as in situ experiments. Previous field experiments exploring

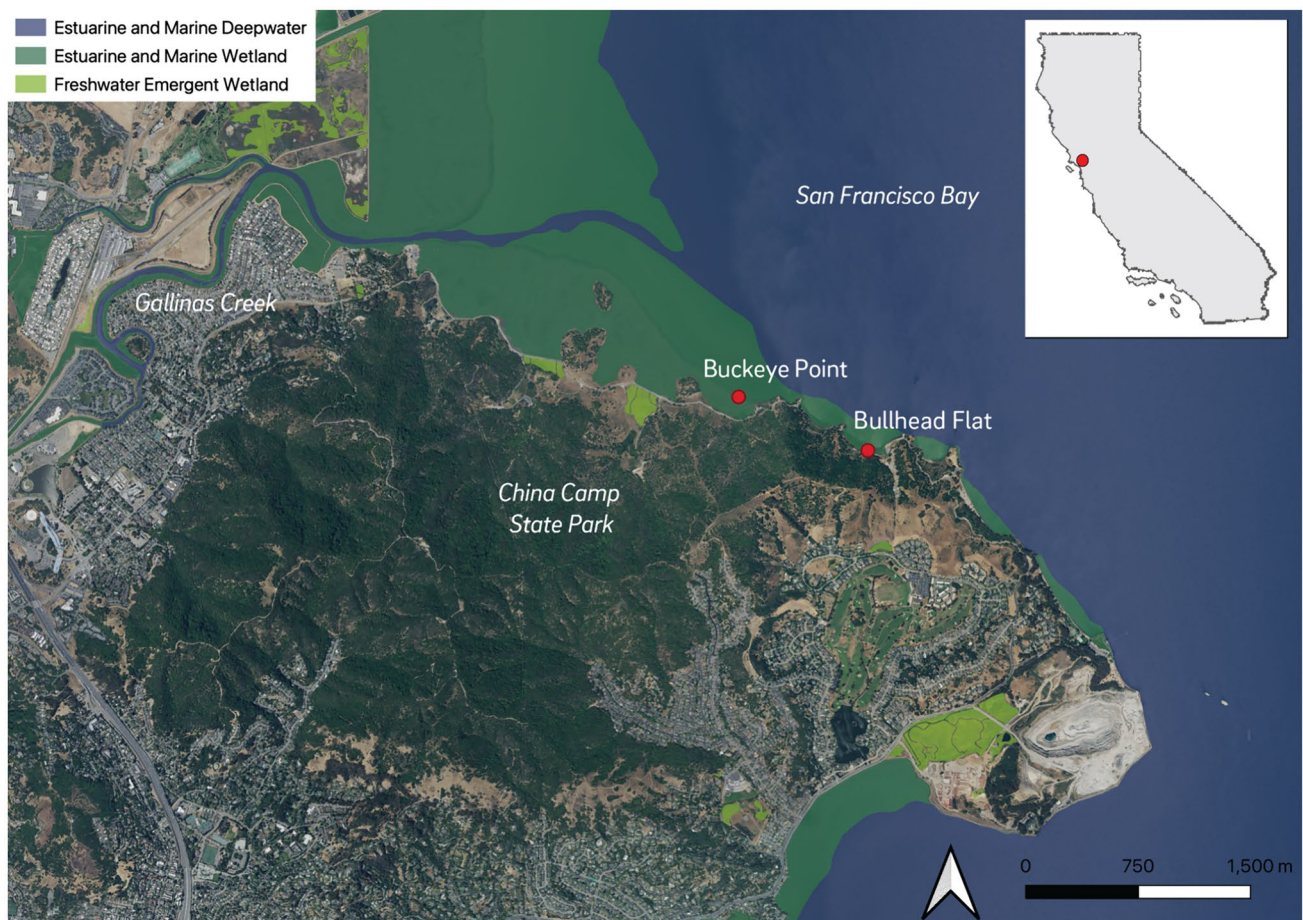


Fig. 1 A map of the study site showing the two experiment locations in China Camp State Park in Marin County, California, with Bullhead Flat and Buckeye Point identified as red points. Inlay shows location

within California, USA. Imagery courtesy of the National Agriculture Imagery Program, 2022. Habitat polygons are courtesy of the California Aquatic Resources Inventory, version 2.2, 2023

impacts of inundation and other physical stress on marsh vegetation have used space for time approaches including marsh elevation gradients as inundation treatments and areas with naturally occurring poor drainage (Schile et al. 2011), but these are often confounded by other parameters that are coupled with elevation or lack of tidal flushing. “Marsh organs” are a useful method to quantify effects of tidal inundation on sediment characteristics, but previous studies were limited by the “bottle effect” of the organs (Schile et al. 2017) and the inability to assess changes to animal communities in the soil. We therefore crafted experimental “marsh boxes” to manipulate inundation in situ (based on the design in Cherry et al. 2015), as described below, to explore a larger suite of biological and physical responses.

At Buckeye Point in spring of 2021, we installed eight marsh boxes (1 m×0.6 m×0.6 m) in areas of cordgrass that were inserted 10 cm into the sediment to reduce lateral water drainage and increase inundation (Fig. 2). These plots were accompanied by eight unaltered, ambient control areas of cordgrass for comparison. As boxes may impact sediment characteristics and flow around the plots, we also installed eight box controls, which contained shorter versions of all four walls (0.2 m high) with openings at the four corners to allow water to flow more freely in and out, to account for artifacts associated with the boxes. For manipulation control plots, we dug a thin trough around the plots to simulate disturbance from box or partial box installation and cut through any belowground root masses connected to the plot. Over winter 2021, boxes filled with sediment and/or were broken due to waves and heavy tidal flows, affecting the cordgrass within and likely disrupting natural processes occurring in boxes. Therefore, in spring 2022, we reduced the number of replicates to six for all treatments and moved all boxes approximately 1 m away from the previous box’s location into an area of unaffected cordgrass. Sets of three inundation treatments were contained in blocks which were distributed across the experimental area, with a total of 48 plots and eight blocks in 2021 and 36 plots and six blocks in 2022.

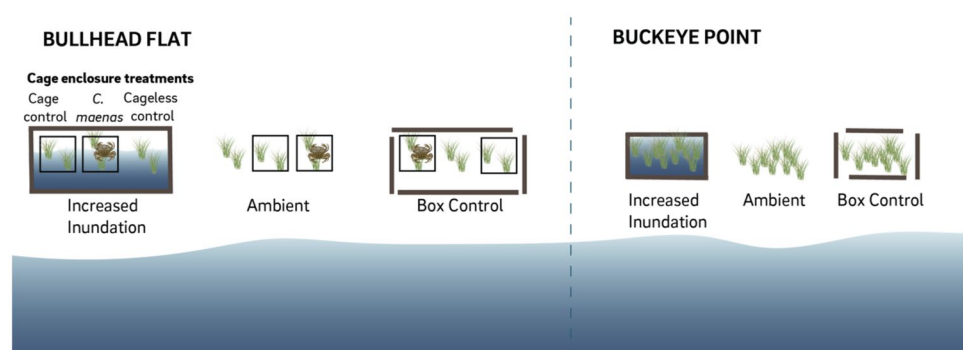
In spring of 2022, we repeated our inundation treatments at an additional site, Bullhead Flat, and added a cage enclosure component (Fig. 2). We enclosed adult green crabs in

plots with established cordgrass as well as cage controls (cages, no crabs) and open unmanipulated controls (no cage) (Fig. 2). The enclosures (0.5 m×0.5 m) were constructed from 7 mm Vexar® mesh into which two adult green crabs were added (based on natural local green crab densities, carapace width ranged from 45 to 82 mm, J. Gonzalez, unpublished data). Cage controls used the same cages but with no crabs. Green crab individuals used in the experiment were acquired at nearby sites using Fukui collapsible crab traps (60×45×20 cm, 1.25-cm mesh). Due to the difficulty of visually assessing crab presence in plots, one green crab was added in each cage in July to account for death or escape of crabs and ensure the treatment was maintained. Even with crab additions, green crab density in cages (between 1 and 3 crabs over the course of the experiment with additions) remained within the realm of natural abundances in San Francisco Bay (mean of 0.6–4 crabs/trap day, E. Grosholz and J. Gonzalez, unpublished data).

