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Ecological and Societal Considerations in Marsh Restoration and Adaptation to Sea-Level Rise

Author
Gonzalez, Julie

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Ecological and Societal Considerations in Marsh Restoration and Adaptation to Sea-Level Rise

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JULIE ANNE GONZALEZ
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Approved:

Edwin Grosholz, Chair

Catherine de Rivera

John Largier

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Dissertation Abstract

As global environmental challenges intensify, understanding the multifaceted dynamics of ecosystem adaptation, as well as what constitutes effective habitat restoration, becomes paramount. The first part of this dissertation aims to understand the ecological success of habitat restoration efforts and its correlation with public perception for enhanced project outcomes and public support. Focusing on tidal marsh ecosystems, we gathered qualitative and quantitative data on public perceptions and ecological responses to restoration in Oregon, USA. Our analysis revealed an increase in hydrology scores with the number of restoration actions, while no distinct relationship emerged between restoration actions and vegetation scores. To bridge social and ecological metrics, we developed a linking matrix and found that although restorationists and the public shared similar values, community priorities often went unaddressed in project assessments. Furthermore, human perceptions and values were rarely considered in restoration evaluations. These findings highlight the need to integrate social values into restoration projects and improve communication between stakeholders.

An important environmental challenge for tidal marshes is sea-level rise (SLR) and the second part of this dissertation investigates the combined effects of SLR and biological invasions on a tidal marsh cordgrass (*Spartina foliosa*) ecosystem. Field experiments in San Francisco Bay, CA, USA, demonstrated reduced cordgrass survival in the presence of invasive crabs, along with varying responses of benthic microalgae and macrofaunal grazers to tidal inundation. Contrary to expectations, no interactive effects between increased inundation and invasive species were observed. This highlights the importance of considering sequential or latent stressor effects on ecosystems.

In light of the impending changes brought about by SLR, the final part of this dissertation explores the intricate trophic interactions between aquatic and terrestrial habitats within tidal marsh ecosystems. We simulated sea-level rise using experimental structures that increased tidal inundation and assessed changes in various ecological indicators and species responses. Cordgrass exhibited negative responses to increased inundation, likely due to oxygen limitations resulting in elevated sulfide levels. Additionally, insect responses varied with some species showing positive reactions to inundation, while others exhibited negative responses. The presence and abundance of Song Sparrows (*Melospiza melodia*) were influenced by elevation and year, potentially linked to alterations in *S. foliosa* integrity and Chironomid abundance. This underscores the importance of integrating aquatic-terrestrial connections into predictive models for sea-level rise effects and conservation strategies, offering valuable insights for proactive management and sustainable coastal planning.

Collectively, these results suggest that effective restoration and adaptation strategies for tidal marsh ecosystems require a holistic approach that bridges ecological and societal considerations. Recognizing the interplay between human values, ecosystem responses to restoration, and the complexity of trophic and stressor interactions is pivotal to craft strategies that safeguard these vital ecosystems in a changing world.

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CHAPTER 1

Improving Tidal Marsh Restoration Using Both Stakeholder Perceptions and Ecological Metrics

Collaborators: Sabra Comet, Paul Engelmeyer, Shersten Finley, Edwin D. Grosholz, Melissa Haeffner, Vanessa Robertson-Rojas, Shon Schooler, and Catherine E. de Rivera

Abstract

Understanding why habitat restoration is viewed as successful is key to evaluating past projects, planning future projects, and building support. Connecting public perceptions of success to the restoration process can improve project outcomes and generate greater public support. Yet, we lack fundamental information about the extent to which restoration actions align with measured ecological outcomes and social perceptions. Focusing on tidal marshes, we gathered qualitative and quantitative data on public perceptions of these habitats and restoration through focus groups in three estuaries in Oregon, USA. We also gathered environmental data from nine restoration projects spanning these three estuaries to understand ecological responses to restoration focusing on responses of hydrology and vegetation. We searched project reports for mentions of priority project goals from an ecological perspective to compare with community priorities. Lastly, we interviewed restoration managers to provide context for the environmental data. Across our sample, hydrology scores increased with the number of restoration actions, however, no clear relationship emerged between restoration action and vegetation scores. We developed a linking matrix to compare social and ecological metrics, and found that, although restorationists and the public have similar social values, assessments of projects do not often include the highest ranked priorities of community members and rarely track human factors as part of restoration assessment. Based on these findings, we suggest methods to include social values in future projects and for improved communication between restorationists and the general public.

Keywords: assessment; estuarine; habitat restoration; salt marsh; social perceptions

Introduction

Conservationists and restorationists seek to manage their systems in the most informed, economical, and effective way possible. Assessing the efficacy of their efforts in achieving project goals is a key component of this process. However, assessment of project outcomes is restricted by funding, logistics, and other constraints, which often limits metrics scientists and managers choose during assessment design and implementation. Funding opportunities for both study of ecological functions before restoration implementation and extended restoration monitoring after are generally minimal (Thom 2000). Consequently, many projects monitor a few selected metrics intended to represent critical ecological functions. Also, ecological monitoring metrics often do not exceed very minimal permit or contract requirements (Zedler 2000), and as such, observations and data outside of those metrics are lost or disregarded. Monitoring data that is collected often remains in unpublished reports (Zedler 2000), which can make access to this data challenging. Moreover, there is often a lag between relevant scientific advances and their application to environmental management (“science-practice gap”, Cabin et al. 2010). For example, there are recent advances in knowledge of fish life history, and use of tidal marsh and other off-channel habitats, that are not often considered in planning for habitat restoration and salmon management recovery plans (Young et al. 2006, Silver et al. 2017, Gayeski et al. 2018). This lack of valuable information prevents full understanding of project outcomes, development of more informative monitoring metrics, and impedes improvement of management practices (Thom 2000, Wagner et al. 2008). In recent years, tidal marsh restoration has been prioritized due to projected habitat loss from sea-level rise (Callaway et al. 2007). As such, many tidal marsh restoration projects have started, or will break ground in the near future, and there is a need for thorough, informative monitoring to assess restoration success.

The ultimate success of new restoration projects as well as the long-term success of completed ones often depends on public support (Miller and Hobbs 2007). Public perception of restoration success may be based on different metrics than ecologists or land managers use to measure success. What a restoration ecologist perceives as a successful, functioning system may look neglected or messy to members of the public (Nassauer 1995, 1997). In contrast, a monoculture of an invasive weed may look more orderly and appealing. Data gaps in our understanding of public perceptions exist in critical areas that could improve ongoing efforts to prepare for, mitigate, or communicate environmental protection projects. For example, recent work found that community members' understanding of biodiversity can influence their support of biodiversity management (Buijs et al. 2008). In a riverine restoration project, Gardeström et al. (2013) discovered local stakeholders worried that adding boulders would decrease the amount of water in the river and deteriorate fishing conditions. Yet, they found the opposite; boulders decreased flow velocity and increased water depth, improving fish habitat. Public community members tend to find invertebrate species distasteful (Kellert 1993) and show little interest in marine plants, although oysters were ranked more favorably than marine plants in the UK, likely because of their status as a luxury food rather than any ecological purpose (Jefferson et al. 2014). In contrast, the public is captivated by 'charismatic species' like harbor seals, puffins and seahorses (Jefferson et al. 2014). Scientists and managers, however, recognize the benefits of plants and invertebrates as refuge or food, and their contribution to ecosystem function and ecological communities. Although discrepancies between public and management perception is a recognized issue (Miller and Hobbs 2007), to our knowledge, few studies exist that aim to reconcile these perceptions to improve tidal marsh restoration efforts.

Assessments of tidal marsh restoration progress that include both ecological and social indicators would allow practitioners to communicate more effectively with the public about links between restoration and human values. Social indicators, such as familiarity, social cohesion, sense of place, or perceived attractiveness, are based on human values. Social indicators may be used to track change in human values as social functions are realized post-restoration. Other creative efforts used social indicators to evaluate the recreational value of habitats, outcomes of freshwater wetland restoration, and the biocultural function of streams and waterways (Tipa and Teirney 2006, Sun et al. 2015, Hegetschweiler et al. 2020). However, tidal marsh restorationists working in estuaries generally include exclusively environmental metrics in assessments of restoration project progress. This approach assumes that the success of projects is limited primarily by biological and physical factors. If projects include adaptive management strategies, including social indicators could greatly improve restorationists ability to respond to unanticipated social responses, as well as ecological responses, to restoration efforts (Hein et al. 2017).

To assess data gaps and as a step towards developing social indicators to use in assessments, we compared social and environmental data to explore how restorationists approach project evaluation, and whether evaluation criteria and outcomes align with stakeholder perceptions of estuaries and their values. To this end, we ask two primary questions: 1) How do tidal marsh restoration project outcomes compare with restoration goals? and 2) Do restoration project goals and outcomes align with local social values? We accomplish this by examining the perceptions of multiple stakeholder groups using focus groups at three estuaries in Oregon. We also compile and analyze environmental monitoring data from nine restored sites spanning the three estuaries to assess restoration project outcomes. We developed a matrix to compare these ecological and social data at the estuary scale and assess gaps in monitoring data to quantify where alignment and mismatches occur.

Methods

Environmental Monitoring

We assessed nine restoration projects spanning three Oregon estuaries: Kunz, Frederickson, Dalton, and Cox marshes in Coos Bay; Y27, Y3 and Poole Slough in Yaquina Bay; and Lint Slough and Drift Creek in Alsea Bay (Table 1). We reviewed project reports and available data for all projects to determine project characteristics and environmental metrics measured (Table 1). We limited our ecological assessment to metric categories that were measured at most of the projects: vegetation, hydrology, mammal use, and fish use. Other categories of ecological function were also considered including water quality and marsh elevation, but not included due to a lack of these data across estuaries and years at a given site, precluding comparison. We then collected present-day data for vegetation and channel sinuosity (as a proxy for hydrologic function) for comparison to pre-restoration data. Mammal and fish use were recorded as post-restoration presence/absence data due to the logistical inability to standardize those data for comparison and general lack of pre-restoration data for these metrics. If mammal or fish use post-restoration was recorded, we assigned the category a value of "present".

Our hydrology metric was marsh channel sinuosity as a proxy for fish habitat and hydrological function in the study marshes (Stone 2012). Google Earth aerial imagery (Google Earth 2021, Large and Gilvear 2015) was used to view pre-project and post-project channel formation to the most recent year. Using pre- and post- project aerial imagery for each site, we traced main stem marsh channels along the center of the channel, and drew a straight line from the start point of the traced line to the end point. We measured these two lines in meters and calculated a ratio of the length of the curved channel to the length of the straight line (Stone et al. 2012). In small to medium size project sites where channels were sparse, all visible channels were measured. Two projects, Poole Slough and Kunz Marsh, were large sites containing extensive networks of visible channels. In these cases, all of the major channels and over 50% of visible minor channels were measured to avoid over sampling. Using only a subset of these minor channels is supported by the low within-site average variance in sinuosity (variance=0.004 for Poole Slough and 0.15 for Kunz Marsh).

In summer of 2021, we resampled vegetation transects for all nine projects. We reviewed past reports and datasets to obtain baseline and post-project vegetation data in the form of species-specific abundance data along intertidal transects. Data were recollected at previously established transects in each project. A subset of a given project's total transects were sampled in cases where all transects could not feasibly be revisited within the sampling season. All transects and associated plots were resampled or a randomly selected subset of 25 plots were resampled from vegetation datasets containing more than 25 vegetation plots across the entire marsh. Poole

Slough contained the least number of plots (n=8) due to a small original dataset, while Lower Drift, Cox, Dalton, Frederickson, Kunz, Y3 and Y27 all contained the maximum number of plots (n=25). Past report maps and documented coordinates were referenced to relocate all transects. Percent cover by species was collected across select transects at each marsh or "project" location, and a 1-meter plot was used at all sites. Replicating the same methods used to collect the original data, 0 to 100 percent cover was recorded for each species present of each 1-meter plot following protocols in Elzinga et al. (1998). Plants were identified to species using Jepson and/or online resources (Calflora 2021, OregonFlora Project 2021, Jepson et al. 1993).

Simpson's Diversity Index assesses species evenness or relative abundance in addition to the richness or a total number of species present, and values were calculated using the "diversity" function in the "vegan" package in R and averaged across the $1m^2$ sampling quadrats of a project. This function calculates the Gini-Simpson Index as one minus the sum of the proportional abundance of species squared or, $1-(D = \sum(n / N)^2)$, which considers both the number of species and heavily weights the evenness of species. We identified the top five species with greater than 40% cover in each transect in both the pre- and final dataset as "dominant". All plant species were assigned native or nonnative status as listed by the USDA Plant database (USDA 2021). We calculated percent cover of non-native species by averaging the percent cover values of all invasive species across transects in one restoration project, for a site-level value. We also calculated the percent of non-native species in each year of available data.

Plant species were assigned a salinity tolerance level (0 to 5 parts per thousand (ppt), 5 to 10 ppt, or 10 to 30 ppt). Many of these designations were identified in peer reviewed journal articles (Janousek and Folger 2013, 2014). In the case where no peer reviewed article could provide information about the salinity tolerances of specific plant species, researchers' experiential knowledge was consulted to identify obvious ranges (Ex: known freshwater plants were assigned to the lowest tolerance range bin, 0-5 ppt). In some cases, there was no clear salinity tolerance range available through peer reviewed journal articles or researchers' experiential knowledge. Species with a lack of characterizing information were not included in analyses of salinity-tolerant plants. We defined a plant species as "salinity tolerant" if it was in the 5 to 10 ppt or 10 to 30 ppt category. We then calculated the percentage of salinity tolerant plants in each transect, in each project for each year. We averaged transects to produce one value for each project for each year considered. We averaged the percent cover values for salinity tolerant plant species as described above in each transect, and then averaged these transect values to produce one value for each project.

We then calculated percent change over time for all vegetation parameters from the earliest recorded data (usually pre- or just post-restoration) to present day 2021 values. Percent change for all variables was calculated using the equation $(\frac{final\ value}{initial\ value-1}) \times 100$ for scaling considerations.

Social-ecological Data Analysis

In August of 2021, we conducted focus group interviews in each of Coos Bay, Alsea Bay, and Yaquina Bay in Oregon, U.S (Fig. 1), with 15, 17, and 12 participants, respectively. Focus group participants included restoration managers, direct receivers of information about restoration (such as port managers), and indirect receivers of information (such as area residents who may learn about the restorations from the news). We held two activities during the focus groups to gather quantitative social information to compare with environmental monitoring data. The first was a Q-sort (forced ranking) activity where participants were prompted with the phrase

"I value estuaries for…" and ranked provided statements according to that phrase (Table S1). We compiled statements into the same broad metric categories that were used to compile environmental data. We also included three additional categories, "Bird Use", "Invertebrate Use" and "Human Factors", to encompass social data that could not be categorized under the environmental metric categories. For example, we assessed how participants valued estuaries for their ability to support oyster and clam farming (Table S1), which were included in the "Invertebrate Use" category. We also held a photo ranking exercise during the focus groups using a pair of photos for each of five metric categories (i.e. bird use, fish use, mammal use, vegetation, hydrology), where one photo of each pair was chosen to portray a "high ecological function" representation of that metric category and the other photo showed a "low function" representation (Fig. S1). Participants in the breakout groups had to come to a consensus on how to rank these ten photos.

Lastly, we had formal conversations with five habitat restoration managers/practitioners that were involved in the nine restoration projects used in our study. Each conversation was conducted with the same set of questions. These conversations provided background and context for our data summaries.

Report Mining for Project Objectives

Eighteen project reports related to the nine projects considered in this work were mined for goals and objectives using the Atlas.Ti software. These data were collected at the estuary scale and were used to compare social and ecological scores of each estuary to restorationists' priorities, or what they focused on in project reports. Using the Atlas.Ti software, a list of thematic coding terms (Saldaña 2013) were developed to match these goals to the seven metric categories: Fish Use, Bird Use, Mammal Use, Invertebrate Use, Hydrology, Vegetation, and Human Factors. All project reports were identified and loaded into Atlas.Ti. All reports were then searched for mention of the terms: “goal”, “goals”, “objective”, “objectives”, “purpose”, and/or “purposes”. Records were associated with project name, project estuary, implementation year, data collection year, report title, goals listed, and restoration actions used to achieve project goals or objectives. Language describing goals was used to develop a list of goals that fit within the seven metric categories. One or multiple goals were listed within each record, depending on the nature of the text. The terms used to describe goals and objectives with the seven metric categories were then used to develop a list of thematic coding terms for each metric (Table 2). Atlas.Ti was used to search all project reports for these specific lists of terms which describe the seven metric categories. These instances were counted, and the totals were summed by estuary.

Scorecard and Matrix Development

We developed a scorecard to synthesize overall ecological performance at the estuary level to compare with social scores at that scale (Table S2). We identified seven major metric categories that described both the environmental and social data we gathered; Vegetation, Hydrology, Fish Use, Mammal Use, Bird Use, Invertebrate Use, and Human Factors. Spatial and temporal scale must be considered when comparing ecological and social data. Environmental data, including monitoring data from restoration projects, are often high-resolution data collected and reported at small spatial scales. Alternatively, socio-economic data are often gathered and reported on much coarser spatial scales (Herr 2007, de Lange et al. 2010). However, how environmental conservation and restoration projects affect humans can span site-level effects (such as impacts to land or property) to ecosystem-level effects including climate change resilience. Previous studies in forestry management developed methods to integrate biological monitoring data and social data by reconciling the spatial scales of these two data types (Hegetschweiler et al. 2017, Hegetschweiler et al. 2020). Here, we considered both environmental and social data at the estuary scale for comparison. We summarized site level environmental data (Vegetation, Hydrology, Fish Use, Invertebrate Use, and Mammal Use) at the estuary level by normalizing those data on a 1 to 10 scale or transforming those data into presence/absence data. We also binned social ranking data (pertaining to all metric categories above) from the Qsort (Table S3) and photo ranking activity on a 1 to 10 scale.

Both pre-restoration and present-day data for vegetation and hydrology were available, so we were able to assign scores for these categories. For the vegetation category, we assessed multiple vegetation parameters, including: invasive species and percent cover of invasives, salt-tolerant species and percent cover, dominant plant species, plant diversity, and native plant species and percent cover of natives. For dominant plant species, we scored abundance of a native dominant highly and abundance of a non-native dominant as low. We considered both the final value (present-day) of each parameter and the change from pre- or just post-implementation to present-day (“lift” of the restoration). We created a “change index” where we calculated percent change, and normalized those data on a 1 to 10 scale. We also created a present day “2021 value index” by assessing the average value of each vegetation parameter across transects for the data collected in 2021, normalizing those data and putting them on a 1 to 10 scale. These index values were then added together to produce a “performance score” for each vegetation parameter, which were binned on a 1 to 10 scale. We averaged vegetation parameters to calculate an overall vegetation score per project. If there was more than one dominant species, we included only the native dominant species with the highest percent cover, and only the invasive dominant species with the highest percent cover in present day data. We only included the highest scoring value for either percent change or species richness variables (invasive species, native species, salinity-tolerant species).

From our measurements of sinuosity pre-restoration and from present-day aerial imagery (see methods above), we created a “change index” for sinuosity data where we calculated percent change, and normalized those data on a 1 to 10 scale. We created a “2021 value index” by assessing the average channel sinuosity for each project across transects for the data collected in 2021, and normalized those data on a 1 to 10 scale. These index values were then added together to produce a “performance score” for channel sinuosity, and these values were binned on a 1 to 10 scale.

This scaling methodology, which permitted comparison across projects with very different starting points, inherently undervalued restoration projects with initially high or moderately high values for pre-restoration vegetation parameters and/or channel sinuosity. These initially high condition sites consequently had less scope for change. Our scores were meant to encompass a restoration project’s ability to improve these metrics over time, which may or may not be the goal of individual projects.

To assess how restoration actions may have affected these final vegetation and hydrology scores, we compiled a list of all seven potential actions taken across projects, derived from project reports, and identified which actions were taken for each project (Table 1). From these, we summed the number actions taken for each project out of the seven total actions to produce a “restoration action score”. We then compared restoration action scores with both overall vegetation and hydrology scores for each project using a linear mixed effects model, with hydrology or vegetation score as a fixed factor and estuary as a random factor to account for non-independence.

We developed a social scorecard using the quantitative social data obtained from the Qsort and photo-ranking activities in the focus groups (see above). Qsort statement rankings were binned on a 1 to 10 scale. The photo rankings for the high ecological function photos were also binned on a 1 to 10 scale, and scores from the Qsort and photo ranking were averaged to produce the overall social score per estuary. Finally, we created a framework to display these environmental and social data in the form of a matrix (Fig. 2). This matrix includes the final social and environmental scores for each estuary, and the number of mentions of each metric category in project reports.

Results

Environmental Monitoring

Higher scores for hydrological change were correlated with number of restoration actions (Fig. 3, χ^2=12.25, p=0.0004). The same analysis using the composite hydrology score yielded the same qualitative outcome (Fig. 4, χ^2=9.48, p=0.002). Kunz Marsh, with the lowest hydrology score and a low restoration action score, had a moderately-high initial channel sinuosity value and consequently less scope for improvement than other projects, even with a full dike removal. Kunz Marsh's hydrology score contributed to the lower average hydrology score for Coos Bay relative to the other estuaries (Fig. 2, Table S2). The other Coos Bay marshes with more restoration actions undertaken scored higher for hydrology (Table 1). Fish were present at three of the four Coos Bay restoration sites post-restoration and beavers were present at Cox Marsh post-restoration.

We found no correlation between restoration action and vegetation scores (Figs. 3 & 4). Some project's restoration action scores track vegetation score. These include Y27 in Yaquina

Estuary, which had a relatively high restoration action score of 4/6 and vegetation score of 7.33/10, and Poole Slough in Alsea Estuary, with a restoration action score of 1/6 and a relatively low vegetation score of 5.5/10. Other projects did not follow this trend; for example, Kunz Marsh, with a low restoration action score of 2/6 had the second highest vegetation score. One vegetation parameter that may explain some of this variation may be the Gini-Simpson Index score for projects. Although the average Gini-Simpson Index (standardized to a scale of 10 to be comparable to the other metrics) score for all projects was relatively low (4.2 ±1.7/10, Table S2), projects like Y27 with higher Gini-Simpson scores scored higher for vegetation overall with a score of 8/10 contributing to a high vegetation score of 7.33/10.

Social-ecological Data

The top five ranked valued statements from the Qsort activity were (1) increasing habitat for fish and wildlife, (2) increasing ecological function in general, (3) enhancing water quality, (4) reducing pollution, and (5) minimizing the impacts of sea-level rise (Table S1). In all focus groups, the combination of Qsort and photo ranking data resulted in a high score for Mammal Use, always receiving the second highest score of the six factors measured (Fig. 2). Bird Use also scored high, receiving the highest score in Coos and Alsea estuaries and the third highest in Yaquina. Hydrology and Human Factors always received the two lowest scores. In Alsea Bay, Vegetation was ranked highest, yet scored moderately in other estuaries. Scores varied from 4.2 to 9.5, with the greatest differentiation between scores within an estuary in Coos Bay (Fig. 2).

Report Mining

The metrics that practitioners were most focused on, for both goal development and evaluation, were Vegetation and Hydrology, which had moderate to moderately-high ecological performance scores (Fig. 2). Alsea, Coos and Yaquina project reports contained 280, 38 and 324 mentions of vegetation, respectively (Fig. 5). Vegetation was also prioritized for evaluation and measured consistently across projects. Hydrology was mentioned 111 times in Alsea project reports, 109 times in Coos project reports and 250 times in Yaquina estuary project reports. However, practitioners did not often evaluate hydrological function through time, except in Coos where channel sinuosity was measured. Ecological performance scores for vegetation were moderate to moderately-high, ranging from 5.8-6.4/10 (Fig. 5). Hydrological function scored higher overall than vegetation across all estuaries, ranging from 6.3-10/10 (Fig. 5).

Matrix and Scorecard

Across estuaries, generally, the number of report mentions was higher when social scores were higher for hydrology, vegetation, and fish use but not the other categories. This pattern held true in Alsea and Yaquina estuaries for the vegetation metric, which was the most frequently mentioned metric/goal in project reports (280 and 324 mentions, respectively) and had high or moderately-high social scores (6.5/10 and 8.7/10. respectively) (Fig. 2). Fish use in Yaquina was mentioned relatively frequently and had a moderately-high social score (6.3/10). In Coos Bay, fish use was mentioned infrequently (11 times) and received a low social score. However, there were some exceptions. In Yaquina, hydrology was mentioned 250 times in project reports and had a moderately-high ecological performance score (6.8/10) yet was given a relatively low social score (5/10). Similarly, in Coos Bay, hydrology, with more mentions than vegetation (109 vs. 38), received a lower social score (4.2 vs. 6/10) (Fig. 2).

There was no apparent relationship between ecological scores and social scores for any of the categories or bays, in part due to a dearth of available ecological monitoring data in the reports (Fig. 2). For example, there was no mention or evaluation of bird use in Coos estuary project reports despite this metric having the highest social score in that estuary (9.2/10). In Yaquina, fish use was mentioned frequently and had a moderately-high social score (6.3/10), yet only project reports from one out of the four projects there contained any information about fish use of habitat post-restoration. Similarly, bird use in Yaquina had a moderately-high social score yet was not monitored pre- or post-restoration. Mammal use was mentioned infrequently (50 mentions), and had a high social score of 8.2/10, yet we found no information on mammal use of habitat in any project reports from Yaquina estuary (Fig. 2). Although bird, fish, mammal, and invertebrate use had moderately-high to high social scores in Alsea Estuary, reports contained no information on evaluation of these metrics at restoration sites post-restoration. Across estuaries, human factors were rarely mentioned (ranging from one to six total mentions), had relatively low social scores, and were not tracked or measured through time (Fig. 2).

Discussion

The overall results of this study illustrate the ecological outcomes of tidal wetland restoration projects and the extent to which project goals and outcomes align with public values. We found that ecological goals stated in project reports were generally met and that restorationists and the public share similar social values. However, we also found that project assessments generally do not include priorities that are highly ranked by community members.

Despite practitioners and community members sharing similar overarching values, these values are not always reflected in the metrics that practitioners use to assess restoration progress. However, this difference varies with the type of metric we considered.

In this study, many of the actions taken to restore sites to functioning tidal wetlands were related to hydrology, consistent with a recent review of 78 peer-reviewed papers on salt marsh restoration that found salt marshes were primarily restored through recovery of tidal exchange, managed realignment and soil level amendment (Billah et al. 2022). Our findings suggest that the number of restoration actions taken in projects influence the degree of change in channel sinuosity through time, as project restoration action scores were significantly correlated with channel sinuosity performance scores. When the number of restoration actions was directly compared with the score assigned for change in channel sinuosity through time, there was an even more substantial correlation.

Measurements of restoration project progress tended to focus on hydrology and vegetation, which were the most common project goals and objectives outlined in project reports. Furthermore, for many of the projects, environmental data gathered on hydrology and vegetation generally showed that project goals related to those metrics were met. Hydrology and fish use are often the first indicators to reach equivalency to natural marshes after hydrological reconnection (Billah et al. 2022). Over half of the projects across estuaries had higher ecological performance scores for hydrology (channel sinuosity) post restoration than before. However, there were some exceptions that point to how oversimplification from using any metric score cannot always evaluate outcomes. For example, Kunz Marsh had a high initial channel sinuosity and slight decrease over time, resulting in a poor overall ecological performance score for hydrology. However, the project tested “cells” with different initial elevations and the higher areas excelled at establishing vegetation, and may be better suited to mitigate sea-level rise, but had lower channel sinuosity after restoration. We grouped channels across cells to compare the hydrological performance of the site as a whole, but it is important to note that the purpose of this restoration was to determine effective starting elevations and inform future restoration projects, for which it was successful. Conversely, in Drift Creek, Alsea Bay, restorationists performed fewer restoration actions but had one of the highest scores for hydrology. However, this project featured a complete dike removal, whereas most others were partial dike/berm removals or dike breaches. Our restoration action score prioritized the number of restoration actions and not the intensity of any one individual action, and the correlation between restoration action and hydrological performance we found pertains to the number of actions performed at a site and not their intensity. Future research is needed to test the relative influence of number or intensity of restoration actions on hydrological function.

In all estuaries, hydrology was mentioned frequently in reports as a proxy for fish habitat. A recent meta-analysis showed that river restoration projects that implement instream measures to support hydrological function, such as river widening or re-meandering, result in higher fish abundance and/or biomass and diversity or richness relative to pre-restoration conditions (Kail et al. 2015). Consistent with this work, fish have been recorded using the new, sinuous streams of some of the restoration projects in this study (Brophy 2004, Cornu 2005A, 2005B). However, comparable data on fish species and abundance pre- and/or post- restoration were not available at more than half of restoration sites.

Vegetation is an important proxy for other marsh functions and was mentioned frequently as a goal in project reports. Vegetation scores were higher in Alsea and Yaquina Bays, where vegetation was also mentioned as a goal more frequently than hydrology in project reports (Fig.

2). However, unlike hydrology, there was no relationship between ecological performance scores for vegetation and the number of restoration actions (Fig. 3). This may be due to low-moderate Simpson's diversity index scores across projects. In pickleweed-dominant marshes in particular, channel excavation and tidal reintroductions alone are not generally sufficient to increase plant species diversity due to the inability of other species to recruit (Lindig-Cisneros and Zedler 2002). Lower ecological scores for vegetation may be driven by low final diversity index values of plant communities and/or minimal increase in diversity over time. Previous work in California marshes found significant correlations between plant species diversity and salt marsh functions (Keer and Zedler 2002), but it is important to note that plant species diversity alone is not indicative of marsh function (Callaway 2005). Marsh plant diversity is affected by environmental gradients in elevation and salinity (Janousek and Folger 2014) which complicates comparison across restoration sites and assessments of diversity through time as a site develops. Additional research is necessary to understand how to best shift restored plant communities on a desired trajectory. This trajectory could be either towards a) the more diverse plant communities seen in older, less manipulated marshes or b) towards measures of plant-derived ecosystem functions in salt marsh restoration projects, such as carbon sequestration, sediment accretion, and net primary productivity. Therefore, we suggest a comprehensive review of vegetation parameters, in addition to contextual information, to evaluate ecological function in restored marshes.

Importantly, project goals and metrics gathered by restorationists did not align well with values expressed by community members in focus groups. We found that vegetation and hydrology were the most common metrics mentioned in project reports. Although vegetation did receive a high social score in Alsea Estuary, community members tended to prioritize wildlife, general estuarine function, water quality, and sea-level rise resilience, and scored metrics related to mammal and bird use highly. Data from our focus groups and conversations with restoration practitioners suggests that this disconnect is not due to divergent values of these two groups; these groups shared similar values (Haeffner et al., *in review*). The disconnect between project reports and values, however, may be due to the constraints practitioners face when implementing restoration projects, especially funding constraints, which affect their monitoring decisions and the goals they focus on.

