

**Changing foundation species in the Chesapeake Bay:
implications for faunal communities of two dominant seagrass species**

A Thesis
Presented to

The Faculty of the School of Marine Science
The College of William and Mary in Virginia

In Partial Fulfillment
of the Requirements for the Degree of
Master of Science

by
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August 2023

APPROVAL PAGE

This thesis is submitted in partial fulfillment of
the requirements for the degree of
Master of Science

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Acknowledgments

I want to express my gratitude and appreciation for the support of all the people who made this work possible.

First, I'd like to thank my advisor, Dr. Chris Patrick. I am so grateful for your guidance and patience. I'd also like to thank my committee members, Drs. David Johnson, Robert Latour, and Rochelle Seitz, for the feedback and helpful discussions that made this work stronger as a whole.

Thank you to the VIMS community for being an amazing group of people and to my professors for sharing their knowledge and expertise. I really appreciate the logistical and administrative support that Maxine Butler, Jen Hay, and Cathy Cake provided throughout my time in the program. I am also extremely grateful to Jenny Dreyer for generously sharing her expertise in invertebrate taxonomy, especially regarding polychaetes. Many thanks to Katie Whitfield in ITNS for retrieving my files when my laptop decided to die just weeks before my defense.

Thank you to all the members of the CEEL lab and the SAV Monitoring and Restoration Program for being amazing company in the lab and field and for helping me with this project. Thank you to Corey Holbert for always making sure fieldwork ran smoothly and for sharing your epifaunal ID expertise. To Valerie Johnson, thank you for always helping me order the supplies I needed for my research. To Dave Wilcox and Carey Johnston, thank you for helping me with ArcGIS and for creating various study maps throughout the course of this project. Thank you to our post-doctoral researchers for your mentorship and support. I am especially grateful to Dr. Marc Hensel for helping me plan this study and for always making time to help me with statistical issues and coding. Thank you, Dr. Enie Hensel for always providing valuable advice and insightful feedback on my work. To Aly Hall, Alex Solis, and Mickie Edwards, thank you for letting me bounce ideas off you and for always making our shared office a fun space. Thank you to all our interns, especially Jecy and Haden for helping me collect samples as well as Tori, Cassidy, and Caitlin, for helping me with sample processing. To Grace, thank you for learning infauna IDs with me in addition to processing samples. I could not have finished my samples without everyone's hard work.

Thank you to my friends and family for all their encouragement and support. To my mom and dad, thank you for always being curious about seagrass ecology and for being my most enthusiastic supporters. Thank you to my brothers, Francisco and Alejandro, for supporting my passions. Thank you to my Aunt Laurie, who inspired me to pursue marine science. To my cats, Fred and George, who could care less about this accomplishment because they can't read, thank you nonetheless. Lots of love to Jainita, Tor, and Aly, you guys have been such amazing friends. I had so much fun in our fantasy book club (even though we hardly read any books together). To Morgan, I can't thank you enough for the great friendship, emotional support, love, and encouragement you provided when times were tough. Thank you!

Lastly, a special thank you to the approximately 40,596 epifauna and 413 infauna who donated their lives to science and to the 2,042 nekton we caught. Without them, this project really would not have been possible.

This work was funded by the VIMS Office of Academic Studies.

Abstract

Foundation species, such as seagrasses, provide many ecosystem functions in coastal habitats and support diverse food webs. However, environmental changes and human impacts to coastal ecosystems worldwide are threatening these biogenic habitats. When these changes cause shifts in the identity of foundation species, whole food webs dependent on those habitats can be altered. Seagrass meadows in Chesapeake Bay are an ideal study system to investigate these shifts, because the identity of the dominant seagrass in the lower Bay is currently shifting due to climate change. As water temperatures have risen, the once dominant species, *Zostera marina*, has been declining, while *Ruppia maritima* has been expanding. We performed quantitative surveys on epifaunal, infaunal, and nektonic communities of meadows with different seagrass species composition to examine how the structure and function of faunal communities differ between these two seagrass species. We found that seagrass bed type impacted epifaunal, infaunal, and nektonic abundance, biomass, secondary production, and diversity differently depending on trophic level. Epifaunal abundance was higher in *Ruppia* beds, but evenness was higher in *Zostera* beds. Furthermore, while epifauna biomass and secondary production per unit plant biomass was higher in *Ruppia* beds, biomass did not differ per unit area and secondary production was comparatively higher in *Zostera* beds suggesting that shifts to larger fauna and higher *Zostera* plant biomass per unit area offsets the increased abundance of small fauna in comparatively low biomass *Ruppia* beds. And while species composition of deep dwelling infauna differed by bed type, we observed few differences in infaunal abundance, biomass, and production between bed types. Based on current bay wide seagrass coverage, *Ruppia* has approximately 28.6% less gigagrams standing biomass of epifauna and infauna and 22.2% less gigagrams secondary production than *Zostera*. Moreover, in the water column, nektonic abundance, biomass, and richness all increased with the proportion of *Zostera* coverage relative to *Ruppia* coverage. We interpret these patterns to show that replacement of *Zostera* by *Ruppia* in Chesapeake Bay will reduce overall biomass and production of invertebrates and mobile fauna and shift invertebrate size distributions to smaller species. Overall, this study advances our understanding of how the shift in seagrass species occurring in Chesapeake Bay impacts the food web and serves as a case study for predicting how changes in the identity of foundation may affect community structure in other estuaries.

Keywords: Eelgrass, *Zostera*, Widgeongrass, *Ruppia*, Invertebrates, Community composition

Preface

Seagrasses are foundation species, or habitat forming organisms that influence ecosystem structure and function as well as the diversity and composition of the communities dwelling therein (Dayton 1972, Bruno 2001). Unfortunately, due to climate change and anthropogenic stressors, coastal ecosystems are being drastically and rapidly altered worldwide (Lotze et al. 2006, Halpern et al. 2008, Halpern et al. 2019), driving habitat fragmentation and loss of foundation species from local to global scales (Krumhansl et al 2016, Bryan-Brown et al. 2020, Dunic et al. 2021, Thomsen et al 2021, Murray et al. 2022). However, in some cases, rather than being lost as a result of these stressors, the identity of dominant foundation species in these habitats is shifting (Hughes et al. 2017, Kendrick et al. 2019, Hensel et al. 2023). When environmental changes affect foundation species, whole food webs can be altered (Johnston & Gruner 2018, Nelson et al. 2019, Pessarrodona, Foggo, & Smale 2019). Thus, there is a need to understand how shifts in foundation species identity impact the abundance and composition of fauna utilizing these habitats.

Seagrass ecosystems are home to epifauna, infauna, and mobile nekton, all of which provide important ecosystem services and functions. For instance, epifauna are vital to the maintenance of seagrass ecosystems. These invertebrates remove fouling epiphytic algae, which would otherwise shade the seagrass, and act as an important link in the food web between primary producers and higher trophic levels (Orth et al. 1984, Valentine & Duffy 2006). Infauna, such as polychaetes and bivalves, also act as vital food sources for epibenthic feeding-predators (Hines et al. 1990, Lipcius et al. 2007), and drive biogeochemical cycling in the sediment (Smith et al. 2000, Waldbusser et al. 2004, Michaud et al. 2021). Mobile nekton, many of which are

commercially valued fish or shellfish species, are found both living in the seagrass meadows and as occasional visitors. Many resident nekton use seagrass meadows as nursery habitats while others come to the meadows to feed (Heck et al. 2003, Lefcheck et al. 2019). Given the overwhelming importance of these different faunal groups to ecosystem structure and functioning, there is a growing need to understand how shifts in the identity of dominant, foundation species impact food-web dynamics in seagrass meadows.

The Chesapeake Bay provides an ideal case study system for investigating the impact of shifts in the identity of foundation species. Over the last few decades, in the lower Chesapeake Bay, we have been seeing a shift in the identity of the dominant seagrass species. As water temperatures have risen, *Zostera marina* has declined while *Ruppia maritima* has become more abundant (Lefcheck et al. 2017, Richardson et al. 2018, Hensel et al. 2023). Given the structural and life history differences between these plant species, shifts in seagrass species dominance might lead to impacts on the fauna that live in these habitats. This raises the questions: How does faunal habitat use differ between *Z. marina* and *R. maritima*? And how will faunal communities on larger scales respond to a shift from *Z. marina* dominance to *R. maritima* dominance in Chesapeake Bay? To answer these questions, I adopt a space for time approach and investigate spatial variation in the fauna of seagrass meadows with different seagrass species composition. I then apply these results to spatial distributions of each seagrass species now and in the future under different climate change regimes to predict the consequences of ongoing temporal changes in seagrass meadow identity.

**Changing foundation species in the Chesapeake
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Introduction

Foundation species, such as seagrasses and reef-building corals, are critical, habitat-forming species that strongly influence ecosystem structure and function (Dayton 1972, Bruno 2001). Environmental change caused by both natural and anthropogenic stressors, operating from local (e.g., shoreline alteration, dredging) to regional (e.g., eutrophication, overfishing) to global scales (e.g., climate change) is drastically and rapidly altering coastal ecosystems worldwide (Lotze et al. 2006, Halpern et al. 2008, Halpern et al. 2019). Due to these stressors, coastal habitats are being fragmented and foundation species are being extirpated from many local systems (Krumhansl et al. 2016, Bryan-Brown et al. 2020, Dunic et al. 2021, Thomsen et al. 2021, Murray et al. 2022). Consequences of losses of foundation species include disruptions to the provisioning of ecosystem services and reductions in habitat complexity (Ellison et al. 2005, Hoegh-Guldberg & Bruno 2010). For example, after an extreme marine heatwave in 2010, a catastrophic dieback of the dominant seagrass species in Shark Bay, Australia, corresponded with declines in the health of resident megagrazers during the following years (Thomson et al. 2015). However, foundation species habitat is not always completely lost from coastal systems. There is a growing body of evidence that in many cases, coastal ecosystems are instead experiencing a shift in the identity of the dominant foundation species (Hughes et al. 2017, Kendrick et al. 2019, Hensel et al. 2023). Although the literature on this subject is sparse, there is evidence that changes in the identity of marine foundation species can alter benthic ecosystem functioning and have lasting impacts on marine faunal communities by altering entire food webs (Johnston & Gruner 2018, Nelson et al. 2019, Pessarrodona, Foggo, & Smale 2019). Thus, there

is a need to quantify how shifts in the identity of dominant, foundation species affect the structure and function of coastal ecosystems.

Seagrasses are one example of a critically important coastal foundation species that are impacted by climate change and anthropogenic stressors. Seagrass meadows provide many ecosystem functions and services in coastal habitats such as improving water quality (Orth et al. 2020), sequestering carbon (Nordlund et al. 2016), stabilizing sediments (Orth et al. 2006), and acting as a nursery habitat (Lefcheck et al. 2019). Compared to non-vegetated habitat, seagrasses also support diverse food webs and have higher density of infauna and epifauna (Orth et al. 1984, Lefcheck et al. 2019). The infaunal and epifaunal invertebrates associated with seagrass meadows are important to ecosystem maintenance and contribute to secondary production, which supports higher trophic levels, such as commercially valued fish species, within the ecosystem (Orth et al. 1984, Seitz & Ewers Lewis 2018). Globally, seagrasses are impacted by local anthropogenic sediment and nutrient loadings (Orth et al. 2006, Shields et al. 2018), sea level rise (Orth et al. 2006), increased intensity of storms (Orth et al. 2006), and marine heat waves (Thomson et al. 2015). These changes in environmental conditions are enabling new foundation species to establish dominance, with potentially lasting impacts throughout the affected ecosystems.

In the lower Chesapeake Bay, rising water temperatures over the last few decades have caused a shift in the identity of the dominant seagrass species (Hensel et al. 2023), providing an ideal case study system for investigating the impact of shifts in the identity of foundation species. The once-dominant species, *Zostera marina*, has been declining due to heat stress (Moore & Jarvis 2008, Lefcheck et al. 2017), while a second species, *Ruppia maritima*, has been expanding at large spatial scales (Richardson et al. 2018, Hensel et al. 2023). These two species differ in life

history traits and morphology. Historically, *Z. marina* occupied greater depths in the subtidal and dominated mid-depths, whereas *R. maritima* dominated the high-light environment of the nearshore shallows (Orth & Moore 1988, Richardson et al. 2018). Additionally, the temporal distribution of *Z. marina* and *R. maritima* differ in that *Z. marina* experiences biannual peaks in above-ground biomass, while *R. maritima* only experiences a single annual peak. During late-spring or early-summer, *Z. marina* reaches its maximum above-ground biomass, then declines in above-ground biomass during mid to late summer, before experiencing its second annual peak in autumn (Orth & Moore 1982). Above-ground biomass of *R. maritima* reaches its annual peak in mid-summer (Orth & Moore 1982). *Zostera marina* and *R. maritima* are both perennial; however, *Z. marina* meadows exhibit greater permanence and year-to-year stability whereas *R. maritima* is more variable from year to year (Kautsky 1988, Hensel et al. 2023). Morphologically, *Z. marina* shoots have strap-like leaves reaching lengths of ~0.5-m while *R. maritima* has straight, thread-like leaves that remain short (~0.1-m) unless the plants are flowering. These structural and life history differences may drive differences in the ecosystem functions provided by the meadows and impact the fauna living there in a variety of ways.

