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Effects of Green Crab (*Carcinus maenas*) Across Variable Densities of Eelgrass (*Zostera marina*)

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by

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Abstract

Eelgrass (*Zostera marina*) plays a critical role in estuarine ecosystem function by sustaining a variety of marine and freshwater species, but it's increasingly threatened by the aggressive non-native green crab (*Carcinus maenas*). The abundance of *C. maenas* is on the rise within the coastal environment of Oregon and it is imperative to know how these populations will affect the long-term health of *Z. marina*. *C. maenas* have been linked to declines in *Z. marina* coverage and shellfish abundance, but there has been no research on to what extent the density of *Z. marina* affects its capability to survive despite *C. maenas* activity. *Z. marina* density is decreasing globally, leaving beds more vulnerable to disturbance and reducing options for recovery after disturbance. We tested the hypothesis that greater loss in *Z. marina* coverage would occur at low densities because the sparse rhizome mat could be easily uprooted by *C. maenas*. We conducted an enclosure experiment in Netarts Bay, OR to analyze change in *Z. marina* coverage and health over the span of two weeks with or without *C. maenas*. Low density *Z. marina* experienced a greater decrease in coverage regardless of *C. maenas* presence. We also observed greater loss in *Z. marina* coverage in plots with *C. maenas*. However, the interaction between *Z. marina* density and *C. maenas* activity on overall *Z. marina* survival and health was not statistically significant. Given that *C. maenas* contributed to the loss in *Z. marina* coverage and low density *Z. marina* was vulnerable to any type of disturbance removal of *C. maenas* would be beneficial across *Z. marina* densities. These observations suggest that efforts to restore *Z. marina* should include replanting at high densities to create more resilient beds.

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TABLE OF CONTENTS

List of Tables

List of Figures

Introduction

Ecology of Zostera marina

Eelgrass (*Zostera marina*) is a type of seagrass found on the Pacific and Atlantic coasts of North America and Eurasia. It typically grows on soft substrata like mud or sand and provide habitat for species that would otherwise not be able to establish themselves on muddy sediment (Phillips, 1985). *Z. marina* serves as the primary producer that creates the base for a highly productive marine food web associated with rich species diversity (Hemminga, 2000). Its thick, rhizomatous mats create extensive meadows that provide a wide array of ecosystem services including attenuating currents, recycling nutrients, habitat for juvenile fish and invertebrates, food for migratory birds, and protective cover for salmon and Dungeness crab (Mumford Jr., 2007; Phillips, 1985; Walter et al., 2020; Kitting et al., 1984; van der Heide, 2007). The critical role provided by *Z. marina* in supporting a variety of economically important species has been valued at $19,004 per hectare per year (Constanza et al., 1997).

Z. marina has a narrow niche and is constrained by a variety of environmental conditions. In optimum growing conditions, *Z. marina* beds are continuous, while in less suitable areas, beds are patchier. The preferred conditions for *Z. marina* are shallow waters like those of shallow bays and estuaries where light availability is high, temperatures range between 15□ and 20□ C, and salinities are persistently above 15% (Nejrup & Pedersen, 2008). In addition, *Z. marina* requires clean water as suspended solids and excess nutrients can reduce light availability and fuel algal growth. Changes to any of these environmental conditions, are coupled with changes to the reproduction strategy of *Z. marina*, with higher reproductive effort being expended in stressful conditions (Phillips et al., 1983). The species flowers in the spring and produces seeds in mid-summer, which germinate the following spring, though this varies depending on location (Churchill et al., 1985; Phillips et al., 1983). In areas like the Oregon Coast where mild water temperatures allow for perennial growth, flowering and seed production is likely less important and shoot propagation from underground rhizomes may be the most important factor in the growth of *Z. marina* (Phillips et al., 1983).

Z. marina beds are increasingly stressed across the world and are very vulnerable to climatic, anthropogenic, and environmental perturbations (Orth & Moore, 1984). One global assessment has found that seagrasses are disappearing at a similar rate to coral reefs and tropical rainforests, categorizing it as one of the most threatened ecosystems in the world (Waycott et al., 2009). Significant declines in *Z. marina* have occurred in estuaries across the world (Garbary et al., 2014; Matheson et al., 2016; Keser et al., 2003). In the 1970s, some areas of Chesapeake Bay experienced a complete loss in vegetation (Orth et al., 1983).

Declines in *Z. marina* cover and density are due to a wide range of factors. *Z. marina* is sensitive to water quality and clarity and excess nutrients in the water column. Eutrophication and pollution can promote growth of epiphytic algae that grows on the blades of *Z. marina*, reducing light availability and inhibiting growth (Hauxwell et al., 2001). Other significant threats include physical disturbances (dredging, coastal construction, damage from recreational boats), and aquaculture (Orth et al., 2006). However, recent mass disturbances to *Z. marina* have also been attributed to an invasive species, the Green Crab (*Carcinus maenas*). In 2001, *Z. marina* declines of about 95% occurred in Antigonish Harbour (Nova Scotia) due to *C. maenas* (Garbary et al., 2014). This loss of *Z. marina* was swift (2000-2002) especially considering the first detection of *C. maenas* in the area was in the mid-1990s (Garbary et al., 2014; Government of Nova Scotia). The widespread of loss in *Z. marina* coverage caused a collapse in scallop fisheries on the East Coast of North America, a decline in waterfowl populations, and an extinction of a marine gastropod (Orth et al., 2006; Carlton et al., 1991).

Background on the Green Crab, Carcinus maenas

Establishment of *C. maenas* can contribute to altered ecosystem functionality, affecting the native species and human societies that rely on those ecosystems. Like many other marine non-native species, *C. maenas* likely made its way over to North America from Europe in the hulls of ships (Say, 1817 as cited in Behrens Yamada et al., 2018). *C. maenas* were first documented on the East Coast in the early 1800s and later detected in San Francisco Bay in 1989, Oregon in 1997, and British Columbia in 1999 (Yamada et al., 2016). It has successfully invaded coasts of every continent but Antarctica that it is not native to (Klassen & Locke, 2007). It is a generalist species that feeds on a wide variety of benthic organisms. *C. maenas* can survive in a variety of environments and can be found in rocky intertidal, mudflats, cobble beaches, and tidal marshes (Grosholz &

Ruiz, 1996). They are tolerant of a broad range of warm and cold temperatures, and winters that have high Pacific Decadal Oscillation and ENSO events are associated with greater recruitment (Yamada, et al., 2019; Tepolt & Somero, 2014). The limit to their range expansion will likely be temperature as *C. maenas* has a thermal limit of 32 °C and larvae can only develop within a restricted range of 10-32 °C (Cuculescu et al., 1998; de Rivera et al., 2007). *C. maenas* larvae from established populations are transported along strong coastal currents that travel northward. Their wide tolerance for salinity, temperature, and habitat type are traits that make them a model invader in many ways (Klassen & Locke, 2007). A chromosomal inversion that allows for thermal acclimation means *C. maenas* can adapt to temperature within a relatively short period of time. Thus, *C. maenas* can quickly establish in new areas, sometimes going unnoticed, but once they colonize a new area, restoration and management costs increase quickly (Tepolt et al., 2021).

While not all non-native species are damaging to their new environment, *C. maenas* is an ecosystem engineer, both directly and indirectly affecting ecosystems through competition, predation, and habitat modification (Grosholz & Ruiz, 1996). They are known for being aggressive foragers that uproot *Z. marina* rhizomes in search of shelter and bivalve prey (Matheson et al., 2016). They have been shown to outcompete native species like Dungeness crab; a critical resource for local shellfish industries (U.S. EPA, 2008).

Establishment of *C. maenas* populations on the West Coast makes the potential expansion to Alaska much higher (U.S. EPA, 2008). In 2013, modeling suggested that an invasion into Washington would result in an estimated loss of 0.45 to 4.46 million kilograms per year in commercial shellfish harvest which accumulates to $1.03 to $23.8 million loss annually with additional losses in distribution and processing (Mach & Chan, 2013).

Description of C. maenas

C. maenas (Portunidae) are easily identifiable with its wide carapace that has five teeth on each antero-lateral margin and a flattened fifth leg adapted for swimming (Klassen & Locke, 2007) (Figure 1). Carapace width is either measured from fifth tooth to fifth tooth or from just inside the fifth teeth. In Oregon and on the rest of the West Coast of North America, rapid growth rates has been observed compared to other regions, and crabs reach adult size (2-3cm) in their first summer (Behrens Yamada & Gillespie, 2008). Adult males in Oregon have an average size of 65-75mm, but with observed growth rates it is likely that West Coast populations will produce crabs larger than 110mm, possibly due to the lack of predators and fewer parasites in its introduced range (Grosholz & Ruiz, 1996, Behrens Yamada & Gillespie, 2008, Kelley et al., 2015, Tochrin et al., 2001). Despite their common name, *C. maenas* are not always green and can vary in color from green, to yellow-green, to yellow, to orange and even red (Young, Elliott, Incatasciato, & Taylor, 2017).

Figure 1: Photo of *C. maenas*

C. maenas have a life span of six years and as they age, they move to deeper waters (Yamada et al., 2016). Molting occurs about once a year once they have reached adulthood, but is largely affected by food availability and seasonal temperatures (Klassen & Locke, 2007). Mating of *C. maenas* occurs when the female has just molted. A female can spawn up to 185,000 eggs at a time and can have one to two clutches a year (Cohen & Carlton, 1998). Female *C. maenas* in Oregon were matured at 1 year of age and at approximately 3 cm in size (Behrens Yamada et al. 2005). Larvae last 50 to 80 days, with the ability to drift long distances before settlement (Klassen & Locke, 2007). Larvae have been shown to have a narrower temperature tolerance compared to adults, with no larvae developing below 10.0 °C or above 22.5 °C, which likely contributes to the variability in larval dispersal across years (de Rivera et al., 2007; Brasseale et al., 2019).