A consequence of funding limitations is minimal monitoring in some areas of public interest. One clear discrepancy we found was high social rankings for bird and mammal use, along with limited mention in project reports, no reported monitoring of bird use, and minimal monitoring of mammal use of habitats in these restoration projects. Many of the studies that have examined bird density and/or diversity post-restoration (e.g. Lewis and Casagrande 1997, Warren et al. 2002, Adamowicz and Roman 2022) yielded inconclusive results, likely due to the seasonality of bird distributions and their mobile nature coupled with infrequent sampling and variable survey design. However, there is some evidence for higher shorebird density after restoration and subsequent mudflat development (Raposa 2008). Given the social importance of birds and that many birds rely on salt marshes for food and habitat, it is worthwhile for managers to consider tracking bird use of habitat over time, especially because monitoring is relatively cost effective. Konisky et al. (2006) suggest tighter protocols and more frequent monitoring to address variability in bird populations. More rigorous and effective monitoring would allow practitioners to evaluate bird use and other metrics that align better with community member values.

Where lack of capacity hinders collection of monitoring metrics valued by community members, practitioners may consider enlisting citizen/community scientists and volunteers, who can provide high quality data across a wide variety of disciplines (Sullivan et al. 2014, Lewandowski and Specht 2015, Fuccillo et al. 2015, Vermeiren et al. 2016). For restoration sites that are adjacent to an area with public access, managers may consider setting up an iNaturalist project for the site (https://www.inaturalist.org/projects) to allow public end users to easily report any birds or mammals they encounter during their visit. Managers may also consider taking advantage of prior or regularly collected data to address this public value.

Along with increased community involvement through citizen science, improved communication about how restoration outcomes link to public values may resolve disconnects between restorationists and the public. We found that fish use of habitat was ranked of moderate-high importance by community members and mentioned relatively frequently (behind vegetation and hydrology) by managers in project reports. Fish, such as salmonids, are highly valued in Oregon, yet it may be that people do not connect restoration of tidal wetlands with an increase in fish. One challenge both for developing restoration targets and for communicating about the need to support fish is the lack of historical data and the resulting 'shifting baselines' of expectations by managers and the general public (Jackson and Alexander 2011). Hydrology was mentioned frequently by managers in project reports and scored relatively high in ecological assessments yet ranked lower than fish use by public end users. This suggests an opportunity to share findings from relatively recent research that links channel morphology and fish use, and how improved hydrological function benefits fish (Gray et al. 2002, Kail et al. 2015). Educating community members about how fish habitat provides refuge for fish could resolve the disconnect between practitionerd and the public.

As ecological systems often function on much larger scales than management boundaries occur (Sayles & Baggio 2017), there has been a movement towards estuary-scale partnerships to promote estuarine conservation and restoration. Our findings support the need for an estuary- or larger scale understanding of restoration outcomes to communicate project outcomes to community members. Community members valued estuaries for large-scale functions like habitat provision and sea-level rise resilience. There are recently developed methods for evaluating sea-level rise and marsh resilience at larger scales using indices derived from biophysical metrics (Raposa et al. 2016, Wasson et al. 2019). Indices such as this allow scientists to consider ecological function at the site level as well as the estuary or watershed scale. It is also important to note that many metrics become more important with climate change, such as a good understanding of current elevation and accretion potential for sea-level rise mitigation, and carbon sequestration potential. These landscape scale approaches and assessments should be prioritized to communicate restoration progress to community members in areas particularly susceptible to these changes.

One striking, yet not altogether surprising, gap concerns the lack of goals related to human factors in project reports coupled with a low social score for human factors. This suggests that restoration managers and public community members alike perceive human factors as being lower priority than other metrics, or they do not make the connection between human benefits and habitat restoration in marshes. Increased multilingual signage in restoration sites, pathways adjacent to or even into the marsh, access to public fishing platforms, and community tours within those areas could all function to achieve improved public education about tidal marsh ecosystem services and restoration. At minimum, we suggest targeted messaging that describes how the metrics that practitioners do measure align with social values. In many cases, vegetation and hydrology metrics can be a useful proxy for the social value of providing habitat for wildlife.

A discussion of the most common perspectives and associated messaging strategies from this work can be found in Haeffner et al. (*in review*).

Studies such as this one that simultaneously examine social and ecological values and identify where and how these could be better aligned are important to help achieve biocultural restoration. Biocultural restoration approaches aim to restore both biophysical and sociocultural components of the ecosystem to maintain or rebuild cultural interactions with ecosystems (Chang et al. 2019). Many of these approaches require public and other stakeholder involvement at all steps of the conservation/restoration process. Although biocultural restoration has focused on the essential area of restoring cultural ties to the land for groups that have been actively thwarted from such connections due to imperialist dogmas and racism, all restoration projects could benefit from more closely tying the surrounding public to restored tidal wetlands. Project success, the future of restoration, and the land and people all could benefit from these closer ties. We found a high level of complex understanding by the public in our focus groups. This suggests that community members, especially Tribal and Indigenous communities, recreationists, and other members of the public that interact directly with estuaries, could be included in more technical discourse in the planning stages, monitoring design, and/or when reconciling the data collected to synthesize findings. Public input can help determine bioculturally important environmental metrics and social indicators to include in assessments. To achieve this, future work can build on past indices that incorporate both environmental and social data to assess freshwater wetland restoration and the biocultural function of streams and waterways (Tipa and Teirney 2006, Sun et al. 2015), established methods for communication with the public and evaluation of impacts from public engagement (Druschke and Hychka 2015), and previous biocultural approaches in other systems (Tipa and Teirney 2006, Morishige et al. 2018). Recently proposed conceptual frameworks incorporate measurements related to both ecological indicators and social attributes in restoration assessments, which can be adapted for use in tidal marsh restoration settings (Hein et al. 2017, Smith et al. 2022). The social values identified in these focus groups (Haeffner et al., *in review*) in particular can be used to develop social indicators to track restoration progress and assess social values in Oregon estuaries over time.

Conclusion

Overall, this work illuminates the extent to which project goals and outcomes align with public values by linking ecological and social datasets. Practitioners and community members tend to share similar overarching values, although these values are not always directly reflected in the metrics that practitioners use to assess restoration progress. We highlight these values here and suggest that practitioners shift to focus on more metrics that are valued by the public and increase public education on how metrics that restorationists measure are in line with the public's top values. Also, practitioners should work to include designs and processes that intentionally include the community and assessments of social indicators over time to garner support for restoration by demonstrating how restoration projects affect the populace in addition to ecological function.

The estuaries we focused on were in rural areas with smaller communities. Studies focused on larger, urban estuaries surrounded by dense populations may give rise to different community perspectives or central restoration goals. Goals relating to human factors may be higher priority in a more populated estuary, such as those related to sea-level rise resilience which may be highly valued to minimize impacts on human infrastructure on the shoreline. In such cases, tracking metrics of sea-level rise resilience and other larger scale processes would certainly resonate with community members. Where funding constraints prevent restorationists from gathering metrics valued by community members, like bird and mammal use of habitats, citizen science and collaboration across stakeholder groups can be used to fill in data gaps. Lastly, development of social indicators to track pre- and post-restoration would allow practitioners to better address social values and adaptively manage restoration projects based on public responses. These strategies can promote alignment between practitioner and community member goals to the best extent possible through all stages of the restoration process.

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Tables

Table 1. Vegetation and hydrology scores for each restoration project along with GPS coordinates, primary restoration actions taken, and Degree of Action Rating (number of restoration actions). Dike breach or removal category actions include dike breach (DB), partial removal (PR), and full or mostly full removal (R).

			Restoration Actions								
Estuary	**Project**	**GPS Coordinates**	Dike breach or removal	Fill placement	Channel excavation	Woody debris placement	Ditch enhancement/ plug	Nonnative plant removal	**Degree of Action Rating (1-6)**	**Vegetation Score**	**Hydrology Score**
Yaquina	Y27	-123.910041°, 44.594256°	**DB**		X	X	X		**4**	7.33	9
Coos	Kunz	-124.321244°, 43.282124°	**PR**	X					**2**	7.67	4
Alsea	Lint Slough	-124.057340°, 44.428590°	**DB**	X		X			**3**	7.2	NA*
Yaquina	Y3	-123.947632°, 44.6124870°	**DB**						**1**	6.33	5
Coos	Frederickson	-124.319998°, 43.274776°	**PR**			X	X		**3**	6.4	8
Alsea	Drift Creek	-124.013156°, 44.425936°	**R**					X	**2**	5.6	10
Yaquina	Poole Slough	-124.005378°, 44.568143°	**DB**						**1**	5.5	5
Coos	Cox	-124.317196°, 43.271129°	**PR**	X			X		**3**	4.6	9
Coos	Dalton	-124.317886°, 43.279439°	**R**		X	X	X		**4**	4.0	9

* We were unable to assess channel sinuosity (Hydrology) for Lint Slough

Table 2. All identified project goals and objectives from mined project reports, metric categories associated with them, and all subsequent thematic coding terms used to mine reports for number of mentions as related to each metric.

Project Goals	**Associated Metric**	**Thematic Coding Terms**
increased fish presence	Fish Use	fish habitat, juvenile salmonid habitat, salmonid habitat, salmon habitat, fish presence, fish use, salmonid, salmon, salmon use
maintain or improve relationships with the surrounding community	Human Factors	community benefit, community relationship, sense of community, improve community relationship
inform future restoration projects	Human Factors	learning opportunity, learned, informed future, inform future, experiment, test method, lessons learned
increased channel sinuosity	Hydrology	tidal reconnection, sinuosity, channel complexity, channel sinuosity, increased sinuosity,
minimize flooding	Hydrology	flood reduction, decrease flooding, flooding buffer, buffer flooding, reduce flooding, mitigate flooding
sea-level rise resilience	Hydrology	hydrologic function, general function, seal level rise, SLR, sea level rise resilience, climate change
restore or enhance salt marsh plant community	Vegetation	native vegetation, salt marsh vegetation, vegetation function, vegetative function, vegetation habitat, native plants, salt marsh plants, halophyte. halophytic
reduce or limit invasive plant species	Vegetation	Invasive species, invasive, invasions, nonnative plants, noxious weeds, weeds, plant invasion
increased wildlife presence (birds)	Bird Use	bird, bird use, avian, waterfowl, bird habitat
increased wildlife presence (mammals)	Mammal Use	wildlife habitat, animal use, wildlife, animal, animal habitat, wildlife habitat
increased wildlife presence (invertebrates)	Invertebrate Use	invertebrate use, invertebrate habitat, invertebrate, clam, oyster

Figure Captions

Figure 1. Map of three study bays in Oregon, USA, where restoration projects took place.

Figure 2. Matrix linking ecological and social scores for each metric category in each study bay. Values include the number of mentions in project reports, social scores derived from focus group activities, and ecological scores from previously collected monitoring data and our own measurements as described in Methods. Asterisks represent social scores for metric categories that were not included in the photo ranking activity, these were calculated using exclusively Qsort data.

Figure 3. Plot showing the vegetation and hydrology "Change Index" scores for each restoration project as compared with degree of action rating, or number of restoration actions. Each point represents one restoration project.

Figure 4. Plot showing vegetation and hydrology scores for each restoration project as compared with degree of action rating, or number of restoration actions. Each point represents one restoration project.

Figure 5. Plot showing average vegetation and hydrology scores for Alsea (N=2 projects for vegetation, N=1 project for hydrology), Coos (N=4) and Yaquina estuaries (N=3). Number of mentions in project reports of each metric for each estuary are shown at the base of each bar in white. Error bars denote standard error relative to the mean. We were able to assign a hydrology score to one of the two projects in Alsea Bay. The bar shows the score for that project.

Figures

Figure 1

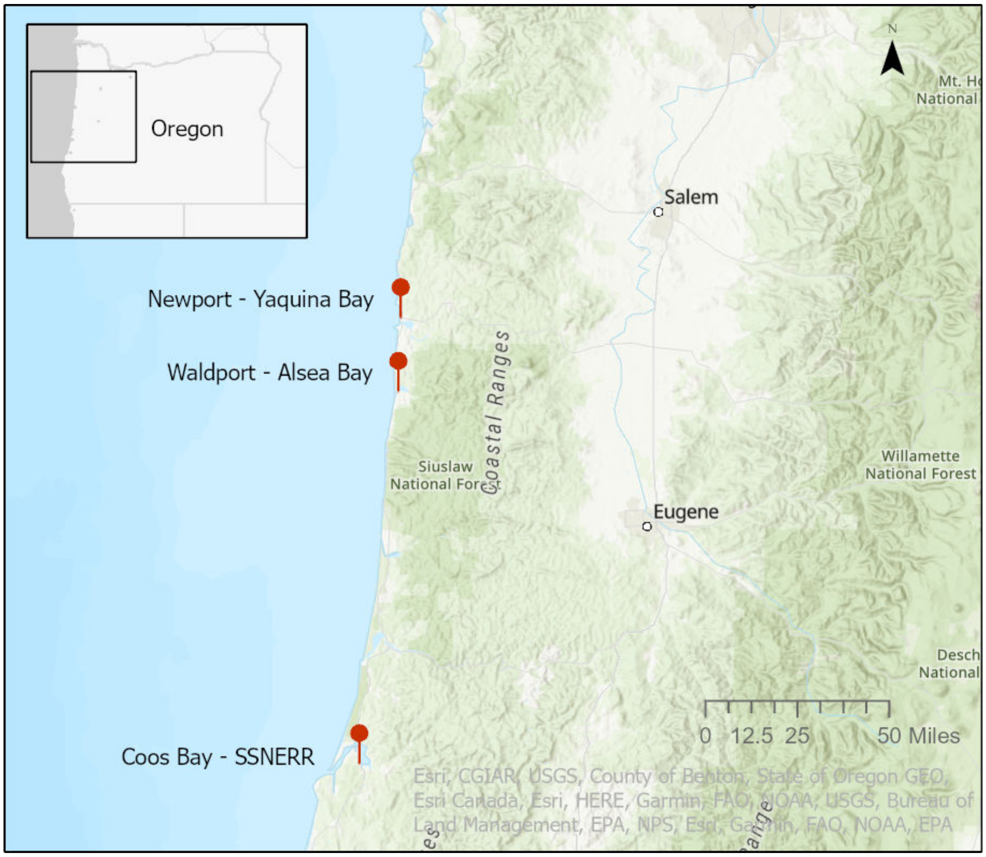


Figure 2

Linking Matrix

Shared Metrics	Alsea Bay			Coos Bay			Yaquina Bay		
	# of Report Mentions	Social Score	Ecological Score	# of Report Mentions	Social Score	Ecological Score	# of Report Mentions	Social Score	Ecological Score
Bird Use	3	9.5	no data	0	9.2	no data	4	6.8	no data
Fish Use	24	5.7	no data	11	5.3	P	144	6.3	P
Mammal Use	33	8.0	no data	2	8.7	P	50	8.2	no data
Invertebrate Use	1	6.0*	no data	14	6.3*	P	0	6.3*	no data
Vegetation	280	6.5	6.4	38	6.0	5.8	324	8.7	6.4
Hydrology	111	5.1	10	109	4.2	7.5	250	5.0	6.3
Human Factors	1	4.8*	no data	1	4.2*	no data	6	4.6*	no data

Figure 3

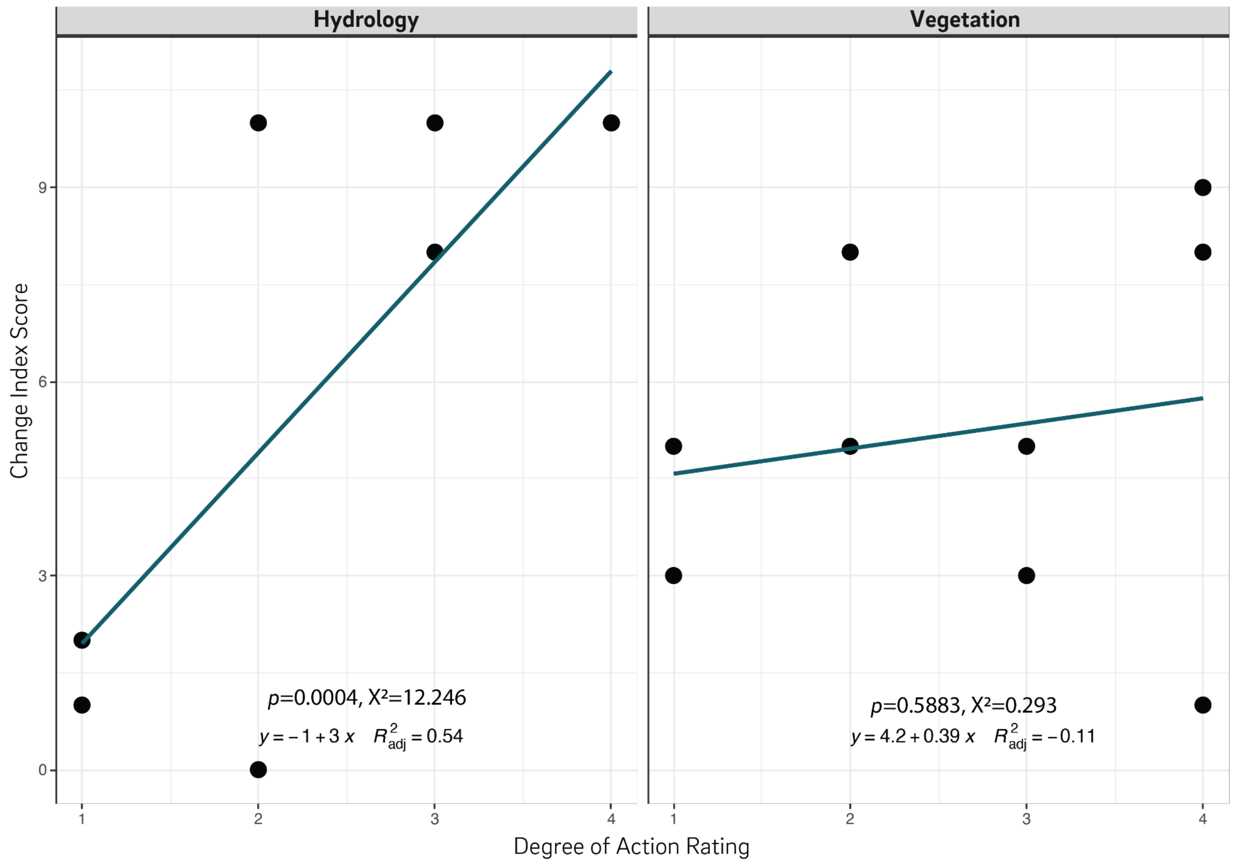
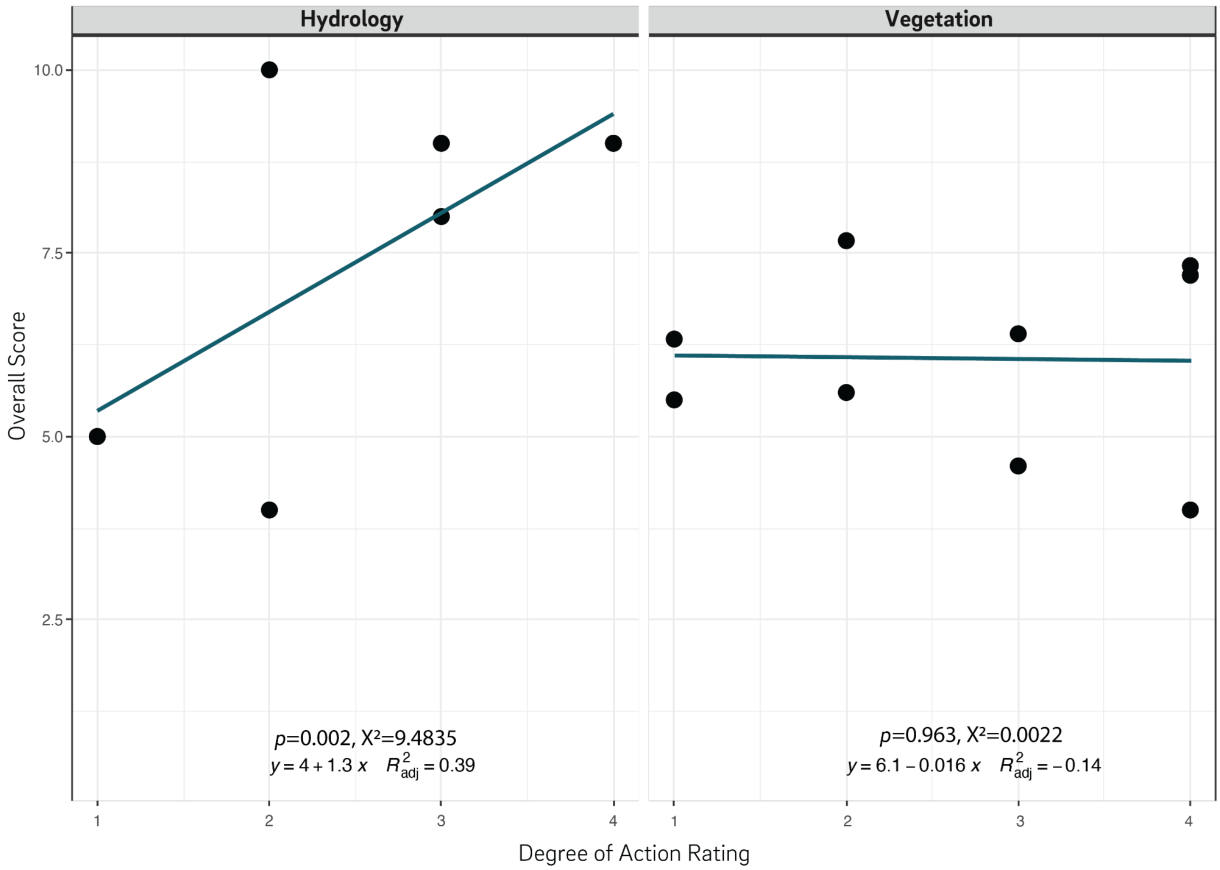
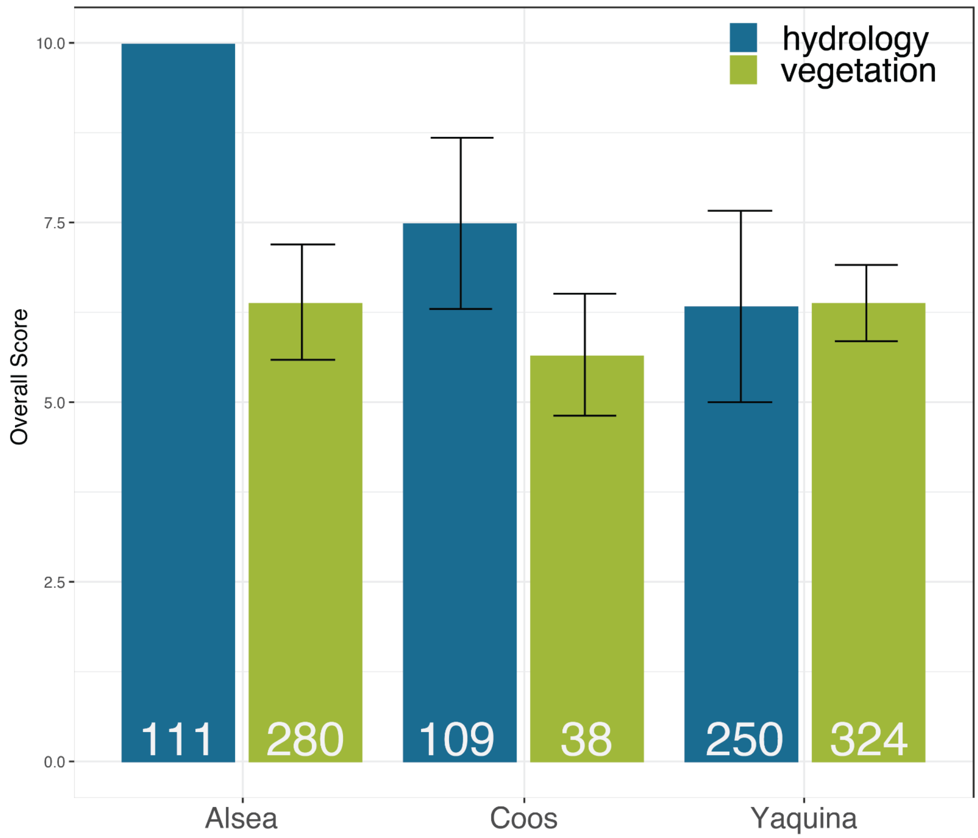

Hydrology
Vegetation
Change Index Score
Degree of Action Rating
p=0.0004, X²=12.246
y = − 1 + 3 x   R²adj = 0.54
p=0.5883, X²=0.293
y = 4.2 + 0.39 x   R²adj = − 0.11
0
3
6
9
1
2
3
4

Figure 4



Hydrology
Vegetation
10.0
7.5
5.0
2.5
Overall Score
p=0.002, X²=9.4835
y = 4 + 1.3 x   R²adj = 0.39
p=0.963, X²=0.0022
y = 6.1 − 0.016 x   R²adj = −0.14
1
2
3
4
Degree of Action Rating

Figure 5



hydrology
vegetation
10.0
7.5
5.0
2.5
0.0
Overall Score
111
280
109
38
250
324
Alsea
Coos
Yaquina

Appendices

Table S1. Statements used for Qsort activity, and their associated ranking, social category (original measure) and environmental monitoring metric category.

Statement	Weighted Score	Original Measure	Metric Category
Increasing habitat for fish and wildlife.	326	Environmental benefit	All categories
Increasing ecological function in general.	300	Environmental benefit	All categories
Enhancing water quality.	296	Environmental benefit	Vegetation, Human Factors, Hydrology
Reducing the amount of pollution in water bodies.	294	Environmental benefit	Vegetation, Human Factors, Hydrology
Minimizing the impacts of sea-level rise.	235	Environmental benefit	Hydrology
Increasing native vegetation.	227	Environmental benefit	Vegetation
Reconnecting tidal channels.	217	Environmental benefit	Hydrology
Places that attract birds.	215	Environmental benefit	Bird Use
The state government's management of the ecosystem.	215	Trust	Human Factors
Recognizing the original Indigenous caretakers.	207	Community values	Human Factors
Reducing coastal erosion.	207	Environmental benefit	Hydrology
Everyone benefits from natural places equally.	206	Community values	Human Factors
Being able to catch native fish in local water bodies.	203	Sense of place/experience	Fish Use, Human Factors
Increasing storm protection for the community.	198	Environmental benefit	Human Factors
Reducing flooding along the coast.	193	Environmental benefit	Hydrology, Human Factors
Outdoor sites for physical well-being, exercise, or recreation.	188	Health	Human Factors
An outdoor place to go to for my mental well-being.	186	Health	Human Factors
Promoting the historical & cultural values of the area.	183	Sense of place/ change over time	Human Factors
Places that attract beavers.	181	Environmental benefit	Mammal Use
Generating long-term jobs.	176	Economic benefit	Human Factors
An aesthetically pleasing environment.	174	Sense of place/ affect	Human Factors
Involving the community in decision-making.	172	Community values	Human Factors
My local government's management of the ecosystem.	170	Trust	Human Factors
The federal government's management of the ecosystem	169	Trust	Human Factors
Increasing my community's resilience.	165	Community values	Human Factors
Generating money for my community.	162	Economic Factors	Human Factors
Being able to harvest local clams.	141	Sense of place/experience	Invertebrate Use, Human Factors
Reducing flood damages to my property.	137	Economic benefit	Hydrology, Human Factors
Being able to harvest local oysters.	135	Sense of place/experience	Invertebrate Use, Human Factors
Reducing waterlogging of crops.	127	Environmental benefit	Hydrology, Human Factors
Projects that don't require heavy machinery.	122	Sentiment	Human Factors
Attracting tourists to the area.	112	Economic Factors	Human Factors
Having a mosquito-free environment.	108	Sentiment	Human Factors
What the majority of my community votes for.	106	Political Factors	Human Factors

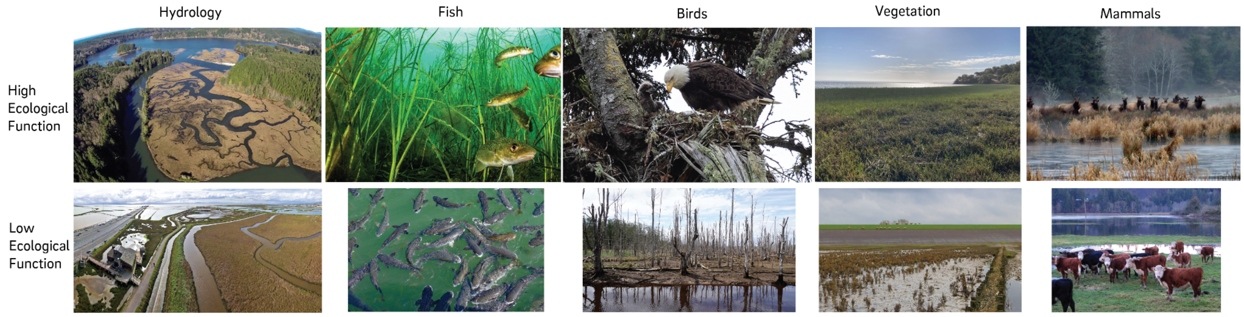


Figure S1. Photos used in the photo ranking activity during focus groups.

Table S2. Tables detailing the scoring process for all metric categories at each restoration site. The Average of Factors for vegetation is noted and consists of all vegetation scoring factors; For invasive, native, and salt-tolerant species percent cover and number of species, we included whichever score (either invasive species number or percent cover) was highest. The Change and 2021 Value Index are, respectively, the Change Value and 2021 Value binned on a 1-10 scale. The Score is the sum of Change and 2021 Value Indices, and the Score Index is the Score binned on a 1-10 scale. NA means data were not available.