These three crab treatments were subject to a tidal inundation treatment that simulates extended tidal inundation within the range projected with SLR, as at Buckeye Point. We installed six marsh boxes (2 m×1 m×0.4 m) which each had two in-flow check valves to let water in, and no exit valve, so that the water slowly drained through the open bottom, as well as six box controls with shorter walls and open corners to allow tidal flushing. As a third treatment, we had areas without boxes experiencing the ambient inundation regime as unmanipulated controls. These three inundation treatments were established as 2×1 m plots separated by at least 2 m. The overall experimental design was set up in both sites as six or eight blocks in a transect parallel to the open bay-marsh edge to account for habitat heterogeneity common in tidal marshes, such as differences in elevation, surface topography, and proximity to tidal channels. Within each of the six blocks, the three inundation treatments were randomly assigned, and within each inundation treatment, the three cage treatments were randomly distributed (Fig. 2).

In the center of each of the inundation treatments at Bullhead Flat ($n=18$) and Buckeye Point ($n=48$ in 2021, $n=36$ in 2022), we took measurements of orthometric height (m NAVD88) using a real-time kinematic (RTK)

Fig. 2 The experimental setup of one block at each site, depicting an aerial view of inundation and crab treatments



GPS GS07 GNSS receiver and CS20 LTE controller (Leica Geosystems) and corrected elevation data using benchmarks taken before and after sampling if necessary. Positions were received via the Leica California SmartNet RTK network. Orthometric heights of inundation treatment areas ranged from 0.80 to 0.98 m (NAVD88) at Bullhead Flat and 0.82 to 1.06 m at Buckeye Point.

Quantification of Biological and Physical Responses

In each site and year, we evaluated water levels in each inundation treatment plot for 8–10-day periods using HOBO U-20L water level loggers (Onset Data Loggers, Cape Cod, MA). Water level in each plot was calculated from temperature and pressure data using the Barometric Compensation Assistant in HOBOWare Pro (version 3.7.23) and corrected using local barometric pressure data (Gnoss Field Airport, NOAA climatological station 00135, <https://www.ncdc.noaa.gov/>). We calculated average inundation time per plot by summing the number of minutes that water level was 2–4 cm above the marsh surface in the plot to avoid effects of rapid data fluctuations during shallower conditions (2 cm in July 2021, 4 cm in June and September 2022). These values then were converted to inundation hours per day. We gathered temperature and light data in two plots without boxes and four plots with boxes using light and temperature loggers (HOBO Pendant Temperature/Light Data Logger).

We monitored plots once a month for 12 weeks (June through August or September) in summer 2021 and 2022 at Buckeye Point and summer 2022 at Bullhead Flat. During each sampling point, we measured the number of total live cordgrass stems and stand height as the average height of the ten tallest stems in each plot. Also monthly, we measured redox potential in each plot at 10 cm below the sediment surface, targeting the area adjacent to the cordgrass root system, using a portable Mettler-Toledo mV meter (Mettler Toledo Seven2Go pH/mV Meter). At the end of the experiment, we collected belowground biomass by taking a sediment core in each plot (5 cm wide PVC corer to a depth of 25 cm). We sieved cores to extract plant roots and rhizomes using a 500- μ m sieve, dried roots at 60 °C, and weighed them. We also took porewater samples using porewater sippers inserted 10 cm into the sediment during low tide (10-cm-long porous tubes [0.15 μ m], Rhizosphere Research Products, Wageningen, The Netherlands) at the end of the experiment. Porewater samples were kept on ice during sampling, frozen on return to the lab, and analyzed within 1 month for ammonium and nitrate (UC Davis Analytical Lab), and sulfides were refrigerated and analyzed within 1 week of collection based on methods by Cline (1969).

Statistics

We performed statistical analyses using R programming software (version 4.0.3 R Core Team 2023). We used linear mixed models and generalized linear mixed models (“lme4” package in R) including a random effect of block or block nested within year, to account for habitat heterogeneity in tidal marshes, and determined the appropriate distribution for each dataset using goodness-of-fit statistics. We included fixed effects of surface elevation and numerical inundation duration if they improved model fit. We applied transformations where necessary to achieve normality and/or heteroscedasticity (Table S1). We evaluated whether partial boxes significantly influenced all responses, and if they were influential, we included those data in the full model (Table S1). We evaluated statistically significant differences in inundation duration among inundation treatments using a generalized linear mixed model with fixed effects of categorical inundation treatment and elevation and a random effect of block nested within date. We also evaluated effects of green crab presence vs. absence, inundation, and the interaction between those two on the following response variables: change in cordgrass stem density as number of stems/m² and stand height over a 12-week period (final stem density – initial stem density), as well as belowground biomass/m², redox potential, and porewater ammonium, nitrate, and sulfide at the end of the experiment. We tested artifactual effects of cages relative to green crabs on change in shoot density by pooling inundation treatment plots and used a linear mixed model with block as a random factor. We compared cordgrass stand height, stem density, and belowground biomass during the 2022 season in control plots at both sites, with measurements taken within 4 days of each other. We evaluated differences in mean temperature/day (°C) and light intensity/day (lumens) among treatments using a generalized linear model. We used the “emmeans” package (estimated marginal means) to evaluate pairwise comparisons post hoc, which performs a multiple comparisons adjustment by default, and deemed differences as significant if *p* values were less than 0.05.

Results

Physical Responses to Inundation

Buckeye Point

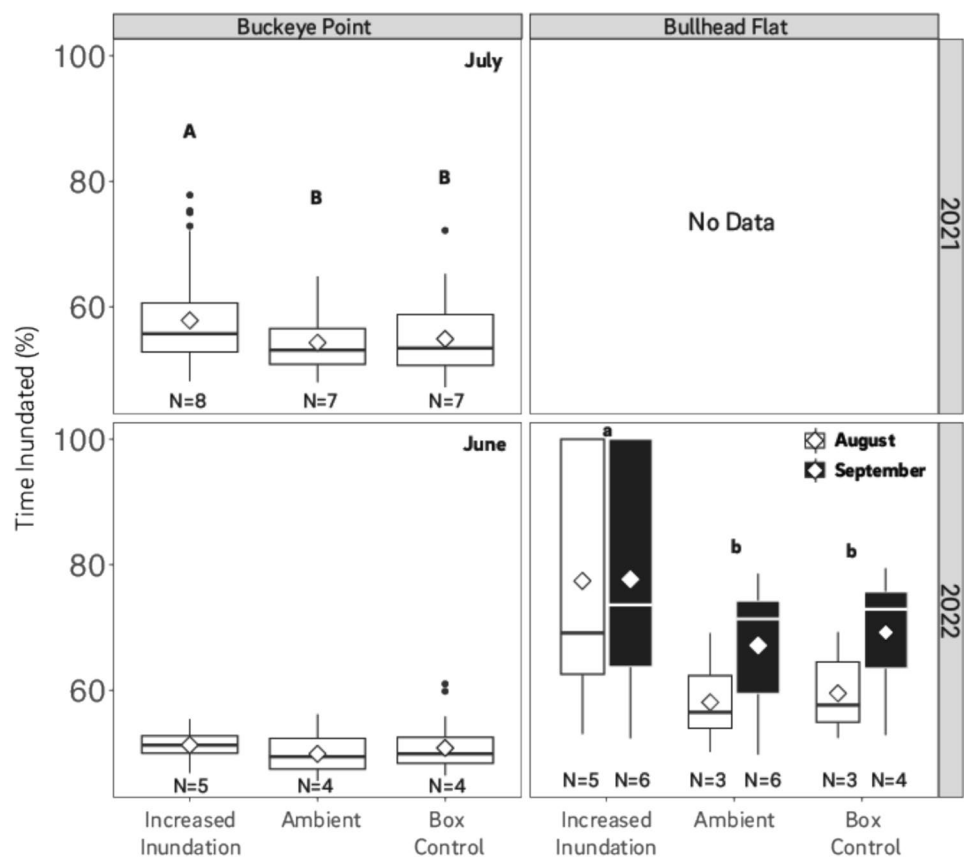
The amount of inundation varied by the categorical inundation treatment, year, surface elevation, and the interaction between treatment and year ($X^2=27.13$, $p<0.001$; $X^2=116.68$, $p<0.001$, $X^2=43.87$, $p<0.001$; $X^2=12.69$,