C. maenas is a generalist species and its omnivorous diet includes a variety of benthic organisms, including clams, mussels, other small crabs, polychaetes, and algae, though they show a preference for bivalve prey (Klassen & Locke, 2007). *C. maenas* ranging from 44mm to 65mm can eat more than 20 (<17mm) clams a day, which is thought to have contributed to major population declines in soft-shell clam (*Mya arenaria*) on the East Coast (Floyd & Williams, 2004; Beal et al., 2018). When *C. maenas* populations are large enough, they can have detrimental impacts to shellfish numbers and result in changes in algal abundance and food web interactions (Trussel et al., 2002; Grosholz et al., 2000). Their dietary preferences overlap with *Cancer* crabs and in food-limited situations, *C. maenas* might outcompete other species (McDonald, 2001). *C. maenas* also possess the unique ability to absorb nutrients through their gills and use those nutrients to survive food limited situations, which has not yet been found for any other marine arthropod (Blewett & Gross, 2017). There is some biotic resistance offered by large red rock crabs (*Cancer productus*) and Pacific brown rock crab (*Cancer antennarius*) that outcompete *C. maenas,* though only in cooler, more saline waters (Hunt & Behrens Yamada, 2003; Jensen et al., 2007). Several shorebirds including great blue heron, cormorants, ducks, gulls, and sandpipers prey upon *C. maenas* (Cohen et al., 1995).

Current status of C. maenas in Oregon

Shortly after the first arrival of *C. maenas* along the West Coast, it was expected that the cohort of *C. maenas* that first colonized the Pacific Northwest would go extinct once they reached the end of their lifespan and no new larvae were supplementing new populations (Behrens Yamada & Randall, 2006). However, *C. maenas* continued expanding northward from California during El Niño events in the 1990s. During El Niño years, strong currents with warm water transported larvae up the coast depositing larvae of *C. maenas* in estuaries across Oregon and Washington. Between 2015 and 2018, there was an increase in the *C. maenas* catch rate across all Oregon estuaries due to a strong arrival of *C. maena*s for several years in a row (Yamada et al., 2019). Before 2016, *C. maena*s were rare in Oregon and Washington averaging less than 0.5 crabs per trap and were not shown to have a strong effect on the benthic community or shellfish industry (Yamada et al., 2019). However, in 2018, over 2,000 *C. maenas* were caught in Oregon and Washington. While the average catch in this region is 3.4 crabs per trap, it is not uncommon to find 20 crabs per trap in some estuaries (Yamada et al., 2019). The estuaries that have more abundant populations are typically well-protected with lower predation and competition from larger crabs (Behrens Yamada et al., 2018; Hunt & Behrens Yamada, 2003; Jensen et al., 2007). A report from Coos Bay in 2020 showed that 77% of the crabs trapped were *C. maenas* and that populations seem to still be growing year to year at most trapping sites (Schooler et al., 2020). Recent research indicates that *C. maenas* are not only coming on warm currents from California, but that there are genetically distinct populations of *C. maenas* from British Columbia that have seeded new populations in estuaries further south, including Netarts and Tillamook (Tepolt, 2021). While populations of *C. maena*s are still low in Oregon and Washington compared to the east coast of North America, California, Europe, and even compared to some enbayments in British Columbia, population sizes are growing, and there is the potential to see similar negative impacts to our critical habitat as has been seen on the East Coast of North America, which is why it is critical to continue monitoring and trapping efforts.

Current Management of Z. marina

Disturbances to *Z. marina* can happen quickly, however recovery is often comparatively slow. Deteriorated and damaged *Z. marina* beds have large restoration costs, between \$100,000 and \$1 million per acre. Transplant survival is still fairly low, around 30 percent, making it an unreliable/inefficient restoration technique (van der Heide, 2007; Fonseca et al., 1998). Thus, managing beds through conservation and preservation is the most effective means for sustaining *Z. marina* beds. Since 1996, *Z. marina* has been designated Essential Fish Habitat under the Magnuson-Stevens Act. This is the primary law governing fisheries in federal U.S. waters. NOAA provides consultations on how to avoid or minimize impacts to *Z. marina* for federal partners, but this is not provided for state or private agencies (Essential Fish Habitat, n.d.).

Washington and California have both taken steps at the state level to establish standards and guidelines for *Z. marina* management, which also include goals for restoration (Sherman & DeBruyckere, 2018). The Oregon Department of State Lands has protection through its No Net Loss policy of submerged aquatic vegetation, including *Z. marina*. Individual projects are reviewed and managed so as to “protect, maintain, where appropriate develop and restore the long-term environmental, economic, and social values, diversity, and benefits of Oregon’s estuaries” (Ekstrom & Young, 2009; Cortright et al., 1987; Sherman & DeBruyckere, 2018). Oregon intends to update its estuary management plans, which were originally written in the 1980s. Environmental groups hope for stronger *Z. marina* protections like those in the California Eelgrass Mitigation Policy which outlines a framework between state and federal agencies to coordinate on *Z. marina* management (Portland Audubon, n.d.).

It is critical to understand the threats facing *Z. marina* in order to create effective policy and maintain overall ecosystem health. *C. maenas* are well adapted for a variety of environmental conditions and pose an increasing threat to West Coast *Z. marina* beds as our waters continue to warm (Tepolt & Somero, 2014). Realistically, full eradication of *C. maenas* is likely not a feasible goal (Green & Grosholz, 2021; Groholz et al., 2021). Therefore, it is critical to understand the effects of *C. maenas* invasion and the potential factors that shift the extent of their effects, so resource managers with limited budgets can focus on asset protection and the species and habitats that could suffer the most.

Research Question and Hypothesis

Previous studies have shown that *C. maenas* can have detrimental impacts to *Z. marina* beds and native invertebrates (Howard et al., 2019; Wong, 2013; Pickering et al., 2017). In some areas, like Antigonish Harbour, there was a 95% decrease in *Z. marina* biomass due to *C. maenas* activity (Garbary et al., 2014; Seymour et al., 2002). However, more complex habitat can reduce foraging efficiency for predators as the rhizome layers provides a protective cover for benthic invertebrates (Wong, 2013; Orth, Heck, & van Montfrans, 1984). Habitat complexity and the ability to mediate predation is significant to determining overall prey abundance (Huffaker, 1958).

No study has been published about whether *C. maenas* effects on *Z. marina* change across *Z. marina* densities. High densities of *Z. marina* typically host more benthic species for *C. maenas* to forage, but high densities of *Z. marina* are often more difficult for *C. maenas* to forage in. Hence, higher *Z. marina* density could increase or decrease *C. maenas* destructive foraging relative to lower densities. Thus, one goal of this study is to understand whether this reduced foraging efficiency protects not only the benthic species, but the overall health of *Z. marina.*

We conducted an enclosure experiment to investigate our research question: Are high densities of *Z. marina* more resilient to *C. maenas* activity and foraging compared to medium and low densities of *Z. marina*? We tested the hypothesis that high densities of *Z. marina* could withstand bioturbation by *C. maenas*, while medium and low densities of *Z. marina* would be more susceptible to loss in percent cover and density due to their sparser rhizome mats that *C. maenas* can more easily uproot. Results from this study are intended to help guide where to prioritize *C. maenas* removal efforts, identify more resilient *Z. marina* beds, and contribute to more successful *Z. marina* transplanting.

Methods

Study area

We examined the impacts of *C. maenas* in Netarts Bay, Oregon located in Lincoln County about 100 km south of the Columbia River and 8km west of the city of Tillamook (Kentula & McIntire, 1986) (Figure 1). Netarts Bay is the sixth largest estuary in Oregon covering 9.41 km^2 and spanning 11 km north to south. The small watershed that drains into Netarts Bay is just 25.7 km^2 in size, fed by 12 small creeks. The volume of freshwater inflow is relatively small when compared with flooding by ocean water (Kreag, 1979). The large amount of ocean water mixing with the freshwater inflow results in high salinity levels, up to 30 ppt in some areas of the bay (Kentula & McIntire, 1986). Annual water temperatures vary from 4° to 25° C with an average summer temperature of 16.0° C. The total volume of the estuary at mean high water (MHW) is 12.6×10^6 m^3. Each tidal cycle, about 75% of that total water volume leaves with a maximum tidal range of 3m (Kreag, 1979).

A shallow, naturally-occurring tidal channel occurs in Netarts bay and extends along the length of the 7 km spit north to south (Figure 2). During the lowest tides, the tide channel is the only submerged part of the bay, leaving the mudflats exposed. Mudflats encompass about two-thirds of the entire bay.

Netarts Bay has Oregon's largest native *Z. marina* bed, extensive clam beds and tidalflats, making it attractive for recreational fishing, clamming, and crabbing. It is one of the main bays in Oregon for finding Dungeness crabs. Netarts Bay has been a designated conservation estuary since 1987. Under the Oregon Estuary Plan, the estuary has limited commercial development and is managed for the long-term use of its natural resources (Kreag, 1979).

Figure 2: Aerial view of Netarts Bay with an inset location map (Google Maps, 2021).

