

**Functional redundancy of a non-native foundation species (eelgrass, *Zostera japonica*)
across intertidal stress gradients**

An Honors Paper for the Department of Biology

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ABSTRACT

Non-native species foundation species can alter ecosystems in both positive and negative ways. The creation of habitat can be beneficial to native species when they provide a limiting resource or in a stressful environment. Yet this creation of habitat can also be detrimental by replacing native species and/or facilitating the presence of more non-native species. In Willapa Bay, WA, a non-native foundation species, *Zostera japonica*, co-exists with the native foundation species *Zostera marina*. *Zostera japonica* persists at the higher intertidal in monocultures, the two species overlap in the mid intertidal, and *Z. marina* persists in monocultures in the low intertidal. Epifaunal invertebrates, the organisms that live on eelgrass blades, connect eelgrass to higher trophic levels. Through a series of transplants and removals, I used this zonation pattern to ask if the two species can fulfill a similar functional role in respect to epifaunal invertebrates (functional redundancy), and if this was due to the identity of the foundation species or a response to the stress gradient of the intertidal. My results suggest that the epifaunal invertebrate community is responding more to the physiological stress gradient, and the functional redundancy of the two species depends on the location they are found. *Z. japonica* is expanding the range of vegetated habitat into to the physiologically stressful high zone, which supports a different community. This experiment highlights that the impacts of non-native species are highly localized and that abiotic and biotic factors are important to trophic interactions.

INTRODUCTION

Non-native foundation species occupy a problematic ecological position regarding ecosystem impacts. Foundation species are numerically abundant and their tissues creates habitat that supports a diverse array of organisms Ellison (2019). Foundation species also alter physical properties of the ecosystem to make it more hospitable for other organisms (Ellison 2019). Where non-native foundation species create a novel habitat type, their effects can be transformative for biogeomorphology, the reciprocal interactions between organisms and landforms (Fei et al. 2014). When non-native foundation species occupy a niche similar to an existing native species, they may be more (or less) likely to displace this species competitively (Daehler 2001, Gioria and Osborne 2014). If a non-native foundation species provides habitat that disproportionately favors other non-native species, a mechanism emerges for “invasional meltdown”, which results in a shift to a community dominated by more non-native species (Simberloff and Von Holle 1999). Yet despite this range of opportunities for non-native foundation species to disrupt biodiversity, such species are also recognized for potential beneficial effects (Katsanevakis et al. 2014), particularly under global change scenarios in which native foundation species are unable to maintain ecological functions or have already disappeared (e.g. Ramus et al. 2017). Habitat modification in environments that are physiologically stressful may allow for the facilitation of native species (Rodriguez 2006). The field of invasion ecology will advance with specific tests of how non-native foundation species perform under increasing environmental stress, and the extent to which the habitat functions they provide are redundant with those of native foundation species.

In a stress gradient, foundation species can ameliorate stress for associated species. The intertidal zone presents an inherent stress gradient for marine organisms that experience longer emersion times at higher elevations (Bertness and Leonard 1997) while also sitting at the land-water interface where non-native foundations species are predicted to create particularly large biogeomorphological change (Fei et al. 2014). On Pacific Northwest tidal flats, a non-native

foundation species (dwarf eelgrass, *Zostera japonica*) has over the past six decades established in an intertidal zone above native eelgrass, *Zostera marina* (Shafer et al. 2014). The distribution may be disjunct (unvegetated between lower *Z. marina* and higher *Z. japonica*), mosaic (patches of *Z. marina*, often in shallow pools, within the high zone with *Z. japonica*), or overlapping (Shafer et al. 2014). This overlapping distribution sets up an opportunity for interspecific competition, but also for a novel habitat type in which the architecture of two different eelgrasses is present, with *Z. japonica* often shorter, denser, and more seasonally variable than *Z. marina* (Ruesink et al. 2010).

Morphological and life-history variation between these two *Zostera* species underlies their response to stress (zonation patterns) and potential competitive interactions. The size of plants, a well-known functional trait, differs substantially between the two species: *Z. marina* has longer and wider blades than *Z. japonica* (Ruesink et al. 2010). Where the two species co-exist *Z. marina* occupies the low tidal elevations, both species occur in the mid zone (typically the upper limit of *Z. marina* and the lower limit of *Z. japonica*), and *Z. japonica* occurs at the high tidal elevations (Shafer et al. 2014). It is thought that the upper limit of *Z. marina* is set by the physiological stress of being exposed to air (Shafer et al. 2007) while the lower limit of *Z. japonica* is set by competition with *Z. marina* (Shafer et al. 2008). *Zostera japonica* has high sexual and asexual reproductive output, faster growth rates, and shorter and narrower blades size (Ruesink et al. 2010). These traits *Z. japonica* can coexist with *Z. marina* in this zone by filling in the bare spaces between *Z. marina* plants (Ruesink et al. 2010). Interspecific competition between these species has been shown to differ depending on environmental conditions. *Zostera japonica* can survive on the more physiologically stressful mounds while *Z. marina* can survive and outcompete *Z. marina* in the less physiologically stressful pools (Hannam and Wyllie-Echeverria 2014). After disturbance events *Z. japonica* can quickly colonize bare patches faster than *Z. marina* (Bando 2006). In competitive interactions between eelgrasses, body size is critical with *Z. japonica* negatively impacting smaller-bodied eelgrasses but not the larger bodied *Z. marina* (Boardman and Ruesink 2022). Prior to the introduction of *Z. japonica*, the high zone was unvegetated habitat, as it is too physiologically stressful for *Z. marina* to thrive (Boese et al. 2005). The smaller *Z. japonica* takes advantage of this typically unvegetated habitat and dominates this zone in monocultures (Harrison and Bigley 1982, Posey 1988).

One of the concerns with *Z. japonica* is that its morphological and ecological differences from *Z. marina* might alter the quality of available habitat. Alternatively, despite morphological differences, these two species might be functionally redundant in terms of abundance of associated species, which may respond more to total surface area rather than to the shape of blades. The epifaunal invertebrate community provides a trophic link between eelgrass species and juvenile fish (Adams 1976) and can serve as a model community to ask the question of functional redundancy: can the two species fill the same functional role within the ecosystem? As climate change alters the distribution of foundation species, functionally redundant non-native foundation species may play critical roles in the resilience of the ecosystem (Walker 1992). Epifaunal communities can shift rapidly seasonally (Ruesink 2016, Gross et al. 2019), but typically occur at high abundance on both *Z. marina* and *Z. japonica* (Posey 1988). Some studies have shown that they can support similar epifaunal invertebrate communities (Knight et al. 2015, Mach et al. 2014), although previous studies have not examined their structure across the stress gradient of tidal elevation. Elevational shifts in epifaunal community structure could reflect direct impacts of prolonged emersion (temperature and desiccation) or could be indirect results of typical shifts in the morphological traits of eelgrass across depths, since larger plants with

longer blades occur at lower tidal elevations and deeper depths (Keller and Harris 1966). Additionally, epifaunal invertebrates may track the abundance of their resource (epiphytes) or be affected by top-down control by predators, which could shift seasonally (Ruesink 2016, Gross et al. 2019) and across tidal elevations (Micheli et al. 2008).

The architecture of a foundation species, for instance, structural complexity or plant body size, is expected to influence its habitat value (Heck and Wetstone 1977, Kovalenko et al. 2012). Overlapping (mixed) conditions of *Z. marina* and *Z. japonica* could therefore provide distinct habitat from either species alone. The larger *Z. marina* creates a canopy while the smaller-bodied *Z. japonica* creates an understory. Ultimately this might create a higher biomass and facilitate a higher abundance of epifauna (Heck and Wetstone 1977, Kovalenko et al. 2012).

Determining the degree to which non-native and native foundation species are functionally redundant in regard to the epifaunal invertebrate community and epiphytes will have important management implications in a changing environment due to climate change. As stressors intensify and potentially cause the native species to reach its physiological limit, the non-native foundation species might provide habitat for native species (Rodriguez 2006). Alternatively, *Z. japonica* might cause an “invasional meltdown” by facilitating the persistence of other non-native species (Simberloff and Von Holle 1999, Ramus 2017), which could come at a cost to native species.

My study addresses the epiphyte and epifaunal response to physical changes across a stress gradient in tidal height. The gradient from native to non-native allows for the testing of by keeping habitat consistent, and to the consequences of having changes in foundation species that shift from mostly native at the low-stress end of the gradient to mostly non-native at the high-stress end. Comparing the quality of habitat that the two species provide is challenging because the two foundation species differ in functional traits as well as typical elevational distribution, a challenge I approached by experimental manipulations of both eelgrass species at multiple intertidal elevations and two sites. This design decoupled the impacts of abiotic changes across zones from the identity of the foundation species to better assess functional redundancy. With this design, I also tested the degree of competition between the non-native and native foundation species at different tidal heights. In this study, I used two sites in a shallow estuary in Willapa Bay, Washington, to conduct a field experiment where I manipulated the presence-absence of the native *Z. marina* and non-native *Z. japonica* at three tidal heights. After 1.5 months, I quantified eelgrass biomass, the epiphyte load, and the abundance and composition of epifaunal invertebrates and nekton (fishes, crabs, etc.) communities. I also quantified the proportion of epifauna consisting of non-natives, in order to address whether invasional meltdown was occurring in this system. Specifically, with these data I address three questions:

1. Zonation: How do eelgrass communities differ across an intertidal stress gradient in which the foundation species shifts from native to non-native? Eelgrass communities were evaluated in terms of zonation patterns in biomass, epiphyte load, epifaunal abundance and type, proportion of non-native epifaunal invertebrates, and nekton. These analyses were carried out on initial observational data and with experimental plots that were unmanipulated, specifically *Z. japonica* monocultures at the high, mixed plots at the mid, and *Z. marina* monocultures at the low zone.
2. Functional Redundancy: To what extent are patterns seen in epifauna and epiphytes due to the direct effects of physiological stress (keeping foundation species identity

- constant) or indirect effects of a shift in foundation species across zones? Further, how much of the epiphyte and epifaunal community patterns at the mid-intertidal zone reflect the intermixing of two foundation species, distinct from what would associate with a monoculture? These analyses were carried out on experimental data only, specifically comparing associated communities on each foundation species across zones, and then comparing monocultures and mixtures especially in the mid zone.
3. Habitat Complexity: Does the increased structural complexity of *Z. marina* growing alongside *Z. japonica*, such as in the mid zones, change the epifaunal community or epiphyte load around the *Zostera* species? Does growing in proximity to *Z. japonica* increase the proportion of non-native species on *Z. marina*? These analyses were done comparing monocultures and mixtures within each foundation species, across sites and zones.