$p=0.002$, respectively). Water level data gathered in July 2021 showed, on average, a $\sim 5\%$ increase in inundation duration in box treatments (hereafter, “increased inundation” treatments) relative to ambient control plots (hereafter, “ambient” treatments, Fig. 3, ambient vs. increased inundation: $Z=4.58$, $p<0.001$ and box controls: $Z=-5.56$, $p<0.001$), yet there was similar average inundation duration among treatments in June 2022 (June 22: $Z=-0.92$, $p=0.630$; $Z=0.51$, $p=0.865$). However, we observed standing water in boxes at several points during both summer 2021 and 2022 when no standing water was in the box controls or ambient plots, which drained over the course of a few hours, confirming that increased inundation treatments were at least intermittently functional in both years. Inundation hours per day was negatively correlated with the surface elevation of the plots in ambient and box control treatments, but not in increased inundation treatments in July 2021 ($R^2=0.23$, $p<0.001$, $R^2=0.43$, $p<0.001$, $R^2=0.04$, $p=0.11$, respectively). Temperature and light intensity did not vary among increased inundation and ambient treatment plots (temperature: $Z=0.10$, $p=0.994$; $Z=1.39$, $p=0.347$, light: $Z=-1.79$, $p=0.173$; $Z=-1.29$, $p=0.400$).

Bullhead Flat

In Bullhead Flat, we observed significantly higher inundation duration in box treatments relative to both ambient controls and box controls (Fig. 3, August: $58 \pm 2\%$ daily inundation in ambient controls, $77 \pm 17\%$ daily inundation with increased inundation, $60 \pm 1\%$ daily inundation in box controls; September: $68 \pm 3\%$ daily inundation in ambient treatments vs. $78 \pm 15\%$ daily inundation with increased inundation and $70 \pm 2\%$ daily inundation in box controls, $Z=-2.69$, $p=0.02$, and $Z=-2.53$, $p=0.031$). Average temperature per day and light intensity per day did not vary between increased inundation and ambient treatments ($Z=-0.90$, $p=0.367$, and $Z=-0.585$, $p=0.558$). The apparent difference in baseline inundation at the Bullhead Flat and Buckeye Point as seen in Fig. 3 is likely due to differences in ambient water levels during the measurement periods in June and August/September. We compared water level data from the two sites across a 5-day period in June 2022 and found that the two sites were inundated for a similar amount of time (12.08 ± 0.32 s.e. vs. 12.14 ± 0.61 s.e. hours/day at Buckeye Point and Bullhead Flat, respectively).

Fig. 3 A box plot showing % daily inundation across inundation treatments for both years in both locations, showing the mean (diamond), spread, and skewness of the data. We did not collect data at Bullhead Flat in 2021. Letters represent significant differences at $p < 0.05$. Sample sizes (N) are shown and represent the number of replicate inundation treatment plots



Response of Redox Potential and Porewater Ammonium, Nitrate, and Sulfide

Buckeye Point

In 2021, redox potential at the end of the experiment was significantly lower in plots with increased inundation relative to ambient treatments (Fig. 4A, mean of -107 ± 17 s.e. Eh in ambient treatments vs. -141 ± 10 s.e. Eh with increased inundation, $t = -2.90$, $p = 0.020$). Redox potential in box control treatments was intermediate between increased inundation and ambient control plots (-132 ± 15 s.e. Eh, $t = 2.23$, $p = 0.086$). Redox potential did not vary between increased inundation and ambient or box control treatments in 2022

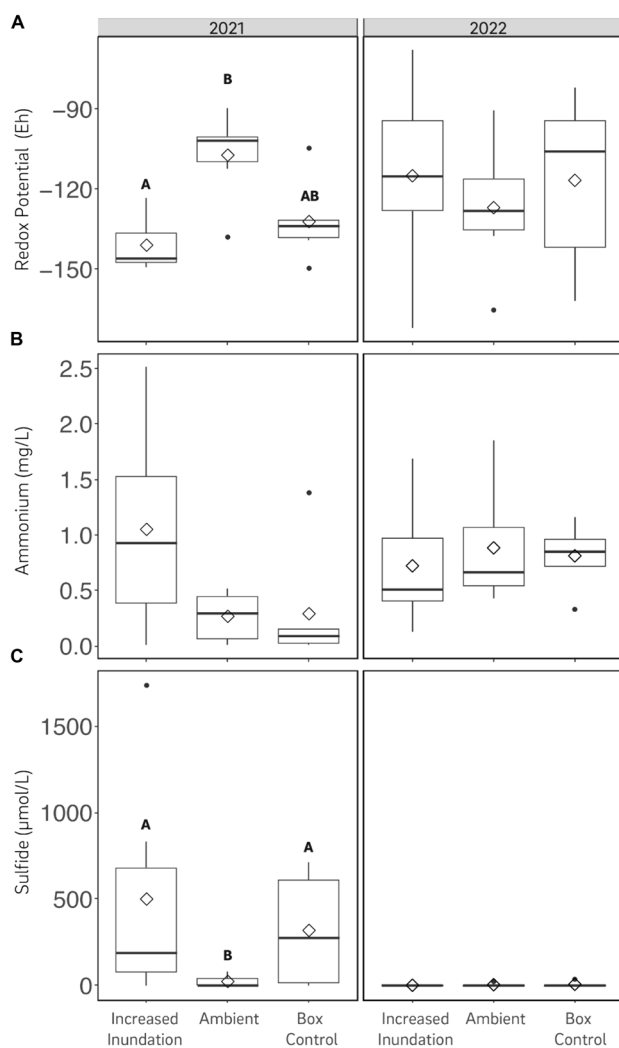


Fig. 4 A multi-panel series of box plots showing **A** redox potential, **B** porewater ammonium, and **C** sulfide concentrations in each plot at the end of the summer season in Buckeye Point for each year. Box-plots and whiskers represent the spread of skew of data, with the diamond representing the mean. Significant differences at $p < 0.05$ are indicated by letters