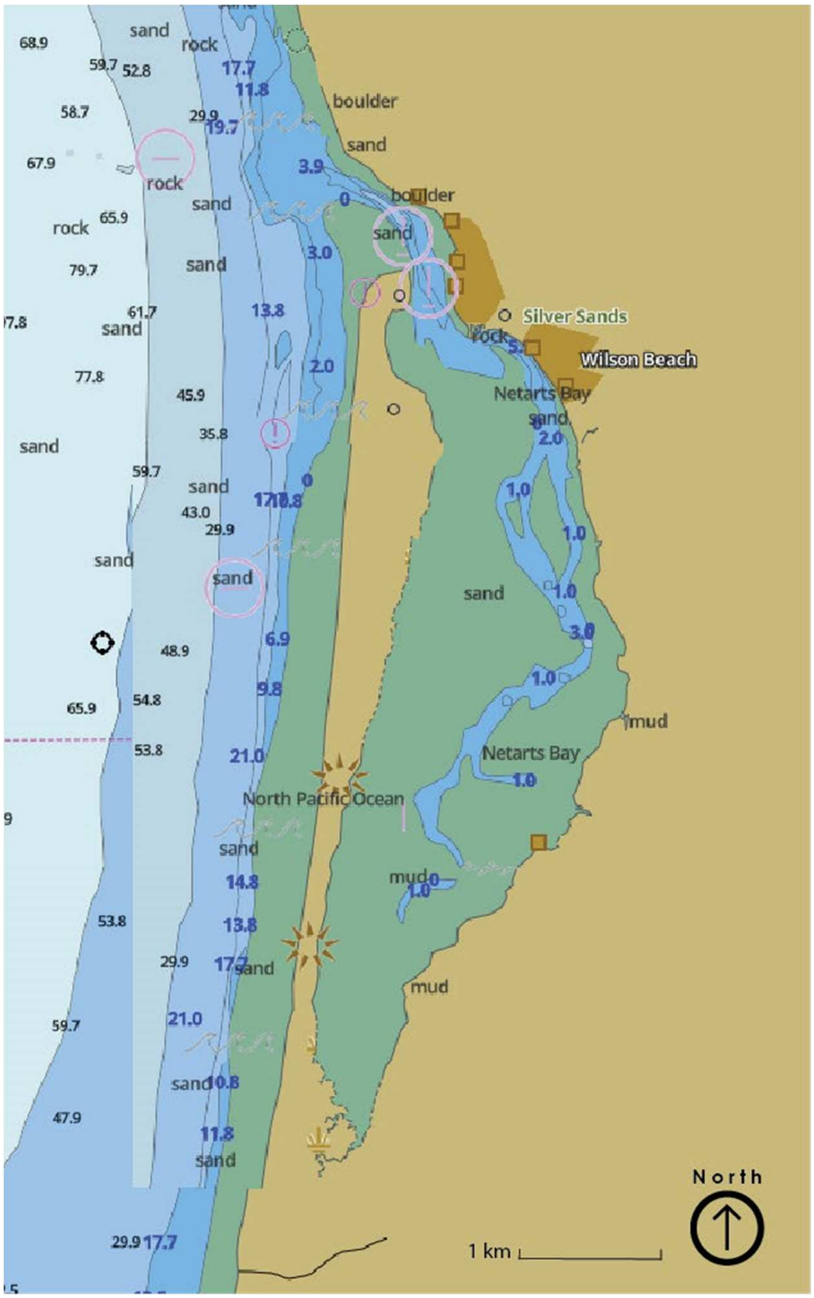

Figure 3: Nautical Map of Netarts Bay showing sediment type and water depth (GPS Nautical Charts, 2021).

C. maenas in Netarts Bay

C. maenas were first documented in Netarts Bay in 1997. In 1998, trapping surveys show that 139 *C. maenas* were caught in the Bay with 0.0057 crabs per trap. Populations decreased from 1998 to 2002 when no *C. maenas* were caught, but started increasing again in 2003. *C. maenas* populations continued to fluctuate between 2003 and 2013 until several strong recruitment classes occurred from 2015-2019. The catch-per unit-effort (CPUE) seen in Netarts Bay in 2019 was 1.4 crabs per trap, 140 crabs caught overall. This is lower than other Oregon estuaries, including Coos Bay (1397 crabs caught) and Yaquina Bay (361 crabs caught) with 3.1 and 3.3 crabs per trap, respectively (Yamada et al., 2019; Behrens Yamada & Gillespie, 2008).

Crab Trapping

We trapped crabs in both intertidal and subtidal regions in Netarts Bay from August to October of 2020 and May to July of 2021. We used collapsible (Fukui) traps which are made of plastic mesh and are 62 x 46 x 23 cm with two 40 cm openings on each end. We deployed three traps at low tide per region. Traps were baited with tilapia enclosed in a plastic bait container. We set four to five traps in total at each deployment with two located ~5m apart near an outflow pipe and two to three traps spaced ~20m apart within the *Z. marina* bed. Traps were deployed for one day and then checked and rebaited before redeployment.

Crabs were kept in the bay and housed in traps and fed periodically until they were placed in enclosures. Any other species of crab or fish found in the traps was removed and set free. Crabs were fed tilapia two days prior to being put in the enclosures to ensure equal hunger levels at the start of the experiment (Malyshev & Quijón, 2011). We collected information on crab species, sex, size of carapace (measured from tip to tip of fifth spine) for each trapping period.

Enclosure Experiments

For our field experiment, we deployed nine plots per replicate for eight replicates in a fully crossed two factor design (*Z. marina* density, *C. maenas* presence) that also included procedural controls (Figure 3). Each density block consisted of one enclosure with crabs, one without crabs (‘control’), and one open plot (‘procedural control’). Each plot within a block was spaced 1-3 m apart and blocks were >5 m away. Blocks of similar densities were located next to each other with all blocks built a similar distance from the shoreline (~45 m). Treatments were randomly assigned to plots within each block.

Plots were 0.5 m^2 in size and were deployed during monthly spring tides when the tide was -1.0 or lower, to ensure that the *Z. marina* was exposed. We built the enclosures with rebar, one in each corner and two additional rebar stakes on each side where the tide would pull against it. The rebar was 1.2 m long and was buried 0.3 m into the sediment. We deployed a 0.91 m tall plastic mesh (2.54 cm openings) 5-sided cube, supported by rebar which was tall enough to allow the *Z. marina* to extend to almost its full height when the tide was in (Figure 4). We inserted the plastic mesh 5 cm into the sediment and secured it with garden staples. To deter outside crab activity, we added a plastic mesh skirt around the bottom of the enclosure that fans out 6 inches from the enclosure and is secured with garden staples. No birds or other large predators could poach the crabs during low tides. We also constructed a 0.46 m^2 frame using 1.9 cm wide polyvinyl chloride (PVC) pipe that we placed in the bottom of our enclosures to ensure they withstood strong tidal currents. Our open procedural plots were marked by two rebar stakes, one in each opposing corner.

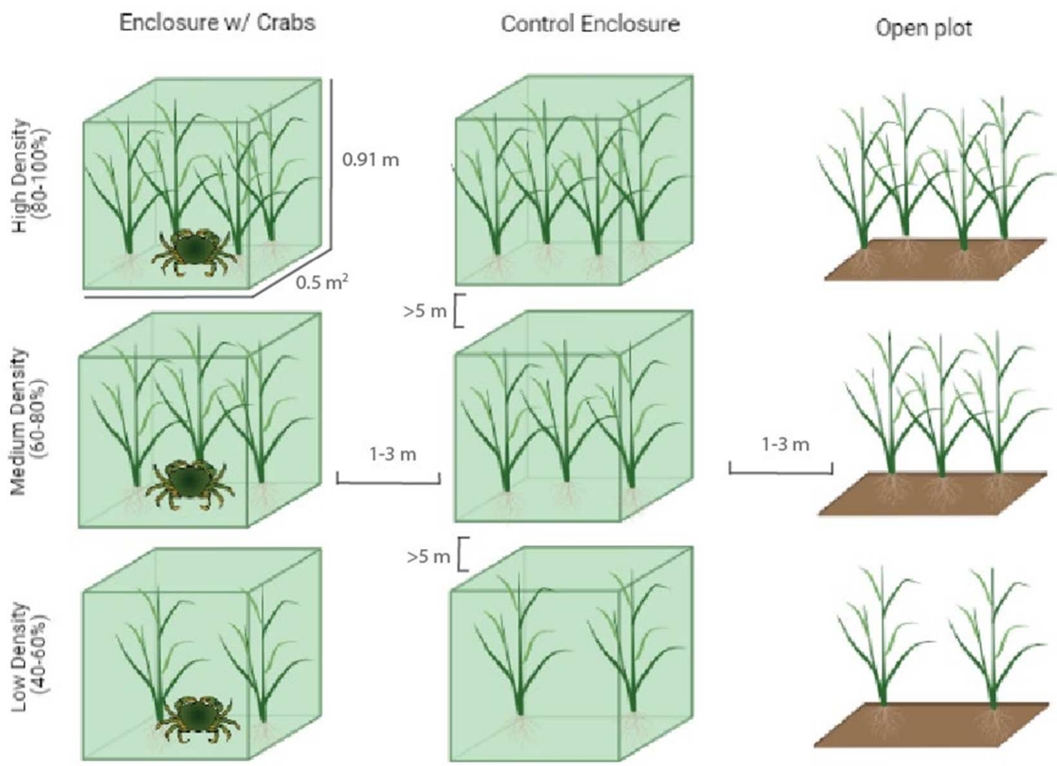

Figure 4: Experimental design with a block of treatment enclosure, control enclosure, and open procedural plot in each of high, medium, and low densities of *Z. marina*. Eight replicate blocks were used per *Z. marina* density, and treatments were randomly assigned.

Figure 5: Medium and low density enclosures and open plots (not visible) during two 9-plot replicates (A) and inside a high density enclosure with a PVC pipe frame before the experiment began (B).:

Enclosure experiments were conducted from May to September of 2021. Before the experiment started, to determine the impact of *C. maenas* on *Z. marina* densities, we did a visual measurement of percent *Z. marina* cover within each plot. Plots were classified as high (80-100% coverage), medium (60-80%), or low *Z. marina* density (<60%). Crabs can impact *Z. marina* by digging it up to access prey underneath or by directly cutting the *Z. marina*. Therefore, we also measured four additional *Z. marina* health metrics both before and after the experiment to determine the extent of each of these impacts that could be driving differences in percent cover. To identify whether the crabs were clipping and tearing the *Z. marina*, we measured the number of blades and the length of the *Z. marina*. For five randomly selected shoots, we measured the longest leaf blade, which is taken from leaf sheath to leaf tip. We also determined the number of blades per shoot by counting the number of blades that extend from the central stem (Bando, 2006; Orth & Moore, 1986; Kim et al., 2015). To quantify the extent at which *C. maenas* is uprooting *Z. marina* rhizomes, we counted the total number of shoots by carefully following each *Z. marina* plant to the base at the sediment surface.

We placed four crabs (8 crabs/m^2) in each of our experimental plots. This density of crabs is in between the high density and very high density seen in other studies that looked at the impacts of these crabs on *Z. marina* (Howard et al., 2019; Davis et al., 1998). Crabs were all male, had both claws, and were of similar size (~80-90mm) because they were the most abundant in our traps and to control for behavioral differences between sexes during mating season (Behrens Yamada, 2001). Procedural control plots were exposed to ambient densities of *C. maenas* and any other crab species present (Howard et al., 2019). Trapped *C. maenas* were not supplemented with any added food other than the bivalve prey that occurred naturally within the plot and the smaller *Hemigrapsus oregonensis* that were able to pass through the openings of the plastic mesh. Open plots were exposed to ambient crab densities.