To understand how the structure and function of faunal communities differ between seagrass foundation species, we performed quantitative surveys of epifaunal, infaunal, and nektonic communities in *Z. marina* and *R. maritima* meadows of the lower Chesapeake Bay in the summer of 2021. We predicted that seagrass meadows dominated by *Z. marina* would have higher levels of epifaunal abundance, biomass, and species richness per unit area since seagrass biomass positively influences epifaunal community abundance and richness (Stoner 1982, Lewis 1984, Attril et al. 2000), and *Z. marina* has greater biomass per unit area than *R. maritima* (Moore et al. 2000). We also expected that infaunal abundance and biomass would be higher in

seagrass meadows dominated *Z. marina* because seagrass roots, rhizomes, and shoots provide some protection from predation and *Z. marina* has more developed and deeper root and rhizomes networks (Orth et al. 1984, Seitz et al. 2001). Furthermore, we hypothesized that due to the greater permanence of *Z. marina* meadows (Hensel et al. 2023), deep-dwelling long lived infaunal species, such as the bivalve *Mya arenaria*, would be more prevalent in *Zostera* meadows. We expected that these effects on epifauna and infauna should, in turn, enhance the abundance and biomass of nekton using the meadows as foraging grounds.

Methods

Study Area:

In 2021, samples were collected on the western shore of the lower Chesapeake Bay (Fig. 1), with the majority of sample sites occurring in Mobjack Bay to minimize among site variation in environmental conditions (e.g., salinity, turbidity, etc.). Mobjack Bay has both *Z. marina* and *R. maritima* meadows and is the site of long-term ground survey data collected by the Submersed Aquatic Vegetation (SAV) Monitoring and Restoration Program at the Virginia Institute of Marine Science. Since 2008, the SAV Monitoring and Restoration Program has conducted annual surveys along 24 permanent transects to supplement aerial mapping which visualizes seagrass percent cover. The transects, which extend from the shore to the deepest end of the seagrass meadow, are used to track the SAV and ground truth bed edges at multiple locations in

Chesapeake Bay. Within fixed 1-m² stations, distributed at 10-m intervals along the entirety of each transect, the total % cover of SAV and the proportional cover of *R. maritima* and *Z. marina* are measured annually. This long-term data set was used to select sampling sites for this study. Samples were collected in three different seagrass bed types, those dominated by *Z. marina* (*Zostera*), those dominated by *R. maritima* (*Ruppia*), and those that were a mix of the two species (Mixed).

Survey Design:

Using transect data collected during 2016–2020, the mean and standard deviation of the proportional cover of each SAV species was quantified for each fixed station (n = 500) along 16 transects within the defined study region. From this pool, we excluded any station that had < 50% total seagrass cover on average over the 5-year pre-study period. Next, we applied the following criteria to categorize sites as either *Ruppia*, *Zostera*, or Mixed. *Ruppia* and *Zostera* were defined as having a mean cover of the target species that was greater than 50% and a standard deviation that was < 25%. Mixed beds were defined as fixed stations that had approximately equal amounts of both species over the 5-year pre-study period.

Epifauna Sampling:

Epifaunal samples for *Zostera*, *Ruppia*, and Mixed beds were collected during mid-June and early July of 2021. We stratified the stations in each seagrass bed type by transect and distance from shore and *a priori* selected a representative 30 total stations per bed type to sample for epifauna (n = 90). Epifauna was sampled using 0.5-mm mesh bags with a 28-cm diameter opening. The bag was brought down over the grass and closed at the sediment level. Then, the

grass was clipped from the rhizomes and sealed before bringing it to the surface. Samples were kept on ice until they were brought back to the lab and frozen until processing.

In the lab, samples were thawed in a sorting tray and vegetation was separated from the epifauna. Epifauna were then sorted into size classes using a series of sieves of increasingly smaller mesh size (5.6 mm, 4.0 mm, 2.8 mm, 2.0 mm, 1.4 mm, 1.0 mm, 0.71 mm, and 0.50 mm), identified to the lowest taxonomic level possible (usually species), and enumerated. Infaunal species that were found incidentally in these samples were excluded. Sorted epifauna were then preserved in 70% ethanol. Vegetation from the samples was separated by species. After, vegetation was dried for 72 hours at 60° C, weighed to determine grams (g) dry weight, then combusted for 5 hours at 500° C, and weighed again to determine g ash-free dry weight (AFDW). Quantification of plant biomass by species was performed to allow epifaunal biomass and abundance to be normalized to plant biomass, accounting for the varying amount of seagrass sampled in each mesh bag due to variation in sampling technique, shoot density, and shoot length.

Infauna Sampling:

Two types of infaunal samples were taken: push-core samples for shallow-dwelling benthos (~15-cm deep) and suction samples for deep-dwelling benthos (~40-cm deep). When sampling the shallow-dwelling benthos, a 15-cm diameter PVC core (176.71-cm²) was pushed into the sediment, and contents were sieved through a 500- μ m mesh. These shallow cores were taken at the same time and sites as epifaunal samples. In total, 50 shallow core samples were taken (n = 15 *Zostera*, n = 15 *Ruppia*, n = 10 Mixed, n = 10 Bare Sediment). Bare Sediment controls were defined as nearby locations of similar depth with no visual above-ground seagrass

biomass. For suction samples, a 60-cm diameter PVC core (2,827.43-cm²) was pushed into the sediment and a suction apparatus was used to vacuum the contents of the core into a coarse mesh bag (3-mm). In total, 28 suction samples were collected from 8 transects in Mobjack Bay during mostly mid to late July 2021. Seven samples were collected from each of four categories (*Zostera*, *Ruppia*, Mixed, or Bare Sediment). All infauna samples were kept on ice until they were brought back to the lab and frozen until processing.

In the lab, push-core samples were thawed in a sorting tray and dyed with Rose Bengal so that infauna were easily visible. Then, vegetation was separated from the fauna. Suction samples were thawed, passed through a 2.8-mm sieve to retain larger deep-dwelling bivalves, and vegetation was separated from the fauna. Organisms from all samples were preserved in 70% ethanol until they were identified and enumerated. Infauna were identified to the lowest taxonomic level possible (typically species for bivalves and family or genus for polychaetes). Epifaunal organisms were excluded from these counts. Following enumeration and identification, organisms were dried for 72 hours at 60° C, weighed, then combusted for 5 hours at 500° C, and weighed again to determine biomass in g AFDW. Vegetation from all samples was separated by species and divided into below-ground and above-ground biomass. After, vegetation was dried for 72 hours at 60° C, weighed to determine dry weight, then combusted for 5 hours at 500° C, and weighed again to determine g AFDW.

Nekton Sampling:

Trawl surveys were conducted in June, July, and August at 11 transects in Mobjack Bay (Fig. 1) to sample the nektonic community. Since nekton are more mobile than epifauna and infauna, and trawls cover much larger spatial areas, seagrass bed type was calculated differently

for these samples. The total and proportional cover of each seagrass species in 2021 was calculated for each transect (Table 1), varying in length from 200 to 880-m. Trawls were performed during the daytime within 2 hours of high tide with a 4.9-m otter trawl (1.9-cm mesh wings and 0.6-cm cod end liner, 0.3 m-by-0.7 m doors) towed along each transect for 2 minutes. Tow length was recorded with a GPS unit, with each tow covering approximately 562-m² of bottom. Nekton were identified to the lowest taxonomic level possible (typically species) and enumerated. Size was recorded for the first 10 randomly selected individuals of each species for each tow. Fish were measured using total length while mature blue crabs were sexed and measured by carapace width.

Statistical Analyses and Calculations:

Several indicators of faunal community structure and function were calculated including: total abundance, total biomass, secondary production, species richness (i.e., number of species present), and evenness. To estimate epifauna biomass, empirical equations relating size class to mass were used to obtain total mg AFDW of each species (Edgar 1990). To estimate nekton biomass, mean mass per individual from measured lengths was used and allometric scaling relationships between length and weight were extracted from FishBase (Froese & Pauly 2011). Secondary production for epifaunal and infaunal communities was estimated using the empirical model $\log Production = \log a + b * \log Biomass + c * \log Temperature$, where a , b , and c are fixed coefficients for different invertebrate faunal groups described by Edgar (1990). Temperature data were obtained from the NOAA 1/4° Daily Optimum Interpolation Sea Surface Temperature Version 2.1 (Huang et al. 2020). To quantify evenness, Shannon diversity was divided by the natural logarithm of species richness to calculate Pielou's evenness (Jost 2010).

Metrics of epifaunal community structure were scaled by both the biomass of seagrass in each sample (per g plant AFDW) and sampled area (per cm²) to allow comparison between metrics per unit plant biomass and metrics per unit area, respectively. Metrics of infaunal community structure were expressed per unit area sampled. Metrics of nektonic community structure were scaled by sample area (trawl length x 2.68-m width) to account for variation in trawl lengths.

Indicators of faunal community structure were compared across seagrass bed type using linear mixed effects models, which were assessed using Akaike's information criteria (AIC) (Burnham & Anderson, 2004). Data were log transformed when necessary to homogenize variances and models were fitted using lme4() function in the lmer library in R (version 4.2.3; Bates et al. 2015). In models assessing epifauna, bed type was treated as a fixed effect and transect was treated as a random effect. Seagrass dry weight (g) was also included as fixed effect when assessing epifaunal abundances per g plant AFDW, biomass per g plant AFDW, and secondary production per g plant AFDW and per cm² (produced lower AIC values). In models assessing infauna, bed type was treated as a fixed effect and transect was treated as a random effect. In models assessing nekton, proportional % cover of *Ruppia* (i.e., bed type) and month were treated as fixed effects and transect was treated as a random effect. Models assessing Pielou's evenness were fitted using glmmTMB() function in the glmmTMB library in R with a beta distribution (Brookes et al. 2017).

To summarize patterns of epifaunal, infaunal, and nektonic assemblages by seagrass bed type, we visualized communities using Bray-Curtis based nonmetric multidimensional scaling (NMDS). NMDS analysis was performed using the metaMDS function in the vegan library in R (Oksanen et al. 2018) and only NMDS ordinations with a stress value below 0.2 were retained as values above this threshold are generally considered uninterpretable (McCune & Grace 2002).

The significance of differences in epifaunal, infaunal, and nektonic community composition among groups was tested using permutational multivariate ANOVA (PERMANOVA) using the `Adonis()` function in the `vegan` library in R (Oksanen et al. 2018).

To estimate current biomass and secondary production of small invertebrates (i.e., epifauna and infauna) in the entire Chesapeake Bay, we used data on the coverage of *Ruppia* and *Zostera* monocultures in 2022 (Patrick et al. 2023b). We also used results from a recent study that forecasts the future of seagrass coverage by species under climate change and nutrient management scenarios described by Shenk et al (2021) to obtain projected coverage of *Ruppia* and *Zostera* monocultures in 2060 under a best-case scenario for nutrient management and a scenario with no further nutrient reductions (Patrick et al. 2023a). We multiplied estimates of combined epifaunal and infaunal biomass ($\bar{x} \pm \sigma$ in g per m²) in *Zostera* and *Ruppia* bed types by projected coverages of each seagrass species to estimate the total biomass (gigagrams) these small invertebrates make up in seagrass habitats of the Chesapeake Bay in 2022 (the most recent year with seagrass coverage currently available) and in 2060 under the two aforementioned scenarios. To estimate secondary production in seagrass meadows of the region currently and in the future, the general empirical model described by Edgar (1990) was applied to our combined epifaunal and infaunal biomass estimates and the projected mean summer temperatures reported by Patrick et al. (2023a). Then, we assumed a four-month growing season (May 15 – September 15) and multiplied these secondary production estimates ($\mu\text{g day}^{-1}$ per m²) by 120 days to calculate growing season secondary productivity per unit area per bed type. These estimates were then similarly multiplied by seagrass cover estimates as we did with biomass.

Results

Epifauna:

In total, 40 unique taxa (Appendix Table A1) were collected in all epifaunal samples (24 in *Zostera*, 33 in *Ruppia*, and 27 in Mixed). The most common species observed were *Bittium* spp., *Caprella penatis*, and *Cymadusa compta* making up respectively 84.97%, 7.88%, and 2.71%, of the total fauna. Epifaunal abundance per g plant AFDW was impacted by bed type and g plant dry weight (Table 2). Bed type also impacted epifaunal abundances per cm² (Table 2) Epifaunal abundances per g plant AFDW (Fig. 2a) and per cm² (Fig. 2b) were higher in *Ruppia* than *Zostera* ($p < 0.0001$, $p = 0.0009$), and were higher in Mixed beds than in *Zostera* ($p = 0.01$, $p < 0.005$). Epifaunal biomass per g plant AFDW was impacted by bed type and g plant dry weight (Table 2) and was higher in *Ruppia* than *Zostera* ($p < 0.005$, Fig. 2c). However, bed type did not affect epifaunal biomass per cm² (Fig. 2d). Additionally, the average size of these individuals tended to be smaller in *Ruppia* beds than *Zostera* beds (Appendix Fig. A1). Secondary production ($\mu\text{g day}^{-1}$) per g plant AFDW and per cm² were both affected by g plant dry weight (Table 2), increasing as seagrass biomass increased. There was no difference in secondary production per g plant AFDW (Fig. 2e) or per cm² (Fig. 2f). While epifaunal species richness did not differ among bed types (Fig. 2g), Pielou's evenness varied among bed types (Table 2). Evenness (Fig. 2h) was higher in *Zostera* than both *Ruppia* ($p < 0.005$) and Mixed beds ($p = 0.01$).

The NMDS fit the data relatively well (Fig. 3a, stress = 0.086). While composition visually overlapped between the mixed beds and the monoculture beds, the PERMANOVA

showed that species composition differed among bed types ($p = 0.001$). These differences appear to be largely driven by the amphipods *Ampithoe longimana*, *C. penatis*, and *C. compta*, the isopod *Erichsonella attenuata*, and gastropods in the genus *Bittium*. *Ampithoe longimana*, and *C. compta* were more common in *Zostera*. *Caprella penatis* and *E. attenuata* were more common in Mixed beds. *Bittium* spp. were more common in *Ruppia* (Appendix Fig. A2).