Site	Metric	Factors Contributing to Score	Max Score	Original Value	2021 Value	% Change Value	Change Index	2021 Value Index	Score	Score Index
Frederickson Marsh	Vegetation	% change in % cover of *Distichlis spicata*	10	43.30%	37.08%	-14%	0	4	4.00	**2**
		% change in % cover of *Juncus balticus*	10	39.58%	64.32%	62%	7	7	14.00	**9**
		% change Simpson Diversity Index	10	0.83	0.67	-20%	0	7	7.00	**4**
		% change % invasive plant species	10	12.50%	33.33%	167%	0	6	6.00	**3**
		% change in invasive species % cover	10	31.61%	5%	-84%	9	9	18.00	**9**
		% change in native plant species	10	87.50%	66.67%	-24%	0	7	7.00	**4**
		% change in native species % cover	10	22.25%	33.54%	51%	6	4	10.00	**5**
		% change in % of salt-tolerant plant species	10	76.39%	83.33%	9%	1	9	10.00	**5**
		% change in salt-tolerant plant % cover	10	25.04%	27.22%	9%	1	3	4.00	**2**
									Average of Factors	**6.40**
	Hydrology	Marsh channel sinuosity percent change over time (total)	10	0.70	1.23	76%	8	7	15.00	**8**
	Fish use	Fish presence/absence	1	NA	NA	NA	NA	NA	NA	NA
	Wildlife Use	Beaver presence/absence	1	NA	NA	NA	NA	NA	NA	NA

Site	Metric	Factors Contributing to Score	Max Score	Original Value	2021 Value	% Change Value	Change Index	2021 Value Index	Score	Score Index
Dalton Marsh	Vegetation	% change in % cover of *Bolboschoenus maratimus*	10	35.00%	0.00%	-100%	0	0	0.00	**0**
		% change in % cover of *Argentina egedei*	10	30.00%	0.00%	-100%	0	0	0.00	**0**
		% change in % cover of *Carex lyngbyei*	10	70.75%	69.78%	-1%	0	7	7.00	**4**
		% change Simpson Diversity index	10	0.61	0.56	-8%	0	6	6.00	**3**
		% change % invasive plant species	10	23.81%	29.17%	23%	0	7	7.00	**4**
		% change in invasive species % cover	10	7.75%	13.90%	79%	0	8	8.00	**4**
		% change in native plant species	10	76.19%	70.83%	-7%	0	8	8.00	**4**
		% change in native species % cover	10	35.38%	43.78%	24%	3	5	8.00	**4**
		% change in % of salt-tolerant plant species	10	61.90%	70.83%	14%	2	8	10.00	**5**
		% change in salt-tolerant plant % cover	10	45.75%	43.78%	-4%	0	5	5.00	**3**
									Average of Factors	**4.00**
	Hydrology	Marsh channel sinuosity percent change over time (total)	10	0.00	1.30	100% (Inf)	10	7	17.00	**9**
	Fish use	Fish presence/absence	1	NA	NA	NA	NA	NA	1	**1**
	Mammal Use	Beaver presence/absence	1	NA	NA	NA	NA	NA	NA	NA

Site	Metric	Factors Contributing to Score	Max Score	Original Value	2021 Value	% Change Value	Change Index	2021 Value Index	Score	Score Index
Cox Marsh	Vegetation	% change in % cover of *Scirpus microcarpus*	10	0.00%	52.50%	100% (Inf)	10	6	16.00	**8**
		% change in % cover of *Argentina egedei*	10	41.70%	33.33%	-20%	0	4	4.00	**2**
		% change in % cover of *Sparganium eurycarpum*	10	0.00%	57.50%	100% (Inf)	10	6	16.00	**8**
		% change in % cover of *Carex lyngbyei*	10	61.18%	27.95%	-54%	0	3	3.00	**2**
		% change Simpson Diversity index	10	0.86	0.89	3%	1	9	10.00	**5**
		% change % invasive plant species	10	5.56%	11.76%	112%	0	8	8.00	**4**
		% change in invasive species % cover	10	0%	20%	19590%	0	8	8.00	**4**
		% change in native plant species	10	94.44%	88.24%	-7%	0	9	9.00	**5**
		% change in native species % cover	10	14.90%	18.87%	27%	3	2	5.00	**3**
		% change in % of salt-tolerant plant species	10	52.63%	35.29%	-33%	0	3	3.00	**2**
		% change in salt-tolerant plant % cover	10	21.39%	21.43%	0%	0	3	3.00	**3**
									Average of Factors	**4.60**
	Hydrology	Marsh channel sinuosity percent change over time (total)	10	0.16	1.53	876%	10	8	18.00	**9**
	Fish use	Fish presence/absence	1	NA	NA	NA	NA	NA	1	**1**
	Mammal Use	Beaver presence/absence	1	NA	NA	NA	NA	NA	1	**1**

Site	Metric	Factors Contributing to Score	Max Score	Original Value	2021 Value	% Change Value	Change Index	2021 Value Index	Score	Score Index
Y27		% change in % cover of *Agrostis stolonifera*	10	49.20%	1.25%	-97%	10	9	19.00	**10**
		% change in % cover of *Carex obnupta*	10	0.00%	39.25%	100% (Inf)	10	4	14.00	**7**
		% change in % cover of *Distichlis spicata*	10	0.00%	31.35%	100% (Inf)	10	4	14.00	**7**
		% change Simpson Diversity index	10	0.26	0.58	126%	10	6	16.00	**8**
		% change % invasive plant species	10	58.33%	33.33%	-43%	5	6	11.00	**6**
		% change in invasive species % cover	10	35.00%	12.96%	-63%	7	8	15.00	**8**
		% change in native plant species	10	41.67%	66.67%	60%	6	7	13.00	**7**
		% change in native species % cover	10	15.45%	25.85%	67%	7	3	10.00	**5**
		% change in % of salt-tolerant plant species	10	58.33%	27.78%	-52%	0	3	3.00	**2**
		% change in salt-tolerant plant % cover	10	12.50%	22.49%	80%	8	3	11.00	**6**
	Vegetation		10						**Average of Factors**	**7.33**
	Hydrology	Marsh channel sinuosity percent change over time (total)	10	0.24	1.49	527%	10	8	18.00	**9**
	Fish use	Fish presence/absence	1	NA	NA	NA	NA	NA	1	**1**
	Mammal Use	Beaver presence/absence	1	NA	NA	NA	NA	NA	NA	NA

Site	Metric	Factors Contributing to Score	Max Score	Original Value	2021 Value	% Change Value	Change Index	2021 Value Index	Score	Score Index
Y3	Vegetation	% change in % cover of *Agrostis stolonifera*	10	32.76%	11.78%	-64%	7	8	15.00	**8**
		% change in % cover of *Carex lyngbyei*	10	14.56%	20.61%	42%	5	3	8.00	**4**
		% change in % cover of *Distichlis spicata*	10	19.90%	55.06%	177%	10	6	16.00	**8**
		% change in % cover of *Juncus balticus*	10	22.92%	19.00%	-17%	0	2	2.00	**1**
		% change Simpson Diversity index	10	0.59	0.62	6%	1	7	8.00	**4**
		% change % invasive plant species	10	16.33%	37.86%	132%	0	6	6.00	**3**
		% change in invasive species % cover	10	40.95%	12.88%	-69%	7	8	15.00	**8**
		% change in native plant species	10	83.67%	62.14%	-26%	0	7	7.00	**4**
		% change in native species % cover	10	17.43%	27.51%	58%	6	3	9.00	**5**
		% change in % of salt-tolerant plant species	10	73.67%	74.88%	2%	1	8	9.00	**5**
		% change in salt-tolerant plant % cover	10	18.93%	26.99%	43%	5	3	8.00	**4**
									Average of Factors	**6.33**
	Hydrology	Marsh channel sinuosity percent change over time (total)	10	1.29	1.46	13%	2	8	10.00	**5**
	Fish use	Fish presence/absence	1	NA	NA	NA	NA	NA	NA	NA
	Mammal Use	Beaver presence/absence	1	NA	NA	NA	NA	NA	NA	NA

Site	Metric	Factors Contributing to Score	Max Score	Original Value	2021 Value	% Change Value	Change Index	2021 Value Index	Score	Score Index
Poole Slough	Vegetation	% change in % cover of *Agrostis stolonifera*	10	19.17%	6.57%	-66%	7	9	16.00	**8**
		% change in % cover of *Juncus balticus*	10	40.51%	12.70%	-69%	0	2	2.00	**1**
		% change in % cover of *Distichlis spicata*	10	29.67%	28.75%	-3%	0	3	3.00	**2**
		% change Simpson Diversity index	10	0.76	0.83	8%	1	9	10.00	**5**
		% change % invasive plant species	10	13.33%	15.66%	18%	0	8	8.00	**4**
		% change in invasive species % cover	10	19.17%	5.46%	-72%	8	9	17.00	**9**
		% change in native plant species	10	86.67%	84.34%	-3%	0	9	9.00	**5**
		% change in native species % cover	10	16.53%	12.53%	-24%	0	2	2.00	**1**
		% change in % of salt-tolerant plant species	10	86.67%	76.39%	-12%	0	8	8.00	**4**
		% change in salt-tolerant plant % cover	10	16.53%	13.25%	-20%	0	2	2.00	**1**
			10						**Average of Factors**	**5.50**
	Hydrology	Sinuosity percent change over time	10	1.66	1.72	3%	1	9	10.00	**5**
	Fish use	Fish presence/absence	1	NA	NA	NA	NA	NA	NA	NA
	Mammal Use	Beaver presence/absence	1	NA	NA	NA	NA	NA	NA	NA

Site	Metric	Factors Contributing to Score	Max Score	Original Value	2021 Value	% Change Value	Change Index	2021 Value Index	Score	Score Index
Lint Slough	Vegetation	% change in % cover of *Jaumea carnosa*	10	17.81%	22.50	-37%	0	3	3.00	**2**
		% change in % cover of *Salicornia virginica*	10	1.96%	46.25	1081%	10	5	15.00	**8**
		% change in % cover of *Distichlis spicata*	10	0.00%	37.50	100% (Inf)	10	4	14.00	**7**
		% change Simpson Diversity index	10	0.66	0.66	1%	1	7	8.00	**4**
		% change % invasive plant species	10	18.57%	0.00%	-100%	10	10	20.00	**10**
		% change in invasive species % cover	10	22.72%	0%	-100%	10	10	20.00	**10**
		% change in native plant species	10	81.43%	100.00 %	23%	3	10	13.00	**7**
		% change in native species % cover	10	9.07%	26.81%	196%	10	3	13.00	**7**
		% change in % of salt-tolerant plant species	10	84.60%	100.00 %	18%	2	10	12.00	**6**
		% change in salt-tolerant plant % cover	10	9.37%	26.81%	186%	10	3	13.00	**7**
									Average of Factors	**7.20**
	Hydrology	Marsh channel sinuosity percent change over time (total)	5	NA	NA	NA	NA	NA	NA	NA
	Fish use	Fish presence/absence	1	NA	NA	NA	NA	NA	NA	NA
	Mammal Use	Beaver presence/absence	1	NA	NA	NA	NA	NA	NA	NA

Site	Metric	Factors Contributing to Score	Max Score	Original Value	2021 Value	% Change Value	Change Index	2021 Value Index	Score	Score Index
Drift Creek	Vegetation	% change in % cover of *Argentina egedei*	10	20.93%	2.60%	-88%	0	1	1.00	**1**
		% change in % cover of *Eleocharus palustris*	10	0.00%	22.50%	100% (Inf)	10	3	13.00	**7**
		% change in % cover of *Distichlis spicata*	10	0.00%	51.58%	100% (Inf)	10	6	16.00	**8**
		% change Simpson Diversity index	10	0.63	0.57	-10%	0	6	6.00	**3**
		% change % invasive plant species	10	50.40%	32.02%	-36%	4	6	10.00	**5**
		% change in invasive species % cover	10	11.26%	18.67%	66%	0	8	8.00	**4**
		% change in native plant species	10	49.60%	67.98%	37%	4	7	11.00	**6**
		% change in native species % cover	10	20.04%	22.49%	12%	2	3	5.00	**3**
		% change in % of salt-tolerant plant species	10	29.37%	47.79%	63%	7	5	12.00	**6**
		% change in salt-tolerant plant % cover	10	24.61%	27.65%	12%	2	3	5.00	**3**
									Average of Factors	**5.60**
	Hydrology	Marsh channel sinuosity percent change over time (total)	10	0.51	1.83	257%	10	10	20.00	**10**
	Fish use	Fish presence/absence	1	NA	NA	NA	NA	NA	NA	NA
	Mammal Use	Beaver presence/absence	1	NA	NA	NA	NA	NA	NA	NA

Site	Metric	Factors Contributing to Score	Max Score	Original Value	2021 Value	% Change Value	Change Index	2021 Value Index	Score	Score Index
Kunz Marsh	Vegetation	% change in % cover of *Agrostis stolonifera*	10	20.96%	0.00%	-100%	10	10	20	**10**
		% change in % cover of *Carex lyngbyei*	10	6.92%	88.26%	1176%	10	9	19	**10**
		% change Simpson Diversity Index	10	0.86	0.36	-58%	0	4	4	**2**
		% change % invasive plant species	10	20.99%	13.10%	-38%	4	8	12	**6**
		% change in invasive species % cover	10	10.99%	1%	-91%	10	9	19	**10**
		% change in native plant species	10	79.01%	86.90%	10%	1	9	10	**5**
		% change in native species % cover	10	5.18%	26.10%	404%	10	3	13	**7**
		% change in % of salt-tolerant plant species	10	65.19%	80.24%	23%	3	8	11	**6**
		% change in salt-tolerant plant % cover	10	5.74%	27.29%	375%	10	3	13	**7**
									Average of Factors	**7.67**
	Hydrology	Marsh channel sinuosity percent change over time (total)	10	1.43	1.37	-5%	0	**7**	7	**4**
	Fish use	Fish presence/absence	1	NA	NA	1	NA	NA	1	**1**
	Mammal Use	Beaver presence/absence	1	NA	NA	NA	NA	NA	NA	NA

Table S3. Tables showing the scoring process for the social scorecards from all three bays.

Coos Bay Social Scorecard	Metric Categories						
Qsort statements	**Vegetation**	**Hydrology**	**Fish Use**	**Bird Use**	**Mammal use**	**Invertebrate Use**	**Human Factors**
Increasing habitat for fish and wildlife.	7	7	7	7	7	7	7
Increasing ecological function in general.	10	10	10	10	10	10	10
Enhancing water quality.	4	4	-	-	-	-	4
Reducing the amount of pollution in water bodies.	4	4	-	-	-	-	4
Minimizing the impacts of sea-level rise.	-	7	-	-	-	-	7
Increasing native vegetation.	5	-	-	-	-	-	-
Reconnecting tidal channels.	-	4	-	-	-	-	-
Places that attract birds.	-	-	-	8	-	-	-
Recognizing the original Indigenous caretakers.	-	-	-	-	-	-	4
Reducing coastal erosion.	-	5	-	-	-	-	-
Everyone benefits from natural places equally.	-	-	-	-	-	-	4
Being able to catch native fish in local water bodies.	-	-	3	-	-	-	3
Increasing storm protection for the community.	-	-	-	-	-	-	1
Reducing flooding along the coast.	-	4	-	-	-	-	4
Outdoor sites for physical well-being, exercise, or recreation.	-	-	-	-	-	-	4
An outdoor place to go to for my mental well-being.	-	-	-	-	-	-	7
Promoting the historical & cultural values of the area.	-	-	-	-	-	-	2
Places that attract beavers.	-	-	-	-	8	-	
Generating long-term jobs.	-	-	-	-	-	-	7
An aesthetically pleasing environment.	-	-	-	-	-	-	1
Involving the community in decision-making.	-	-	-	-	-	-	2
Increasing my community's resilience.	-	-	-	-	-	-	3
Generating money for my community.	-	-	-	-	-	-	5
Being able to harvest local clams.	-	-	-	-	-	2	2
Reducing flood damages to my property.	-	6	-	-	-	-	6
Being able to harvest local oysters.	-	-	-	-	-	6	6
Reducing waterlogging of crops.	-	3	-	-	-	-	3
Attracting tourists to the area.	-	-	-	-	-	-	3
Having a mosquito-free environment.	-	-	-	-	-	-	3
The federal government's management of the ecosystem	-	-	-	-	-	-	3
My local government's management of the ecosystem.	-	-	-	-	-	-	2
What the majority of my community votes for.	-	-	-	-	-	-	3
Projects that don't require heavy machinery.	-	-	-	-	-	-	7
The state government's management of the ecosystem.	-	-	-	-	-	-	6
Photoranking Scores	6	3	4	10	9	NA	NA
Average of Qsort and photoranking	**6.00**	**4.20**	**5.33**	**9.17**	**8.67**	**6.25**	**4.24**

Alsea Bay Social Scorecard	Metric Categories						
Qsort statements	**Vegetation**	**Hydrology**	**Fish Use**	**Bird Use**	**Mammal use**	**Invertebrate Use**	**Human Factors**
Increasing habitat for fish and wildlife.	10	10	10	10	10	10	10
Increasing ecological function in general.	7	7	7	7	7	7	7
Enhancing water quality.	4	4	-	-	-	-	4
Reducing the amount of pollution in water bodies.	6	6	-	-	-	-	6
Minimizing the impacts of sea-level rise.	-	6	-	-	-	-	6
Increasing native vegetation.	8	-	-	-	-	-	-
Reconnecting tidal channels.	-	7	-	-	-	-	-
Places that attract birds.	-	-	-	10	-	-	-
Recognizing the original Indigenous caretakers.	-	-	-	-	-	-	4
Reducing coastal erosion.	-	6	-	-	-	-	-
Everyone benefits from natural places equally.	-	-	-	-	-	-	4
Being able to catch native fish in local water bodies.	-	-	2	-	-	-	2
Increasing storm protection for the community.	-	-	-	-	-	-	4
Reducing flooding along the coast.	-	6	-	-	-	-	6
Outdoor sites for physical well-being, exercise, or recreation.	-	-	-	-	-	-	8
An outdoor place to go to for my mental well-being.	-	-	-	-	-	-	6
Promoting the historical & cultural values of the area.	-	-	-	-	-	-	2
Places that attract beavers.	-	-	-	-	10	-	-
Generating long-term jobs.	-	-	-	-	-	-	6
An aesthetically pleasing environment.	-	-	-	-	-	-	2
Involving the community in decision-making.	-	-	-	-	-	-	3
Increasing my community's resilience.	-	-	-	-	-	-	6
Generating money for my community.	-	-	-	-	-	-	6
Being able to harvest local clams.	-	-	-	-	-	1	1
Reducing flood damages to my property.	-	5	-	-	-	-	5
Being able to harvest local oysters.	-	-	-	-	-	6	6
Reducing waterlogging of crops.	-	5	-	-	-	-	5
Attracting tourists to the area.							3
Having a mosquito-free environment.	-	-	-	-	-	-	5
The federal government's management of the ecosystem	-	-	-	-	-	-	7
My local government's management of the ecosystem.	-	-	-	-	-	-	1
What the majority of my community votes for.	-	-	-	-	-	-	2
Projects that don't require heavy machinery.	-	-	-	-	-	-	6
The state government's management of the ecosystem.	-	-	-	-	-	-	5
Photoranking Scores	6	4	5	10	7	NA	NA
Average of Qsort and photoranking	**6.50**	**5.10**	**5.67**	**9.50**	**8.00**	**6.00**	**4.76**

Yaquina Bay Social Scorecard	Metric Categories						
Qsort statements	**Vegetation**	**Hydrology**	**Fish Use**	**Bird Use**	**Mammal use**	**Invertebrate Use**	**Human Factors**
Increasing habitat for fish and wildlife.	10	10	10	10	10	10	10
Increasing ecological function in general.	9	9	9	9	9	9	9
Enhancing water quality.	5	5	-	-	-	-	5
Reducing the amount of pollution in water bodies.	5	5	-	-	-	-	5
Minimizing the impacts of sea-level rise.	-	6	-	-	-	-	6
Increasing native vegetation.	8	-	-	-	-	-	-
Reconnecting tidal channels.	-	7	-	-	-	-	-
Places that attract birds.	-	-	-	7	-	-	-
Recognizing the original Indigenous caretakers.	-	-	-	-	-	-	3
Reducing coastal erosion.	-	4	-	-	-	-	
Everyone benefits from natural places equally.	-	-	-	-	-	-	4
Being able to catch native fish in local water bodies.	-	-	4	-	-	-	4
Increasing storm protection for the community.	-	-	-	-	-	-	2
Reducing flooding along the coast.	-	6	-	-	-	-	6
Outdoor sites for physical well-being, exercise, or recreation.	-	-	-	-	-	-	5
An outdoor place to go to for my mental well-being.	-	-	-	-	-	-	6
Promoting the historical & cultural values of the area.	-	-	-	-	-	-	2
Places that attract beavers.	-	-	-	-	9	-	
Generating long-term jobs.	-	-	-	-	-	-	5
An aesthetically pleasing environment.	-	-	-	-	-	-	2
Involving the community in decision-making.	-	-	-	-	-	-	3
Increasing my community's resilience.	-	-	-	-	-	-	6
Generating money for my community.							9
Being able to harvest local clams.	-	-	-	-	-	2	2
Reducing flood damages to my property.	-	6	-	-	-	-	6
Being able to harvest local oysters.	-	-	-	-	-	4	4
Reducing waterlogging of crops.	-	1	-	-	-	-	1
Attracting tourists to the area.	-	-	-	-	-	-	1
Having a mosquito-free environment.	-	-	-	-	-	-	3
The federal government's management of the ecosystem	-	-	-	-	-	-	6
My local government's management of the ecosystem.	-	-	-	-	-	-	3
What the majority of my community votes for.	-	-	-	-	-	-	5
Projects that don't require heavy machinery.	-	-	-	-	-	-	3
The state government's management of the ecosystem.	-	-	-	-	-	-	7
Photoranking Scores	10	4	5	5	7	NA	NA
Average of Qsort and photoranking	**8.70**	**4.95**	**6.33**	**6.83**	**8.17**	**6.25**	**4.59**

CHAPTER 2

Variable effects of Experimental Sea-Level Rise Conditions and Invasive Species on a California Tidal Marsh Community

Collaborators: Matthew E. Ferner and Edwin D. Grosholz

Abstract

Sea-level rise (SLR) will produce unprecedented changes in tidal marsh systems that already cope with daily tidal perturbations, disturbances from storms, and salinity changes from droughts and runoff events. Additionally, negative impacts from non-native invasive species may alter marsh plants' susceptibility to SLR stressors like inundation and salinity. To persist, tidal marsh communities must tolerate both changes in the physical environment from SLR and invasive species impacts. To assess the response of a tidal marsh cordgrass (*Spartina foliosa*) ecosystem to both stressors, we implemented a field experiment in San Francisco Bay, CA, USA, where cordgrass was enclosed with or without the invasive European green crab, *Carcinus maenas*. These enclosures were subject to a second treatment that simulated the extended tidal inundation projected with SLR using a recently developed *in situ* method. We found that cordgrass survival was lower in the presence of invasive crabs relative to controls, and there was a slight negative effect of crabs on benthic microalgae. In contrast, benthic macrofaunal grazers responded favorably to inundation, likely in response to increased benthic microalgal biomass. This study provides quantitative biological responses to invasive species and specific levels of inundation. We did not find interacting effects of increased inundation and *C. maenas* on any

response variables, which highlights the need to consider how latent or sequential, rather than simultaneously occurring, effects of multiple stressors may affect ecosystems. Evaluating relative effects 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

Introduction

Sea-level rise will produce unprecedented changes in tidal marshes that have experienced habitat degradation from land use change and other stressors (Dahl 1990). Tidal marshes already must cope with daily tidal perturbations as well as stochastic disturbances from large storms and salinity changes from droughts and runoff events. Sea-level rise 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 ecological communities. Increased inundation associated with sea-level rise can negatively impact plant communities through increased levels of hydrogen sulfide or other toxins that directly impact rhizomes and roots (Cronk & Fennessy 2001), and limit biomass, growth, and nutrient uptake (Mendelssohn and Seneca 1980, Koch and Mendelssohn 1989). Tidal marsh plant tolerance to inundation, salinity stress from tidal fluctuations, and competition often determine the range limits of plant species along an estuarine gradient (Bertness and Ellison 1987). How inundation affects tidal marsh community structure depends on the plant species' susceptibility to inundation stress and the rate of increased inundation from sea-level rise.

Other biotic interactions, like predation and facilitation through the amelioration of low oxygen or high salinity conditions (Zhang and Shao 2013), can also structure tidal marsh communities (Bertness 1985, Bertness and Grosholz 1985, Bruno and Bertness 2001). For example, benthic macrofauna provide several important functions including sediment stabilization and oxygenation from bioturbation or formation of burrows, promoting nutrient deposition, and promoting phosphorus retention and denitrification (Hall et al. 1994, Karlson et al. 2007, Holdredge et al. 2010) all of which can affect vegetation. Benthic microalgae is an important primary producer in tidal marsh systems and serves as food for benthic macrofaunal grazers (Kwak and Zedler 1997, Page 1997). Previous work found that the microphytobenthos was reduced in sea-level rise scenarios, perhaps due to a switch to planktonic production, reduced light, or increased grazing (Boyer and Fong 2005, Whitcraft and Levin 2007, O'Meara et al. 2017). A loss of microphytobenthos with sea-level rise could be detrimental to the grazer populations that rely on it, which could in turn limit the functions they provide for vegetation. Additionally, non-native species invasions are increasingly common, and especially prevalent in coastal systems that experience heavy shipping traffic and human use. Non-native invasive species can decimate native coastal plant populations and impact nutrient cycling in coastal and other systems (Garbary et al. 2014, Gallardo et al. 2016). As such, negative impacts from non-native species may alter marsh plants' susceptibility to sea-level rise stressors like inundation and salinity. Also, changes to native plant communities due to invasion can alter native macrofaunal communities (Neira et al. 2005), potentially limiting the functions they provide. In tidal marshes, non-native crabs in particular feed on smaller benthic invertebrate grazers, like amphipods and annelids, and can additionally reduce the food availability for these benthic macroinvertebrates by disturbing or consuming benthic algae (Neira et al. 2006). For example, the European green crab, *Carcinus maenas*, has significant negative impacts on establishing native cordgrass (Gonzalez et al. 2023, *in press*) and may reduce redox potential through a loss of bioturbating subsurface deposit feeders (Neira et al. 2006) at other sites in California. As such, invasive species have the potential to alter tidal marsh systems through both physical and trophic mechanisms.

In order to persist, marsh vegetation and the organisms that inhabit it will likely need to withstand or adapt to both physical changes from sea-level rise and impacts from invasive species. Effects of multiple stressors can be additive, synergistic or antagonistic. On the east coast of the US, Crotty et al. (2017) found synergistic negative impacts of increased inundation and native crabs on a native foundational plant species. Increased inundation resulted in sediment softening that facilitated burrowing and grazing by crabs (*Sesarma reticulatum*) which decreased both above and belowground cordgrass (*Spartina alterniflora*) biomass. Using projections from models assessing sea-level rise scenarios, they found that marshes previously impacted by die-off were projected to be more impacted by future sea-level rise. Since crabs will readily move from areas with harder sediment to adjacent habitat with softer sediment to forage (Crotty et al. 2017), it is likely that marsh die-offs will increase exponentially with sea-level rise and without control of *S. reticulatum*. However, the sign and magnitude of crab impacts, both direct and indirect, on tidal marsh plants are context-dependent, ranging from severe negative to positive associations (Silliman and Bertness 2002, Alberti et al. 2007, Bertness and Coverdale 2013, Bertness et al. 2014). Additionally, many physical factors are influenced by inundation in addition to sediment hardness which could influence impacts and feedbacks within the community. Lastly, physical and ecological variables, such as tidal regime, and plant and animal species, differ across tidal marshes and may elicit different outcomes.

In this study on the west coast, USA, we experimentally increased inundation *in situ* in areas of tidal marsh vegetation, and additionally exposed these experimental areas to invasive crabs *Carcinus maenas*. We gathered physical and biological data to understand how tidal marsh vegetation, and the organisms that inhabit that community, respond to these two stressors. We hypothesized that: 1) in the presence of increased inundation, tidal marsh cordgrass growth and survival, redox potential, and benthic microalgae would decline, benthic macrofaunal species would remain neutral or increase, and ammonium would increase due to lower redox potential inhibiting transformation to nitrate, 2) in the presence of invasive crabs, tidal marsh cordgrass growth and survival and benthic microalgae would decrease, and redox potential, and ammonium from crab excrement (Montague 1980), would increase, and 3) invasive crabs and inundation would interact to produce negative impacts on redox potential, cordgrass growth and survival and benthic microalgae, and result in more ammonium.

Methods

Study Site

China Camp State Park, a component site of the San Francisco Bay National Estuarine Research Reserve (NERR), is an ancient and centennial marsh complex with extensive meadows of California cordgrass (*Spartina foliosa*) and little anthropogenic impact in comparison to surrounding marshes. San Francisco Bay experiences mixed semi-diurnal tides and is projected to experience between 10 and 20 cm of sea-level rise by the year 2050 (Vitousek et al. 2017). In this area, MLLW-MHHW tidal range is 1.80m (Gallinas Creek, NOAA tide station 9415052, http://tidesandcurrents.noaa.gov). An increase of 20 cm of sea-level is projected to result in nearly double the inundation time at current mean higher high water at a site near where this study took place (Janousek et al. 2016). The native *S. foliosa* is a low marsh "foundation" species in San Francisco Bay that serves as habitat and nesting ground for a range of species including endangered animals such as Ridgway's Rail (*Rallus obsoletus*) and Salt Marsh Harvest Mouse (*Reithrodontomys raviventris*). San Francisco Bay is a highly invaded estuary and the number of invasions are rapidly accelerating (Seebens et al. 2013). *Spartina foliosa* is also threatened by invasion of hybrid cordgrass (*Spartina foliosa x Spartina alterniflora*, Ayres et al. 2003). *Spartina foliosa* is relatively tolerant of inundation and predicted to increase at moderate rates of sea-level rise, but significantly decline at higher rates (Parker et al. 2011). It is a focus of restoration throughout San Francisco Bay via efforts of California Coastal Conservancy's Invasive *Spartina* Project. This current study was conducted in *Spartina foliosa* meadows in the Bullhead Flat area of China Camp State Park (38.003610, -122.469279, Fig. 1).

Green Crabs

In addition to sea-level rise, another potential stressor for *S. foliosa* is the non-native European green crab, *Carcinus maenas*, which was introduced to San Francisco Bay in the 1980s and has spread along the U.S. west coast (Cohen 1998). In San Francisco Bay, these crabs are abundant mostly in low marsh areas, often co-occurring with *S. foliosa*, and can negatively impact the establishment of newly planted *S. foliosa* in San Francisco Bay (Gonzalez et al. 2023, *in press*). *C. maenas* 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). *C. maenas*-induced changes in composition and abundance of benthic macrofaunal organisms could in turn influence sediment characteristics that impact *S. foliosa.*

Experimental Design

Previous studies that attempted to understand impacts of increased inundation used small-scale mesocosm experiments (Spalding and Hester 2007, Cherry et al. 2009) that did not reflect natural conditions as well as *in situ* experiments. Previous work exploring impacts of inundation and other physical stress on marsh vegetation often 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 were often confounded by other parameters that were 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 used experimental 'marsh boxes' to manipulate inundation *in situ* (based on the design in Cherry et al. 2015), as described below, to explore community level changes due to increased levels of inundation.