We followed our plots for a period of two weeks for each replicate, visiting every 2-3 days to make sure the enclosures were still standing and that the crabs had not escaped. At the end of each replicate, we re-measured for percent cover, number of blades, blade length, rhizome count, and algal mass. The vast majority of *C. maenas* (80 of the 96 deployed crabs, 83%) were successfully recovered over the duration of the experiment. We observed that *C. maenas* were often burrowed one to three inches below the sediment surface, sometimes creating large holes near the enclosure edges.

Benthic sampling

To estimate the quantity of food available to the crabs during the experiment, we counted the number of clam holes in each plot and took benthic samples both before and after the experiment. Three samples were taken pre-experiment just outside of each enclosure and only one sample were taken post-experiment within each enclosure to reduce the impact in a small area to this important habitat. We used a 10.16 cm wide plastic clam gun to take sediment cores. Core samples were sifted over a 2.0-mm sieve. Benthic infauna were identified in the field, counted and sorted into morphologically based groups. Pre-experiment infauna abundance was divided by three for comparison to post-experiment species abundance. We also noted observable signs of predation including broken shell fragments and empty carapaces of *Hemigrapsus oregonensis* within *C. maenas* treatment plots at the end of each round of the experiment, which would likely require minimal to no disturbance of *Z. marina*.

Statistical Analysis

For our statistical analysis, we conducted two-way analysis of variance (ANOVA) tests with additional covariates and a blocking variable on three *Z. marina* variables: change in percent cover, change in *Z. marina* shoots, and the ratio of change in percent cover compared to initial coverage. Statistical analysis uses data from closed plots to observe the effect between treatment and control. Statistical analysis between all plots, open and closed is located in Appendix A. Our explanatory variables (crab treatment and density, both fixed) and blocking variable (date, random) were all categorical data. The covariables (blade length, blade number, number of shoots, number of clam holes, and algal mass) were all continuous data. To account for high density plots having the ability to lose more percent coverage, our response variable is a ratio of percent change in *Z. marina* coverage divided by the initial percent coverage. We developed a series of models using stepwise eliminations that omitted variables in the model if they had weak effects ($p \leq 0.10$). Then, we used the Akaike Information Criterion (AIC) to find the model with the best fit for the data. The model with the lowest AIC score was chosen for further evaluation. ANOVA assumptions for normality and homoscedasticity were checked with the Shapiro-Wilk test and Levene's Test, respectively. A power analysis indicated limited statistical power behind the output of our ANOVA models ($n = 8$). We would need a total sample of 27 in order to obtain statistical power at the recommended 0.80 level, so we should be mindful of this as we interpret the results.

Benthic core data visualization was performed in R using the "vegan" package. A nonmetric multidimensional scaling (NMDS) ordination plot based on functional group abundance in the benthic core samples was created using the Bray-Curtis distance matrices. The data underwent a Wisconsin double standardization to account for the effect of absolute species abundance and abundance between sites. However, the stress level of this analysis was 0.25, exceeding the commonly accepted limit of 0.2 that would indicate a good and interpretable plot, which means we should interpret this graph with caution (Clarke, 1993). Analysis of similarity (ANOSIM) calculations were used to test if there were significant differences in benthic infauna communities across sample date and treatments. No diversity analysis was conducted due to a low number of replicates, differing levels of taxonomic identification, and transformations of the data failing to approximate a normal distribution. Instead, we provide a qualitative discussion of our observations.

Results

Crab Trapping

Catch per unit effort (CPUE) for each sampling date ranged from 3.33 to 8.0 in 2020 with an average CPUE of 6.7. The 2021 catch ranged from 6.2 to 16.6 with an average CPUE of 11.2. Males comprised 88% of the total 2020 catch and 83% of the total 2021 catch. Catch rate was higher in 2021 than 2020 with a total of 64 *C. maenas* caught from August to September of 2020 and 223 from June to September of 2021 (Figure 6). The average size of a male was 79mm in 2020, and 80mm in 2021. The average size of a female in 2020 was 64mm and 69mm in 2021. The range in carapace size for males was larger in the 2020 catch (20-95mm), but smaller for females (50-80mm). Total CPUE for *C. magister* was lower than the total for *C. maenas*; 0.9 in 2020 and 0.35 in 2021. We also had zero Red Rock Crab (*C. productus*) within our traps either year, but both these species were rarely seen in our study site until later in the season (August-September).

Figure 6: Box plots of C. maenas sex and carapace size (mm) from 2020 and 2021 trapping seasons. Dots represent individual crabs caught. A small random jitter was added to each point to show their density. The lower and upper bounds of the box correspond to the first and third quartiles and the line in between represents the median. The upper and lower whisker represent the maximum and minimum value, respectively.

Enclosure Experiment

Our 2-way ANOVA model for change in *Z. marina* shoots also showed no significant interaction between *Z. marina* density and *C. maenas* ($F = 1.022$, $df = 2$, $p = 0.3695$). *C. maenas* treatment demonstrated a moderately significant impact to the change in *Z. marina* shoots ($F = 4.983$, $df = 1$, $p = 0.0316$; Table 2). For example, on average all *Z. marina* densities with enclosed *C. maenas* experienced a higher average loss in shoots compared to plots with no *C. maenas* (Table 1, Figure 7). High densities of *Z. marina* with *C. maenas* experienced two to six times greater loss in *Z. marina* shoots compared to low or medium densities, respectively (Table 1). This is compared to all plots without *C. maenas* that experienced an increase in *Z. marina* shoots including high densities which grew seven times more shoots over the two-week period than low densities and medium densities which grew five times more shoots than low densities (Table 1).

Table 1: Average change in Z. marina coverage, change in number of Z. marina shoots, and average ratio of change in coverage across densities in enclosed plots versus without C. maenas, with standard deviation values (n=8).

Density	***C. maenas* Treatment**	**Average change in % *Z. marina* coverage**	**Average change in *Z. marina* shoots**	**Ratio of % change in final cover compared to initial % cover**
High	No	0.00 ± 5.00	14.00 ± 11.92	0.00 ± 0.06
High	**Yes**	**-6.43 ± 9.00**	**-6.54 ± 16.58**	**-0.08 ± 0.10**
Medium	No	-3.33 ± 8.66	11.11 ± 22.84	-0.05 ± 0.13
Medium	**Yes**	**- 6.00 ± 6.99**	**1.54 ± 43.35**	**-0.09 ± 0.14**
Low	No	-3.13 ± 9.23	2.13 ± 12.19	-0.07 ± 0.23
Low	**Yes**	**-10.70 ± 7.32**	**-2.91 ± 20.00**	**-0.25 ± 0.21**

Table 2: 2-way ANOVA output for change in the number of *Z. marina* shoots in low, medium and high *Z. marina* density closed plots with and without crab treatment, and with date as a blocking factor.

	Change in number of *Z. marina* shoots				
	Df	Sum Sq	Mean Sq	F Value	Pr (>F)
Z. marina Density	2	14	6.8	0.014	0.9859
Crab Treatment	1	2377	2377.3	4.983	0.0316 *
Date	1	766	765.6	1.604	0.2130
Crab Treatment: Density	2	976	487.8	1.022	0.3695
Residuals	38	18133	477.2		

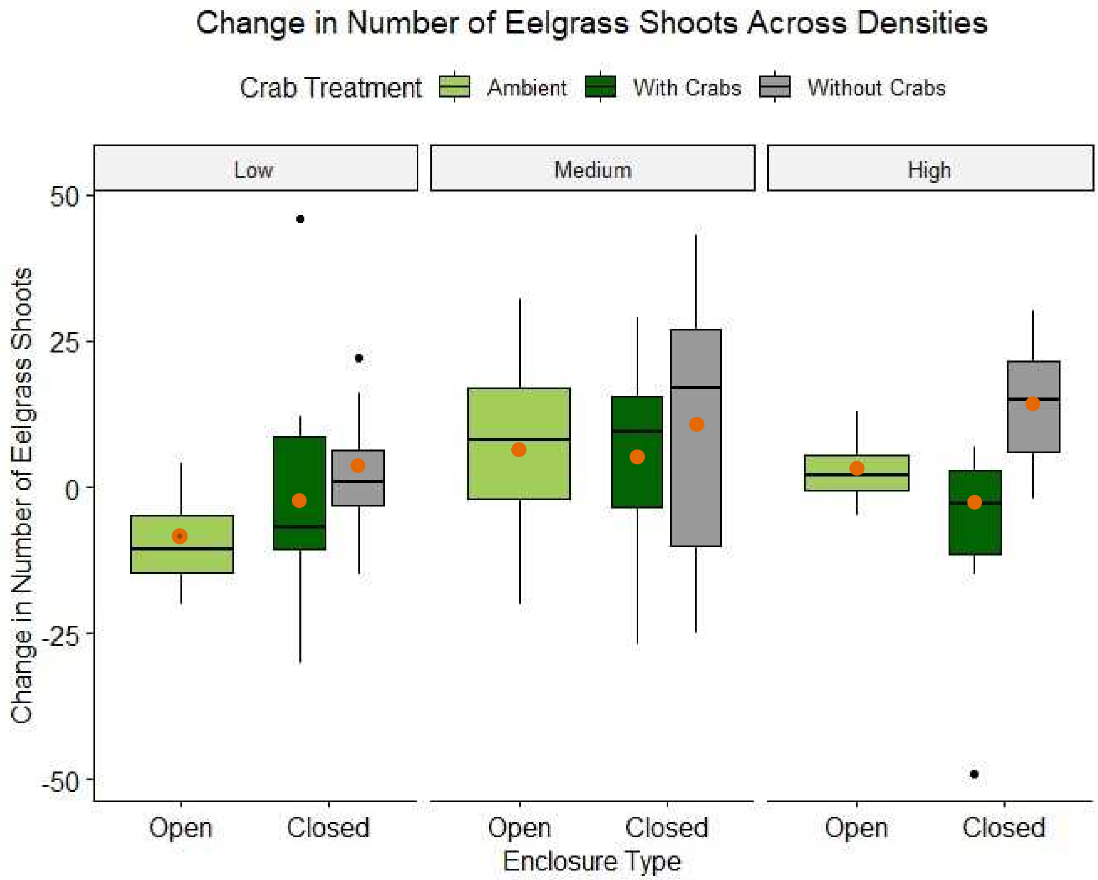

Figure 7: Change in the number of *Z. marina* shoots across low, medium, and high densities of *Z. marina* in open and closed plots. Open plots were exposed to ambient densities of crabs. Closed plots were with or without crab treatment. Orange dots represent the average change (mean). The lower and upper bounds of the box correspond to the first and third quartiles and the line in between represents the median. The upper and lower whisker represent the maximum and minimum value, respectively.