Infauna:

In total, 16 infaunal taxa (Appendix Table A2) were collected in shallow core samples (11 in *Zostera*, 10 in *Ruppia*, 7 in Mixed, and 8 in Bare Sediment). The most common species observed were the polychaetes *Alitta succinea* and *Clymenella toquata* and the bivalve *Arcuatula papyria*, making up respectively 55.56%, 11.64%, and 8.99%, of the total fauna. On average, below-ground plant biomass (Fig. 4f) was 0.703 ± 1.950 SD g in bare sediment, 1.077 ± 0.312 SD g in Mixed, 1.293 ± 0.680 SD g in *Ruppia*, and 2.172 ± 1.650 SD g in *Zostera*. For these samples, bed type did not impact infaunal abundance (Fig. 4a), biomass (Fig. 4b), secondary production (Fig. 4c), species richness (Fig. 4d), or evenness (Fig. 4e, Table 3).

In total, 12 infaunal taxa (Appendix Table A2) were collected in suction samples (8 in *Zostera*, 9 in *Ruppia*, 9 in Mixed, and 4 in Bare Sediment). The most common species observed were the bivalves *A. papyria*, *Mulinia lateralis*, and *Tagelus plebeius*, making up respectively 53.57%, 18.75%, and 17.41%, of the total fauna. On average, below-ground plant biomass (Fig. 5f) was 0.240 ± 0.635 SD g in bare sediment, 7.531 ± 5.039 SD g in Mixed, 6.808 ± 3.988 SD g in *Ruppia*, and 10.016 ± 3.868 SD g in *Zostera*. For these samples, bed type impacted infaunal abundances per cm^2 (Table 3). Infaunal abundance (Fig. 5a) was higher in Mixed beds than in bare sediment ($p < 0.01$), but otherwise similar between all seagrass bed types. Infaunal biomass

(Fig. 5b), secondary production (Fig.5c), richness (Fig. 5d), and evenness (Fig. 5e) did not differ among bed types (Table 3).

For shallow-dwelling infauna, the NMDS fit the data well and revealed no consistent difference in community composition as a function of bed type (Fig. 3b, stress = 0.137). PERMANOVA confirmed this visual inspection, suggesting that bed type did not significantly influence shallow-dwelling infaunal community composition. For deep-dwelling infauna, the NMDS fit the data well (Fig. 3c, stress = 0.104). Composition visually overlapped between all bed types and bare sediment as well as between Mixed and *Zostera* beds. However, the PERMANOVA showed that species composition differed among bed types ($p < 0.05$). These differences appear to be largely driven by the bivalves *Mulina lateralis* and *Tagelus plebeius*. *Mulina lateralis* was more common in *Ruppia*, while *T. plebeius* was more common in Mixed beds (Appendix Fig. A4).

Nekton:

In total, 22 unique taxa (Appendix Table A3) were collected through trawl surveys. The most common species observed across all months were *Bairdiella chrysoura* (American silver perch), *Leiostomus xanthurus* (spot), *Anchoa mitchilli* (bay anchovy), *Callinectes sapidus* (blue crab), and *Sygnathus* spp. (pipefish), making up respectively 45.19%, 20.41%, 14.99%, 7.55%, and 7.44% of the total fauna. Nektonic abundance, biomass, and species richness all significantly varied with proportional % *Ruppia* coverage along the transect (Table 4). All indicators of faunal community structure, except for Pielou's evenness, decreased as proportional % cover of *Ruppia* increased (Fig. 6). These patterns persisted across all months (Appendix Fig. A5). The proportional abundance of *B. chrysoura* was highest in *Zostera* dominated meadows (Appendix

Fig. A6) and abundance of *C. sapidus* increased with % *Zostera* due to higher abundances being observed in August (Appendix Fig. A7).

The NMDS fit the data well and revealed no consistent difference in nektonic community composition as a function of bed type (Fig. 3d, stress = 0.154). PERMANOVA confirmed this visual inspection, suggesting that bed type as a categorical variable did not significantly influence community composition.

Estimates of Biomass and Secondary Production in Chesapeake Bay:

We estimate that in the entire Chesapeake Bay in 2022, *Zostera* holds 0.35 ± 0.27 SD gigagrams of small invertebrate (i.e., epifauna and infauna) biomass and supports 0.18 gigagrams of secondary production per year, while *Ruppia* holds 0.25 ± 0.17 SD gigagrams of small invertebrate biomass and supports 0.14 gigagrams of secondary production per year (Appendix Table A4). Under a best-case scenario for nutrient management, we estimate that in 2060, *Zostera* will hold 0.11 ± 0.08 SD gigagrams of small invertebrate biomass and will support 0.06 gigagrams of secondary production per year, while *Ruppia* will hold 0.35 ± 0.23 SD gigagrams of small invertebrate biomass and will support 0.21 gigagrams of secondary production per year (Appendix Table A4). Under a scenario with no further nutrient reductions, we estimate that in 2060, *Zostera* will hold 0.09 ± 0.07 SD gigagrams of small invertebrate biomass and will support 0.05 gigagrams of secondary production per year, while *Ruppia* will hold 0.12 ± 0.08 SD gigagrams of small invertebrate biomass and will support 0.07 gigagrams of secondary production per year (Appendix Table A4).

Discussion

We set out to quantify how faunal community structure and function differ between *Z. marina* and *R. maritima* meadows in the lower Chesapeake Bay, because the impact on the food web due to shifting identity of dominant seagrass species in this region is not well known. In general, we found that seagrass bed type impacted faunal abundance, biomass, secondary production, and diversity differently depending on trophic level. Epifauna biomass and production per unit plant biomass was higher in *Ruppia* beds than *Zostera* beds. However, biomass did not differ per unit area and secondary production was comparatively higher per unit area in *Zostera* beds. This suggests that shifts to larger fauna and higher *Zostera* plant biomass per unit area offsets the increased abundance and biomass of small fauna per unit plant biomass in *Ruppia* beds with comparatively lower plant biomass. In contrast, while species composition of deep dwelling infauna differed by seagrass bed type, we observed few differences in infaunal abundance, biomass, and secondary production between the bed types. In the water column, nektonic abundance, biomass, and richness all increased with the proportion of *Zostera* coverage relative to *Ruppia* coverage. These results suggest that the ongoing shift in seagrass species dominance from *Zostera* to *Ruppia* has had significant impacts on community structure and function that will continue to accelerate with climate change.

While *Ruppia* beds were characterized by a higher abundance of small epifauna in comparison to *Zostera* and Mixed beds, epifaunal biomass scaled by the biomass of seagrass (per g plant AFDW) was significantly higher in *Ruppia* compared to *Zostera* and Mixed beds. However, when scaled by sampled area (per cm²), epifaunal biomass was not impacted by bed type. This is likely because *Ruppia* has a relatively high surface area-to biomass ratio due to its

narrow leaves but has overall lower biomass per unit area than *Zostera* (Parker et al. 2001). *Ruppia* beds were dominated by high abundances of smaller epifaunal species, such juvenile *Bittium* snails, whereas *Zostera* and Mixed beds had greater abundances of comparatively larger fauna like the isopod *Erichsonella attenuata*. *Zostera* beds also had greater abundances of the amphipods *A. longimana*, *C. compta*, *Elasmopus levis*, and *Gammarus mucronatus* compared to other seagrass bed types. Our results contrast those of a previous study conducted in the same region which found no effect of seagrass species on the abundance of epifaunal assemblages (French & Moore 2018). This may be due to the comparatively low sample size of the French & Moore study (3 sites and 10 samples per site) and the presence of the algae *Gracilaria vermiculophylla* in their samples, potentially confounding the habitat complexity difference between the seagrass meadow types. Additionally, the patterns we observed should be interpreted cautiously bearing in mind that the study was a snapshot in the summer, with samples being taken over a relatively short period of time. However, this sample period was optimal for observing differences in seagrass bed types as it encompasses summer peaks in seagrass above-ground biomass and takes place after spring benthic recruitment. Similar to French & Moore (2018), we also found no difference in species richness among bed type. The lack of differences between bed type in epifaunal species richness might be due to the overall low richness of small, epifaunal invertebrates like gastropods, isopods, decapods, and amphipods in the lower Chesapeake Bay and the high dispersal that they have as larvae (Parker et al. 2001, Valentine & Duffy 2006).

Infauna like bivalves and polychaetes are important food sources for higher trophic levels and predators, such as blue crabs (*C. sapidus*) (Lipcius et al. 2007). However, for the shallow benthos (~15-cm), no differences in infaunal abundance were observed among seagrass bed

types and there was no difference between bare sediment and any of the seagrass beds when it came to infaunal biomass, secondary production, species richness, or evenness. In part, this was due to high numbers of small *A. succinea* occurring in all vegetated habitats, which had negligible effects on total biomass and secondary production. For the deep benthos (~40-cm), there was no difference between bare sediment and *Zostera* or *Ruppia* beds when it came to infaunal abundance, biomass, and secondary production, but Mixed beds had significantly higher infaunal abundance than bare sediment. Differences in abundance between bare sediment and Mixed beds were driven by higher numbers of *A. papyria* in Mixed beds. These findings contrast a past, local study where abundance, diversity, and secondary production were higher in *Zostera* beds than unvegetated habitats (Seitz & Ewers Lewis 2018). Additionally, increased infaunal abundances (Orth et al. 1984, Edgar 1990) and high benthic secondary productivity (Edgar 1990, Wong et al. 2011) have been previously documented in seagrass meadows compared to unvegetated habitats. Low sample size combined with rare large fauna may be responsible for the discrepancy as the comparatively high mean biomass in our bare sediment samples was driven by the presence of one very large hard clam (*Mercenaria mercenaria*) in a single sample. When this outlier was removed, we found that biomass of deep-dwelling infauna was comparatively higher in vegetated habitats.

Nektonic communities showed a clear pattern of response to different seagrass species identity. Nektonic abundance, biomass, and species richness declined with increasing proportional cover of *Ruppia* across the entire growing season while evenness showed the opposite pattern. These observations were driven by decreases in the abundance of all nektonic species as proportional cover of *Ruppia* increased. There were also overall greater abundances of certain species in *Zostera* such as *Sygnathus* spp. (*pipe fish*), *Orthopristis chrysoptera* (*pigfish*),

and *C. sapidus* (blue crab). However, certain species, like *L. xanthurus* (spot), were overall the most abundant in *Ruppia* and had a much higher abundance in Mixed beds than *Zostera*. These effects are particularly important considering the economic value of blue crabs and spot. A possible explanation for the patterns we observed is that thin-bladed *Ruppia* shoots fail to provide comparable canopy structure and prey refuge for animals, like blue crabs and pipefish, relative to *Z. marina* (French & Moore 2018). Another factor may be the comparatively higher production of epifauna and higher biomass per individual we observed in *Zostera* beds provides higher quality foraging grounds to mobile fauna, like pigfish, that forage on epifauna. Conversely, for bottom feeders like spot that feed more on infauna, such as burrowing polychaetae species (Chao & Musick 1997), lower below-ground biomass observed in *Ruppia* beds may make foraging in these meadows easier than among the denser and more robust *Zostera* rhizomes. Similar results have been documented in other seagrass ecosystems, such as in the Mira estuary in Portugal. In the Mira estuary, after the loss of *Z. marina* meadows, *Z. noltii* (dwarf eelgrass) supported lower long-term fish diversity and abundance after gaining dominance (Castro et al. 2019). It is also worth considering the potential effect that differences in sampling efficiency had on these observations. Trawling has less efficient catch rates over seagrass than bare sediment and efficiency drops with increasing seagrass biomass per unit area (Orth & van Montfrans 1987, Rozas & Minello 1997, Stallings et al. 2014). Given that *Zostera*, which has more seagrass biomass per unit area than *Ruppia* (Moore et al. 2000), had both higher catch per unit effort and higher nektonic biomass per unit area, the differences we observed between *Zostera* and *Ruppia* beds might be an underestimate of the true difference in nektonic abundance between these seagrass bed types.

These results have several serious implications for Chesapeake Bay and the results are an important case study for how similar shifts in biogenic habitat identity may impact coastal ecosystems. In 2022, there are approximately 8,104.41 hectares of *Zostera* and 9,778.34 hectares of *Ruppia* in the lower Chesapeake Bay (Patrick et al. 2023b), a shift from just a few decades ago when *Zostera* made up 50% of all SAV in the system (Hensel et al. 2023). Extrapolating our epifaunal and infaunal observations to the whole system, we estimate a total service of 0.60 ± 0.33 SD gigagrams standing biomass and 0.32 gigagrams growing season production currently provided by seagrass in the Chesapeake Bay (Appendix Table A4) that supports higher trophic levels and fisheries. Under a best-case scenario for nutrient management, we estimate that continued predicted shifts in *Ruppia* dominance will cause a 23.3% decrease in biomass and a 18.8% decrease in secondary production of epifauna and infauna in seagrass meadows. By 2060, this equates to a loss of 0.14 gigagrams of biomass and 0.06 gigagrams of growing season production. These estimates consider predicted increases in overall seagrass coverage with successful nutrient management. Focusing on shifts in just seagrass species identity with no further nutrient reductions, we estimate a 65.0% decrease in biomass and a 62.5% decrease in secondary production of epifauna and infauna in seagrass meadows. By 2060, this equates to a loss of 0.38 gigagrams of biomass and 0.20 gigagrams of growing season production. While these estimates do not consider how other factors, such as temperature changes, will simultaneously affect organism body size and abundance per unit area or how infauna remaining in the bare sediments might contribute to secondary production, it underscores the massive importance of both seagrass presence and seagrass identity to provisioning of services.