METHODS

Study Site

Experimental manipulations of native *Z. marina* and non-native *Z. japonica* were conducted in Willapa Bay, Washington, USA (Fig. 1). Willapa Bay is estuary with a mean tidal range of 1.9m (Hickey and Banas 2003). During the summer, the bay experiences a decrease in river water input along with an increase of effects associated with oceanic upwelling. Two sites were about 10 km apart (Fig. 1). The two sites differed in sediment type and the slope of the tidal flat (Table 1). At these two sites, both species of *Zostera* occurred with distinct tidal zonation (see RESULTS, Table 3). At both sites, *Z. japonica* occurred as a monoculture at the higher tidal elevation, while both species coexisted at mid and low tidal elevations in varying proportions. Of the two sites, the site with the more extensive tidal flat (Sloughville) had a larger area of overlap, in which *Z. marina* extended to higher elevations in pools, and, even at the low zone, some *Z. japonica* was present. Tidal zone was split into three categories, low, mid, and high; and was determined by the *Zostera* species present. The low zone had only or mostly *Z. marina*, mid zone included the two species interspersed, and the high zone had only *Z. japonica*, corresponding to an absolute elevation difference of 1.4 to 1.8 m (Table 1).

Zonation

The density of each eelgrass species was measured at each site and tidal height. Since *Z. marina* did not occur at the high tidal height, the total number of shoots in the 6, 1 m² plots were counted at the mid and low tidal heights. These were averaged across samples (n=6). For *Z. japonica*, 6, 10 cm cores were taken at each zone and number of shoots was averaged by zone. The counts from the cores were then scaled to be equivalent of the densities in 1 m². To characterize the epifaunal invertebrate community before experimental manipulations, the epifaunal community was sampled initially in each zone, early June 2022. This allowed for the examination of important factors before experimental manipulation. All epifauna species were collected on *Zostera* blades in shallow (10-20 cm depth) water during ebb tide, with a mesh bag (diameter of 20 cm, 80 µm mesh) slipped over the blades, which were then severed above the sediment. At the mid tidal height, where the two species were interspersed, one sample containing at least one plant of only *Z. marina* and one containing only *Z. japonica* were

collected at each sample location. Within two hours, each sample was agitated three times with fresh water to dislodge epifauna, and the water was then passed through a 0.5 mm sieve. Material caught on the sieve was preserved in ethanol for later identification of invertebrates. Eelgrass from each sample was dried (60 C for >3 days) and weighed for later standardization of epifauna to the amount of eelgrass biomass collected, as samples included varying amounts of eelgrass. Samples were examined under a dissecting microscope at 10-20x power, and all invertebrates were identified to the taxonomic resolution of family, with select taxa to genus or species. Taxon were identified using a key (Light 2007) and verified by Bob Oxborrow a graduate student at the University of Washington. To quantify if there was an invasional meltdown, or that *Z. japonica* was facilitating the establishment of non-native species compared to native species, the proportion of non-native species to the total number of species was calculated for each plot. Native vs. non-native species were categorized by non-native species listed in Wonham and Carlton (2005) with the exclusion of *Apithoe valida* due to its recently contested invasion history (Harper et al. 2022).

One week before the end of the experiment, nekton (fish, crabs, shrimp) were sampled at the three zones at each site. Nekton were collected in a custom beach seine deployed when the water was 40-70 cm above the sediment. The seine (3 mm mesh) had 6-m wings that were walked out in a circle, and then compressed to chase nekton into the cod end. The cod end was lifted into a tub of seawater, all individuals were identified and counted, and the first 10 of each species was measured for length, as they were removed and immediately released. Seines were replicated about 10 m apart at each zone and site (N=3).

Functional redundancy

To test if the epifauna community was associated with one of the foundation species, rather than site and zone, I manipulated the composition of *Zostera* species (“foundational structure”) in experimental plots. At each study site, three foundation structure treatments were established in 1 m² plots in each of the three tidal heights. The three treatments were: i. monoculture of *Z. marina* (Zm), ii. monoculture of *Z. japonica* (Zj), and ii. mixture of the two (Zm & Zj). Each zone had a 6 replicate plots for each treatment, giving a total of 18 plots per zone (1 m²). Plots were spaced at least 2 m apart along a horizontal transect and treatments were assigned in a stratified random design. Depending on whether an eelgrass species was already present in the zone, transplants and/or removals were performed to create the treatments (Table 2) Transplants were done at low tide, when the eelgrass plants had fewer epifaunal invertebrates on them. Epifaunal invertebrates and epiphytes were not removed before transplanted. Removals of the plant, including the rhizomes were done in the 1 m² plots and transplants were only added to the center 0.25 m² to create a 0.375 m buffer zone between the new transplants and the environment. Transplants included the rhizomes. Due to their differences in size, *Z. marina* transplants were transplanted as individual shoots with rhizomes, and *Z. japonica* was transplanted using cores that included sediment. There were approximately 250 shoots of *Z. japonica* transplanted into the center 0.25 m².

For the high zone treatments (Zm and Zm & Zj), all *Z. marina* was transplanted from either mid or low to the high zone. For *Z. marina* monoculture (Zm) and mixture treatments (Zm & Zj), 25 shoots at Stackpole and 35 shoots at Sloughville were placed into the central 0.25 m² area of plots. These densities were chosen to maintain the slightly higher density of *Z. marina* at Sloughville compared to Stackpole. For *Z. japonica* monoculture treatments (Zj) plots were not

manipulated for density. Starting biomass of *Z. japonica* was not controlled for but appeared visually to have similar coverage of eelgrass across the zone.

At the mid tidal zone, *Z. marina* shoots were removed from the mid plots to create *Z. japonica* monoculture treatments (Zm), and *Z. japonica* was removed to create *Z. marina* monoculture treatments (Zj). For mixture treatments at the mid-intertidal both species were left unmanipulated (Zm & Zj). At the low tidal zone, *Z. marina* monoculture treatments (Zm) were unmanipulated (Stackpole) or involved removing some *Z. japonica* (Sloughville). Also at the low tidal height, *Z. japonica* monoculture treatments (Zj) were constructed by adding 16 cores (10 cm depth 10 cm diameter) with *Z. japonica* collected from a monoculture area. These cores, placed in the central 0.25 m² of plots, resulted in a density of approximately 1000 shoots per 1m². For the mixture treatments at the low, 16 cores of *Z. japonica* were added at Stackpole. At Sloughville, where *Z. japonica* was already present at low elevation, cores were added only to the portions of the central 0.25 m² that did not contain *Z. japonica* shoots. To control for the disturbance created by the removals and transplants, the process was mimicked by digging by hand into the center 0.25 m² of the plots that received neither treatment. These treatment and zone combinations are indicated by “0” in Table 2. Starting densities and biomass of either eelgrass species were not controlled for in all conditions that had no manipulations, however, the plots had similar amounts of coverage of eelgrass.

Experimental plots were set up during the last week of May and through mid June 2022. All treatments were in place on June 14th, 2022. The experiment ran for 6 weeks before the start of a week and a half data collection period on July 25th, 2022. Collection at the end of the experiment coincided with the timing of maximum eelgrass biomass (Ruesink 2016).

To contrast different communities in these plots and test for functional redundancy, the epifaunal invertebrate community was sampled at the end of experiment from the center of the plots in a 0.25m² area, following the same methods as the initial invertebrate sampling described in *Zonation* (above). Eelgrass grows rapidly, with leaf plastochrone intervals less than two weeks in summer (Ruesink et al. 2018), which means the biomass of each plant was entirely replaced over the course of the 6-week experiment. All epifaunal and epiphyte communities, as well as traits of eelgrass, were therefore generated during the experiment. One sample was collected in the plots with monoculture treatments and two samples, one sample per foundation species, were collected in the mixture treatment plots. To determine the relative amount of food resources available to the epifauna, a subset of shoots was collected from each plot, and all epiphytes were scraped off the eelgrass within 24 hours, dried in a drying oven (60 C for >5 days), and weighed to the nearest 0.1mg. The epiphyte community was largely diatoms. For *Z. marina* one shoot was collected, and five shoots were collected for *Z. japonica*. Multiple *Z. japonica* plants were collected as these plants are smaller and the mass of epiphytes would not have been detected from one plant. Epiphyte biomass was standardized to shoot mass, which was also measured to the nearest 0.1 g.

Data Analysis

To test if there was zonation, analyses of variance (ANOVA) models were used on the data for biomass, epiphyte load, total epifaunal abundance, proportion of crustaceans, proportion of non-native. For total epifaunal abundance, proportion of crustaceans, and proportion of non-native species, there are two time points, the initial sampling, and the sampling at the end of the experiment. When analyzing the experimental plots for zonation patterns, only the unmanipulated plots (*Z. japonica* monocultures at the high, mixture of both species at the mid,

and *Z. marina* monocultures at the low) were used. Since all species did not co-occur at all zones the data was split in three ways. To compare between the species, only data from the mid zone where the two species co-occur was analyzed, and a two-factor ANOVA model with two levels of site (Stackpole and Sloughville) and two levels of species (*Z. japonica* and *Z. marina*) was used. To test if there were zonation effects within each *Zostera* species, the data was separated by species and a two-factor ANOVA model with the levels of site (Stackpole and Sloughville) and three levels of zone (mid and low) was used. For the overall abundance of nekton, the data was analyzed with a two-factor ANOVA model with the two-levels of site (Stackpole and Sloughville) and three-levels of zone (high, mid, and low). The same analysis was repeated for each category of nekton (crustaceans, eelgrass mimics, benthic, and pelagic). To meet assumption of normality, the biomass, epiphyte load, epifaunal abundance, and nekton were all log transformed before analysis. Finally, a permutational analysis of variance (PERMANOVA) was used to analyze the initial and unmanipulated epifaunal invertebrate community (Oksanen J et al. 2022, R Core Team 2023). The community data was relativized by taking the observed number of individuals for each species and dividing it by the maximum number of that species. The data was split in the same ways as the univariate analysis (mid zone, all *Z. marina* data, all *Z. japonica* data) then analyzed with PERMANOVA epifaunal community analysis.