The ANOVA model for the effect on the ratio of percent change in final cover compared to initial cover showed *C. maenas* treatment was significant (F = 6.318, *df* = 1, p = 0.0163). However, density was not significant (F = 2.063, *df* = 2, p = 0.1410) nor was there a significant interaction between *C. maenas* and *Z. marina* density (F= 0.772, *df* = 2, p = 0.4691) (Table 3, Figure 8). Low-density plots with *C. maenas* experienced the highest averaged loss, two times the average loss than plots without *C. maenas* (Table 1). Low density plots also experienced a high degree of variability in both plots with and without *C. maenas*. Medium density plots with and without *C. maenas* had similar averaged losses (Table 1). High density plots with *C. maenas* experienced greater change than plots without (Table 1). Examination of percent cover (without comparison to initial cover) yielded qualitatively similar results.

Table 3: 2-way ANOVA outputs for the ratio of percent change in final Z. marina cover compared to initial percent cover between closed plots of low, medium, and high densities of Z. marina with and without crab treatment. Date was used as a blocking factor.

	Ratio of % change in final cover compared to initial % cover				
	Df	Sum Sq	Mean Sq	F Value	Pr (>F)
Crab Treatment	1	0.0923	0.04616	2.063	0.0163 *
Density	2	0.1414	0.14136	6.318	0.1463
Date	1	0.0067	0.00667	0.298	0.5882
Crab Treatment: Density	2	0.0346	0.01728	0.772	0.4691
Residuals	38	0.8503	0.02238		

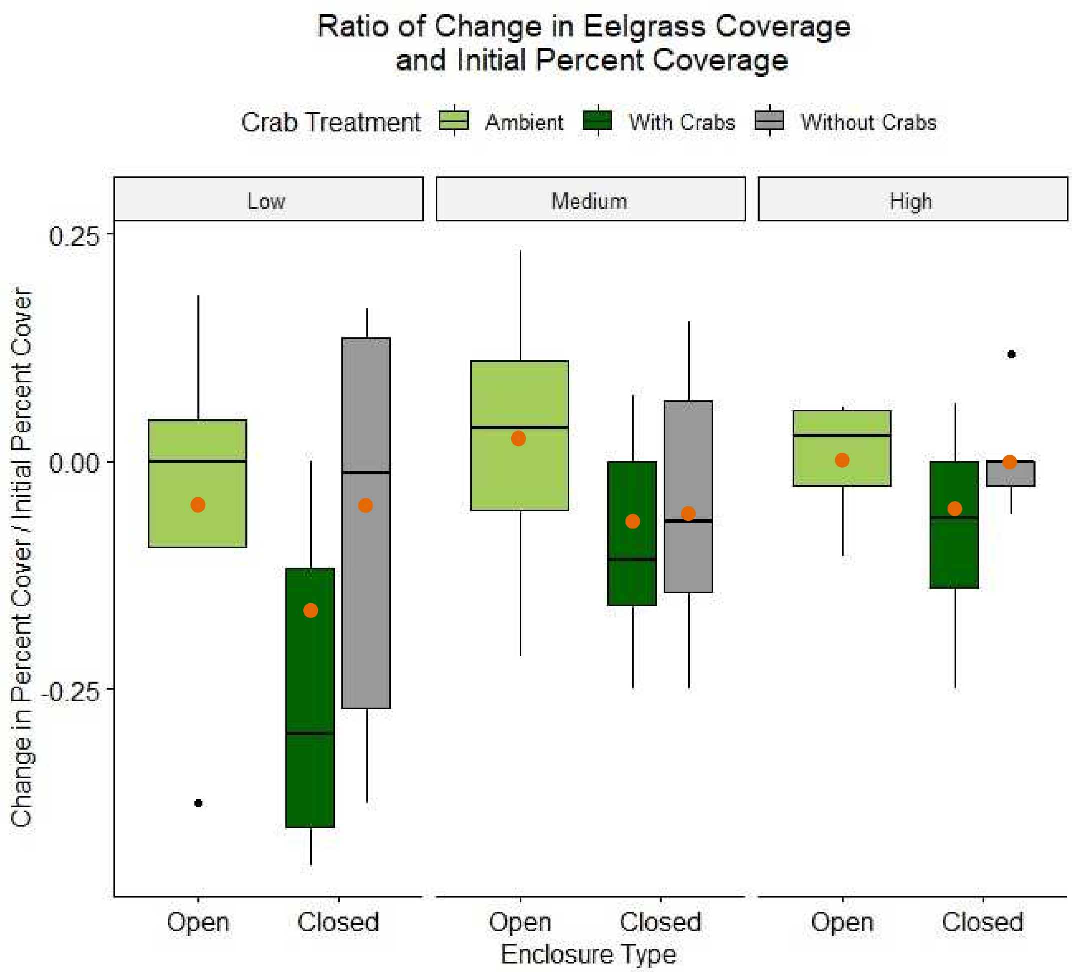

Figure 8: Ratio of change in Z. marina coverage and initial percent coverage across low, medium, and high densities of Z. marina in open and closed plots. Open plots were exposed to ambient densities of crabs. Closed plots were with or without crab treatment. Orange dots represent the average change (mean). The lower and upper bounds of the box correspond to the first and third quartiles and the line in between represents the median. The upper and lower whisker represent the maximum and minimum value, respectively.

Benthic Sampling

The analysis of benthic core samples showed a diverse community of benthic fauna including polychaetes, bivalves, nemerteans, crustaceans, and gastropods across *Z.*

marina densities (Figure 9). Taxonomic group composition was fairly consistent across densities with polychaete and bivalve species having the highest average abundance (Figure 9). *Eupolymnia heterobranchia, Mya arenaria,* and *Notomastus tenuis* were the three most common species found in core samples across *Z. marina* densities. We observed *Notomastus tenuis* abundance happened in clusters with a large abundance in a single core as opposed to being present across core samples. Their absence in ending core samples does not necessarily indicate that they were not present rather that our one core sample did not capture their clustering (Figure 9). We observed a 35% decrease in abundance in ending high density *Z. marina* with *C. maenas,* but a 32% increase in low density *Z. marina* with *C. maenas*. Medium density *Z. marina* saw little change in average abundance. In closed plots with no *C. maenas*, we observe two times more prey abundance in low *Z. marina* densities in ending core samples compared to initial samples. In medium and high densities of *Z. marina* we observe an increase of 18 and 25% respectively.

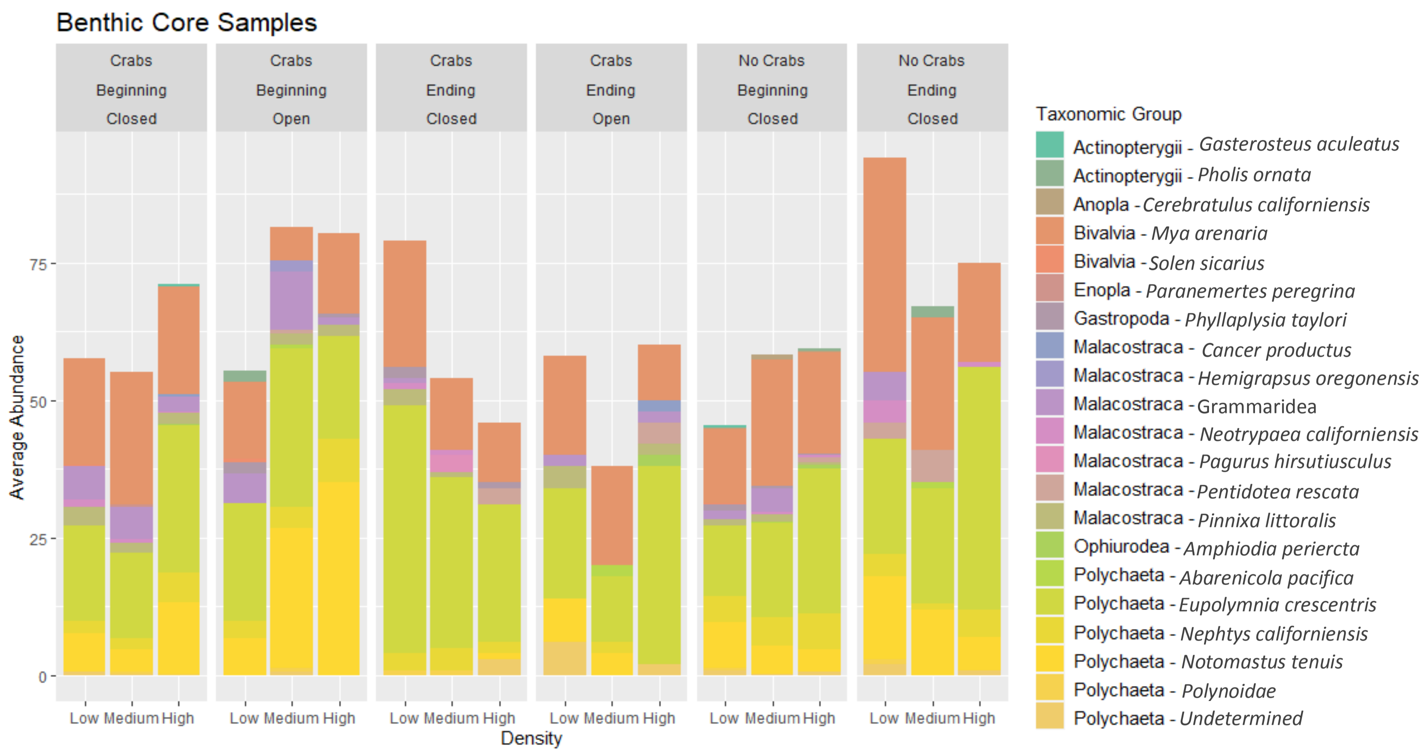

Figure 9: Bar graph of average benthic abundance from initial and ending core samples in open and closed plots across low, medium and high Z. marina densities with and without C. maenas treatment. Open plots were exposed to ambient crab densities.