While we do not attempt similar estimates with more mobile fauna, we expect that similarly large changes will result from changes in the coverage and identity of seagrass in the

Chesapeake under climate change. Our results show that overall abundance, richness, and biomass of nekton are lower in *Ruppia* dominated meadows. While direct extrapolation of these results is not defensible because we are unable to separate the potential fish aggregation effects from differences in habitat provisioning, several lines of reasoning suggest that that proportional reductions in *Zostera* coverage over the next century will cause declines in mobile fauna at the fishery scale. First, overall reductions in biomass and production of epifauna and infaunal forage should translate to reductions in potential fishery production. For example, 33% of prey consumption by silver perch (*Bairdiella chrysoura*) in seagrass meadows of the Chesapeake Bay is estimated to go directly into growth during the summer (Sobocinski & Latour 2015). Second, *R. maritima* has less year-to-year stability in coverage and bed locations (Hensel et al. 2023), and long-term fisheries declines have been documented in response to reductions in habitat consistency (Castro et al. 2019). Greater year-to-year variability in *Ruppia* coverage could also be problematic for important transient or juvenile species like blue crabs and spot. Overall, the management message is clear, there is a continued need to push attainment of water quality standards to ensure that these essential habitats are preserved (Lefcheck et al. 2018), particularly in the face of climate change (Hensel et al. 2023).

In a global context, the full impact shifting dominant seagrass species identities has yet to be quantified but there is an emerging literature that suggests that these shifts, which are accelerating with climate change, have potential to reshape the structure and function of ecosystems worldwide. For example, climate change and introduced pests in forests across North America have facilitated various hardwoods replacing Eastern hemlock (*Tsuga canadensis*), considerably altering nitrogen dynamics, associated bird communities in the forests, and insect communities of nearby watersheds (Kizlinski et al. 2002, Snyder et al. 2002, Ellison et al 2005).

In coastal ecosystems, the current evidence suggests that the poleward shift of the mangrove-marsh ecotone may lead to changes in fish and invertebrate community composition (Armitage et al. 2021), and studies have reported differences in faunal community structure that vary by taxonomic group (Osland et al. 2022 and references therein). For instance, along the Atlantic coast of Florida, macrofaunal communities of small fish and decapod crustaceans differed in marsh versus mangrove-dominated vegetation, because of the influence of differences in vegetation type and physical structure (Johnston & Gruner 2018). The replacement of cold-water kelp (*Laminaria hyperborea*) by warm-temperate golden kelp (*Laminaria orchroleuca*) has caused orders-of-magnitude losses in structure and function of associated fauna that support a diverse food web (Pessarrodona, Foggo, & Smale 2019, Smale et al. 2022). Thus, when considering examples from other marine and terrestrial ecosystems experiencing climate change-driven shifts in foundation species identity, it becomes clear that impacts to ecosystem functioning depend on the magnitude of changes to positive interactions, habitat cascades, and food web facilitation.

Because foundation species form critical habitats which influence biodiversity, evaluating how different faunal groups respond to shifting identity of foundation species can inform our understanding of broader community change. Overall, this study advances our understanding of how the shift occurring in the lower Chesapeake Bay is impacting both lower and intermediate levels of the food web as well as serves as a case study for predicting how changes in the identity of foundation species may affect community structure and function in other coastal ecosystems.

Figures

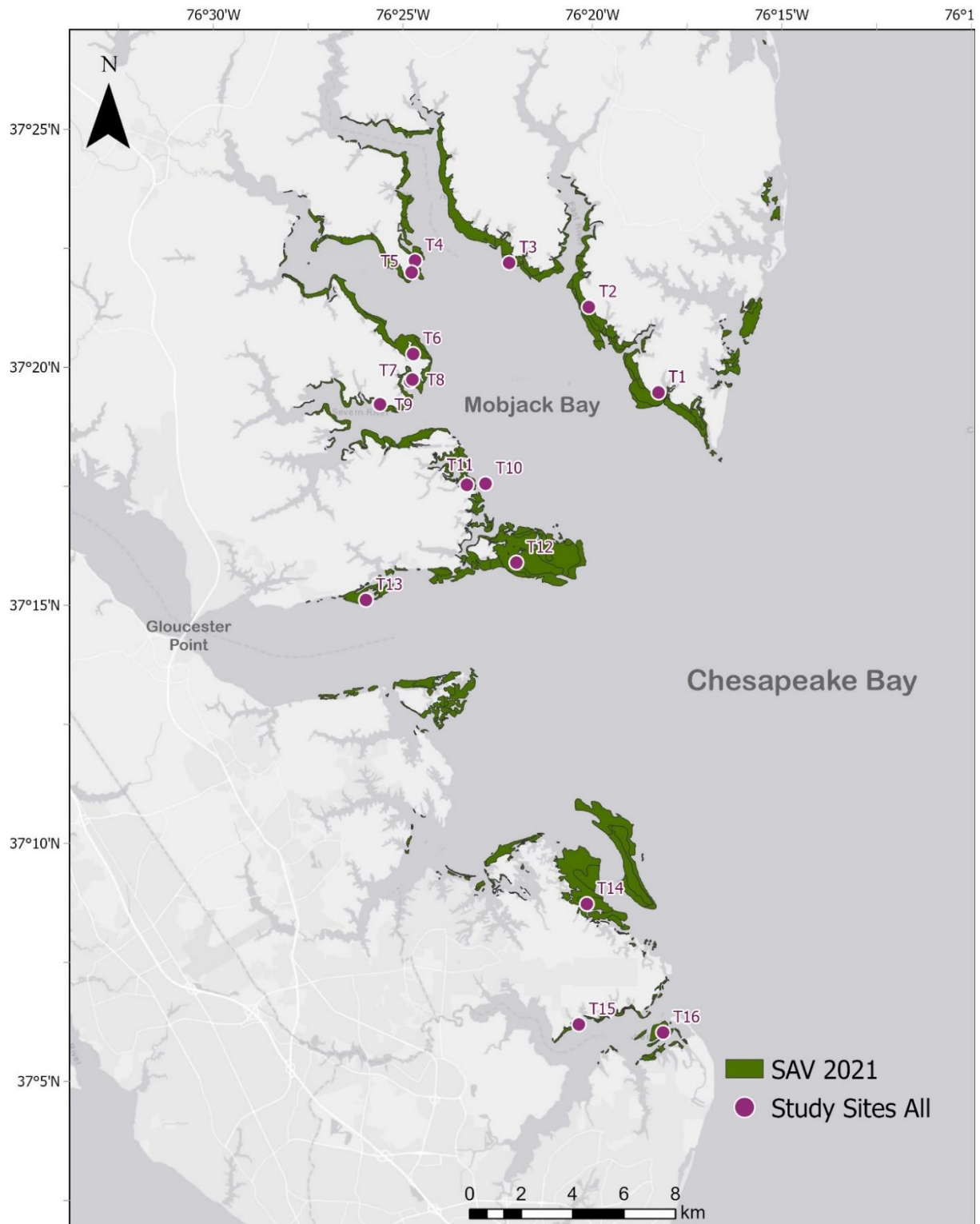


Figure 1: Map of the lower Chesapeake Bay, VA. Study sites are indicated by purple dots and the coverage of submerged aquatic vegetation (SAV), or seagrass meadows, is shown in green.

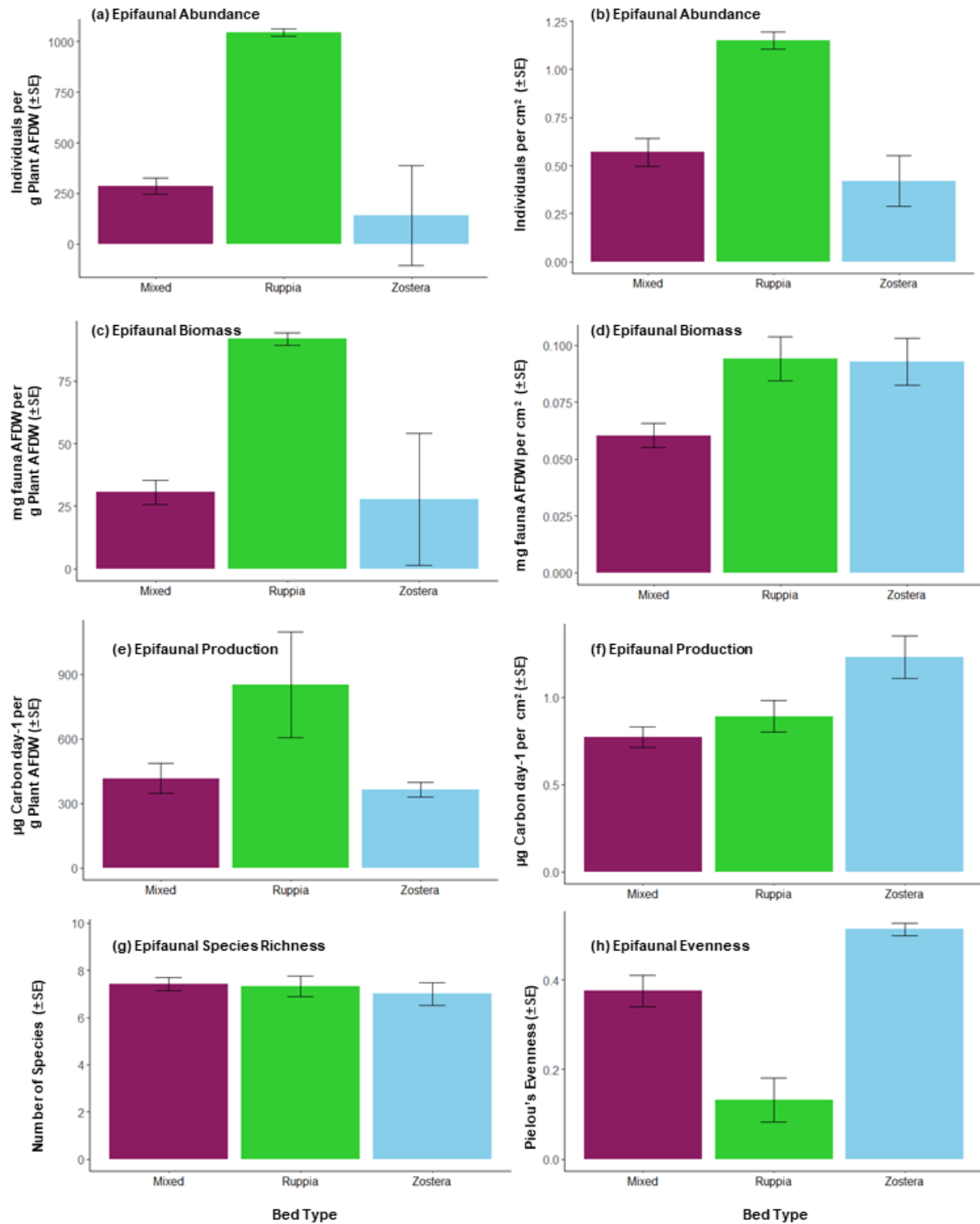


Figure 2: Indicators of epifaunal community structure in three seagrass bed types, those dominated by *Zostera marina* (*Zostera*), those dominated by *Ruppia maritima* (*Ruppia*), and those that were a mix of the two species (Mixed). **(a)** Epifaunal abundance per g plant ash free

dry weight (AFDW). **(b)** Epifaunal abundance per cm². **(c)** Epifaunal biomass per g plant AFDW. **(d)** Epifaunal biomass per cm². **(e)** Secondary production per g plant AFDW. **(f)** Secondary production per cm². **(g)** Epifaunal species richness. **(h)** Pielou's evenness of epifaunal assemblages.

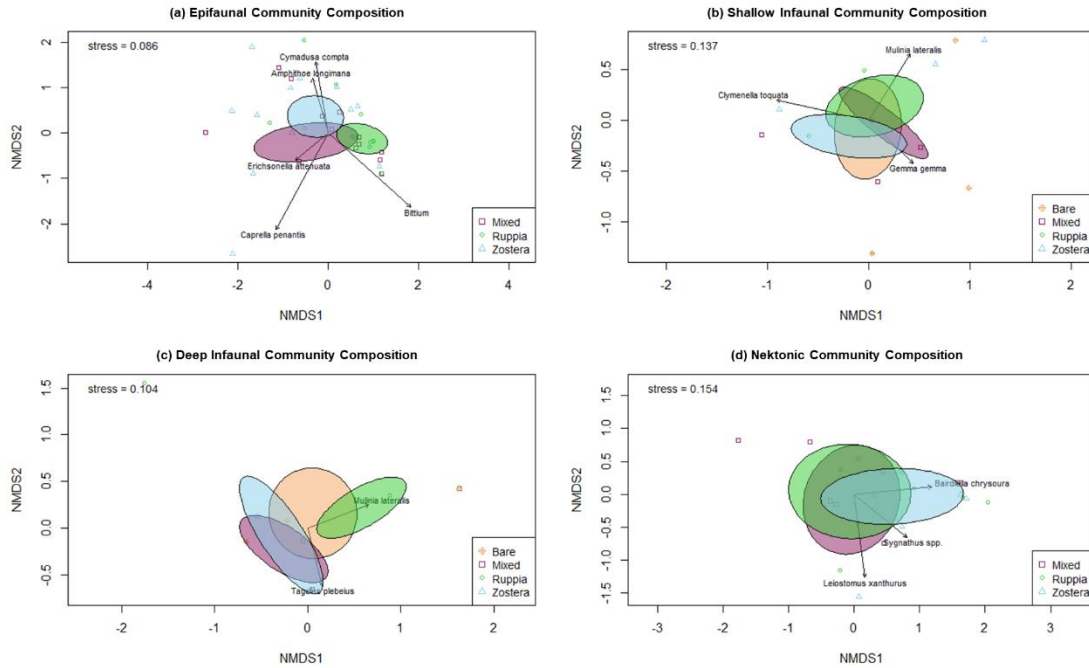


Figure 3: Faunal community composition in three seagrass bed types, those dominated by *Zostera marina* (*Zostera*), those dominated by *Ruppia maritima* (*Ruppia*), and those that were a mix of the two species (Mixed). Infaunal communities also included a fourth bed type category for bare sediment controls (Bare). Color and shape of symbols correspond to these categories. **(a)** NMDS plot of epifaunal community composition. **(b)** NMDS plot of community composition for shallow-dwelling infauna. **(c)** NMDS plot of community composition for deep-dwelling infauna. **(d)** NMDS plot of nektonic community composition.