To test functional redundancy of the eelgrass species, the data from the experimental plots was used to compare if it was the identity of the foundation species or if it was the zonation patterns that created differences in abundance or community structure. For biomass, epiphyte load, total epifaunal abundance, proportion of crustaceans, and proportion of non-native, the data was split into three ways. The first model was to compare between species. To do this, mixed plots at all elevations were excluded from the analysis to ask the question: do the species on their own facilitate different communities? This three-factor ANOVA model included the two-level factor site (Stackpole and Sloughville), the three-level factor zone (high, mid, and low), and two-level factor species (*Z. japonica* and *Z. marina*). To compare if growing in monocultures and mixtures altered the habitat created by each species, the data was separated into each species (*Z. japonica* and *Z. marina*) then analyzed with a three-factor ANOVA model with the two-level factor site (Stackpole and Sloughville), the three-level factor zone (high, mid, and low), and the two-level factor monoculture vs. mixture (monoculture vs. mixture). If there was a three-way interaction, estimated marginal means (EMMs) were used to compare zones within each site (Lenth 2023, R Core Team 2023). As in the zonation analysis, the biomass, epiphyte load, total epifaunal abundance, and nekton were all log transformed to meet the assumptions of normality. The effect size that the species had on each other was calculated by comparing the biomass in monocultures vs. in mixtures at all zones. This was done with the `esc_mean_sd` function in the `esc` R package and visualized by plotting the effect size by the biomass of the competitor (Lüdecke 2019, R Core Team 2023). The mean biomass of each species in mixtures and monocultures by site and zone was used to calculate the effect size. The same three ANOVA models described above were also used to analyze the community data with a PERMANOVA. The experimental data was relativized in the same way as the zonation community data. Where three-way interactions occurred, the data was separated by site and zone to find which combinations still had significant. For these analyses, p-values were adjusted with a Bonferroni correction.

Results

Zonation

Initial sampling

The initial sample included gammarid amphipods, tanaids, isopods, cumaceans, barnacles, *Crepidula spp.*, mollusks, mollusk egg cases, *Lacuna spp.*, *Mytilus spp.*, polychaetes, and anemones (Supplemental Table 1). The most abundant species was the gammarid amphipod *Ampithoe valida* (Supplemental Table 1). In terms of community structure, the epifaunal community varied by site and foundation species (Supplemental Fig. 1, Table 3, Mid, Community; Site x Foundation Species effect) and by site on *Z. marina* (Supplemental Fig. 1, Table 3, *Z. marina*, Community; Site effect). On *Z. japonica* the community varied by site and zone (Supplemental Fig. 1, Table 3, *Z. japonica*, Community; Site x Zone effect).

In the initial sampling, the abundance of epifaunal invertebrates at the mid zone differed by foundation species with higher abundance on *Z. japonica* compared to *Z. marina* (Supplemental Fig. 2a, Table 3, Mid, Abundance; Site x Foundation Species effect). On *Z. marina* the abundance of epifauna varied by site and zone (Supplemental Fig. 2a, Table 3, *Z. marina*, Abundance: Site x Zone effect). On *Z. marina*, there were more epifauna at the mid zone at Stackpole compared to the other two zones and more epifauna in the low zone at Sloughville compared to the other two zones. There were no initial patterns by zone, site, or foundation species in the proportion of crustaceans in epifaunal samples (Supplemental Fig. 2b, Table 3, Mid, Proportion Crustacean). The proportion of non-native species at the mid zone varied by site and foundation species with *Z. japonica* having more non-native epifaunal species (Supplemental Fig. 2c, Table 3, Mid, Proportion non-native; Site x Foundation Species effect) and by site and zone on *Z. japonica* with there being more non-native epifaunal species at the high zone at Stackpole compared to more at the mid zone in Sloughville (Supplemental Fig. 2c, Table 3, *Z. japonica*, Proportion Non-native; Site x Zone effect).

Post experiment

There were distinct patterns in zonation with *Z. japonica* with the highest biomass in the high zone and *Z. marina* in the low zone. The zonation showed the biomass of each species varied in different ways by site at the mid zone (Supplemental Fig. 3, Table 4, Mid, Biomass; Site x Foundation Species effect). In *Z. marina* the biomass differed by site with Sloughville having a higher biomass than Stackpole (Supplemental Fig. 3, Table 4, *Z. marina*, Biomass; Site effect). Biomass of *Z. japonica* differed by both site and zone with Stackpole than Sloughville having more biomass generally and the high zone having more biomass than the other zones (Supplemental Fig. 3, Table 4, *Z. japonica*, Biomass; Site and Zone effects). The biomass of *Z. marina* was lowest and the high zone and increased until reaching its peak biomass at the low zone. *Zostera japonica* had the highest biomass at the high zone. The highest biomass of *Z. marina* occurred at Sloughville, while *Z. japonica* reached the highest biomass at Stackpole.

Epiphytes varied more by site than by zone. In the mid zone, Stackpole had more epiphytes than Sloughville (Supplemental Fig. 4, Table 4, Mid, Epiphytes; Site effect). Epiphyte load on *Z. marina* also varied by site with Stackpole having more epiphytes than Sloughville (Supplemental Fig. 4, Table 4, *Z. marina*, Epiphytes; Site effect). In *Z. japonica* there was no pattern of epiphyte biomass by site or zone.

At the end of the experiment, and in the unmanipulated epifaunal samples, the average abundance of epifaunal invertebrates differed by foundation species and site at the mid zone, with *Z. marina* supporting more individuals than *Z. japonica* at Stackpole and the opposite at

Sloughville (Supplemental Fig. 5a, Table 4, Mid, Abundance; Site x Foundation Species effect). The proportion of crustaceans at the mid varied by site and foundation species, where both species supported similar amounts of crustaceans at Stackpole, but *Z. japonica* had a higher proportion at Sloughville (Supplemental Fig. 5b, Table 4, Mid, Proportion of Crustaceans; Site x Foundation Species effect). On *Z. marina* there was a higher proportion of crustaceans at Stackpole than at Sloughville (Supplemental Fig. 5b, Table 4, *Z. marina*, Proportion of Crustaceans; Site effect). The proportion of non-native species varied in different ways across site and zone on *Z. marina* with there being a higher proportion of non-native invertebrates at the low zone at Stackpole compared to the other two zones, and a higher proportion of non-natives at the mid at Sloughville compared to the other two zones (Supplemental Fig. 5c, Table 4, *Z. marina*, Proportion of Non-native; Site x Zone effect).

The overall abundance of nekton depended on site and zone (Table 5, Abundance; Site x Zone effect). Stackpole has a higher abundance of nekton at the low mid zone and Sloughville has the highest abundance at the low zone. Nekton were split into four groups, benthic, crustaceans, eelgrass mimics, and pelagic (See Supplemental Table 2 for full list of species). The nekton groups varied by both site and zone. For benthic, crustaceans, and pelagic fish, there was an interaction between site and zone (Table 5, Site x Zone effect). Benthic nekton at Stackpole were highest at the low, but highest at the high at Sloughville. Crustaceans at Stackpole increased until they reached their peak at the low but at Sloughville, they were at their highest at the high zone and decreased in the lower zones. Pelagic fish at Stackpole were most abundant at the mid zone, followed by the low, and increased until their peak low zone. For eelgrass mimics there was a main effect of both site and zone with the highest abundance being at Stackpole and nekton being more abundant at the mid and low zones (Table 5, Site and Zone effect).

Functional redundancy

The two foundational species showed striking differences in biomass across the three zones which depended on an apparent competitive effect between species (Fig. 2, Table 6, Biomass). For *Z. japonica*, biomass reached the greatest value in the high zone and generally declined with decreasing height, but the specific relationship between biomass and zone depended on site and the presence or absence of *Z. marina* (Fig. 2). Specifically, the presence of *Z. marina* suppressed the biomass of *Z. japonica*, as indicated by the significant zone x mono vs. mixture interaction in the three-way ANOVA (Fig. 3, Table 6, *Z. japonica*, Biomass; Zone x mono vs. mixture effect). In contrast, *Z. marina* shows the opposite general pattern with respect to zone: increasing biomass with decreasing height, and the presence of *Z. japonica* has no statistical effect on this biomass zonation (Fig. 2). This pattern is confirmed by the significant two-way interaction between zone x site (Table 6, *Z. marina*, Biomass; Zone x Site effect) and a lack of significant two- or three-way terms that include mono vs. mixture (Table 6, *Z. marina*, interaction terms). Effect sizes appear to increase with the biomass of the competitor and *Z. japonica* generally had a higher effect size than *Z. marina* (Fig. 3).

Epiphytes

If the two foundation eelgrass species are ecologically redundant, similar patterns in epiphytes biomass across zones are expected between sites regardless of the identity of the foundation species. Further, the presence of the second foundational species should have weak or no effect on epiphyte abundance. My data essentially reject this idea, with the biomass of epiphytes being strongly dependent on foundation species in a site-specific pattern (Fig. 4, Table

6, Monocultures, Epiphytes; Site x Zone x Foundation species effect). In monoculture, the two foundation species diverge in epiphyte load, with *Z. japonica* having the highest epiphyte biomass across zones and between the two sites ($p < 0.001$, one-way ANOVA) but not at Sloughville. Within *Z. marina*, epiphyte load varied by site, and monocultures vs. mixtures (Fig. 4, Table 6, *Z. marina*, Epiphytes; Site x Monoculture vs. Mixture effect).

At Stackpole, there were more epiphytes on plants that were in mixtures and at Sloughville plots in mixtures had less epiphytes (Fig. 4). Many blades of *Z. marina* in the high zone, where *Z. marina* highest epiphyte load at Sloughville appeared necrotic. Epiphyte load on *Z. japonica* also varied in different ways between site and monoculture vs. mixture (Fig. 4, Table 6, *Z. japonica*, Epiphytes; Site x Monoculture vs. mixture effect). At Stackpole, there was not much difference between the monocultures and mixtures however, at Sloughville, monocultures had higher epiphyte loads (Fig. 4).

Epifaunal community

The epifaunal invertebrate community that colonized the experimental plots included gammarid amphipods, tanaids, isopods, cumaceans, barnacles, insect larvae, *Crepidula spp.*, mollusks, mollusk egg cases, *Lacuna spp.*, *Mytilus spp.*, polychaetes, leeches, and anemones (Supplemental Table 3). The most abundant species was the amphipod *Ampithoe valida* complex, which made up 55% of all epifaunal invertebrates collected (Supplemental Table 3). Between the observational sampling and the experimental sampling, there was an overall increase in epifaunal abundance, consistent with previously observed seasonal phenology in abundance (Ruesink 2016, Gross et al. 2019). In the monocultures epifaunal invertebrate communities differed between the two foundation species in different ways across zones and site (Fig. 5, Table 6, Monocultures, Community; Site x Zone x Foundation Species effect). The communities differed between foundation species at Stackpole high, Sloughville mid, and Sloughville low. Within *Z. marina* and within *Z. japonica*, the invertebrate community varied by site and zone (Fig. 5, Table 6, *Z. marina*, *Z. japonica*, Community; Site x Zone effect).

