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Understanding the non-trophic effects of animals on community dynamics in California salt marshes

I. Introduction

Animals influence community structure and ecosystem function via trophic interactions. For example, consumer effects on prey density (consumptive effects; Estes and Palmisano 1994) and prey traits (nonconsumptive effects; Konar and Estes 2003) can have cascading impacts on entire communities. However, animals can also impact communities through non-trophic pathways, such as trampling (Cumming and Cumming 2003), pollination (Memmott 1999), mutualism (Bascompte et al. 2003), and ecosystem engineering via burrowing (Wright et al. 2002). Although burrowing animals may commonly alter community dynamics by changing abiotic conditions (Jones et al. 1994), there is a paucity of information surrounding the role of burrowing animals in determining the composition of plant communities. The activities of such organisms may mitigate the impacts of climate change by reducing environmental stress that would otherwise change plant communities. In salt marshes, for example, crabs can burrow into soils surrounding marsh vegetation and thereby alleviate submergence and hypoxic stress (Bertness 1985). Importantly, such stress reductions could shift plant-plant interactions towards more negative, competitive interactions according to the Stress-Gradient Hypothesis (Bertness and Hacker 1994, Bertness and Ewanchuk 2002, He et al. 2003). These impacts of burrowing animals may shape the distribution and abundance of plant species and may be especially pronounced at lower latitudes where temperature-related stress is already high. *The central goal of this research is to address how animals can influence community dynamics by modifying plant interactions via non-trophic pathways in Pacific coast salt marshes.*

Two reasons suggest that animals may commonly drive the composition of salt marsh plant communities via non-feeding pathways. First, burrowing animals in these marshes can influence the performance and fitness of plants (Bertness 1985, Boyer and Fong 2005, Escapa et al. 2015, Walker and Long *in* prep). For example, burrowing crabs can decrease environmental stress for cordgrass by oxygenating sediment, facilitating drainage, depositing nutrients, and decreasing interstitial salinity (Bertness 1985, Smith et al. 2009, Holdredge et al. 2010), potentially shifting plant competition in favor of cordgrass. Second, burrowing activities can reduce overall stress such that interactions between marsh plants can completely switch from facilitation to competition (Bertness 1991, Pennings and Callaway 1992, Boyer and Zedler 1999, He et al. 2013). For example, in San Diego salt marshes, the dominant plants, cordgrass (*Spartina foliosa*) and pickleweed (*Sarcocornia* spp.), only compete under reduced nutrient stress (Boyer and Zedler 1999). However, *we lack direct tests of the hypothesis that burrowing animals shift the composition of mixed-species assemblages in salt marshes.*

Additionally, the role of burrowing animals in shaping salt marsh plant communities may vary across latitude. In California, precipitation generally increases and temperature decreases with latitude, so environmental stress tends to occur more frequently in southern California salt marshes (Weigert and Freeman 1990, Boyer and Zedler 1999, Pennings and Bertness 1999, Allen et al. 2006). Thus, I predict that burrowing animals play a greater role in determining the makeup of southern salt marshes because they reduce environmental stress, and thereby increase competition between plants.

II. Objectives

I will examine how burrowing crabs (*Pachygrapsus crassipes, Hemigrapsus oregonensis, Uca crenulata*) impact the interactions of two dominant salt marsh plants (cordgrass and pickleweed) at different latitudes on the California coast. I hypothesize:

> **(H1)** Plant competition overall will be stronger at northern sites where conditions are less stressful,
> **(H2)** Reduction of stress by crab burrowing will increase the competitive ability of cordgrass (relative to pickleweed) (C>P), and thereby
> **(H3)** Crabs will influence the directionality of interactions and overall community dynamics.