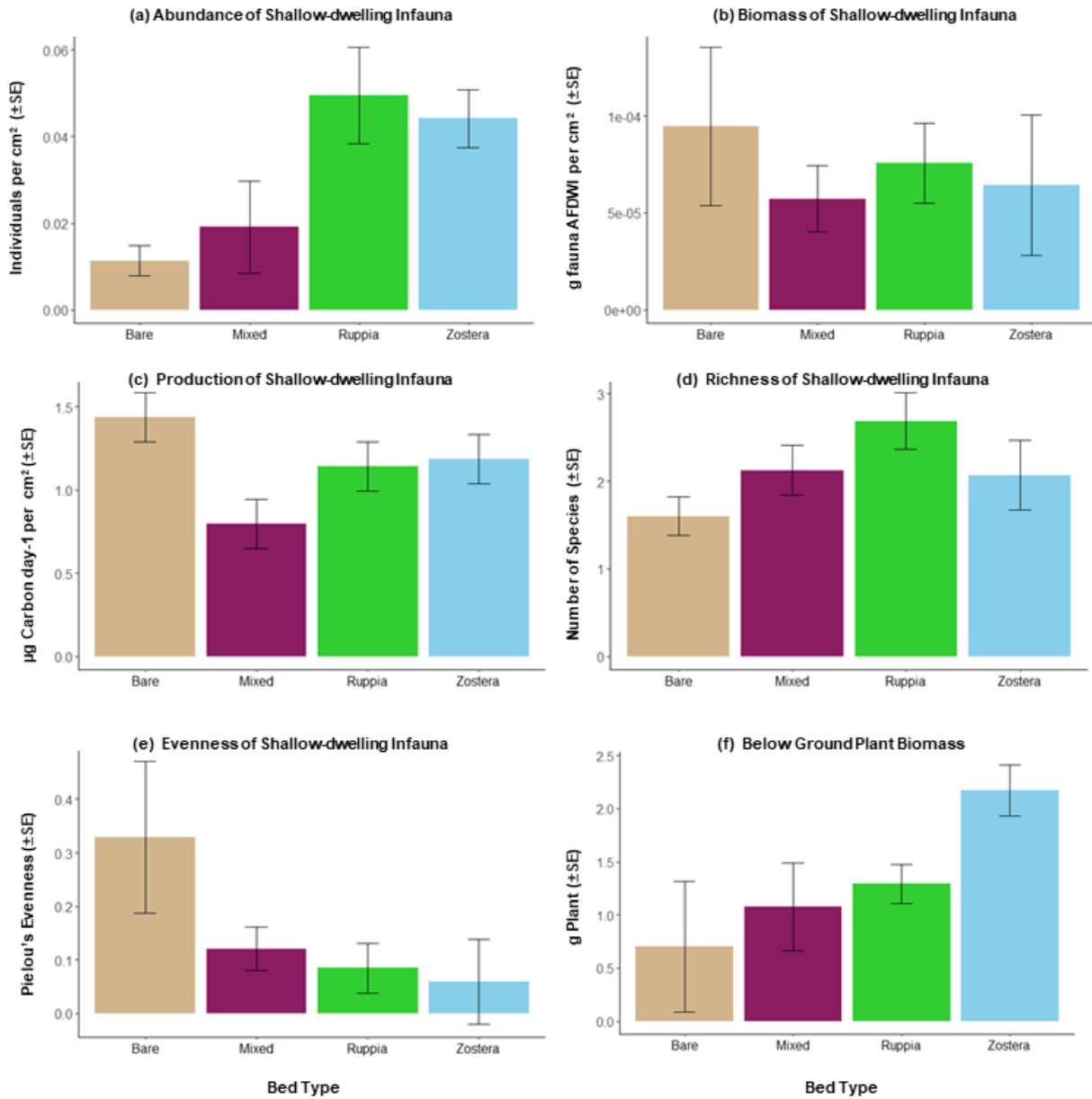


Figure 4: Indicators of shallow-dwelling infaunal community structure in four bed types, bare sediment, *Zostera marina* (*Zostera*), *Ruppia maritima* (*Ruppia*), and those that were a mix of the two seagrass species (Mixed). **(a)** Abundance. **(b)** Biomass. **(c)** Secondary production. **(d)** Species richness. **(e)** Pielou's evenness. **(f)** Below-ground plant biomass in samples.

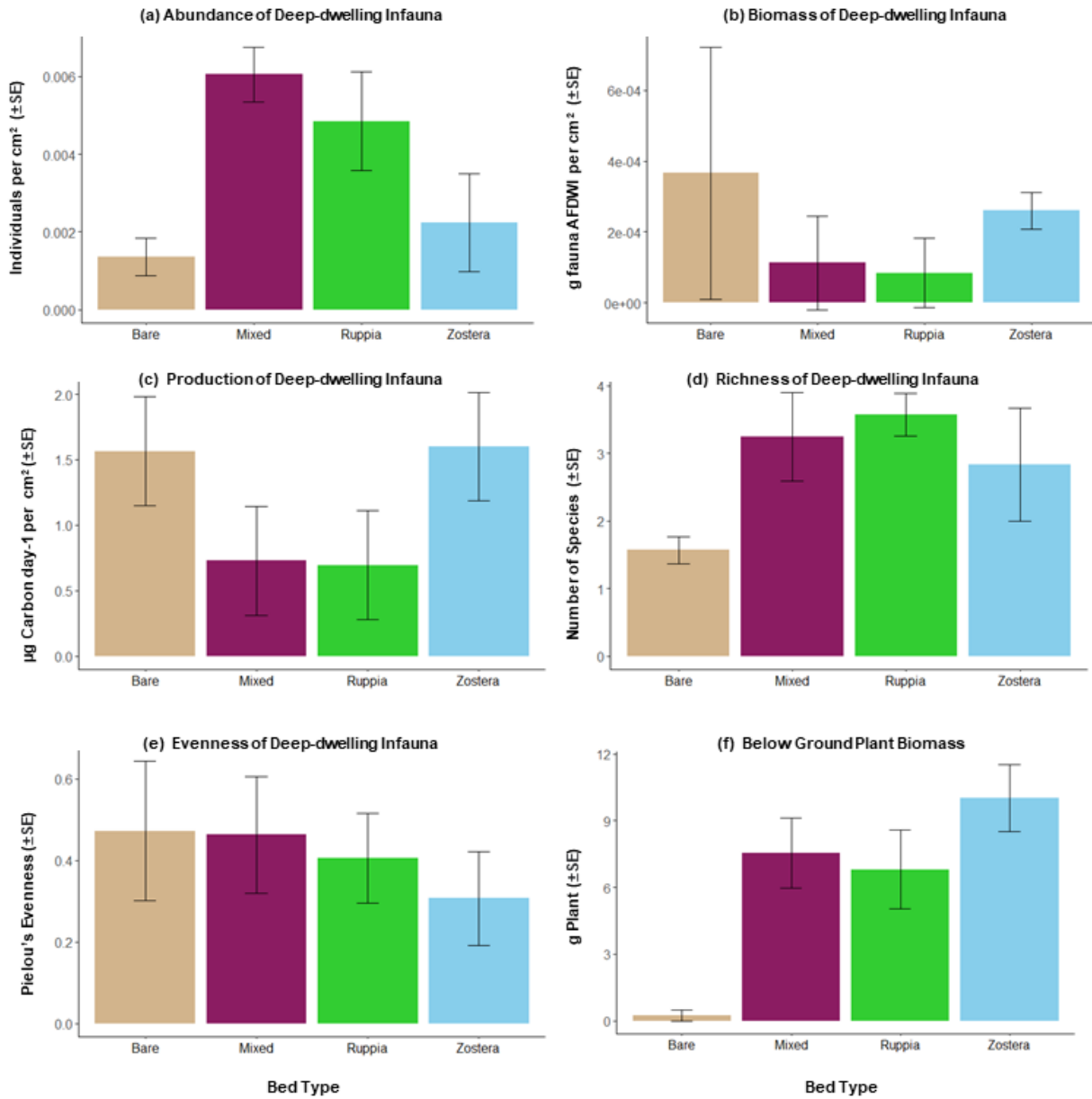


Figure 5: Indicators of deep-dwelling infaunal community structure in four bed types, bare sediment, *Zostera marina* (*Zostera*), *Ruppia maritima* (*Ruppia*), and those that were a mix of the two seagrass species (Mixed). **(a)** Abundance. **(b)** Biomass. **(c)** Secondary production. **(d)** Species richness. **(e)** Pielou's evenness. **(f)** Below-ground plant biomass in samples.

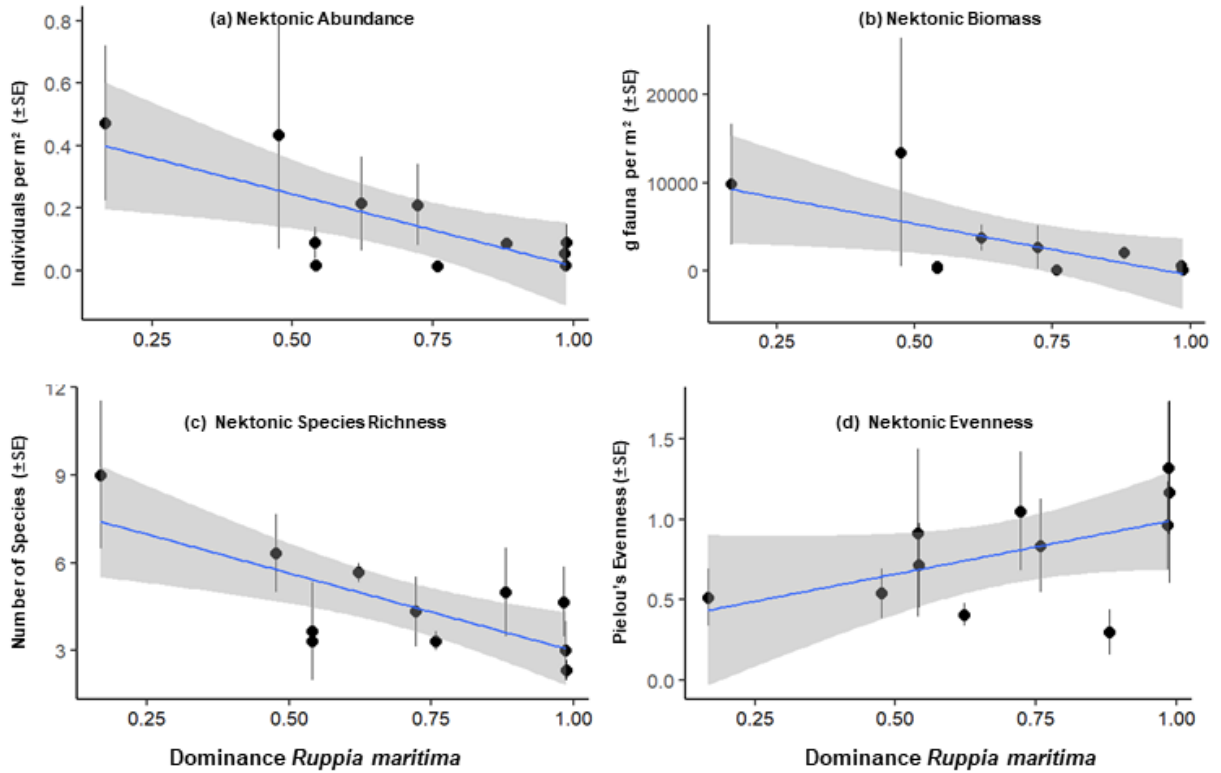


Figure 6: Indicators of nektonic community structure vs. dominance of *Ruppia maritima*. (The further right along the x-axis means that the benthos becomes more dominated by *Ruppia* compared to *Zostera marina* (i.e., 0.25 equates to 25% cover of *Ruppia* and 75% cover of *Zostera*.) Black circles indicate site averages over three months. The gray shading around the line represents the 95% confidence interval. **(a)** Nektonic abundance. **(b)** Nektonic biomass. **(c)** Nektonic species richness. **(d)** Pielou's evenness of nektonic assemblages.

Tables

Transect #	Transect Name	% Dominance <i>Ruppia</i>	% Dominance <i>Zostera</i>
T10	Browns Bay North	99%	1%
T5	Warepoint South	99%	1%
T2	East River East	98%	2%
T3	East River West	88%	12%
T4	Warepoint North	76%	24%
T8	Four Points Cove	72%	28%
T7	Four Points South	62%	38%
T11	Browns Bay South	54%	46%
T6	Four Points North	54%	46%
T1	Pepper Creek	48%	52%
T12	Guinea Marsh	17%	83%

Table 1: The total, proportional cover of *Zostera marina* (*Zostera*) and *Ruppia maritima* (*Ruppia*) in 2021 for each transect in Mobjack Bay where trawl surveys were conducted.