Yet, the NMDS plots of community structure revealed that the largest differences between epifaunal communities were determined by zone at both sites (Fig. 5). At both sites the epifaunal community sampled from the high zone was a small subset those communities sampled at the mid and low zones. Also apparent in the NMDS plots, was a separation of epifaunal communities by foundation species at the Stackpole high zone, a pattern that did not occur at the Sloughville high zone.

One species or zone did not consistently support a higher abundance of invertebrates. The species that was able to support the highest abundance of epifauna depended on the site and zone (Fig. 6a, Table 6, Monocultures, Abundance; Site x Zone x Foundation Species effect). At Stackpole, there was a higher abundance of invertebrates on *Z. marina* while at Sloughville there was a higher abundance on *Z. japonica* (Fig. 6a, high-mid $p = 0.001$, high-low $p < 0.001$, EMMs). abundance at the high zone (Fig. 6a). On *Z. marina*, the varied by site and zone with abundance increasing until the low zone at Stackpole and slightly decreasing until the low at Sloughville (Fig. 6a, Table 6, *Z. marina*, Abundance; Site x Zone effect). At Stackpole mid and low there was a higher abundance of invertebrates on monocultures than mixtures but were similar at Sloughville (Fig. 6a). The total abundance of epifauna on *Z. japonica* varied by zone and monoculture vs. mixture, with the mixtures at the mid and low zone having higher abundances while the mixtures at the high zone had higher abundances (Fig. 6a, Table 6, *Z. japonica*, Abundance; Zone x Monoculture vs. Mixture effect).

The high zone supports a higher number of crustaceans than other zones (Fig. 6b). Regardless of species, or monoculture or mixture, the proportion of crustaceans varied by site and zone decreasing at the lower zones (Fig. 6b, Table 6, Mid, *Z. marina*, *Z. japonica*, Proportion of Crustaceans; Site x Zone effect).

Neither the non-native foundation species nor the novel habitat of the high zone facilitates a higher proportion of non-native species (Fig. 6c). The proportion of non-native varied in different ways across site, zone, and foundation species (Fig. 6c, Table 6, Monocultures, Proportion of Non-native; Site x Zone x Foundation Species effect). At Stackpole both foundation species supported similar proportion of non-native species at the high, but *Z. japonica* had a larger proportion of non-natives at the low zones (Fig. 6c). At Sloughville, the proportion of non-native invertebrate species increased at the lower zones on *Z. japonica* but decreased with zone in *Z. marina* (Fig. 6c). On *Z. marina* the proportion of non-native invertebrates varied in different ways by site, zone, and monoculture vs. mixture (Fig. 6c, Table 6, *Z. marina*, Proportion of Non-native; Site x Zone x Monoculture vs. Mixture effect). On *Z. japonica* the proportion of non-native species varied by zone (Fig. 6c, Table 6, *Z. japonica*, Proportion of Non-native; Zone effect).

DISCUSSION

Ecological communities across multiple trophic levels responded more to the abiotic stress gradient associated with increasing tidal height than to the structural aspects of eelgrass habitats. Along this stress gradient, foundation species composition shifted from native to non-native. The presence of the non-native *Z. japonica* has extended the vegetated habitat on the mudflat and is not replacing *Z. marina* habitat, since *Z. marina* cannot survive in the high zone that *Z. japonica* inhabits (Fig 2). The increased time exposed to air at the high zone is likely outside the physiological limits of *Z. marina* (Shafer et al. 2007). At the low zone at Sloughville, *Z. japonica* in monocultures was able to reach higher biomass than when grown in mixtures (Fig 2). This suggest that the lower limits of *Z. japonica* are set by competition rather than physiological limits consistent with previous studies in both species invaded and native range (Shafer et al. 2007, Kim et al. 2016). However, at the Stackpole site and in low zone, *Z. japonica* was unable to reach a high biomass regardless of growing in a monoculture or a mixture, potentially limited by light availability (Fig 2). When comparing competition across zones, I found there was asymmetrical competition with *Z. japonica* being negatively impacted by the presence of *Z. marina* (Fig. 3). This result is consistent with previous studies that have shown that in mid and low elevations *Z. marina* is competitively dominant, and that the small-bodied *Z. japonica* does exert competitive pressure on *Z. marina* (Bando 2006, Boardman and Ruesink 2022). At high tidal elevations *Z. japonica* was shown to have a negative impact on *Z. marina* (Bando 2006), however the results from this study suggests otherwise as even at high biomasses, *Z. japonica* appears to have a low competitive effect on *Z. marina* (Fig. 3).

The experiment was established to separate two plausible explanations for different epifaunal communities associated with eelgrass in the high zone: emersion stress, or distinct foundation species. At both sites, the epifaunal communities in the high zone were distinct from the other two zones, although this pattern was complicated by site-specific differences in epifaunal communities between foundation species (Fig. 5). In the high zone at Stackpole, the two foundation species supported different communities, which converged at the mid and low zone (Fig. 5). This result at the mid zone and low is consistent with Knight et al. (2015) found that the two species were able to support similar communities when testing at a similar tidal

height. In contrast, in the high zone at Sloughville, *Z. marina* and *Z. japonica* supported similar communities, which diverged by foundation species at lower zones (Fig. 5). This difference could be due to the differences in site. Overall, epifauna were denser on eelgrass at Stackpole than Sloughville, and densities sometimes increased and sometimes declined across the intertidal gradient (Fig. 6a). The empirical evidence for functional redundancy of the non-native and native eelgrass was site- and zone-specific and depended on whether epifauna biomass or community structure was considered. The results from this experiment suggest that functional redundancy between the two species depends on the environmental stress and the ability of the foundation species to withstand this stress. Other studies support this idea and suggest that the impact of a non-native foundation species is often site specific (Scott and terHorst 2020). Additionally, the interaction between eelgrasses and their associated communities are heavily dependent on both the abiotic and biotic context (Moore and Duffy 2016, Meysick et al. 2019, Scott and terHorst 2019).

Non-native foundation species provide a mechanism for invasional meltdown if they disproportionately provide habitat and conditions suitable for other non-native species. *Zostera japonica* persists in the high zone which is typically unvegetated habitat. When non-native foundation species are introduced to typically unvegetated habitat, especially where native foundation species have been lost, they can increase the presence and diversity of epifaunal invertebrates (Ramus et al. 2017). Yet in my study, the extension of the vegetated habitat into the high intertidal, does not appear to consistently support a higher proportion of non-native species than other zones (Fig. 6c). The high zone that is created by *Z. japonica* supports a higher proportion of crustaceans (Fig. 6b). This means there are less soft bodied organisms that are less equipped to handle desiccation stress. *Zostera japonica* growing in either monocultures or mixtures also does not appear to support a higher proportion of non-native species than *Z. marina* (Fig 6c). This suggests that *Z. japonica* is not facilitating the presence of other non-native species even though it is creating a new niche within the ecosystem. A similar result has been shown with invasive blackberry, *Rubus fruticosus*, that increased the abundance of small mammals when it created novel habitat. (Packer et al. 2016).

Abundance of invertebrates changed on *Z. japonica* depending on if the larger canopy forming species *Z. marina* was present. Where *Z. japonica* grows alongside *Z. marina*, it adds additional structural complexity by creating an understory to the canopy formed by *Z. marina*. *Zostera japonica* grows at a higher density which has been linked to creating a more structurally complex habitat (Jenkins et al. 2002, Knight et al. 2015). Despite this increase in complexity of having the two species there was no difference in the community that mixtures supported when compared to monocultures (Fig. 5). This finding is contradictory to the Watt and Scrosati (2013). When *Z. marina* grew in plots with *Z. japonica* there was also no difference between the epifaunal abundance. However, the abundance of epifauna decreased on *Zostera japonica* when grown in mixtures compared to monocultures of *Z. japonica*. This suggests that epifaunal species found in the canopy influences understory that is created by *Z. japonica*. Previous studies in eelgrass ecosystems have found that above ground biomass is more closely correlated with increase in epifaunal invertebrate abundance and number of than the number of foundation species (Heck and Wetstone 1977). The empirical evidence demonstrates that the abundance on the understory community changes if there is a canopy community above it. Previous studies show that the canopy community is likely to influence the understory community (Watt and Scrosati 2013). At the two lower zones, monocultures of *Z. japonica* have a higher abundance of invertebrates. At the high zone, where the most physiological stress occurs, the presence of a

larger foundation species facilitates a higher abundance of epifauna on *Z. japonica*, while at the less stressful elevations, the larger foundation species inhibits the abundance of epifauna on *Z. japonica*. This result is consistent with studies of intertidal and saltmarsh communities, where increased stress changes the species interactions (Bertness and Leonard 1997, Alberti et al. 2010).

The results from my experiment provide another example of the functional redundancy of a non-native species that is heavily dependent on environmental factors (Moore and Duffy 2016, Meysick et al. 2019). These factors can dictate the distribution of these species, and consequently impact the communities that form around the eelgrass species. Previous studies have also highlighted that it is the abundance of eelgrass that is more likely to dictate the presence of the epifaunal community that forms around the eelgrass species than the identity of the foundation species (Moore and Duffy 2016). Since climate change is projected to increase ocean temperatures, *Z. marina* could reach its desiccation threshold at lower tidal elevations and therefore be forced lower in the intertidal. If this were to happen, *Z. japonica*, with its higher thermal tolerance (Shafer et al. 2008), could potentially survive these warmer temperatures. Intriguingly, *Z. japonica* could support similar communities and fulfill the same functional role as *Z. marina* in Pacific Northwest soft sediment communities, however the degree of ecological redundancy appears to interact with other environmental factors.