($t = 0.07$, $p = 0.998$; $t = -1.51$, $p = 0.305$). Ammonium concentrations tended to be higher in increased inundation relative to ambient treatments and box control treatments in 2021 (Fig. 4B, $t = 2.43$, $p = 0.055$; $t = 2.39$, $p = 0.060$), but these differences were not significant. Ammonium concentrations did not vary between increased inundation and ambient or box control treatments in 2022 ($t = -0.445$, $p = 0.897$; $t = -0.362$, $p = 0.931$). Ammonium values were similar in 2022 relative to 2021 ($t = 1.01$, $p = 0.316$; $t = -1.81$, $p = 0.078$; $t = -1.68$, $p = 0.100$). Sulfide concentrations were significantly higher in increased inundation in 2021 relative to ambient treatments (Fig. 4C, ambient: 23 ± 36 s.e. $\mu\text{mol/l}$ vs. increased inundation: 499 ± 676 s.e.; $Z = 3.28$, $p = 0.003$). Sulfide in box controls was intermediate between increased inundation and ambient treatments yet substantially higher than in ambient plots (318 ± 336 s.e. $\mu\text{mol/l}$; $Z = -3.41$, $p = 0.002$). We found no difference between increased inundation and ambient or box controls in 2022 (increased inundation-ambient: $Z = -0.89$, $p = 0.649$; increased inundation-box control: $Z = -1.60$, $p = 0.247$).

Bullhead Flat

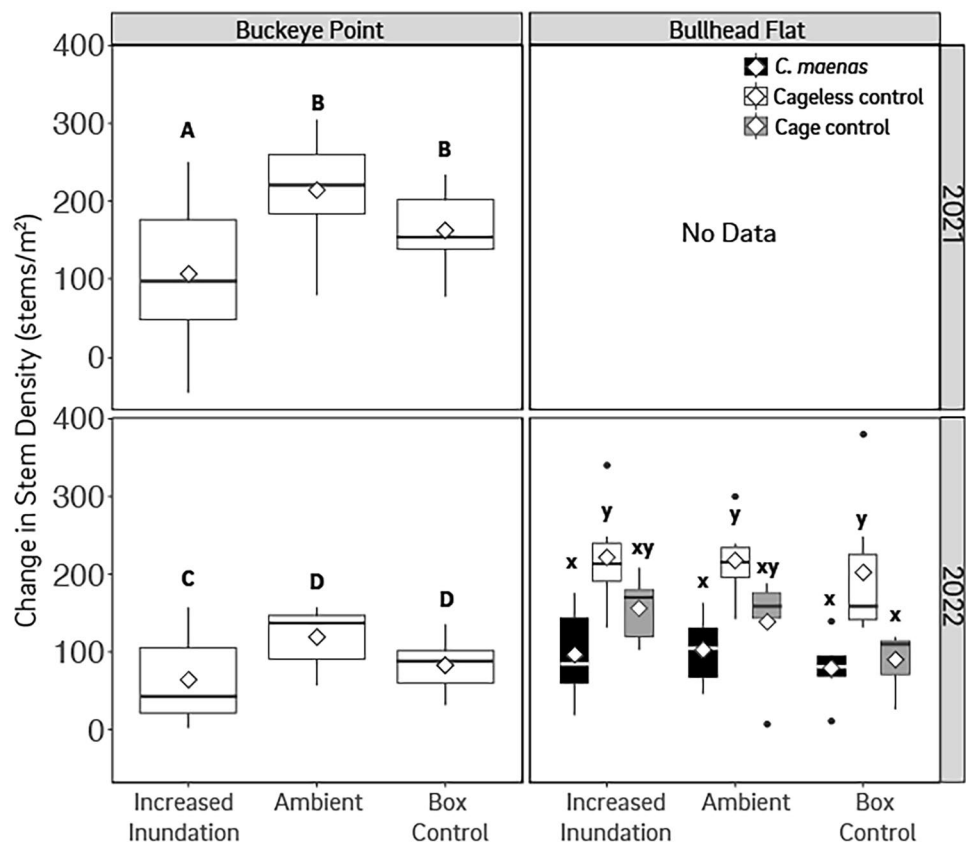
Redox potential in August did not vary by crab or inundation treatment, and there was no interaction between those two factors ($X^2 = 1.20$, $p = 0.548$; $X^2 = 1.99$, $p = 0.158$; $X^2 = 0.10$, $p = 0.950$, respectively). Crab treatments and inundation did not affect porewater ammonium in plots, nor did their interaction ($X^2 = 3.10$, $p = 0.212$; $X^2 = 0.092$, $p = 0.765$; $X^2 = 1.65$, $p = 0.437$). Nitrate concentrations in all plots rarely were higher than zero, and values above zero were negligible. We found no effect of inundation, crabs, or the interaction of the two on sulfide concentrations in August ($X^2 = 2.32$, $p = 0.314$; $X^2 = 0.12$, $p = 0.944$, $X^2 = 1.47$, $p = 0.832$).

Response of Vegetation

Buckeye Point

Cordgrass plots within increased inundation treatments gained 51% fewer stems, and average stand height gained over the course of the experiment was 14% lower than ambient treatments in 2021 (Fig. 5, $Z = -10.04$, $p < 0.001$ and $Z = 2.53$, $p = 0.031$, respectively). In 2022, cordgrass plots gained 46% fewer stems in increased inundation treatments relative to ambient treatment plots (Fig. 5, $Z = -5.30$, $p < 0.001$), and there was no treatment effect on change in stand height in 2022. We observed yearly variation in cordgrass growth and survival that may have resulted in reduced treatment effects in 2022. All treatments gained fewer stems over the course of the growing season in 2022 relative to 2021 (Fig. 5, increased inundation: $Z = -5.46$, $p < 0.001$; ambient treatment: $Z = -5.71$, $p < 0.001$; box controls: $Z = -5.48$, $p < 0.001$). Also, change in cordgrass stand

Fig. 5 A box plot showing the change in *S. foliosa* stem density in inundation and crab treatment plots at Bullhead Flat and Buckeye Point over a 12-week period each summer season, for each year. Inundation treatments are shown on the x axis and colored bars denote crab treatments. Box and whiskers show the spread and skew of the data, diamonds represent the mean, and letters represent significant differences among treatments at $p < 0.05$



height within ambient treatments and box control plots in 2022 was significantly less than the year prior (Fig. 5, $Z = -3.85$, $p < 0.001$; $Z = -4.06$, $p < 0.001$).

We also found that, in treatments plots with increased inundation only, in both years, final cordgrass stem density increased with the surface elevation of the plot, significantly so in 2021 (Fig. 6, 2021: $R^2 = 0.68$, $p = 0.012$; 2022: $R^2 = 0.61$, $p = 0.067$). A similar pattern emerged when we compared change in cordgrass stem density over 12 weeks with surface elevation (2021: $R^2 = 0.61$, $p = 0.022$; 2022: $R^2 = 0.29$, $p = 0.27$). The amount of belowground biomass per plot did not differ across inundation treatments in August 2022 ($X^2 = 1.56$, $p = 0.459$).

In addition, treatments with increased inundation gained 43% fewer stems and average stand height increase was 13% lower relative to box controls in 2021 ($Z = -4.32$, $p < 0.001$ and $Z = 3.06$, $p = 0.006$, respectively). In 2022, there were 22% fewer stems in increased inundation treatments relative to box controls ($Z = -2.85$, $p = 0.012$).