Predictors	log(EpiAbunPerPlantBio)				log(EpiBioPerPlantBio)				log(EpiProdPerPlantBio)				Epi Richness			
	Estimates	CI	p-value	df	Estimates	CI	p-value	df	Estimates	CI	p-value	df	Estimates	CI	p-value	df
Fixed Effects																
(Intercept)	2.75	2.53 – 2.96	<0.001	85	1.44	1.26 – 1.63	<0.001	86	2.75	2.60 – 2.91	<0.001	85	6.78	5.55 – 8.01	<0.001	83
Bedtype (<i>Ruppia</i>)	0.12	-0.05 – 0.28	0.172	85	0.22	0.03 – 0.41	0.027	86	0.12	-0.03 – 0.27	0.102	85	-0.10	-1.35 – 1.16	0.878	83
Bedtype (<i>Zostera</i>)	-0.31	-0.52 – -0.11	0.003	85	-0.04	-0.27 – 0.18	0.709	86	0.04	-0.13 – 0.21	0.661	85	-0.64	-2.06 – 0.78	0.373	83
g Plant Dry Mass	-0.12	-0.15 – -0.08	<0.001	85					-0.1	-0.12 – -0.07	<0.001	85	0.31	0.05 – 0.56	0.020	83
Random Effects																
σ^2	0.05				0.08				0.05				3.82			
Transect	0.06				0.04				0.02				0.84			
Marginal R ² / Conditional R ²	0.498 / 0.778				0.104 / 0.382				0.384 / 0.547				0.067 / 0.236			
ANOVA		<i>Chisq</i>	<i>p-value</i>	<i>df</i>		<i>Chisq</i>	<i>p-value</i>	<i>df</i>		<i>Chisq</i>	<i>p-value</i>	<i>df</i>		<i>Chisq</i>	<i>p-value</i>	<i>df</i>
Bedtype		23.065	<0.001	2		9.1053	0.011	2		3.05	0.218	2		0.94	0.624	2
g Plant Dry Mass		51.003	<0.001	1						40.74	<0.001	1		5.59	0.018	1

Predictors	log(EpiAbunPerArea)				log(EpiBioPerArea)				log(EpiProdPerArea)				Epi Evenness			
	Estimates	CI	p-value	df	Estimates	CI	p-value	df	Estimates	CI	p-value	df	Estimates	CI	p-value	
Fixed Effects																
(Intercept)	-0.15	-0.34 – 0.05	0.132	86	-1.19	-1.35 – -1.03	<0.001	86	-0.27	-0.37 – -0.18	<0.001	85	0.35	0.18 – 0.68	0.002	
Bedtype (<i>Ruppia</i>)	-0.01	-0.16 – 0.14	0.893	86	0.05	-0.11 – 0.21	0.524	86	0.05	-0.06 – 0.16	0.366	85	0.980	0.64 – 1.50	0.922	
Bedtype (<i>Zostera</i>)	-0.32	-0.51 – -0.13	0.001	86	0.03	-0.16 – 0.22	0.720	86	0.10	-0.02 – 0.22	0.092	85	2.06	1.27 – 3.33	0.003	
g Plant Dry Mass									0.06	0.04 – 0.09	<0.001	85				
Random Effects																
σ^2	0.4				0.05				0.04				0.05			
Transect	0.07				0.03				0.001				1.04			
Marginal R ² / Conditional R ²	0.173 / 0.692				0.006 / 0.343				0.280 / 0.298				0.095/0.959			
ANOVA		<i>Chisq</i>	<i>p-value</i>	<i>df</i>		<i>Chisq</i>	<i>p-value</i>	<i>df</i>		<i>Chisq</i>	<i>p-value</i>	<i>df</i>		<i>Chisq</i>	<i>p-value</i>	<i>df</i>
Bedtype		16.52	<0.001	2		0.410	0.815	2		2.92	0.233	2		13.29	0.001	2
g Plant Dry Mass										23.50	<0.001	1				

Table 2: Model outputs for indicators of epifaunal (epi) community structure in three seagrass bed types, those dominated by *Zostera marina* (*Zostera*), those dominated by *Ruppia maritima* (*Ruppia*), and those that were a mix of the two species (Mixed). Bed type was treated as a fixed effect and transect was treated as a random effect. Seagrass dry weight was also included as fixed effect when assessing epifaunal abundances per g plant AFDW and per cm², biomass per g plant AFDW and per cm², and secondary production per g plant AFDW and per cm². Significant *p*-values are bolded.

Shallow-dwelling Infauna

	AbunPerArea				BioPerArea				log(ProductionPerArea)				Richness			Evenness			
Fixed Effects																			
Predictors	Estimates	CI	P-value	df	Estimates	CI	P-value	df	Estimates	CI	P-value	df	Estimates	CI	P-value	df	Estimates	CI	P-value
(Intercept)	0.0168	-0.0114 – 0.0449	0.234	32	0.00009	0.00004 – 0.00015	0.002	44	-0.086	-0.404 – 0.231	0.585	40	1.601	0.899 – 2.304	<0.001	44	0.187	0.079 – 0.444	<0.001
Bedtype [Mixed]	0.0105	-0.0365 – 0.0574	0.653	32	-0.00003	-0.00012 – 0.00005	0.462	44	-0.249	-0.706 – 0.208	0.277	40	0.54	-0.519 – 1.599	0.31	44	0.791	0.272 – 2.299	0.666
Bedtype [Ruppia]	0.0342	0.0003 – 0.0682	0.048	32	-0.00002	-0.00009 – 0.00005	0.625	44	0.03	-0.330 – 0.391	0.866	40	1.075	0.185 – 1.966	0.019	44	0.731	0.295 – 1.814	0.5
Bedtype [Zostera]	0.0327	-0.0004 – 0.0658	0.053	32	-0.00004	-0.00011 – 0.00004	0.318	44	-0.136	-0.489 – 0.217	0.44	40	0.436	-0.454 – 1.326	0.329	44	0.711	0.287 – 1.761	0.461
Random Effects																			
σ^2	<0.001				<0.001				0.14				1.18			1.73			
Transect	<0.001				<0.001				0.06				0.04			<0.001			
Marginal R ² / Conditional R ²	0.128 / 0.312				0.022 / 0.111				0.053 / 0.345				0.114 / 0.141			0.010 / NA			
ANOVA	Chisq	p-value	df		Chisq	p-value	df		Chisq	p-value	df		Chisq	p-value	df		Chisq	p-value	df
Bedtype	5.809	0.121	3		1.165	0.762	3		2.654	0.448	3		6.257	0.0998	3		0.619	0.892	3

Deep-dwelling Infauna

	AbunPerArea				BioPerArea				log(ProductionPerArea)				Richness			Evenness			
Fixed Effects													***Linear Model						
Predictors	Estimates	CI	P-value	df	Estimates	CI	P-value	df	Estimates	CI	P-value	df	Estimates	CI	P-value	df	Estimates	CI	P-value
(Intercept)	0.001	-0.001 – 0.003	0.306	22	0.000001	-	0.991	22	-0.975	-1.585 – -0.364	0.003	22	1.571	0.448 – 2.695	0.008	24	0.257	0.078 – 0.847	0.026
Bedtype [Mixed]	0.005	0.002 – 0.008	0.001	22	0.00014	0.000173 – 0.000175	0.194	22	0.65	-0.073 – 1.374	0.076	22	1.679	0.140 – 3.217	0.034	24	1.915	0.443 – 8.281	0.384
Bedtype [Ruppia]	0.004	0.001 – 0.006	0.016	22	0.00002	-0.00020 – 0.00024	0.858	22	0.248	-0.462 – 0.958	0.477	22	2	0.411 – 3.589	0.016	24	0.848	0.208 – 3.459	0.818
Bedtype [Zostera]	0.001	-0.002 – 0.004	0.647	22	0.00026	0.00002 – 0.00049	0.033	22	0.501	-0.257 – 1.259	0.184	22	1.262	-0.391 – 2.915	0.128	24	0.79	0.194 – 3.225	0.743
Random Effects																			
σ^2	<0.001				<0.001				0.37							0.98			
Transect	<0.001				<0.001				0.25							1.14			
Marginal R ² / Conditional R ²	0.358 / 0.522				0.172 / 0.381				0.096 / 0.459				R ² = 0.247			0.060 0.567			
ANOVA	Chisq	p-value	df		Chisq	p-value	df		Chisq	p-value	df		Sum Sq	F Value	p-value	df	Chisq	p-value	df
Bedtype	17.228	<0.001	3		2.640	0.451	3		1.29	0.525	3		16.35	2.63	0.073	3	1.321	0.724	3
Residuals													49.76			24			

Table 3: Model outputs for indicators of shallow-dwelling and deep-dwelling infaunal community structure in four bed types, bare sediment, *Zostera marina* (*Zostera*), *Ruppia maritima* (*Ruppia*), and those that were a mix of the two seagrass species (Mixed). Bed type was treated as a fixed effect and transect was treated as a random effect. Significant *p*-values are bolded.

Predictors	log(Biomass)				log(Abundance)				Richness				Evenness			
	Estimates	CI	p-value	df	Estimates	CI	p-value	df	Estimates	CI	p	df	Estimates	CI	p-value	
Fixed Effects																
(Intercept)	4.46	3.15 – 5.77	<0.001	25	0.03	-1.10 – 1.16	0.955	25	12.03	7.92 – 16.15	<0.001	25	0.42	-0.51 – 1.35	0.381	
RmPerDom	-1.87	-3.64 – -0.09	0.04	25	-1.92	-3.45 – -0.39	0.016	25	-9.97	-15.54 – -4.40	0.001	25	0.61	-0.65 – 1.87	0.345	
Month [July]	-1.14	-2.72 – -0.44	0.151	25	-0.81	-2.20 – 0.58	0.241	25	-5.06	-10.69 – -0.57	0.076	25	-0.18	-1.50 – 1.13	0.788	
Month [June]	-1.15	-2.73 – -0.43	0.145	25	-0.89	-2.29 – 0.50	0.198	25	-6.14	-11.77 – -0.51	0.034	25	-0.1	-1.42 – 1.21	0.879	
RmPerDom × Month [July]	0.75	-1.39 – 2.89	0.478	25	1.09	-0.79 – 2.98	243	25	6.22	-1.40 – 13.85	0.105	25	0.34	-1.44 – 2.12	0.709	
RmPerDom × Month [June]	0.86	-1.28 – 3.00	0.416	25	1.49	-0.39 – 3.38	0.115	25	7.77	0.15 – 15.40	0.046	25	-0.12	-1.90 – 1.66	0.892	
Random Effects																
σ^2	0.36				0.28				4.6				0.28			
Transects	0.14				0.09				0.32				<0.001			
Marginal R ² / Conditional R ²	0.286 / 0.482				0.217 / 0.408				0.346 / 0.388				0.133 / NA			
ANOVA																
		Chisq	p-value	df		Chisq	p-value	df		Chisq	p-value	df		Chisq	p-value	df
Bedtype		4.61	<0.05	1		4.08	<0.05	1		10.21	0.001	1		3.342	0.068	1
Month		7.00	<0.05	2		0.83	0.662	2		0.84	0.656	2		1.286	0.526	2
RmPerDom:Month		0.81	0.667	2		2.86	0.239	2		4.94	0.855	2		0.2767	0.871	2

Table 4: Model outputs for indicators of nektonic community structure where the proportional % cover of *Ruppia maritima* (RmPerDom) and month were treated as fixed effects and transect was treated as a random effect. Significant *p*-values are bolded.

Appendix

Supplemental Figures:

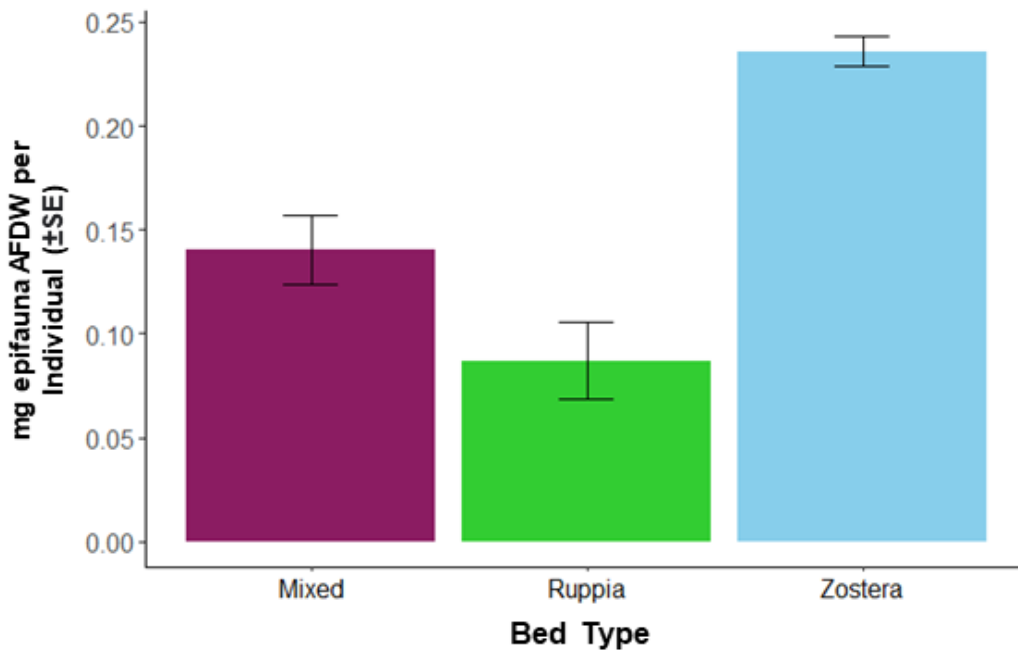


Figure A2: Average size of epifauna (mg fauna ash free dry weight (AFDW) per individual) in three seagrass bed types, those dominated by *Zostera marina* (*Zostera*), those dominated by *Ruppia maritima* (*Ruppia*), and those that were a mix of the two species (Mixed).