FIGURES

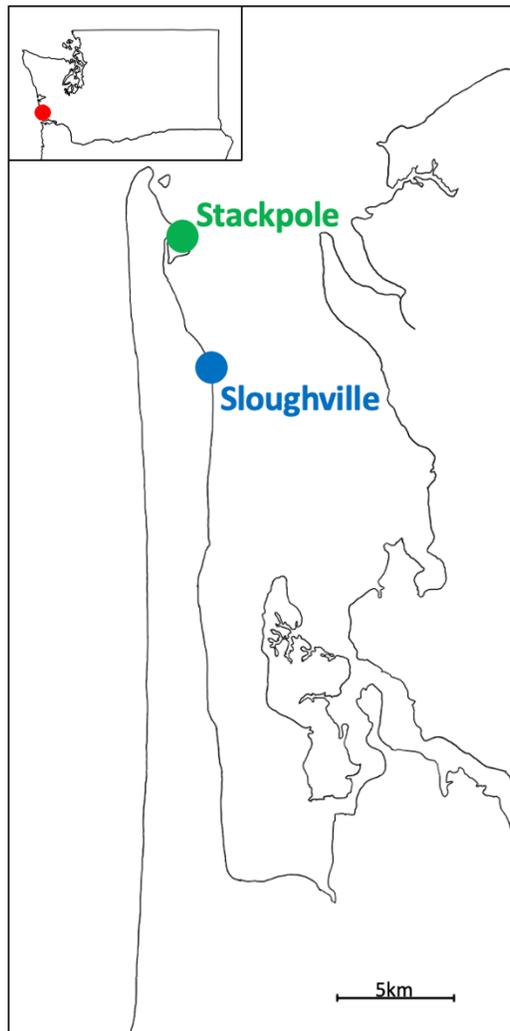


Fig. 1. Map depicting study sites. Willapa Bay is in southeastern corner of Washington State, USA. The experiment was conducted at two sites in Willapa bay: Stackpole, them more northern site in green, and Sloughville, the more southern site in blue.

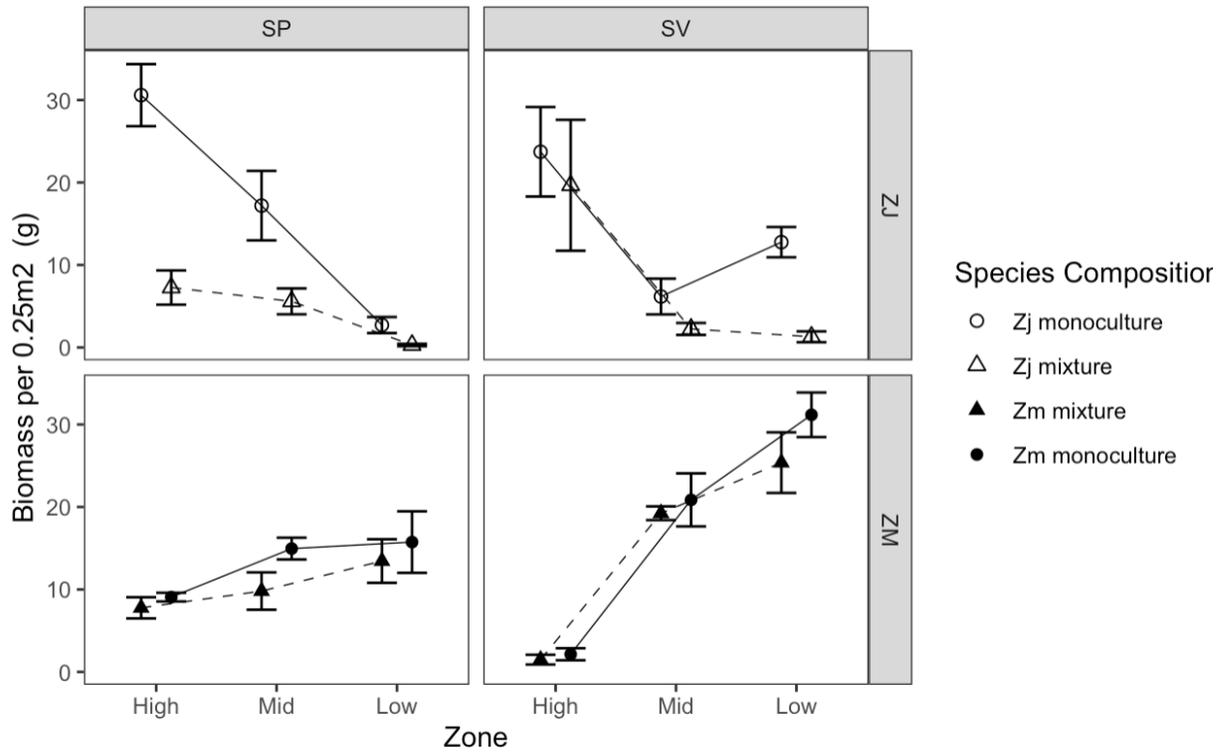


Fig. 2. Biomass by site, zone, foundation species, and monoculture vs. mixture from experimental plots ($n = 6$). Site (SP and SV) is in columns, foundation species (ZM and ZJ) is in rows. Mixtures are represented with triangles and circles are monocultures. Solid lines connect monocultures while dashed lines connect mixtures. Error bars are one standard error of the mean. Unmanipulated plots are ZJ monocultures at the high, ZJ and ZM mixtures at the mid, and ZM monocultures at the low.

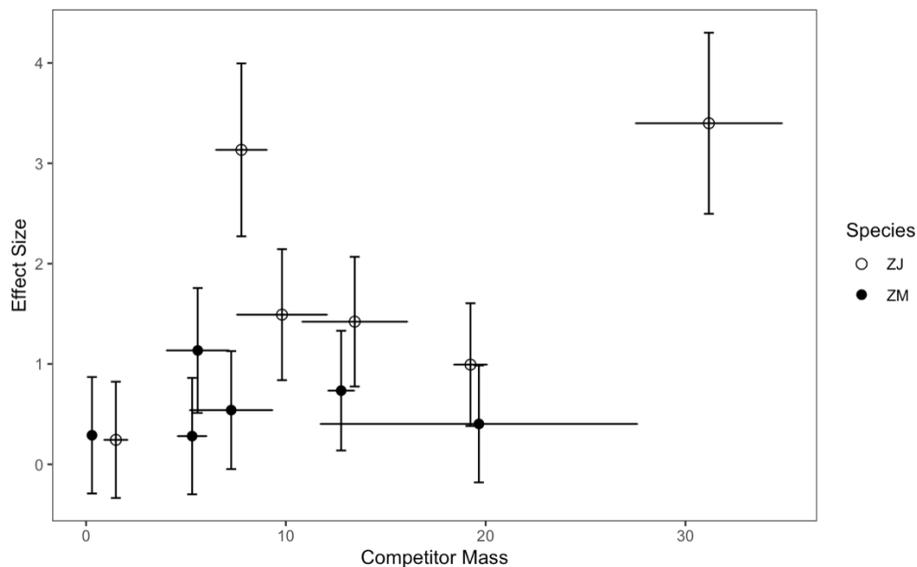


Fig. 3. Effect size by competitor mass of eelgrass within a site, zone, and species ($n = 6$). Filled in circles are ZM and open circles are ZJ. Generally, as competitor mass increases, so

does effect size. Even at higher competitor masses, *Z. marina* had lower effect size than *Z. japonica*.

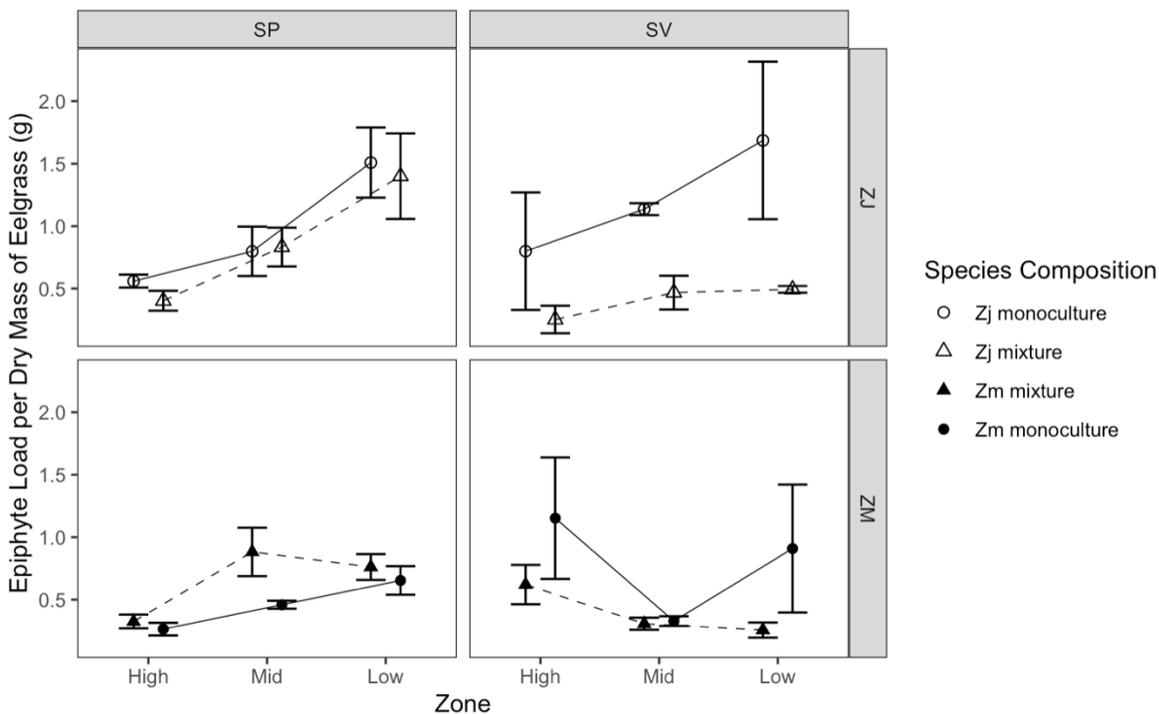


Fig. 4. Average epiphyte load as gram per gram dry mass of eelgrass by site, zone, foundation species, and monoculture vs. mixture (n=6). Epiphytes, consisting of mostly diatoms, were scraped off one *Z. marina* plant and five *Z. japonica* plants, dried, and standardized to the dry mass of the eelgrass. Site (SP and SV) are in columns and foundation species (ZM and ZJ) are in rows. Circles and solid lines represent monocultures, and triangles and dashed lines represent mixtures. Error bars are one standard error from the mean. Note that unmanipulated plots are ZJ monocultures at the high, ZJ and ZM mixtures at the mid, and ZM monocultures at the low.