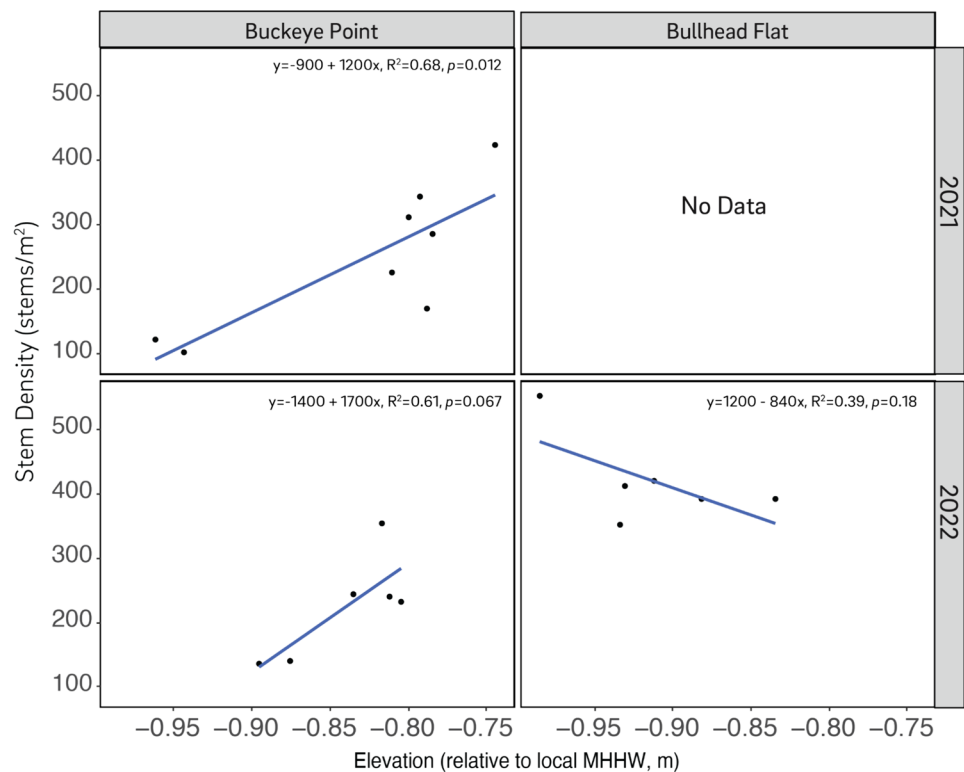
Bullhead Flat

We found negative effects of green crabs on cordgrass stem density when exposed to both increased and ambient inundation

regimes. Overall, change in cordgrass stem density was influenced by crab treatment ($X^2 = 18.29$, $p < 0.001$). In increased inundation treatments, cordgrass stem density increased to a greater extent over the course of the summer in cageless controls (mean of 56 ± 7 s.e. stems, $Z = -3.20$, $p = 0.004$) relative to green crab treatments (mean 24 ± 6 s.e. stems). Similarly, in ambient inundation treatments, gains in cordgrass stem density were greater in cageless controls (55 ± 5 s.e. stems, $Z = -2.87$, $p = 0.011$) relative to green crab treatments (26 ± 5 s.e. stems). We did not find an effect of inundation or the interaction of crab treatment and inundation on the change in stem density ($X^2 = 0.39$, $p = 0.535$ and $X^2 = 0.30$, $p = 0.859$, respectively). Change in stand height over the course of the experiment also was similar across crab treatments ($X^2 = 1.99$, $p = 0.369$). Belowground biomass did not change in plots across inundation and green crab treatments ($X^2 = 0.62$, $p = 0.433$ and $X^2 = 4.68$, $p = 0.096$, respectively), nor was there an interaction between inundation and green crab treatments ($X^2 = 1.04$, $p = 0.593$).

We tested for cage effects specifically and found that when inundation treatment plots were pooled, change in shoot density from the initial to final time point in green crab treatment plots was significantly lower than cage control treatments ($t = -2.04$, $p = 0.049$).

Fig. 6 A regression of the elevation relative to MHHW of each increased inundation treatment plot with *S. foliosa* stem density at the end of each 12-week period at each site and for each year. Each plot shows the equation, R^2 value, and p value for the associated regression



Site Comparison

Cordgrass stem density in ambient control plots in Bullhead Flat was 82% greater than Buckeye Point in 2022 (Fig. 7, $Z = -2.79$, $p = 0.019$). Cordgrass stand height was 10% greater on average in Bullhead Flat than Buckeye Point the same year ($Z = -2.57$, $p = 0.028$). Also in ambient control plots, we found a positive correlation between belowground biomass and surface elevation at both sites (Bullhead Flat: $R^2 = 0.42$, $p = 0.006$; Buckeye Point: $R^2 = 0.73$, $p = 0.014$).

Discussion

Through our novel approach of manipulating both the presence of an invasive species and tidal inundation in situ, we found negative effects of increased inundation and green crabs (*Carcinus maenas*) on stem density and height of native cordgrass, *Spartina foliosa*.

Marsh boxes increased inundation relative to box control and ambient control treatments at both sites. However, in 2022, at Buckeye Point, this increase was not statistically significant due to considerable variability in water retention among box treatments, possibly exacerbated by lower replication that year. Similarly, at Bullhead Flat, there was substantial variability in inundation duration among boxes, likely

stemming from differences in the functioning of individual units, perhaps influenced by factors such as the presence of roots, rocks, or variations in soil characteristics affecting the seal with the surrounding sediment. Inundation duration in box control treatments was intermediate between ambient and increased inundation treatments, which likely contributed to intermediate responses in soil conditions and plant growth and survival. This suggests the presence of some artifact effects from the marsh boxes, possibly due to their structure retaining water to a lesser extent than full boxes but more than ambient treatment plots. Additionally, the mean inundation duration we achieved using boxes is on the low end of what we might expect with sea-level rise (SLR, i.e., a doubling of inundation time relative to MHHW, Janousek et al. 2016). Cordgrass populations are predicted to be unaffected, or even increase, with moderate rates of SLR, yet decline with substantial increases as sea level continues to rise (Parker et al. 2011). This modeled prediction is supported by experimental work that found *Spartina alterniflora* stem density to increase with moderate increases in inundation yet decline under extreme SLR scenarios (Ober and Martin 2018). Significant impacts on stand height and belowground biomass may only manifest with higher inundation levels sustained over prolonged periods. Consequently, the responses observed in our study may intensify or undergo changes as sea levels rise and inundation duration increases.

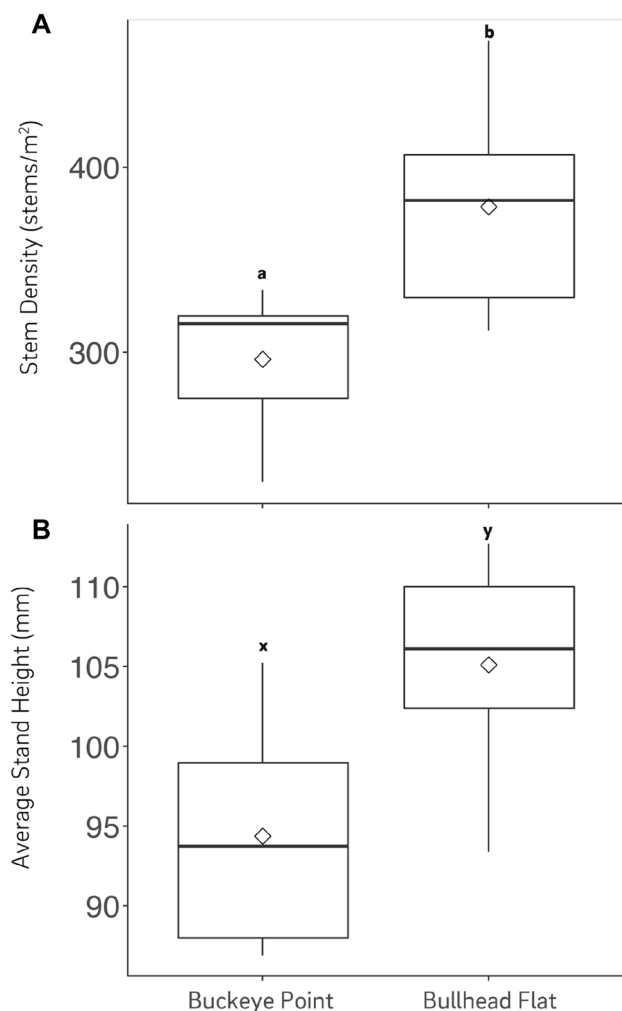


Fig. 7 Box plots comparing **A** stand height and **B** stem density in ambient, control treatments at Bullhead Flat and Buckeye Point in 2022. Box and whiskers show the spread and skew of the data and diamonds represent the mean. Letters indicate significant differences among sites at $p < 0.05$