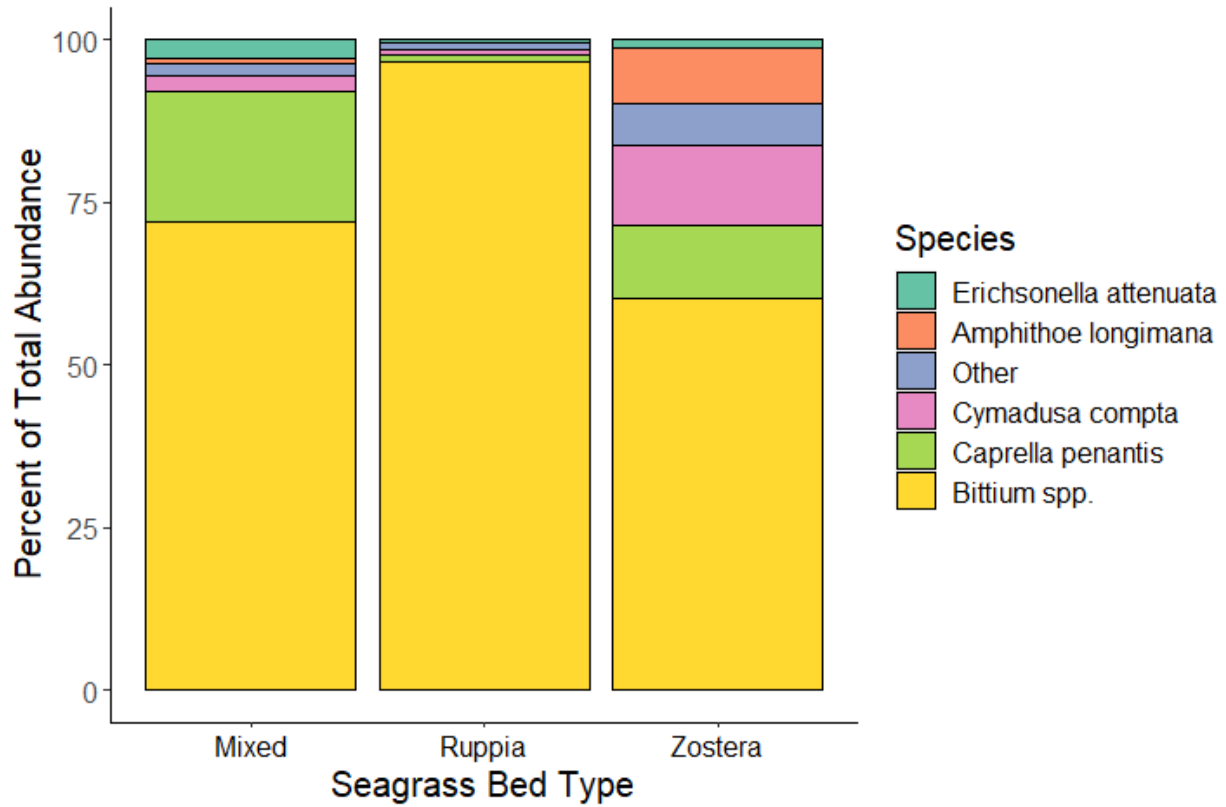


Figure A1: The percent of total abundance of epifaunal species in three seagrass bed types, those dominated by *Zostera marina* (*Zostera*), those dominated by *Ruppia maritima* (*Ruppia*), and those that were a mix of the two species (*Mixed*). Different colors indicate the most common species.

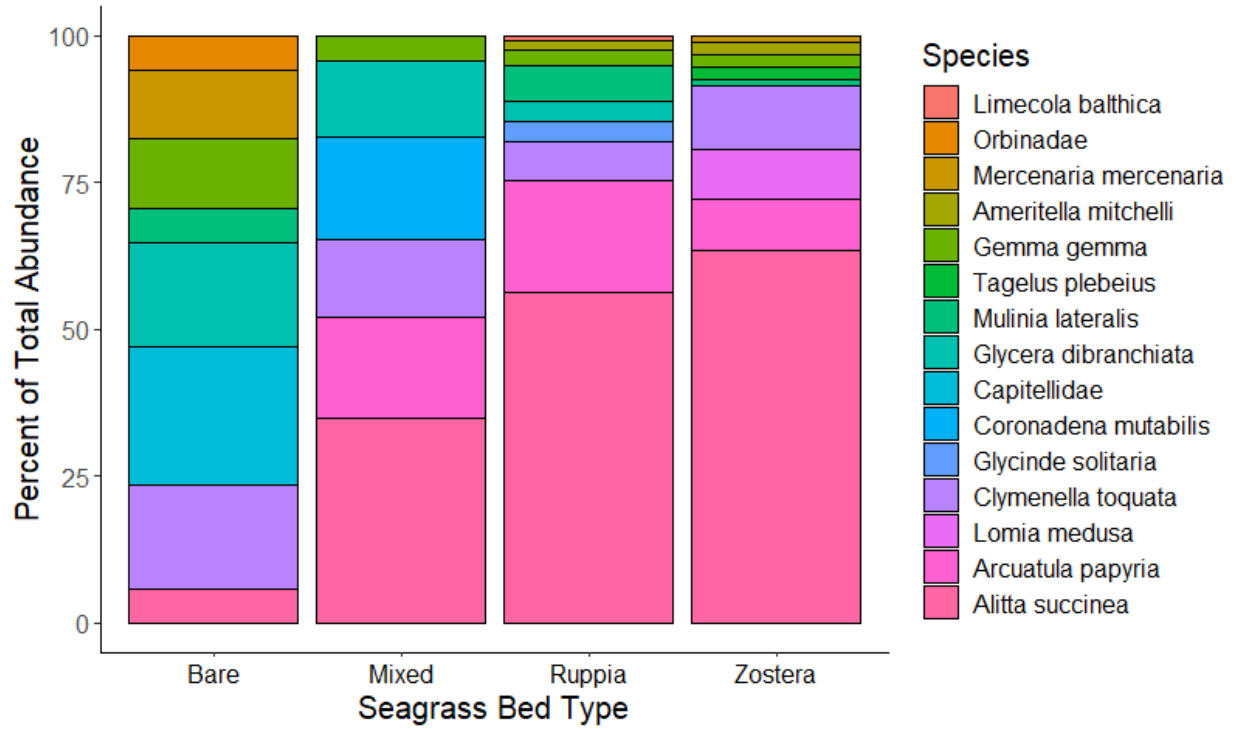


Figure A3: The percent of total abundance of shallow-dwelling infaunal taxa in four bed types, bare sediment, *Zostera marina* (*Zostera*), *Ruppia maritima* (*Ruppia*), and those that were a mix of the two seagrass species (Mixed). Different colors indicate infaunal taxa.

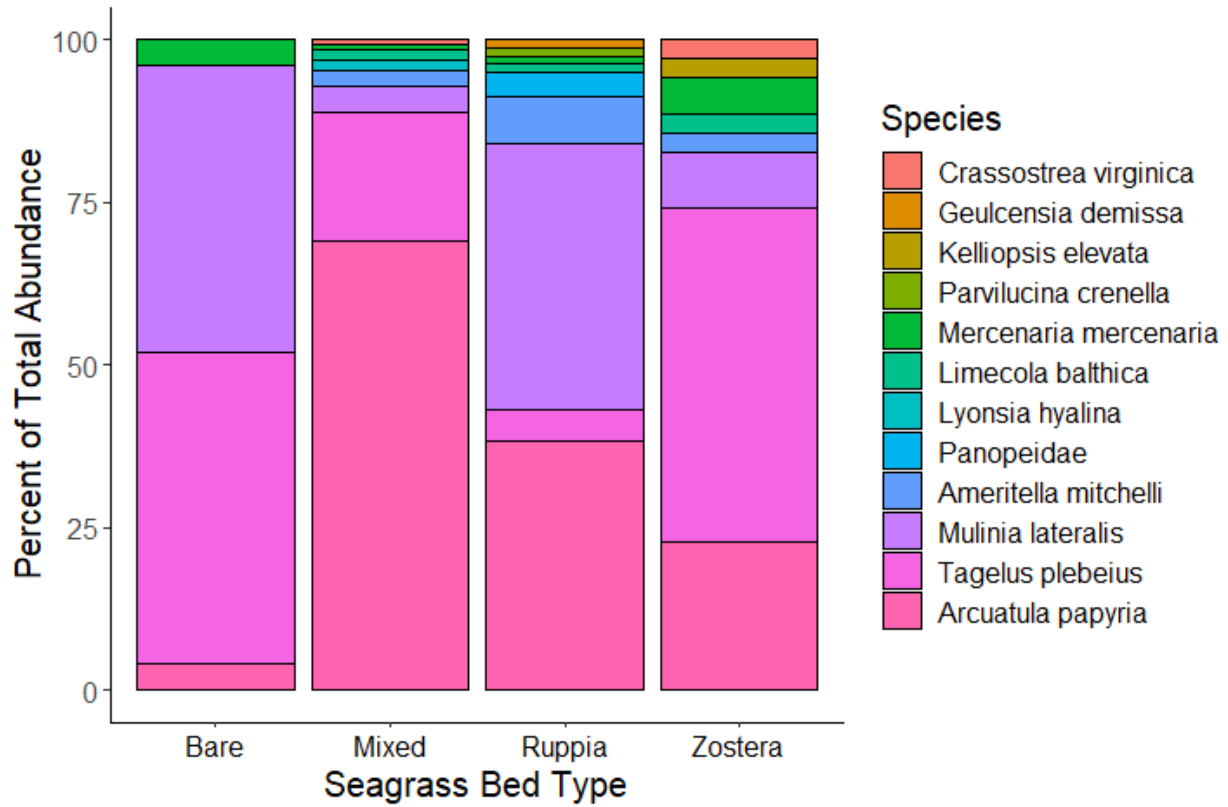


Figure A4: The percent of total abundance of deep-dwelling infaunal bivalves in four bed types, bare sediment, *Zostera marina* (*Zostera*), *Ruppia maritima* (*Ruppia*), and those that were a mix of the two seagrass species (Mixed). Different colors indicate infaunal taxa.

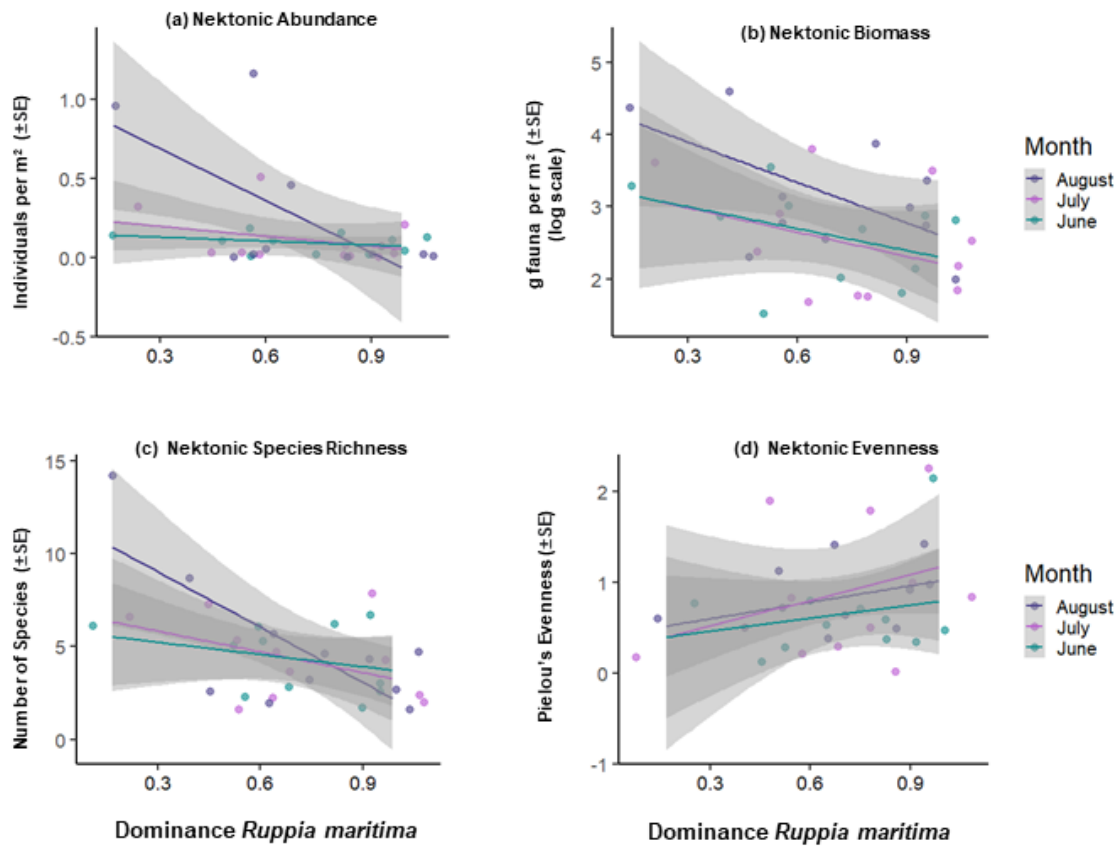


Figure A5: Indicators of nektonic community structure vs. dominance of *Ruppia maritima* (*Ruppia*) over time. (The further right along the x-axis means that the benthos becomes more dominated by *Ruppia* compared to *Zostera marina* (i.e., 0.3 equates to 30% cover of *Ruppia* and 70% cover of *Zostera*)). Different colors indicate month. The gray shading around the lines represents the 95% confidence interval. **(a)** Nektonic abundance. **(b)** Nektonic biomass (log scale). **(c)** Nektonic species richness. **(d)** Pielou's evenness of nektonic assemblages.