III. Approach

I will conduct a multi-factorial, manipulative caging experiment at four salt marshes - two southern California sites (Kendall-Frost Marsh Reserve, San Dieguito Lagoon) and two northern California sites (Bolinas Lagoon, Tomales Bay). At each site, I will manipulate Plant Neighbors (Present, Absent), Focal Plant Species (Pickleweed, Cordgrass), and Crabs (Present, Removal) at each of three intertidal elevations (High, Mid, Low; n=8). Neighbor presence will be manipulated by clipping non-focal species in Neighbor Absent plots. I will maintain Neighbor treatments every two weeks. Crab presence will be manipulated by surrounding plots (0.7 x 0.7-m) with galvanized mesh cloth that extends into the marsh substrate to minimize crab migration. In May 2017, I will remove crabs from Crab Removal treatments at the start of the experiment by hand, and then throughout the experiment with pitfall traps. In contrast, ambient crabs will be left in Crab Present treatments and replaced as needed. During cage deployment, plant rhizomes will be severed at cage borders to prevent nutrient and resource exchange with plants outside of my manipulated plots. To account for possible caging effects in my experiments (e.g. shading), I will also deploy two-sided cage controls at each elevation.

During the experiment, plant community structure will be assessed within each plot non-destructively by recording the percent cover of different plant species. Additionally, I will collect all aboveground biomass and a core sample of belowground biomass at the end of the experiment in order to determine the dried biomass of each species in each plot. I predict that crabs will increase the relative abundance of cordgrass, particularly in the southern marshes. Furthermore, the neighbor manipulation will identify if crabs modify how plants interact with each other. To help understand the mechanisms underlying changes in community structure, I will also measure several plant traits, including morphology (stem density, plant height), nutritional content (% carbon and % nitrogen), and reproduction (number of flowers and seeds). To understand the physical mechanism by which crabs alter environmental stress, I will measure porewater salinity, sediment pH, bulk density, carbon: nitrogen ratios, sediment texture, and organic matter to inorganic material ratios. I will analyze these data with a multi-factor ANOVA across sites, and within a single site.

IV. Preliminary Data

In summer 2016, a manipulative caging experiment was deployed in order to examine how burrowing crabs impacted the prevalence of cordgrass and pickleweed at two salt marshes in southern California. At three sites, I manipulated Crabs (Present, Removal) (n=5). The goal of this experiment was to determine 1) if there is a crab effect on plants in Pacific coast salt marshes, and 2) if crabs alter the plant community assemblage. Crabs changed the plant community at two of our three sites (Fig 1: F=3.99, p = 0.09; for difference in cover between treatments at site KF1).

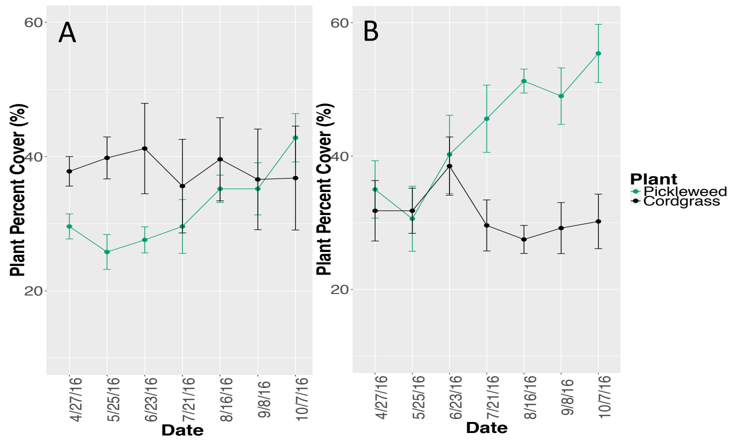

Figure 1. Plant percent cover for pickleweed and cordgrass from April to October at Kendall-Frost Marsh Reserve, site 1. (A) Crab Removal. (B) Crab Present.

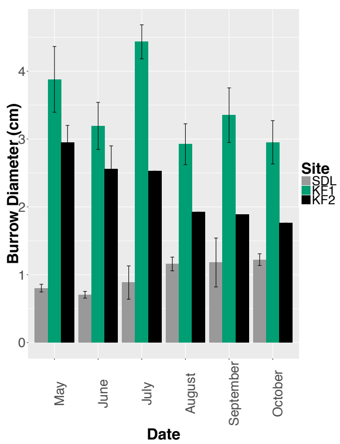

Figure 2: Average burrow diameter from May to October, where diameter was site-specific (KF1 > KF2 > SDL; values are means +/- SE).