In summer of 2022, we implemented a cage experiment involving *C. maenas* enclosed in plots with established *S. foliosa* as well as cage controls (cages, no crabs) and open unmanipulated controls (no cage) (Fig 2). The enclosures (0.5 m x 0.5 m) were constructed from 7 mm Vexar mesh into which two *C. maenas* were added (based on natural local *C. maenas* densities, J. Gonzalez, unpublished data). The cages controls used the same cages but with no crabs (Fig 2). *Carcinus maenas* individuals used in the experiment were acquired at nearby sites using Fukui collapsible crab traps (60 × 45 × 20 cm, 1.25-cm mesh). Two *C. maenas* were added in each cage in July to account for death or escape of crabs. Even with crab additions, *C. maenas* density in cages remained within the realm of natural abundances in San Francisco Bay, which can reach up to four crabs per trap (J. Gonzalez, unpublished data).

These three crab treatments were also subject to a tidal inundation treatment that simulates the extended tidal inundation projected with sea-level rise. We altered inundation using experimental 'marsh boxes' placed parallel to shore that delayed the draining of tidal waters and increased the inundation time experienced by experimental *S. foliosa*. The marsh boxes (2m x 1m x 0.4m) were sunk 10cm into the mud to reduce lateral water drainage and had two in-flow check valves to let water in, and no exit valve, so that the water slowly drained through the open bottom. We also used a partial box as a control, which contained shorter versions of all four walls (0.2m high) with openings at the four corners to allow water to flow freely in and out. As a third treatment, we had no box areas as unmanipulated controls. These three inundation treatments were established as 2 x 1 m plots separated by at least 2 m. In the center of each of the 18 inundation treatments, we took measurements of orthometric height using a Real-Time Kinematic (RTK) GPS GS07 GNSS receiver and CS20 LTE controller (Leica Geosystems), and corrected elevation data using benchmarks taken before and after sampling. Positions were received via the Leica California SmartNet RKT network. Orthometric heights of inundation treatment areas ranged from 0.80m to 0.98m. The overall experimental design was set up as six blocks to account for habitat heterogeneity common in tidal marshes, including such factors as elevation and proximity to channels. Within each of the six blocks, the three inundation treatments were randomly assigned, and within each inundation treatment, the three cage treatments were also randomly distributed (Fig. 2).

Quantification of Biological and Physical Responses

We evaluated water levels in each inundation treatment plot over the course of two weeks at both the beginning and the end of the experiment 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. We then corrected water level data to account for varying elevation of inundation plots. From those water level data, we calculated average inundation time per inundation plot by summing the number of minutes where the water level was above 3cm to account for any baseline noise in the data. These values were then 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**)**.

Plots were monitored once a month for twelve weeks (June through August) in summer 2022 for the number of total cordgrass stems and the average height of the ten tallest stems. Also monthly, we measured redox potential in each plot at 10cm below the sediment surface, which is meant to sample the area adjacent to the *S. foliosa* 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 at the end of the experiment (5cm wide PVC corer to a depth of 25cm). We sieved cores to extract plant roots, dried roots at 60°C and weighed. We calculated belowground biomass for the entire plot (0.25m^2). We also took porewater samples using porewater sippers inserted 10cm into the sediment during low tide (10cm long porous tubes [0.15µm], Rhizophere Research Products, Wageningen, The Netherlands). Porewater samples were later analyzed for ammonium and nitrate (UC Davis

Analytical Lab), and sulfides were analyzed based on methods by Cline (1969). We also took small, surface sediment cores ($1.23cm^2$ x 5mm deep), to evaluate chlorophyll *a* concentration as a proxy for benthic microalgal biomass. We extracted these cores using 90% acetone and used a spectrophotometer to quantify chlorophyll *a* according to Plante-Cuny (1973). We also counted the number of snails (*Ilyanassa obsoleta*) on the surface of each plot in August.

Crab consumption of prey species, including small clams and other invertebrates as found in a similar caging experiment by Gonzalez et al. (2023, *in press*), may subsequently alter sediment characteristics driven by changes to prey populations. Changes to physical conditions in the soil may impact vegetation. As such, sediment cores were collected to quantify macrofauna in each treatment and control plot at the end of the experiment, using a 5cm wide PVC corer to a depth of 10cm. The sample was sieved through a 500 µm mesh sieve, and invertebrates were fixed in 10% formalin, stored in 70% ethanol and sorted to the lowest taxonomic level possible (Neira et al. 2006).

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, to account for habitat heterogeneity in tidal marshes, and determined the appropriate distribution for each dataset using goodness-of-fit statistics. We evaluated whether partial boxes significantly influenced all responses, and if they were influential, included those data in the full model (Table S1). We evaluated statistically significant differences in inundation hours per day among categorical inundation determinations. We focus reporting on box and no box treatments. For some responses, partial boxes produced intermediate effects due to small increases in inundation, which we report when those effects were significant. Otherwise, we excluded data from partial boxes in our analysis. We also evaluated effects of *C. maenas* presence vs. absence and inundation as well as their interaction on the following variables: change in *S. foliosa* stem density and stem height from June through August, sediment chlorophyll *a*, porewater ammonium, redox potential, number of snails (*I. obsoleta*) on surface, belowground biomass, number of amphipods, and number of oligochaetes in core samples at the end of the experiment in August. We evaluated difference in mean temperature/day (°C) and light intensity/day (lumens) among four box and two no box plots using a generalized linear model. We used the "emmeans" package (estimated marginal means) to evaluate pairwise comparisons post hoc, and deemed differences as significant if p values were less than 0.05.

Results

Physical Responses to Inundation

We found moderate increases to inundation in experimental box treatments. Boxes were inundated for approximately 9% and 6% longer than controls without boxes and partial boxes, respectively, although these were not significant increases (Fig. 3, 16.5±1.6 hours/day vs. 15.2±0.1 and 15.6±0.3 hours/day, Z=-1.70, p=0.207, and Z=-1.30, p=0.396). Average temperature per day and light intensity per day did not vary between boxes and treatment areas without boxes (Z=-0.90, p=0.367 and Z=-0.585, p=0.558). Redox potential also did not significantly change as a function of inundation treatment (X^2=1.89, p=0.169).

Response of Vegetation

We found negative effects of *C. maenas* on cordgrass exposed to both increased and ambient inundation regimes. Overall, green crabs reduced *S. foliosa* stem density over the course of the experiment (X^2=18.29, p<0.001). In box treatments, fewer *S. foliosa* stems were gained over the course of the experiment in *C. maenas* treatments (mean 24 ± 6 s.e. stems) relative to cageless controls (mean of 56±7SE stems, Z=-3.20, p=0.004) and cage controls (mean 39 ± 4 s.e. stems, Z=1.95, p=0.126), although this was not a significant change (Fig. 5). Similarly, in controls without boxes, the amount of *S. foliosa* stems gained was less in *C. maenas* treatments (26±5SE stems) relative to cageless controls (55±5SE stems, Z=-2.87, p=0.011) and tended to be less in cage controls (Fig. 5, 35±7SE stems, Z=1.20, p=0.453). We did not find an effect of inundation or the interaction of crab treatment and inundation on the change in stem density (X^2=0.01, p=0.911 and X^2=0.85, p=0.653, respectively). Change in stem 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 *C. maenas* treatments (X^2=0.27, p=0.606 and X^2=3.93, p=0.140, respectively), nor was there an interaction between inundation and *C. maenas* treatments (X^2=0.64, p=0.726).

Response of Microalgal Biomass, Redox, and Ammonium/Nitrate

We found that microalgal biomass (chlorophyll *a*) on the sediment surface was affected by inundation (X^2=12.64, p=0.002) and *C. maenas* (X^2=8.03, p=0.018), but was not significantly affected by their interaction (X^2=0.08, p=0.782). There was significantly more chlorophyll (chl) *a* in box treatments overall relative to treatments without boxes (Fig. 4, t=3.09, p=0.009). We also found effects of intermediate levels of inundation in partials boxes that, when crab treatments were pooled, had significantly higher chl *a* concentrations than treatments without boxes (t=-2.41, p=0.05). We found 43% less chl *a* in *C. maenas* treatments relative to cageless controls and 35% less in cage controls within boxes (t=-1.20, p=0.458; t=1.12, p=0.507, respectively). We also found 85% less chl *a* in *C. maenas* treatments relative to cageless controls and 55% less than cage controls, without boxes ($t=-1.63$, $p=0.244$; $t=1.59$, $p=0.258$, respectively), although these reductions were not significant (Fig. 4). Reductions in chl *a* due to *C. maenas* were slightly less in inundated treatments than non-inundated treatments due to generally higher levels of chl *a* in inundated treatments. This is supported by data showing that chl *a* increased with increasing inundation hours per day in crab control treatments (significantly so in cageless controls), but not *C. maenas* treatments, due to lower chl *a* concentrations in all *C. maenas* plots despite inundation duration (Fig. S1). Redox potential in August did not vary by crab or inundation treatment, and there was no interaction between those two factors ($X^2=1.26$, $p=0.533$; $X^2=1.89$, $p=0.169$; $X^2=0.130$, $p=0.937$, respectively). Crab treatments and inundation did not affect porewater ammonium in plots, nor did their interaction ($X^2=3.89$, $p=0.143$; $X^2=0.004$, $p=0.953$; $X^2=2.84$, $p=0.241$). Nitrate concentrations in all plots rarely were higher than zero, and values above zero were negligible.

Response of Soil and Surface Feeding Macrofauna

Amphipod abundance increased with inundation but was not affected by crab treatment or the interaction of those two factors ($X^2=27.77$, $p<0.001$; $X^2=0.16$, $p=0.925$; $X^2=3.41$, $p=0.182$, respectively). Number of amphipods in crab and crab control treatments declined in plots without boxes relative to treatments within boxes (Fig. 6A, cage controls: $Z=6.15$, $p<0.001$, *C. maenas*: $Z=5.26$, $p<0.001$; cageless controls: $Z=9.39$, $p<0.001$) and partial boxes (cage controls: $Z=10.52$, $p<0.001$, *C. maenas*: $Z=7.54$, $p<0.001$; cageless controls: $Z=11.43$, $p<0.001$). Cageless controls in plots without boxes had the fewest amphipods relative to all other treatments (Fig. 6A). Inundation significantly increased oligochaete abundance ($X^2=8.03$, $p=0.018$). There were more oligochaetes in cageless controls within boxes than cageless controls in plots without boxes (Fig. 6B, $Z=3.14$, $p=0.005$). We found that partial box controls increased both amphipod and oligochaete abundance relative to controls without boxes (Z=-16.53, $p<0.001$; t=-2.82, $p=0.013$, respectively). We also found a significant effect of inundation on the number of snails (*I. obsoleta*) in plots ($X^2=23.18$, $p<0.001$), with 77% more snails in cageless controls (t=2.69, $p=0.011$) and cage controls (t=1.93, $p=0.062$), and 86% more snails in *C. maenas* plots in boxes (Fig. 7, t=2.88, $p=0.007$) relative to their counterparts without boxes. There was no effect of the partial box control on the number of snails relative to the control without a box (t=0.257, $p=0.964$).

Discussion

Through our novel approach of manipulating both the presence of an invasive species and tidal inundation *in situ*, we found strong negative effects of green crabs and generally neutral effects of moderate increases in tidal inundation on the aboveground growth of *Spartina foliosa*. Interestingly, increased tidal inundation had largely positive effects on animal communities, perhaps due to increased levels of microalgae, an important food source for benthic invertebrates in tidal marshes.

Marsh boxes increased inundation relative to partial and no box treatments, but this increase was not significant due to high variability in water retention among box treatments. Additionally, the inundation levels that these boxes captured are on the low end of what we might expect with sea-level rise (i.e., a doubling of inundation time, Janousek et al. 2016). Also, *S. foliosa* is relatively tolerant of inundation and predicted to increase at moderate rates of sea-level rise, but significantly decline at higher rates (Parker 2011). As such, the responses we found in the present study may increase in magnitude or potentially change sign as sea-levels rise and inundation levels increase. We found an effect of the partial box on chlorophyll *a*, and the number of amphipods and oligochaetes, likely due to intermediate levels of inundation in partial boxes. No other factors we considered in this study were significantly affected by the presence of the partial box relative to treatment areas without boxes.

Contrary to our hypothesis, microalgal biomass increased with increasing inundation. Previous studies have found that chlorophyll (chl) *a* increases with soil moisture in tidal marsh sediments during periods of low rainfall (Green et al. 2010). Moderate increases in inundation may result in greater production and deposition of benthic chl *a* to a point, after which benthic chl *a* production shifts to planktonic production as suggested by O'Meara et al. (2017). Consistent with our hypotheses, we found that *C. maenas* reduced chl *a* concentrations. These reductions are consistent with a previous *C. maenas* caging study that found depletion of benthic chl *a* in crab treatments (Neira et al. 2006). Although some of the differences in our study were not significant, they could become more substantial with time. Alternatively, increased grazing from significantly more snails in box treatments could have suppressed microalgal cover in both the *C .maenas* and reference treatments, reducing our ability to accurately estimate the amount of reduction due to crabs. Future studies should explore the possibility that inundation may ameliorate reductions of chl *a* due to crab activities. We found no effect of either factor on redox potential, ammonium, or nitrate. However, changes to chl *a* and redox and subsequent changes to ammonium or nitrate may operate on a longer timescale than this study encompassed.

As hypothesized, we found that cordgrass survival decreased in the presence of *C. maenas*. This finding is consistent with a previous cage study that also found reduced *S. foliosa* stem density in the presence of *C. maenas* (Gonzalez et al. 2023, *in press*). Physical disturbance by *C. maenas* is a likely mechanism, as it disturbs estuarine vegetation in other systems by digging large pits and tearing eelgrass stems (Garbary et al. 2014). Cordgrass did not respond to increased levels of inundation. This neutral response is supported by the physical data; Increased inundation did not statistically affect redox potential. Nutrient concentrations remained consistent across inundation treatments as did the response of vegetation. Impacts to stem height and belowground biomass may only be affected at higher levels of inundation over prolonged periods. *Spartina* populations are predicted to be unaffected, or even increase, with moderate rates of sea-level rise, yet decline with substantial increases as sea level continue to rise (Parker et al. 2011). This modeled prediction is supported by experimental work that found *Spartina alterniflora* stem density increases with moderate increases in inundation yet declines under extreme sea-level rise scenarios (Ober and Martin 2018). It may be that the inundation levels simulated in this experiment were not severe enough to result in significant changes to cordgrass stem density or growth.

Contrary to our hypotheses, we found an increase in amphipods and oligochaetes, as well as snails, with increased inundation in boxes. For amphipods and snails, this could be due in part to the increase in microalgal biomass we found in inundation treatments. Previous studies by Levin and Talley (2002) found a positive association between chl *a* and macrofauna abundance. However, the structure of the box, as represented by partial box treatments, did significantly affect chl *a* as well as the number of amphipods and oligochaetes, which may be due to intermediate levels of inundation in partial boxes or other favorable conditions created by the box structures, such as protection from predators. However, cage controls also functioned to exclude predators, and we found significantly more amphipods in cage controls in box treatments relative to cage controls in no box treatments, suggesting that positive effects of inundation were in addition to increased survival due to predator exclusion.

Additionally, 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). *Carcinus maenas* 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 *S. foliosa* are likely to be captured, as we found in this study. *S. foliosa* senesces 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 & Fennessy 2001). It is possible that effects of increased inundation may impact *S. foliosa*'s senescent root structure 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 *S. foliosa* and other marsh vegetation over a longer timescale, spanning both the winter, and summer growing season. Negative effects of inundation on *S. foliosa* belowground biomass in the winter may influence its growth in the summer, producing sequential effects rather than simultaneous. As such, and consistent with Cheng et al. (2015), we suggest that ecologically relevant local conditions are considered in empirical tests of multiple stressors across systems.

Conclusion

We found variable responses of a tidal marsh community to inundation and the presence of an invasive crab, including positive responses of benthic microalgae and macrofauna to inundation and a negative response of cordgrass to *C. maenas.* Importantly, this work suggests that moderate increases in inundation from sea-level rise may affect less visible parts of the ecosystem, such as benthic algae and macrofaunal communities, before affecting vegetation. Changes to lower trophic levels could in turn affect higher trophic level organisms like fish and birds. The initial positive responses to inundation we found here may turn negative as higher levels of inundation create hypoxic conditions in increasingly higher elevations in tidal marshes. These data can also be used to guide management decisions in coastal areas with green crabs. The quantitative responses associated with specific levels of inundation we found in this study can be used to parameterize models that predict future effects of sea-level rise along with invasive species, and provide guidance on priority areas for removal, conservation and/or restoration.

Finally, considering sea-level rise impacts and biological invasions in the context of multiple stressor theory is useful to determine tipping points for organisms and foundation species in particular (Silliman and He 2018). Future work should examine additional levels of inundation along with *C. maenas* presence, and responses over a larger timescale, to identify these tipping points and better contribute to our understanding of the persistence of this community with sea-level rise.

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Figure Captions

Figure 1. A map of the study site showing China Camp State Park in Marin County, California, as component site of the San Francisco Bay National Estuarine Research Reserve.

Figure 2. The experimental setup of one block, depicting an aerial view of box and crab treatments.

Figure 3. A bar plot showing mean hours the marsh surface was inundated per day across inundation treatments. Error bars represent ± one standard error about the mean.

Figure 4. A bar plot showing average chlorophyll *a* concentration in the top layer (5mm) of the sediment (per $0.6cm^3$ core) in plots with different crab and inundation treatments. Inundation treatments are shown on the x axis and crab treatments are denoted by color. Error bars represent ± one standard error. Asterisk indicates significant differences among pooled crab treatments within inundation treatments at $p<0.05$.

Figure 5. A bar plot showing the mean change in *S. foliosa* stem density in inundation and crab treatment plots over the twelve week period. Inundation treatments are shown on the x axis and colored bars denote crab treatments. Error bars show ± one standard error and asterisks represent significant differences among treatments at $p<0.05$.

Figure 6. A panel showing bar plots of the average number of (A) amphipods and (B) oligochaetes per $491cm^3$ core in each treatment plots at the end of the experiment in August. Inundation treatments are shown on the x axis and crab treatments are denoted by color. Error bars represent ± one standard error and asterisks show significant differences among treatments at $p<0.05$.

Figure 7. A bar plot showing the average number of snails (*Ilyanassa obsoleta*) per 0.25m^2 crab treatment plot. Inundation treatments are shown on the x axis and crab treatments are denoted by color. Error bars represent ± one standard error and asterisks denote significance at p<0.05.

Figures

Figure 1

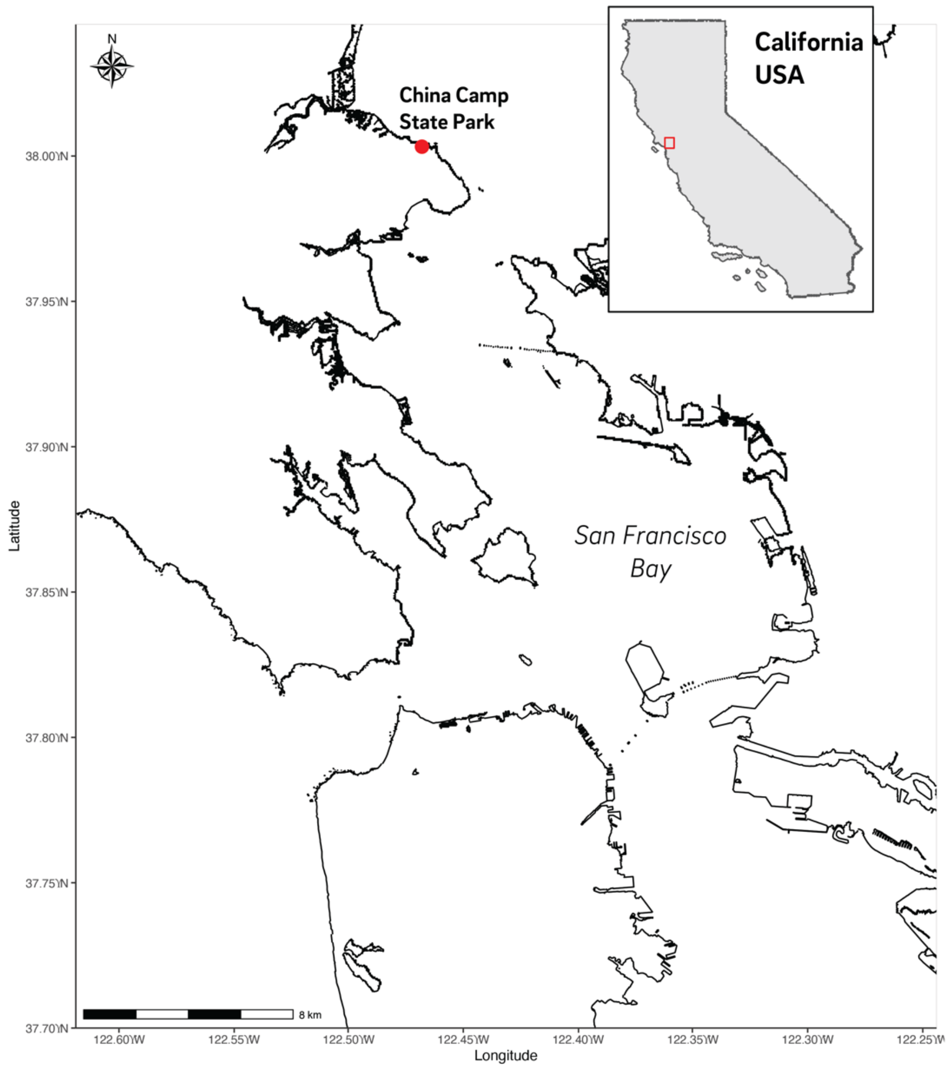


Figure 2

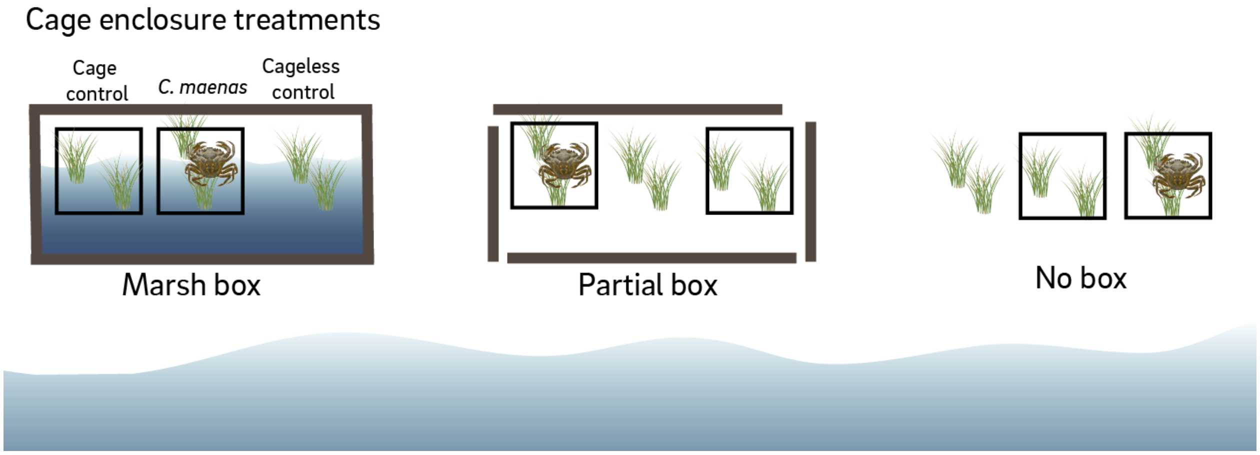


Figure 3

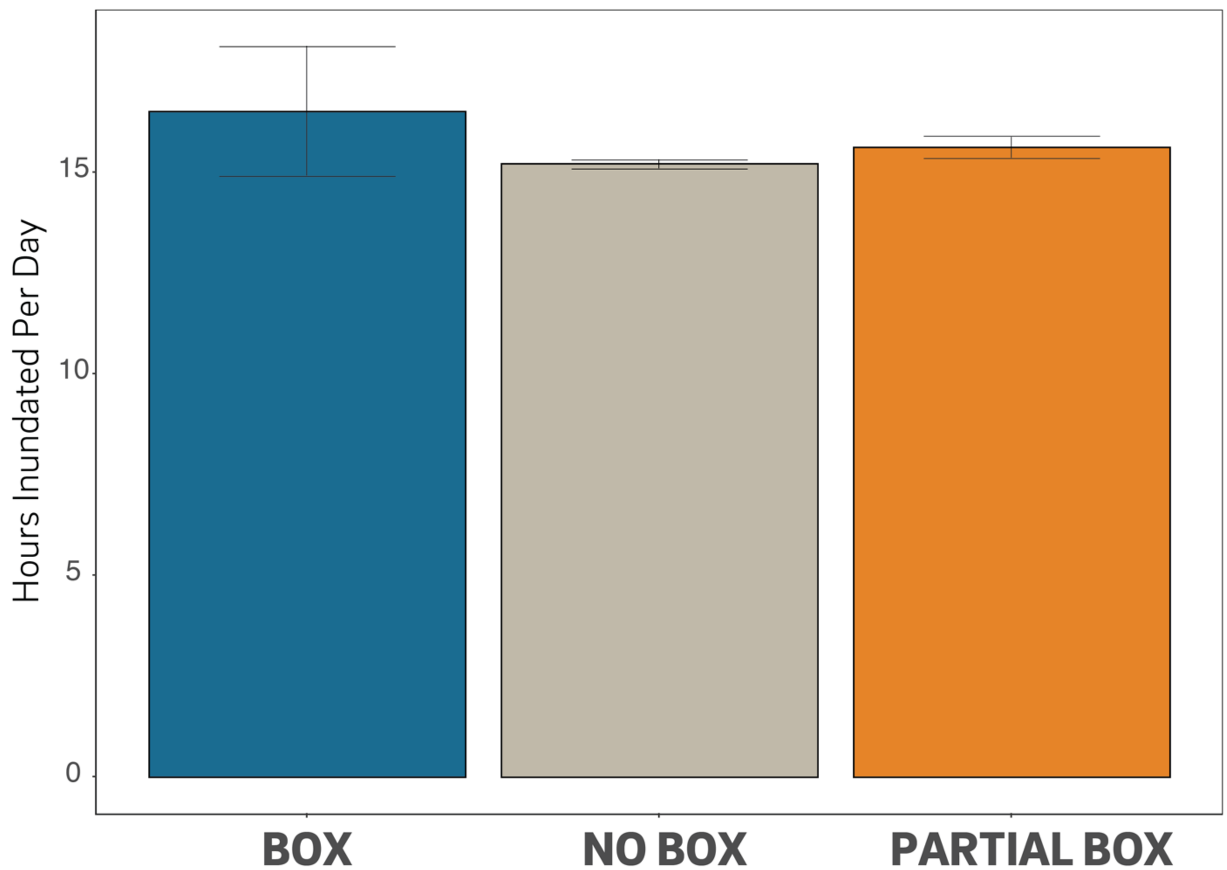


Figure 4

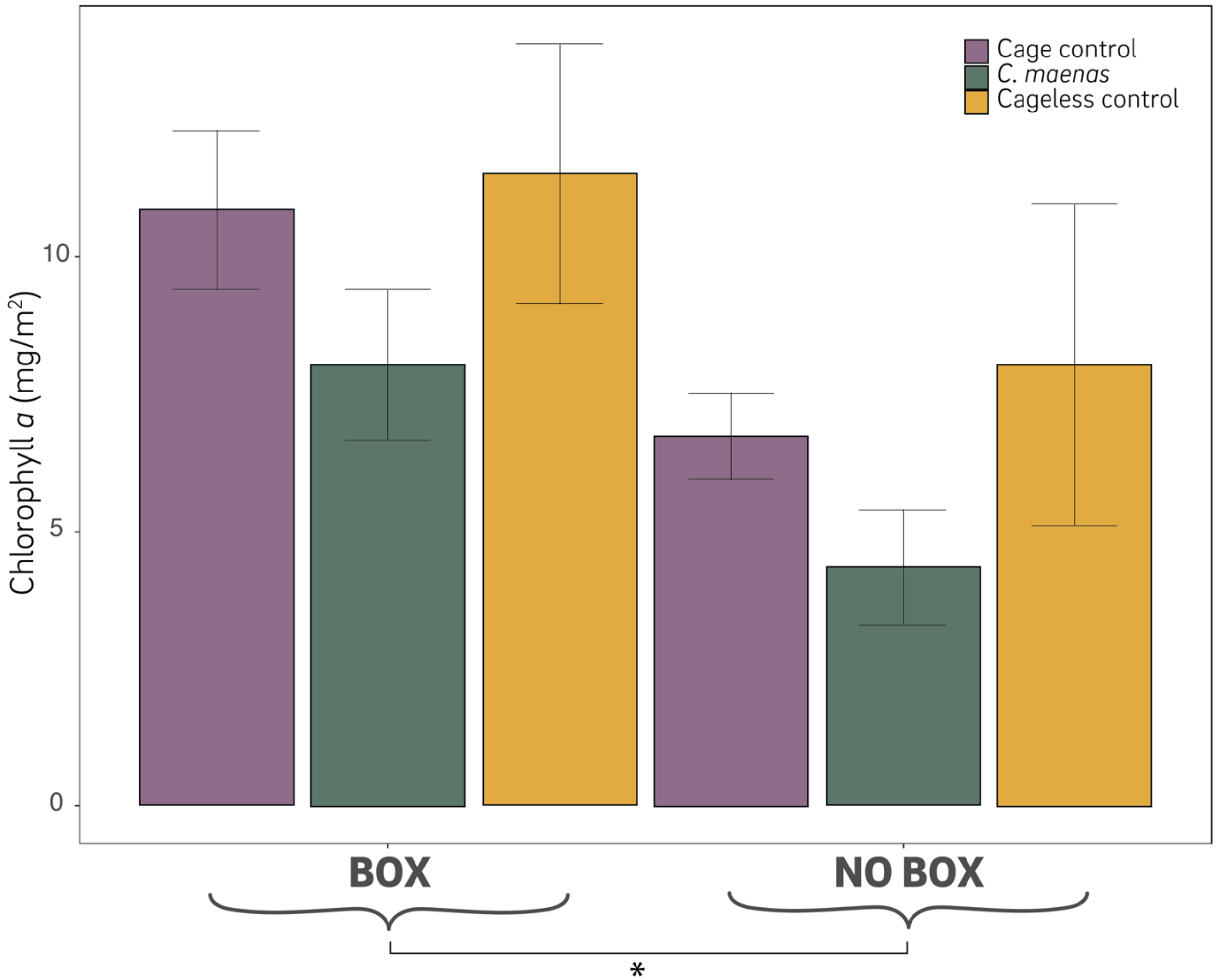
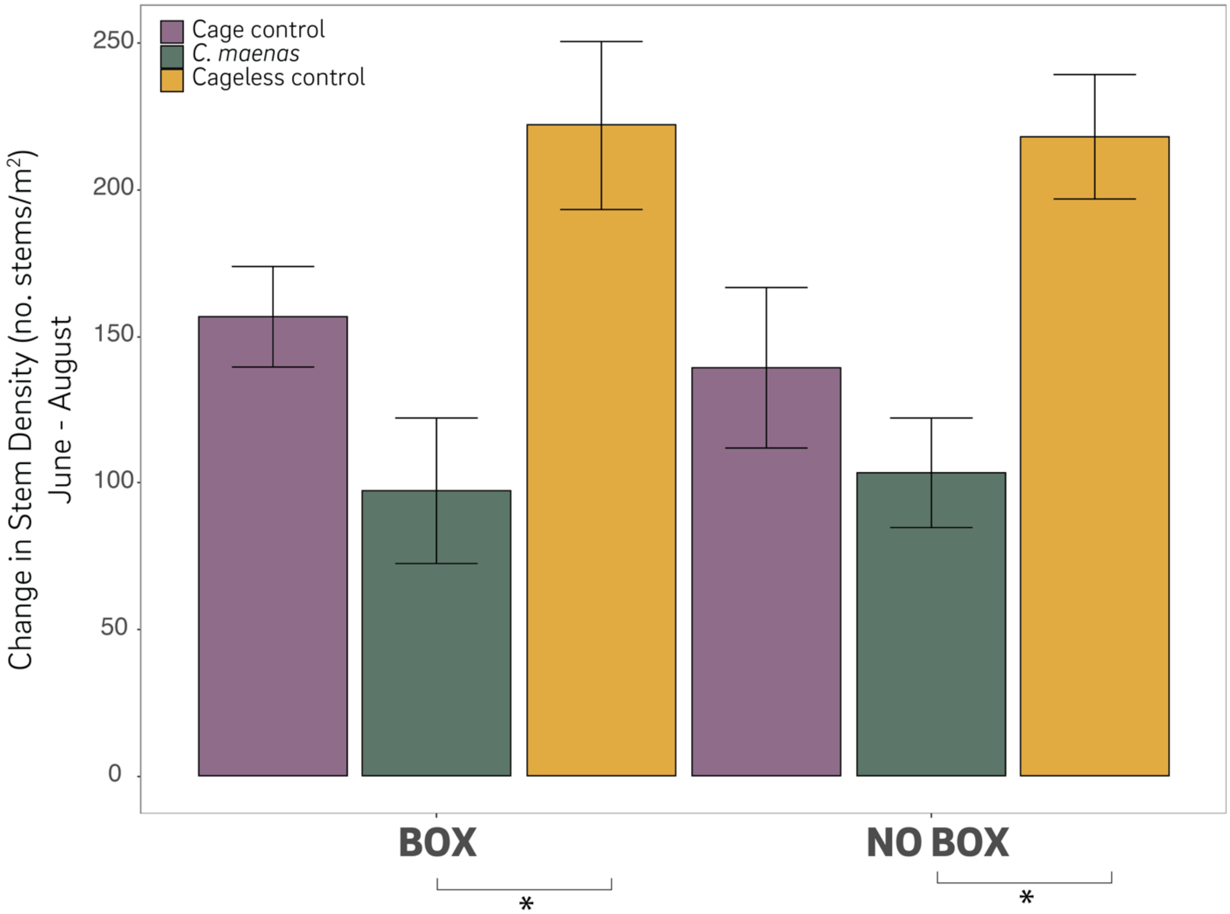