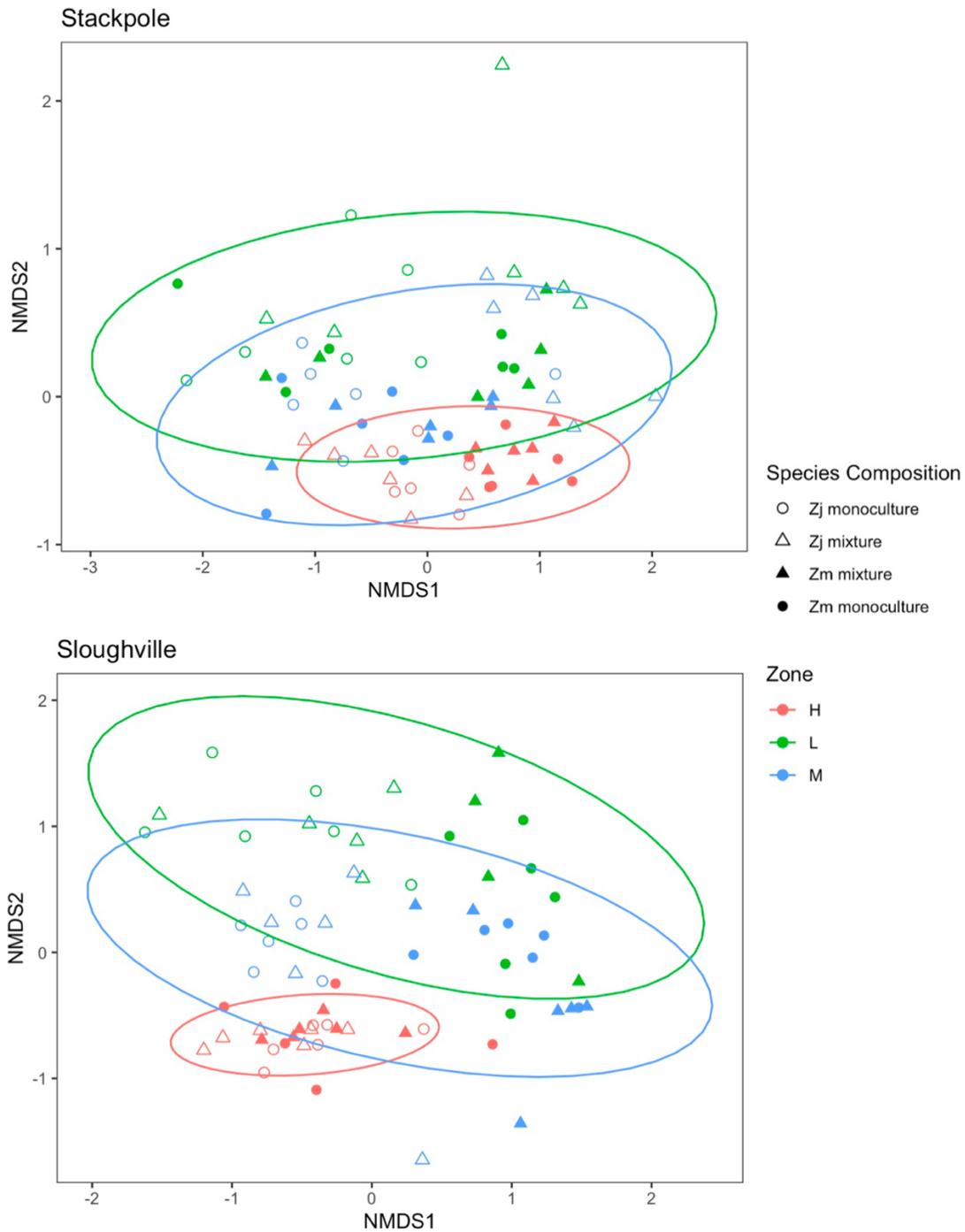


Fig. 5. NMDS of invertebrate community separated by site. Factors included site, zone, foundation species, and monoculture vs. mixture (n=6). Colors are zone, filled in shapes are *Z. marina* and open shapes are *Z. japonica*, and triangles are mixtures while circles are monocultures. Ellipses are 95% confidence interval around zones. Both sites have a large amount of overlap between the two foundation species and monoculture vs. mixture.

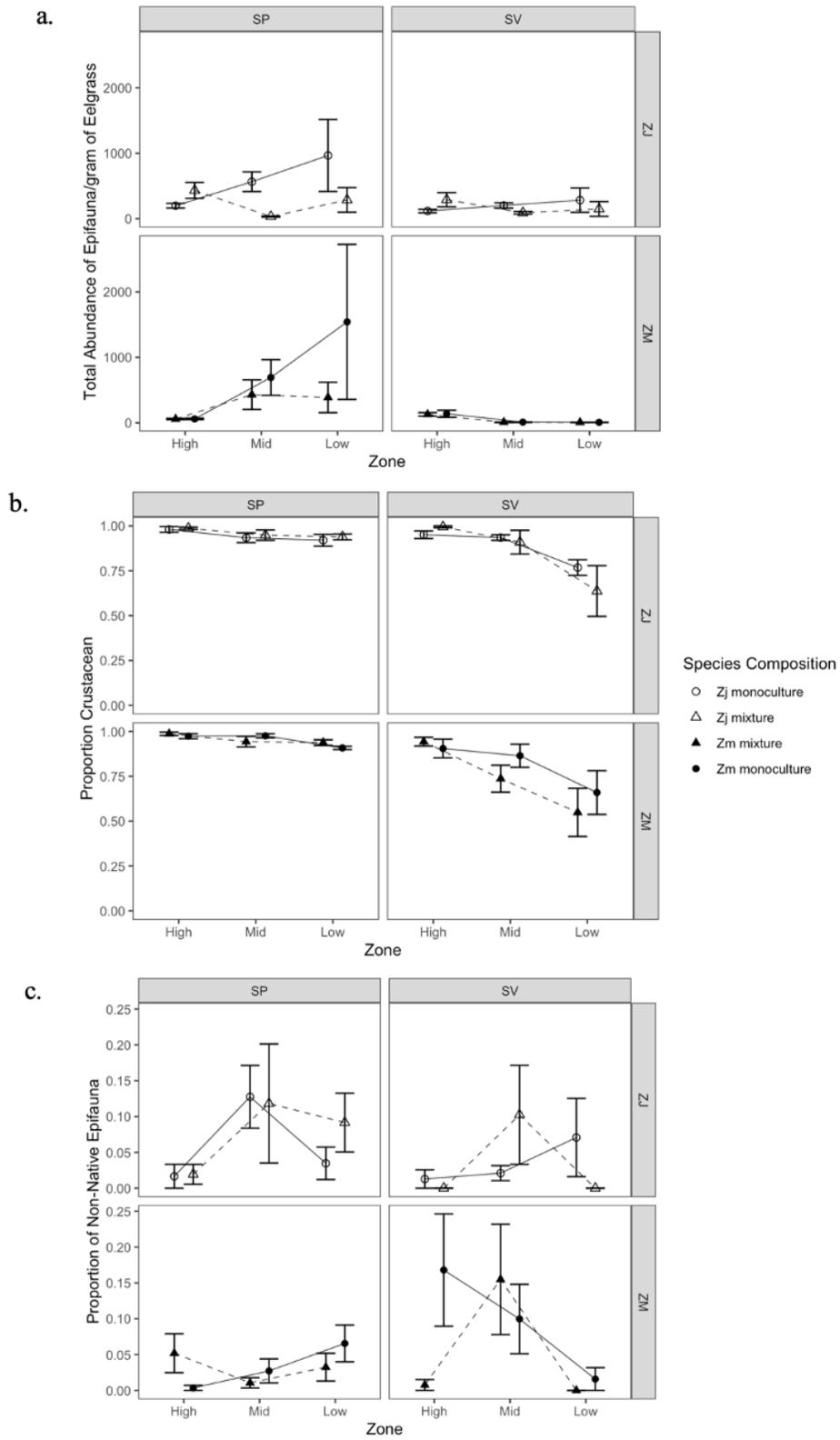


Fig. 6. Average, epifaunal abundance per gram of dry eelgrass (a), proportion of crustaceans (b), and proportion of non-native epifaunal invertebrates (c) by site, zone, foundation species, and monoculture vs. mixture for experimental plots (n=6). Site (SP and SV) are separated by columns and foundation species (ZM and ZJ) is separated by rows. Circles connected with solid lines represent monocultures and triangles with dashed lines represent mixtures. Error bars are one standard error of the mean. Unmanipulated plots are ZJ monocultures at the high, ZJ and ZM mixtures at the mid, and ZM monocultures at the low.

TABLES

Table 1. Environmental attributes of two study sites in Willapa Bay, Washington. Sediment conditions are based on N=3 samples per site and tidal height, which were dried, ashed at 500C for 3 hours to determine loss-on-ignition (organic content), and subsequently sieved (RoTap sieve shaker). The bathymetric slope at Stackpole was 28.192 and 1.620 at Sloughville, based on vertical distance per horizontal distance.

| Site | Stackpole (North) | | | Sloughville (South) | | |
|--------------------------|-------------------------|-------------------------|-------------------------|-------------------------|------------------------|-------------------------|
| Tidal height | Low zone | Mid zone | High zone | Low zone | Mid zone | High zone |
| % organic (SE) | 0.034 | 0.027 | 0.026 | 0.013 | 0.012 | 0.018 |
| % silt (SE) | 0.02 | 0.024 | 0.033 | 0.108 | 0.1 | 0.083 |
| Geolocation | 46.59480, -124.02763 | 46.59471, -124.02782 | 46.59464, -124.02782 | 46.52657, -124.01436 | 46.52661, -124.0176 | 46.52677, -124.02336 |
| Tidal elevation (m MLLW) | 0 | 0.6 | 1.8 | 0 | 0.7 | 1.4 |

Table 2. Experimental treatments by site and zone. Transplants or removals were dependent on which species were abundant. 0 indicates plots that received no manipulation besides a disturbance control.

| Site | Stackpole | | | Sloughville | | |
|-----------|-----------|----------|---------|----------------------|----------|---------|
| | Zm | Zj | Zm & Zj | Zm | Zj | Zm & Zj |
| Treatment | | | | | | |
| High | -Zj + Zm | 0 | + Zm | -Zj + Zm | 0 | + Zm |
| Mid | -Zj | -Zm | 0 | -Zj | -Zm | 0 |
| Low | 0 | -Zm + Zj | +Zj | 0 (-Zj if necessary) | -Zm + Zj | +Zj |