In contrast to my original prediction (**H2**), crabs increased or maintained pickleweed cover at two of the sites, but did not influence cordgrass cover. Additionally, the strength and direction of the crab effect on the two dominant plants was related to the identity of the dominant crab species and the associated size and number of their burrows (Fig 2). KF1 was dominated by larger crabs (*P. crassipes*), whereas SDL was dominated by smaller crabs (*U. crenulata*). Therefore, I plan to continue these experiments through another growing season in order to monitor plant community assemblage through time, and add additional experiments (as proposed) in order to identify whether crabs alter the strength and magnitude of competitive interactions between plants.

V. Benefits to Wetlands

Salt marshes provide key ecosystem services, including carbon sequestration, habitat provisioning, shoreline protection, and water filtration. Environmental stress on salt marshes will likely increase, particularly at lower latitudes, with projected increases in global temperatures associated with climate change. Identifying factors that mitigate this environmental stress (e.g. the activities of burrowing crabs) would contribute to conservation strategies and enhance our appreciation for the resilience of these ecosystems in the face of climate change. This project will use a biogeographic approach to enhance our understanding of the non-trophic effects of animals on community dynamics across varying abiotic conditions.

Additionally, salt marshes are important ecosystems along the coast of California providing habitat for endangered species, such as the Ridgway's Rail. The landscapes and biological communities of California salt marshes have been transformed, some beyond recognition due to landscape transformations, pollution, and introduced species. Management and restoration has become of utmost importance; however, to construct successful restorations, the community structure of California salt marshes must be identified and understood. My project will serve to enhance our understanding of the impact of animal modifiers on community interactions in order to better recognize the complex relationships that build and create community structures.

VI. Funding

The primary expenses for conducting my research will be the materials needed to assemble crab-exclusion cages, as well as travel to field sites. The biogeographic aspect of my experiments will involve travel to four sites along the California coast in order to fully understand how communities respond to environmental stress across a large spatial scale. I have access to two marine laboratories – San Diego State University's Coastal Marine Institute (CMIL) and University of California, Davis' Bodega Marine Lab (BML). I will have access to field vehicles at each marine lab, therefore funding will cover gasoline expenses from CMIL to Kendall-Frost Marsh Reserve and San Dieguito Lagoon, and travel from BML to Tomales Bay and Bolinas Lagoon. Additionally, flights will be needed to fly between Northern and Southern field sites once a month.

VII. Outreach and Broader Impacts

Restoration and management

Restoration has become of utmost importance, however to construct successful restorations, the community structure of California salt marshes must be identified and understood in the context of potential climate change impacts. I will conduct scientific workshops for marsh managers at the California Fish and Wildlife, as well as San Dieguito River Valley Conservancy, in order to provide a holistic and inclusive report regarding abiotic and biotic conditions of salt marshes in California. Additionally, the findings of this study will be shared with local restoration groups (e.g., ReCon) and resource managers through annual reports and oral presentations to volunteers and staff, in particular - Kendall-Frost Marsh Reserve, San Dieguito Restoration, and Bolinas Lagoon Wildlife Reserve. With information regarding marsh community structure, these groups will be able to make more informed decisions regarding salt marsh restoration.

Community outreach and education

As part of the unique joint-doctoral program with San Diego State University (SDSU) and UC Davis, I have the opportunity to impact and share my science with two different communities. I will continue working with the Marine Ecology and Biology Student Association (MEBSA) to continue initiatives, such as the Annual CMIL Marine Science Day and Making Waves, which seek to enhance the San Diego community's awareness of local marine issues. As an executive member of MEBSA, I intend to grow our membership and the number of STEM specific outreach activities. While at UC Davis, I will contribute service and public workshops to the Society of Conservation Biology, Davis chapter.

My proposed project will serve to train six undergraduate students each year in basic field, laboratory, and data analysis techniques. In 2016, I mentored and trained seven undergraduate students, influencing many students to pursue higher education in ecological studies. SDSU is ranked number 20 in the nation for racial and ethnic diversity by the US News & World Report, as well as number 13 in the nation for bachelor's degrees awarded to minorities according to the Diverse Issues in Higher Education. Conducting my research at SDSU will allow me the unique opportunity to engage and train minority students in field techniques and data analysis. Additionally, I will utilize high school volunteers in order to maintain crab cages, which will expose volunteers to field work.

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