Cage control
C. maenas
Cageless control
Chlorophyll a (mg/m²)
10
5
0
BOX
NO BOX
*

Figure 5



Cage control
C. maenas
Cageless control
Change in Stem Density (no. stems/m²)
June - August
250
200
150
100
50
0
BOX
NO BOX
*
*

Figure 6

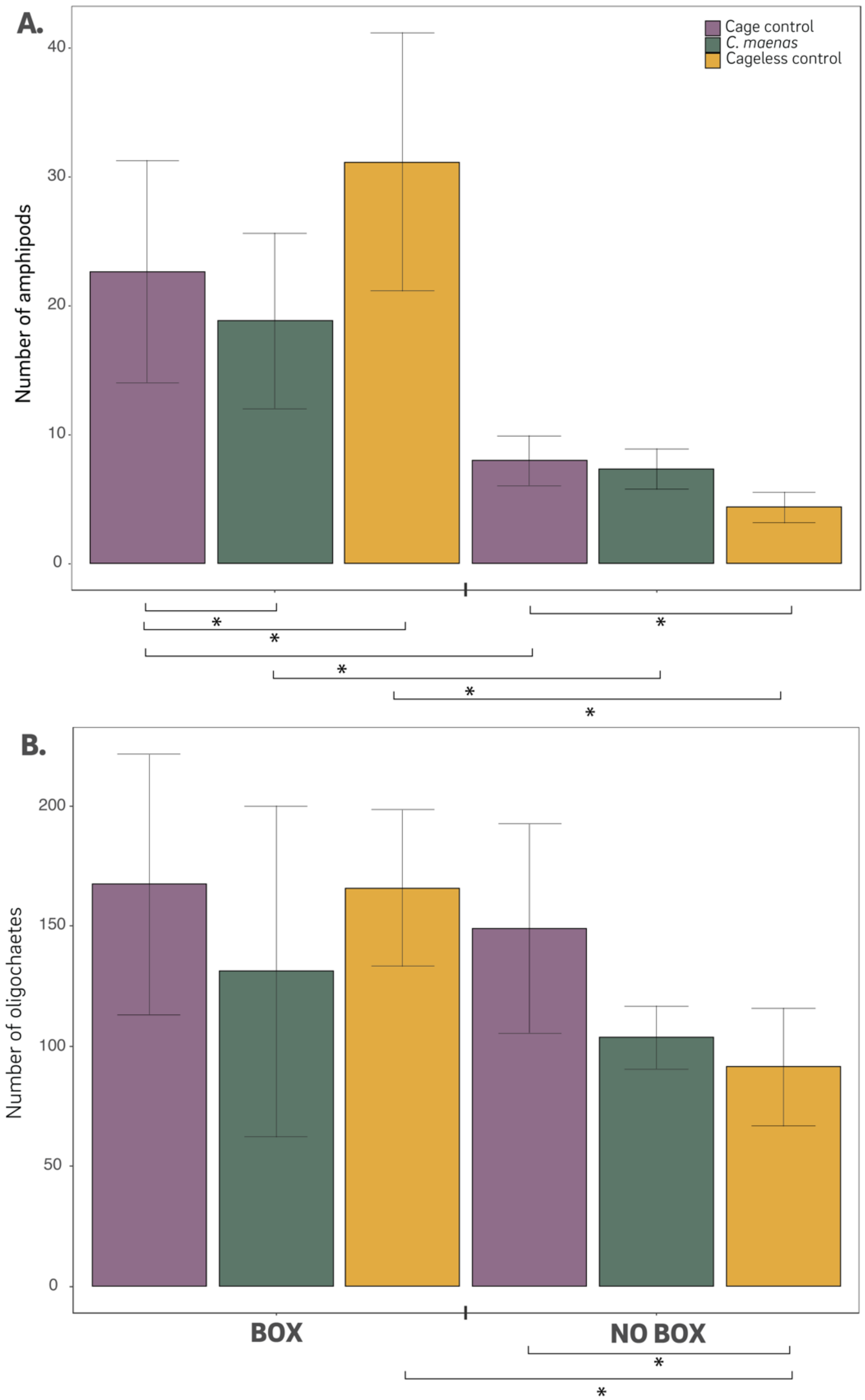
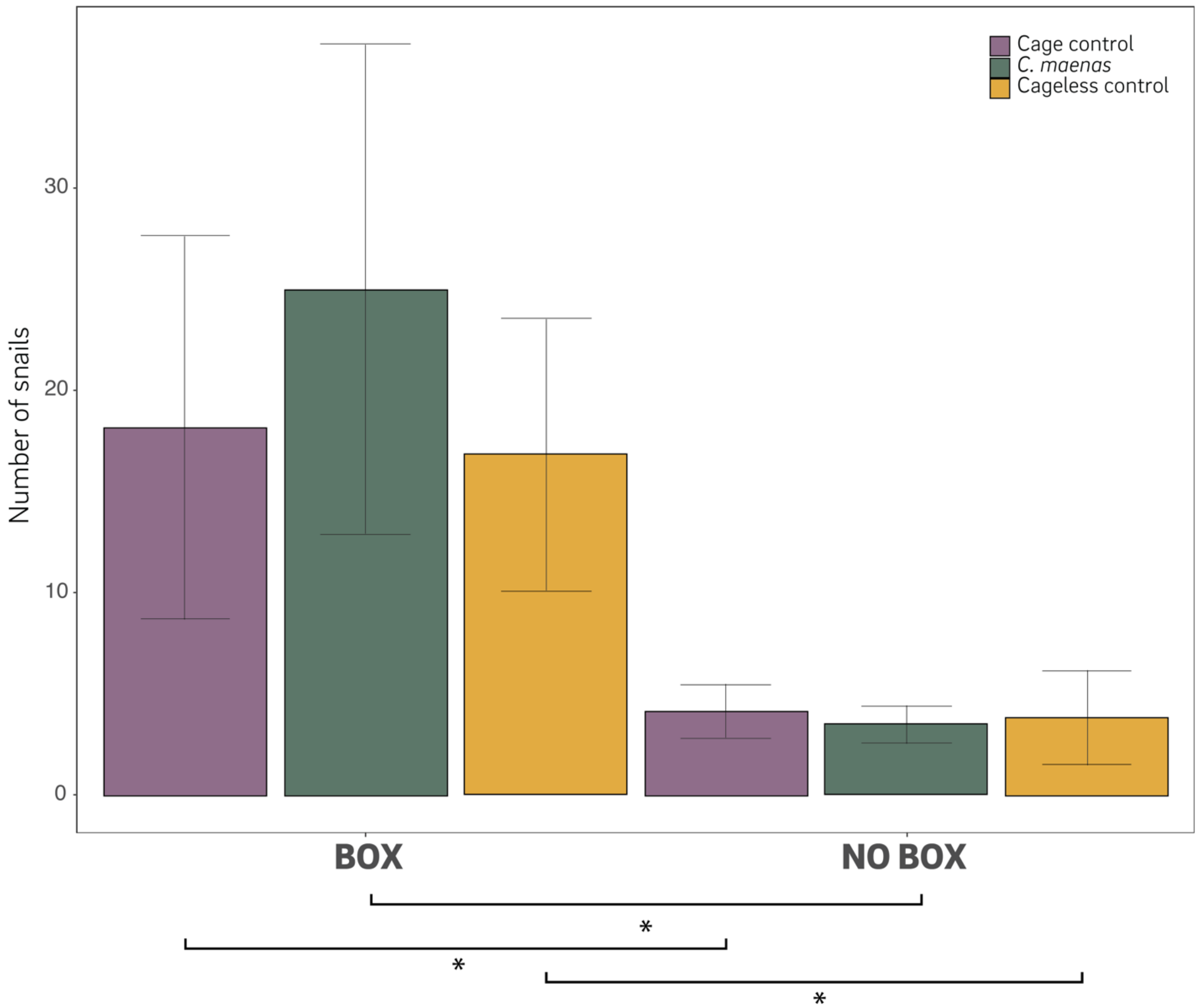

A.
Cage control
C. maenas
Cageless control
Number of amphipods
40
30
20
10
0
*
*
*
*
*
*
B.
Number of oligochaetes
200
150
100
50
0
BOX
NO BOX
*
*

Figure 7


Cage control
C. maenas
Cageless control
Number of snails
0
10
20
30
BOX
NO BOX
*
*
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Appendices

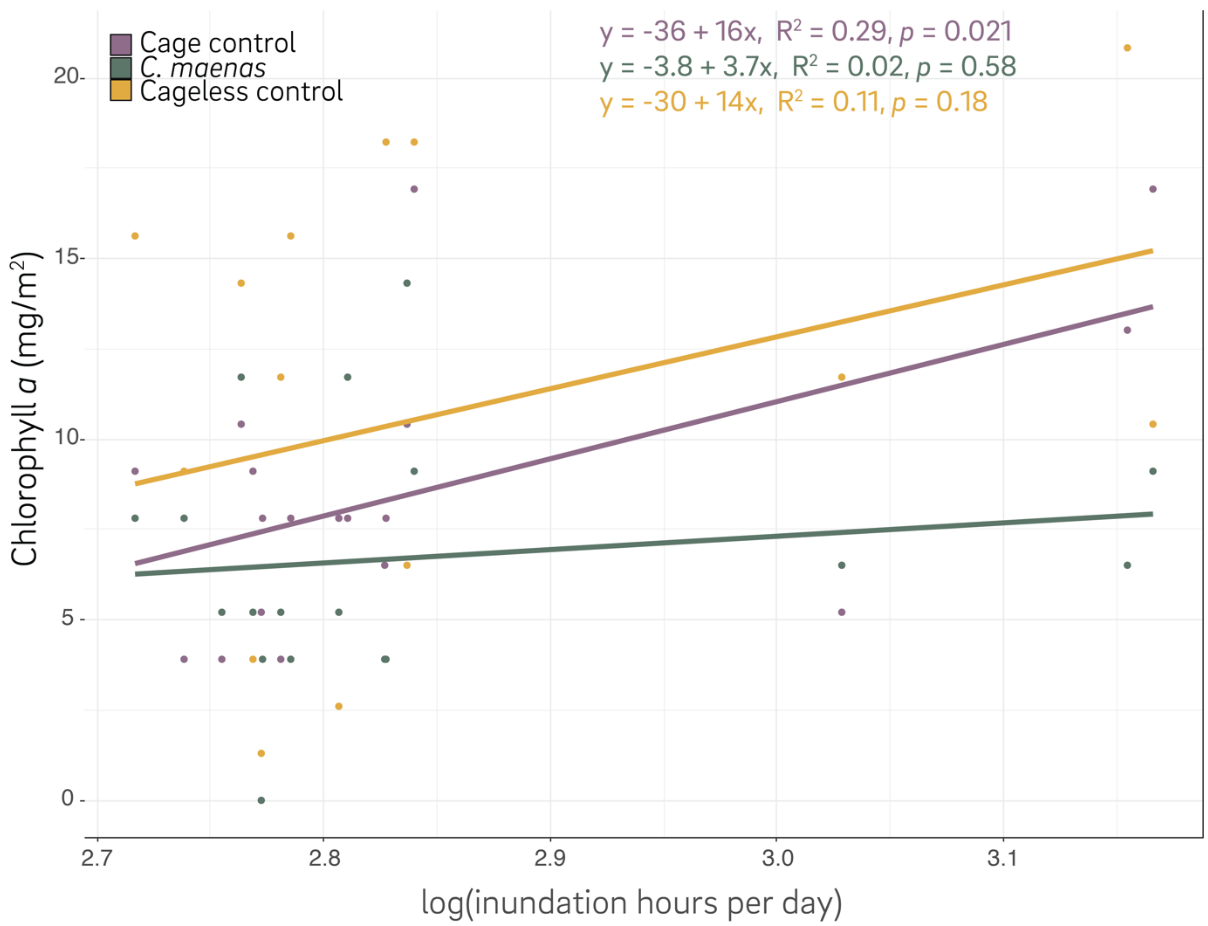
Table S1. Table outlining all statistical models discussed in manuscript. SE = standard error, DF=degrees of freedom, EGC = European green crab (*Carcinus maenas*). Bolded p-values highlight significant values.

Response Variable	Model	Fixed factor	Random Effect	Distribution	Comparison	Estimate	SE	DF	Test score	Score value	p-value
Inundation hours per day	GLMM	Inundation Treatment	Block	Gamma	Box vs. no box	-0.005218	0.00308	Inf	Z score	-1.695	0.207
					Box vs. partial box	-0.004602	0.00354	Inf	Z score	-1.299	0.3957
					No box vs. partial box	0.000615	0.00343	Inf	Z score	0.179	0.9825
Temperature (ºC)	GLM	Inundation Treatment	None	Gamma	Box vs. no box	-0.000799	0.000885	Inf	Z score	-0.903	0.3667
Light intensity (lumens)	GLM	Inundation Treatment	None	Gamma	Box vs. no box	-0.000142	0.000243	Inf	Z score	-0.585	0.5583
Redox potential + 396 Square Root Transformed No partial box effects	LMM	Inundation Treatment*Crab Treatment	Block	Normal	Box, cage vs. box, egc	-0.598	1.1	36	t ratio	-0.545	0.8497
					Box, cage vs. box, no cage	0.208	1.1	36	t ratio	0.189	0.9805
					Box, EGC vs. box, no cage	0.806	1.1	36	t ratio	0.734	0.745
					No box, cage vs. no box, egc	-0.351	1.1	36	t ratio	-0.319	0.9455
					No box, cage vs. no box, no cage	0.687	1.1	36	t ratio	0.625	0.8073
					No box, EGC vs. no box, no cage	1.037	1.1	36	t ratio	0.944	0.6162
Chlorophyll a Square Root Transformed Partial box effects	LMM	Inundation Treatment*Crab Treatment Orthometric height	Block	Normal	Box treatment	NA	NA	2	X2 (ANOVA)	12.6374	**0.001802**
					Crab treatment	NA	NA	2	X2 (ANOVA)	8.0267	**0.018073**
					Elevation	NA	NA	1	X2 (ANOVA)	0.0768	0.781641
					Box treatment*crab treatment	NA	NA	4	X2 (ANOVA)	2.5306	0.63917
					Box vs. no box	0.766	0.248	55.9	t ratio	3.085	**0.0087**
					Box vs. partial box	0.155	0.255	58.6	t ratio	0.61	0.8152
					No box vs. partial box	-0.611	0.254	58.2	t ratio	-2.407	**0.0498**
					Cage: box vs. no box	0.6911	0.43	55.9	t ratio	1.607	0.2512
					Cage: partial vs. no box	-0.148	0.433	56.7	t ratio	-0.342	0.9377
					EGC: box vs. no box	0.895	0.43	55.9	t ratio	2.081	0.103
					EGC: partial vs. no box	-0.8388	0.433	56.7	t ratio	-1.936	0.1379
					No cage: box vs. no box	0.7121	0.43	55.9	t ratio	1.656	0.2313
					No cage: partial vs. no box	-0.8451	0.433	56.7	t ratio	-1.951	0.134
					Box, cage vs. EGC	0.48068	0.43	55.9	t ratio	1.118	0.5073
					Box, cage vs. no cage	-0.0353	0.43	55.9	t ratio	-0.082	0.9963
					Box, EGC vs. no cage	-0.51598	0.43	55.9	t ratio	-1.2	0.4583
					No box, cage vs. EGC	0.68461	0.43	55.9	t ratio	1.592	0.2575
					No box, cage vs. no cage	-0.01431	0.43	55.9	t ratio	-0.033	0.9994
					No box, EGC vs. no cage	-0.69892	0.43	55.9	t ratio	-1.625	0.2436
Change in stem density over 12 week period No partial box effects	GLMM	Inundation treatment*Crab treatment Orthometric height Inundation Hours Per Day	Block	Negative Binomial	Box treatment	NA	NA	1	X2 (ANOVA)	0.3858	0.5345158
					Crab treatment	NA	NA	2	X2 (ANOVA)	18.2879	**0.0001069**
					Orthometric Height	NA	NA	1	X2 (ANOVA)	1.1434	0.2849426
					Inundation Hours Per Day	NA	NA	1	X2 (ANOVA)	1.156	0.2823059
					Box*Crab	NA	NA	2	X2 (ANOVA)	0.3038	0.8590553
					Cage: box vs. no box	0.22006	0.287	Inf	Z score	0.766	0.4436
					EGC: box vs. no box	0.00882	0.275	Inf	Z score	0.032	0.9744
					No cage: box vs. no box	0.12401	0.289	Inf	Z score	0.429	0.6681
					Box, cage vs. EGC	0.534	0.274	Inf	Z score	1.946	0.126

					Box, cage vs. no cage	-0.35	0.266	Inf	Z score	-1.314	0.3871
					Box, EGC vs. no cage	-0.883	0.276	Inf	Z score	-3.198	**0.0039**
					No box, cage vs. EGC	0.323	0.269	Inf	Z score	1.2	0.4532
					No box, cage vs. no cage	-0.446	0.266	Inf	Z score	-1.676	0.2145
					No box, EGC vs. no cage	-0.768	0.268	Inf	Z score	-2.87	**0.0114**
Change in stem height over 12 week period No partial box effects	LMM	Inundation treatment*Crab treatment Orthometric height	Block	Normal	Box treatment	NA	NA	1	X2 (ANOVA)	0.0124	0.91142
					Crab treatment	NA	NA	2	X2 (ANOVA)	1.9933	0.36911
					Elevation	NA	NA	1	X2 (ANOVA)	3.575	0.05866
					Box*Crab	NA	NA	2	X2 (ANOVA)	0.8531	0.65275
					Box, cage vs. EGC	-2.59	2.88	36.2	t ratio	-0.9	0.6441
					Box, cage vs. no cage	-2.9	2.88	36.2	t ratio	-1.007	0.5772
					Box, EGC vs. no cage	-0.31	2.88	36.2	t ratio	-0.108	0.9936
					No box, cage vs. EGC	0.628	2.88	36.2	t ratio	0.218	0.9741
					No box, cage vs. no cage	-2.258	2.88	36.2	t ratio	-0.784	0.7149
					No box, EGC vs. no cage	-2.887	2.88	36.2	t ratio	-1.003	0.58
Belowground Biomass No partial box effects	LMM	Inundation treatment*Crab treatment Orthometric height	Block	Normal	Box, cage vs. EGC	-1.2147	0.938	21.9	t ratio	-1.295	0.4128
					Box, cage vs. no cage	0.4071	0.991	22.6	t ratio	0.411	0.9116
					Box, EGC vs. no cage	1.6218	0.991	22.6	t ratio	1.637	0.2513
					No box, cage vs. EGC	0.0485	1.044	23.3	t ratio	0.046	0.9988
					No box, cage vs. no cage	1.0359	0.991	22.6	t ratio	1.045	0.5568
					No box, EGC vs. no cage	0.9875	0.992	22.5	t ratio	0.996	0.5869
Ammonium Log Transformed No partial box effects	LMM	Inundation treatment*Crab treatment Orthometric height	Block	Normal	Box treatment	NA	NA	2	X2 (ANOVA)	2.7883	0.248
					Crab treatment	NA	NA	1	X2 (ANOVA)	0.9884	0.3201
					Elevation	NA	NA	1	X2 (ANOVA)	0.1788	0.6724
					Box*Crab	NA	NA	2	X2 (ANOVA)	1.6811	0.4315
Number of amphipods Partal box effects	GLMM	Inundation treatment*Crab treatment Orthometric height	Block	Poisson	Crab treatment	NA	NA	2	X2 (ANOVA)	0.1558	0.92504
					Box Treatment	NA	NA	1	X2 (ANOVA)	27.7657	**1.369E-07**
					Elevation	NA	NA	1	X2 (ANOVA)	4.5997	**0.03198**
					Box*Crab	NA	NA	2	X2 (ANOVA)	3.4123	0.18156
					Partial vs. No Box	-1.797	0.109	Inf	Z score	-16.533	**<.0001**
					Box vs. No Box	1.31	0.107	Inf	Z score	12.206	**<.0001**
					Cage: box vs. no box	1.033	0.168	Inf	Z score	6.153	**<.0001**
					Cage: partial vs. no box	1.698	0.161	Inf	Z score	10.522	**<.0001**
					EGC: box vs. no box	0.934	0.178	Inf	Z score	5.261	**<.0001**
					EGC: partial vs. no box	1.315	0.174	Inf	Z score	7.538	**<.0001**
					No cage: box vs. no box	1.964	0.209	Inf	Z score	9.391	**<.0001**
					No cage: partial vs. no box	2.379	0.208	Inf	Z score	11.428	**<.0001**
					Box, cage vs. EGC	0.1853	0.1271	Inf	Z score	1.457	0.3117
					Box, cage vs. no cage	-0.3185	0.1126	Inf	Z score	-2.829	**0.013**
					Box, EGC vs. no cage	-0.5037	0.119	Inf	Z score	-4.233	**0.0001**
					No box, cage vs. EGC	0.087	0.2085	Inf	Z score	0.417	0.9084
					No box, cage vs. no cage	0.6131	0.2432	Inf	Z score	2.521	**0.0314**
					No box, EGC vs. no cage	0.5261	0.2471	Inf	Z score	2.129	0.084
					EGC: partial vs. no box	0.287	0.264	Inf	Z score	1.086	0.523
					Cage: partial vs. no box	1.545	0.278	Inf	Z score	5.554	**<.0001**
					No cage: partial vs. no box	1.258	0.275	Inf	Z score	4.573	**<.0001**
Number of oligochaetes Partial box effects	GLMM	Inundation treatment*Crab treatment Orthometric height	Block	Negative Binomial	Crab treatment	NA	NA	2	X2 (ANOVA)	0.9882	0.61012
					Box Treatment	NA	NA	2	X2 (ANOVA)	8.0315	**0.01803**

					Elevation	NA	NA	1	X2 (ANOVA)	0.3203	0.57145
					Box*Crab	NA	NA	4	X2 (ANOVA)	9.0669	0.05945
					Partial vs. No Box	-0.498	0.177	Inf	Z score	-2.817	**0.0134**
					Box vs. No Box	0.311	0.173	Inf	Z score	1.795	0.1712
					Cage: box vs. no box	0.0446	0.298	Inf	Z score	0.15	0.9877
					EGC: box vs. no box	-0.0406	0.301	Inf	Z score	-0.135	0.99
					No cage: box vs. no box	0.9301	0.296	Inf	Z score	3.138	**0.0048**
					Box, cage vs. EGC	0.2994	0.294	Inf	Z score	1.018	0.5653
					Box, cage vs. no cage	-0.11816	0.295	Inf	Z score	-0.4	0.9155
					Box, EGC vs. no cage	-0.41756	0.299	Inf	Z score	-1.398	0.3417
					No box, cage vs. EGC	0.21419	0.297	Inf	Z score	0.722	0.7506
					No box, cage vs. no cage	0.76741	0.297	Inf	Z score	2.585	**0.0264**
					No box, EGC vs. no cage	0.55322	0.296	Inf	Z score	1.868	0.1481
					EGC: partial vs. no box	0.311	0.173	Inf	Z score	1.795	0.1712
					Cage: partial vs. no box	-0.186	0.179	Inf	Z score	-1.039	0.5519
					No cage: partial vs. no box	-0.498	0.177	Inf	Z score	-2.817	**0.0134**
Number of snails Square Root Transformed No partial box effects	LMM	Inundation treatment*Crab treatment Orthometric height	Block	Normal	Box Treatment	NA	NA	1	X2 (ANOVA)	23.1839	**1.472E-06**
					Crab Treatment	NA	NA	2	X2 (ANOVA)	0.373	0.829854
					Elevation	NA	NA	1	X2 (ANOVA)	8.7961	**0.003019**
					Box*Crab	NA	NA	2	X2 (ANOVA)	0.6335	0.728509
					Cage: box vs. no box	1.6	0.83	36.8	t ratio	1.926	**0.0618**
					EGC: box vs. no box	2.39	0.83	36.8	t ratio	2.881	**0.0066**
					No cage: box vs. no box	2.24	0.83	36.8	t ratio	2.694	**0.0106**
					Box, cage vs. EGC	-0.574	0.83	36.8	t ratio	-0.692	0.7697
					Box, cage vs. no cage	-0.175	0.83	36.8	t ratio	-0.211	0.9759
					Box, EGC vs. no cage	0.399	0.83	36.8	t ratio	0.481	0.8806
					No box, cage vs. EGC	0.218	0.83	36.8	t ratio	0.263	0.9626
					No box, cage vs. no cage	0.462	0.83	36.8	t ratio	0.557	0.8435
					No box, EGC vs. no cage	0.244	0.83	36.8	t ratio	0.294	0.9536

Figure S1. Chlorophyll *a* concentrations per plot regressed with the log of inundation hours per day per treatment. Individual points represent one plot. Linear equations, R^2 values, and *p* values shown. Colors denote crab treatments.



CHAPTER 3

Trophic Implications of Experimentally Prolonged Inundation on a Tidal Marsh Community

Collaborators: Matthew E. Ferner, Philip B. Georgakakos, and Edwin D. Grosholz

Abstract

Sea-level rise has the potential to drive significant changes in tidal marsh ecosystems, impacting habitat availability and species interactions. However, we understand little about the trophic links between aquatic and terrestrial habitats in the context of sea-level rise management. In this study, we experimentally increased inundation *in situ* using 'marsh boxes' to simulate sea-level rise and flooding at a tidal marsh in China Camp State Park, San Rafael, CA, USA. We examined changes in porewater metrics, redox potential, microalgal cover, responses of insects and benthic invertebrates and use of habitats by marsh nesting birds to better understand the potential impacts on higher trophic level organisms and inform effective conservation strategies. We found that cordgrass, *Spartina foliosa*, responds negatively to longer inundation, likely due to low oxygen conditions creating high levels of sulfide in box treatments. These effects varied by year, perhaps due to shorter *S. foliosa* stems and lower stem density in 2022. Additionally, we found a positive response of inundation on some insects (Chironomidae) and a negative response of inundation on others like Planthoppers (*Prokelisia* spp.) We found more Song Sparrows (*Melospiza melodia*) in lower elevation *S. foliosa* relative to mid/high elevation *Sarcocornia pacifica* areas, and fewer Song Sparrows in 2022, potentially due to reduced *S. foliosa* integrity

coupled with lower Chironomid abundance in 2022. These findings underscore the importance of incorporating such aquatic-terrestrial linkages into predictive models for sea-level rise effects and management strategies, providing valuable insights for proactive conservation and sustainable coastal planning.

Keywords: aquatic-terrestrial linkages; birds; insects; Song Sparrow; planthopper; chironomid

Introduction

Sea-level rise is a pressing environmental challenge with far reaching consequences for coastal systems world-wide. Increased inundation from sea-level rise is projected to affect coastal systems in a variety of ways, from habitat loss to salinity intrusion further into estuaries (Day and Templet 1989; Scavia et al. 2002). This will likely affect the distributions or survival of organisms that are not adapted to deal with greater inundation and salt stress. Tidal marsh habitats are particularly vulnerable to sea-level rise, which may lead to significant degradation of this habitat and potential loss. On the west coast of the USA alone, approximately 85% of tidal marsh habitat has been lost due to having been diked, drained, or otherwise converted (Zedler and Kercher 2005; Brophy et al. 2019). Sea-level rise will produce unprecedented changes to inundation and salinity, potentially exacerbating habitat loss and complicating conservation and restoration efforts in tidal marshes.