Table 3. Variation in the epifaunal community in unmanipulated plots in the beginning of the experiment. Results from two-way ANOVA and PERMANOVA models. All results are from an ANOVA except for the community data where a PERMANOVA was used. Models for the mid zone (left column) focus on the effects of the two foundation species where they naturally co-occur, while models for each foundation species (middle, right column) consider their individual effect across zones.

| | Mid | | | | <i>Z. marina</i> | | | | <i>Z. japonica</i> | | | | | |
|----------------------------------|-----|---------|---------|-----------|------------------|---------|---------|--------|--------------------|-------------|---------|--------|-------|---------|
| | Df | Mean sq | F value | Pr(>F) | Df | Mean sq | F Value | Pr(>F) | Df | Mean sq | F Value | Pr(>F) | | |
| Abundance | | | | | | | | | | | | | | |
| Site | 1 | 0.02 | 0.03 | 0.866 | Site | 1 | 1.86 | 3.30 | 0.085 | Site | 1 | 2.94 | <0.01 | 0.029* |
| Foundation S | 1 | 36.09 | 66.98 | <0.001*** | Zone | 1 | 0.58 | 1.03 | 0.324 | Zone | 1 | 0.03 | 0.06 | 0.803 |
| Site x Found: | 1 | 0.38 | 0.70 | 0.414 | Site x Zone | 1 | 1.08 | 1.91 | 0.183 | Site x Zone | 1 | 0.64 | 1.26 | 0.279 |
| | | | | | | | | | | | | | | |
| Proportion of Crustaceans | | | | | | | | | | | | | | |
| Site | 1 | 0.06 | 0.49 | 0.492 | Site | 1 | 0.05 | 0.47 | 0.501 | Site | 1 | 0.03 | 0.74 | 0.403 |
| Foundation S | 1 | 0.40 | 3.27 | 0.089 | Zone | 1 | 0.44 | 4.18 | 0.055 | Zone | 1 | 0.02 | 0.38 | 0.549 |
| Site x Found: | 1 | 0.07 | 0.55 | 0.468 | Site x Zone | 1 | 0.08 | 0.81 | 0.380 | Site x Zone | 1 | 0.04 | 0.88 | 0.363 |
| | | | | | | | | | | | | | | |
| Proportion Non-native | | | | | | | | | | | | | | |
| Site | 1 | 0.03 | 0.98 | 0.336 | Site | 1 | 0.00 | 0.19 | 0.670 | Site | 1 | 0.04 | 0.98 | 0.339 |
| Foundation S | 1 | 0.04 | 1.30 | 0.270 | Zone | 1 | 0.00 | 0.00 | 0.950 | Zone | 1 | 0.01 | 0.29 | 0.597 |
| Site x Found: | 1 | 0.02 | 0.59 | 0.452 | Site x Zone | 1 | 0.01 | 2.01 | 0.173 | Site x Zone | 1 | 0.24 | 5.51 | 0.033 * |
| | | | | | | | | | | | | | | |
| Community (PERMANOVA) | | | | | | | | | | | | | | |
| Site | 1 | 0.64 | 2.04 | 0.029* | Site | 1 | 1.61 | 5.45 | <0.001*** | Site | 1 | 0.64 | 1.45 | 0.194 |
| Foundation S | 1 | 1.37 | 4.38 | <0.001*** | Zone | 1 | 0.57 | 1.93 | 0.0853 | Zone | 1 | 1.37 | 1.15 | 0.328 |
| Site x Found: | 1 | 0.51 | 1.63 | 0.087 | Site x Zone | 1 | 0.26 | 0.87 | 0.5083 | Site x Zone | 1 | 0.51 | 3.64 | 0.005** |

Table 4. Variation in the epifaunal community in unmanipulated plots at the end of the experiment. Results from two-way ANOVA and PERMANOVA models. All results are from an ANOVA except for the community data where a PERMANOVA was used. Models for the mid zone (left column) focus on the effects of the two foundation species where they naturally co-occur, while models for each foundation species (middle, right column) consider their individual effect across zones.

| | Mid | | | | <i>Z. marina</i> | | | | <i>Z. japonica</i> | | | |
|----------------------------------|-----|---------|---------|------------|------------------|---------|---------|------------|--------------------|---------|---------|------------|
| | Df | Mean sq | F Value | Pr(>F) | Df | Mean sq | F Value | Pr(>F) | Df | Mean sq | F Value | Pr(>F) |
| Biomass | | | | | | | | | | | | |
| Site | 1 | 0.44 | 0.46 | 0.505 | 1 | 6.56 | 7.06 | 0.015 * | 1 | 4.77 | 5.01 | 0.037 * |
| Foundation Species | 1 | 17.00 | 17.93 | <0.001 *** | 1 | 0.47 | 0.51 | 0.485 | 1 | 33.13 | 34.80 | <0.001 *** |
| Site x Foundation Species | 1 | 7.62 | 8.04 | 0.010 * | 1 | 0.22 | 0.23 | 0.636 | 1 | 1.53 | 1.61 | 0.220 |
| Epiphytes | | | | | | | | | | | | |
| Site | 1 | 3.09 | 11.78 | 0.003 ** | 1 | 2.41 | 4.94 | 0.038 ** | 1 | 0.49 | 1.72 | 0.204 |
| Foundation Species | 1 | 0.03 | 0.10 | 0.760 | 1 | 0.11 | 0.23 | 0.636 | 1 | 0.01 | 0.02 | 0.880 |
| Site x Foundation Species | 1 | 0.05 | 0.20 | 0.659 | 1 | 0.96 | 1.96 | 0.177 | 1 | 0.33 | 1.15 | 0.296 |
| Epifaunal Abundance | | | | | | | | | | | | |
| Site | 1 | 30.16 | 37.46 | <0.001 *** | 1 | 118.56 | 63.03 | <0.001 *** | 1 | 0.63 | 0.56 | 0.459 |
| Foundation Species | 1 | 10.23 | 12.71 | 0.002 ** | 1 | 0.35 | 0.19 | 0.668 | 1 | 3.18 | 2.81 | 0.101 |
| Site x Foundation Species | 1 | 13.47 | 16.73 | <0.001 *** | 1 | 1.27 | 0.68 | 0.415 | 1 | 1.84 | 1.63 | 0.208 |
| Proportion of Crustaceans | | | | | | | | | | | | |
| Site | 1 | 0.05 | 2.72 | 0.115 | 1 | 0.31 | 9.64 | 0.006 ** | 1 | 0.01 | 0.80 | 0.383 |
| Foundation Species | 1 | 0.09 | 5.13 | 0.035 * | 1 | 0.02 | 0.59 | 0.453 | 1 | 0.01 | 0.91 | 0.351 |
| Site x Foundation Species | 1 | 0.04 | 2.38 | 0.138 | 1 | 0.00 | 0.08 | 0.777 | 1 | 0.00 | 0.02 | 0.903 |
| Proportion Non-native | | | | | | | | | | | | |
| Site | 1 | 0.00 | 0.09 | 0.769 | 1 | 0.01 | 0.93 | 0.346 | 1 | 0.00 | 0.01 | 0.921 |
| Foundation Species | 1 | 0.02 | 0.88 | 0.360 | 1 | 0.02 | 1.59 | 0.223 | 1 | 0.05 | 3.36 | 0.083 |
| Site x Foundation Species | 1 | 0.03 | 1.37 | 0.257 | 1 | 0.05 | 4.98 | 0.038 * | 1 | 0.00 | 0.01 | 0.910 |
| Community (PERMANOVA) | | | | | | | | | | | | |
| Site | 1 | 0.28 | 2.11 | 0.089 | 1 | 1.71 | 12.54 | <0.001 *** | 1 | 0.05 | 0.50 | 0.723 |
| Foundation Species | 1 | 0.20 | 1.54 | 0.190 | 1 | 0.10 | 0.77 | 0.550 | 1 | 0.63 | 6.87 | <0.001 *** |
| Site x Foundation Species | 1 | 0.78 | 5.88 | <0.001 *** | 1 | 0.09 | 0.68 | 0.612 | 1 | 0.25 | 2.70 | 0.0401 * |

Table 5. Variation in the nekton community at two sites and three zones at the end of the experiment. All results are from ANOVA models. See supplement for list of Nekton.

| | | Df | Mean sq | F Value | Pr (>F) |
|-----------------------|-------------|----|---------|---------|------------|
| Abundance | | | | | |
| | Site | 1 | 15.666 | 99.82 | <0.001 *** |
| | Zone | 2 | 1.587 | 10.113 | 0.003** |
| | Site x Zone | 2 | 0.366 | 2.333 | 0.139 |
| Benthic | | | | | |
| | Site | 1 | 0.48 | 2.27 | 0.054 |
| | Zone | 2 | 0.00 | 0.00 | 0.021* |
| | Site x Zone | 2 | 6.13 | 29.17 | 0.007 ** |
| Crustacean | | | | | |
| | Site | 1 | 0.48 | 2.27 | 0.146 |
| | Zone | 2 | 0.00 | 0.00 | 0.978 |
| | Site x Zone | 2 | 6.13 | 29.17 | <0.001 *** |
| Elgrass mimics | | | | | |
| | Site | 1 | 5.54 | 19.02 | <0.001 *** |
| | Zone | 2 | 47.32 | 162.36 | <0.001 *** |
| | Site x Zone | 2 | 1.12 | 3.85 | 0.051 |
| Pelagic | | | | | |
| | Site | 1 | 4.59 | 7.56 | 0.008 |
| | Zone | 2 | 2.71 | 4.46 | 0.056 |
| | Site x Zone | 2 | 2.92 | 4.81 | 0.029* |

Table 6. Variation in eelgrass biomass, epiphyte biomass, and epifaunal community from all experimental plots. All statistical tests were ANOVAs except for the community data where a PERMANOVA was used. Data was separated by monocultures of both species to compare between species (left), and by foundation species (middle and right).