We did not detect a statistical difference in benthic community composition across the different densities (ANOSIM R= 0.011, P = 0.206). We also did not have a statistical difference in benthic communities based on sample date (ANOSIM R = 0.01, P = 0.2; Figure 9).

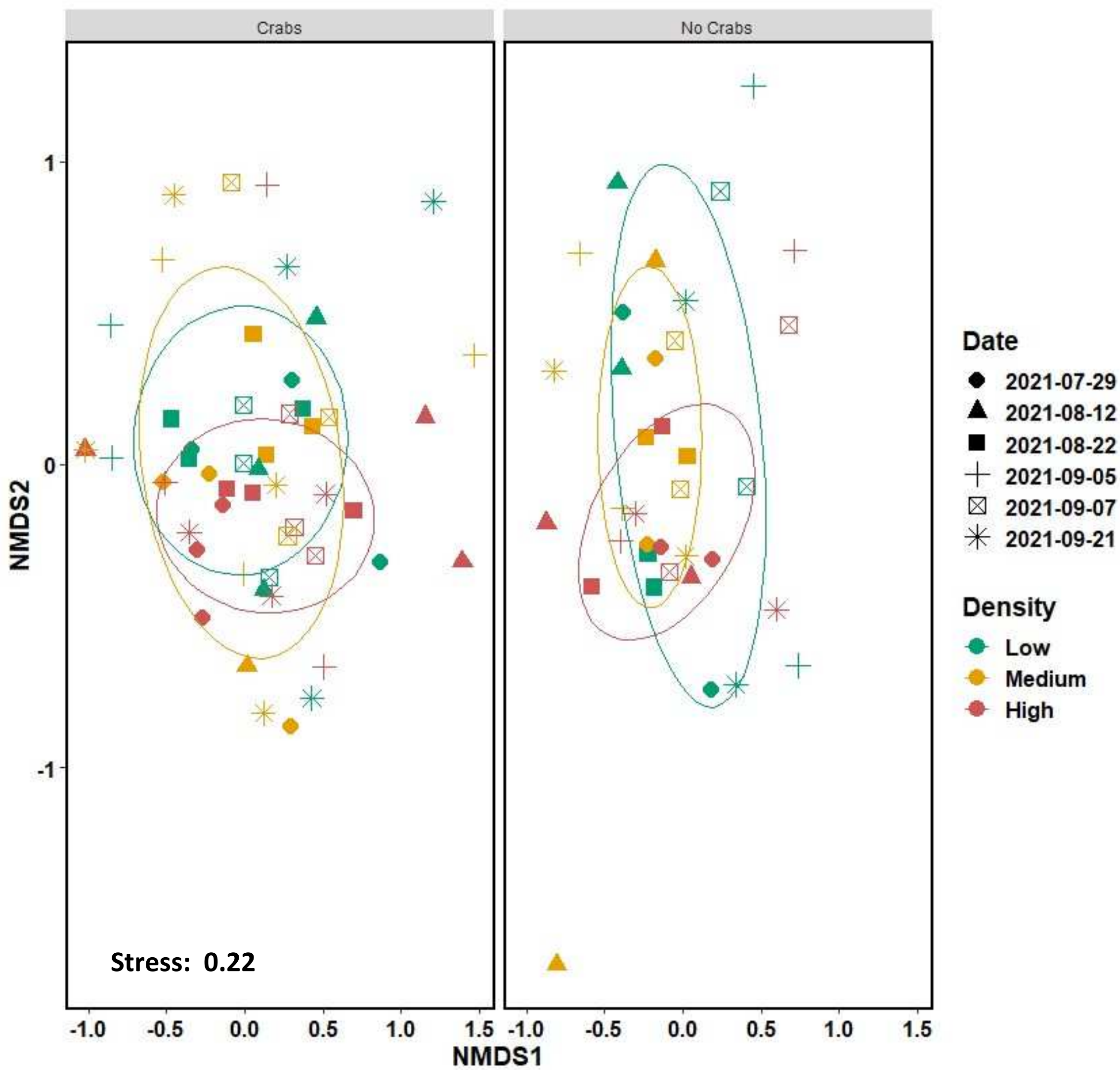

Figure 10: Differences in the benthic core samples across time and densities and between crab treatments. Ellipses represent 60% of the average NMDS scores for each density. Stress value = 0.25.

Discussion

We did not observe a statistically significant interaction between *Z. marina* density and *C. maenas* activity on the *Z. marina* cover and shoots. However, in general, low densities of *Z. marina* experienced the greatest decrease in coverage regardless of *C. maenas* activity and plots with *C. maenas* had greater percent coverage loss than control plots. Our outcomes align with previous research carried out with both transplanted and established *Z. marina* (Davis et al., 1998; Garbary et al., 2014; Howard et al., 2019). Below, we discuss the current status of *C. maenas* populations in Netarts Bay, OR and the observed effects on benthic abundance. In addition, we examine the interaction of *Z. marina* density and *C. maenas* activity to understand how these variables contribute to *Z. marina's* ability to persist.

C. maenas *Abundance and Impacts to Benthic Abundance*

The total number and CPUE of *C. maenas* caught in 2021 was greater than any previous trapping done in Netarts Bay illustrating a growing annual population of *C. maenas* (Behrens Yamada et al., 2018). We caught a greater ratio of males (83%) compared to females (17%) which is not uncommon as females are less frequently found in traps after their first year of life and are more likely to be found in subtidal zones compared to intertidal zones (Behrens Yamada et al., 2005; Warman et al., 1993). The average size of the *C. maenas* caught was greater than what is seen on the Atlantic Coast of North America, but consistent with what is seen on the Pacific Coast of North America where *C. maenas* can grow in excess of 100mm (Young et al., 2017; Kelley et al., 2015). *C. maenas* of this size are effective predators and can have detrimental effects on bivalve populations (Pickering et al., 2017). However, we placed 4 crabs per $0.5m^2$ in our enclosures and saw little to no impact to benthic abundance for the groups we sampled. This is contrary to other studies that show significant decreases in abundances of bivalve species due to *C. maenas* predation (Walton, 2003; Elner, 1981; Floyd & Williams, 2004; Grosholz et al., 2000), but was a similar outcome to a previous study in British Columbia, BC (Howard et al., 2019). In plots that had no *C. maenas* activity we observe increased abundance across all densities from pre-experiment to post-experiment particularly with polychaete species in high density and bivalve species in low density. Increases for specific populations is likely linked to a decrease in predation in enclosures with no *C. maenas* (Janke, 1990). Low and high density open plots experienced no change in abundance, but we do see a decrease in medium density, which could be attributed to having cores that happen to catch organisms that congregate together like *Notomastus tenuis*. For epifauna, we observed a high abundance of *Phyllaplysia taylori* and their eggs on the blades of *Z. marina*, but few other organisms.

Interaction between Z. marina *and* C. maenas

While there was no significant interaction between *Z. marina* density and *C. maenas* on *Z. marina* health, we did observe *Z. marina* density and *C. maenas* activity as separate significant variables when looking at metrics of *Z. marina* health. While there was almost no loss in *Z. marina* shoots due to *C. maenas* activity in low and medium density plots, we observed an average decrease of 6.54 shoots in high density plots over a two-week period. This is compared to an increased in shoots seen across all densities that did not have *C. maenas* activity. Contrary to the findings of Howard et al. (2019), we did not observe the same drastic decline in *Z. marina* shoots with *C. maenas*. The difference in findings could be a result of experimental duration as our study was carried out over the course of two weeks while Howard et al. (2019) conducted their experiment over four weeks. There was also a significant difference in the average total number of shoots: 796 shoots m^{-2} in their study and 184 shoots m^{-2} in our study. This difference in shoot density could be an important factor to explain why we did not observe a significant interaction between *Z. marina* density and *C. maenas.* Fewer total shoots could have allowed *C. maenas* to forage without having to uproot *Z. marina* as they were able to easily dig for prey where *Z. marina* was sparse or absent. This is notable because Garbary et al. (2014) found that much of the decline in *Z. marina* coverage was due to the extension of bare batches in *Z. marina* beds where *C. maenas* was foraging.

A number of factors may contribute to our observation of fewer changes in *Z. marina* compared to earlier studies. First, given its status as designated conservation estuary, Netarts Bay may experience fewer environmental stressors compared to other estuaries, which could contribute to more resilient *Z marina* beds (Demeter Design, 2008). Nonetheless, *Z. marina*, especially at low densities, experienced a loss in percent coverage over the course of two weeks. This degree of loss in such a short period of time still indicates a vulnerability that could be further exacerbated by climate change. In addition, while we saw no strong discernable interaction between *C. maenas* presence and *Z. marina* density, *C. maenas* contributed to a loss in *Z. marina* percent coverage and shoots. Our low sample size combined with high variability in *Z. marina* estimated percent cover means it is possible the statistical tests did not detect a real pattern that exists. Power analysis showed that an increase of three to four times ins ample size would be needed to demonstrate statistical significance.