The availability of suitable habitat for organisms in tidal marsh systems is strongly influenced by the underlying physical processes shaping marsh structure and function. Tidal marshes are exposed to daily tidal fluctuations, wind and wave action from storm events, nutrient runoff, and other stressors. Tidal marsh organisms have varying tolerances to these stressors and different competitive abilities that determine where they exist along the tidal marsh gradient (Bertness and Ellison 1987; Pennings and Callaway 1992). In addition, positive and negative biotic interactions contribute to the community structure of these systems (Bertness 1984; Bertness 1985; Bertness and Callaway 1994). Sea-level rise will likely further influence these interactions by altering physical conditions.

While some research has been conducted on species interactions in the context of increased inundation due to sea-level rise or flooding, a comprehensive understanding of these intricate relationships remains a crucial knowledge gap. Increased flooding in tidal marshes can displace terrestrial tidal marsh species with wide ranging consequences. Avian predators in marshes generally consume fish, larvae, small mammals and birds, and crustaceans (Takekawa et al. 2011) and capture attempts by avian predators and successful capture rates increased with increased flooding in marshes (Thorne et al. 2019). During extreme flooding events, nest failure of Seaside Sparrows increased due to their building nests at high elevations exposed to terrestrial predators (Hunter 2017). However, little is known about how bird prey items will respond to increasing levels of inundation. Changes to these interactions from increased inundation may prove especially influential, since the repercussions of altered interactions between species in tidal marshes may extend beyond the marshes themselves.

Despite their importance in shaping ecosystem dynamics, the trophic links between aquatic and terrestrial habitats have been largely overlooked in the context of sea-level rise adaptation planning. Tidal marshes are transitional systems that are positioned between aquatic and terrestrial habitats. Aquatic and terrestrial systems are linked by invertebrate species that are either fully or partially aquatic, and the organisms that eat those invertebrates (e.g. birds and fish). These food subsidies from aquatic systems can affect the growth and abundance of their terrestrial consumers (Baxter et al. 2005). In the Tijuana Estuary in southern California, organic material from low marsh native cordgrass *Spartina foliosa,* as well as benthic micro- and macroalgae, supports invertebrates in that system and further, the higher trophic level organisms that consume those invertebrates, like fish and the endangered Light Footed Clapper Rail (*Rallus longirostris levipes*) (Kwak and Zedler 1997). Investigating the role of these food subsidies, as well as habitat, in transitional systems like tidal marshes can offer valuable insights into the potential impacts of sea-level rise on higher trophic level organisms, like threatened and endangered bird species, and inform effective conservation strategies.

In this study, we experimentally increased inundation to simulate the flooding expected with future sea-level rise and examined responses of physical parameters and organisms across trophic levels. We additionally evaluated bird use of habitats within tidal marshes to understand how impacts to vegetation or invertebrates may affect bird abundance and distribution. We hypothesized that greater inundation would trigger a suite of physical and biological effects including decreased redox potential, and increased ammonium and sulfide levels. We postulated that these physical changes would decrease *S. foliosa* growth and abundance, and together these changes would affect marsh invertebrate abundance, which could cascade up to affect bird habitat use.

Methods

Site Description

This study took place in China Camp State Park (SP), located in San Rafael, CA, USA. China Camp SP contains a large, remnant historic marsh. The site where this work took place is characterized by a low elevation band of cordgrass, or *Spartina foliosa*, that leads into a middle/higher elevation area dominated primarily by pickleweed (*Sarcocornia pacifica*) with *Jaumea carnosa* and *Limonium californicum* scattered throughout. Channel edges within *S. pacifica* habitat also contain gumplant *Grindelia stricta*, as well as *S. foliosa* at the base of the channel interior. Higher elevation *S. pacifica* habitat can also contain saltgrass, *Distichlis spicata*, throughout. This study focused primarily on the *S. pacifica* dominated mid/high marsh, mudflat, and the low elevation band of *S. foliosa* that bisects the two.

Experimental Design

We used three inundation treatment levels. In spring of 2021, we installed eight marsh boxes (1m x 0.6m x 0.6m) in areas of *Spartina*. These plots were accompanied by eight unaltered areas of *S. foliosa* for comparison. As boxes may impact sediment characteristics and flow around the plots, we also installed eight partial marsh boxes, which allowed water to flow out at the corners, to account for any artefactual effects of the boxes. For control plots, we dug a thin strip around the plots to simulate disturbance from box or partial box installation and cut through any belowground root masses connected to the plot. Each set of three inundation treatments were contained in blocks which were distributed across the experimental area. Over winter 2021, the boxes filled with sediment and/or were broken due to heavy tidal flows, affecting the *S. foliosa* 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 one meter away from the previous box’s location into an area of unaffected cordgrass.

Inundation, Physical Conditions, and Vegetation Response

We evaluated inundation hours per day using water level data captured by HOBO U20L water level loggers (Onset Data Loggers, Cape Cod, MA) placed in each plot for a two-week period in June and July 2021, and June 2022. To account for atmospheric variation, we corrected raw water level data using barometric pressure readings from the closest NOAA Climatological Data Station (Gnoss Field Airport, CA) and the barometric compensation assistant in HOBOware Pro. Water level data deemed unusable due to logger failure or sensor disruption by particulates were excluded from statistical analyses. We used HOBO Temperature/Light loggers to evaluate any differences in temperature and light among inundation treatments. We took elevation measurements in the center of each plot using a Real-Time Kinematic (RTK) GPS GS07 GNSS receiver and CS20 LTE controller (Leica Geosystems), and corrected elevation data using benchmarks taken before and after sampling. Positions were received via the Leica California SmartNet RKT network.

We monitored plots approximately monthly for five months in summer 2021 and three months in summer 2022. Measurements were taken approximately 10cm from the edges in each plot to account for potential edge effects of the boxes. Response variables included the change in *S. foliosa* stem density (no. stems per m^2) and average height of the ten tallest *S. foliosa* stems over approximately a 12 week period from June to August or September each year, and redox potential (Eh), which we measured using a Mettler-Toledo mV meter at 10cm below the surface of the sediment (Neira et al. 2005). We collected belowground biomass by taking a sediment core at the end of the experiment in September 2022 (5cm diameter PVC corer to a depth of 25cm). As inundation is also generally coupled with physical changes to sediment characteristics and nutrient cycling (Schile et al. 2011), we used porewater sippers established in each plot to sample porewater for ammonium, nitrate and sulfide each year. Porewater was collected using 10 cm long, porous (0.15 μm) soil moisture samplers (Rhizophere Research Products, Wageningen, The Netherlands). At the start of the sampling period each summer, porewater sippers were submerged approximately 10cm to collect soil porewater at or near the root assemblages of vegetation (Walker et al. 2020). Porewater sippers were capped at the exposed end to prevent entry of oxygen. We evaluated sulfide concentrations from porewater samples based on methods by Cline (1969) and other porewater samples were analyzed for ammonium and nitrate (UC Davis Analytical Lab). We also gathered data on microalgal biomass, an important food source for benthic invertebrates and insects like Chironomidae with a larval stage that occurs in the sediment. We took a soil core (1.23cm^2 diameter x 5mm deep) to quantify chlorophyll *a* concentrations in the top layer of the sediment according to Plante-Cuny (1973).

Bird Prey Items – Insects and Soil Infauna

To quantify food resources for birds in different habitats, we deployed sticky traps (Gideal brand, Amazon.com) (Sabo and Power 2002) to collect flying insects in treatment plots approximately monthly throughout the experiment. Simultaneously, we deployed 6-8 sticky traps in the mid marsh area dominated primarily by *S. pacifica* to compare with control treatments in low marsh *S. foliosa*. Sticky traps were made of 310 cm^2 plastic sheets covered with Tanglefoot insect trap coating (Tanglefoot, Grand Rapids, Michigan, USA) and rolled in a cylinder around PVC posts just above the vegetation to capture insects flying from all directions. After field collection, each sticky trap was scanned to generate a digital image suitable for analysis in FIJI/ImageJ. The image was then overlaid with a grid, allowing for the counting and identification of insects in each cell, down to the finest possible classification. To quantify soil infauna and surface feeding invertebrates, we took a sediment core in each treatment plot at the end of each growing season in 2021 and 2022 using a 5cm PVC corer to a depth of 10cm. The sample was sieved through a 500µm mesh sieve, and invertebrates were fixed in 10% formalin, stored in 70% ethanol and sorted into broad taxonomic categories (Neira et al. 2006).

Bird Abundance and Use of Habitat

In addition to the response of vegetation and soil parameters, and bird prey items, we also assessed potential impacts on higher trophic levels by quantifying bird presence and foraging in habitat treatments. Bird species identification and enumeration in low and mid/high marsh habitats was assessed using a standardized Area Search Census protocol (Point Blue 1999, Patten and O'Casey 2007) and we took point counts using spotting scope (Vortex Optics, Barnveld, WI) to identify birds in mudflat habitat. In this study we focus primarily on three species that were found consistently in the low marsh: Song Sparrow (*Melospiza melodia*), Marsh Wren (*Cistothorus palustris*) and Common Yellowthroat (*Geothlypis trichas*). Surveys occurred during low tide and were timed to coincide with high bird densities in the fall, winter and spring migration periods for various groups. We completed four surveys in the fall through winter between 9/21 and 1/22 and four surveys between 10/22 and 4/23. Bird data were stratified by habitat type (pickleweed plain (mid/high marsh), fringing *S. foliosa* meadow (low marsh), and mudflat). Each of the three habitats were contained in one area, and we surveyed three replicate areas.

Statistics

Using R statistical software (R Development Core Team 2012) we used linear mixed models ("lme4" package in R) to quantify the following response parameters: change in *S. foliosa* stem density and height over a ~12 week period each growing season, belowground biomass, redox potential, chlorophyll *a*, ammonium, number of amphipods and oligochaetes, total number of insects, number of chironomids and planthoppers (*Prokelisia* spp.), and number of Song Sparrows per hectare per hour. For among year comparisons, 2022 data were collected within two weeks of the initial sample date in 2021. The full model included inundation hours per day and orthometric tidal elevation as fixed factors. Block was included as a random factor, and block nested within year was included as a random factor when data encompassed both years of the experiment as block numbers varied across years. We evaluated full and reduced versions of the model using Goodness-of-fit statistics to determine the best model for each dataset (Table S1, Quinn and Keough 2002). We used a generalized linear mixed model to evaluate inundation hours per day during three distinct tidal cycles (June and July 2021, and June 2022) to account for non-normal data distribution and heteroscedastic variances. We included fixed factors of treatment, elevation, the time period of the tidal cycle, and the interaction of treatment and tidal cycle, as well as a random effect of block nested within cycle. For post hoc comparisons of model outputs, we used the "emmeans" package in R (estimated marginal means) that calculates degrees of freedom using the Kenward-Rogers method.

Results

Inundation Treatments

The amount of inundation varied by the categorical box treatment designation, the tidal cycle in which water level data were gathered, the orthometric height of the plot, and the interaction of treatment and tidal cycle ($X^2 = 10.12$, $p=0.006$; $X^2 = 51.21$, $p<0.001$, $X^2 = 28.37$, $p<0.001$; $X^2 = 26.16$, $p<0.001$, respectively). Water level data gathered in July 2021 showed, on average, a 5-6% increase in inundation hours per day in box treatments relative to control plots without boxes (Fig. 1, 14.5±0.6 s.e. vs. 13.6±0.2 s.e. inundation hours per day, Z=-4.03, $p<0.001$) and partial box controls (13.7±0.4 s.e. inundation hours per day, Z=-5.25, $p<0.001$), yet there was similar average inundation time per day across treatments in June 2021 and June 2022 (June 21: Z=1.57, $p=0.260$; Z=1.08, $p=0.530$, June 22: Z=-0.76, $p=0.727$; Z=0.53, $p=0.858$).

However, we observed standing water in boxes at several points during both summer 2021 and 2022 when no standing water was in the partial boxes or control plots, confirming that box treatments were at least intermittently functional in both years (Fig. S1). Inundation hours per day was negatively correlated with the orthometric height of the plots in controls without boxes and partial box treatments, but not in box 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 box and control 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).

Response of Vegetation

Spartina foliosa plots within boxes gained 51% fewer stems than controls without boxes and 43% fewer stems than partial box controls over the course of the summer growing season in 2021 (Fig. 2, Z=-7.10, p<0.001 and Z=-3.10, p=0.006, respectively). In addition, average stem height gained over the course of the experiment was 14% lower in box treatments relative to boxless controls and 13% lower relative to partial box treatments in 2021 (Fig 3, Z=2.79, p=0.015; Z=3.62, p<0.001, respectively). In 2022, *S. foliosa* plots gained 46% fewer stems in box treatments relative to plots without boxes, and 22% fewer stems in partial boxes (Fig. 2, Z=-3.85, p<0.001, Z=-2.00, p=0.112, respectively). We found no treatment effect on change in stem height in 2022 (Fig. 3). We also found that, in box treatments only in both years, *S. foliosa* survival increased with the orthometric height of the plot, significantly so in 2021 (Fig. 4, 2021: R^2=0.68, p=0.012; 2022: R^2=0.61, p=0.067). We observed yearly variation in *S. foliosa* growth and survival that may have resulted in reduced treatment effects in 2022. Plots with boxes, without boxes and with partial boxes gained fewer stems over the course of the growing season in 2022 relative to 2021 (Fig. 2, Z=5.02, p<0.001; Z=5.31, p<0.001; Z=5.15, p<0.001). Also, change in *S. foliosa* height within control plots without boxes and partial box control plots in 2022 was significantly less than the year prior (Fig. 3, Z=-3.52, p<0.001; Z=3.23, p<0.001). The amount of belowground biomass per plot in boxes did not differ from boxless and partial box controls at the end of the experiment in August 2022 (t=-2.06, p=0.128; t=-1.83, p=0.201).

Response of Soil Characteristics and Benthic Microalgae

In 2021, redox potential at the end of the experiment was significantly lower in box plots relative to controls without boxes, and tended to be lower than partial box treatments as well (Fig. 5, mean of -115±15 s.e. in boxes vs. -127±10 s.e. and -117±35 s.e., t=-2.90, p=0.020; t=2.23, p=0.086). Redox potential did not vary between box and no box or partial box treatments in 2022 (t=0.07, p=0.998; t=-1.51 p=0.305). Ammonium concentrations were significantly higher in boxes relative to both controls without boxes and with partial boxes in 2021 (Fig. 6, t=2.52, p=0.048; t=2.52, p=0.048), but concentrations did not vary between box and control treatments in 2022 (Fig. 6, t=0.68, p=0.778; t=-0.02, p=0.999). On average, ammonium was higher in 2022 across box, no box, and partial box treatments relative to 2021 (t=-31.78, p<0.001; t=-31.10, p<0.001; t=-31.24, p<0.001). Sulfide concentrations were significantly higher in both box and partial box treatments in 2021 relative to controls (Fig 7, Z=3.28, p=0.003; Z=-3.41, p=0.002), yet we found no difference between boxes and controls in 2022 (box-no box: Z=-0.89, p=0.649; box-partial: Z=-1.60, p=0.247). Chlorophyll *a* concentration tended to be lower in boxes in 2021 relative to controls without boxes (Fig. 8, t=-2.39, p=0.057). There was no evidence of treatment effects in 2022, yet on average significantly lower chlorophyll *a* concentration in 2022 relative to 2021 across treatments (box: t=2.02, p=0.049; partial box: t=4.35, p<0.001; no box: t=3.76, p<0.001).

Bird Prey Items – Insects and Soil Infauna

In total, we identified 6,991 insect specimens collected at the end of the summer in 2021 and 1,505 specimens collected at the end of the summer in 2022. On average, there were significantly more insects in 2021 across treatments in the *S. foliosa* habitat despite the same effort, largely driven by an abundance of Chironomids and *Prokelisia* sp, or planthoppers (box: mean of 74±29 s.e. total insects per plot in 2021 vs. 24±8 s.e. in 2022, $Z=2.91$, $p=0.004$; no box: mean of 55±18 s.e. in 2021 vs. 20±6 s.e. in 2022, $Z=2.18$, $p=0.029$; partial box: mean of 59±20 s.e. in 2021 vs. 21±7 s.e. in 2022, $Z=2.47$ $p=0.014$). Comparison among control plots in the higher elevation *S. pacifica* zone revealed more insects in areas with *S. foliosa* relative to areas where *S. pacifica* is dominant, with, on average, 13±4 s.e. insects in *S. pacifica* vs. 55±18 s.e. insects in *Spartina* in 2021, and 8±2 s.e. insects in *S. pacifica* and 20±6 s.e. insects in *S. foliosa* in 2022 (2021: $Z=3.73$, $p<0.001$; 2022: $Z=2.91$, $p=0.004$). During an emergence event in 2021, we observed, on average, 41% more chironomids in box treatments relative to plots without boxes, and 33% more chironomids in boxes relative to plots with partial boxes (Fig. 9, $t=3.29$, $p=0.009$; $t=2.75$, $p=0.028$). Chironomid abundance data gathered within two weeks of that date during 2022 revealed significantly fewer chironomids across treatments relative to 2021 (box: $t=3.02$, $p=0.004$, partial: $t=2.19$, $p=0.032$, no box: $t=2.26$, $p=0.027$), and no difference between box and partial box, or box and control treatments. We found, on average, 81% fewer *Prokelisia* sp., or plant hoppers, in inundation treatments relative to partial boxes and 44% fewer relative to plots without boxes in 2021 (Fig. 10, $Z=-9.23$, $p<0.001$; $Z=-3.18$, $p=0.004$), but no treatment effects in 2022. There were fewer planthoppers on average in partial treatments in 2022 relative to 2021 ($Z=3.04$, $p=0.002$). We found no significant difference in oligochaete abundance in boxes relative to controls without boxes and partial box controls in 2021 (t=-0.72, p=0.756; t=-0.94, p=0.618, respectively) or 2022 (t=0.74, p=0.739; t=2.21, p=0.086). Similarly, amphipod abundance did not change in the presence of boxes compared with partial boxes and plots without boxes in either 2021(t=0.94, p=0.623; t=-0.35, p=0.934) or 2022 (t=-0.90, p=0.648; t=-0.51, p=0.867).

Bird Abundance and Use of Habitat

We identified a total of 53 bird species across the three habitat types surveyed in 2021 and 2022 (Fig. S2). Of those 53 species, three were present in one or both of the non-mudflat habitats, low marsh cordgrass or slightly higher elevation pickleweed plain, during most surveys: Song Sparrow, Marsh Wren, and Common Yellowthroat. In 2021, Song Sparrows were 53% more abundant in the low marsh cordgrass habitat compared with the higher elevation pickleweed plain (Fig. 11, Z=3.04, p=0.002). In the low marsh cordgrass habitat in particular, song sparrow abundance was 37% higher in 2021 than in 2022 (Z=1.99, p=0.047). Song sparrow abundance did not change from 2021 to 2022 in the higher elevation pickleweed plain habitat (Z=0.16, p=0.873).

Discussion

Overall, we found that marsh boxes increased inundation, altering the physical environment and negatively affecting *S. foliosa*, which had variable effects on invertebrate and insect prey for birds within the *S. foliosa* habitat. Birds responded negatively to shorter and less dense cordgrass in 2022, suggesting that decreased habitat integrity with sea-level rise in conjunction with changes to prey items may significantly impact bird abundance and distribution.

Marsh boxes successfully increased inundation and increased percent of time inundated per day from 57% to 60%. Boxes increased hours inundated per day in box treatments by ~6% in July, but water level data in June 2021 and 2022 revealed no difference in inundation hours per day in boxes relative to controls. However, we observed boxes holding water at various times during summer 2021 and 2022 (Fig. S1), suggesting that the inundation treatment, although variable, was present intermittently throughout both summers. Regardless, even at peak functionality of the boxes, the increase in inundation we achieved is far below what is expected in a local 2050 sea-level rise scenario, which predicts a doubling of inundation time relative to MHHW (10-19%, Janousek et al. 2016).

Despite the modest increase in inundation, and consistent with our hypothesis, we found that *S. foliosa* responded negatively to increased inundation, although these effects varied by year. The increase in *S. foliosa* stem density and height over the course of the growing season in 2021 was significantly less in box treatments relative to controls without boxes and/or partial boxes. However, there was generally less dense and shorter *S. foliosa* in 2022 making significant treatment effects harder to capture. Notably, we found that *Spartina* survival within box treatments was largely dependent on the elevation of the plot; stems in higher elevation plots tended to have higher survival than in lower elevation plots (Fig. 4). These data can be used to determine optimal planting locations to establish *S. foliosa* in restoration sites so that it may persist with sea-level rise. This information can 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 ~6% increase in inundation time, managers may consider planting *S. foliosa* higher than ~0.97m to achieve full growth potential in a salt marsh with similar characteristics as this site.

The decreased number of *S. foliosa* stems and height were likely driven by the increased inundation and subsequent decreased oxygen and cascading changes in the sediment in 2021. Redox potential was lower in 2021 in inundated plots, and these low oxygen conditions may have contributed to higher 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 & 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 & Fennessy 2001, Koch & Mendelssohn 1989). Despite high levels of ammonium in 2022 relative to the year prior, *S. foliosa* was relatively shorter and less dense. This could be due to variability in weather patterns from year to year affecting wave energy and sediment deposition, as previous studies found correlations between shorter and less dense *S. foliosa* and increased wave energy and reduced accretion (Swales et al. 2004). Fewer or more stressed *S. foliosa* could have resulted in decreased uptake of ammonium.

Aquatic insects serve as critical components of salt marsh food webs and act as an important trophic link between aquatic and surrounding terrestrial systems (LaSalle and Bishop 1987). Insects in tidal marshes are consumed by both tidal marsh birds and spiders (Cameron 1972, Throckmorton 1989, Giberson et al. 2001). We found that Chironomid abundance was higher in plots with increased inundation in 2021, and we found significantly lower Chironomid abundance across treatments in 2022. As larval Chironomids can be both herbivores and saprovores (Butakka et al. 2016), abundances have been highest during peak periods of plant productivity and litter accumulation. These periods also likely coincide with emergence as adults

(Cameron 1972). Chironomids spend their larval stage in the sediment and require water to emerge. The pupa ascends, swimming to the surface of the water, after which it emerges (Oliver 1971). Variation in emergence relies on the length of larval period, which is influenced by water level, temperature, oxygen concentration and photoperiod (Armitage 1995). As such, increased inundation duration may have positively influenced the number of chironomid larvae that successfully emerged. Infaunal samples collected after insect trap data each year revealed very few insect larvae, suggesting that emergence had occurred prior to soil core collection. Conversely, we found fewer planthoppers in inundated treatments in 2021. Planthoppers, that do not have an aquatic larval stage, may have been negatively impacted by reduced *S. foliosa* stem density and height in inundated treatments, since it feeds exclusively and reproduces on cordgrass (Denno et al. 1987; Denno et al. 1996). Chironomid larvae are found in and consume benthic microalgal mats that commonly occur in sparsely vegetated areas of the marsh (Goldfinch and Carman 2000; Levin and Talley 2002), which could explain the slight reduction of microalgal biomass on the sediment surface in boxes in 2021. We found no changes to soil infauna (amphipods and oligochaetes) in response to inundation, which may be due to inadequate levels of inundation duration to affect a response, variability in invertebrate abundance within the treatment plots, or the slower responses of these species to the experimental changes.

Bird surveys revealed a preference of Song Sparrows for *S. foliosa* habitat relative to the higher elevation pickleweed plain at this site. Within the *S. foliosa* habitat, Song Sparrows were located primarily in the transitional area that is still mostly composed of cordgrass yet directly adjacent to *S. pacifica*, so they had easy access to both habitats. Their preference may be due to higher availability of insects in *S. foliosa* vs. *S. pacifica* habitat, as well as seasonal access to *S. foliosa* seeds for consumption. We noticed fewer Song Sparrows in 2022, potentially due to a generally shorter and less dense *S. foliosa* population. We observed Song Sparrows eating *S. foliosa* seeds post-flowering in 2021, so changes to their abundance in 2022 may be due to lower food availability from fewer seeds or less ideal habitat due to reduced *S. foliosa* density and height. Fewer chironomids in 2022 may also have contributed to reduced abundance of Song Sparrows. Unfortunately, there is little information on temporal variation in Song Sparrow use of tidal marsh habitat. Future studies should examine how bird distributions are impacted by variability in habitat availability and seed abundance from less and more successful plant growing seasons, and changes to prey items.

The quantitative responses to inundation that we describe here can be used to parameterize models that predict future responses to sea-level rise. For example, models that predict bird distributions often are based on models of vegetation responses, like habitat suitability models based on sea-level rise projections (Veloz et al. 2013). However, factors that aren't included in models like small-scale decreases in density or height of plants, as well as prey items, may have large effects on how birds are distributed. Change in *S. foliosa* height and density in box treatments in 2021 was similar to height and density across treatments in summer 2022. Song Sparrows in *S. foliosa* habitats tend to be absent from *S. foliosa* that is less than ~45cm, and pairs are found further apart in shorter vegetation (Marshall 1948). If shorter *S. foliosa* does indeed correlate with fewer Song Sparrows, we might see similar reductions in Song Sparrow use if greater inundation with sea-level rise results in shorter and less dense *S. foliosa*. Incorporating measurements of plant density and vertical growth, as well as bird prey abundance and distribution, like planthoppers and chironomids, into models that evaluate effects of future sea-level rise on bird distributions, would make these models more ecologically relevant. This detailed vegetation data can be achieved through finer resolution aerially imagery provided by unmanned aerial vehicles (Klemas 2015). It is also important to track bird food availability through time and under multiple inundation scenarios. Song Sparrows may benefit from higher chironomid numbers due to inundation in the short term. However, increasingly longer inundation with sea-level rise may reach a point beyond which *S. foliosa*, without access to upland areas for migration, is extirpated. The loss of this habitat may outweigh any benefits of greater Chironomid abundances for Song Sparrows.

Conclusion

In closing, this study supplies evidence that increased inundation can have significant negative impacts on tidal marsh foundation species by altering the physical environment. As we found here, even small increases in inundation can affect the physical environment in tidal marshes and consequently *S. foliosa* growth and abundance. This is especially concerning because in certain areas in San Francisco Bay, *S. foliosa* occurs frequently at tidal elevations below which it is most productive, perhaps due to competition from *S. pacifica* encroaching on the higher end of its elevational distribution (Janousek et al. 2016). Importantly, in large, urban estuaries like San Francisco Bay, *S. foliosa* may not have available upland area to migrate as sea levels rise. The loss of this crucial habitat, combined with increasingly stressful environmental conditions due to inundation, may significantly impact the abundances of resident species, consequently altering the trophic structure of tidal marsh ecosystems.

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Figure Captions

Figure 1. Mean inundation hours per day across treatments in July 2021 (N=7 for no box and partial box treatments, and N=8 for box treatments). Error bars represent ±1 standard error about the mean. Letters denote significance at $p<0.05$)

Figure 2. Bars represent mean change in *Spartina* stem density (number of stems/0.5m^2) from July through August each year for each treatment. Error bars show ±1 standard error about the mean, and asterisks show significant differences between treatments.

Figure 3. Bar plot representing the average change in *Spartina* stem height (average of ten tallest stems) from June through August in 2021 and 2022 across treatments, denoted by color. Error bars represent ±1 standard error about the mean and asterisks show significant differences among treatments.

Figure 4. The linear relationship between shoot density at the end of the summer and the orthometric height of plots during (A) 2021 and (B) 2022. Each point represents one plot. The R^2 and p-values for each linear regression are shown on the plot.

Figure 5. Bars show mean redox potential across treatments at the end of the summer in 2021 and 2022. Error bars are ±1 standard error about the mean and asterisks show significant differences.

Figure 6. Barplots showing mean concentration of ammonium across treatments (denoted by colored bars) in both years of the experiment. Error bars represente ±1 standard error about the mean. Asterisks show significant differences in ammonium among treatments and years.

Figure 7. Boxplot showing mean sulfide concentrations at the end of the experiment across treatments in each year. Error bars represent ±1 standard error about the mean and asterisks show significant differences among treatments and years.

Figure 8. Bars represent mean chlorophyll *a* concentrations as a proxy for microalgal biomass on the sediment surface, across treatments and years. Colored bars show different treatments and error bars denote ±1 standard error about the mean. Asterisks show differences across years.

Figure 9. Bars represent Chironomid density, or mean number of Chironomids per $310cm^2$ trap. Error bars denote ±1 standard error about the mean, and asterisks show significant changes to density across treatments and years at $p<0.05$.

Figure 10. Bars represent *Prokelesia* sp., or planthopper, density as number of planthoppers per $310cm^2$ trap. Error bars show ±1 standard error, and asterisks denote significant differences among treatments and years at $p<0.05$.

Figure 11. Mean song Sparrow density (number of Song Sparrows per hectare per hour) in lower elevation cordgrass habitat (low marsh) and mid/high elevation pickleweed plain (mid/high marsh) in 2021 and 2022. Error bars represent variability in sampling dates, at ±1 standard error about the mean. Asterisks denote significant *p* values at <0.05, also shown below the plot.

Figure 12. A conceptual diagram using data from figure 4 to suggest optimal elevations for *Spartina* planting and survival with sea-level rise.