| | Monocultures | | | <i>Z. marina</i> | | | <i>Z. japonica</i> | | | | | | | |
|----------------------------------|--------------|---------|---------|------------------|---------------------------------------|---------|--------------------|--------|------------|---------------------------------------|---------|--------|-------|------------|
| | DF | Mean sq | F Value | Pr(<F) | DF | Mean sq | F Value | Pr(<F) | DF | Mean sq | F Value | Pr(<F) | | |
| Biomass | | | | | | | | | | | | | | |
| Site | 1 | 0.01 | 0.01 | 0.909 | Site | 1 | 0.29 | 0.48 | 0.491 | Site | 1 | 0.06 | 0.04 | 0.852 |
| Zone | 2 | 0.52 | 0.93 | 0.400 | Zone | 2 | 21.56 | 35.85 | <0.001 *** | Zone | 2 | 96.07 | 29.18 | <0.001 *** |
| Foundation Species | 1 | 0.03 | 0.05 | 0.832 | Monoculture vs. Mixture | 1 | 1.13 | 1.87 | 0.176 | Monoculture vs. Mixture | 1 | 69.16 | 42.02 | <0.001 *** |
| Site x Zone | 2 | 10.72 | 19.14 | <0.001 *** | Site x Zone | 2 | 14.80 | 24.61 | <0.001 *** | Site x Zone | 2 | 14.82 | 4.50 | 0.015 * |
| Site x Foundation Species | 1 | 0.12 | 0.21 | 0.652 | Site x Monoculture vs. Mixture | 1 | 0.08 | 0.13 | 0.715 | Site x Monoculture vs. Mixture | 1 | 0.43 | 0.26 | 0.609 |
| Zone x Foundation Species | 2 | 16.36 | 29.20 | <0.001 *** | Zone x Monoculture vs. Mixture | 2 | 0.39 | 0.64 | 0.530 | Zone x Monoculture vs. Mixture | 2 | 21.44 | 6.51 | 0.003 ** |
| Site x Zone x Foundation Species | 2 | 2.97 | 5.30 | 0.008 ** | Site x Zone x Monoculture vs. Mixture | 2 | 0.56 | 0.93 | 0.402 | Site x Zone x Monoculture vs. Mixture | 2 | 5.38 | 1.63 | 0.204 |
| Epiphytes | | | | | | | | | | | | | | |
| Site | 1 | 0.515 | 1.15 | 0.288 | Site | 1 | 0.51 | 1.32 | 0.256 | Site | 1 | 1.64 | 4.36 | 0.041 * |
| Zone | 2 | 2.107 | 4.71 | 0.013 * | Zone | 2 | 0.11 | 0.29 | 0.746 | Zone | 2 | 4.99 | 13.29 | <0.001 *** |
| Foundation Species | 1 | 6.792 | 15.18 | <0.001 *** | Monoculture vs. Mixture | 1 | 0.09 | 0.23 | 0.634 | Monoculture vs. Mixture | 1 | 4.83 | 12.88 | <0.001 *** |
| Site x Zone | 2 | 0.732 | 1.64 | 0.204 | Site x Zone | 2 | 5.18 | 13.37 | <0.001 *** | Site x Zone | 2 | 0.15 | 0.39 | 0.679 |
| Site x Foundation Species | 1 | 0.05 | 0.11 | 0.740 | Site x Monoculture vs. Mixture | 1 | 2.74 | 7.06 | 0.010 * | Site x Monoculture vs. Mixture | 1 | 3.11 | 8.28 | 0.006 ** |
| Zone x Foundation Species | 2 | 0.976 | 2.18 | 0.122 | Zone x Monoculture vs. Mixture | 2 | 0.44 | 1.12 | 0.332 | Zone x Monoculture vs. Mixture | 2 | 0.02 | 0.04 | 0.961 |
| Site x Zone x Foundation Species | 2 | 2.143 | 4.79 | 0.012 * | Site x Zone x Monoculture vs. Mixture | 2 | 0.04 | 0.09 | 0.914 | Site x Zone x Monoculture vs. Mixture | 2 | 0.23 | 0.60 | 0.553 |
| Abundance | | | | | | | | | | | | | | |
| Site | 1 | 43.84 | 33.75 | <0.001 *** | Site | 1 | 82.37 | 59.90 | <0.001 *** | Site | 1 | 1.08 | 0.77 | 0.196 |
| Zone | 2 | 3.09 | 2.38 | 0.588 | Zone | 2 | 0.50 | 0.36 | 0.139 | Zone | 2 | 1.10 | 0.78 | 0.210 |
| Foundation Species | 1 | 34.39 | 26.63 | <0.001 *** | Monoculture vs. Mixture | 1 | 1.65 | 1.20 | 0.344 | Monoculture vs. Mixture | 1 | 10.10 | 7.14 | 0.004 ** |
| Site x Zone | 2 | 10.57 | 8.14 | <0.001 *** | Site x Zone | 2 | 34.96 | 25.43 | <0.001 *** | Site x Zone | 2 | 1.48 | 1.05 | 0.386 |
| Site x Foundation Species | 1 | 11.05 | 8.51 | 0.002 ** | Site x Monoculture vs. Mixture | 1 | 0.25 | 0.18 | 0.420 | Site x Monoculture vs. Mixture | 1 | 5.55 | 3.92 | 0.054 |
| Zone x Foundation Species | 2 | 3.01 | 0.00 | 0.327 | Zone x Monoculture vs. Mixture | 2 | 0.71 | 0.52 | 0.505 | Zone x Monoculture vs. Mixture | 2 | 9.45 | 6.68 | <0.001 *** |
| Site x Zone x Foundation Species | 2 | 9.96 | 7.67 | 0.002 ** | Site x Zone x Monoculture vs. Mixture | 2 | 0.71 | 0.51 | 0.911 | Site x Zone x Monoculture vs. Mixture | 2 | 1.49 | 1.05 | 0.444 |
| Proportion of Crustaceans | | | | | | | | | | | | | | |
| Site | 1 | 0.19 | 14.35 | <0.001 *** | Site | 1 | 0.59 | 24.68 | <0.001 *** | Site | 1 | 0.13 | 8.75 | 0.004 ** |
| Zone | 2 | 0.13 | 9.81 | <0.001 *** | Zone | 2 | 0.21 | 8.84 | <0.001 *** | Zone | 2 | 0.17 | 11.12 | <0.001 *** |
| Foundation Species | 1 | 0.02 | 1.60 | 0.210 | Monoculture vs. Mixture | 1 | 0.02 | 0.71 | 0.402 | Monoculture vs. Mixture | 1 | 0.00 | 0.18 | 0.676 |
| Site x Zone | 2 | 0.04 | 3.32 | 0.043 * | Site x Zone | 2 | 0.11 | 4.44 | 0.016 * | Site x Zone | 2 | 0.09 | 5.96 | 0.004 ** |
| Site x Foundation Species | 1 | 0.03 | 2.34 | 0.131 | Site x Monoculture vs. Mixture | 1 | 0.02 | 1.01 | 0.319 | Site x Monoculture vs. Mixture | 1 | 0.01 | 0.77 | 0.385 |
| Zone x Foundation Species | 2 | 0.00 | 0.25 | 0.778 | Zone x Monoculture vs. Mixture | 2 | 0.02 | 0.67 | 0.514 | Zone x Monoculture vs. Mixture | 2 | 0.01 | 0.67 | 0.517 |
| Site x Zone x Foundation Species | 2 | 0.00 | 0.16 | 0.851 | Site x Zone x Monoculture vs. Mixture | 2 | 0.01 | 0.45 | 0.641 | Site x Zone x Monoculture vs. Mixture | 2 | 0.01 | 0.88 | 0.421 |
| Proportion Non-native | | | | | | | | | | | | | | |
| Site | 1 | 0.00 | 0.47 | 0.498 | Site | 1 | 0.03 | 3.54 | 0.065 | Site | 1 | 0.02 | 2.16 | 0.147 |
| Zone | 2 | 0.01 | 0.76 | 0.472 | Zone | 2 | 0.01 | 1.94 | 0.153 | Zone | 2 | 0.04 | 4.17 | 0.020 * |
| Foundation Species | 1 | 0.00 | 0.17 | 0.679 | Monoculture vs. Mixture | 1 | 0.00 | 0.44 | 0.512 | Monoculture vs. Mixture | 1 | 0.00 | 0.15 | 0.697 |
| Site x Zone | 2 | 0.01 | 2.10 | 0.132 | Site x Zone | 2 | 0.03 | 4.49 | 0.015 * | Site x Zone | 2 | 0.00 | 0.45 | 0.642 |
| Site x Foundation Species | 1 | 0.03 | 4.87 | 0.031 * | Site x Monoculture vs. Mixture | 1 | 0.01 | 0.79 | 0.377 | Site x Monoculture vs. Mixture | 1 | 0.00 | 0.13 | 0.718 |
| Zone x Foundation Species | 2 | 0.01 | 2.05 | 0.137 | Zone x Monoculture vs. Mixture | 2 | 0.01 | 1.02 | 0.368 | Zone x Monoculture vs. Mixture | 2 | 0.00 | 0.35 | 0.707 |
| Site x Zone x Foundation Species | 2 | 0.03 | 4.75 | 0.012 * | Site x Zone x Monoculture vs. Mixture | 2 | 0.03 | 4.27 | 0.019 * | Site x Zone x Monoculture vs. Mixture | 2 | 0.02 | 1.89 | 0.160 |
| Community (PERMANOVA) | | | | | | | | | | | | | | |
| Site | 1 | 1.15 | 5.33 | <0.001 *** | Site | 1 | 2.10 | 9.26 | <0.001 *** | Site | 1 | 0.72 | 3.30 | 0.062 |
| Zone | 2 | 3.42 | 7.90 | <0.001 *** | Zone | 2 | 3.17 | 6.99 | <0.001 *** | Zone | 2 | 4.48 | 10.25 | <0.001 *** |
| Foundation Species | 1 | 1.51 | 6.99 | <0.001 *** | Monoculture vs. Mixture | 1 | 0.09 | 0.41 | 0.973 | Monoculture vs. Mixture | 1 | 0.65 | 2.96 | 0.051 |
| Site x Zone | 2 | 0.94 | 2.18 | <0.001 *** | Site x Zone | 2 | 2.50 | 5.51 | <0.001 *** | Site x Zone | 2 | 0.92 | 2.10 | 0.016 * |
| Site x Foundation Species | 1 | 0.74 | 3.41 | 0.009 ** | Site x Monoculture vs. Mixture | 1 | 0.14 | 0.61 | 0.782 | Site x Monoculture vs. Mixture | 1 | 0.21 | 0.98 | 0.120 |
| Zone x Foundation Species | 2 | 0.55 | 1.27 | 0.086 | Zone x Monoculture vs. Mixture | 2 | 0.09 | 0.21 | 0.989 | Zone x Monoculture vs. Mixture | 2 | 1.13 | 2.58 | 0.073 |
| Site x Zone x Foundation Species | 2 | 1.14 | 2.6333 | 0.002 ** | Site x Zone x Monoculture vs. Mixture | 2 | 0.37 | 0.82 | 0.491 | Site x Zone x Monoculture vs. Mixture | 2 | 0.30 | 0.68 | 0.984 |

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