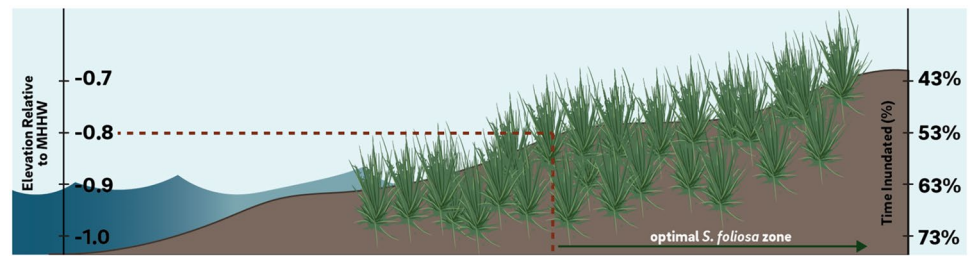
Despite the modest increase in inundation, and consistent with our hypothesis, we found that cordgrass responded negatively to increased inundation, although these effects varied by year and site. At Buckeye Point, the increase in cordgrass stem density and height over the course of the growing season in 2021 was significantly less in increased inundation treatments relative to ambient controls and box controls. Decreased cordgrass stem density and stand height was likely driven by increased inundation and subsequent decreased oxygen and cascading changes in the sediment in 2021. Redox potential was lower in 2021 in plots where inundation was experimentally increased, and these low oxygen conditions may have contributed to elevated levels of sulfide and ammonium coupled with low concentrations of nitrate, as oxygen is needed to transform ammonium

into nitrate and sulfide is produced in anaerobic conditions. These redox potential, sulfide, and ammonium responses are consistent with previous work that evaluated sediment chemistry in response to inundation (Koch and Mendelssohn 1989; Schile et al. 2017). High levels of sulfide may have functioned to reduce growth and increase stem loss by negatively impacting roots and rhizomes (Cronk and Fennessy 2016; Koch and Mendelssohn 1989). However, there was generally less dense and shorter cordgrass in Buckeye Point in 2022 relative to 2021 making significant treatment effects harder to capture. This could be due to year-to-year variability in environmental conditions affecting wave energy and sediment deposition, as previous studies found correlations between increased wave energy and reduced accretion and shorter and less dense cordgrass (Swales et al. 2004). Fewer or more stressed cordgrass could have resulted in decreased uptake of ammonium as well.

However, in Bullhead Flat, cordgrass did not respond to increased levels of inundation. Increased inundation did not statistically affect redox potential, and nutrient concentrations remained consistent across inundation treatments. Our sampling approach may not have sufficiently captured the full spectrum of edaphic conditions within the plot, as we only collected one sediment and porewater measurement per plot. Or, the inundation that plots experienced was not sufficiently elevated in increased inundation treatments and therefore did not affect edaphic conditions and consequently did not affect cordgrass. Alternatively, the variation in geomorphic context and the integrity of cordgrass stands between the two sites might account for the difference in cordgrass response. Cordgrass in the Bullhead Flat experimental area is significantly taller and more dense on average compared to that in Buckeye Point (Fig. 7). This disparity could be attributed to site-specific characteristics that offer more favorable conditions for cordgrass growth and survival. Bullhead Flat, characterized by a sheltered cove with a gently sloping mudflat, likely experiences better wave attenuation from the Bay, unlike the more exposed Buckeye Point (Fig. 1). Given that sites with differing cordgrass conditions may respond diversely to increased inundation from SLR, future investigations could explore how variation in geomorphic settings and hydrodynamic exposure influence the resilience of habitat-forming vegetation to SLR.

Notably, we found that cordgrass survival in plots with boxes that increased inundation duration was largely dependent on the elevation of the plot; we observed higher stem density in higher elevation plots at the end of the experiment (Fig. 6) and less stem loss through time than in lower elevation plots. We did not see this trend in inundation control treatments. These data can be used to inform optimal planting locations to establish cordgrass in restoration sites so that it may persist with SLR (Fig. 8). This information can

Fig. 8 A conceptual diagram showing the optimal *S. foliosa* zone for Buckeye Point given sea-level rise, using data from Fig. 6



also be used to select sites for conservation purposes or sites to restore that have the highest likelihood of persisting with increasing levels of inundation. For example, given a ~5% increase in inundation time, managers may consider planting cordgrass higher than ~0.8 m relative to MHHW to achieve full growth potential in a salt marsh with similar geomorphic characteristics as Buckeye Point. Also, we found that cordgrass belowground biomass increases with increasing surface elevation at both sites. Belowground biomass is generally used as a proxy for plant productivity, and Turner et al. (2004) documented lower cordgrass belowground biomass in impaired wetland sites relative to healthy sites. This disparity suggests that the specific position within the narrow elevation range where these plants exist may influence their response to SLR and may have contributed to variability in plant responses in our inundation treatments. This also supports planting *S. foliosa* at higher elevations within their elevational distribution. Lower elevation plants, characterized by lower productivity, could face more severe impacts from rising sea level over time.

In addition, we found that cordgrass survival decreased in the presence of green crabs. This finding is consistent with a previous cage study that found reduced cordgrass stem density in the presence of green crabs (Gonzalez et al. 2024). Physical disturbance by green crabs is a potential mechanism, as they have been observed to disrupt estuarine vegetation in other systems through activities such as digging large pits and tearing eelgrass stems (Garbary et al. 2014). Although we did find evidence of cage effects, likely from shading or disturbance during installation, cordgrass responded more negatively to green crabs than cage controls suggesting that crab effects on cordgrass were in addition to any deleterious effects of cage presence. Crabs sometimes inhabit higher elevation areas, such as mudflats and cordgrass meadows, during high tide when these habitats are inundated, and retreat to lower elevation or subtidal zones at low tide to avoid terrestrial predators (Klein Breteler 1976; Hines and Ruiz 1995). As such, increased inundation duration of cordgrass may amplify its accessibility to crabs. Strategic planting of cordgrass in higher elevations may additionally minimize its exposure to green crabs and mitigate potential negative effects on cordgrass growth and structure. It is worth noting that while our focus has been

on the impacts of non-native, invasive species like green crabs in this region, it is important not to overlook the potential deleterious effects that native species can also have on ecosystems. For instance, although Gonzalez et al. (2024) compared effects of native shore crabs (*Hemigrapsus oregonensis*) and invasive green crabs on recently planted native cordgrass San Francisco Bay and only green crabs negatively affected cordgrass survival, others have found that native crab species may also disrupt ecosystems through habitat alterations (Crotty et al. 2017). As such, when considering the implications of this study in a broader context, it is critical to understand system-specific effects of non-native, invasive, and native species to effectively interpret and apply results from this study towards comprehensive ecosystem management and SLR adaptation planning efforts.