Figures

Figure 1

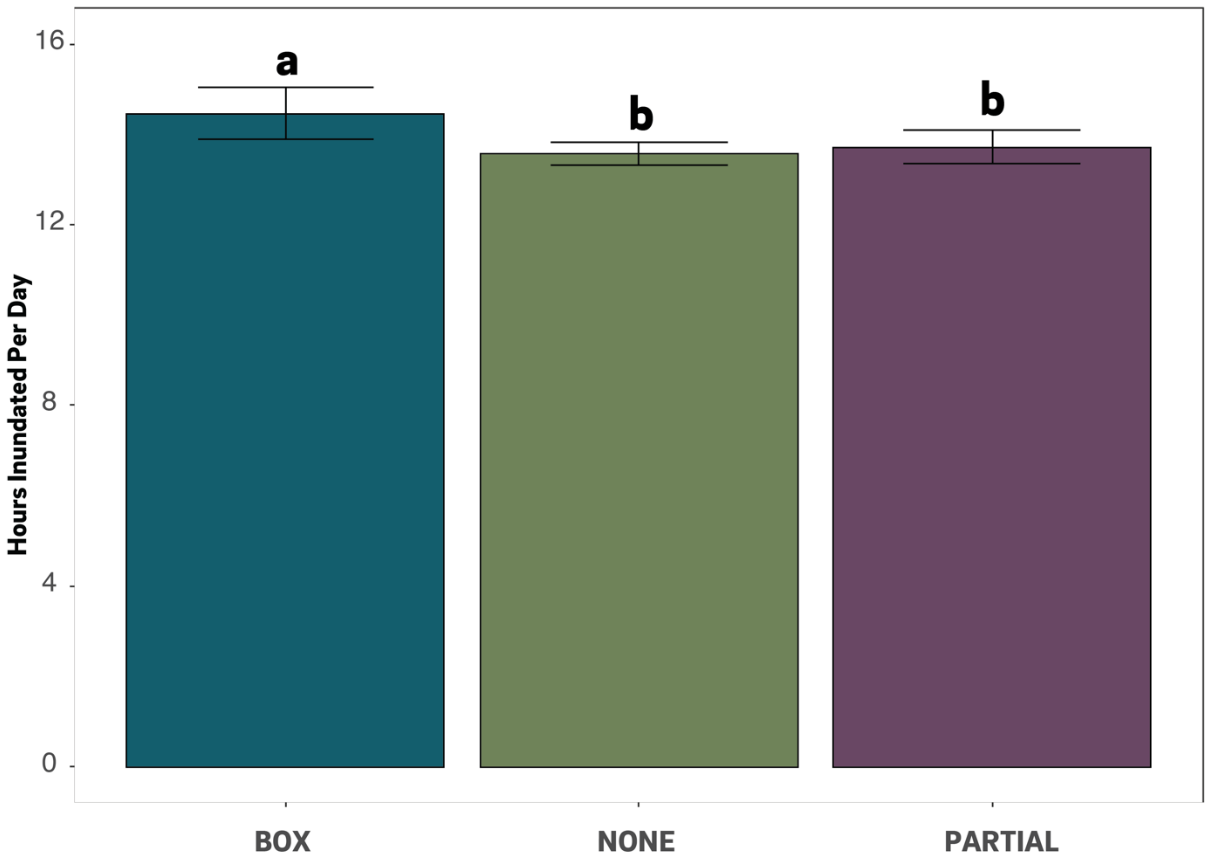


Figure 2

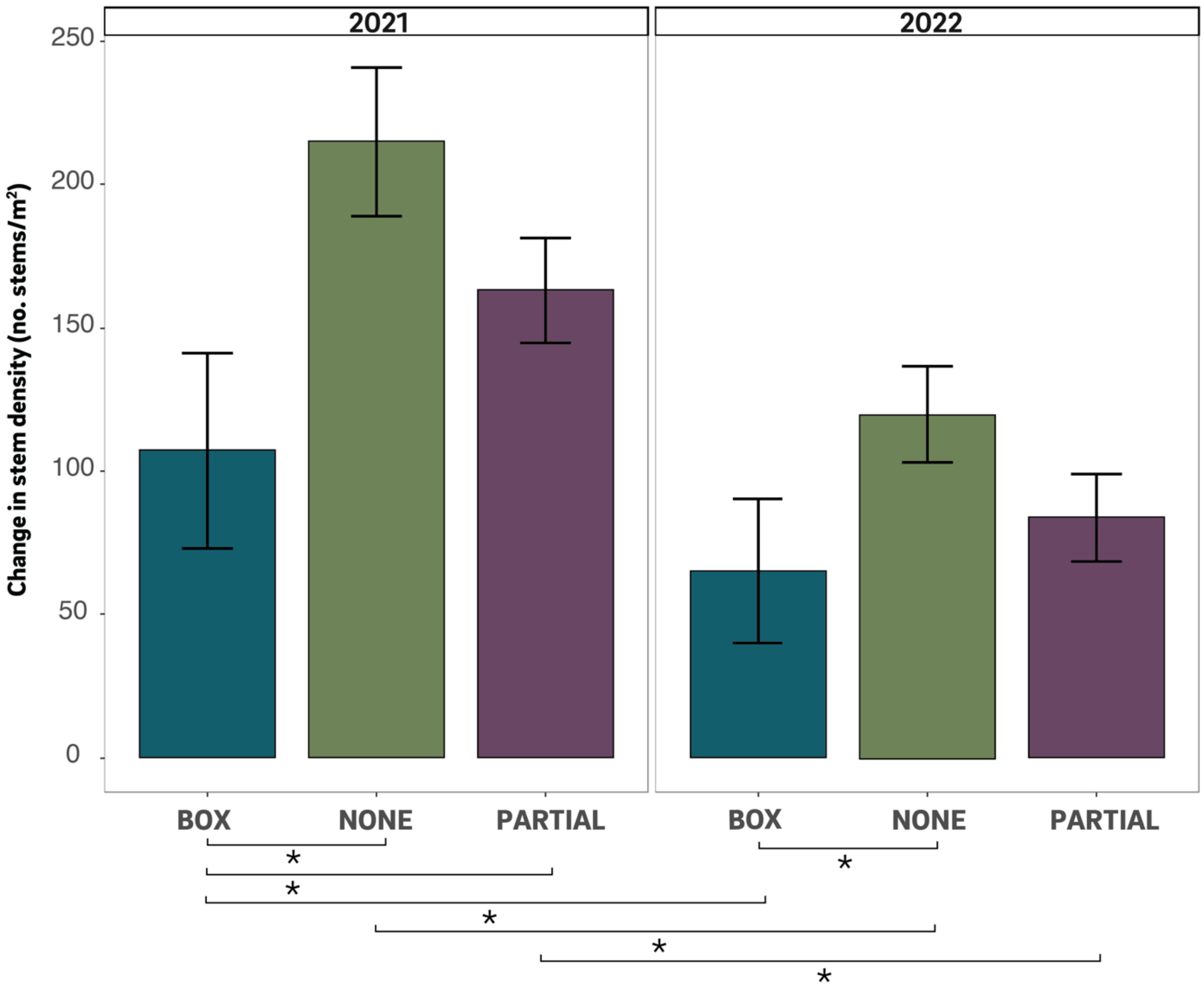

2021
2022
250
200
150
100
50
0
Change in stem density (no. stems/m²)
BOX
NONE
PARTIAL
BOX
NONE
PARTIAL
*
*
*
*
*
*
*

Figure 3

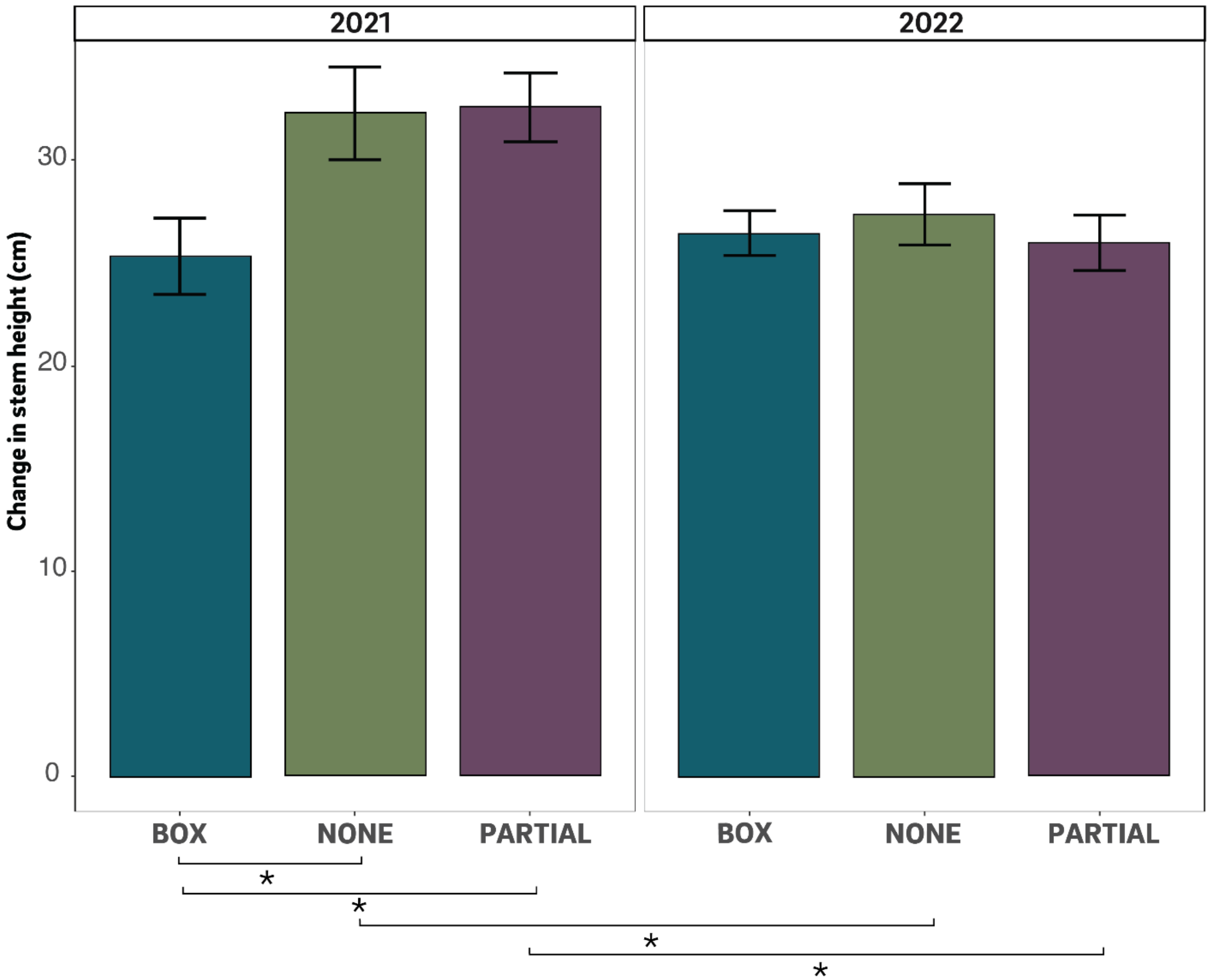
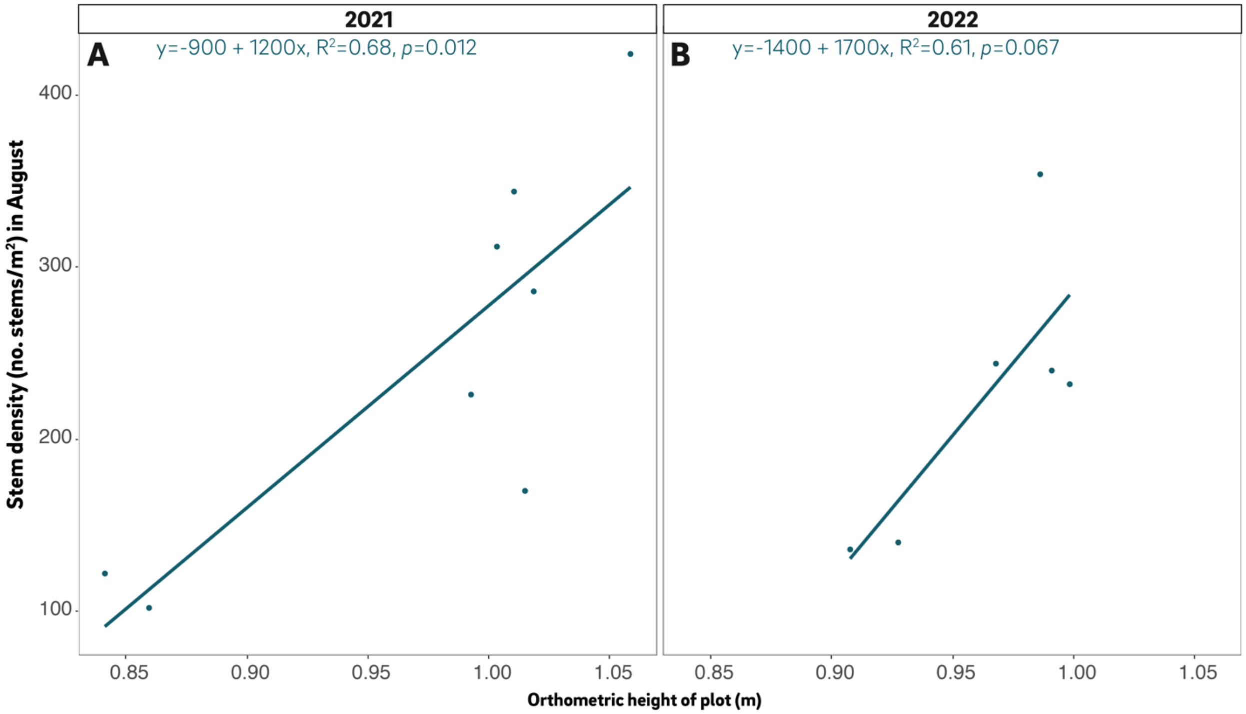

2021
2022
Change in stem height (cm)
30
20
10
0
BOX
NONE
PARTIAL
BOX
NONE
PARTIAL
*
*
*
*

Figure 4



2021
2022
A
y=-900 + 1200x, R²=0.68, p=0.012
B
y=-1400 + 1700x, R²=0.61, p=0.067
400
300
200
100
Stem density (no. stems/m²) in August
0.85
0.90
0.95
1.00
1.05
Orthometric height of plot (m)

Figure 5

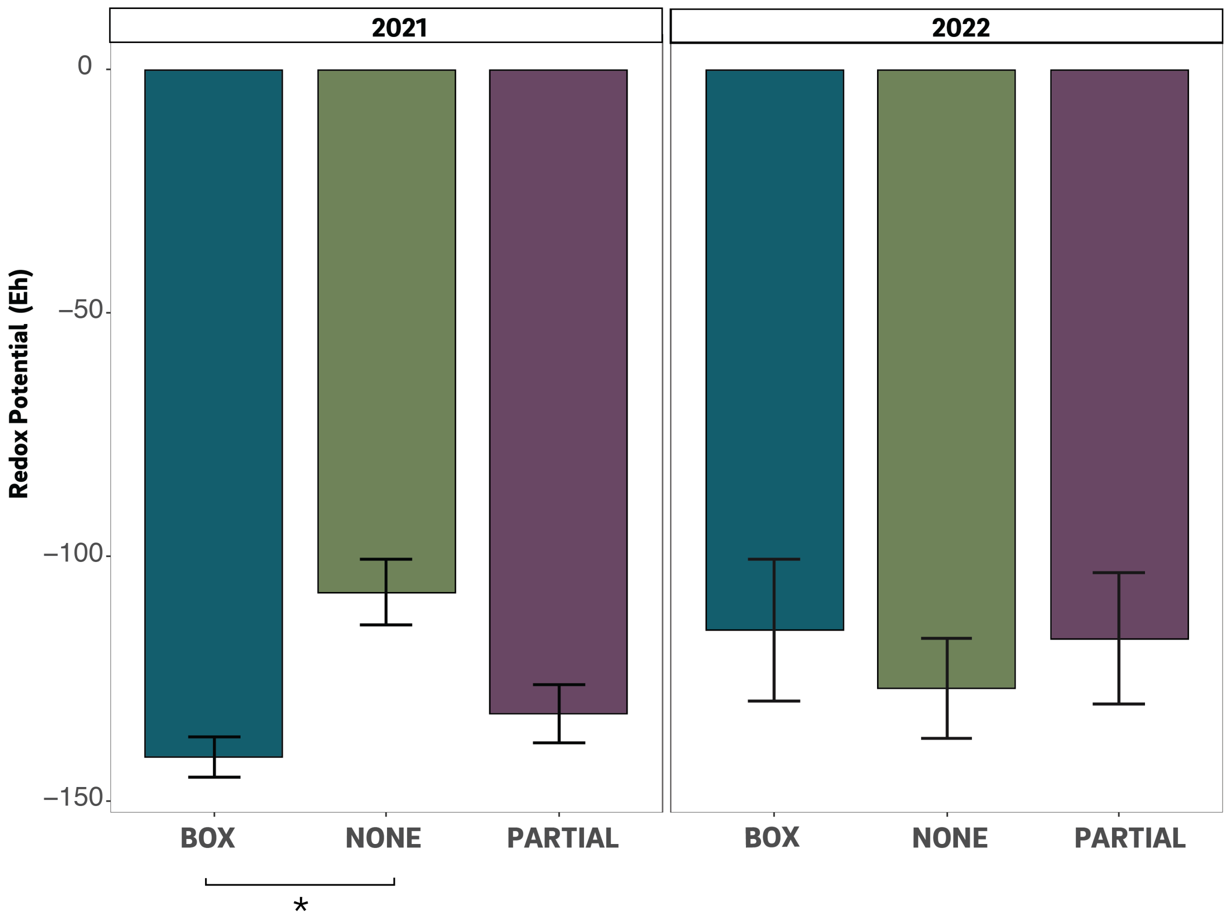

2021
2022
0
−50
−100
−150
Redox Potential (Eh)
BOX
NONE
PARTIAL
BOX
NONE
PARTIAL
*

Figure 6

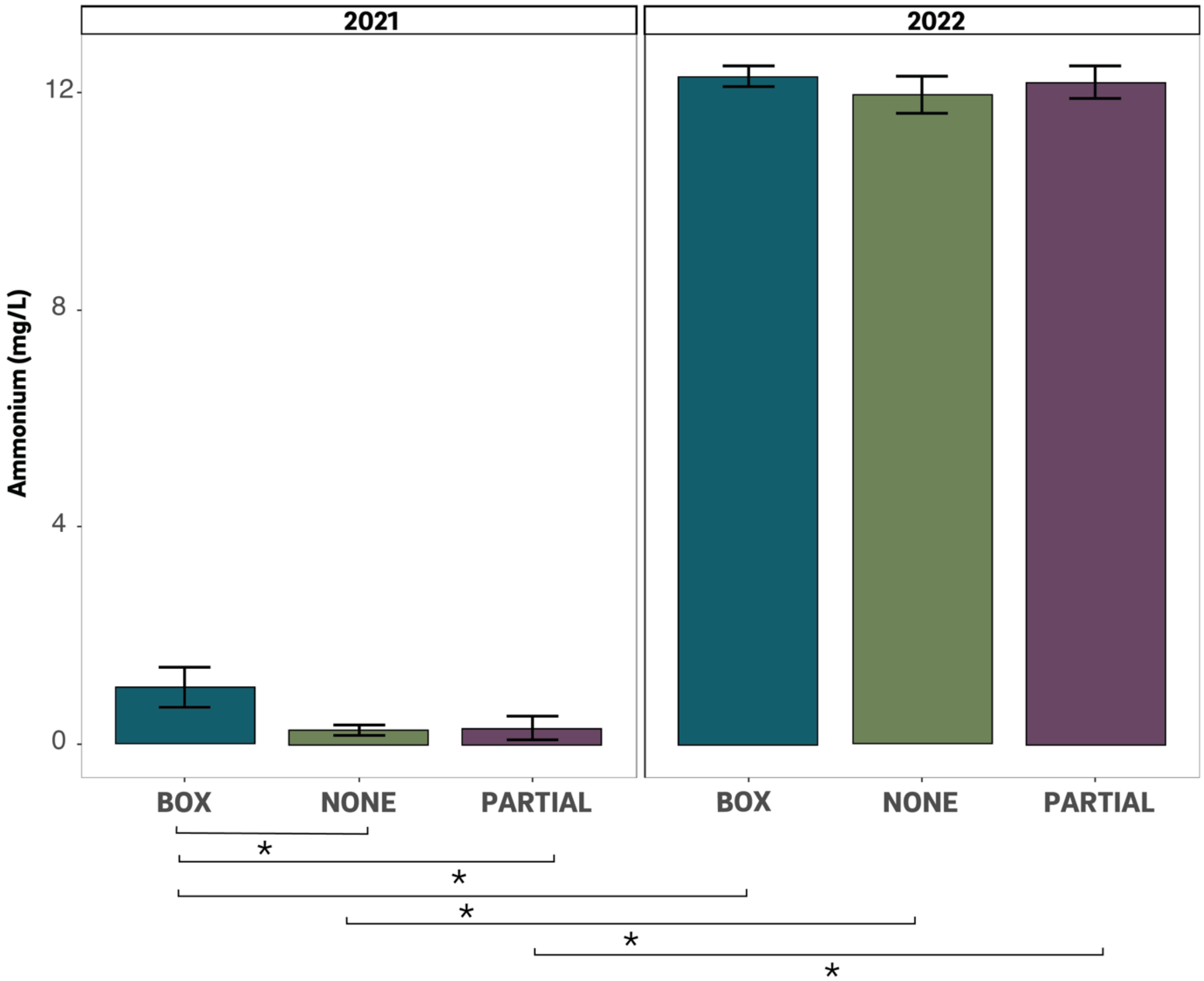

2021
2022
Ammonium (mg/L)
12
8
4
0
BOX
NONE
PARTIAL
BOX
NONE
PARTIAL
*
*
*
*
*

Figure 7

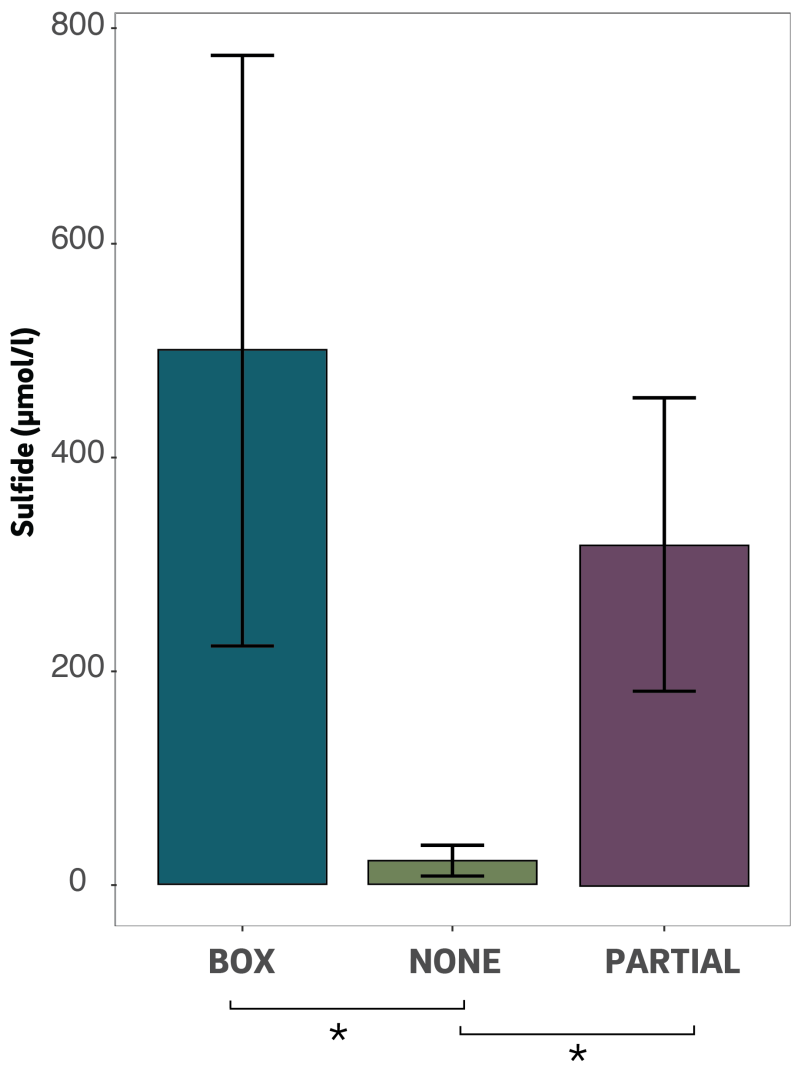


Figure 8

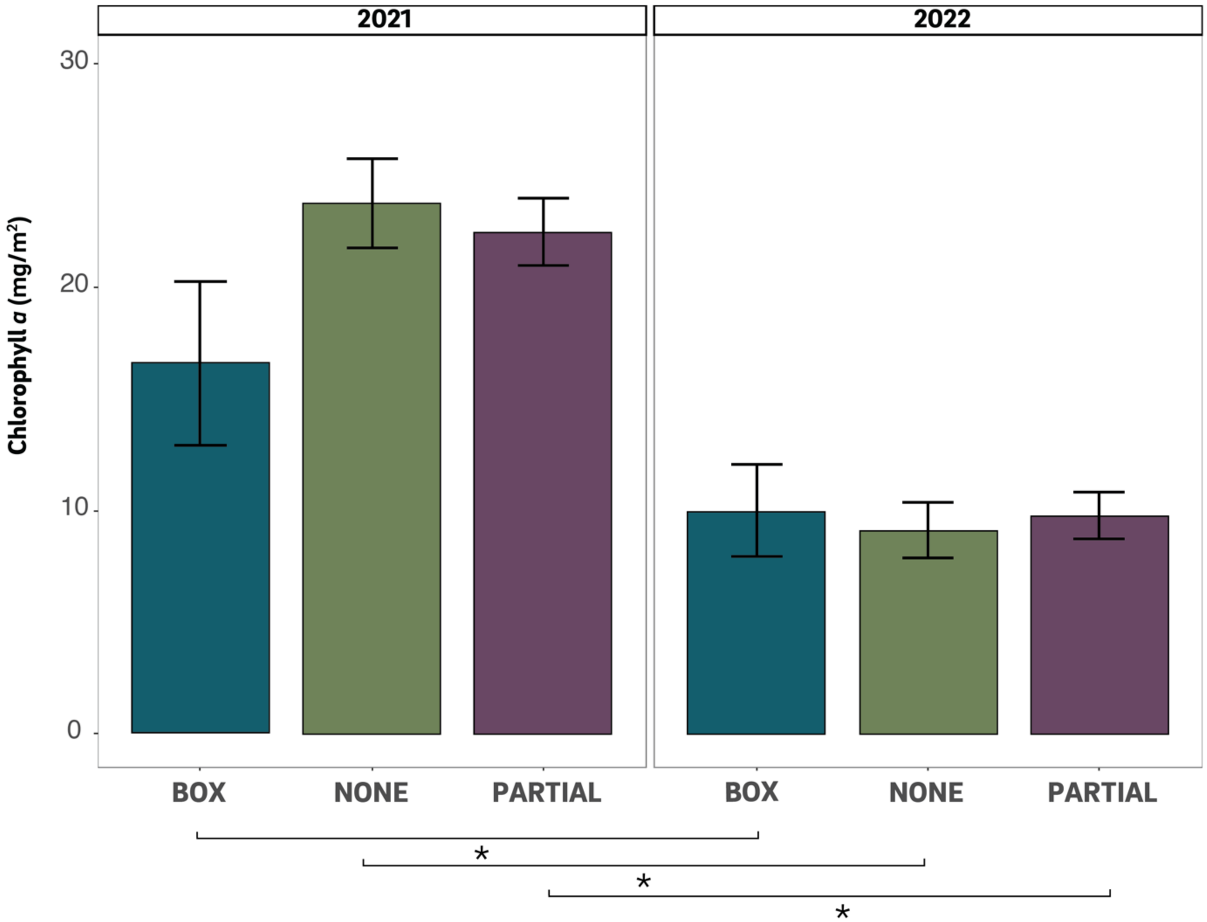

2021
2022
Chlorophyll a (mg/m²)
30
20
10
0
BOX
NONE
PARTIAL
BOX
NONE
PARTIAL
*
*
*

Figure 9

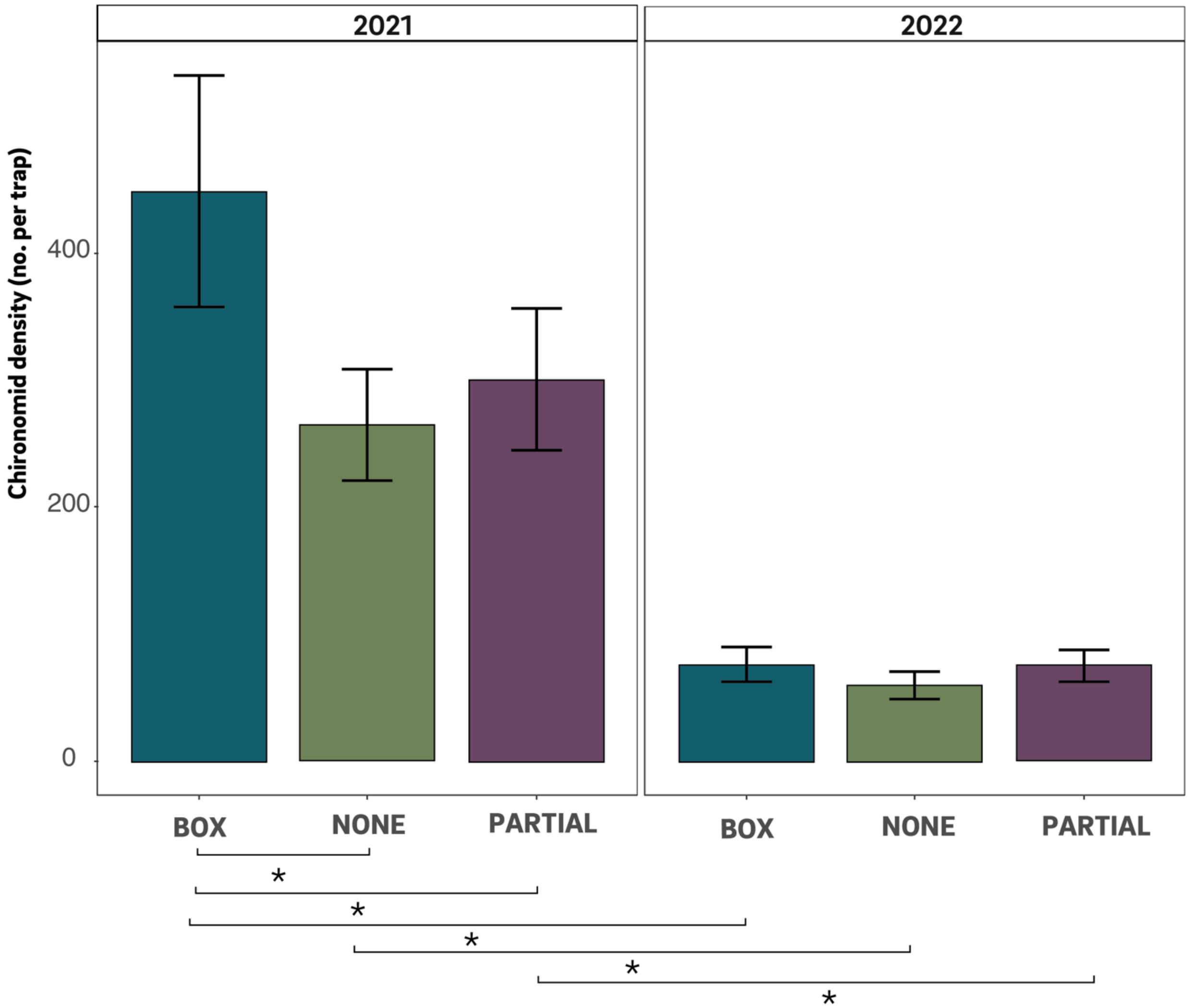

2021
2022
Chironomid density (no. per trap)
400
200
0
BOX
NONE
PARTIAL
BOX
NONE
PARTIAL
*
*
*
*
*