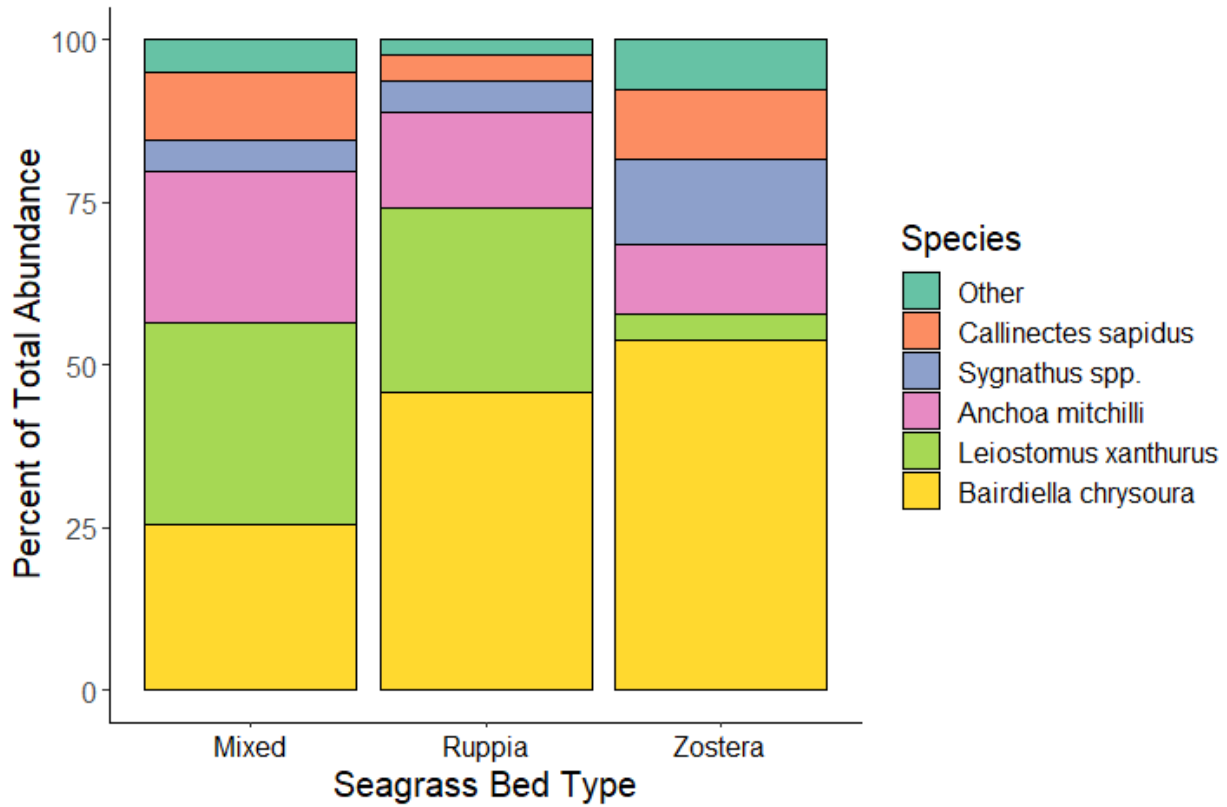


Figure A6: The percent of total abundance of nektonic species across all months combined in three seagrass bed types, those dominated by *Zostera marina* (*Zostera*), those dominated by *Ruppia maritima* (*Ruppia*), and those that were a mix of the two species (Mixed). Different colors indicate the most common nekton species.

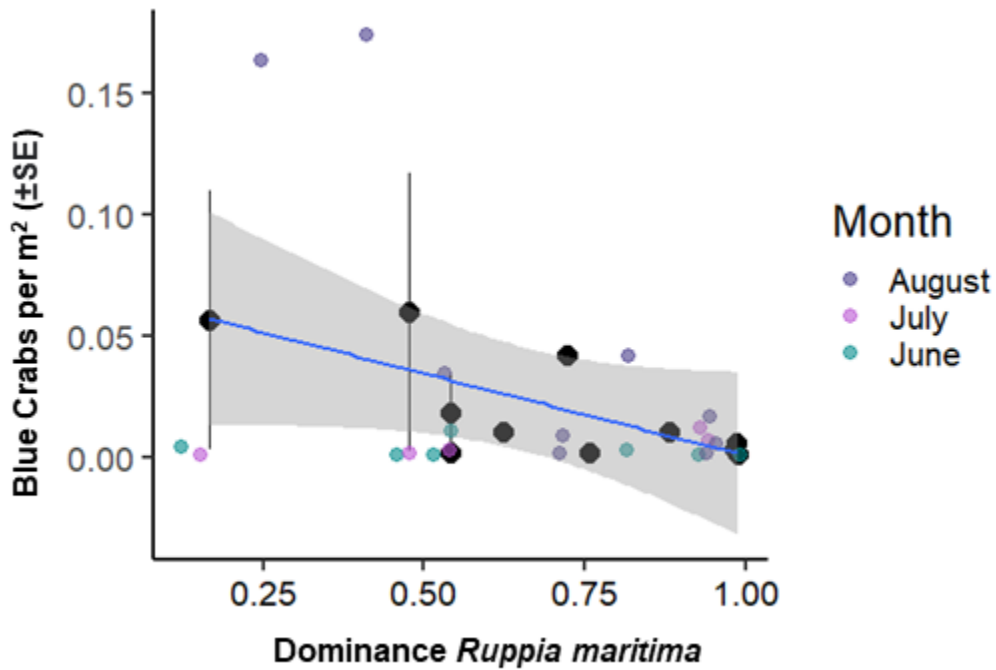


Figure A7: Abundance of blue crabs (*Callinectes sapidus*) vs. dominance of *Ruppia maritima*. (The further right along the x-axis means that the benthos becomes more dominated by *Ruppia* compared to *Zostera marina* (i.e., 0.25 equates to 25% cover of *Ruppia* and 75% cover of *Zostera*.) Different colored circles indicate abundances in three different months and black circles indicate averages over all three months. The gray shading around the line represents the 95% confidence interval.

Supplemental Tables:

Table A1: Presence/absence table for the 40 unique epifaunal taxa collected in three seagrass bed types, those dominated by *Zostera marina* (*Zostera*), those dominated by *Ruppia maritima* (*Ruppia*), and those that were a mix of the two species (Mixed).

Taxa	Seagrass Bed Type		
	Mixed	<i>Ruppia</i>	<i>Zostera</i>
<i>Acteocina canaliculata</i>	+	+	+
<i>Acteon punctostriatus</i>		+	
<i>Alpheus</i> sp.		+	
Amphipod A	+	+	
<i>Amphithoe longimana</i>	+	+	+
<i>Ampileasca</i> sp.	+	+	+
<i>Ampithoe valida</i>	+	+	+
<i>Anthuridae</i>	+	+	
<i>Bittium</i> spp.	+	+	+
<i>Caprella penantis</i>	+	+	+
<i>Cerithiopsis greeni</i>	+	+	+
<i>Copepod</i>	+	+	+
<i>Crangon</i> sp.	+		
<i>Crepidula convexa</i>	+	+	+
<i>Cumacea</i>	+	+	+
<i>Cymadusa compta</i>	+	+	+
<i>Edotea triloba</i>	+	+	+
<i>Elasmopus levis</i>	+	+	+
<i>Erichsonella attenuata</i>	+	+	+
<i>Gammarus mucronatus</i>	+	+	+
<i>Hippolyte</i> sp.	+	+	+
<i>Lembos smithi</i>	+	+	+
<i>Mangelia plicosa</i>		+	
<i>Melita nitida</i>		+	
<i>Microdeutopus gryllotalpa</i>	+	+	+
<i>Microprotopus raneyi</i>	+		
<i>Mitrella lunata</i>			+
<i>Nassarius vibex</i>		+	
<i>Odostomia bisaturalis</i>	+	+	+
<i>Paracaprella tenuis</i>		+	
<i>Penaeid</i> sp.	+		

<i>Rudilemboides naglei</i>	+		+
Shrimp A	+	+	+
Shrimp B		+	+
Snail B	+		
Snail E		+	
Snail G		+	+
Snail J		+	
Snail K		+	+
<i>Unicola serrata</i>	+		

Table A2: Presence/absence table for the 16 unique taxa collected in push core samples which targeted shallow-dwelling infauna (~15-cm depth) and for the 12 unique infauna taxa collected in suction samples which targeted deep-dwelling infauna (~40-cm depth). All samples were collected from four bed types, bare sediment (Bare), *Zostera marina* (*Zostera*), *Ruppia maritima* (*Ruppia*), and those that were a mix of the two seagrass species (Mixed).

Shallow-dwelling Infauna				
Seagrass Bed Type				
Taxa	Bare	Mixed	<i>Ruppia</i>	<i>Zostera</i>
<i>Alitta succinea</i>	+	+	+	+
<i>Ameritella mitchelli</i>			+	+
<i>Arcuatula papyria</i>		+	+	+
<i>Capitellidae</i>	+			
<i>Clymenella toquata</i>	+	+	+	+
<i>Coronadena mutabilis</i>		+		
<i>Gemma gemma</i>	+	+	+	+
<i>Glycera dibranchiata</i>	+	+	+	+
<i>Glycinde solitaria</i>			+	+
<i>Limecola balthica</i>			+	
<i>Lomia medusa</i>				+
<i>Mercenaria mercenaria</i>	+			+
<i>Mulinia lateralis</i>	+		+	+
<i>Orbinadae</i>	+			
<i>Tagelus plebeius</i>				+
<i>Terebellidae</i>	+	+	+	+
Deep-dwelling Infauna				
Seagrass Bed Type				
Taxa	Bare	Mixed	<i>Ruppia</i>	<i>Zostera</i>

<i>Ameritella mitchelli</i>		+	+	+
<i>Arcuatula papyria</i>	+	+	+	+
<i>Crassostrea virginica</i>		+		+
<i>Geukensia demissa</i>			+	
<i>Kelliopsis elevate</i>				+
<i>Limecola balthica</i>		+	+	+
<i>Lyonsia hyaline</i>		+		
<i>Mercenaria mercenaria</i>	+	+	+	+
<i>Mulinia lateralis</i>	+	+	+	+
<i>Panopeidae</i>			+	
<i>Parvilucina crenelle</i>			+	
<i>Tagelus plebeius</i>	+	+	+	+

Table A3: Presence/absence table for the 22 unique taxa collected in trawl surveys in three seagrass bed types, those dominated by *Zostera marina* (*Zostera*), those dominated by *Ruppia maritima* (*Ruppia*), and those that were a mix of the two species (Mixed).

Taxa	Seagrass Bed Type		
	Mixed	<i>Ruppia</i>	<i>Zostera</i>
<i>Anchoa mitchilli</i>	+	+	+
<i>Archosargus probatocephalus</i>			+
<i>Bairdiella chrysoura</i>	+	+	+
<i>Callinectes sapidus</i>	+	+	+
<i>Centropristis striata</i>	+		
<i>Chaetodipterus faber</i>		+	+
<i>Chilomycterus schoepfii</i>	+	+	+
<i>Cynoscion nebulosus</i>	+		+
<i>Gobiosoma bosc</i>		+	
<i>Hippocampus erectus</i>	+	+	
<i>Hypsoblennius hentz</i>	+		+
<i>Lagodon rhomboides</i>		+	
<i>Leiostomus xanthurus</i>	+	+	+
<i>Menidia menidia</i>	+	+	+
<i>Micropogonias undulatus</i>	+		
<i>Opsanus tau</i>			+
<i>Orthopristis chrysoptera</i>	+	+	+
<i>Paralichthys dentatus</i>		+	+
<i>Sphoeroides maculatus</i>		+	+

<i>Sygnathus</i> spp.	+	+	+
<i>Synodus foetens</i>		+	
<i>Tautoga onitis</i>	+		+

Table A4: Estimated hectares of submerged aquatic vegetation (SAV) (under nutrient management scenarios modeled by Hensel et al. 2023) and extrapolated mean biomass and secondary production of epifaunal and infauna invertebrates in *Ruppia maritima* (*Ruppia*) and *Zostera marina* (*Zostera*) seagrass meadows in the Chesapeake Bay. (The general allometric equation described by Edgar 1990 to calculate estimates of production based on mean invertebrate biomass.)

Current Bay (2022)			
	SAV Area (hectares)	Mean Biomass ± SD (Gg)	Mean Production (Gg)
<i>Ruppia</i>	9,778.34	0.25 ± 0.17	0.14
<i>Zostera</i>	8,104.41	0.35 ± 0.27	0.18
Total		0.60 ± 0.33	0.32
Further Nutrient Reductions (2060)			
	SAV Area (hectares)	Mean Biomass ± SD (Gg)	Mean Production (Gg)
<i>Ruppia</i>	13,717.48	0.35 ± 0.23	0.21
<i>Zostera</i>	2,525.20	0.11 ± 0.08	0.06
Total		0.46 ± 0.25	0.26
No Further Nutrient Reductions (2060)			
	SAV Area (hectares)	Mean Biomass ± SD (Gg)	Mean Production (Gg)
<i>Ruppia</i>	4,851.73	0.12 ± 0.08	0.07
<i>Zostera</i>	2,094.89	0.09 ± 0.07	0.05
Total		0.21 ± 0.12	0.12

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