Contrary to our hypothesis, we did not find interactive effects of inundation and green crabs. At Bullhead Flat, we did not find evidence of physical or biological responses to increased inundation, precluding the possibility of interactive effects. However, stressor interactions may be simultaneous, sequential, or latent, and it could be that there is a temporal decoupling of the most severe effects of these two factors in this specific system that confounds interpretation of these results (Cheng et al. 2015). Green crabs are less active in the winter and early spring in San Francisco Bay and more active in the summer season as water and air temperatures warm. This is when their effects on cordgrass are likely to be captured, as we found in this study. Cordgrass senescences in the winter and regrows from its rhizomal root system each spring through late summer. In the winter, fewer aboveground stems containing aerenchyma that funnel oxygen to their root system may reduce oxygen availability in the soil, leading to increased sulfide production, which can in turn have deleterious effects on roots and rhizomes (Cronk and Fennessy 2016). It is possible that effects of increased inundation may impact the senescent root structure of cordgrass more severely than its aboveground growth through the summer growing season. This work focused on the summer growing season, and future studies should evaluate how increased inundation affects soils and marsh vegetation over a longer timescale, spanning both the winter, and summer growing season. Negative effects of inundation on cordgrass belowground biomass in the winter may influence

its growth in the summer, producing sequential multiple stressor effects rather than simultaneous. As such, and consistent with Cheng et al. (2015), we suggest that ecologically relevant local conditions be considered in empirical tests of multiple stressors across systems.

Conclusion

We found a negative response of a threatened habitat-forming plant species to increased inundation and an invasive crab. We also found that these effects varied by site and year due to site-specific factors and possibly water retention dynamics. These findings align with predictions of previous studies about cordgrass populations responding to sea-level rise (SLR), indicating that more significant impacts may manifest with higher levels of inundation over prolonged periods.

Additionally, we observed that green crabs negatively influenced cordgrass survival, but did not interact with inundation to affect cordgrass. Sequential or latent interactions of these two stressors were not studied here but warrant further investigation. Our findings emphasize the need to consider site-specific integrity of vegetation and local ecological conditions when studying the impacts of multiple stressors across different ecosystems. This information can also be used to guide management decisions in coastal areas with green crabs. Notably, this work reinforces the importance of considering surface elevation in planting locations and conservation planning. We found that cordgrass had higher survival rates at higher elevations, even within its typical range, which is critical for ensuring its survival in the face of SLR. Also, the quantitative responses associated with inundation time we found in this study can be used to parameterize models that predict future effects of SLR with the added stress of invasive species and provide guidance on priority areas for removal, conservation, and/or restoration. Overall, this study contributes valuable insights into the complex dynamics of salt marsh ecosystems in the context of environmental changes and invasive species.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s12237-024-01393-0>.

Acknowledgements We sincerely thank the editor and three anonymous reviewers for their time spent reviewing this manuscript and for their thoughtful comments and suggestions. We would also like to thank scientists and staff with the San Francisco Bay National Estuarine Research Reserve and the Friends of China Camp for their enthusiastic support in the field and beyond, especially A. Good, B. Mayorga, A. Deck, M. Vasey, S. Siegel, and C. Young. We thank California State Parks staff for their support and for allowing us to carry out this study in China Camp State Park, especially B. Hardcastle and R. Schneider. We thank C. de Rivera, J. Largier, and J. Stachowicz for their insight while developing this study. This study would not have been possible without the volunteers and technicians that assisted in experimental installation and removal and sample collection and

processing, including A. Korabik, P. Shukla, B. Rubinoff, O. Sereni, C. Dunn, A. Olsen, M. Li, A. Ibanez-Ramos, A. Laws-Mcneill, A. Le, N. Connor, and E. Barajas-Carmona.

Funding This study was supported by the Margaret A. Davidson fellowship program, NOS Office for Coastal Management award number NA20NOS4200118, and annual operating awards to San Francisco Bay National Estuarine Research Reserve from the National Oceanic and Atmospheric Administration's Office for Coastal Management.

Data Availability The data supporting the findings of this study are available through the Dryad Digital Repository. The dataset can be accessed at <https://doi.org/10.5061/dryad.pg4f4qrwx>.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Alberti, J., M. Escapa, P. Daleo, O. Iribarne, B. Silliman, and M. Bertness. 2007. Local and geographic variation in grazing intensity by herbivorous crabs in SW Atlantic salt marshes. *Marine Ecology Progress Series* 349: 235–243.
- Ayres, D.R., D.R. Strong, and P. Baye. 2003. *Spartina foliosa* (poaceae)—a common species on the road to rarity? *Madroño* 50: 209–213.
- Bertness, M.D. 1985. Fiddler crab regulation of *Spartina alterniflora* production on a new England salt marsh. *Ecology* 66: 1042–1055.
- Bertness, M.D., C.P. Brisson, T.C. Coverdale, M.C. Bevil, S.M. Crotty, and E.R. Suglia. 2014. Experimental predator removal causes rapid salt marsh die-off. *Ecology Letters* 17: 830–835.
- Bertness, M.D., and A.M. Ellison. 1987. Determinants of pattern in a new England salt marsh plant community. *Ecological Monographs* 57: 129–147.
- Bertness, M.D., and E. Grosholz. 1985. Population dynamics of the ribbed Mussel, *Geukensia demissa*: The costs and benefits of an aggregated distribution. *Oecologia* 67: 192–204.
- Bruno, J.F., and M.D. Bertness. 2001. Habitat modification and facilitation in benthic marine communities. In *Marine Community Ecology*, ed. M.D. Bertness, S.D. Gaines, and M.E. Hay, 201–218. Sinauer.
- California Aquatic Resources Inventory (CARI), San Francisco Estuary Institute, 2.2. 2023. <https://www.sfei.org/data/california-aquatic-resource-inventory-cari-version-22-gis-data#sthash.HxIvwMSC.dpbs>.
- Cheng, B.S., J.M. Bible, A.L. Chang, M.C. Ferner, K. Wasson, C.J. Zabin, M. Latta, A. Deck, A.E. Todgham, and E.D. Grosholz. 2015. Testing local and global stressor impacts on a coastal foundation species using an ecologically realistic framework. *Global Change Biology* 21: 2488–2499.
- Cherry, J.A., K.L. McKee, and J.B. Grace. 2009. Elevated CO₂ enhances biological contributions to elevation change in coastal wetlands by offsetting stressors associated with sea-level rise. *Journal of Ecology* 97: 67–77.