While not significant, we did see notable differences in number of shoots in high density plots with *C. maenas* compared to without. We did not use juvenile *C. maenas* in our study, which are known to impact blades more than shoots, so a subsequent study using juvenile *C. maenas* might find a decrease in percent cover through damage to blades rather than the uprooting of entire shoots (Malyshev & Quijón, 2011). *Z. marina* is likely well adapted for the pressure brought on by the cutting and grazing of *C. maenas* during foraging. *Zostera spp.* have the ability to reallocate resources to ungrazed shoots on the same rhizome and store carbohydrates during specific seasons to ensure long-term survival (Dawes & Guiry, 1992; Harrison, 1978). *Zostera spp*. are likely not adapted to being uprooted entirely and the differences in cover is likely more noticeable in low density plots. Overall, *Z. marina* likely has compensatory mechanisms that reduce effects from *C. maenas* foraging, but with additional stressors like climate change, this could put *Z. marina* beyond its threshold. Our results add to mounting evidence of the negative effects of *C. maenas* on *Z. marina* ecosystems. If *C. maenas* populations continue to increase on the Oregon Coast, a trend that is likely to continue under climate change, coastal ecosystems will suffer especially those that are already vulnerable and less resilient.

Conclusion

C. maenas are one of the more well studied invasive species and previous studies have found bioturbation due to *C. maenas* negatively effects *Z. marina* ecosystems (Garbary et al., 2014; Grosholz, 2011; Malyshev & Quijón, 2011; Matheson et al., 2016). However, the ability for *C. maenas* to forage seems to depend on habitat complexity and food availability (Orth et al., 1984; Wong, 2013). This led us to ask whether the density of *Z. marina* would affect its overall health and survival through *C. maenas* activity.

It was hypothesized that higher densities of *Z. marina* would inhibit the ability for *C. maenas* to forage efficiently due to a thicker rhizome mat and therefore there would be less effect on *Z. marina* coverage. We found that *C. maenas* do contribute to greater *Z. marina* loss across densities compared to control plots which is consistent with earlier findings that did not focus on *Z. marina* density (Garbary et al., 2014; Howard et al., 2019). However, we did not find a significant relationship between *C. maenas* activity and *Z. marina* density on the change in *Z. marina* coverage. We observed that low density *Z. marina* experiences greater loss in percent cover compared to medium and low density regardless of *C. maenas* presence, averaging a 10% decrease in percent coverage with *C. maenas* presence and 3% decrease without *C. maenas* after a period of two weeks. Our results and those from British Columbia, show that even healthy, established *Z. marina* beds with low eutrophication, *C. maenas* still has measurable impacts (Howard et al., 2019). A rapid loss of *Z. marina* habitat due to *C. maenas* activity could have major implications for coastal ecosystems and food web dynamics.

Currently, there is still a relatively low abundance of *C. maenas* in Oregon, which has meant that concern has not reached the point of action. However, there is data that indicates that populations are growing (Behrens Yamada et al., 2018). Since *C. maenas* live up to six years, if current populations include young of the year, they could continue producing larvae until 2027. *C. maenas* have been identified as ecosystem engineers with the ability to modify their environment, changing the biotic and abiotic characteristics of a particular ecosystem (Crooks, 2002). Growing populations of *C. maenas* could have negative impacts for native and transplanted *Z. marina* beds across Oregon, endangering the variety of invertebrate, fish, and bird species that depend on it for habitat, and threatening local shellfish economies (Grosholz, 2011; Matheson et al., 2016; Davis et al., 1998; U.S. EPA, 2008).

Estuaries are major hubs for biodiversity, but they are also one of the more highly invaded ecosystems today. Successful invasive species like *C. maenas* have the potential to make environmentally and economically costly changes to our coastal habitat as has been documented on the Atlantic Coast.

Management implications

This species is still a relatively new invader to Pacific coastlines and with a well targeted management plan, its populations can be controlled and its spread to new estuaries prevented. In areas, were *C. maenas* have yet to establish, it is recommended to have ships manage their ballast water, including between invaded to non-invaded bays along the same coast. However, there is evidence that there are estuaries in Oregon and Washington where *C. maenas* have high larval supply that can seed future populations in other regional bays (Tepolt & Somero, 2014). Because of larval dispersal, *C. maenas* can spread quickly to new areas so ridding ourselves of *C. maenas* is an unlikely goal, but controlled populations should help keep *C. maenas* at numbers that will not be detrimental to native species, *Z. marina* ecosystems, and the aquaculture industry (Green & Grosholz, 2021).

The population of *C. maenas* in Netarts Bay appears to be established and growing, so population control through trapping to minimize impacts is crucial in addition to attempting to create financial incentives for the public to harvest *C. maenas* as part of a bounty program or encouraging recreational fishing for *C. maenas* as a food (U.S. EPA, 2008). Eradication through trapping is most effective when the species population is low, but widespread populations can also be eradicated (Simberloff, 2003).

Unlike Washington or British Columbia, Oregon does not have a coordinated effort to actively manage *C. maenas*. In order to stay on top of maintaining this species' population, a region wide management plan is needed. Not managing for *C. maenas* means endangering vulnerable ecosystems not just in Oregon, but up and down the West Coast of North America. These ecosystems will only continue to become more vulnerable as climate change exacerbates the problem of invasive species especially with *C. maenas* which is better adapted to a variety of habitats and warmer waters. If Oregon's resource managers routinely controlled invading populations, including *C. maenas*, before they were a problem, this could avoid the heavy monetary costs associated with addressing established populations of invasive species. More weight should be put on controlling populations before they are a problem. The Oregon Invasive Species Council whose stakeholders span various federal, state, and local agencies, could work toward creating a streamlined approach to *C. maenas* management and outreach, in addition to creating easily accessible information on identification and management strategies for the public through published resources.

Beyond just management solutions, striving to increase public awareness about *Z. marina* ecosystems and the negative impacts of *C. maenas* could bring public assistance in controlling *C. maenas* populations and create more conscientious users of *Z. marina* beds. *Z. marina* ecosystems are critical habitat and the public perception of *Z. marina* should be similar to that of coral reefs and mangroves. Continued public outreach, monitoring, and research of seagrasses should be a high priority as seagrass habitat is often subject to a variety of human impacts due to being in easily accessible, shallow areas. Additionally, since *Z. marina* is sensitive to various environmental variables including extreme temperatures, changes in salinity, light attenuation, and epiphyte load, continued monitoring of these variables and its effects on *Z. marina* fitness are critical for maintaining Oregon's native *Z. marina* distribution. Netarts Bay is a highly trafficked recreational clamming area and disturbance due to extensive clamming can inhibit *Z. marina* growth. Hence, better public awareness about avoiding low density *Z. marina* during recreation would minimize impacts to already vulnerable habitat. This is also an opportunity to engage with the public about trapping and eating *C. maenas*. Fostering and encouraging this activity for those who are interested could help improve resiliency to recreational crabbing in Oregon and provide additional food and subsistence for lower income residents.

Estuaries across Oregon have already experienced a loss in *Z. marina* cover and there have been management projects done to restore native beds with *Z. marina* transplants. These projects are costly and have low success rates (Park & Lee, 2007). The results of our study show that when *Z. marina* transplant projects are done they should strive to plant in higher densities as low densities were more susceptible to loss in cover. In addition, *C. maenas* trapping should be prioritized in areas with low densities of *Z. marina* as they are the most at risk to loss in coverage.

Study Limitations

We noticed on several occasions that other *C. maenas* would be buried next to or on top of our enclosure skirts. Since crab behavior is impacted by interactions with other crabs and habitat complexity, it is unclear whether this was seen as protective cover and a way to avoid to desiccation during low tides or if this was some type of hormonal response to the *C. maenas* within the enclosures (Gehrels et al., 2017).

We also noticed that the *C. maenas* in our enclosures tended to distance themselves from each other within the enclosures often hiding under the PVC pipe frame, crawling the plastic mesh, and burying themselves in opposing corners. This could be due to trying to avoid predation and desiccation or an agonistic behavior could have changed feeding behaviors and influenced prey choices within our enclosures (Boudreau, Boudreau, & Hamilton, 2013). Conspecific interference inhibits *C. maenas* feeding rates, especially with high densities of crab, and can involve kleptoparasitism (Griffen & Williamson, 2008; Sneddon, Huntingford, & Taylor, 1997; Quinn et al., 2012). We also had two replicates that were conducted during the 2021 heatwave that corresponded with low tides, which could have also altered *C. maenas* behavior.

Crab recovery was not 100% at the end of the experiment. We assumed that crabs were within the enclosures for the duration of the experiment, and due to a change in tides, we were unable to fully check the enclosures for crab presence after they were deployed. So, results could be skewed if *C. maenas* were able to escape early on in the two-week period. Additional staples around the bottom of the enclosure, especially in areas where the sediment height changes, would likely further reduce the likelihood of *C. maenas* escape.

Netarts Bay is heavily trafficked and as a result, we experienced theft of several minnow traps that resulted in a discontinuation in their use. Minnow traps typically select for smaller crabs, which likely caused the distribution of our crab trappings to be skewed towards larger crabs and are not indicative of the actual population distribution present in that portion of Netarts Bay. Setting minnow traps out of public view and with signage about their use could potentially reduce theft.

Lastly, we had a limited number of field workers who could be out in the field together. A team of researchers would be able to put up and take down the experiment more swiftly, thus having the ability to do more replicates in less amount of time. It took two people twenty to thirty minutes to set up each enclosure and take data collection. So, with an experienced team of six, we were able to set up two replicates in one day. However, with more people in the field, the impacts to *Z. marina* is greater. We found that our foot paths were still visible for several weeks after we moved the enclosures. Avoiding heavy foot traffic in low density *Z. marina* would reduce the overall impact. We checked our enclosures

Future Considerations

Our power analysis indicated that we would need 27 replicates to find a relationship between *C. maenas* and *Z. marina* density. We set eight replicates to minimize the impact to *Z. marina*. The number of replicates required to find significance would have been detrimental to the health of *Z. marina* in Netarts Bay due to the impact of the enclosures, *C. maenas*, and researcher foot traffic in a limited area. Working in *Z. marina* beds that allow for the ability to move each round of replicates to a new area would allow for the recovery of *Z. marina* and limit the repeated impact from the experiment returning to a similar area. A natural experiment that takes advantage of varying *C. maenas* abundance is an alternative to our enclosure experiment that could limit the impact of enclosures and foot traffic.