Figure 10

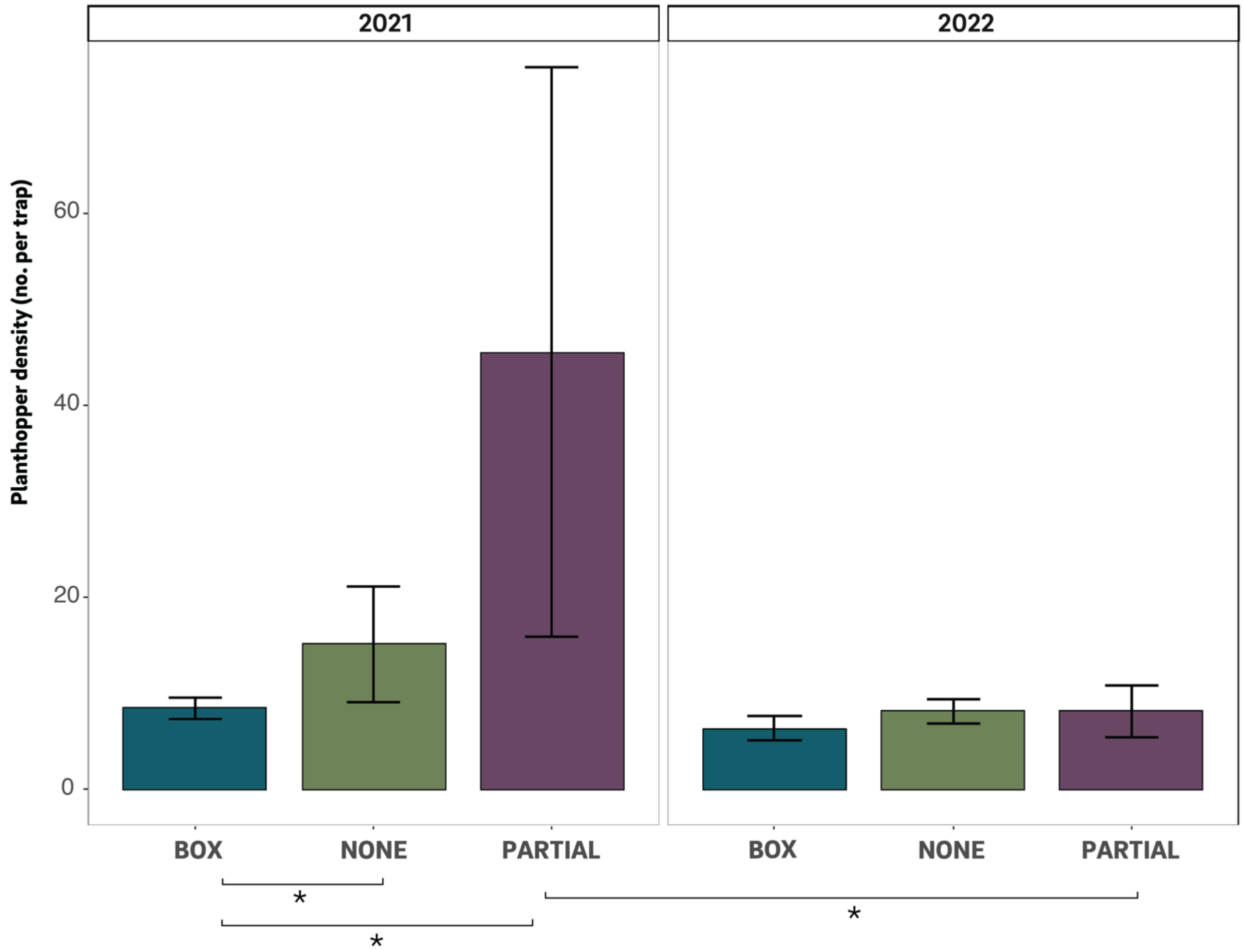

2021
2022
Planthopper density (no. per trap)
60
40
20
0
BOX
NONE
PARTIAL
BOX
NONE
PARTIAL
*
*
*

Figure 11

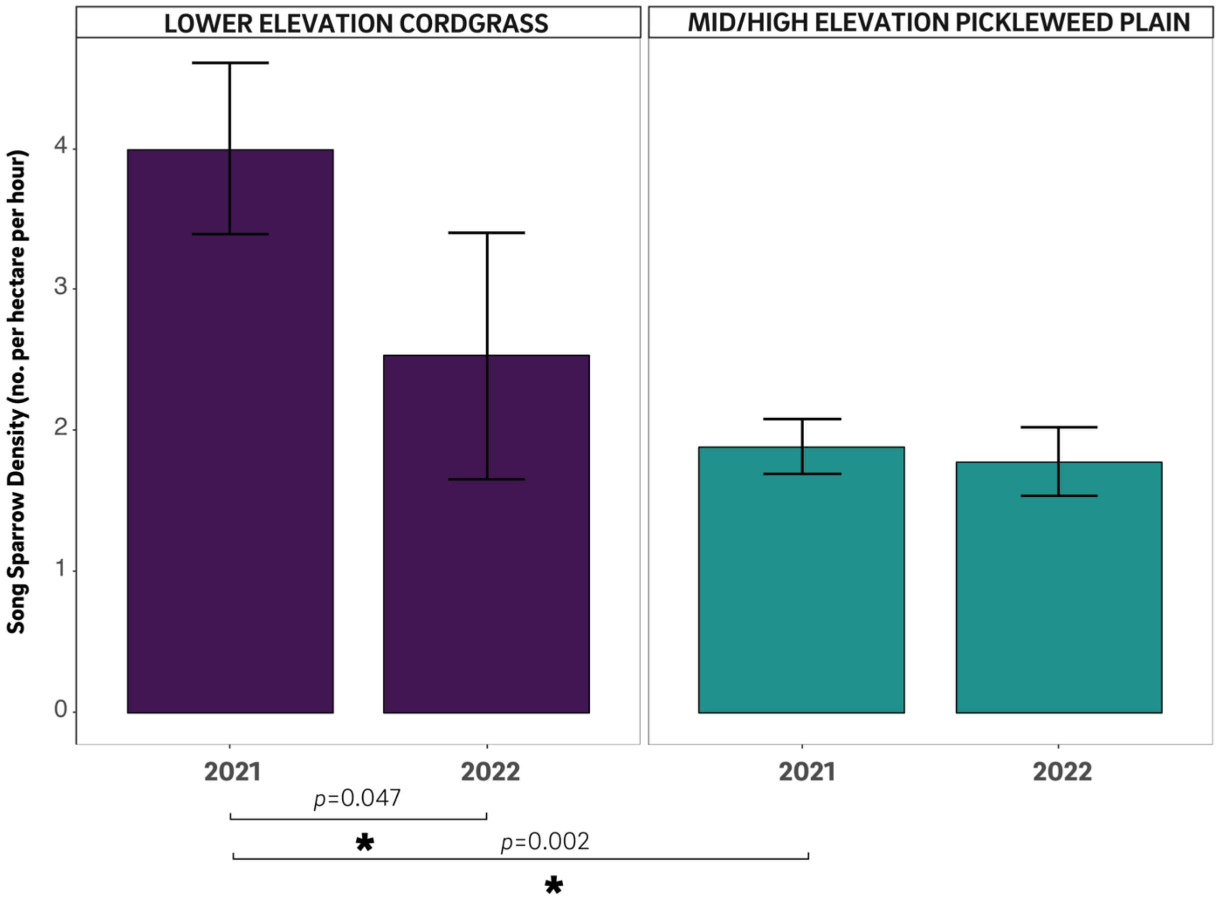
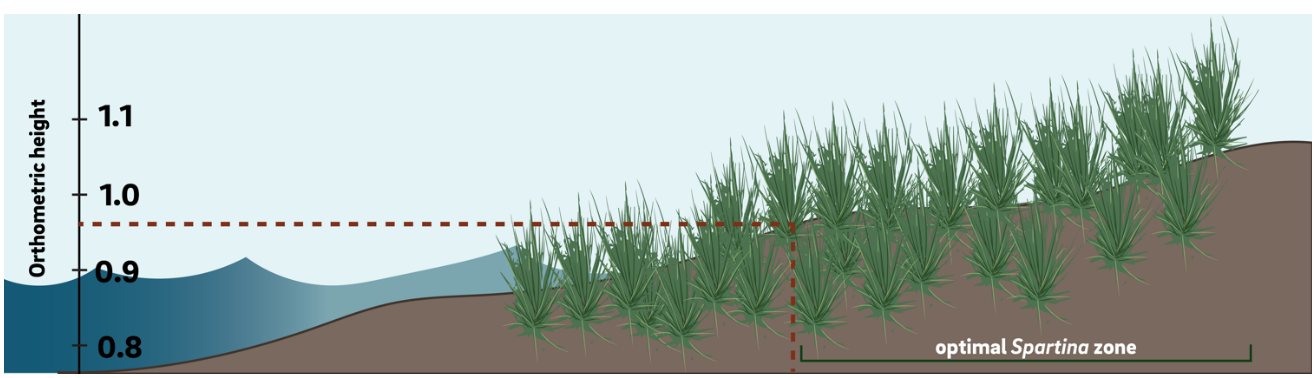


Figure 12



Appendices

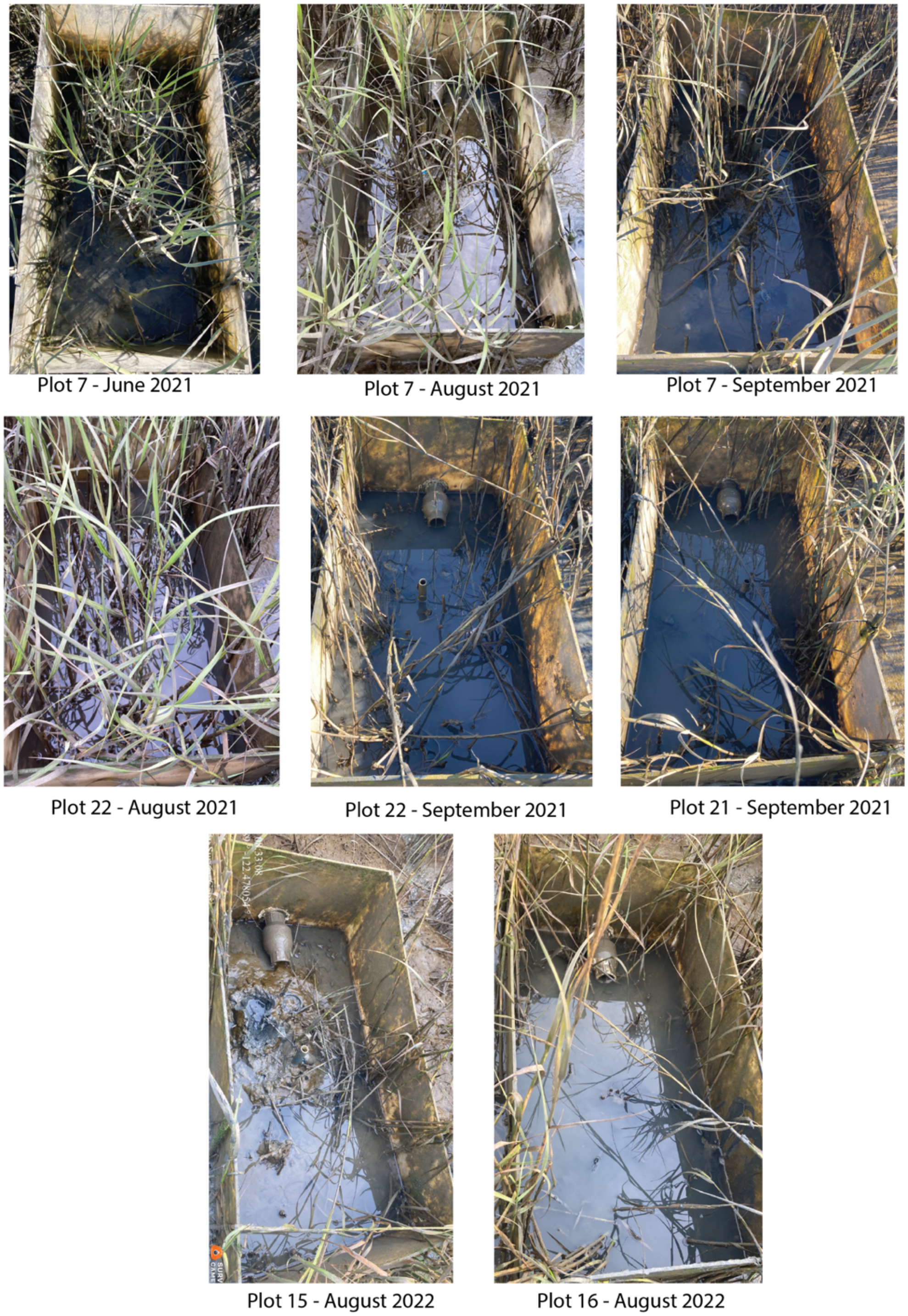


Figure S1. Photos of boxes retaining water throughout the two-year experiment, taken after the tide receded during a negative tide series.

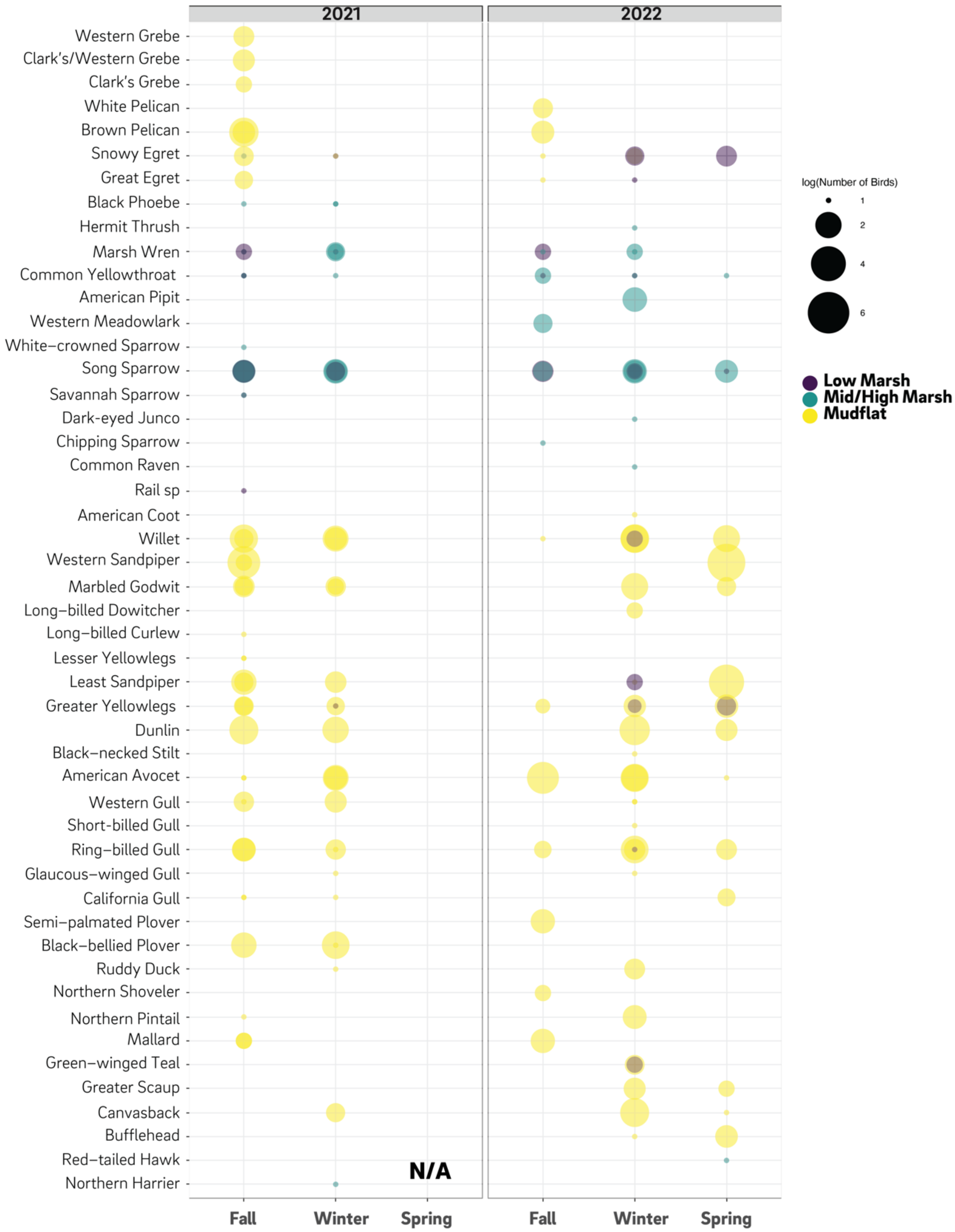


Figure S2. Bird species identified in three different habitats (low marsh, mid/high marsh and mudflat) across three seasons in 2021 and 2022, organized by family. Size of points imply the natural log of the number of total birds per sample date.

Table S1. Table outlining all statistical models discussed in manuscript. SE = standard error, DF=degrees of freedom. Bolded p-values highlight significant values.

Response Variable	Model	Fixed factor	Random Effect	Distribution	Comparison	Estimate	SE	DF	Test	Score value	p-value
Inundation hours per day	GLMM	Treatment *Cycle Elevation	Block:Cycle	Gamma	Treatment	NA	NA	2	X2	12.319	**0.002114**
					Cycle	NA	NA	2	X2	108.906	**2.20E-16**
					Elevation	NA	NA	1	X2	53.483	**2.61E-13**
					Treatment*Cycle	NA	NA	4	X2	25.096	**4.81E-05**
					July 2021, Box vs. None	-0.003875	0.000905	Inf	Z score	-4.281	**0.0001**
					July 2021, Box vs. Partial	-0.004811	0.000918	Inf	Z score	-5.241	**<.0001**
					July 2021, None vs. Partial	-0.000936	0.001003	Inf	Z score	-0.934	0.619
					June 2021, Box vs. None	0.001878	0.001261	Inf	Z score	1.49	0.2959
					June 2021, Box vs. Partial	0.001373	0.001329	Inf	Z score	1.033	0.556
					June 2021, None vs. Partial	-0.000504	0.001318	Inf	Z score	-0.382	0.9225
					June 2022, Box vs. None	-0.001299	0.001419	Inf	Z score	-0.916	0.6304
					June 2022, Box vs. Partial	0.000701	0.001364	Inf	Z score	0.513	0.8648
					June 2022, None vs. Partial	0.002	0.001491	Inf	Z score	1.341	0.3725
Temperature (ºC)	GLM	Treatment	None	Gamma	Box vs. None	5.93E-05	0.000586	Inf	Z score	0.101	0.9944
					Box vs. Partial	1.03E-03	0.00074	Inf	Z score	1.389	0.3467
					None vs. Partial	9.69E-04	0.00077	Inf	Z score	1.257	0.4195
Light Intensity (lumens)	GLM	Treatment	None	Gamma	Box vs. None	0.0289	0.23	Inf	Z score	0.126	0.9913
					Box vs. Partial	-0.054	0.294	Inf	Z score	-0.184	0.9815
					None vs. Partial	-0.0829	0.306	Inf	Z score	-0.271	0.9603
Change in Stem density from June - August + 47 (accounts for negative values)	GLMM	Treatment *Year	Block:Year	Poisson	2021, Box vs. None	-0.393	0.0392	Inf	Z score	-10.04	**<.0001**
		Elevation Inundation hours per day	Year		2021, Box vs. Partial	-0.184	0.0426	Inf	Z score	-4.321	**<.0001**
					2021, None vs. Partial	0.209	0.0386	Inf	Z score	5.417	**<.0001**
					2022, Box vs. None	-0.362	0.0684	Inf	Z score	-5.299	**<.0001**
					2022, Box vs. Partial	-0.196	0.0688	Inf	Z score	-2.847	0.0123
					2022, None vs. Partial	0.166	0.0748	Inf	Z score	2.224	0.0671
					Box, 2021 vs. 2022	0.898	0.164	Inf	Z score	5.464	**<.0001**
					None, 2021 vs. 2022	0.928	0.163	Inf	Z score	5.71	**<.0001**
					Partial, 2021 vs. 2022	0.886	0.162	Inf	Z score	5.478	**<.0001**
Change in Stem Height from June - August	GLMM	Treatment *Year Elevation Inundation hours per day	Block:Year Year	Gamma	2021, Box vs. None	0.005449	0.00216	Inf	Z score	2.527	**0.0309**
					2021, Box vs. Partial	0.00658	0.00215	Inf	Z score	3.058	**0.0063**
					2021, None vs. Partial	0.001132	0.00193	Inf	Z score	0.587	0.8269
					2022, Box vs. None	-0.002943	0.00311	Inf	Z score	-0.945	0.6117
					2022, Box vs. Partial	-0.002005	0.0031	Inf	Z score	-0.647	0.7938
					2022, None vs. Partial	0.000937	0.00343	Inf	Z score	0.273	0.9597
					Box, 2021 vs. 2022	-0.00624	0.0039	Inf	Z score	-1.601	0.1093
					None, 2021 vs. 2022	-0.01463	0.0038	Inf	Z score	-3.85	**0.0001**
					Partial, 2021 vs. 2022	-0.01482	0.00365	Inf	Z score	-4.056	**<.0001**
Belowground Biomass (mass/plot) (Square Root Transformed)	LMM	Treatment Inundation hours per day	Block	Normal	Box vs. None	-2.627	1.166	17.4	t ratio	-2.253	**0.09**
					Box vs. Partial	-2.029	0.953	12.1	t ratio	-2.128	0.1251
					None vs. Partial	0.598	0.955	13.9	t ratio	0.627	0.8081
Redox Potential	LMM	Treatment *Year			2021, Box vs. None	-38.595	13.3	25.1	t ratio	-2.901	**0.0202**

		Inundation hours per day	Block:Year	Normal	2021, Box vs. Partial	-9.361	13.3	27.4	t ratio	-0.705	0.7629
					2021, None vs. Partial	29.233	13.1	25.9	t ratio	2.225	0.0856
					2022, Box vs. None	0.929	14.1	28.9	t ratio	0.066	0.9976
					2022, Box vs. Partial	-20.716	13.7	24.7	t ratio	-1.507	0.3051
					2022, None vs. Partial	-21.645	14.7	27.3	t ratio	-1.469	0.321
Ammonium	LMM	Treatment *Year Elevation	Block:Year	Normal	2021, Box vs. None	0.779095	0.31	24.1	t ratio	2.517	0.0479
					2021, Box vs. Partial	0.779887	0.31	24.1	t ratio	2.518	0.0477
					2021, None vs. Partial	0.000792	0.31	24.2	t ratio	0.003	1
					2022, Box vs. None	0.254595	0.375	31	t ratio	0.678	0.7778
					2022, Box vs. Partial	-0.008306	0.371	27.4	t ratio	-0.022	0.9997
					2022, None vs. Partial	-0.262901	0.395	30.8	t ratio	-0.666	0.7846
					Box, 2021 vs. 2022	-11.2	0.353	39.8	t ratio	-31.783	**<.0001**
					None, 2021 vs. 2022	-11.8	0.378	40	t ratio	-31.095	**<.0001**
					Partial, 2021 vs. 2022	-12	0.385	39.8	t ratio	-31.239	**<.0001**
Sulfide	LMM	Treatment *Year Inundation hours per day	Block:Year	Negative Binomial	2021, Box vs. None	4.935	1.5	Inf	Z score	3.281	**0.003**
					2021, Box vs. Partial	1.039	1.2	Inf	Z score	0.869	0.6598
					2021, None vs. Partial	-3.896	1.14	Inf	Z score	-3.413	**0.0019**
					2022, Box vs. None	-1.163	1.31	30.1	Z score	-0.887	0.6485
					2022, Box vs. Partial	-2.044	1.28	27.3	Z score	-1.597	0.247
					2022, None vs. Partial	-0.881	1.21	33.3	Z score	-0.729	0.7462
					Box, 2021 vs. 2022	10	1.92	185	Z score	5.212	**<.0001**
					None, 2021 vs. 2022	3.91	1.32	Inf	Z score	2.968	**0.003**
					Partial, 2021 vs. 2022	6.92	1.51	Inf	Z score	4.575	**<.0001**
Chlorophyll *a* (Square Root Transformed)	GLMM	Treatment *Year	Block:Year	Normal	2021, Box vs. None	-0.9527	0.398	32.7	t ratio	-2.392	0.0574
					2021, Box vs. Partial	-0.8281	0.398	32.7	t ratio	-2.079	0.1099
					2021, None vs. Partial	0.1246	0.398	32.7	t ratio	0.313	0.9476
					2022, Box vs. None	0.0484	0.46	32.7	t ratio	0.105	0.9939
					2022, Box vs. Partial	-0.0795	0.46	32.7	t ratio	-0.173	0.9837
					2022, None vs. Partial	-0.1278	0.46	32.7	t ratio	-0.278	0.9584
					Box, 2021 vs. 2022	0.868	0.43	49	t ratio	2.018	**0.0491**
					None, 2021 vs. 2022	1.869	0.43	49	t ratio	4.345	**0.0001**
					Partial, 2021 vs. 2022	1.617	0.43	49	t ratio	3.758	**0.0005**
Total No. Insects	GLMM	Treatment *Year Elevation Inundation hours per day	Block:Year Year	Negative Binomial	2021, Box vs. None	0.4766	0.447	Inf	Z score	1.066	0.5355
					2021, Box vs. Partial	0.5515	0.422	Inf	Z score	1.308	0.3905
					2021, None vs. Partial	0.0749	0.415	Inf	Z score	0.18	0.9823
					2022, Box vs. None	0.0406	0.588	Inf	Z score	0.069	0.9974
					2022, Box vs. Partial	0.1639	0.567	Inf	Z score	0.289	0.955
					2022, None vs. Partial	0.1233	0.628	Inf	Z score	0.196	0.979
					Box, 2021 vs. 2022	1.75	0.601	Inf	Z score	2.914	**0.0036**
					None, 2021 vs. 2022	1.31	0.603	Inf	Z score	2.181	**0.0292**
					Partial, 2021 vs. 2022	1.36	0.552	Inf	Z score	2.471	**0.0135**
No. Chironomids (Square Root Transformed)	LMM	Treatment *Year	Block:Year	Normal	2021, Box vs. None	6.247	1.9	23.4	t ratio	3.292	**0.0085**
		Elevation Inundation hours per day	Year		2021, Box vs. Partial	5.326	1.94	26.2	t ratio	2.748	**0.0279**
					2021, None vs. Partial	-0.921	1.86	26.1	t ratio	-0.494	0.8749
					2022, Box vs. None	1.565	2.02	29.9	t ratio	0.774	0.7215
					2022, Box vs. Partial	0.896	1.98	26.2	t ratio	0.452	0.8939
					2022, None vs. Partial	-0.669	2.13	29.8	t ratio	-0.313	0.9474
					Box, 2021 vs. 2022	16.4	5.44	58.3	t ratio	3.015	**0.0038**
					None, 2021 vs. 2022	11.7	5.35	69.1	t ratio	2.192	**0.0318**
					Partial, 2021 vs. 2022	12	5.29	65.2	t ratio	2.263	**0.027**
No. Prokelesia	GLMM	Treatment *Year Elevation	Block:Year Year	Poisson	2021, Box vs. None	-0.6535	0.205	Inf	Z score	-3.181	**0.0042**
					2021, Box vs. Partial	-1.6921	0.183	Inf	Z score	-9.227	**<.0001**

		Inundation hours per day			2021, None vs. Partial	-1.0386	0.137	Inf	Z score	-7.564	**<.0001**
					2022, Box vs. None	-0.4014	0.265	Inf	Z score	-1.513	0.2846
					2022, Box vs. Partial	0.0126	0.278	Inf	Z score	0.045	0.9989
					2022, None vs. Partial	0.414	0.299	Inf	Z score	1.383	0.3501
					Box, 2021 vs. 2022	-0.105	0.548	Inf	Z score	-0.191	0.8483
					None, 2021 vs. 2022	0.147	0.52	Inf	Z score	0.283	0.7769
					Partial, 2021 vs. 2022	1.6	0.527	Inf	Z score	3.038	**0.0024**
No. Amphipods (Square Root Transformed)	LMM	Treatment *Year Inundation hours per day	Block:Year	Normal	2021, Box vs. None	-0.437	1.25	29.7	t ratio	-0.351	0.9344
					2021, Box vs. Partial	1.124	1.2	30.8	t ratio	0.935	0.6226
					2021, None vs. Partial	1.562	1.2	31.1	t ratio	1.301	0.405
					2022, Box vs. None	-0.798	1.56	34.7	t ratio	-0.51	0.867
					2022, Box vs. Partial	-1.376	1.54	29.9	t ratio	-0.895	0.6476
					2022, None vs. Partial	-0.578	1.64	32.8	t ratio	-0.353	0.9338
					Box, 2021 vs. 2022	0.724	1.65	43.8	t ratio	0.438	0.6639
					None, 2021 vs. 2022	0.364	1.65	44.6	t ratio	0.22	0.8269
					Partial, 2021 vs. 2022	-1.776	1.61	43.6	t ratio	-1.105	0.2754
No. Oligochaetes (Square Root Transformed)	LMM	Treatment *Year	Block:Year	Normal	2021, Box vs. None	-1.273	1.78	29.4	t ratio	-0.717	0.7555
		Elevation Inundation hours per day			2021, Box vs. Partial	-1.672	1.77	31.6	t ratio	-0.943	0.6176
					2021, None vs. Partial	-0.399	1.74	31.9	t ratio	-0.23	0.9713
					2022, Box vs. None	1.632	2.19	36.1	t ratio	0.744	0.7391
					2022, Box vs. Partial	4.83	2.19	32.2	t ratio	2.205	0.0856
					2022, None vs. Partial	3.198	2.32	35.6	t ratio	1.378	0.3629
					Box, 2021 vs. 2022	-2.448	2.48	45.4	t ratio	-0.987	0.3287
					None, 2021 vs. 2022	0.457	2.38	44.7	t ratio	0.192	0.8486
					Partial, 2021 vs. 2022	4.053	2.27	45.2	t ratio	1.788	0.0805
No. Sparrows per hectare per hour (Log Transformed)	GLM	Habitat *Year	None	Normal	Low Marsh, 2021 vs. 2022	0.5801	0.272	Inf	t ratio	2.129	**0.0332**
					Mid Marsh, 2021 vs. 2022	0.0811	0.246	Inf	t ratio	0.33	0.7414
					2021, Low Marsh vs. Mid Marsh	0.654	0.257	Inf	t ratio	2.545	**0.0109**
					2022, Low Marsh vs. Mid Marsh	0.155	0.262	Inf	t ratio	0.59	0.555