- Cherry, J.A., G.S. Ramseur, E.L. Sparks, and J. Cebrian. 2015. Testing sea-level rise impacts in tidal wetlands: A novel *in situ* approach. *Methods in Ecology and Evolution* 6: 1443–1451.
- Cline, J.D. 1969. Spectrophotometric determination of hydrogen sulfide in natural waters 1. *Limnology and Oceanography* 14 (3): 454–458.
- Cloern, J.E., N. Knowles, L.R. Brown, D. Cayan, M.D. Dettinger, T.L. Morgan, D.H. Schoellhamer, M.T. Stacey, M. van der Wegen, R.W. Wagner, and A.D. Jassby. 2011. Projected evolution of California's San Francisco Bay-Delta-River system in a century of climate change. *PLoS ONE* 6: e24465.
- Cohen, A.N. 1998. *The invasion of the Pacific coast by the European green crab Carcinus maenas*. San Francisco Estuary Institute.
- Cronk, J.K., and M.S. Fennessy. 2016. *Wetland plants: Biology and ecology*. Boca Raton, FL: CRC Press.
- Crotty, S.M., C. Angelini, and M.D. Bertness. 2017. Multiple stressors and the potential for synergistic loss of New England salt marshes. *PLoS ONE* 12: e0183058.
- Dahl, T.E. 1990. *Wetlands losses in the United States, 1780's to 1980's*. US Department of the Interior, Fish and Wildlife Service.
- Daleo, P., E. Fanjul, A.M. Casariego, B.R. Silliman, M.D. Bertness, and O. Iribarne. 2007. Ecosystem engineers activate mycorrhizal mutualism in salt marshes. *Ecology Letters* 10 (10): 902–908.
- Emery, N.C., P.J. Ewanchuk, and M.D. Bertness. 2001. Competition and salt-marsh plant zonation: Stress tolerators may be dominant competitors. *Ecology* 82 (9): 2471–2485.
- Gallardo, B., M. Clavero, M.I. Sánchez, and M. Vilà. 2016. Global ecological impacts of invasive species in aquatic ecosystems. *Global Change Biology* 22: 151–163.
- Garbary, D.J., A.G. Miller, J. Williams, and N.R. Seymour. 2014. Drastic decline of an extensive eelgrass bed in Nova Scotia due to the activity of the invasive green crab (*Carcinus maenas*). *Marine Biology* 161: 3–15.
- Gonzalez, J.A., G.M. Ruiz, A.L. Chang, and K.E. Boyer. 2024. Effects of a non-native crab on the restoration of cordgrass in San Francisco Bay. *Ecological Restoration* 42 (1): 28–41.
- Grosholz, E.D., G.M. Ruiz, C.A. Dean, K.A. Shirley, J.L. Maron, and P.G. Connors. 2000. The impacts of a nonindigenous marine predator in a California bay. *Ecology* 81: 1206–1224.
- Hines, A.H., and G.M. Ruiz. 1995. Temporal variation in juvenile blue crab mortality: Nearshore shallows and cannibalism in Chesapeake bay. *Bulletin of Marine Science* 57: 884–901.
- Holdredge, C., M.D. Bertness, and A.H. Altieri. 2009. Role of crab herbivory in die-off of New England salt marshes. *Conservation Biology* 23 (3): 672–679.
- Janousek, C., K. Buffington, K. Thorne, G. Guntenspergen, J. Takekawa, and B. Dugger. 2016. Potential effects of sea-level rise on plant productivity: Species-specific responses in northeast Pacific tidal marshes. *Marine Ecology Progress Series* 548: 111–125.
- Klein Breteler, W.C.M. 1976. Settlement, growth and production of the shore crab, *Carcinus maenas*, on tidal flats in the Dutch Wadden Sea. *Netherlands Journal of Sea Research* 10 (3): 354–376.
- Koch, M.S., and I.A. Mendelssohn. 1989. Sulphide as a soil phytotoxin: Differential responses in two marsh species. *Journal of Ecology* 77: 565–578.
- Mendelssohn, I.A., and E.D. Seneca. 1980. The influence of soil drainage on the growth of salt marsh cordgrass *Spartina alterniflora* in North Carolina. *Estuarine and Coastal Marine Science* 11: 27–40.
- Montague, C. 1980. *The net influence of the mud fiddler crab, Uca pugnax, on carbon flow through a Georgia salt marsh: the importance of work by macroorganisms to the metabolism of ecosystems*. University of Georgia.
- Morris, J.T., P.V. Sundareshwar, C.T. Nietch, I.B. Kjerfve, and D.R. Cahoon. 2002. Responses of coastal wetlands to rising sea level. *Ecology* 83: 2869–2877.
- National Agriculture Imagery Program (NAIP). 2022. U.S. Department of Agriculture. <https://gis.apfo.usda.gov/arcgis/rest/services/NAIP>.
- Neira, C., E.D. Grosholz, L.A. Levin, and R. Blake. 2006. Mechanisms generating modification of benthos following tidal flat invasion by a *Spartina* hybrid. *Ecological Applications* 16: 1391–1404.
- Ober, G.T., and R.M. Martin. 2018. Sea-level rise and macroalgal blooms may combine to exacerbate decline in *Spartina patens* and *Spartina alterniflora* marshes. *Hydrobiologia* 823: 13–26.
- Parker, V.T., J.C. Callaway, L.M. Schile, M.C. Vasey, and E.R. Herbert. 2011. Climate change and San Francisco bay-delta tidal wetlands. *San Francisco Estuary & Watershed Science* 9 (3). <https://doi.org/10.15447/sfews.2011v9iss3art3>.
- Parker, V.T., and K.E. Boyer. 2019. Sea-level rise and climate change impacts on an urbanized Pacific Coast estuary. *Wetlands* 39: 1219–1232.
- Pennings, S.C., M.B. Grant, and M.D. Bertness. 2005. Plant zonation in low-latitude salt marshes: Disentangling the roles of flooding, salinity and competition. *Journal of Ecology* 93 (1): 159–167.
- R: A Language and Environment for Statistical Computing. 2023. R Core Team, <https://www.R-project.org/>.
- Schile, L.M., J.C. Callaway, V.T. Parker, and M.C. Vasey. 2011. Salinity and inundation influence productivity of the halophytic plant *Sarcocornia pacifica*. *Wetlands* 31: 1165–1174.
- Schile, L.M., J.C. Callaway, K.N. Suding, and N.M. Kelly. 2017. Can community structure track sea-level rise? Stress and competitive controls in tidal wetlands. *Ecology and Evolution* 7: 1276–1285.
- Seebens, H., T.M. Blackburn, E.E. Dyer, P. Genovesi, P.E. Hulme, J.M. Jeschke, S. Pagad, P. Pyšek, M. Winter, M. Arianoutsou, S. Bacher, B. Blasius, G. Brundu, C. Capinha, L. Celesti-Grapow, W. Dawson, S. Dullinger, N. Fuentes, H. Jäger, J. Kartesz, M. Kenis, H. Kreft, I. Kühn, B. Lenzner, A. Liebhold, A. Mosena, D. Moser, M. Nishino, D. Pearman, J. Pergl, W. Rabitsch, J. Rojas-Sandoval, A. Roques, S. Rorke, S. Rossinelli, H.E. Roy, R. Scalera, S. Schindler, K. Štajerová, B. Tokarska-Guzik, M. van Kleunen, K. Walker, P. Weigelt, T. Yamanaka, and F. Essl. 2017. No saturation in the accumulation of alien species worldwide. *Nature Communications* 8: 14435.
- Spalding, E.A., and M.W. Hester. 2007. Interactive effects of hydrology and salinity on oligohaline plant species productivity: Implications of relative sea-level rise. *Estuaries and Coasts* 30: 214–225.
- Swales, A., I.T. MacDonald, and M.O. Green. 2004. Influence of wave and sediment dynamics on cordgrass (*Spartina anglica*) growth and sediment accumulation on an exposed intertidal flat. *Estuaries* 27: 225–243. <https://doi.org/10.1007/BF02803380>.
- Turner, R., E.M. Eugene, C.S. Swenson, J.M. Milan, and Lee, and T. A. Oswald. 2004. Below-ground biomass in healthy and impaired salt marshes". *Ecological Research* 19 (1): 29–35.
- Vitousek, S., P.L. Barnard, C.H. Fletcher, N. Frazer, L. Erikson, and C.D. Storlazzi. 2017. Doubling of coastal flooding frequency within decades due to sea-level rise. *Scientific Reports* 7: 1399.