Netarts Bay, in comparison to other Oregon estuaries, has denser and more robust *Z. marina* with greater belowground biomass that makes it more resilient. Conducting this research in a different bay would likely provide different results and more evidence of *C. maenas* as an added stressor to *Z. marina* health.

There is a clear need for further studies of the potential threats to *Z. marina*, especially those that focus on compounding effects. In addition, more studies that focus on how climate change will impact established and transplanted *Z. marina* beds and the dispersal of *C. maenas*. Lastly, because *Z. marina* is sensitive to a variety of environmental variables, continuing to understand what contributes to successful transplanting of *Z. marina,* specifically under climate change on the Oregon Coast.

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Appendix. Additional Figures

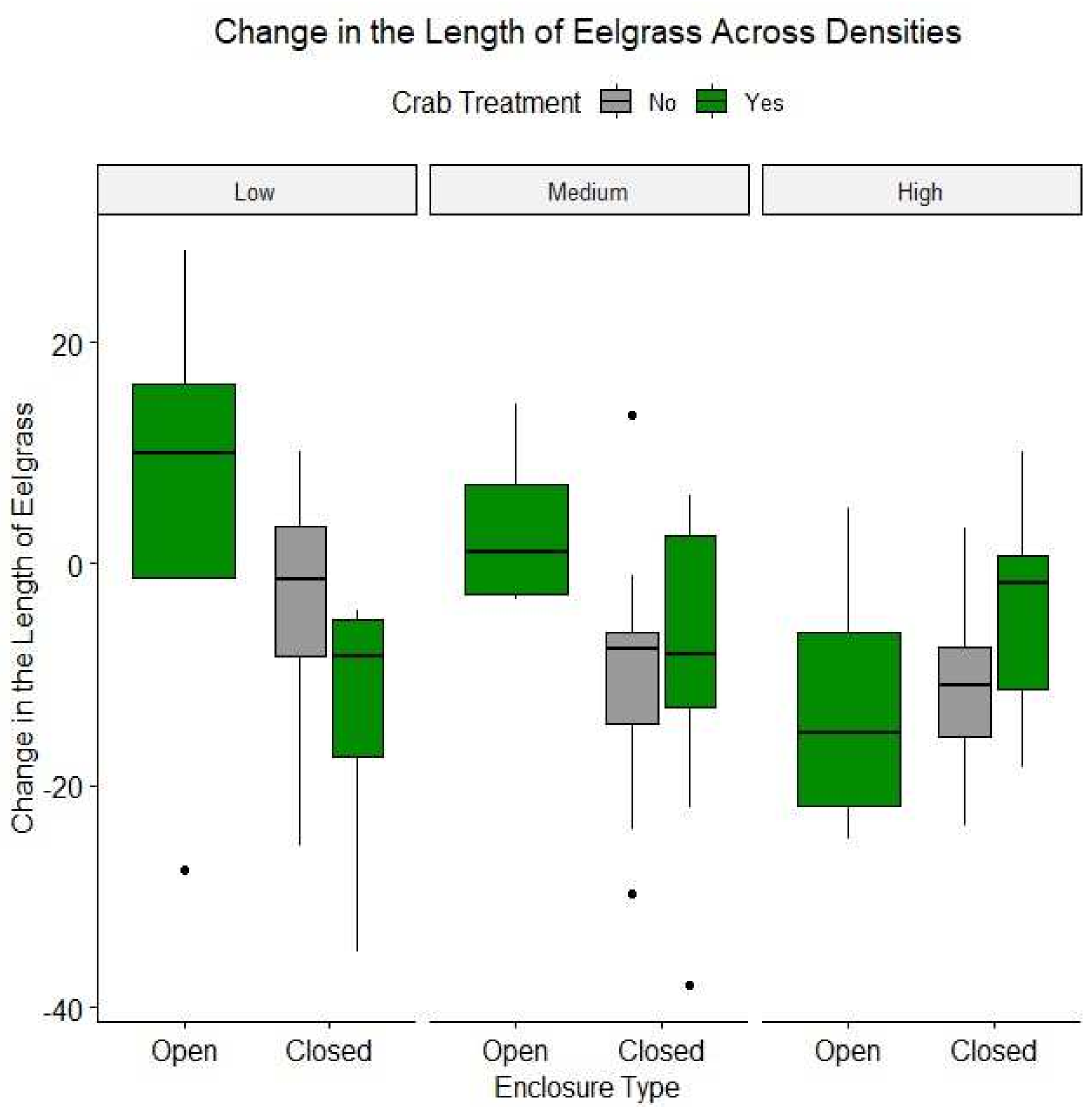

Figure 11: Change in *Z. marina* length in open and closed plots. Open plots were exposed to ambient densities of crabs. Closed plots were with or without crab treatment. The lower and upper bounds of the box correspond to the first and third quartiles and the line in between represents the median. The upper and lower whisker represent the maximum and minimum value, respectively.

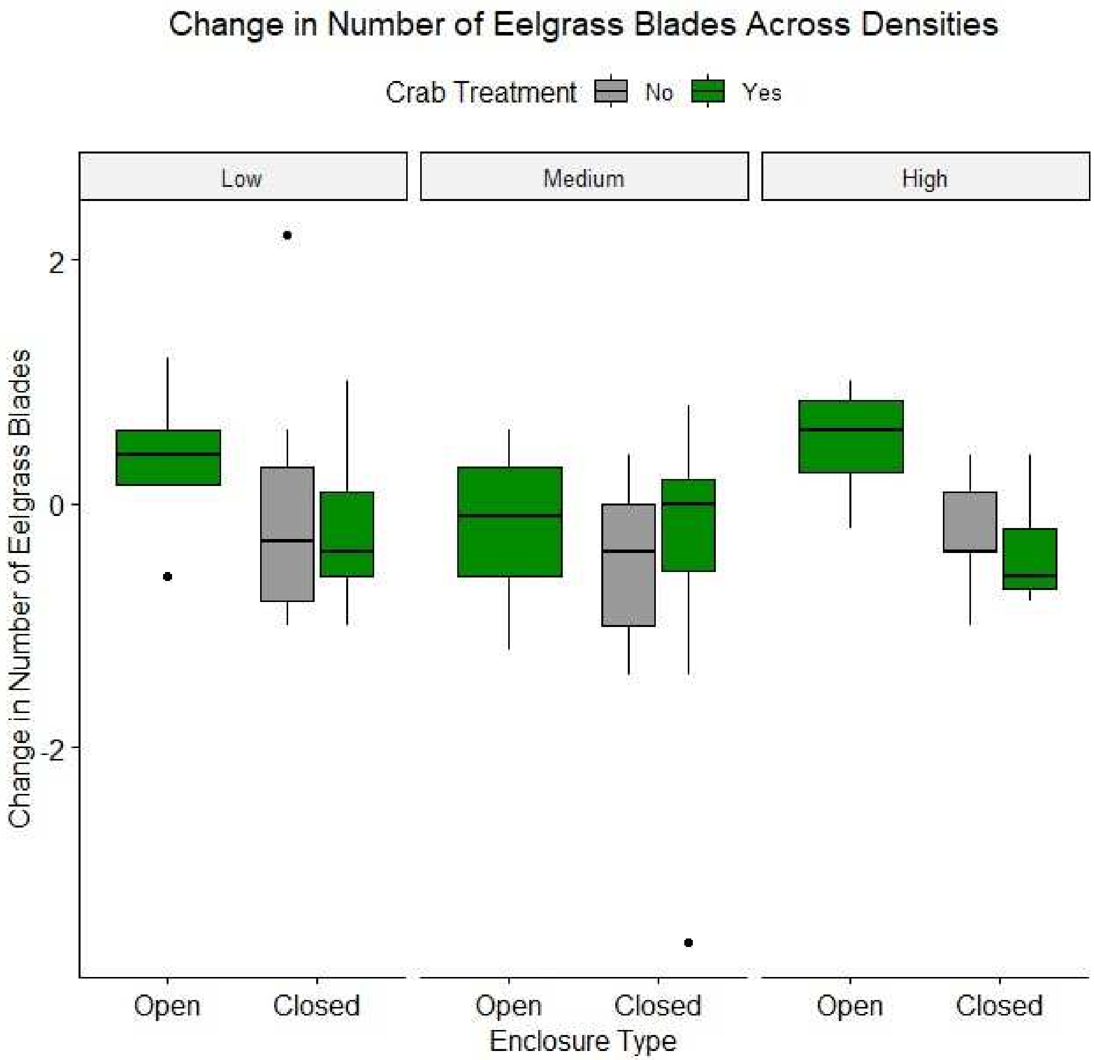

Figure 12: Change in number of *Z. marina* blades across *Z. marina* densities in open and closed plots. Open plots were exposed to ambient densities of crabs. Closed plots were with or without crab treatment. The lower and upper bounds of the box correspond to the first and third quartiles and the line in between represents the median. The upper and lower whisker represent the maximum and minimum value, respectively.

Table 4: 2-way ANOVA output for change in the number of Z. marina shoots in low, medium and high Z. marina density closed plots with and without crab treatment, open plots with ambient crab density, and with date as a blocking factor.

	Change in number of *Z. marina* shoots				
	Df	Sum Sq	Mean Sq	F Value	Pr (>F)
Z. marina Density	2	202	101.1	0.234	0.7921
Crab Treatment	1	2126	2125.8	4.975	0.0311 *
Date	1	421	420.9	0.975	0.3282
Crab Treatment: Density	2	401	200.3	0.464	0.6315
Residuals	50	21587	431.7		

Table 5: 2-way ANOVA outputs for the ratio of percent change in final *Z. marina* cover compared to initial percent cover in closed plots with and without crab treatment, open plots with ambient crab density, and with date as a blocking factor.

	Ratio of % change in final cover compared to initial % cover				
	Df	Sum Sq	Mean Sq	F Value	Pr (>F)
Crab Treatment	1	0.0488	0.04885	1.870	0.178
Density	2	0.0975	0.04877	1.867	0.165
Date	1	0.0050	0.00500	0.192	0.664
Crab Treatment: Density	2	0.0285	0.01425	0.546	0.583
Residuals	50	1.3059	0.02612		